

## **Tube morphology, ultrastructures and mineralogy in recent Spirorbinae (Annelida: Polychaeta: Serpulidae). III. Tribe Circeini**

**A.P. Ippolitov<sup>1</sup>, A.V. Rzhavsky<sup>2</sup>**

<sup>1</sup> *Geological Institute of Russian Academy of Sciences (GIN RAS), 7 Pyzhevskiy per., Moscow, Russia 119017, e-mail: ippolitov.ap@gmail.com*

<sup>2</sup> *A.N. Severtsov Institute of Ecology and Evolution of Russian Academy of Sciences (IPEE RAS), 33 Leninskiy prosp., Moscow, Russia. 119071, e-mail: rzhavskij@mail.ru*

**ABSTRACT:** This paper is a third part of the series started by Ippolitov and Rzhavsky (2014, 2015) and providing detailed descriptions of Recent spirorbin tubes, their mineralogy and ultrastructures. In the present part we describe species of the small tribe Circeini Knight-Jones, 1978, which includes the genera *Circeis* Saint-Joseph, 1894 and *Paradexiospira* Caullery et Mesnil, 1897. Mineralogically, tubes of both genera are purely calcitic. Ultrastructurally, most studied *Circeis* had three-layered tubes with spherulitic irregularly oriented prismatic (SIOP) structure of the main middle layer, while inner and outer surfaces were consolidated by dense spherulitic prismatic (SPHP) layers. All *Paradexiospira* species tend to have unilayered tubes with simple prismatic (SP) structure resulting in tube transparency. One unique species (*Circeis vitreopsis* Rzhavsky, 1992), shows a transition between these two types. A direct observation of ultrastructures at early stages of a tube development suggests that the presence of thick middle SIOP layer is a plesiomorphic state, while unilayered SP wall is apomorphic. Most plesiomorphic structures among Circeini look similar to structures of certain Spirorbini, probably indicating close phylogenetic relationships of these taxa. Development of apomorphic unilayered SP wall in *Paradexiospira* providing consolidation and strengthening of the tube is probably a result of adaptation to living on hard substrates with strong rate of sand abrasion in bottom waters. How to cite this article: Ippolitov A.P., Rzhavsky A.V. 2015. Tube morphology, ultrastructures and mineralogy in recent Spirorbinae (Annelida: Polychaeta: Serpulidae). III. Tribe Circeini // *Invert Zool.* Vol.12. No.2. P.151–173. doi: 10.15298/invertzool.12.2.03

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

## **Морфология, ультраструктуры и минералогия трубок современных Spirorbinae (Annelida: Polychaeta: Serpulidae). III. Триба Circeini**

**А.П. Ипполитов<sup>1</sup>, А.В. Ржавский<sup>2</sup>**

<sup>1</sup> *Геологический институт РАН, Пыжевский пер. 7, Москва, Россия, 119017, e-mail: ippolitov.ap@gmail.com*

<sup>2</sup> *Институт проблем экологии и эволюции им. А.Н. Северцова РАН, Ленинский пр. 33, Москва, Россия, 119071, e-mail: rzhavskij@mail.ru*

**РЕЗЮМЕ:** Эта статья — третья часть серии (Ippolitov, Rzhavsky, 2014, 2015), посвящённой описанию морфологии, минералогии и ультраструктур трубок современных спирорбин. В статье описываются виды, относящиеся к небольшой трибе *Circeini* Knight-Jones, 1978, включающей два рода — *Circeis* Saint-Joseph, 1894 и *Paradexiospira* Caullery et Mesnil, 1897. Трубки всех изученных видов состоят из кальцита. С точки зрения ультраструктур трубки представлены двумя типами. У большинства изученных видов *Circeis* трубки имеют трехслойную стенку: плотные внешний и внутренний слои имеют сферулитовую призматическую структуру, а менее плотный средний слой имеет структуру хаотически ориентированных призматических сферулитов. У представителей рода *Paradexiospira* стенка трубки однослойная с простой призматической структурой, обуславливающей прозрачность трубки. У одного из видов (*Circeis vitreopsis* Rzhavsky, 1992) в пределах трубки найдена комбинация обоих типов строения стенки, демонстрирующая переход между ними. Изучение ультраструктур стенок на ранних стадиях развития трубки показывает, что трехслойная стенка является исходной (архаичной), а однослойная стенка с простой призматической структурой — вторичной (прогрессивной). Виды цирцеин с наиболее архаичным строением стенки трубки обнаруживают высокое сходство по особенностям структуры с некоторыми представителями трибы *Spirorbini*, изученными нами ранее, что, вероятно, указывает на близкое родство этих таксонов. Появление однослойной стенки с простой призматической структурой в пределах рода *Paradexiospira*, по-видимому, было обусловлено необходимостью консолидации и упрочнения трубки в связи с переходом к поселению на камнях в местообитаниях с интенсивной песчаной абразией в придонном слое воды.

Как цитировать эту статью: Ippolitov A.P., Rzhavsky A.V. 2015. Tube morphology, ultrastructures and mineralogy in recent Spirorbinae (Annelida: Polychaeta: Serpulidae). III. Tribe *Circeini* // *Invert Zool.* Vol.12. No.2. P.151–173. doi: 10.15298/invertzool.12.2.03

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

## Introduction

Introductory remarks, including key terminology of tubes and their ultrastructures, were provided in the first part of the present series (Ippolitov, Rzhavsky, 2014).

## Material and methods

Detailed information on material and methods is provided in the first part of the series (Ippolitov, Rzhavsky, 2014). Current investigation covers 6 out of 9 (10?) known species belonging to the genera *Circeis* Saint-Joseph, 1894 and *Paradexiospira* Caullery et Mesnil,

1897 of the tribe *Circeini*. All examined tubes are obtained from the collection of A.V. Rzhavsky deposited in A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow (IPEE RAS).

## Results

### Tribe *Circeini* Knight-Jones, 1978

**Diagnosis.** The embryos stick to each other and then directly to the inner side of the tube; accordingly, the only type of operculum throughout life time is an endplate, usually with a talon. Other important features are: 1) thoracic uncini

wide rasp-shaped, with 3–15 longitudinal rows of teeth and blunt anterior peg; 2) abdominal uncini distributed quite asymmetrically, on convex body side they may be present on last chaetigers only or absent altogether; 3) abdominal chaetae are flat geniculate, pennant-shaped (blade width decreasing gradually towards the 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 sometimes present only on the last abdominal chaetigers; 5) larvae without white attachment glands.

**Distribution.** All species of *Circeini* are found in the North Hemisphere only. Most of them are arcto-boreal, while others are boreal Atlantic or Pacific (Knight-Jones P. et al., 1991; Rzhavsky, 1992a, b, 1992[1994], 1998; Rzhavsky et al., 2014).

**Remarks.** The tribe includes two genera: *Circeis* Saint-Joseph, 1894 and *Paradexiospira* Caullery et Mesnil, 1897.

### Genus *Circeis* Saint-Joseph, 1894

**Type species:** *Circeis armoricana* Saint-Joseph, 1894.

**Diagnosis.** Tubes usually dextral (anticlockwise), but in some species may be regularly or occasionally sinistral (clockwise); margins of collar and thoracic membranes not fused over thoracic groove; large collar chaetae bent (usually strongly), modified with vestigial lateral cross-striation or cross-striated from “frontal side” of blade, not visible laterally under a dissecting microscope; sickle chaetae absent; three thoracic chaetigers.

**Composition.** The genus includes 6 recent species, 3 of them are described below and the rest are not covered in the present study. However, real number of species in the genus may be larger (see Remarks for *C. armoricana*).

**Distribution.** As for the tribe (see above).

#### *Circeis armoricana* Saint-Joseph, 1894

Fig. 1A–K.

For descriptions see Knight-Jones P., Knight-Jones E.W., 1977: 468–470, Fig. 5A–C, E–M [non *Circeis armoricana paguri*, p. 470, Fig. 5D]; Knight-Jones P. et

al., 1979: 427–429, Fig. 3A (a–d); Rzhavsky et al., 2014: 77–80, Fig. 16A–K.

**Material examined.** Two specimens were studied with SEM in longitudinal sections (IPEE No. 54/1204, Kit Bay, Primorsky Krai, Sea of Japan, on a bivalve shell cast ashore). Mineralogy was analyzed twice: using a single tube and couple of fused tubes from the same sample. External tube morphology was illustrated using specimens from different samples to demonstrate intraspecific variability [IPEE No. 33/1183, Kamenka Bay, Primorsky Krai, Sea of Japan, several meters deep, on *Laminaria* (Fig. 1C); IPEE No. 96/2051, Jarnyshnaja Inlet, Barents Sea, depth 10 m, on filamentous algae (Fig. 1B, E); IPEE No. 148/2871, Rifovaja Bay, Primorsky Krai, Sea of Japan, tidal pool, on hydrozoans (Fig. 1A); IPEE No. 149/2889, Rifovaja Bay, Primorsky Krai, Sea of Japan, tidal pool, on *Laminaria* (Fig. 1D)].

**Tube morphology.** Tubes are normally dextral, but some sinistral specimens are recorded from Pacific coast of North America (Knight-Jones P. et al., 1979) and Kiel, Baltic Sea (Bock, 1953, as “*Spirorbis spirillum*”). Coil diameter up to 2.5 mm. Tube typically unsculptured (Fig. 1C) or bearing distinct (Fig. 1A, B) or vestigial (Fig. 1D) median keel. Rarely tube with up to 3 keels. Coils usually planospiral, but overlapping in specimens from filamentous algae or uneven substrates (Fig. 1E), sometimes ascending over substrate, or the last coil may be erected. Tube walls white opaque, but usually with narrow semitransparent transverse bands; slightly porcellaneous. Indistinct peripheral flange may be present (Fig. 1D).

**Tube ultrastructures.** Wall is three-layered (Fig. 1F). Outer covering layer (Fig. 1G) is 6–7  $\mu\text{m}$  wide (corresponding wall width is 55  $\mu\text{m}$ ) with spherulitic prismatic (SPHP) structure. Spherulites are usually oriented almost perpendicular to the surface by their long axes, but often somewhat slightly inclined. The thickest (35–40  $\mu\text{m}$  wide) middle layer (Fig. 1H) with spherulitic irregularly oriented prismatic (SIOP) structure is composed of densely packed typical irregular isometric or slightly elongated spherulites up to 3–4  $\mu\text{m}$  long and some smaller (~1  $\mu\text{m}$ ) isometric crystals also considered here as irregularly-shaped spherulites. The inner layer (Fig. 1I) has width ~10  $\mu\text{m}$ , and, like the outer layer, is represented by spherulites, arranged along the tube surface as SPHP structure.

The lower part of the tube, adhering to the substrate, has SIOP structure (Fig. 1J). Internal

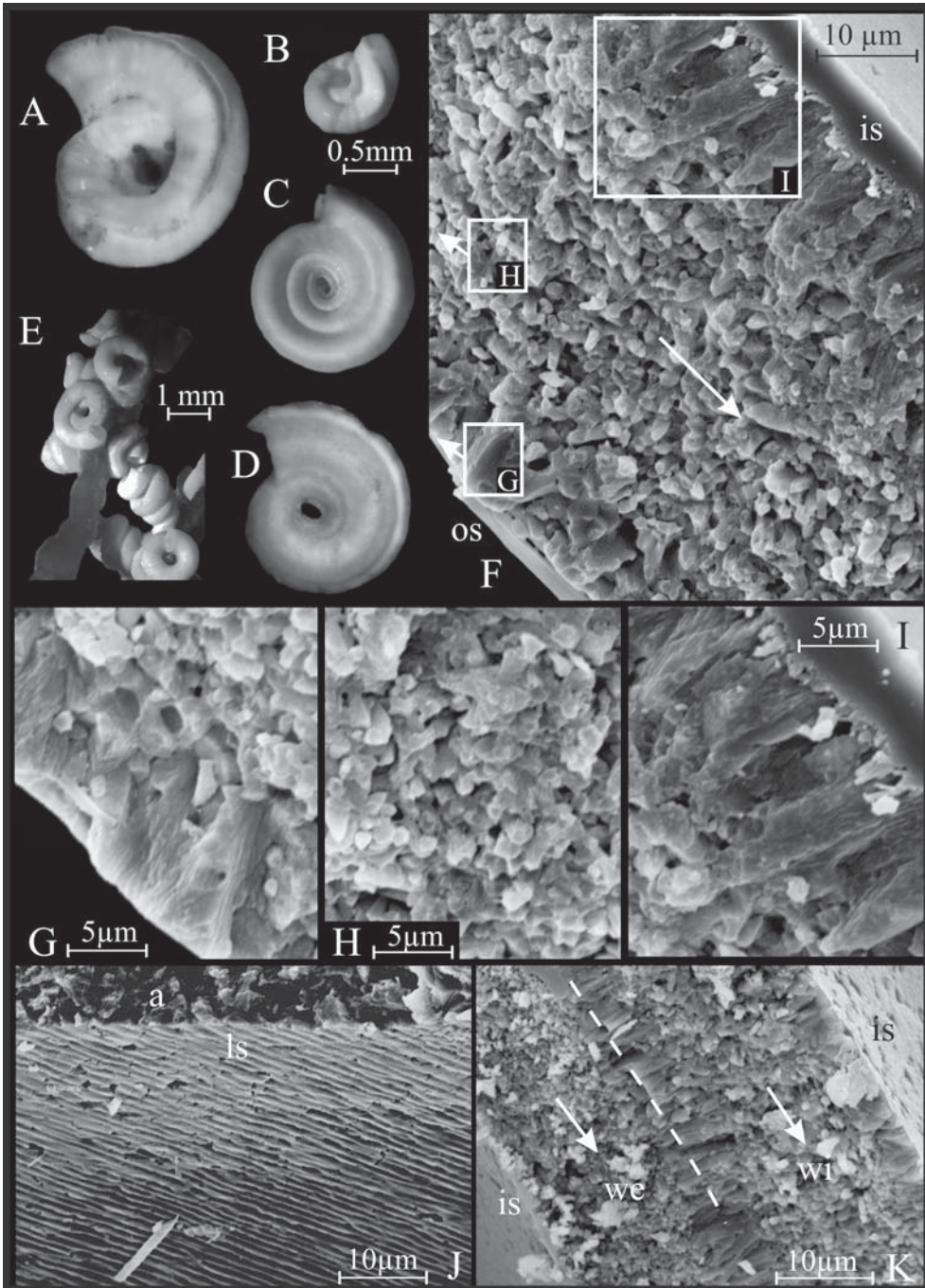


Fig. 1. *Circeis armoricana*. A–E — tubes: A — adult tube with a distinct median keel (IPEE No. 148/2871); B — juvenile with distinct median keel (IPEE No. 96/2051); C — unsculptured tube of mature specimen (IPEE No. 33/1183); D — tube with indistinct median keel and peripheral flange (IPEE No. 149/2889); E — aggregation of unsculptured tubes with overlapping coils from filamentous algae (IPEE No. 96/20); F–K — tube ultrastructures, specimen 1 (F–J), specimen 2 (K): F — general view of the longitudinal section; G —

wall has three-layered structure (Fig. 1K) similar to that of external wall. Early coils (Fig. 1K) have main layer relatively thicker than in that of later coils, and consist of smaller isometric and elongated crystals, forming typical irregularly oriented prismatic (IOP) structure similar to that of Paralaeospirini and Spirorbini (Ippolito, Rzhavsky, 2014, 2015).

Inner organic lining was not observed.

**Tube mineralogy.** 100% low-Mg calcite ( $I_{\text{calc}} = 99$  and 225 in two different samples, respectively).

**Distribution.** In the Arctic *C. armoricana* is reported from Chukchi, East-Siberian, Laptev, Kara, Barents, White, Norwegian (the mainland coast) and Greenland Seas (Spitsbergen coast) and from the central Arctic Ocean (Rzhavsky, 1992a, 1992[1994], 2001; Rzhavsky et al., 2014). Also known from Barrow Point, Arctic coast of Alaska (Knight-Jones P. et al., 1979, 1991) and Iceland coast of the Greenland Sea (Knight-Jones P. et al., 1991). In the North Pacific its distribution range extends south to Possiet Bay (Sea of Japan, Russia), Japan coasts and Acapulco (Mexico); in the North Atlantic it extends to Brittany (France) and Nova Scotia (Canada) (see Knight-Jones P., Knight-Jones E.W., 1977;

Knight-Jones P. et al., 1979, 1991; Rzhavsky, 1992a, 1992[1994]; Rzhavsky et al., 2014).

**Ecology.** *C. armoricana* is one of the most common and abundant species in arctic and boreal waters. It occupies various substrates — rocks, stones, shells, live crustaceans, macrophytes, other polychaete tubes, ascidians, artificial substrates, rarely bryozoans and hydrozoans. The species was recorded from intertidal zone up to 271 m deep, although its preferable bathymetric range is 0–50 m.

**Remarks.** It is not obvious if *C. armoricana*, which is extremely widely distributed, variable morphologically and showing a wide ecological range, is a true cosmopolitan species or a complex of sibling species. This problem should be solved using molecular data.

### *Circeis spirillum* (Linnaeus, 1758)

Fig. 2A–G.

For descriptions see Knight-Jones P., Knight-Jones E.W., 1977: 471, Fig. 5N–U; Knight-Jones et al., 1979: 429, Fig. 3B (a–d); Rzhavsky et al., 2014: 81–83, Fig. 17A–G, Pl. 2H.

**Material examined.** One specimen was studied with SEM in longitudinal section (IPEE No. 3/1130, Kamen' Morskoj Cliff, Pacific coast of Kamchatka, depth 30 m, on bryozoan). Mineralogy was analyzed twice: using a single

outer part of the wall showing SPHP structure; H — middle part of the wall showing SIOP structure; I — innermost part of the wall showing SPHP structure; J — attachment surface, substrate matter detached; K — longitudinal section through the contact of coils in early growth stages, showing elongated rice grain-like appearance of crystals in the middle layer (IOP structure) and relatively poorly developed SPHP layers.

Abbreviations: os — outer surface, is — inner surface, a — attachment side of the tube, ls — lower side of the tube, wi — tube wall on the internal side of the last coil, we — tube wall on the external side of the next-to-last coil. Large arrows indicate the direction of tube growth.

Рис. 1. *Circeis armoricana*. А–Е — трубки: А — взрослая особь с четким медианным килем (IPEE No. 148/2871); В — трубка ювенильной особи с хорошо выраженным медианным килем (IPEE No. 96/2051); С — не скульптурированная трубка взрослой особи (IPEE No. 33/1183); D — трубка со слабо выраженным медианным килем и периферийным флангом (IPEE No. 149/2889); Е — агрегация не скульптурированных трубок с налегающими оборотами на водоросли с узким талломом; F–K — ультраструктуры трубок, экземпляр № 1 (F–J), экземпляр № 2 (K): F — общий вид стенки в продольном сечении; G — внешняя часть стенки, демонстрирующая сферулитовую призматическую (SPHP) структуру; H — средняя часть трубки со структурой из хаотически ориентированных сферулитов (SIOP); I — внутренняя часть стенки со сферулитовой призматической структурой (SPHP); J — поверхность прикрепления к субстрату, вещество субстрата не сохранилось; K — продольное сечение через область смыкания оборотов на ранних стадиях роста; в среднем слое хорошо заметны удлиненные кристаллы в форме зерен риса, слагающие структуру хаотически ориентированных призматических кристаллов (IOP) и относительно слабо развитые сферулитовые призматические слои на наружной и внутренней поверхностях трубки.

Условные обозначения: os — наружная поверхность, is — внутренняя поверхность, а — поверхность прикрепления трубки, wi — стенка внутренней стороны позднего оборота; we — стенка наружной стороны раннего оборота. Большие стрелки указывают направление роста трубки.

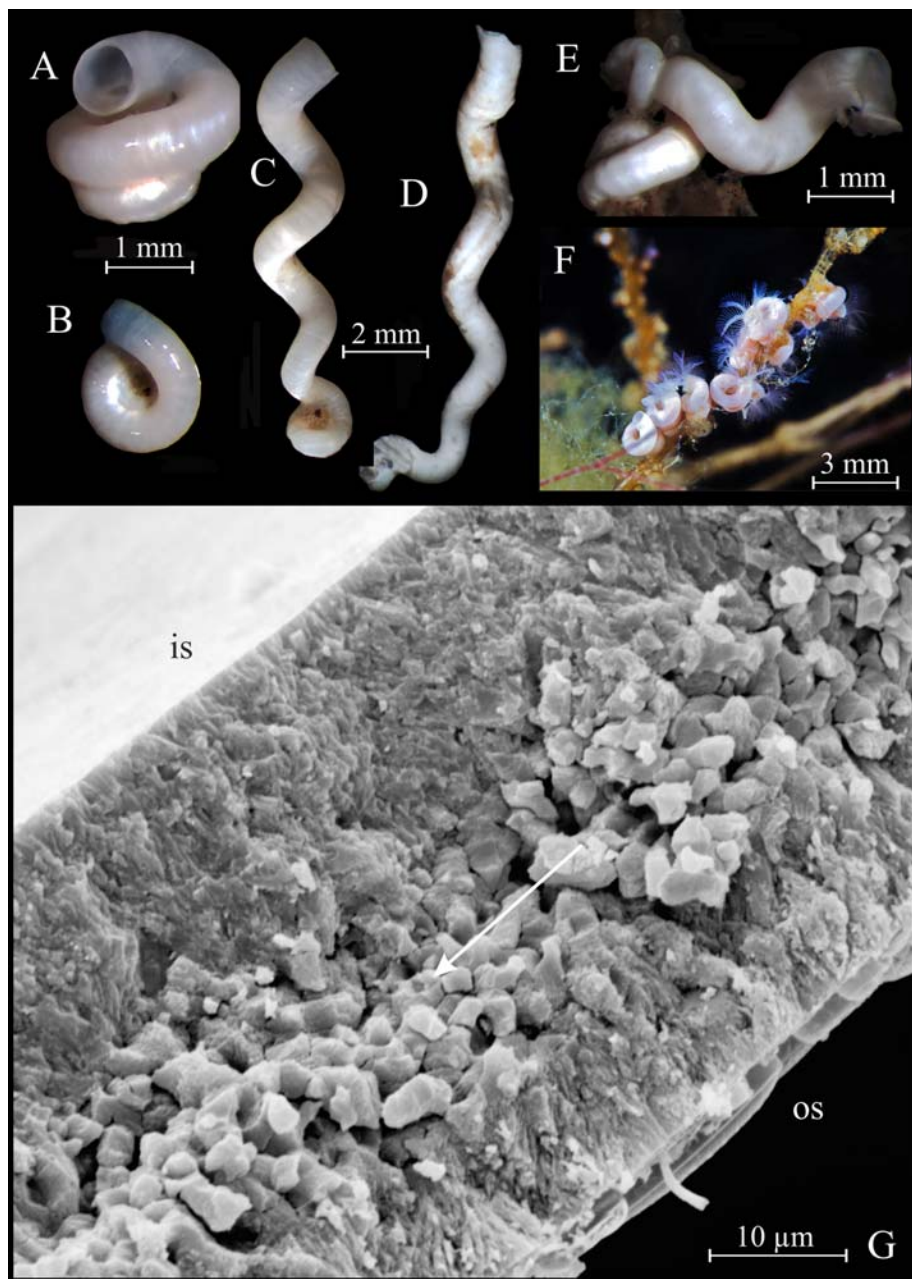


Fig. 2. *Circeis spirillum*. A–F — tubes (A–E: IPEE No. 13/1140; F — underwater photo *in situ*). A — tube with overlapping coils from the lateral side of view; B — juvenile tube with overlapping coils, view from the top; C — typical mode of coiling (tube, ascending over substratum like a spring); D — the same with slightly irregular initial coiling and almost straight posteriorly; E — specimen with irregular coiling; F — group of specimens on a hydroid colony; G — tube ultrastructure, longitudinal section of the wall showing three-layered structure (outer SPHP, middle SIOP and thick inner SPHP layers).

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

Рис. 2. *Circeis spirillum*. А–F — трубки (А–Е: ИПЕЕ No. 13/1140; F — подводное фото в естественных условиях). А — трубка с налегающими оборотами, вид сбоку; В — ювенильная трубка с налегающи-

tube and a set of 4 tubes (IPEE No. 21/1148, Atlasova Island, North Kurile Islands, depth 19 m, on bryozoan). External tube morphology was illustrated using preserved specimens (IPEE No. 13/1140, Atlasova Island, North Kurile Islands, depth 17–18 m, on bryozoans and underwater photo taken in vicinity of Velikaja Salma Strait, White Sea).

**Tube morphology.** Tubes are dextral. Only initial coils planospiral, further ones overlapping (Fig. 2A–B, F) or ascending over substrate like a spring (Fig. 2C–D) so that tube height sometimes reaches up to 6–7 mm. Also tubes may be somewhat irregularly coiled (Fig. 2E). Sculpture absent. Tube walls white but semi-transparent because thin-walled; porcellaneous.

**Tube ultrastructures.** Wall is three-layered, having very recognizable structure with irregular, non-rectilinear boundaries between layers (Fig. 2G). Outer layer is 8–10  $\mu\text{m}$  wide (corresponding wall width 40  $\mu\text{m}$ ), and has SPHP structure with well-defined spherulites. Middle layer is 8–15  $\mu\text{m}$  wide, composed of irregularly oriented spherulites (SIOP structure), smaller of them are more or less isometric (size  $\sim 2 \mu\text{m}$ ), larger ones irregularly elongated up to 4–5  $\mu\text{m}$ . Inner layer with SPHP structure is 15–25  $\mu\text{m}$  wide comprising up to 1/2 of total wall thickness.

Position of the axial part of parabolic growth lamellae is slightly displaced to outer surface, roughly coinciding with central part of the middle (SIOP) layer.

Inner organic lining was not observed.

**Tube mineralogy.** 100% low-Mg calcite ( $I_{\text{calc}} = 48$  and 246).

**Distribution.** In the Arctic this species is recorded from Chukchi, Laptev, Kara, Barents, White, Greenland Seas, and Central Arctic Ocean (Rzhavsky, 1992a, 1992[1994], 2001; Rzhavsky et al., 2014) as well as from Norwegian Sea (Knight-Jones P. et al., 1991). In the North Pacific its distribution range extends south

to Possiet Bay (Sea of Japan, Russia), Japan and California, USA; in the North Atlantic it extends to Brittany, France, and Nova Scotia, Canada (see Knight-Jones P. & Knight-Jones E.W., 1977; Knight-Jones P. et al., 1979; 1991; Rzhavsky, 1992a, 1992 [1994]).

**Ecology.** *C. spirillum* mainly colonizes hydrozoans and bryozoans, but as an exception it was recorded from the White Sea on red algae *Ptilota* sp. (Jakovis, 1997) and on some red algae from British coasts (Knight-Jones P., Knight-Jones E.W., 1977); juveniles sometimes are found on mussel byssus in the Sea of Japan (Rzhavsky, pers. observation). Worms are recorded at depths of 0–550 m with preferable bathymetric range 50–100 m.

### *Circeis vitreopsis* Rzhavsky, 1992

Fig. 3A–H.

For description see Rzhavsky, 1992b: 167–170, Figs 1A–C, 2A–I.

**Material examined.** Two specimens were studied with SEM in longitudinal sections [IPEE No. 4/2873, Vostok Bay, Primorsky Krai, Sea of Japan, depth 4–5 m, on the shell of bivalve *Swiftopecten swiftii* (Bernardi, 1858)]. Mineralogy was analyzed using a set of 7 tubes [IPEE No. 5/2891, Vostok Bay, Primorsky Krai, Sea of Japan, depth 5–15 m, on shells of bivalve *Crenomytilus grayanus* (Dunker, 1853)]. External tube morphology was illustrated using specimens from the sample also used for SEM analysis.

**Tube morphology.** Tubes are sinistral, usually planospiral (Fig. 3A), or with last whorl slightly overlapping preceding one (Fig. 3B). One distinct median longitudinal keel may form a small pointed projection over aperture. Coil diameter up to 2.5 mm. Wall vitreous (transparent or semitransparent); fields of transparent and semitransparent appearance are irregularly distributed over the surface, providing an impression of some “clouding” of the tube. In some specimens well-defined transparent longitudinal band running along outer median keel side (Fig. 3A).

---

ми оборотами, вид сверху; С — типичная форма, трубка приподнята над субстратом в виде растянутой пружины; D — то же, но с неправильным завиванием на начальных стадиях роста и более распрямленным последним завитком; E — трубка с неправильным клубкообразным завиванием; F — группа особей на колонии гидроидов; G — ультраструктура трубки, продольное сечение стенки с трехслойной структурой (внешний сферулитовый призматический, средний слой из хаотически ориентированных сферулитов и внутренний сферулитовый призматический слои).  
Условные обозначения: os — наружная поверхность, is — внутренняя поверхность. Большая стрелка указывает направление роста трубки.

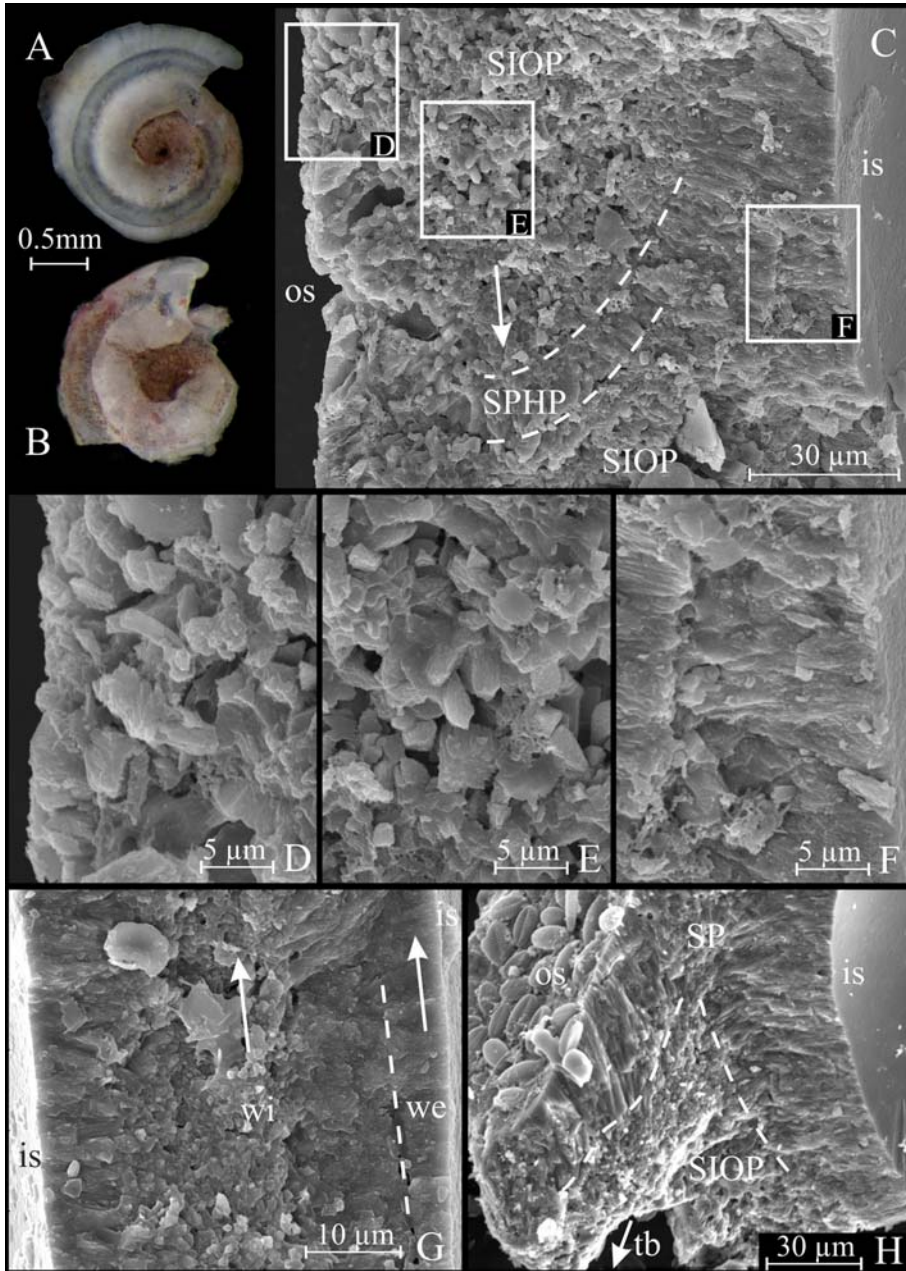


Fig. 3. *Circeis vitreopsis*. A, B — tubes (IPEE No. 4/2873): A — with longitudinal transparent band running along the lateral side of the median keel; B — semitransparent, locally with “cloudy” appearance; C–H — tube ultrastructures, specimen 1 (C–G), specimen 2 (H): C — general view of the longitudinal section, note parabolic growth lamellae and SPHP bands penetrating along them to the central part of the wall; D — outer part of the wall showing irregular SIOP structure; E — middle wall part showing SIOP structure; F — inner wall part showing SPHP structure along the lumen; G — section through the area of coils contact in early growth stages showing SPHP structure of the internal wall; H — general view of oblique section near the tube base, showing transition from three-layered structure near the attachment area (inner SPHP, middle SIOP, outer SP) to unilayered SP in the middle part of the wall by reduction of the middle SIOP layer.



**Tube ultrastructures.** Wall was found to be different in two studied specimens. In the first specimen (Fig. 3C–G) longitudinal section running nearby the tube base revealed two-layered structure. Inner SPHP layer (Fig. 3F) is 15–35  $\mu\text{m}$  wide (corresponding wall thickness is 90  $\mu\text{m}$ ) and locally penetrates into the inner part of the wall along certain growth lamellae (Fig. 3C). Outer layer (55–75  $\mu\text{m}$  wide) had SIOP structure consisting of irregularly shaped angular elongated spherulites (up to 5  $\mu\text{m}$  long and 2–2.5  $\mu\text{m}$  wide; Fig. 3D, E). Early coils (Fig. 3G) showed three-layered structure with developed outer SPHP, middle SIOP and inner SPHP layers, where inner and outer layers had equal thickness.

In the second specimen (Fig. 3H) the wall in standard longitudinal section was unilayered with simple prismatic (SP) structure. The wall was not homogenous as its middle part was less consolidated than outer and inner parts. Near the base of the tube chaotically oriented isometric spherulites appear in the middle part of the wall, thus transforming the structure into three-layered with inner and outer SPHP layers and middle SIOP. No details on spherulite morphology of SIOP layer were obtained for this specimen. The axis of parabolic growth lamellae was slightly displaced to the outer side of the wall, outer branch of parabola was partly reduced, so that crystals were inclined towards outer surface with angle  $\sim 45^\circ$  (Fig. 3H).

Internal wall of the coil, as observed from two different sections, was simplified, the only layer had SPHP structure (Fig. 3G). This layer probably corresponds to the inner SPHP layer, while middle SIOP layer and outer SPHP layers were absent in the contact zone of coils. Early growth stages had large amount of cement in the middle layer (Fig. 3G).

Inner organic lining was not observed.

**Tube mineralogy.** Probably 100% low-Mg calcite ( $I_{\text{calc}}=41$ ), doubtful weak aragonite peak was observed.

**Distribution.** Primorsky Krai, Sea of Japan (Rzhavsky, 1992b and unpubl.).

**Ecology.** Known from bivalve shells (live and dead) of *S. swifti* and *C. grayanus* at depths of 4–15 m.

**Remarks.** The tubes of *C. vitreopsis* are untypical for the genus because of their sinistral vitreous (transparent/semitransparent) tubes being far thicker and more solid than tube of any other *Circeis* species. They resemble the tubes belonging to *Paradexiospira*, but somewhat more fragile.

Variations of wall structure, observed in studied sections, may explain the “cloudy” wall appearance and the presence of a transparent band running along the outer side of the median keel. As unilayered SP structure tends to be related to transparency in serpulid tubes (Ippolitov, Rzhavsky, 2008; Vinn et al., 2008;

---

Abbreviations: os — outer surface, is — inner surface, tb — tube base, wi — tube wall on the internal side of the last coil, we — tube wall on the external side of the next-to-last coil. Large arrows indicate the direction of tube growth. Рис. 3. *Circeis vitreopsis*. А, В — трубки (ИПЕЕ No. 4/2873): А — полупрозрачная с продольной прозрачной полосой с наружной стороны срединного продольного кия; В — полупрозрачная, местами замутнённая; С–Н — ультраструктуры трубок, экземпляр № 1 (С–Г), экземпляр № 2 (Н): С — общий вид продольного сечения трубки, хорошо заметны параболические линии роста и слои с призматической сферулитовой (SPHP) структурой, проникающие вдоль отдельных линий роста в среднюю часть стенки; D — наружная часть трубки со структурой хаотически ориентированных сферулитов (SIOP); E — средняя часть стенки со структурой хаотически ориентированных сферулитов (SIOP); F — внутренняя часть стенки со сферулитовой призматической (SPHP) структурой; G — продольное сечение через смыкание оборотов на ранних стадиях роста; стенка на внутренней стороне позднего оборота имеет сферулитовую призматическую (SPHP) структуру; H — продольное сечение близ основания трубки, демонстрирующее переход от трехслойного строения (внутренний сферулитовый призматический (SPHP), средний слой со структурой хаотически ориентированных сферулитов (SIOP); наружный слой с простой призматической (SP) структурой) к однослойной стенке с простой призматической (SP) структурой за счёт выклинивания среднего слоя. Условные обозначения: os — наружная поверхность, is — внутренняя поверхность, tb — основание трубки, wi — стенка внутренней стороны позднего оборота; we — стенка наружной стороны раннего оборота. Большие стрелки указывают направление роста трубки.

Ippolitov et al., 2014), such structure found in longitudinal sections in the middle wall part seems to correspond to the longitudinal transparent band. Middle SIOP layer found in other sections, tapers out here. On the contrary, sections with a developed SIOP structure in middle (and sometimes in outer) zones of the wall obviously correspond to semitransparent areas of the tube.

The doubtful aragonite peak ( $I_{\text{arag}^0} = 8$ , reflecting content ~16%) in mineralogical analysis was somewhat shifted (spacing between diffracting planes  $d = 3.39 \text{ \AA}$ ). Due to the weakness of this signal we cannot be sure if any aragonite is really present.

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

**Type species:** *Spirorbis violaceus* Levensen, 1884.

**Diagnosis.** Tubes dextral, one species occasionally may be coiled sinistrally. Margins of collar and thoracic membrane not fused over thoracic groove. Large collar chaetae bent, cross-striated or fin-and-blade cross-striated. Only sickle (*Apomatus*-type) chaetae present on 3<sup>rd</sup> thoracic chaetigers. Four thoracic chaetigers in adults (juveniles rarely with only 3 chaetigers).

**Composition.** Genus includes subgenera *Paradexiospira* Caullery et Mesnil, 1897 and *Spirorbides* Chamberlin, 1919.

**Distribution.** All known species are arctic-boreal.

#### Subgenus *Paradexiospira* Caullery et Mesnil, 1897

**Type species:** *Spirorbis violaceus* Levensen, 1884.

**Diagnosis.** Modified collar chaetae cross-striated, groove may present in basal part of blade, but fin never forms.

**Composition.** *P. (P.) violacea* only.

#### *Paradexiospira (Paradexiospira) violacea* (Levensen, 1884)

Fig. 4A–H.

For descriptions see Knight-Jones et al., 1979: 429–430, Fig. 3C (a–e); Rzhavsky et al., 2014: 84–86, Fig. 18A–F, Pl. 2B.

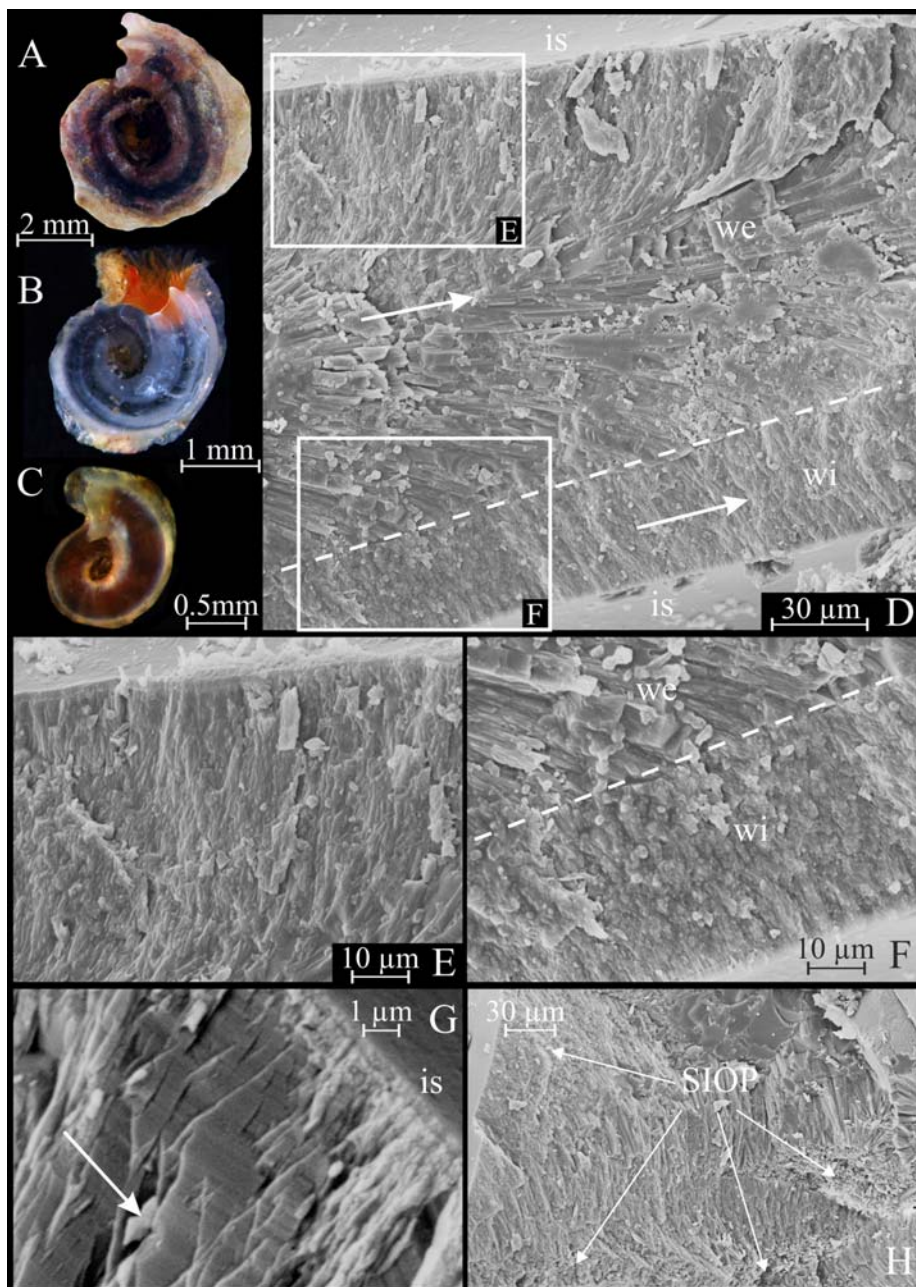
**Material examined.** Five specimens were studied with SEM in longitudinal sections (IPEE No. 41/2430, Vhodnoj Reef Point, Bering Island, Commander Islands, depth 8 m, on brachiopod). Mineralogy was analyzed using a single tube and by a set of 3 tubes from the same sample as was used for SEM. External tube morphology was illustrated using specimens from Telegraph Bay, Tromsø, Norway, littoral, on stones (IPEE No. 51/2880).

**Tube morphology.** Tubes are dextral, planospiral, thick-walled, up to 3.5 mm in coil

Fig. 4. *Paradexiospira (Paradexiospira) violacea*. A–C — tubes (IPEE No. 51/2880): A — typical live mature specimen, with three distinct keels ending with projections over the aperture; B — younger live specimen with a single median keel; C — preserved juvenile unsculptured specimen with small rounded projection over the aperture; D–H — tube ultrastructures, specimen 1 (D–F), specimen 2 (G), specimen 3 (H): D — general view of the longitudinal section of the contact of coils in late growth stages, showing unilayered SP structure in both external and internal walls (note gradually changing crystal orientation across the wall, giving a false impression of three-layered structure); E — inner part of the external wall; F — contact of coils; G — details of consolidated SP structure near the lumen, note tiny growth lines on the crystals subparallel to the lumen; H — longitudinal section near the tube base showing intercalating zones of SP and SIOP structures.

Abbreviations: os — outer surface, is — inner surface, wi — tube wall on the internal side of the last coil, we — tube wall on the external side of the next-to-last coil. Large arrows indicate the direction of tube growth.

Рис. 4. *Paradexiospira (Paradexiospira) violacea*. А–С — трубки (IPEE No. 51/2880): А — типичная живая взрослая особь с тремя продольными киями, оканчивающимися зубцами над устьем; В — более молодая живая особь с одним медианным килем, оканчивающимся зубцом над устьем; С — ювенильная фиксированная особь с нескульптированной трубкой и закруглённым выступом над устьем напротив будущего медианного кия; D–F — ультраструктуры трубок, экземпляр № 1 (D–F), экземпляр № 2 (G), экземпляр № 3 (H): D — общий вид продольного сечения через смыкание оборотов на поздних стадиях роста, демонстрирующий однослойную стенку с простой призматической (SP) структурой как на внешней, так и на внутренней сторонах оборота, хорошо заметны



постепенные изменения ориентировки кристаллов в стенке, создающие ложное впечатление наличия трёх слоев; E — внутренняя часть стенки на наружной стороне оборота; F — смыкание оборотов; G — детали строения консолидированной простой призматической (SP) структуры близ устья трубки, на кристаллах хорошо заметны тончайшие линии роста, идущие субпараллельно внутренней полости; H — продольное сечение основания трубки с выраженным переслаиванием зон с простой призматической (SP) структурой и структурой хаотически ориентированных сферулитов (SIOP). Условные обозначения: os — наружная поверхность, is — внутренняя поверхность, wi — стенка внутренней стороны позднего оборота; we — стенка наружной стороны раннего оборота. Большие стрелки указывают направление роста трубки.

diameter; adults with up to three massive keels ending as three projections over aperture (Fig. 4A, B), juvenile tubes unsculptured (Fig. 4C). Tube walls vitreous (transparent); deep violet inner tube lining visible through tube walls, so that tubes of live animals appearing almost black (Fig. 4A, B). This lining may change colour to brown in freshly preserved material (Fig. 4C) and to light-brown in long-stored material.

**Tube ultrastructures.** Tube wall is unilayered with SP structure (Fig. 4D–H). Prismatic crystals are merged together during the growth process, so that individual units, having the same cleavage, can be hardly recognized within the wall. The surface of crystals often demonstrates very fine transverse growth lines (Fig. 4G). The axis of parabolic growth lamellae slightly displaced to the outer side of the wall. External branch of parabola is partly reduced: crystals are inclined to outer surface at  $\sim 45^\circ$  angle (Fig. 4D, F). Structure of the internal wall is also unilayered SP (Fig. 4D, F). Outer and middle parts of the wall are absent in the coils contact zone, as suggested by the configuration of growth lamellae of the internal wall. Near the tube base there are numerous areas with SIOP structure (Fig. 4H), forming intercalating zones with normal SP structure.

Inner organic lining is about 1  $\mu\text{m}$  thick and well-separated from the wall.

**Tube mineralogy.** 100% low-Mg calcite ( $I_{\text{calc}}=130$  and 231).

**Distribution.** In the Arctic the species was recorded from Chukchi, Kara, Barents, White, and Greenland Seas (Rzhavsky, 1992a, 1992 [1994], 2001; Rzhavsky et al., 2014); also off the Arctic coast of West Greenland (Wesenberg-Lund, 1950) and Iceland (Knight-Jones P. et al., 1991). In the North-Western Pacific its distribution range to the south extends to North Kurile Islands, Russia (Rzhavsky, 1992a, 1992 [1994]); off American coast of Pacific the species is known only from Alaska (Knight-Jones P. et al., 1979). In the North Atlantic the species is recorded only from off Newfoundland, Canada (Knight-Jones P. et al., 1979).

**Ecology.** Worms live on stones, mollusk, brachiopod and barnacle shells, other serpulid

tubes, and solid erect branched bryozoans at depths of 0–130 m (preferable range 5–50 m).

**Remarks.** In *P. (P.) violacea*, as well as in all other members of the genus *Paradexiospira* described below, the general pattern of crystal orientation of SP structure is perpendicular to parabolic growth lamellae. As a result, the orientation of individual crystals changes gradually across the wall: in the middle part of the wall crystals are more or less parallel to the surface, while in outer part they are inclined to outer surface, and in the inner part of the wall crystals become almost perpendicular to the inner surface (Fig. 4D). This provides false impression of a three-layered tube. Because smallest crystal units in different zones of the wall look the same and are oriented in the same way (perpendicular to the growth lamellae), while distinct boundaries between these zones are absent, such wall is considered unilayered.

### Subgenus *Spirorbides* Chamberlin, 1919

**Type species:** *Serpula cancellata* Fabricius, 1780.

**Diagnosis.** Modified collar chaetae fin-and-blade cross-striated.

**Composition.** Only two species described below. Additionally, Knight-Jones P. et al. (1979) recorded specimens of *P. (S.) vitrea* (Fabricius, 1780) from Oregon with domed operculum, which may be a new species of the subgenus *Spirorbides* (Knight-Jones P., pers. comm.), but as it was never described, it was not included in our study.

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

Fig. 5A–J.

For descriptions see Bergan, 1953: 38, Fig. 3a–d; Rzhavsky et al., 2014: 86–88, Fig 19A–D.

**Material examined.** Two specimens were studied with SEM in longitudinal and transverse sections [IPEE No. 3/898, Olutorsky Gulf, Bering Sea (East Kamchatka), depth 52 m, on gravel]. Mineralogy was analyzed using a single tube and set of 2 tubes (IPEE No. 1/896, Morzhovaja Bay, Pacific coast of East Kamchatka, depth 25 m, on stones). External tube morphology was illustrated using specimens from the sample also used for SEM.

**Tube morphology.** Tubes are dextral, planospiral, thick-walled, up to 4 mm in coil diameter, usually with regularly spaced alveoli (pits) along the tube periphery (Fig. 5A–C). Alveoli often absent in juveniles (Fig. 5D), but very rarely in adults. Adult tubes with 2–3 distinct keels ending as projections over the aperture (Fig. 5A–B); juvenile tubes are unsculptured (Fig. 5D). Specimens of intermediate age between juveniles and adults have 1–2 vestigial keels (Fig. 5C). Tube walls are vitreous (transparent); inner tube lining is transparent and macroscopically invisible, while the body is uncoloured, so that tubes of live specimens appear greyish-white.

**Tube ultrastructures.** The wall in longitudinal section is unilayered, having SP structure (Fig. 5E–G). Individual crystals are poorly discernible. In the central wall part crystals are spiculi-like, over 15 µm long, while their width does not exceed 0.5–1 µm (Fig. 5E, I). Crystals making SP structure grow across parabolic lamellae. Locally near the inner and outer margins of the wall prismatic crystals can be gradually replaced by spherulites (SPHP structure; Fig. 5E, F), preserving the same orientation within the wall. In transverse section near the lumen we observed interbedding of typical SP/SPHP structure with thin layers composed of spherulites up to 9–10 µm length, oriented irregularly, densely packed and growing through each other (SIOP structure). The latter type of structure was also found near the attachment area (Fig. 5H–J), where relatively thin outer and inner sides of the wall are consolidated and have SP/SPHP structure, while thick middle zone has SIOP structure.

The axis of parabolic growth lamellae is located centrally or slightly displaced to the outer side of the wall (Fig. 5E). The outer branch is partly reduced: crystals are inclined towards outer surface at ~45° angle. In the internal wall, which is very thin, growth lamellae run almost parallel to the tube wall, being slightly inclined to lumen backwards, thus indicating that outer part of the wall is absent here.

Inner organic lining is well-discernible, 1–2 µm thick.

**Tube mineralogy.** 100% low-Mg calcite ( $I_{\text{calc}}=445$  and 436 in different samples).

**Distribution.** In the Arctic the species was recorded from Kara, Barents, White, and Greenland Seas (Rzhavsky, 1992a, 1992[1994], 2001; Rzhavsky et al., 2014); also reported off the Arctic coast of West Greenland (Wesenberg-Lund, 1950, 1953; Knight-Jones P. et al., 1991). In the North Pacific the species is known only off Russian coast where its range extends south to North Kurile Islands and northern part of Sakhalin (Rzhavsky, 1992a, 1992[1994]). In the North Atlantic the species is recorded only from Newfoundland, Canada (Knight-Jones P. et al., 1991).

**Ecology.** Worms attach to stones and shells at depths of 3–120 m (preferable range 5–50 m).

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

Fig. 6A–J.

For descriptions see Knight-Jones P., Knight-Jones E.W., 1977: 472–474, Fig. 6A–J; Knight-Jones P. et al., 1979: 430, Fig. 3D (a–f); Rzhavsky et al., 2014: 88–91, Fig. 20A–I, Pl. 2A.

**Material examined.** Six specimens were studied with SEM in longitudinal and transverse sections (three from IPEE No 23/978, Poludennaja Bay, Bering Island, Commander Islands, Russia, depth 9 m, on stones, and three from No. 39/994, Shirokaja Bay, Jurij Island, South Kurile Islands, Russia, depth 3 m, on stones). Mineralogy was analyzed using a single tube and the set of 4 tubes from the same sample as used for SEM (IPEE No 23/978). External tube morphology was illustrated using specimens from the Telegraph Bay, Tromsø, Norway, littoral, on stones (IPEE No. 117/2879) and the same sample as for SEM (No. 39/994).

**Tube morphology.** Tubes are normally dextral, sinistral specimens also recorded from Pacific coast of North America (Knight-Jones P. et al., 1979; Macdonald, 2007). Whorl diameter up to 2.5 mm, not exceeding 2 mm when tube is turret-shaped. Tubes of mature specimens thick, hard, vitreous (transparent), with 1–3 massive keels often ending as projections over the aperture (Fig. 6A–C). In live specimens red body colour visible through transparent tube walls, giving bright-pink appearance to tubes (Fig. 6A, B). Tubes may be overgrown by green-coloured algae (Fig. 6A). Walls of preserved or dead specimens sometimes lose transparency (Fig.

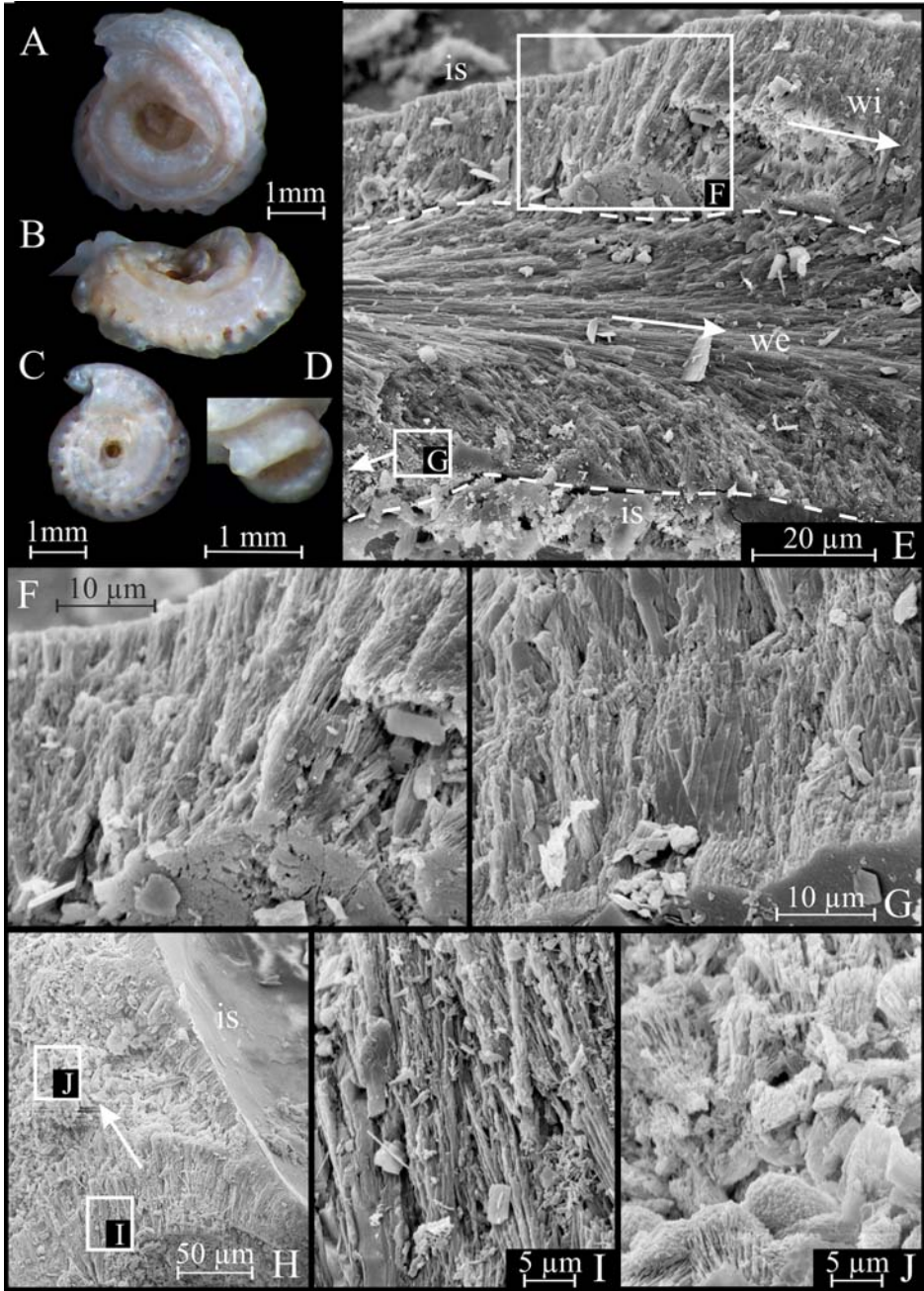


Fig. 5. *Paradexiospira (Spirorbides) cancellata*. A–D — tubes (IPEE No 3/898): A — mature tube, view from the top; B — the same specimen, from the lateral side of view; C — younger specimen with well-developed peripheral row of alveoli and only vestigial longitudinal keel; D — juvenile, yet without sculpture and without alveoli; E–J — tube ultrastructures: E — general view of the longitudinal section of the contact of coils in late growth stages showing unilayered SP structure in both external and internal walls; F — internal wall of the last coil; G — innermost part of the external wall showing calcite crystals of typical rhomboidal shape; H — general view of section along the tube base showing residual SIOP structure in

6C, D). Whorls usually planospiral (Fig. 6A, B) or overlapping giving turret-like shape to tubes (Fig. 6C, D), when tube height exceeds diameter 1.5–2 times. Tubes of juveniles unsculptured and planospiral; their walls having narrow transverse wavy transparent zones alternating with milky-white coloured ones.

**Tube ultrastructures.** In the last coils wall is unilayered, with SP structure (Fig. 6E–H). Inner and middle wall parts show high degree of consolidation, and isolated crystals are usually not distinguishable in these zones. In outer part individual crystals are sometimes better discernible, being composed of a bundles of tiny parallel crystallites (Fig. 6H). Their precise size is unclear as crystals grow continuously through consequent growth lamellae forming long crystal units with the same cleavage. Locally along the outer surface there are regions with spherulitic irregularly oriented structure (SIOP; Fig. 6I), and the tube surface is covered by spherulitic prismatic structure (SPHP) with somewhat loose orientation.

The axis of parabolic growth lines is located in the central part of the wall, being slightly displaced towards the outer side. In the internal wall middle and inner wall parts are completely declined (Fig. 6J), as it follows from the orientation of crystals, and parabolic growth lamellae are not visible.

Early (juvenile) coils have three-layered walls with thin inner and outer SPHP layers

(Fig. 6J), while the widest middle part of the wall has IOP (or irregular SIOP?) structure with crystals of 1, rarely 2  $\mu\text{m}$  long, embedded into amorphous organic matter. During tube growth this middle layer gradually reduces, being replaced by increasing inner and outer SP layers, finally merging together into a single layer.

Inner organic lining is thin, less than 0.5  $\mu\text{m}$ .

**Tube mineralogy.** 100% low-Mg calcite ( $I_{\text{calc}}=130$  and 345 in different samples).

**Distribution.** In the Arctic the species was recorded from Chukchi, Kara, Barents, White, Norwegian, and Greenland Seas (Rzhavsky, 1992a, 1992[1994], 2001; Rzhavsky et al., 2014); also reported from off Arctic coasts of Greenland (Wesenberg-Lund, 1950, 1953) and Iceland (Knight-Jones P. et al., 1991). In the North Pacific its range extends south the Russian coast of Sea of Japan (Rzhavsky, 1992a, 1992[1994]), Japan and California, USA (Knight-Jones P. et al., 1979, 1991). In the North Atlantic it extends to Brittany, France (Knight-Jones P., Knight-Jones E.W., 1977) and New England, USA (Knight-Jones P. et al., 1979, 1991).

**Ecology.** The species occupies only hard substrates, such as rocks, stones, mollusk, brachiopod and barnacle shells, other serpulid tubes and artificial substrates with rough surface. Juveniles are occasionally found on laminarian folds and *Abietinaria* sp. (Hydrozoa) at depths of 0–242 m (preferable range 3–50 m).

interspaces between zones with SP structure; I — parallel rod-like crystallites forming SP structure; J — irregularly oriented spherulites forming SIOP structure.

Abbreviations: is — inner surface, wi — tube wall on the internal side of the last coil, we — tube wall on the external side of the next-to-last coil. Large arrows indicate the direction of tube growth.

Рис. 5. *Paradexiospira (Spirorbides) cancellata*. A–D — трубки (IPEE No. 3/898) А — взрослая особь, вид сверху; В — тот же экземпляр, вид с боку; С — более молодая особь с периферический рядом альвеол, но только с одним зачаточным медианным килем; D — ювенильная особь без скульптуры и альвеол; E–J — ультраструктуры трубок: E — общий вид продольного сечения через смыкание оборотов на поздних стадиях роста, демонстрирующий однослойную стенку с простой призматической (SP) структурой как на наружной, так и на внутренней сторонах оборота; F — стенка на внутренней стороне последнего оборота; G — внутренняя часть стенки на наружной стороне оборота, видна типичная ромбическая форма кристаллов кальцита; H — продольное сечение близ основания трубки, демонстрирующее участки с остаточной структурой хаотически ориентированных призматических кристаллов между участками с простой призматической (SP) структурой; I — параллельные палочковидные кристаллиты, слагающие простую призматическую структуру (SP); J — хаотически ориентированные сферулиты, слагающие одноименную структуру (SIOP).

Условные обозначения: os — наружная поверхность, is — внутренняя поверхность, wi — стенка внутренней стороны позднего оборота; we — стенка наружной стороны раннего оборота. Большие стрелки указывают направление роста трубки.

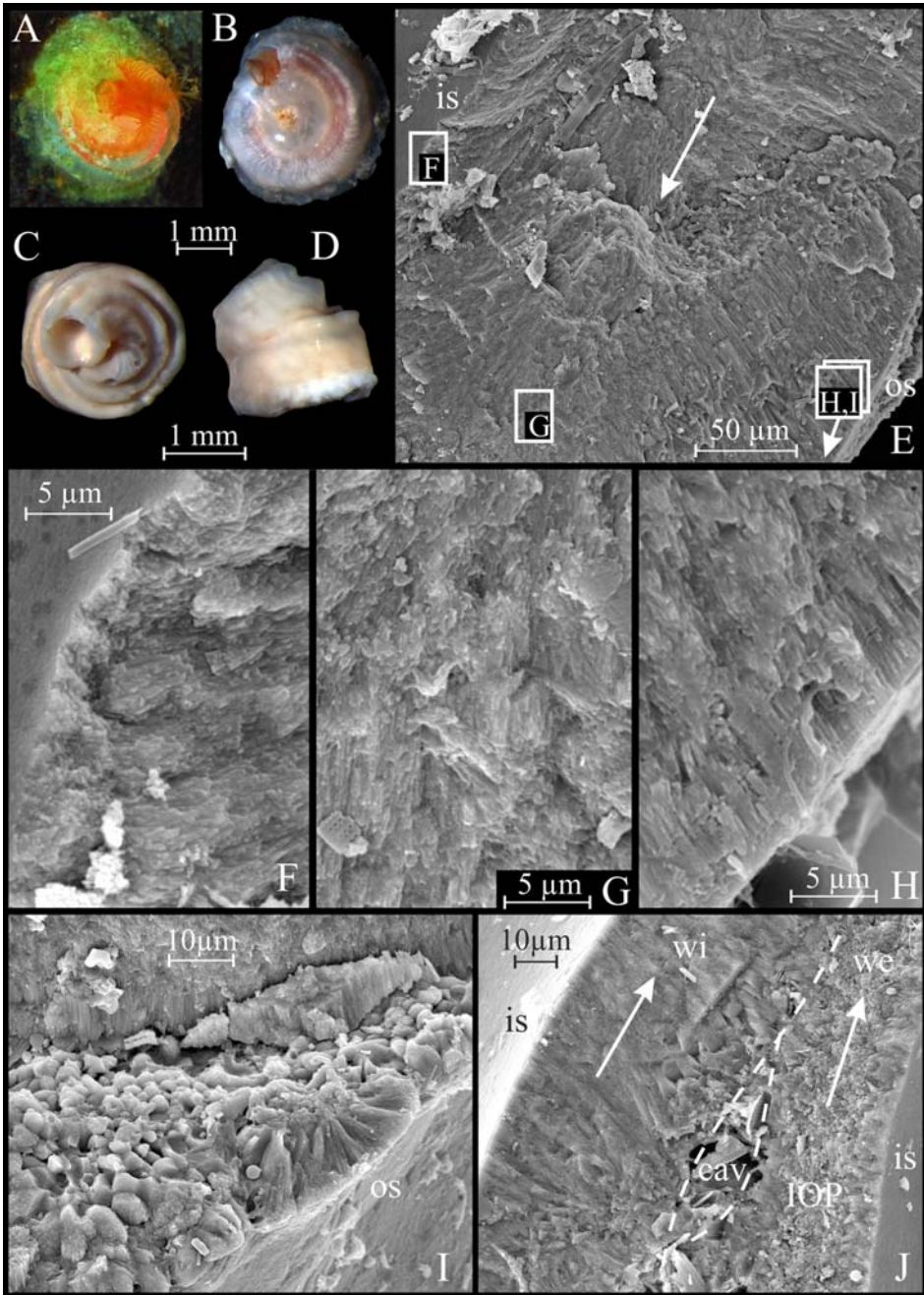


Fig. 6. *Paradexiospira (Spirorbides) vitrea*. A–D — tubes: A (IPEE No. 117/2879) — mature tube of live animal with three well-defined keels, view from the top; B–D (IPEE No. 39/994), B — mature tube of preserved worm with vestigial median keels, transparent tube and still kept light-red colour of the body (view from the top); C — preserved worm with turret-like tube, which has lost its original transparency, view from the top; D — the same specimen, from the lateral side view; E–J: tube ultrastructures: E — general view of the longitudinal section showing unilayered wall with SP structure; F — innermost part of the wall; G — middle part of the wall; H — outermost part of the wall; I — outermost part of the wall with unique residual



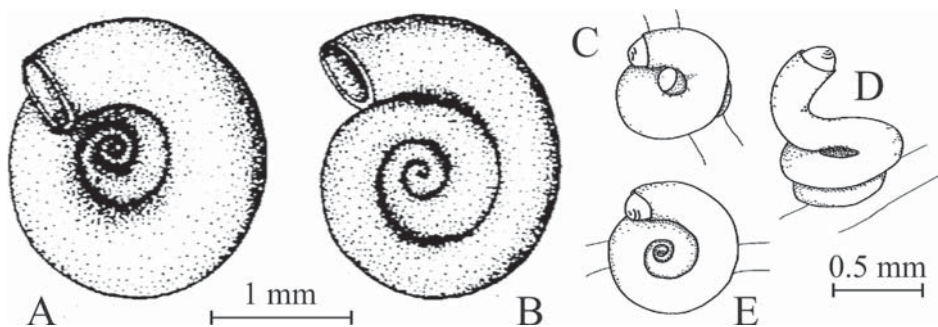


Fig. 7. Tubes of *Circeini* species not covered in the present study. A, B — *Circeis gurjanovae* (from Rzhavsky, 1992a, fig. A, B); C–E — *C. oshurkovi* (from Rzhavsky, 1998, fig. 1A–C).

Рис. 7. Трубки представителей трибы *Circeini*, не изученные в ходе настоящего исследования. А, В — *Circeis gurjanovae* (из Rzhavsky, 1992a, fig. A, B); С–Е — *C. oshurkovi* (из Rzhavsky, 1998, fig. 1A–C).

**Remarks.** Internal tube surface demonstrates small imprints up to 1  $\mu\text{m}$  in diameter, somewhat similar to those described for *Spirorbini* and interpreted as traces of anchoring by chaetae (Ippolitov, Rzhavsky, 2015).

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

Only three species of *Circeis* were not covered by our SEM and mineralogical studies: *Circeis paguri* Knight-Jones P. et Knight-Jones

E.W., 1977, *C. gurjanovae* Rzhavsky, 1992 and *C. oshurkovi* Rzhavsky, 1998.

*C. paguri* was originally described as a subspecies of *C. armoricana* by Knight-Jones P. and Knight-Jones E.W. (1977) and later was erected as valid species by Al-Ogily and Knight-Jones E.W. (1981) on the basis of the differences in ecology and larval morphology. Tube morphology of *C. paguri* (planospiral and unsculptured) is identical to that typical for representatives of *C. armoricana*, but tubes are smaller (coil diameter up to 1.5 mm only versus 2.5 mm in *C. armoricana*); its tube walls are white

area with SIOP structure; J — longitudinal section of the contact of early coils, showing three-layered external wall of the early coil, with thin outer SPHP, thick middle IOP, and thin inner SPHP layers. Note the cavity between coils, filled with carbonate debris and immured diatoms.

Abbreviations: cav — cavity between coils; is — inner surface, os — outer surface, wi — tube wall on the internal side of the last coil, we — tube wall on the external side of the next-to-last coil. Large arrows indicate the direction of tube growth.

Рис. 6. *Paradexiospira (Spirorbides) vitrea*. A–D — трубки: А (IPEE No. 117/2879) — взрослая живая особь с тремя килями, вид сверху; В–D (IPEE No. 39/994), В — взрослая зафиксированная особь с зачаточным срединным килем, прозрачной трубкой и всё ещё сохранившейся светло-красной окраской тела (вид сверху); С — трубка взрослой зафиксированной особи, потерявшая прозрачность с налегающими оборотами (башенковидная), вид сверху; D — тот же, вид сбоку; Е–J: ультраструктуры трубок: Е — общий вид продольного сечения, демонстрирующий однослойную стенку с простой призматической (SP) структурой; F — внутренняя часть стенки; G — средняя часть стенки; H — внешняя часть стенки; I — то же самое, уникальный реликтовый участок со структурой хаотически ориентированных сферулитов (SIOP); J — продольное сечение через смыкание оборотов на ранних стадиях, хорошо видно трехслойное строение стенки раннего оборота, состоящее из тонкого внешнего сферулитового призматического слоя (SPHP), более мощного среднего со структурой из хаотически ориентированных призматических кристаллов (IOP) и тонкого внутреннего сферулитового призматического (SPHP) слоя. Между оборотами заметна полость, заполненная неструктурированным карбонатным веществом и замурованными в процессе роста трубки створками диатомей.

Условные обозначения: cav — полость между оборотами, os — наружная поверхность, is — внутренняя поверхность, wi — стенка внутренней стороны позднего оборота; we — стенка наружной стороны раннего оборота. Большие стрелки указывают направление роста трубки.

opaque, slightly porcellaneous. It was never illustrated in literature.

Tubes of *C. gurjanovae* (Fig. 7A–B) look just the same as unsculptured tubes of *C. armoricana*, and have approximately the same size (2 mm in coil diameter versus 2.5 mm in *C. armoricana*); planospiral or their last whorls may overlap previous ones. Tubes examined by Rzhavsky (1992a) were non-porcellaneous, but this may be a result of long preservation time, which resulted in degradation.

The third species, *C. oshurkovi*, is very similar to *C. spirillum* by having thin, semi-transparent and unsculptured tubes (Rzhavsky, 1998). On the other hand, tubes of *C. oshurkovi* usually have last whorls covering the inner ones or last whorl may turn upwards away from the substrate (Fig. 7C–E), but never ascend over substrate like a spring as seen in *C. spirillum*; sometimes tubes of *C. oshurkovi* are planospiral with coil diameter up to 1.3 mm.

A potential new species of *Paradexiospira* (See Remarks to the subgenus *Spirorbides*) was not examined.

## Discussion

**Patterns and variations.** All Circeini have purely calcitic tubes with various numbers of layers having different structures, and can be classified into the following groups (Table 1).

Group A. Three-layered tube wall with well-developed inner and outer spherulitic prismatic (SPHP) covering layers, while middle part of the wall in juveniles has irregularly oriented prismatic (IOP) structure that in mature tubes transfers into spherulitic irregularly oriented prismatic (SIOP) structure with large spherulites (up to 5  $\mu\text{m}$ ). Macroscopically tubes are not transparent and tend to be unsculptured or to have a single median keel, rarely 3 keels. This group includes *C. armoricana* and *C. spirillum*.

Group B. Unilayered tubes with simple prismatic (SP) structure, which may locally transform to SPHP in inner and outer zones of the tube wall. Locally (for example in the attachment area) large slightly elongated spherulites without certain orientation (SIOP structure) may

also appear. Macroscopically tubes are always transparent, and mature specimens tend to have planospiral tubes with 3 massive keels. This group includes all studied species of *Paradexiospira*.

Spatial and ontogenetic interrelationships of two ultrastructural groups described above may be observed even within a single species — for example, *P. (S.) vitrea* obviously has type A of structure in early coils, while in later coils structure represents type B. One more species, *C. vitreopsis*, not included in the lists above, has tube features intermediate between groups A and B: a three-layered wall with a well-developed inner SIOP layer (characteristic of Group A) in the lower part of the tube, nearby the attachment area, but an unilayered SP wall (characteristic for Group B) slightly above. Also, general tube morphology of *C. vitreopsis* is also somewhat similar to that of the genus *Paradexiospira* (see Remarks above). In typically unilayered tubes (Group B) SIOP structure may appear locally, tending to be localized near the tube base.

As three *Circeis* species not covered by SEM studies, have opaque or semitransparent tubes, most probably they belong to Group A. Therefore, ultrastructural groups are well-correlated with generic subdivision of Circeini into *Circeis* and *Paradexiospira*, allowing in most cases the determination of generic affiliation of mature specimens (except for *C. vitreopsis*) by tube structure only. Representatives of the subgenera *Paradexiospira* s. str. and *Paradexiospira* (*Spirorbides*) do not differ by ultrastructures.

Both studied species of Group A (i.e. *Circeis* species) are more or less individual by their ultrastructures, differing in relative thickness of middle layer with spherulites. However, number of studied species is too small (3 out of 6 described species) to conclude that ultrastructures are a certain specific character for the members of the genus. SIOP structure of the middle layer, described here for Circeini, is much different from that known for other serpulids (e.g., Vinn et al., 2008; Vinn, 2013): crystals do not grow through each other, but are lying loosely in the wall and have more irregular

Table 1. Main tube characters for studied Circeini and their subdivision into groups. Abbreviations: arag — aragonite; calc — calcite; D — dextral (anti-clockwise) coiling; S — sinistral (clockwise) coiling.  
 Таблица 1. Основные черты строения трубок изученных видов Circeini. Условные обозначения: arag — арагонит; calc — кальцит; D — правозакрученные (против часовой стрелки) трубки; S — левозакрученные (по часовой стрелке) трубки.

Group	Species	External morphology							Mineralogy		Ultrastructures		
		Max. coil diameter (mm)	Coiling	Longitudinal keels	Alveoli	Transparency	Surface*	Inner lining colour**	arag/calc content (%)	Mg content in calc	Dense outer layer	Main layer and max crystal length (µm)	Dense inner layer
A	<i>C. armoricana</i>	2.5	D (rarely S)	0–3 vestigial or well-defined	no	opaque with narrow semitransparent transverse bands	slightly porcelaneous		0/100	low	SPHP	SPOP 3–4	SPHP
	<i>C. spirillum</i>	~2	D	0	no	semitransparent	30% cel-laneous		0/100	low	SPHP	SPOP 4–5	SPHP
	<i>C. vitreopsis</i>	2.5	S	1 median well-defined	no	vitreous unevenly transparent: “cloudy” or with transparent longitudinal bands		no	0/100	low	SPHP	SPOP 5	SPHP
B	<i>P. (P.) violacea</i>	3.5	D	3 massive	no	vitreous (transparent)		violet	0/100	low	consolidated SP		consolidated SP
	<i>P. (S.) can-cellata</i>	4	D	2–3 distinct	1 peripheral row	vitreous (transparent)		no	0/100	low	consolidated SP		consolidated SP
	<i>P. (S.) vitrea</i>	2.5	D (rarely S)	1–3 distinct	no	vitreous (transparent)		no	0/100	high	consolidated SP		consolidated SP

\* for non-transparent tubes only/только для непрозрачных трубок.

\*\* for transparent tubes only/только для прозрачных трубок.

shapes. They are more likely to be somewhat intermediate between well-defined spherulites and simple elongated prismatic crystals typical for IOP structure.

**Comparison with other Spirorbinae.** Both *Circeis* and *Paradexiospira* are clearly different by ultrastructure from spirorbins of the tribes Paralaespirini and Spirorbini studied before (Ippolitov, Rzhavsky, 2014, 2015).

Members of both Paralaespirini and Spirorbini have well-defined main layer with IOP structure, which is found in Circeini only in juveniles. Many Spirorbini have an outer SPHP layer, which is, unlike in Circeini, usually thin and unevenly developed. However, among studied Spirorbini, one unique species, *Spirorbis* (*Spirorbis*) *rothlisbergi* Knight-Jones, 1978, has three-layered tube (Ippolitov, Rzhavsky, 2015, "Spirorbini group C"), principally similar with the Circeini Group A. However, the middle layer of *S. (S.) rothlisbergi* consists of small rice grain-like crystals (not spherulites) typical within Spirorbinae, and therefore, has IOP structure which cannot be confused with SIOP structure of the middle layer in Circeini.

Among published data on species of other spirorbini tribes, unilayered SP tubes similar to Circeini Group B, were found in *Protolaeospira* (*Protolaeospira*) *augeneri* (Vine, 1977) (Ippolitov, Rzhavsky, 2008: fig. 1d), while a combination of middle SIOP layer with covering inner and outer SPHP layers, like in Circeini Group A, is known for *Protolaeospira* (*Dextralia*) *stalagmia* Knight-Jones P. et Walker, 1972 (Ippolitov, Rzhavsky, 2008: fig. 1 c, d); both species belonging to the tribe Romanchellini Knight-Jones P., 1978. Comparison with other species of Romanchellini as well as with species of tribes Januini and Pileolariiini will be provided in subsequent parts of the present series.

**Phylogenetic significance.** Altogether all species of the tribe Circeini form a continuous spectrum of tube structures. It includes three-layered tubes with well-developed middle SIOP layer (*C. armoricana*), three-layered tubes with thin, but still distinct middle SIOP layer (*C. spirillum*), complex uni- and three-layered tubes

(*C. vitreopsis*), and presumably unilayered SP tubes with residual spherulitic zones (all members of *Paradexiospira*). Early coils of unilayered SP tubes, as observed for *P. (S.) vitrea*, are essentially similar to those of *Circeis* by structure, being three-layered with well-developed middle IOP/SIOP layer. This means that within the range of ultrastructural variability of Circeini the presence of well-developed SIOP middle layer is a plesiomorphic state, while unilayered SP tubes are produced by strong reduction of SIOP elements during the ontogeny, and are evidently apomorphic. From this point of view, ultrastructurally *Paradexiospira* may be considered as a derivate of *Circeis*, and *C. vitreopsis* as an advanced member of the genus, close to the bifurcation point of *Circeis/Paradexiospira* in the phylogeny. However, *Circeis* looks more apomorphic from the point of soft body, having three thoracic chaetigers instead of four in *Paradexiospira*, thus illustrating a trend for oligomerization as a basic principle of metazoan evolution (Dogiel, 1954). The progressive soft-body characters in *Circeis* in combination with plesiomorphic tube wall structure and *vice versa* in *Paradexiospira* probably mean that the last common ancestor or both genera had three-layered *Circeis*-like tube wall, and four thoracic segments, like *Paradexiospira*. So, we can suppose that *Circeis* lineage evolved to oligomerization of thorax, while its tube structures remained more or less archaic, and in *Paradexiospira* lineage major evolutionary changes touched the tube structure.

Ontogenetic transition in Circeini from IOP structure in juveniles to SIOP structure in mature specimens, observed in *C. armoricana*, fits well the hypothesis of Vinn (2013), who suggested the idea of derivation of SIOP structure from IOP or RHC (rounded homogeneous crystal) structure. Also, our data suggest reasonably close relationships between Spirorbini and Circeini based on tube ultrastructures. Early ontogenetic stages showing IOP structure and uneven outer SPHP layer in *C. armoricana* fully repeat characteristics of some Spirorbini, having outer SPHP layer (Ippolitov, Rzhavsky, 2015). The striking morphological, mineralog-

ical, and ultrastructural similarity of adults in most ultrastructurally “plesiomorphic” Circeini (*C. armoricana*), having well-developed middle layer with unoriented type of structure with certain three-layered Spirorbini (*S. (S.) rothlisbergi*) having well-developed outer and inner SPHP layers, also supports the close phylogenetic relation of the tribes.

**Evolutionary interpretation of tube structure in *Paradexiospira*.** The present study suggests that unilayered tubes with SP wall structure is an evolutionary result of gradual swelling of dense inner and outer oriented spherulitic layers (usually having SPHP structure) combined with the total suppression of crumbly middle layer with unoriented structure (IOP or SIOP). Ippolitov and Rzhavsky (2015) discussed the explanation for the formation of dense outer layers in serpulids, introduced by Vinn and Kupriyanova (2011). We concluded that unlike in non-spirorbin serpulids, the appearance of SPHP layers in Spirorbini is related to their substrate preferences and the need of tube mechanical consolidation as protection from abrasion in high-energy environments. A similar explanation, suggesting development of SPHP layers as a factor resisting mechanical stress, was introduced by Chan et al. (2015), who hypothesized that outer SPHP layer may be important for preventing crack propagation on the juvenile tubes in *Hydroides elegans* Haswell, 1883. From this point of view, further transition to unilayered SP structure within Circeini could be interpreted as an extreme degree of strengthening the tube wall, allowing the species to settle in shallow-water bottom environments with high rates of sand abrasion. All species having unilayered SP tubes (*C. vitreopsis* and all *Paradexiospira*) are found only in such environments, settling on stones, shells etc. Therefore, Circeini group B may be interpreted as spirorbin branch that made a back evolutionary transition from inhabiting macrophytes and floating ephemeral substrata to hard-sediment benthic environments, like the serpulid ancestors of the subfamily Spirorbinae (Ippolitov, 2010; Ippolitov et al., 2014). In the frame of this hypothesis,

tube transparency, which is the most remarkable macroscopic character for all *Paradexiospira* tubes, is nothing but an accessory result of adaptation to high-energy bottom environments, not having strong adaptive significance itself.

The combination of SP and SPHP structures, making the tubes transparent, was also found in some unrelated serpulid genera (*Placostegus* Philippi, 1844 and *Vitreotubus* Zibrowius, 1979 — see Hove, Zibrowius, 1986; Vinn et al., 2008). An application of our hypothesis to these non-spirorbin Serpulidae is not fully consistent and needs to be discussed.

### Acknowledgements

We thank L.T. Protasevich, A.V. Kravtsev and R.A. Rakitov (Office of Instrumental Analytics, Paleontological Institute of Russian Academy of Sciences), N.N. Surovenkova (IPEE RAS), V.L. Kosorukov (Geological Faculty of Moscow State University) for their kind help with technical part of the study and A.A. Semenov (N.A. Pertsov White Sea Biological Station, Department of Biology of V.M. Lomonosov Moscow State University, Moscow, Russia for the kindly provided underwater photo of *C. spirillum*. We are grateful to E.K. Kupriyanova (Australian Museum Research Institute), R. Sanfilippo (University of Catania, Italy) and O. Vinn (University of Tartu, Estonia) who reviewed this manuscript and provided invaluable remarks and suggestions, greatly improving the paper. We also thank specialists and Institutions who donated materials to the collection of A.V. Rzhavsky (see full list in Ippolitov and Rzhavsky, 2014). The investigation was supported by the RFBR grant No. 14-05-31413 and RAS Presidium Program No. 28.

### References

- Al-Ogily S.M., Knight-Jones E.W. 1981. *Circeis paguri*, the spirorbid polychaete associated with the hermit-crab *Eupagurus bernhardus* // Journal of the Marine Biological Association of the United Kingdom. Vol.61. No.4. P.821–826.
- Bergan P. 1953. The Norwegian species of *Spirorbis* (Daudin) // Nyt Magasin for Zoologi. Vol.1. P.27–48.

- Bernardi M. 1858. Description d'espèces nouvelles // Journal de Conchyliologie. Vol.7. P.301–303.
- Bock K.-J. 1953. Linksqwundene Formen des Polychaeten *Spirorbis spirillum* (L.) // Zoologischer Anzeiger. Bd.150. H.7–8. S.200–201.
- Caulley M., Mesnil F. 1897. Études sur la morphologie comparée et la phylogénie des espèces chez les *Spirorbes* // Bulletin scientifique de la France et de la Belgique. T.30. P.185–233.
- Chamberlin R.V. 1919. The Annelida Polychaeta [Albatross Expeditions] // Memoirs of the Museum of Comparative Zoology at Harvard College. Vol.48. P.1–514.
- Chan V.B.S., Vinn O., Li C., Lu X., Kudryavtsev A.B., Schopf J.W., Shih K., Zhang T., Thiyagarajan V. 2015. Evidence of compositional and ultrastructural shifts during the development of calcareous tubes in the biofouling tubeworm, *Hydroides elegans* // Journal of Structural Biology. Vol.189. Iss.3. P.230–237.
- Dogiel V.A. 1954. Oligomerizatsiya gomologicheskikh organov kak odin iz glavnykh putej evolutsii zhivotnykh [The oligomerization of homologous organs as one of the main ways of the animals evolution]. Leningrad: Leningrad State University Press. 368 p. [in Russian].
- Fabricius O. 1780. Fauna Groenlandica, systematicae sistens, Animalia Groenlandiae occidentalis hactenus indagata, quoad nomen specificum, triviale, vernaculumque synonyma auctorum plurium, descriptionem, locum, victum, generationem, mores, usum, capturamque. Copenhagen, Leipzig. 452 pp.
- Haswell W.A. 1883. On some new Australian tubicolous annelids // Proceedings of the Linnean Society of New South Wales. Vol.7. P.633–638.
- Hove H.A., ten, Zibrowius H. 1986. *Laminatubus alvini* gen. et sp. n. and *Protis hydrothermica* sp. n. (Polychaeta, Serpulidae) from the bathyal hydrothermal vent communities in the eastern Pacific // Zoologica Scripta. Vol.15. No.1. P.21–31.
- Ippolitov A.P. 2010. Serpulid (Annelida, Polychaeta) evolution and ecological diversification patterns during Middle-Late Jurassic // Earth Science Frontiers. Vol. 17. Special issue. P.207–208.
- Ippolitov A.P., Rzhavsky A.V. 2008. On the tube microstructure of recent spirorbids (Annelida, Polychaeta) // Doklady Biological Sciences. Vol.418. P.20–22.
- Ippolitov A.P., Rzhavsky A.V. 2014. Tube morphology, ultrastructures and mineralogy in recent Spirorbinae (Annelida; Polychaeta; Serpulidae). I. General Introduction. Tribe Paralaeospirini // Invertebrate Zoology. Vol.11. No.2. P.293–314.
- Ippolitov A.P., Rzhavsky A.V. 2015. Tube morphology, ultrastructures and mineralogy in recent Spirorbinae (Annelida; Polychaeta; Serpulidae). II. Tribe Spirorbini // Invertebrate Zoology. Vol.12. No.1. P.61–92.
- Ippolitov A.P., Vinn O., Kupriyanova E.K., Jäger M. 2014. Written in stone: history of serpulid polychaetes through time // Memoirs of Museum Victoria. Vol.71. P.123–159.
- Jakovis E.L. 1997. [Preliminary data on the fauna polychaetes worms of the family Spirorbidae (Polychaeta, Sedentaria) of the White Sea] // Anichkovskij Vestnik Vol.1. P.33–54 [in Russian].
- Knight-Jones P. 1978. New Spirorbidae (Polychaeta: Sedentaria) from the East Pacific, Atlantic, Indian and Southern Oceans // Zoological Journal of the Linnean Society, London. Vol.64. No.3. P.201–240.
- Knight-Jones P., Walker A.J.M. 1972. Spirorbinae (Serpulidae, Polychaeta) on limpets from the South Orkney Islands // British Antarctic Survey Bulletin. Vol.31. P.33–40.
- Knight-Jones P., Knight-Jones E.W. 1977. Taxonomy and ecology of British Spirorbidae (Polychaeta) // Journal of the Marine Biological Association of the United Kingdom. Vol.57. No.2. P.453–499.
- Knight-Jones P., Knight-Jones E.W., Buzhinskaja G.N. 1991. Distribution and interrelationships of Northern spirorbid genera // Bulletin of Marine Science. Vol.48. No.2. P.189–197.
- Knight-Jones P., Knight-Jones E.W., Dales R.P. 1979. Spirorbidae (Polychaeta: Sedentaria) from Alaska to Panama // Journal of Zoology. Vol.189. No.4. P.419–458.
- Levinson G.M.R. 1884. Systematisk-geografisk oversigt over de nordiske Annulata, Gephyrea, Chaetognathi, og Balanoglossi // Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i København. 1882. P.160–251.
- Linnaeus C. [as Linné C.] 1758. Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Holmiae: Laurentius Salvius. 10<sup>th</sup> ed. 824 p.
- Macdonald T.A. 2007. Evolution of tube coiling direction in the dimorphic *Paradexiospira vitrea* (Fabricius, 1780) (Sabellida, Spirorbinae) // Abstracts of the 9<sup>th</sup> International Polychaete Conference, Portland, Maine, USA, August 12–18, 2007. P.56.
- Philippi A. 1844. Einige Bemerkungen ueber die Gattung *Serpula*, nebst Aufzählung der von mir im Mittelmeer mit dem Thier beobachteten Arten // Annals and Magazine of Natural History. Vol.14. P.153–162.
- Rzhavsky A.V. 1992[1994]. [Distribution of the Spirorbidae (Polychaeta) of the Russian shores] // Issledovaniya Fauny Morej. Vol.43(51). P.99–105 [in Russian].
- Rzhavsky A.V. 1992a. [A review of Circeinae and Spirorbinae (Polychaeta, Spirorbidae) of the Russian seas with description of the new species *Circeis gurjanovae*] // Zoologicheskij Zhurnal. Vol.71. No.7. P.5–13 [in Russian, with English summary].
- Rzhavsky A.V. 1992b. *Circeis vitreopsis* sp. n. (Polychaeta, Spirorbidae) from the Japan Sea // Ophelia. Vol.36. No.3. P.167–170.
- Rzhavsky A.V. 1998. *Circeis oshurkovi* sp. n. (Polychaeta, Spirorbidae) from the North Pacific // Ophelia. Vol.48. No.3. P.207–210.
- Rzhavsky A.V. 2001. Spirorbidae // I.A. Jirkov (ed.). Polichety Severnogo Ledovitogo okeana [Polychaeta of the Arctic Ocean]. Moscow. Yanus-K Press. P.572–606 [in Russian].
- Rzhavsky A.V., Kupriyanova E.K., Sikorski A.V., Dahle S. 2014. Calcareous tubeworms (Polychaeta, Serpulidae) of the Arctic Ocean. Moscow: KMK Sci. Press. 191 pp.

- Saint-Joseph M., de. 1894. Les Annélides polychètes des côtes de Dinard. Troisième Partie // Annales des sciences naturelles, Paris. Ser.7. T.17. No.1. P.1–395.
- Vine P.J. 1977. The marine fauna of New Zealand: Spirorbinae (Polychaeta: Serpulidae) // New Zealand Oceanographic Institute Memoir. Vol.68. P.1–66.
- Vinn O. 2013. SEM study of semi-oriented tube microstructures of Serpulidae (Polychaeta, Annelida): implications for the evolution of complex oriented microstructures // Microscopy Research and Technique. Vol.76. P.453–456.
- Vinn O., Kupriyanova E.K. 2011. Evolution of a dense outer protective tube layer in serpulids (Polychaeta, Annelida) // Carnets de Géologie [Notebooks on Geology]. Letter CG2011/05 (CG2011\_L05).
- Vinn O., Hove H.A., ten, Mutvei H., Kirmsmæ K. 2008. Ultrastructure and mineral composition of serpulid tubes (Polychaeta, Annelida) // Zoological Journal of the Linnean Society. Vol.154. P. 633–650.
- Wesenberg-Lund E. 1950. The Polychaeta of West Greenland, with special reference to the Fauna of Nordre Strømfjord, Kvane- and Bredefjord // Meddelelser om Grønland. Vol.151. No.2. P.1–171.
- Wesenberg-Lund E. 1953. The zoology of East Greenland. Polychaeta // Meddelelser om Grønland. Vol.122. No.3. P.1–170.
- Zibrowius H. 1979. *Vitreotubus digeronimoi* n. g., n. sp. (Polychaeta Serpulidae) du Pléistocène inférieur de la Sicile et de l'étage bathyal des Açores et de l'Océan Indien // Tethys. Vol.9. Iss.2. P.183–190.

*Responsible editor E.N. Temereva*