

Tube morphology, ultrastructures, and mineralogy in recent Spirorbinae (Annelida: Polychaeta: Serpulidae). IV. Tribe Romanchellini

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ABSTRACT: This is the fourth paper of the series (see Ippolitov & Rzhavsky, 2014, 2015a, b) that provides descriptions of the morphology of tubes of Recent spirorbins, their mineralogies and ultrastructures. Here, we discuss members of the tribe Romanchellini P. Knight-Jones, 1978 which comprises genera *Eulaeospira* Pillai, 1970, *Helicosiphon* Gravier, 1907a (including *Knightjonesia* Pillai, 2009), *Metalaeospira* Pillai, 1970, *Protolaeospira* Pixell, 1912 and *Romanchella* Caullery et Mesnil, 1897. Romanchellini's tube ultrastructures demonstrate an outstanding variability, which includes three types of unoriented structures (irregularly oriented prismatic — IOP, with several subtypes of crystal fabric described for the first time; spherulitic irregularly oriented prismatic — SIOP; rounded homogeneous crystal — RHC) and three types of oriented and semi-oriented structures (oriented fibrillar — OF; spherulitic prismatic — SPHP; simple prismatic — SP). Mineralogically, all studied tubes are 100% calcitic, with doubtful aragonite content registered in sample. Based on tube morphology, ultrastructures, and mineralogy, all Romanchellini can be subdivided into four groups, roughly corresponding to the subdivision into genera. Genus *Eulaeospira* differs from most other members of the tribe and should possibly be re-installed within the tribe Paralaeospirini, as was proposed by Phyllis Knight-Jones in her early papers. In the genus *Protolaeospira*, thick tubes, strengthened by the dominance of SP/SPHP structures, are an evolutionary adaptation to the environments characterised by aggressive hydrodynamics and sand abrasion — in particular, to the settlement on rocky substrates and pebbles in the upper sublittoral zone. In contrast, thin walls of tubes in *Metalaeospira*, also characterised by “loose” microstructure, are likely to relate to settlement on algae.

How to cite this article: Ippolitov A.P., Rzhavsky A.V. 2024. Tube morphology, ultrastructures, and mineralogy in recent Spirorbinae (Annelida: Polychaeta: Serpulidae). IV. Tribe Romanchellini // Invert. Zool. Vol.21. No.4. P.433–477, Suppl. Table. doi: 10.15298/invertzool.21.4.02

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

Морфология, ультраструктуры и минералогия трубок современных Spirorbinae (Annelida: Polychaeta: Serpulidae). IV. Триба Romanchellini

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РЕЗЮМЕ: Эта статья — четвертая часть серии (см. Ippolitov, Rzhavsky, 2014, 2015a, b), посвящённой описанию морфологии, минералогии и ультраструктур трубок современных спирорбин. В статье описываются виды, относящиеся к трибе Romanchellini P. Knight-Jones, 1978, в состав которой входят рода *Eulaeospira* Pillai, 1970, *Helicosiphon* Gravier, 1907a (включая *Knightjonesia* Pillai, 2009), *Metalaespira* Pillai, 1970, *Protolaespira* Pixell, 1912, and *Romanchella* Caullery et Mesnil, 1897. Микроструктуры трубок трибы обнаруживают чрезвычайное разнообразие, которое включает в себя три типа неориентированных структур (хаотически ориентированных призматических кристаллов (IOP) с несколькими подтипами, описываемыми впервые; сферулитовую хаотическую структуру (SIOP), структуру однородных изометричных кристаллов (RHC)), а также три различных типа ориентированных структур (ориентированная фибриллярная (OF); сферулитовая призматическая (SPHP); простая призматическая (SP)). Минералогически почти все изученные трубки сложены чистым кальцитом, присутствие арагонита под вопросом отмечено только для одного вида. По микроструктуре, минералогии и морфологии трубок все Romanchellini можно разделить на четыре группы, коррелирующие с подразделением на роды по признакам мягкого тела. Род *Eulaeospira* отличается от большинства других представителей трибы и, возможно, должен быть вновь отнесен к трибе Paralaeospirini, как это предлагалось первоначально в ранних работах Филлис Найт-Джонс. У рода *Protolaespira* толстые трубки, усиленные за счет развития структур SP/SPHP, являются эволюционным приспособлением к обитанию в обстановках, характеризующимся агрессивной гидродинамикой и песчаной абразией — в частности, на гальках и скальных грунтах в верхней сублиторали. Напротив, тонкостенные *Metalaespira* с рыхлой структурой стенки, вероятно, адаптированы к поселению преимущественно на водорослях. Как цитировать эту статью: Ippolitov A.P., Rzhavsky A.V. 2024. Tube morphology, ultrastructures, and mineralogy in recent Spirorbinae (Annelida: Polychaeta: Serpulidae). IV. Tribe Romanchellini // Invert. Zool. Vol.21. No.4. P.433–477, Suppl. Table. doi: 10.15298/invertzool.21.4.02

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

Introduction by A.P. Ippolitov to parts IV–VII

After Alexander V. Rzhavsky passed away in late July 2018, our series on the morphological and ultrastructural diversity within recent Spirorbinae remained partly unfinished. Shortly before his death, Alexander was preparing the materials to be published in parts IV, V, and VI, in particular, providing tube descriptions and photographs as well as reviewing the taxonomy of the described species. He died while working on part VI, leaving most of the materials necessary for the compilation of parts IV and V to me.

Starting from the present part, the following should be noted.

First, I did not discuss the interpretative part of our studies in detail with my co-author. However, new studies reconstructing spirorbin phylogeny (Rzhavsky, Kupriyanova, 2019; Rouse *et al.*, 2024) made it necessary to include these data in the discussion, providing a good ground for checking the assumptions deriving from our observations. Therefore, I am responsible for any erroneous deductions and conclusions in the Discussion of the present and subsequent parts of our series.

Second, I left principally unrevised parts of the text by Alexander dealing with the taxonomic aspects of extant spirorbins, even where they contradict the newer classifications (e.g., the position of some genera in Rouse *et al.*, 2024) or contain inconsistencies. However, the appropriate discussion or remarks are provided everywhere, and besides, the original diagnoses by Alexander were subjected to technical edits. A.V. Rzhavsky's diagnoses of supraspecific taxa (tribes and genera, but not subgenera), initially prepared for the present series, both from published parts I–III and unpublished drafts of parts IV–VI, were included in the serpulid chapter of the “Handbook of Zoology” series (Kupriyanova *et al.*, 2020), while some of them were published even earlier (Rzhavsky *et al.*, 2014, 2018). These diagnoses are repeated below in full to preserve the overall integrity of our work.

Third, the spirorbin collection by A.V. Rzhavsky, previously kept in his office at A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow (IPEE RAS), has been transferred to the Zoological Museum of Moscow University, Moscow

(ZMMU). As this huge collection remains mostly unregistered in this new repository, the original registration numbers of A.V. Rzhavsky at IPEE are retained throughout the text. However, some specimens used for our study remained unregistered in the original collection as well, as follows from Alexander's notes — some of them are likely to be lost shortly after being examined.

The obituary to Alexander, outlining his life and scientific career and containing a full list of his publications, was published by E.K. Kupriyanova (2020). In my turn, I hope that the present and subsequent parts of our series will help preserving immense knowledge on spirorbins accumulated by Alexander over decades of his scientific activity for future generations of marine biologists and everybody who loves serpulids.

Material and methods

Introductory remarks, including the critical terminology of tube morphology and ultrastructures, can be found in the first part of our series (Ippolitov, Rzhavsky, 2014), which also contains details of the material and methods. Since that paper had been published, additional materials from the collections of the Australian Museum Research Institute (AMRI) were received, which allowed us to obtain new observations on the morphology of several species and to extend the total coverage of our microstructural and mineralogical study by three species (two belonging to Romanchellini and one to Januini). As a result, our study now covers 19 out of 28 known valid species belonging to all five genera of the tribe Romanchellini P. Knight-Jones, 1978. Most of the examined specimens are from the collection of A.V. Rzhavsky, currently deposited in the Zoological Museum of Moscow University, Moscow (ZMMU).

Results

Tribe Romanchellini P. Knight-Jones, 1978

DIAGNOSIS (see also Kupriyanova *et al.*, 2020: 263–264). Embryos are incubated inside the parent's tube in the sac attached to the thorax or to the abdomen by an epithelial stalk, sometimes poorly developed. The only type of operculum throughout the lifetime is an endplate (which may be a multiplate in some species) with a talon or rarely without a talon. Other essential features are: 1) thoracic uncini have variable morphology — typically rasp-shaped with 3–7 longitudinal rows of teeth, rarely with 2–3 rows or saw to rasp-shaped, but a single species (*Romanchella quadricostalis* P. Knight-Jones, 1973) has 12–15 rows of teeth; anterior peg flat and often gouged,

thus, looking bifurcated under a light microscope, but sometimes flat anterior peg is fluted and looking serrated or wavy (see Vine, 1972: fig. 1F; Knight-Jones P., Fordy, 1979: fig. 84); 2) abdominal uncini are distributed asymmetrically: they are absent on the convex side of body or present only on last chaetigers; 3) abdominal chaetae are flat geniculate, brush-type with very short sharply narrowing blades and around 10 denticles; 4) abdominal capillary hooked chaetae may be present on the last chaetigers; 5) larvae usually without white abdominal attachment gland, reported only for *Protolaeospira striata* (Quiévreux, 1963) (see Quiévreux, 1963; Knight-Jones P., Knight-Jones E.W., 1977), while for many Romanchellini larvae remain completely undescribed).

DISTRIBUTION. Most species of Romanchellini are distributed throughout the Southern Hemisphere from the Antarctic coast to the tropical zone (but mainly in the subtropical areas). Some species of *Protolaeospira* Pixell, 1912 were recorded from both the North Pacific subtropical/tropical and boreal waters, while the distribution of a single species *Protolaeospira (Protolaeospira) striata* Quiévreux, 1963 ranges from the boreal to tropical waters in the north-eastern and west-southern Atlantic. One species of *Eulaeospira*, *E. arguta* (Bush in Moore, Bush, 1904), is distributed within the northern Indian Ocean and was described from Japan¹.

REMARKS. The tribe includes 5 genera: *Eulaeospira* Pillai, 1970, *Helicosiphon* Gravier, 1907a (including *Knightjonesia* Pillai, 2009), *Metalaeospira* Pillai, 1970, *Protolaeospira* Pixell, 1912, and *Romanchella* Caullery et Mesnil, 1897.

Although all Romanchellini incubate embryos inside the tube within a sac attached to the body by an epithelial stalk and in some species details of this attachment are undescribed or remain unclear, we suggest that there are two different types of incubation. *Romanchella*, *Helicosiphon*, and *Protolaeospira* have a distinct large stalk in the posterior part of the thorax. This stalk is visible even when embryos are not incubated. In *Eulaeospira* and *Metalaeospira*, the stalk is thin and short, attached to the abdominal fecal groove or to the thorax/abdomen boundary. Thus, the sac sometimes looks like a string of embryos lying freely in the fecal groove. For this reason, the latter group of genera had been considered as Paralaeospirini (= "Paralaeospirinae" in Knight-Jones P., Fordy, 1979) until P. Knight-Jones and E.W. Knight-Jones (1994) transferred them to Romanchellini (= "Romanchellinae" in Knight-Jones P., Knight-Jones E.W., 1994).

¹ In the original draft of the present paper A.V. Rzhavsky called this species "*Eulaeospira orientalis* (Pillai, 1960)", not mentioning the name "*arguta*" at all. However, as it follows from his unpublished manuscripts, he undoubtedly considered *orientalis* to be a junior subjective synonym of *arguta*. Therefore, the species name has been emended throughout the present paper — *A.P.I.*

Genus *Eulaeospira* Pillai, 1970

(see also description in Kupriyanova *et al.*, 2020: 264)

TYPE SPECIES: *Spirorbis argutus* Bush in Moore et Bush, 1904.

DIAGNOSIS (see also Kupriyanova *et al.*, 2020: 264). Tubes are sinistral (clockwise); margins of collar and thoracic membranes are not fused over thoracic groove; large collar chaetae are bent, without cross-striation, modified fin-and-blade as well as limbate are in the same fascicle; fin-and-blade chaetae are more common on convex body side than on the concave side; sickle chaetae absent; there are three thoracic chaetigers.

COMPOSITION. The genus includes 2 species (or 3, if we include a doubtful record of "*?Eulaeospira* sp." by Rzhavsky (1997) from Adelie Land, Antarctic shelf); only one is described below.

DISTRIBUTION. Tropical and subtropical regions of the Northern and Southern Hemispheres in the Indo-Pacific and probably, in the southern temperate waters, questionably, Antarctic shelf (Rzhavsky, 1997).

REMARKS. Initially, this genus was placed into Paralaeospirini because embryos were considered to lie freely in the tube (Knight-Jones P., Fordy, 1979). Later Knight-Jones P. and Knight-Jones E.W. (1994) demonstrated the presence of a poorly developed and hardly distinguishable attachment stalk. The brush-type abdominal notochoetae provide additional support for the placement of *Eulaeospira* in Romanchellini. This viewpoint has been accepted over the last decades (e.g., Macdonald, 2003; Rzhavsky, Kupriyanova, 2019; Kupriyanova *et al.*, 2020). Recently, Rouse *et al.* (2024) re-interpreted *Eulaeospira* as a member of Paralaeospirini; this agrees with the ultrastructural data represented below.

Eulaeospira convexis (Wisely, 1962)

Fig. 1A–E.

For descriptions see Wisely, 1962: 243–244, fig. 1–10 (as "*Spirorbis convexis*"); Knight-Jones E.W. *et al.*, 1974: 118–120, fig. 7a–p.

MATERIAL EXAMINED. Two specimens were studied with SEM in longitudinal sections (IPEE No. 1/2518, Sydney, Australia, lower littoral zone, on algae). Mineralogy was analysed using a bulk set of fragments of five tubes from the same sample. External tube morphology was illustrated using an unregistered specimen (Watson Bay, Sydney, depth 3–6 m, on brown algae *Ecklonia*) and supplemented by an additional figure from E.W. Knight-Jones *et al.* (1974: fig. 7a).

TUBE MORPHOLOGY. Tube is sinistral, small (coil diameter is about 1 mm), thin-walled. Coiling is planospiral (Fig. 1A) or with the last whorl covering the previous ones (Fig. 1B). There is no sculpture, cross-section is rounded. Tube surface is smooth and porcellaneous.

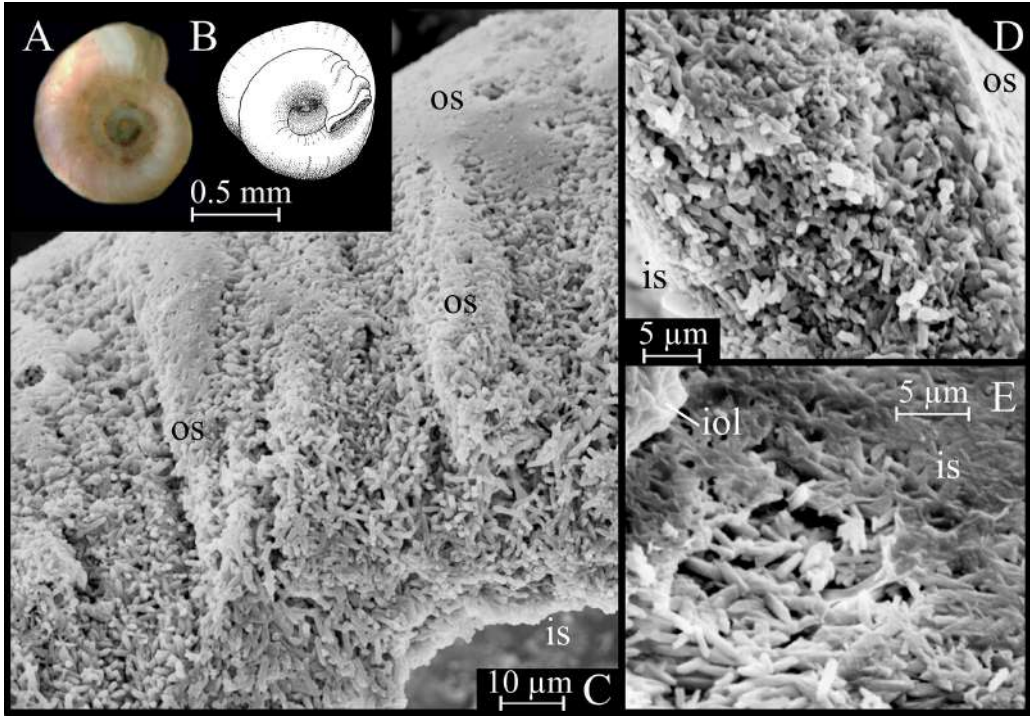


Fig. 1. *Eulaeospira convexis*: details of tube morphology and ultrastructures. A, B — tubes: A — adult planospiral tube (unregistered specimen from Watson Bay, Sydney); B — tube with ascending last whorl (from Knight-Jones E.W. *et al.*, 1974: fig. 7a); C–E — tube ultrastructures: C — specimen 1; general view of the oblique longitudinal section and adhering outer surface; D — specimen 2, longitudinal section of the wall, showing IOP structure; E — specimen 1, internal surface of the wall just below the inner organic lining (detached). Abbreviations: iol — inner organic lining; is — inner surface; os — outer surface.

Рис. 1. *Eulaeospira convexis*: детали строения трубок и их ультраструктуры. А, В — трубки: А — взрослая планоспиральная трубка (экземпляр без номера, Уотсонс Бэй, Сидней, Австралия); В — трубка с налегающим последним оборотом (из Knight-Jones E.W. *et al.*, 1974: fig. 7a); С–Е — ультраструктуры трубок: С — экземпляр №1; общий вид косого продольного сечения и прилегающего участка внешней поверхности трубки; D — экземпляр №2, продольное сечение однослойной стенки со структурой хаотически ориентированных призматических кристаллов (IOP); E — экземпляр №1, внутренняя поверхность трубки под органической мембраной (частично удалена). Обозначения: iol — внутренняя органическая мембрана; is — внутренняя поверхность; os — наружная поверхность.

TUBE ULTRASTRUCTURES. The wall is unilayered, having a typical IOP structure (Fig. 1C, D). Crystals are $\sim 3 \mu\text{m}$ long, with a corresponding width of $0.75 \mu\text{m}$; they are uniform in size and shape throughout the wall. Near the inner wall, elongated crystals are 1.5–2 times smaller than those in the middle part of the wall and lie parallel to the surface (Fig. 1D, E). The outer zone of the wall is consolidated by micritic matter (Fig. 1C).

Inner organic lining is thin, $\sim 1 \mu\text{m}$.

TUBE MINERALOGY. 100% high-Mg calcite ($I_{\text{calc}}=42$, average data reliability).

DISTRIBUTION. Species recorded only off the southern coast of Australia from Sydney to Geographe Bay, Western Australia, including Tasmania (Knight-Jones P., Knight-Jones E.W., 1984).

ECOLOGY. Shallow water species settling on algae, usually *Ecklonia* sp., from the littoral zone to several meters deep.

REMARKS. *Eulaeospira convexis* differs from most species of *Protolaeospira*, *Metalaeospira*, and *Helicosiphon* by its ultrastructure, as described below, but is undistinguishable from the members of the tribe Paralaeospirini (see Ippolitov, Rzhavsky, 2014), thus principally supporting the placement of the genus *Eulaeospira* within that tribe by Rouse *et al.* (2024; see the details in the Discussion section below).

Genus *Helicosiphon* Gravier, 1907a

(see also description in Kupriyanova *et al.*, 2020: 264)

TYPE SPECIES: *Helicosiphon biscoeensis* Gravier, 1907a.

DIAGNOSIS. Tubes are sinistral (clockwise); margins of collar and thoracic membranes are not fused over the thoracic groove; large collar chaetae are limbate without cross-striation; sickle chaetae are absent; there are four thoracic chaetigers.

COMPOSITION. 2 species (see Remarks).

DISTRIBUTION. Known from off the subantarctic islands of the South Atlantic and Indian Oceans, as well as some localities off the Antarctic coast.

REMARKS. Pillai (2009) established a monotypic genus *Knighjtjonesia* for the species *Helicosiphon platyspira* P. Knight-Jones, 1978. According to his opinion, this species (and, respectively, the genus *Knighjtjonesia*) differs from *Helicosiphon* in having a somewhat winged peduncle. The taxonomic importance of this feature is doubtful, contrary to our previous assumption (Ippolitov, Rzhavsky, 2014), so we do not support Pillai's new genus and below classify this species as a member of the genus *Helicosiphon*.

Helicosiphon biscoeensis Gravier, 1907a

Fig. 2A–I.

For descriptions see Gravier, 1907b: 63–68, figs 44–47, Pl. V, figs 49–52; Knight-Jones E.W. *et al.*, 1973: 10–14, figs 1A–K, 2A, 4E, 5 (partim); Monteiro *et al.*, 2013: 204–207, figs 1a–z, 2a–f; for additional figures of tubes, see also Pillai, 2009: fig. 1A–C.

MATERIAL EXAMINED. Two specimens were studied with SEM in longitudinal and transverse sections (IPEE No. 2/2895, Nella Fjord, Prydz Bay, Cooperation Sea, Antarctica, on stones and serpulid tubes, depth 8–9 m). Mineralogy was analysed using fragments of two tubes from the sample, which was used for SEM. External tube morphology was illustrated using a specimen from the sample also used for SEM and supplemented by a figure from E.W. Knight-Jones *et al.* (1973: fig. 1A).

TUBE MORPHOLOGY. Tube is sinistral, initially tightly coiled with a pronounced single keel on the upper side, but for most of its length (attaining 20 mm or more) forming an ascending disjunct spiral with a rounded unsculptured or subangular cross-section (Fig. 2A, B). In their erect part, tubes may be fluted proximally but unsculptured distally (Fig. 2A). At the transition from attached to erect part of the tube, there is a small constriction, where tubes often break (Fig. 2A, B; also see Ecology). The tube surface is white, opaque, and non-porcellaneous.

TUBE ULTRASTRUCTURES. The wall is two-layered (Fig. 2C). The outer layer is 8–12 μm thick with a corresponding wall thickness of $\sim 115 \mu\text{m}$, very distinct and has a somewhat irregular SPHP structure (Fig. 2D). Locally, this layer can disappear. Along certain growth lines, prismatic spherulites constituting the SPHP layer penetrate the middle part of the wall, sometimes up to the lumen, connecting the outer SPHP layer with the uneven inner SPHP layer (Fig. 2G). The outer SPHP layer is distinct in all studied sections. It is absent near the aperture of the tube (Fig. 2G) but is present backwards from it.

The main layer shows a transitional IOP structure represented by crystals of diverse shape, ranging from isometric varieties (2 μm in diameter) to elongated ones (length 5–6 μm , width 2–2.5 μm); both may have rounded or angular blunt ends. In a single studied cross-section (Fig. 2H), the inner part of the main layer shows elongated crystals arranged parallel to the transverse section (Fig. 2I), resembling the OF (ordered fibrillar) structure of Vinn *et al.* (2008). However, such an arrangement was not found elsewhere. The innermost part of the main layer is $\sim 20 \mu\text{m}$ thick (corresponding wall thickness is 120–130 μm) and shows the strongest consolidation by micritic matter. Crystal sizes vary throughout the wall. They are the

the transverse section; I — details of crystal orientation in the inner part of the wall (\sim ordered fibrillar (OF) structure *sensu* Vinn *et al.*, 2008).

Abbreviations: is — inner surface; os — outer surface.

Рис. 2. *Helicosiphon biscoeensis*: детали строения трубок и их ультраструктуры. А, В — трубки; А — трубка типичной морфологии с неясно-угловатым, бороздчатым поперечным сечением участка, поднимающегося над субстратом (IPEE No. 2/2895), также на прикрепленном участке заметен мидианный киль; В — трубка с сечением выраженной угловатой формы на приподнимающемся участке (из Knight-Jones E. W. *et al.*, 1973: fig. 1A); С–I — ультраструктуры трубок (С–F, экземпляр №1; G–I, экземпляр №2): С — общий вид продольного сечения; D — внешняя часть стенки, показывающая присутствие тонкого приповерхностного слоя со сферулитовой призматической структурой (SPHP); E — центральная часть стенки со структурой хаотически ориентированных призматических кристаллов (IOP); F — внутренняя часть стенки, заметна неясная ориентировка кристаллов длинной вдоль внутренней поверхности трубки; G — экземпляр №2, общий вид продольного сечения в приустьевой части трубки, хорошо заметно проникновение внешнего сферулитового призматического слоя (SPHP) вдоль отдельных параболических слоев роста; H — общий вид поперечного сечения; I — ориентировка кристаллов во внутренней части стенки, видимые в поперечном сечении (\sim ориентированная фибриллярная структура (OF), согласно классификации (Vinn *et al.*, 2008)).
Обозначения: is — внутренняя поверхность; os — наружная поверхность.

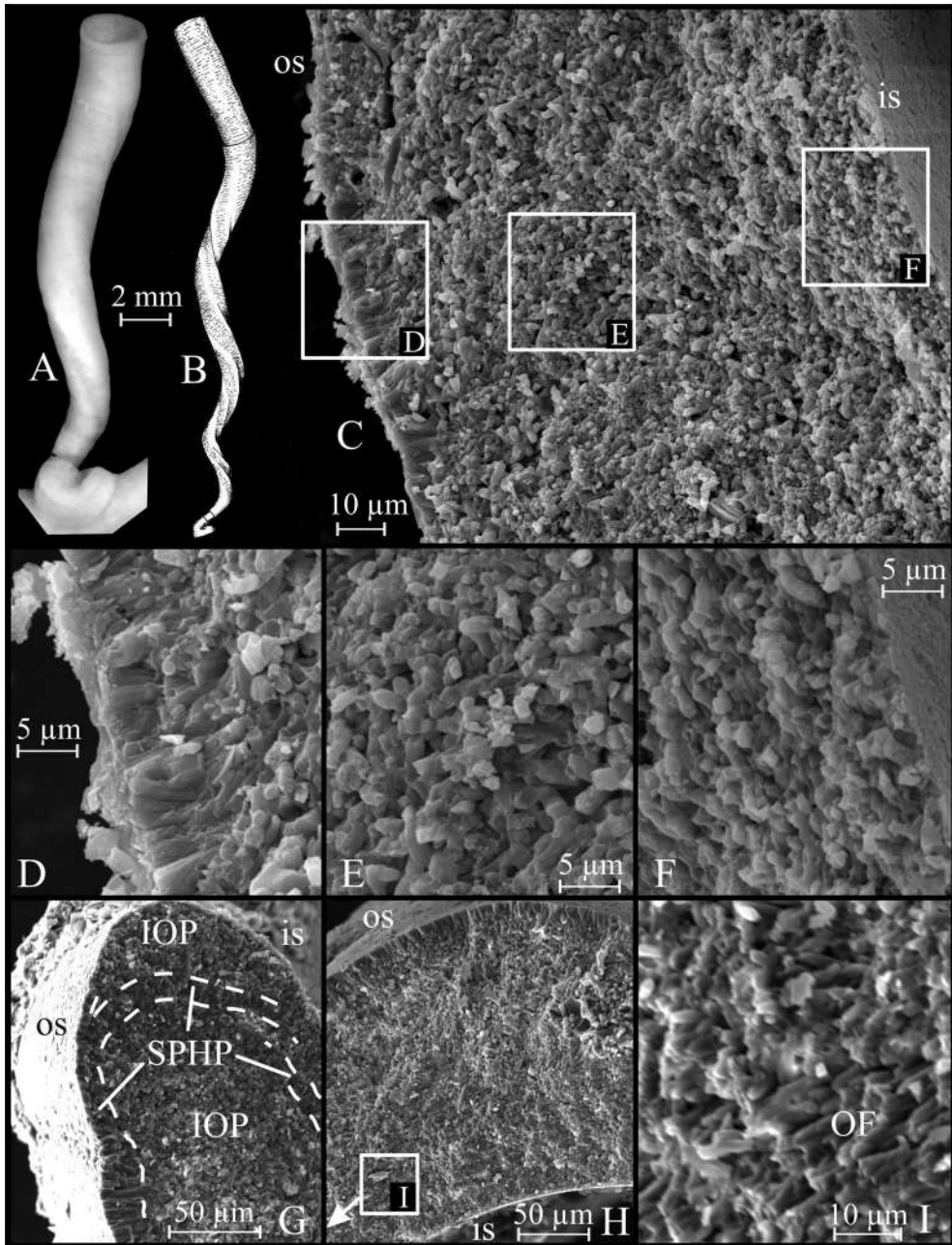


Fig. 2. *Helicosiphon biscoeensis* details of tube morphology and ultrastructures. A, B — tubes; A — typical tube with unclear angular, fluted cross-section (IPEE No. 2/2895), also showing a keel on the upper side of the attached part; B — tube with pronounced angular cross-section of the ascending part (from Knight-Jones E.W. *et al.*, 1973: fig. 1A); C–I — tube ultrastructures (C–F, specimen 1; G–I, specimen 2): C — general view of the longitudinal section; D — outer part of the wall showing irregular SPHP structure along the surface; E — central part of the wall showing IOP structure; F — innermost zone of the wall showing unclear orientation of prismatic crystals parallel to the lumen; G — specimen 2, general view of apertural part of the wall also showing penetration of SPHP outer layer along parabolic growth lamellae; H — general view of

largest in the central part of the wall, while the inner and outer zones contain smaller crystals.

Inner organic lining was not observed, judging from the appearance of the inner zone (Fig. 2F); it is easily detachable from the wall and not preserved in our specimens.

TUBE MINERALOGY. 100% calcite ($I_{\text{calc}}=525$).

DISTRIBUTION. South Atlantic: off South Georgia, the South Shetlands and South Orkney Islands; Antarctic coast: Biscoe Bay, Antarctic Peninsula (Bellingshausen Sea), Ross Sea (Monteiro *et al.*, 2013) and Cooperative Sea (Rzhavsky, unpubl.).

ECOLOGY. *Helicosiphon biscoeensis* is recorded at depths of 2–200 from stones and tubes of other serpulids sunk in silt or silty sand. According to Gravier (1907b) and E.W. Knight-Jones *et al.* (1973), the initial, coiled part of the tube breaks off at the small constriction at the transition to the erect part (Fig. 2A, B), and afterwards, the tube sits “freely” in the sediment in an upright position. However, Monteiro *et al.* (2013) demonstrated that some tubes have the initial part preserved and unbroken. It is possible that “free” anterior parts result from mechanical damage during the sampling.

REMARKS. Records from the Kerguelen Islands, initially attributed to *H. biscoeensis* by E.W. Knight-Jones *et al.* (1973), belong to *H. platyspira* (Knight-Jones P., 1978).

Helicosiphon platyspira P. Knight-Jones, 1978

Fig. 3A–E.

For description see Knight-Jones P., 1978: 233–234, fig. 18A–K.

MATERIALEXAMINED. Only one tube (IPEE No. 1/2507, Crozet Islands, Indian Ocean, depth 155–156 m) was available both for SEM examination (longitudinal section) and for mineralogical analysis.

External tube morphology is illustrated by the figures from P. Knight-Jones (1978: fig. 18A, B).

TUBE MORPHOLOGY. Tubes are sinistral, planospiral or with overlapping whorls (Fig. 3A, B). Coil diameter is 5 mm or more in planospiral specimens. Tube is unsculptured, with opaque white, non-porcellaneous walls.

TUBE ULTRASTRUCTURES. The wall is two-layered (Fig. 3C). Near the outer surface, there are numerous irregularly oriented spherulites, with a tendency to form SPHP structure (Fig. 3C, D), but locally transforming into hemispheres with a common nucleation centre. The spaces between loosely lying spherulites are filled with small isometric crystals (diameter 0.5 μm). The outer half of the wall has intermixed crystals of different types, ranging from smaller, slightly elongated varieties (length 2 μm , width 1 μm) to more elongated and regular-shaped cylindrical forms (length 5 μm , width 1.5 μm). The inner half of the wall contains micritic matter, and larger-sized elongated crystals seem to be absent here.

Inner organic lining is $\sim 2 \mu\text{m}$ thick (Fig. 3E).

TUBE MINERALOGY. 100% calcite ($I_{\text{calc}}=458$).

DISTRIBUTION. *Helicosiphon platyspira* is known only from the Southern Indian Ocean off the Kerguelen, Marion, Prince Edwards and Crozet Islands (Knight-Jones P., 1978; Knight-Jones P., Knight-Jones E.W., 1984; Rzhavsky, 1998).

ECOLOGY. According to the published data, *H. platyspira* inhabits hard substrates in a low littoral zone (Knight-Jones P., 1978), while some records lack information about the habitat. The specimen we examined was collected from depths of 155–156 m (Rzhavsky, unpublished data).

REMARKS. Specimens of *H. platyspira* from the Kerguelen Islands were initially identified as “*Spirorbis perrieri*” by Ehlers (1913; =*Romanchella perrieri*, according to actual classification) and later as *H. biscoeensis* by E.W. Knight-Jones *et al.* (1973; see discussion in Knight-Jones P., 1978).

general view of a longitudinal section in the mouth area.

Abbreviations: is — inner surface; os — outer surface. Large arrows indicate the direction of tube growth.

Рис. 3. *Helicosiphon platyspira* (A–E) и *Metalaeospira armiger* (F–J): детали строения трубок и их ультраструктуры. A–E — *Helicosiphon platyspira*: A, B — трубки (из Knight-Jones P., 1978: fig. 18A, B); A — планоспиральный вариант; B — с перекрывающимися оборотами и приподнятым последним оборотом; C–E — ультраструктуры трубок: C — общий вид продольного сечения; D — внешняя часть стенки, со сферулитовым призматическим слоем (SPHP); E — внутренняя часть стенки, хорошо видна органическая мембрана на внутренней поверхности трубки. F–J — *Metalaeospira armiger*. F–H — трубки: F — планоспиральная; G — с приподнимающимся последним оборотом; F — раскрученная, с приподнимающимися оборотами; I–J — ультраструктуры трубок; I — экземпляр №1, общий вид продольного сечения, хорошо видно, что внешняя часть трубки сложена хаотически ориентированными сферулитами (структура SIOP), у поверхности локально приобретающими ориентировку, характерную для сферулитовой призматической структуры (SPHP), также хорошо заметен постепенный переход от сферулитов к призматическим кристаллам близ внутренней поверхности трубки; J — экземпляр №2, общий вид продольного сечения через устьевую часть трубки.

Обозначения: is — внутренняя поверхность; os — наружная поверхность. Большие стрелки показывают направление роста трубки.

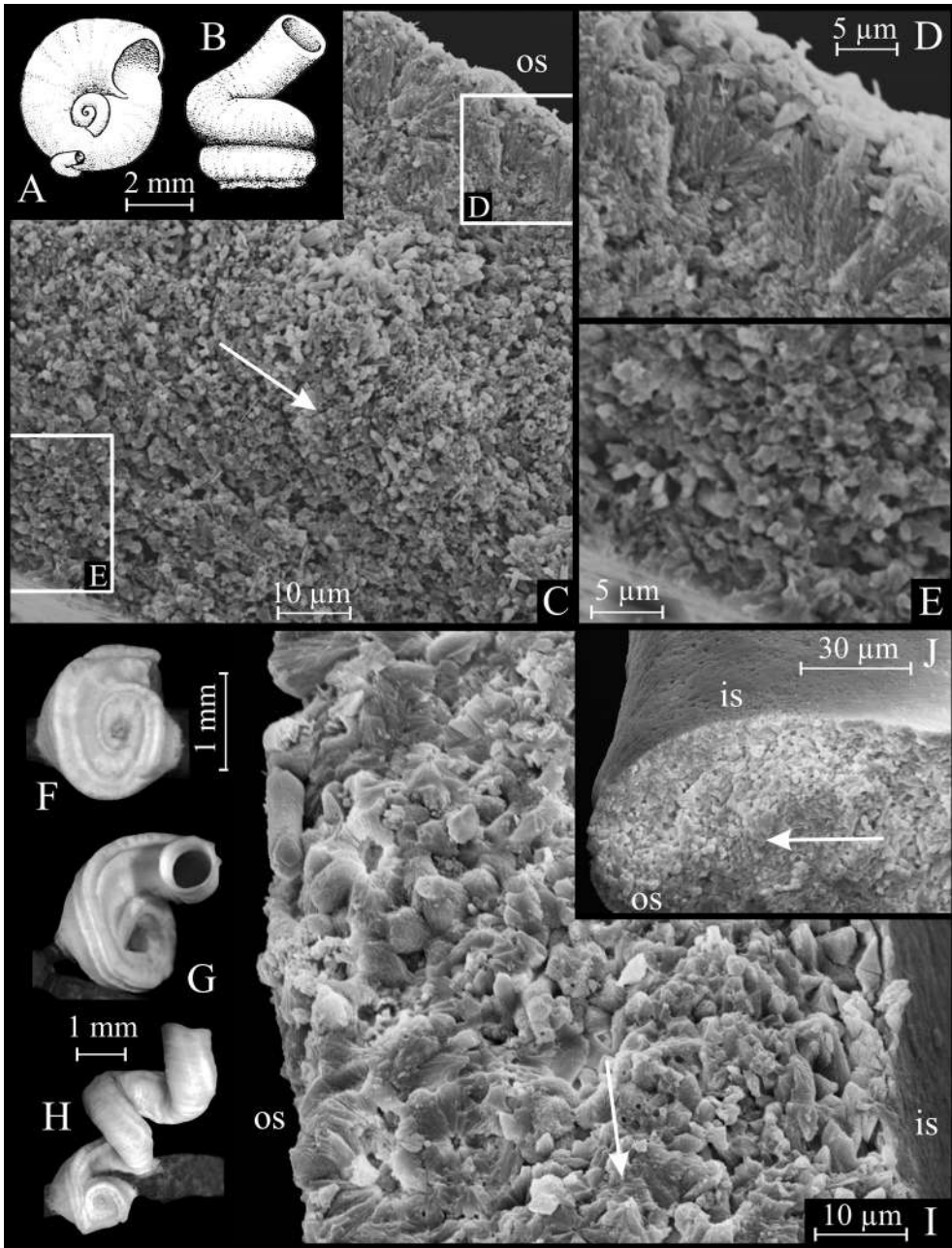


Fig. 3. *Helicosiphon platyspira* (A–E) and *Metalaeospira armiger* (F–J): details of tube morphology and ultrastructures. A–E — *Helicosiphon platyspira*: A, B — tubes (from Knight-Jones P., 1978: fig. 18A, B); A — planospiral modification; B — tube with ascending whorls; C–E — tube ultrastructures: C — general view of the longitudinal section; D — outer part of the wall showing irregular SPHP structure; E — innermost zone of the wall showing inner organic lining. F–J — *Metalaeospira armiger*. F–H — tubes; F — planospiral tube; G — tube with last whorls ascending over substrate; H — evolved tube, with whorls ascending from the substrate; I–J — tube ultrastructures; I — specimen 1, general view of the longitudinal section showing irregularly oriented spherulites in the outer zone (SIOP structure), locally transforming to SPHP covering layer, note the gradual transition from spherulites to prismatic crystals across the wall; J — specimen 2,

Genus *Metalaespira* Pillai, 1970(see also description in Kupriyanova *et al.*, 2020: 264)

TYPE SPECIES: *Spirorbis antarcticus* Pixell, 1913 (= *Spirorbis pixelli* Harris, 1969).

DIAGNOSIS. Tubes are sinistral (clockwise); margins of collar and thoracic membranes are not fused over thoracic groove; large collar chaetae are limbate without cross-striation; sickle chaetae present in the third fascicle; there are four thoracic chaetigers.

COMPOSITION. 4 species, all covered in the present study.

DISTRIBUTION. It was recorded from subantarctic waters off the islands of the South Atlantic and Indian Oceans, New Zealand, the south coast of Australia and some locations off the Antarctic coast.

REMARKS. Like *Eulaespira*, this genus was initially placed in *Paralaespirini* by P. Knight-Jones and Fordy (1979) because its incubation type was insufficiently known. Later P. Knight-Jones and E.W. Knight-Jones (1994) revealed the presence of the attachment stalk, thus justifying its placement within *Romanchellini*. This assumption is supported by the presence of brush-type abdominal chaetae.

***Metalaespira armiger* Vine, 1977**

Fig. 3F–J.

For descriptions see Vine, 1977: 12, figs 2c, 3a–d, 4a–g, 17 c; Knight-Jones P., Knight-Jones E.W., 1994: 88–89, fig. 2E–L.

MATERIAL EXAMINED. Two specimens (IPEE No. 1/2402, South Orkneys Islands, depth 97 m, on bryozoans) were studied with SEM in longitudinal sections. Mineralogy was analysed using two broken tubes and numerous fragments from the same sample.

External tube morphology was illustrated using the specimens from the same sample.

TUBE MORPHOLOGY. Tubes are sinistral, may be planospiral (Fig. 3F), but late whorls are usually positioned upright (Fig. 3G, H; see also Knight-Jones P., Knight-Jones E.W., 1994: fig. 2M). Coil diameter is up to 3 mm (see Vine, 1977: fig. 3a, b). The sculpture is represented by three narrowly spaced longitudinal keels, among which the central one may look thicker and more elevated in mature specimens. Tube walls are white porcellaneous, hard to break.

TUBE ULTRASTRUCTURES. Tube wall formally can be considered two-layered, but the typical structures of both layers are strongly fused along their boundary, making it indistinct (Fig. 3I). The outer zone of the wall (1/3–1/2 of the entire tube thickness in one specimen, not over 1/6 in another) contains irregularly arranged pyramid-shaped spherulites (SIOP structure), with a slight tendency to consolidate outer surface by the “basement” sides of the pyramids (=irregular SPHP structure; Fig. 3I). Locally spherulites develop into hemispheres and spheres with common initiation nucleus, and in some sections, an extremely thin (2.5 μm) simple prismatic (SP) outer layer was observed. The central part of the wall in one specimen is also composed of SIOP structure (Fig. 3I), while in another (Fig. 3J), it is represented by cylindrical elongated crystals with blunt ends (transitional from IOP to SIOP type), attaining a length of 4–5 μm and a width of 2–3 μm. Inner 1/4 of the wall of the second specimen is consolidated by micritic matter. Such a “consolidated” structure stretches along the parabolic growth lamellae, making “intercalation” with a typical loose structure in the central part of the tube.

Inner organic lining has a thickness of ~1–2 μm.

TUBE MINERALOGY. 100% calcite ($I_{\text{calc}} = 253$).

of peripheral flange showing its nature as an extension of the outer SPHP/SIOP layer; J — the surface of the lumen showing substructure of inner organic lining.

Abbreviations: iol — inner organic lining; is — inner surface; os — outer surface; pf — peripheral flange; we — tube wall on the external side of the next to last whorl; wi — tube wall on the internal side of the last whorl. Large arrows indicate the direction of tube growth.

Рис. 4. *Metalaespira clansmani*: детали строения трубок и их ультраструктуры. А–С — трубки; А, В — планоспиральная (типичная) разновидность с широким периферическим базальным краем; С — трубка с перекрывающимися оборотами (нетипичный вариант; из Vine, 1977: fig. 5a); D–J — ультраструктуры трубок (D–G, J — экземпляр №1; H, I — экземпляр №2); D — общий вид продольного сечения, хорошо виден внешний слой, имеющий сферулитовую призматическую структуру (SPHP) с невыдержанной ориентировкой сферулитов и мощным основным слоем, со структурой переходного типа от хаотически ориентированных сферулитов (SIOP) к призматическим кристаллам (IOP); E, F — продольные сечения через зону соприкосновения оборотов, показывающие однослойное строение (структура хаотически ориентированных кристаллов, IOP) внутренней стенки оборота; G — облик призматических кристаллов в зоне соприкосновения оборотов; H — общий вид продольного сечения, сделанного в основании трубки через периферический базальный край; I — его строение, показывающее, что этот край образован расширяющимся наружным сферулитовым призматическим (SPHP) слоем; J — внутренняя поверхность трубки, хорошо видна тонкая структура органической мембраны. Обозначения: iol — внутренняя органическая мембрана; is — внутренняя поверхность; os — наружная поверхность; pf — периферический базальный край; we — стенка наружной стороны раннего оборота; wi — стенка внутренней стороны позднего оборота. Большие стрелки показывают направление роста трубки.

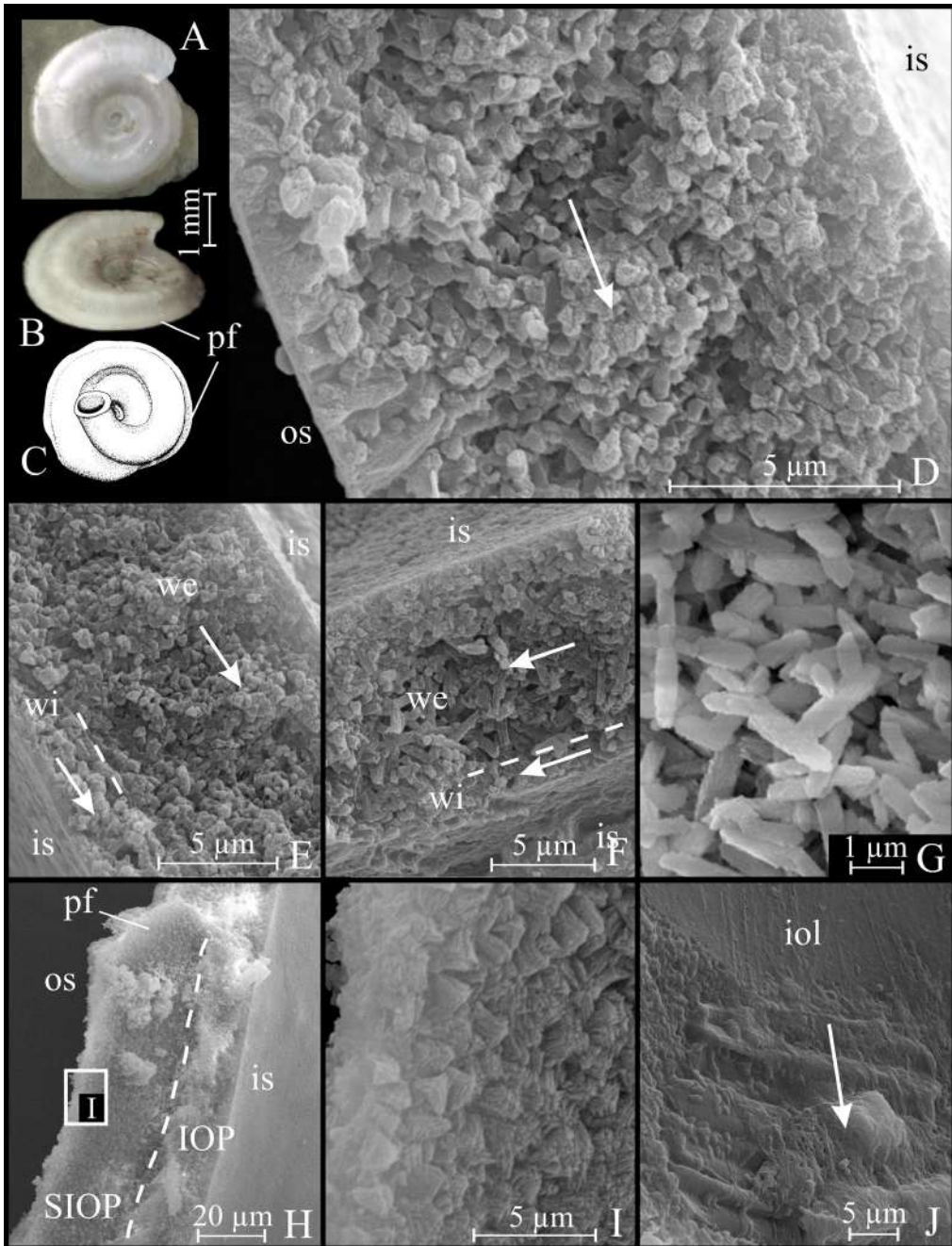


Fig. 4. *Metalaospira clansmani*: details of tube morphology and ultrastructures. A–C — tubes; A, B — planospiral (most typical) modification, note a wide peripheral flange; C — tube with ascending whorls (untypical; from Vine, 1977: fig. 5a); D–J — tube ultrastructures (D–G, J — specimen 1; H, I — specimen 2); D — general view of the longitudinal section showing outer SPHP layer with unclearly oriented spherulites and thicker main layer of IOP to SIOP transitional type; E, F — longitudinal section through the area of whorls contact, showing unlayered internal walls with IOP structure; G — details of IOP structure in the whorls contact zone; H — general view of the longitudinal section along the peripheral flange; I — details

DISTRIBUTION. *Metalaeospira armiger* is known from Signy Island of the South Orkney Islands, South Atlantic (Knight-Jones P., Knight-Jones E.W., 1994), the Ross Sea (Vine, 1977) and Adelie Land (d'Urville Sea, Antarctic) (Rzhavsky, 1998).

ECOLOGY. Recorded from bryozoans at 7–158 m depth.

REMARKS. *Metalaeospira armiger* was tentatively placed within the genus *Helicosiphon* by P. Knight-Jones and Fordy (1979) and later by P. Knight-Jones and E.W. Knight-Jones (1984).

***Metalaeospira clansmani* Vine, 1977**

Fig. 4A–J.

For description see Vine, 1977: 12–16, figs 2b, 5a–k, 6a.

MATERIAL EXAMINED. Two specimens (IPEE No. 1/2893, Portobello, Dunedin, New Zealand, on algae—a donation from AMRI, No. W.46256) were studied with SEM in longitudinal sections. Mineralogy was analysed using a sample made of two tubes and a few fragments from the same sample. External tube morphology was illustrated using specimens from the same sample and supported by the figure from Vine (1977: fig. 5a).

TUBE MORPHOLOGY. Tubes are sinistral, planospiral (Fig. 4A, B) or with overlapping last whorls (Fig. 4C); peripheral flange may be present (Fig. 4B, C). Coil diameter is up to 3 mm. No sculpture is present. Tube walls are thin, smooth, white opaque, with porcellaneous outer surface.

TUBE ULTRASTRUCTURES. The wall is extremely thin (up to 20 μm in adults), two-layered (Fig. 4D). The outer layer has SPHP structure, with somewhat irregularly oriented spherulites, usually variously inclined to the outer surface by their long axes (Fig. 4D). This layer is not continuous in the last whorl and seems to be absent in early whorls of both studied specimens (Fig. 4E, F). The thickness of the outer layer in adults does not exceed 2 μm (corresponding wall thickness $\sim 15 \mu\text{m}$). The main inner layer has a transitional from IOP to SIOP structure, with crystals of about 0.5–1 μm long of somewhat isometric and irregular appearance, sometimes slightly elongated (Fig. 4D). Crystals are loosely packed. Locally, in the sections of the early whorls, crystals may have the appearance of chaotically oriented rice grains with angular ends (IOP structure; Fig. 4F, G), the length of such crystals is up to 2.5 μm (usually 1.5–2 μm), corresponding width is 0.5 μm . Crystals also may have such an appearance in the central part of the wall at the external sides of whorls at middle growth stage (Fig. 4F). In a longitudinal section made along the tube base, the outer SPHP layer is clearly transformed into a thicker SIOP zone with densely packed pyramid-like spherulites lacking space between them (Fig. 4H, I), while the inner part of the wall retains its usual structure as described above.

Consequently, the peripheral flange is produced by the extension of the outer layer.

On the internal side of the whorl, only the main inner IOP/SIOP layer is seen in the wall (Fig. 4E, F), while the outer SPHP layer is absent.

Details of the inner organic lining were not clarified. The lining is likely to be extremely thin, with a thickness of $\sim 0.2 \mu\text{m}$, and the adjacent innermost 1.5 μm of the wall is also cemented with organic matter. The lining shows a distinct microrelief, represented by embedded chords of 0.5–1.5 μm wide, running subparallel in both transverse and longitudinal directions (Fig. 4J); the transverse ones were observed only locally.

TUBE MINERALOGY. 100% calcite ($I_{\text{calc}}=53$), low reliability. There is a questionable aragonite peak, which may indicate the presence of 17% aragonite ($I=11$), but is somewhat atypically shifted at the diagram and therefore dubious.

DISTRIBUTION. It is known only from New Zealand (Vine, 1977; Knight-Jones P., Knight-Jones E.W., 1984 and unpublished data of A.V. Rzhavsky).

ECOLOGY. *Metalaeospira clansmani* was recorded from brown algae in shallow waters. The depth was recorded only for one sample (“10 m”), while for all others, data on depth are absent.

***Metalaeospira pixelli* (Harris, 1969)**

Fig. 5A–D.

For descriptions see Pixell, 1913: 351, fig. 3a–c (as “*Spirorbis antarcticus*”); Harris, 1969: 165–167, fig. 17a–l (as “*Spirorbis pixelli*”).

MATERIAL EXAMINED. A single specimen (IPEE No. 2/2509, Signy Islands, South Atlantic, on algae) was studied with SEM in longitudinal sections. Mineralogy was analysed using a single tube from the same sample. External tube morphology was illustrated using another specimen from the same sample as used for SEM and mineralogy, and was additionally supported by a figure from P. Knight-Jones and E.W. Knight-Jones (1994: fig. 2E).

TUBE MORPHOLOGY. Tubes are sinistral, up to 3 mm (4 mm fide Pixell, 1913) in coil diameter, unsculptured or with a single variably pronounced median keel (Fig. 5A, B). Tube walls are white and thin, semitransparent and fragile. Tube surface is smooth and porcellaneous.

TUBE ULTRASTRUCTURES. The wall is two-layered. The outer layer (about 6–7 μm thick) is composed of sectorial spherulites arranged in an SPHP structure (Fig. 5D). The orientation of spherulites is imperfect, but most of them are perpendicular to the outer surface by their axes. The main part of the tube wall consists of loosely lying, irregular-shaped, fine angular crystals of isometric ($\sim 1 \mu\text{m}$) and elongated irregular shape (length up to 3 μm , width 1 μm), slightly variable in size and making IOP structure (Fig. 5C). The largest crystals can be found near the

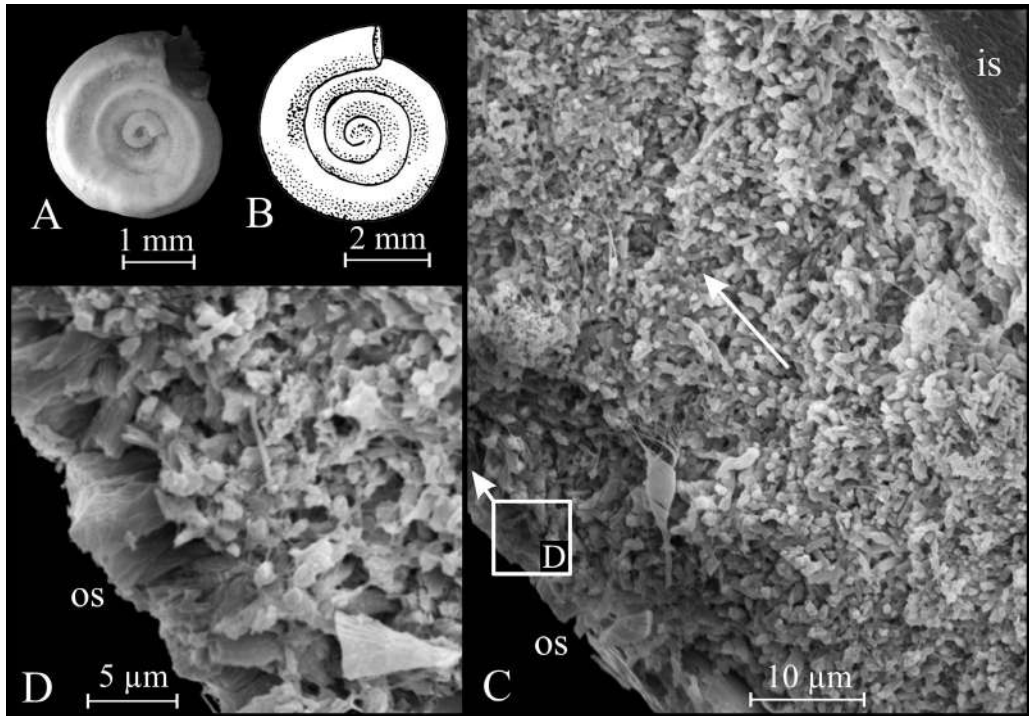


Fig. 5. *Metalaeospira pixelli*: details of tube morphology and ultrastructures. A, B — tubes; A — variety with a median keel; B — unsculptured variation (from Knight-Jones P., Knight-Jones E.W., 1994: fig. 2E); C, D — tube ultrastructures: C — general view of longitudinal section; D — details of outer zone of the wall, showing thin covering SPHP layer.

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

Рис. 5. *Metalaeospira pixelli*: детали строения трубок и их ультраструктуры. А, В — трубки; А — скульптурированная разновидность с медианным килем; В — нескульптурированная разновидность (из Knight-Jones P., Knight-Jones E.W., 1994: fig. 2E); С, D — ультраструктуры трубок: С — общий вид продольного сечения; D — строение наружной части трубки, где фиксируется присутствие тонкого сферулитового призматического слоя (SPHP).

Обозначения: is — внутренняя поверхность; os — наружная поверхность. Большая стрелка показывает направление роста трубки.

inner surface, where elongated forms dominate. The structure of the wall at the internal side of the whorl is similar to that described above, but the outer SPHP layer was not observed.

Inner organic lining is thin, less than 1 μm .

TUBE MINERALOGY. 97% low-Mg calcite, 3% aragonite ($I_{\text{calc}}=138$; $I_{\text{arag}}=6$).

DISTRIBUTION. The South Shetland and South Orkney Islands, the South Atlantic; Australia: Victoria (Melbourne), Tasmania and South Australia (Pixell, 1913; Harris, 1969; Knight-Jones P., Knight-Jones E.W., 1984; 1994).

ECOLOGY. This species is known from 10–53 m depth and is usually found attached to algae or mussels (*vide* Pixell, 1913).

REMARKS. Pixell (1913) described this species as “*Spirorbis antarcticus*.” This name is invalid because the binomen is preoccupied by Lesson (1831),

who introduced it to describe a spirorbini of currently unclear taxonomic position.

SEM examination of the wall at the early ontogenetic stage revealed crystals of smaller sizes than in the last whorl (length 1.5–2 μm , width 0.5–1 μm), having a regular shape with bluntly rounded ends, similar to the typical IOP structure of Paralaespirini and Spirorbini (see Ippolitov, Rzhavsky, 2014, 2015a).

Metalaeospira tenuis P. Knight-Jones, 1973 Fig. 6A–K.

For description see Knight-Jones P., 1973: 233–236, figs 1a–p, 6b, 7b; see also Rouse *et al.*, 2024: fig. 1J.

MATERIAL EXAMINED. 4 specimens were studied with SEM in different orientations (unregistered sample; probably lost). Mineralogy was analysed using a set of several tubes from the same

sample. External tube morphology was illustrated using specimens from another unregistered sample (Sydney, Australia, 2014; on algae, depth 2–4 m) and AMRI No. W.46249 (Mallacoota, Victoria, Australia, St. 6A, 19.02.1973; from algal washing, depth unknown).

TUBE MORPHOLOGY. Tubes are sinistral up to 3 mm in coil diameter, typically unsculptured (Fig. 6A), but sometimes with a distinct keel that rarely may be somewhat tuberculated (Fig. 6B). Usually, all the whorls (3 to 5 in adults) are planospiral, though in adults the mouth may ascend slightly. The mouth has a tiny denticle protruding ahead from the keel (Fig. 6B). The central part of the spiral looks like a shallow dish-like depression, as the basal part of the tube wall splits and flattens the step between adjoining whorls (Fig. 6H). Tube walls are white or slightly semitransparent (thin-walled) and fragile; tube surface is smooth and porcellaneous.

TUBE ULTRASTRUCTURES. The wall is two-layered. The outer layer is only ~6–7 μm thick and represented by more or less regularly oriented sectorial spherulites arranged into SPHP structure (Fig. 6C). The main inner layer of the wall consists of irregular-shaped, fine angular crystals of isometric (~1 μm) and elongated irregular shape (length up to 3 μm , width 1 μm), poorly sorted by size and making IOP structure (Fig. 6C, I–K). Crystals differ in the studied sections. The smallest crystals are observed near the lumen (Fig. 6F). Along the lumen, crystals can be oriented more or less parallel to the inner surface and transversely to the growth direction (Fig. 6I), thus

having the OF structure. The wall at the inner side of the whorl is extremely thin (not exceeding 1.5–2 μm) and unlayered, without the outer SPHP layer (Fig. 6E). Basal part of the tube shows low micrite content (Fig. 6H, J).

The characteristic feature of the species is a divergence of the wall base into two parts at the place of whorl contact on the upper side (Fig. 6H), resulting in the formation of a hollow spiral secondary tube in-between (“tubules” of Ippolitov, 2007a, b; Fig. 6K).

The inner organic lining is only about 0.2–0.4 μm thick.

TUBE MINERALOGY. A single sample made from a set of several tubes failed to provide reliable results: the main inferred component was rhodochrosite (MnCO_3 , 72%), while calcite and aragonite were both represented by minor peaks (16 and 12%, respectively). We interpret this result as a device error.

DISTRIBUTION. The southeast coast of Australia (including Tasmania) from Adelaide and Kangaroo Island to Sydney (Knight-Jones P., 1973; Knight-Jones P., Knight-Jones E.W., 1984).

ECOLOGY. *Metalaespira tenuis* is known from the littoral zone to several meters deep. Usually, it can be found on brown alga *Ecklonia* (Rzhavsky, unpubl.), but it is also recorded from other brown and red algae, as well as angiosperms (Knight-Jones P., 1973).

REMARKS. According to P. Knight-Jones (1973, fig. 1a), there is a swollen ring just behind the tube mouth. This feature occurs occasionally in our Australian material, spaced irregularly along the tube and seems to be associated with growth stops.

tation of prismatic crystals nearby the lumen (OF structure); J — basal part of the tube showing relatively loose packing of prismatic crystals at the basal, extended part of the wall; K — zone of contacting whorls at the upper side, note hollow structure formed in the basal part of the later whorl (“tubule”).

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

Рис. 6. *Metalaespira tenuis*: детали строения трубок и их ультраструктуры. А, В — трубки; А — некульптированная (типичная) разновидность (AMRI No. W.46249); В — разновидность с бугорчатым медианным килем (экземпляр без номера из Сиднея, Австралия); С–К — ультраструктуры трубок (С, D — экземпляр № 1; Е, F — экземпляр № 2; G — экземпляр № 3; H–K — экземпляр № 4); С — общий вид продольного сечения; D — детали строения внутренней части стенки, вдоль поверхности хорошо заметен сферулитовый призматический (SPHP) слой с несколько невыдержанной ориентировкой сферулитов; E — зона соприкосновения оборотов, хорошо видна структура хаотически ориентированных призматических кристаллов (IOP) внутренней стороны оборота; F — внутренняя поверхность трубки, органическая мембрана частично удалена, под ней хорошо заметны призматические кристаллы; темная полоса в центральной части изображения — это трещина (артефакт); G — детали строения структуры хаотически ориентированных призматических кристаллов (IOP); H–K — некоторые особенности строения и структуры трубок, выявленные на поперечном сечении: H — общий вид поперечного сечения; I — ориентация призматических кристаллов близ внутренней полости (“ориентированная фибриллярная” структура, OF); J — базальная часть трубки, в которой хорошо заметно разуплотнение упаковки кристаллов материала в области расширения стенки; K — зона смыкания оборотов на верхней стороне трубки, хорошо заметна полость в основании стенки более позднего оборота, имеющая спиральную форму соответственно характеру контакта оборотов (“тубула”).

Обозначения: is — внутренняя поверхность; ls — нижняя сторона трубки; os — наружная поверхность; we — стенка наружной стороны раннего оборота; wi — стенка внутренней стороны позднего оборота. Большие стрелки показывают направление роста трубки.

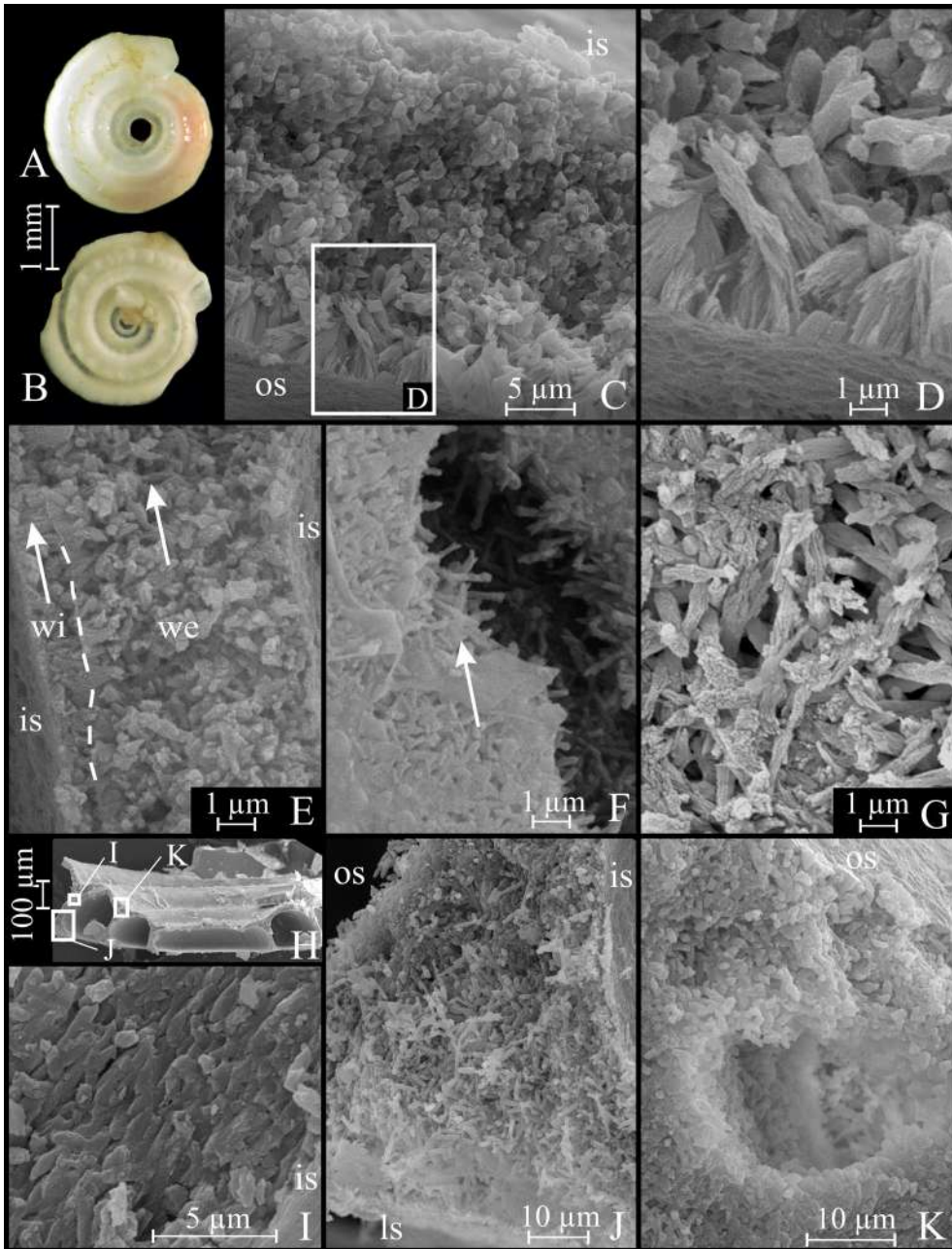


Fig. 6. *Metalaeospira tenuis*: details of tube morphology and ultrastructures. A, B — tubes; A — typical unsculptured modification (AMRI No. W.46249); B — modification with tuberculated median keel (unregistered specimen from Sydney, Australia); C–K — tube ultrastructures (C, D — specimen 1; E, F — specimen 2; G — specimen 3; H–K — specimen 4); C — general view of the longitudinal section; D — details of the innermost zone with covering SPHP layer, note somewhat irregular orientation of spherulites; E — whorl contact zone, showing unilayered IOP structure of the internal wall; F — internal side of the tube with inner organic lining partly removed, showing small prismatic crystals just below it; in the central part of a figure there is a crevice (artifact); G — details of the IOP structure; H–K — some details of tube architecture and ultrastructure, obtained from the transverse section: H — general view of the transverse section; I — orien-

Genus *Protolaeospira* Pixell, 1912(see also description in Kupriyanova *et al.*, 2020: 264)

TYPE SPECIES: *Spirorbis* (*Protolaeospira*) *ambilateralis* Pixell, 1912.

DIAGNOSIS. Tubes are usually sinistral (clockwise) but may be dextral (anticlockwise) in some species; margins of collar and thoracic membranes are not fused over thoracic groove; large collar chaetae are bent, modified fin-and-blade (at least from the convex side of the body), cross-striated or not; simple limbate and sickle chaetae in third thoracic fascicles; there are four thoracic chaetigers.

COMPOSITION. The genus includes 12 extant species arranged in 2 subgenera — *Protolaeospira* s.str. (with sinistrally coiled tubes) and *Dextralia* (with dextrally coiled tubes).

DISTRIBUTION. Though distribution for most *Protolaeospira* species is poorly documented, in general, members of the genus are typically found in the Southern Hemisphere, from the Antarctic to the subtropical zone (Knight-Jones P., Knight-Jones E.W., 1984, 1991, 1994). However, two species (*P. eximia* (Bush, 1905) and *P. capensis* (Day, 1961) — which, however, can be easily confused, see Remarks to *P. capensis* below) were recorded from subtropical/tropical and boreal waters in the North Pacific; Knight-Jones *et al.*, 1979; Rzhavsky, unpubl.) and one (*P. striata* Quiévreux, 1963) from boreal-tropical waters of the north-eastern Atlantic (Knight-Jones P., Knight-Jones E.W., 1977).

REMARKS. Tube coiling direction, traditionally used for subdivision of *Protolaeospira* into subgenera, has doubtful or even no taxonomic value (see Knight-Jones P. *et al.*, 1979: 420). Within the other tribes, certain species may demonstrate intraspecific variation in coiling direction (e.g., *Spirorbis* (*Spirorbis*) *bifurcatus* P. Knight-Jones, 1978), while some genera comprise species with different coiling directions (e.g., *Spirorbis*, *Circeis*; see Knight-Jones P. *et al.*, 1979; Rzhavsky, 1992). Indeed, the subdivision of the genus *Protolaeospira* into subgenera should be revised, and the 12 species included in this genus by us below are nothing but a list of names that were thought to be valid by different authors. Such a revision is beyond the scope of

this paper, so we follow the traditional subdivisions into subgenera and species.

Subgenus *Protolaeospira* s.str. Pixell, 1912

TYPE SPECIES: *Spirorbis* (*Protolaeospira*) *ambilateralis* Pixell, 1912.

DIAGNOSIS. Tube is sinistral (clockwise).

COMPOSITION. 10 species, 6 of which are described below.

***Protolaeospira* (*Protolaeospira*) *augeneri* Vine, 1977**

Fig. 7A–G.

For description see Vine, 1977: 25, figs 2g, 11b, 13a–n.

MATERIAL EXAMINED. Two specimens were studied with SEM in longitudinal sections (unregistered; lost). Mineralogy was analysed using a set of two tubes (IPEE No. 2/2894, Moreton Bay, eastern coast of Australia, depth 1 m, on spines of sea urchins — a donation from AMRI W.201760). External tube morphology was illustrated using specimens from the same sample as were used for mineralogy.

TUBE MORPHOLOGY. Tubes are sinistral, initially planospiral with an initial coil diameter of up to 2.5 mm; the last whorl often ascends over the substrate (Fig. 7A–C), mouth often forms trumpet-like extension (Fig. 7A), later preserved as peristomes. Tube walls are thick, hard, vitreous or semi-vitreous. Some specimens have a petite keel on the outer margin of the upper side (Fig. 7B), and sometimes a second keel of the same appearance is visible on the inner margin (Fig. 7C). Outer surface has faint transverse growth lines (Fig. 7A, B).

TUBE ULTRASTRUCTURES. The wall can be considered two-layered but with an indistinct boundary between the layers (Fig. 7D). Both layers are of comparable thickness. The outer one has simple prismatic (SP) sensu Vinn *et al.* (2008) structure, with well-discernible densely packed needle-like crystals, up to 10 µm long or over, while the corresponding width is less than 0.5 µm (Fig. 7D, E). Locally, crystal ends are aligned to certain growth lines, interrupting the needles. The outer surface can be covered with a distinct thin layer of curved fang-shaped spherulites

Рис. 7. *Protolaeospira* (*Protolaeospira*) *augeneri*: детали строения трубок и их ультраструктуры. А–С — трубки: А — нескульптированная (типичная) разновидность; В — разновидность с одним слабо выраженным килем на внешней стороне оборота; С — разновидность с двумя небольшими килями на внешней и внутренней сторонах оборота; D–G — ультраструктуры трубок, экземпляр №1: D — общий вид продольного сечения; E — детали строения внешней части стенки, с внешним простым призматическим (SP) слоем и сферулитами клыкообразной формы близ внешней поверхности трубки; F — вид с нижней стороны трубки, показывающий сферулитовую призматическую (SPHP) структуру пластинки прикрепления и простую призматическую структуру (SP) стенки над ней; G — детали строения зоны прикрепления, видная невыдержанная ориентировка сферулитов. Обозначения: is — внутренняя поверхность; os — наружная поверхность. Большие стрелки показывают направление роста трубки.

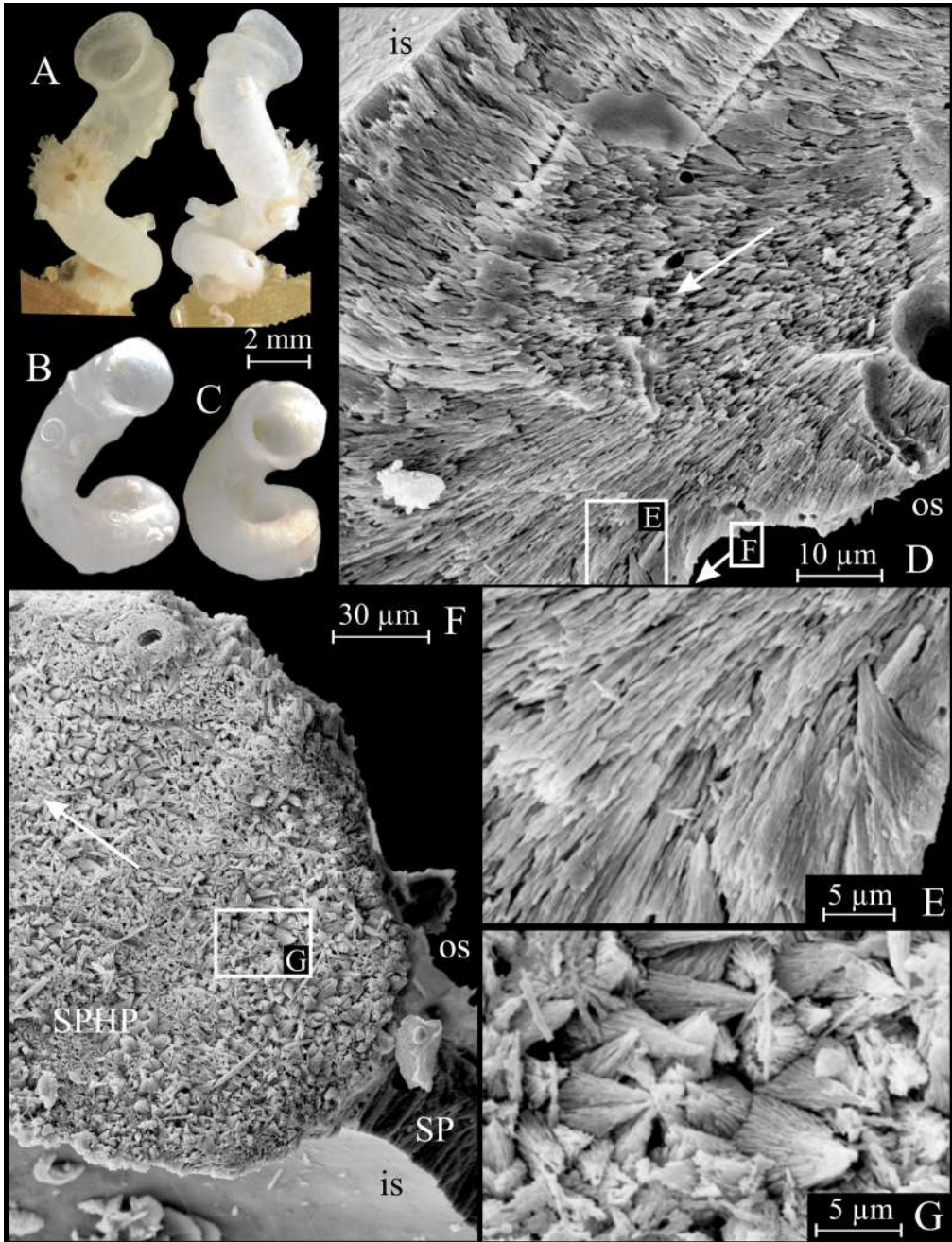


Fig. 7. *Protolaeospira (Protolaeospira) augeneri*: details of tube morphology and ultrastructures. A–C—tubes: A — typical unsculptured variety; B — variety with a single keel running along the outer side of the whorl; C — variety with two small keels on the inner and outer sides of the whorl; D–G — tube ultrastructures, specimen 1: D — general view of the longitudinal section; E — details of the outer layer of the wall having SP structure and fang-like spherulites at the outer surface, and their transition to SP structure; F — view from the lower side of the tube showing the attachment with SPHP structure and broken wall with SP structure; G — details of unevenly oriented SPHP structure of the attachment area. Abbreviations: is — inner surface; os — outer surface. Large arrows indicate the direction of tube growth.

(Fig. 7E). Some of them show the finest growth lines positioned perpendicular to the spherulite growth axis. The inner zone of the wall is represented by spherulitic prismatic (SPHP) structure, forming several spherulitic "layers" over each other and sometimes separated by surfaces of major growth stops (Fig. 7D). The boundary between the inner and outer layers is well-discernible in standard longitudinal sections, but while studying the wall at the internal side of the whorl, we found that the outer SP layer in some local zones laterally transforms into multi-layered SPHP structure. And *vice versa*, the inner SPHP layer locally transforms into SP structure.

Parabolic growth lines are distinct, with the outer branch of the parabola reduced, so the crystals of the SP structure are inclined to the outer tube surface at 30–40° angle (Fig. 7E). The axis is strongly displaced to the outer side of the wall, running at a distance of about 1/4 of the wall thickness from its outer surface.

The tube attachment area at the lower side has SPHP structure with somewhat irregularly oriented spherulites (Fig. 7F, G). Spherulites have pyramidal shapes, are 3–8 µm long, with the diameter of the base about 1.5–5 µm and grow in the direction away from the substrate. Acicular crystallites comprising spherulites are well discernible. Spherulites are uniform in size and form zones with larger regular and smaller irregular spherulites only locally (Fig. 7F); zones with smaller spherulites also include even smaller elongated to isometric crystals (probably irregular spherulites, but the details were not visible).

Inner organic lining is thin, less than 0.3 µm in thickness.

TUBE MINERALOGY. 100% low-Mg calcite ($I_{\text{calc}}=129$).

DISTRIBUTION. New Zealand (Vine, 1977), Queensland, Australia (Rzhavsky, unpubl.), and Marion Island, the Southern Indian Ocean (Rzhavsky, 1998). A record of *P. (P.) augeneri* was drawn on the Romanchellini distribution map for New South Wales, Australia (Knight-Jones P., Knight-Jones E.W., 1984:

fig. 6); however, it is not shown on a more detailed map of spirorbin distribution off south-eastern Australia (Knight-Jones P., Knight-Jones E.W., 1984: fig. 2).

ECOLOGY. Specimens were collected at depths of ~1 m, 15–20 m, and 180 m from the undersides of stones and the spines of sea urchins, while in some cases, the substrate remains unknown. Juveniles often settle on the adult tubes.

REMARKS. An additional longitudinal section of *P. (P.) augeneri* tube, using another specimen from the same sample as was used for SEM herein, was published earlier (Ippolitov, Rzhavsky, 2008: fig. 1d).

Protolaeospira (Protolaeospira) capensis
(Day, 1961)
Fig. 8A–H.

For descriptions see Day, 1961: 554–556, fig. 18a–h (as "*Spirorbis (Paralaeospira) capensis*"); Vine, 1977: 27, figs 11c, 12h, 14a–i; Knight-Jones P. *et al.*, 1979: 450, fig. 7B(a–e).

MATERIAL EXAMINED. One tube (IPEE No. 1/2511, Cape Town, South Africa, substrate and depth unknown) was studied with SEM in the longitudinal section. Mineralogy was analysed using fragments of three broken tubes from the same sample. External morphology was illustrated by specimens from the same sample and IPEE No. 2/2572 (Kalk Bay, South Africa, 5 m depth, substrate unknown).

TUBE MORPHOLOGY. Tubes (Fig. 8A, B) are sinistral, planospiral, but with the last whorl hiding the previous ones, so that the umbilicus of the spiral is very narrow. Coil diameter is 2 mm. Longitudinal sculpture is absent (Fig. 8A) or represented by a single, poorly defined median keel (Fig. 8B). Walls are very thick and resistant to breakage. Appearance of the outer surface is uneven: there are multiple thin transverse transparent or semitransparent irregular bands on the normally porcellaneous background. Specimens available for our study only partially cover the morphological diversity described in the literature (see Remarks).

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

Рис. 8. *Protolaeospira (Protolaeospira) capensis*: детали строения трубок и их ультраструктуры. А, В — трубки: А — трубка с хорошо выраженными тонкими прозрачными и полупрозрачными полосами; В — сросшаяся пара трубок; С–Н — ультраструктуры трубок: С — общий вид продольного сечения; D — детали строения внешней части стенки, видны сферулиты невыдержанной ориентировки, слагающие сферулитовую призматическую структуру (SPHP); Е — центральная часть стенки, видны сферулиты угловато-неправильной формы, смешанные с призматическими кристаллами; F — детали строения внутренней части трубки, хорошо видны ряды мелких отверстий, ориентированных параллельно стенке трубки и приуроченных к линиям роста сферулитов; G — общий вид продольного сечения через перистом, показывающий его внутреннее строение; H — область смыкания оборотов на ранней стадии развития, видна однослойная структура внутренней стороны трубки и распространение приповерхностного сферулитового призматического (SPHP) слоя во внутреннюю часть стенки вдоль линий роста.

Обозначения: is — внутренняя поверхность; os — наружная поверхность; we — стенка наружной стороны раннего оборота; wi — стенка внутренней стороны позднего оборота. Большие стрелки показывают направление роста трубки.

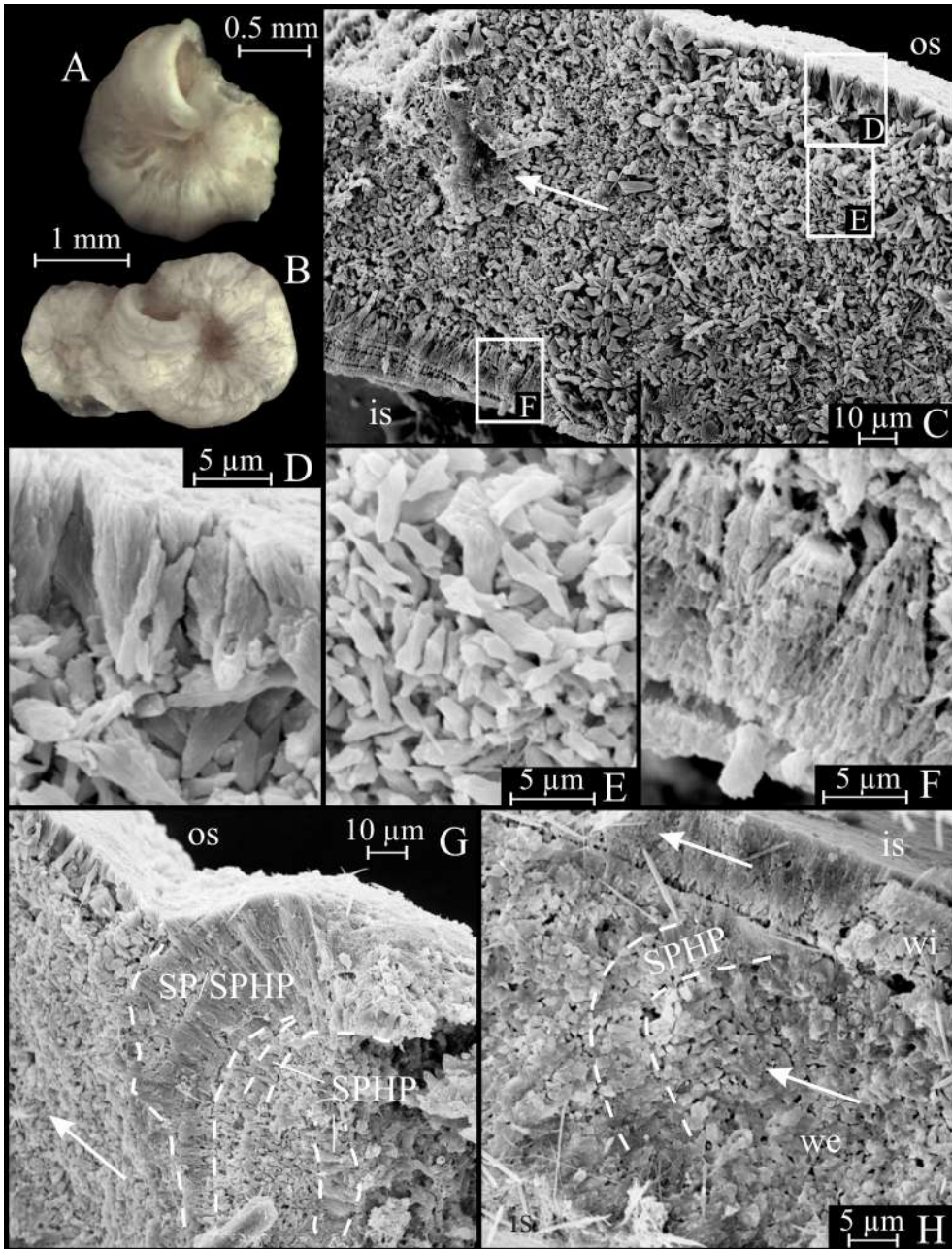


Fig. 8. *Protolaeospira (Protolaeospira) capensis*: details of tube morphology and ultrastructures. A, B — tubes: A — a tube with well-visible thin semitransparent to transparent bands; B — two coalescent tubes; C–H — tube ultrastructures: C — general view of the longitudinal section; D — details of the outer part of the wall showing somewhat irregularly oriented spherulites making up SPHP structure; E — details of the central part of the wall, showing knotty-shaped spherulites intermixed with prismatic crystals; F — details of the innermost part of the tube covered with uneven SPHP layer; note rows of tiny cavities in the spherulites of outer SPHP layer marking isochronous surfaces of their growth; G — general view of a longitudinal section through a peristome, revealing its internal structure; H — contact of whorls of the early whorls, showing unilayered structure of the internal wall and penetration of SPHP/SP structure along growth lamellae.

TUBE ULTRASTRUCTURES. The wall is three-layered (Fig. 8C). The outer layer has SPHP structure and is ~10 µm thick (corresponding wall thickness is 100 µm). Sectorial spherulites have a pyramidal shape; their orientation is somewhat irregular (Fig. 8D). They are often curved, with the narrow end bending backwards. The boundary between the outer and middle layers shows some smaller irregularly shaped pyramidal spherulites oriented irregularly. The middle part of the wall consists of narrow elongated spherulites of irregular shape, lying loosely and intermixed with irregularly shaped elongated prismatic crystals having rounded blunt to pointed irregular ends (Fig. 8E). There are numerous intermediate variations, and together all these crystals form irregularly oriented prismatic (IOP) structure. The size of smaller prismatic crystals varies from 2 to 4 µm long and from 0.5 to 2 µm wide. Spherulites are usually larger but rarely attaining 6 µm in length. All the crystals are variable in size; however, locally larger and more regularly shaped spherulites may dominate, while smaller crystals are rare, and *vice versa* (Fig. 8C).

The inner layer, like the outer one, has SPHP structure (Fig. 8F). Crystal growth lines can be discerned by rows of small holes piercing the crystals, reflecting oscillations in the amount of carbonate matter (Fig. 8F). Locally, the outer layer may become thicker, transforming to SP structure (Fig. 8G; also see Discussion). This is often associated with growth stops and peristome formation.

The internal side of the whorl, examined in 3 different sections, had an unilayered wall with SPHP structure of the inner layer (Fig. 8H), while the middle and outer layers were absent.

The axis of the parabolic growth lines is strongly displaced to the outer side of the wall, located approximately at a distance of 1/3 of the total wall thickness from the outer surface.

Inner organic lining was not observed.

TUBE MINERALOGY. 100% calcite ($I_{\text{calc}}=33$).

DISTRIBUTION. In the Southern Hemisphere, *P. (P.) capensis* is known from South Africa (Day, 1961), New Zealand (Vine, 1977), the Galapagos Islands (Bailey, Harris, 1968, as “*translucens*”) and

Tonga Islands (Bailey-Brock, 1987). In the Northern Hemisphere — off Hawaii (Bailey-Brock, 1976, as “*translucens*”) and the Pacific coast of North America (west coast of Vancouver Island to Pacific Grove, California; Knight-Jones *P. et al.*, 1979).

ECOLOGY. Recorded from the intertidal zone up to 37 m deep; in some cases, depth was not reported. Specimens were found on stones, shells, rocky outcrops, and lobster carapaces.

REMARKS. Some records of *P. (P.) capensis* are probably a mixture of at least two species (“*capensis*” and “*eximia*”) or a larger number of taxa. Different authors describe very different morphology of *P. (P.) capensis* tubes. Day (1961), Vine (1977), and Bailey and Harris (1968) indicate that the tube wall is vitreous or semivitreous, while P. Knight-Jones *et al.* (1979) state that the tube surface is porcellaneous. Day (1961) and Vine (1977) described the tubes as tightly coiled, with overlapping coiling and whorl diameter not exceeding 1.5 mm, with 2–3 longitudinal keels appearing near the mouth. Bailey and Harris (1968: fig. 6h, as “*translucens*”) also indicate that the tube mouth grows upwards or covers previous whorls and that the tube has irregular transverse ridges. Contrarily, in P. Knight-Jones *et al.* (1979: fig. 7Ba), the figured tube looks planospiral (no details provided in the text) and reaches 3.5 mm in coil diameter. It also has “irregular transverse growth rings that may be quite distinct in the last part of the whorl ... or may meander in such a way as to suggest incipient longitudinal ridges” (Knight-Jones *P. et al.*, 1979). Notably, these authors also synonymised *Spirorbis translucens* Bailey et Harris, 1968 with “*capensis*” without any explanation, so their *P. (P.) capensis* may include multiple species. Our examined material best fits the description by P. Knight-Jones *et al.* (1979). Apparently, *P. (P.) capensis* needs a revision, which is beyond the scope of this article.

The wall of *P. (P.) capensis* shows clear growth stops, sometimes marked by the peristomes and sometimes not seen macroscopically. During periods of growth stops, the SPHP layer is often running either from outside or from inside along the growth lines, with gradually reducing sizes of crystals towards the middle part of the wall (Fig. 8G, H). The outer

Рис. 9. *Protolaeospira (Protolaeospira) eximia*: детали строения трубок и их ультраструктуры. А, В — трубки: А — коричневая, прозрачная разновидность; В — белая фарфоровидная разновидность с поперечной скульптурой (изображена также в нашей более ранней работе — Ippolitov, Rzhavsky, 2014, fig. 1D); С–Н — ультраструктуры трубок: С — общий вид продольного сечения, хорошо заметна поперечная скульптура; D — то же самое, увеличено; Е — внешняя часть стенки, хорошо заметен внешний сферулитовый призматический слой (SPHP); F, G — детали строения центральной части стенки, в которой видны различные переходные типы от структуры хаотически ориентированных призматических кристаллов (IOP) к структуре хаотически ориентированных сферулитов (SIOP); H — детали строения внутренней части стенки, хорошо заметен тонкий приповерхностный слой с простой призматической структурой (SP).
Обозначения: is — внутренняя поверхность; os — наружная поверхность. Большая стрелка показывает направление роста трубки.

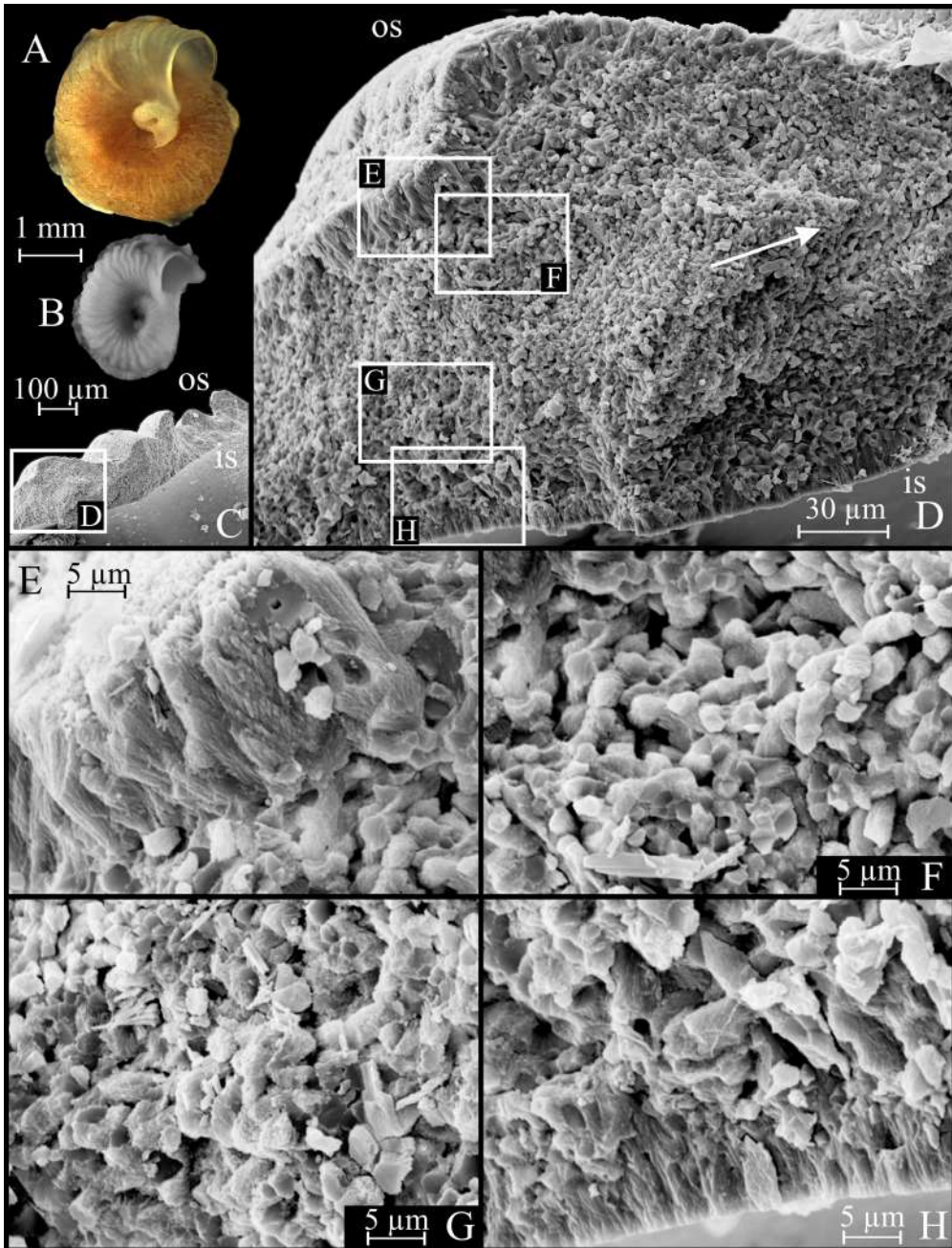


Fig. 9. *Protolaeospira (Protolaeospira) eximia*: details of tube morphology and ultrastructures. A, B — tubes: A — brownish vitreous variety; B — white porcellaneous modification with regular transverse peristomes (was also illustrated in Ippolitov, Rzhavsky, 2014: fig. 1D); C–H — tube ultrastructures: C — general view of the longitudinal section showing multiple transverse ridges; D — the same, enlarged; E — details of the outer part of the wall showing outer covering SPHP layer; F,G — details of the central zone of the wall showing different variations of transitional IOP to SIOP structure; H — details of the inner part of the wall showing thin covering layer with SP structure.

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

SPHP layer can be very thick at such growth stops (Fig. 8G). Very rarely, the inner SPHP layer connects along the growth lines with the outer SPHP layer. We observed such stops both on early whorls (Fig. 8H) and on the last whorl, indicating that their appearance is not age-related. Macroscopically, the penetration of SPHP layers across the wall is reflected in well-visible, frequent, thin, transparent and semi-transparent transverse lines (Fig. 8A, B).

We also observed ontogenetic changes of ultrastructure in the studied specimen. In both early growth stages (wall thickness 17–18 μm) and in late ones, the wall on the external whorl side of is three-layered. Outer and inner SPHP layers are each $\sim 5\text{--}8\ \mu\text{m}$ thick, while the middle layer is 10 μm wide, composed of irregular-shaped spherulites and irregular crystals 1–2 μm long, intermixed with spherulites up to 3 μm long. Smaller crystals in the middle layer are usually isometric. In the next whorl, wall thickness increases up to $\sim 30\ \mu\text{m}$ due to the extension of the middle layer, while in SPHP layers, crystal sizes and shapes do not change compared to the earlier whorl.

Protolaeospira (Protolaeospira) eximia

(Bush, 1905)

Fig. 9A–H.

For descriptions see Bush, 1905: 239, pl. XLI, figs 7, 18, 20, pl. XLIII, figs 6, 11, 17 (as “*Spirorbis eximus*”); Knight-Jones P. *et al.*, 1979: 449–450, fig. 7A(a–e).

MATERIAL EXAMINED. A single specimen having a white tube (IPEE No. 1/2573, Vancouver, Canada, on the rocks, littoral zone) was studied with SEM. Vitreous brownish tubes (see Tube morphology and Remarks) were not examined. Mineralogy was analysed by powdering a single specimen from the same sample as used for SEM. External tube morphology was illustrated using two specimens, both from the same sample as used for SEM.

TUBE MORPHOLOGY. Tubes are sinistral with coil diameters up to 5 mm. P. Knight-Jones *et al.* (1979) mentioned “prominent transverse growth rings (e.g., fig. 7Ba)”, which in our terminology (Ippolitov, Rzhavsky, 2014) are “transverse ridges” (Fig. 9B). Observed tubes are planispiral or with whorls slightly overlapping each other. Tube walls are thick, white porcellaneous (Fig. 9B) or brownish, vitreous (Knight-Jones P. *et al.*, 1979 and Fig. 9A).

TUBE ULTRASTRUCTURES. The wall is three-layered (Fig. 9D). The outer layer is represented by spherulitic prismatic (SPHP) structure and is up to 17–18 μm thick, but usually about 10 μm (Fig. 9E). On the border with the middle layer, the spherulites may be irregularly oriented, not perpendicular towards the tube surface, but inclined.

The middle layer has a complicated structure transitional from IOP to SIOP (Fig. 9D–H), includ-

ing several crystal fabric types. In zones underlying both inner and outer SPHP layers (Fig. 9E, H), the fabric is represented by elongated, angular crystals of irregular shape with blunt to flat ends (6–8 μm long, $\sim 3\ \mu\text{m}$ wide), densely packed. In the middle part of the layer (Fig. 9F, G), crystals may have a very characteristic elongated shape with rounded ends (6–7 μm long, 2–2.5 μm wide). Locally, they are smaller and are consolidated by micritic matter (Fig. 9G).

The inner layer underlying the lumen is 6–7 μm wide and has SPHP structure. Spherulites here are irregularly pyramidal and can be locally transformed into SP structure (Fig. 9H).

Inner organic lining was not observed.

TUBE MINERALOGY. 100% calcite ($I_{\text{calc}}=283$).

DISTRIBUTION. The Pacific coast of North America, from La Paz, Mexico, to Vancouver Island, Canada (Knight-Jones P. *et al.*, 1979). In the South Pacific, *P. (P.) eximia* is known from Lima, Peru to Concepcion, Chile (Knight-Jones P., Knight-Jones E.W., 1991) and was also reported from Auckland, New Zealand (as “*ambilateralis*”, see Vine, 1977) and, questionably, Japan (Rzhavsky *et al.*, 2010).

ECOLOGY. The studied material was collected from the littoral up to 160 m deep, from stones, dead corals, mollusc shells, barnacles, and sunken wood fragments.

REMARKS. The species is unique in having variable tube morphology — as both vitreous brownish and white porcellaneous tubes can be found within the same population. We agree with P. Knight-Jones *et al.* (1979), who considered them as belonging to the same species, though a special study is needed. Our ultrastructural and mineralogical study was limited to the “white” (non-vitreous) morphotype. According to the vitreous appearance of the unstudied brownish variety, it can be predicted that it must have the unilayered SP/SPHP wall with reduced main IOP to SIOP layer, by analogy with *P. (P.) augeneri* and *P. (P.) striata* (see also discussions on transparency in spirorbins in Ippolitov, Rzhavsky, 2008; 2015b). Indeed, the synonymy of this species and most other *Protolaeospira* spp. is confusing and doubtful because most records and original descriptions of synonymised species were not supported by any tube illustrations.

The tube cross-section (Fig. 9D) shows that the regular transverse ridges are formed by the thickenings of the middle layer, while the inner and outer SPHP layers have more or less uniform thickness. Interestingly, the outer SPHP layer can completely disappear locally. In such areas, the tube surface is not smooth like elsewhere but somewhat rough, formed by the middle layer’s outer part (SIOP structure).

Protolaeospira (Protolaeospira) pedalis
P. Knight-Jones et E.W. Knight-Jones, 1994
 Fig. 10A–D.

For description see Knight-Jones P., Knight-Jones E.W., 1994: 81–83, fig. 3A–P.

MATERIAL EXAMINED. Three fragments (IPEE No. 1/2519, Signy Island, South Orkney Islands, the Atlantic sector of the Southern Ocean, on brachiopods at depths of 18–28 m; C11.12.1971, British Antarctic Survey) were studied with SEM in longitudinal sections. Mineralogy was analysed using fragments of several tubes from the same sample. External tube morphology is illustrated by figures from the original description (Knight-Jones P., Knight-Jones E.W., 1994: fig. 3A).

TUBE MORPHOLOGY. Tubes are sinistral, planospiral with coil diameters up to 2 mm (Fig. 10A). The cross-section is rounded, usually without sculpture, but sometimes with three low and thick keels running towards the mouth. Tube walls are white, easily breakable.

TUBE ULTRASTRUCTURES. The wall is unilayered, having irregularly oriented prismatic (IOP) structure (Fig. 10B). The fabric is represented by small, slightly elongated crystals up to 5 µm long and 2 µm wide (corresponding tube wall thickness is 80 µm). Typically, crystals are smaller, up to 2.5 µm long, 1–1.5 µm wide (the corresponding thickness of the walls in studied fragments are 60, 30 and 10 µm). Their shapes are irregular, often angular. Crystals are highly variable in size. Near the lumen, crystals are proportionally 1.5–2 times smaller (Fig. 10B) than in the central and outer zones of the wall and are consolidated by micrite. The crystals have the largest sizes and less regular shapes near the outer side of the wall. One specimen had a local thin (about 3 µm) covering layer having a simple prismatic (SP) structure on the inner side of the wall (Fig. 10C).

Inner organic lining was not observed.

TUBE MINERALOGY. 100% low-Mg calcite ($I_{\text{calc}}=68$).

DISTRIBUTION. *Protolaeospira (P.) pedalis* is known only from its type locality, Signy Island of the South Orkney Islands in the Atlantic sector of the Southern Ocean (Knight-Jones P., Knight-Jones E.W. 1994).

ECOLOGY. Recorded from the 6–28 m depth range, mainly from brachiopod shells; some specimens were collected from the stones and bryozoans.

Protolaeospira (Protolaeospira) striata
Quiévreux, 1963
 Fig. 10E–H.

For description see Quiévreux, 1963: 70–76, figs 1, 2A–B, 3, 4A–B, 5A–E, 6, 7; Knight-Jones P., Knight-Jones E.W., 1977: 476–478, fig. 8A–J.

MATERIAL EXAMINED. A single specimen (IPEE No. 1/2538, Malta, Mediterranean Sea, on a piece of metal, depth 38 m) was studied with SEM in a longitudinal section. Mineralogy was not studied due to insufficient material. External tube morphology was illustrated using specimens from the same sample as used for SEM.

TUBE MORPHOLOGY. Tubes are sinistral, with coil diameters up to 3 mm (Fig. 10E, F). Coiling is planospiral, but sometimes the last whorl sometimes slightly overlaps previous ones (Fig. 10F). The tube is sculptured with transverse ridges, which may be irregularly or indistinctly regularly spaced, well-pronounced or poorly defined. Tube walls are hard and vitreous.

TUBE ULTRASTRUCTURES. Tube wall has a complex structure. In the standard longitudinal section of mature specimens (Fig. 10G), the wall is unilayered, having SPHP to SP structure and with the axis of parabolic growth lamellae strongly displaced towards the outer surface of the tube. The inner half of the wall has SP structure (crystal length over 15 µm). The outer half contains the axial part of parabolic growth lamellae and has SPHP structure, but in the axial zone, there are areas of irregular spherulites oriented chaotically (~IOP structure) — such areas interchange with SPHP structure longitudinally in a regular manner. The outer wall is consolidated with crystals forming SPHP structure. Longitudinal section made along the upper part of the tube shows that chaotically oriented spherulites here are significantly more developed. The internal side of the whorl, observed in early growth stages, shows the unilayered wall (Fig. 10H), with SPHP structure underlying the lumen, while the middle and outer layers are reduced.

Inner organic lining was not observed.

TUBE MINERALOGY. Not studied due to insufficient material.

DISTRIBUTION. *Protolaeospira (P.) striata* is recorded from the north-east Atlantic from the West African coast to the south and even to the central part of Great Britain, the Canary Islands and Cape Verde Islands (Quiévreux, 1963; Zibrowius, 1973; Knight-Jones P., Knight-Jones E.W., 1977). It is especially common in the Mediterranean Sea (Bianchi, 1981). Also, this species was recorded from Rio de Janeiro, the Atlantic coast of Brazil (Knight-Jones P., Knight-Jones E.W., 1991).

ECOLOGY. Specimens from the northwest Atlantic are recorded from the low littoral zone up to the depth of 25 (rarely up to 40) m. They can be found on rocks and stones free from silt (Knight-Jones P., Knight-Jones E.W., 1977). Ecological data for the south-eastern Atlantic records (Knight-Jones P., Knight-Jones E.W., 1991) are absent.

REMARKS. At early growth stages (Fig. 10H; wall width ~15–18 µm), the wall on the external side of the whorl is distinctly three-layered. The inner

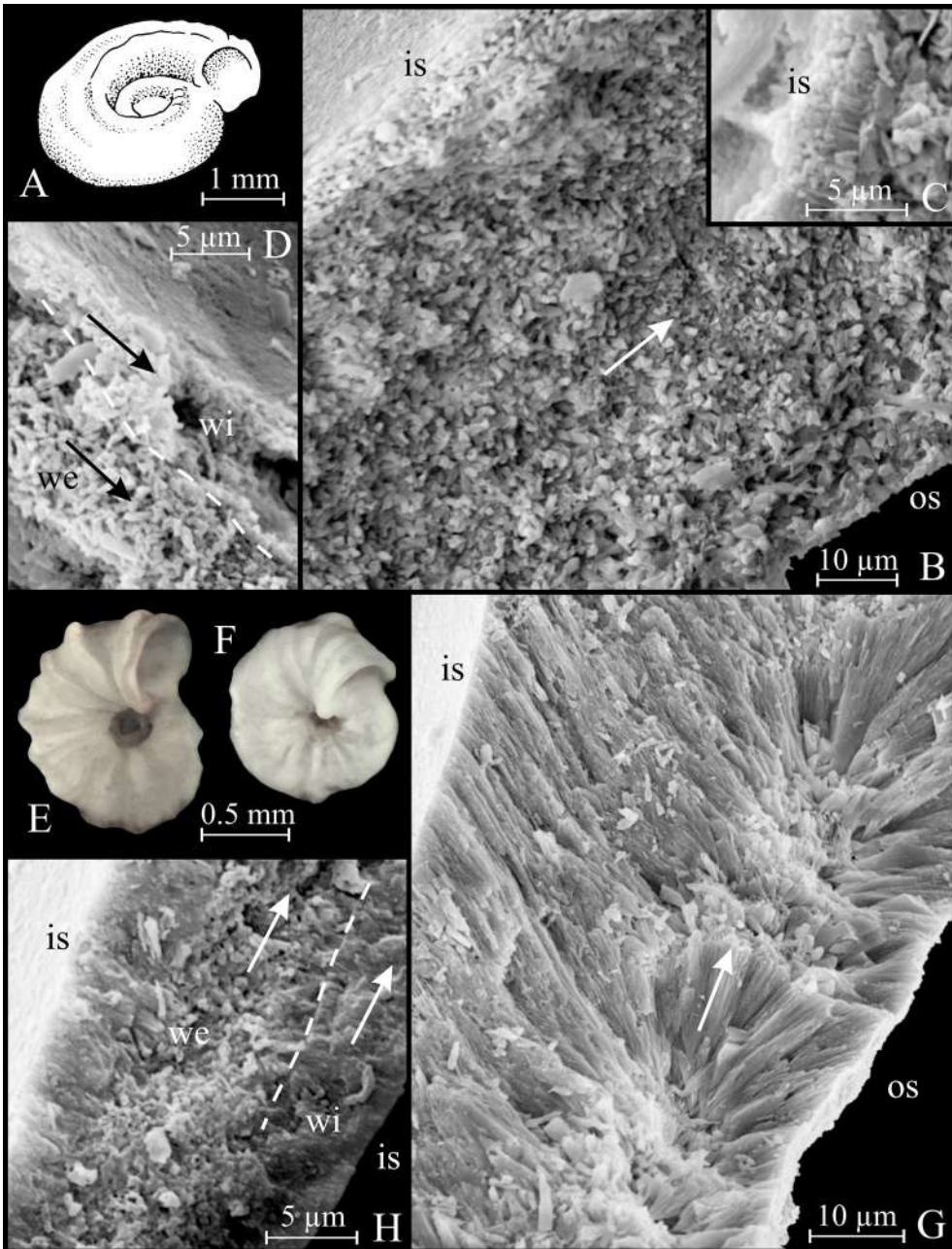


Fig. 10. *Protolaeospira (Protolaeospira) pedalis* (A–D) and *P. (P.) striata* (E–H): details of tube morphology and ultrastructures. A–D — *P. (P.) pedalis*: A — tube (from Knight-Jones P., Knight-Jones E.W., 1994: fig. 3A); B–D — tube ultrastructures (all three figures may belong to one, two, or three different specimens): B — general view of the longitudinal section; C — an area at the inner surface showing very thin layer with SP structure; D — contact of whorls in the early whorls. E–H — *P. (P.) striata*. E, F — tubes; G — general view of the longitudinal section of the last whorl, showing SP/SPHP structure with areas of residual IOP structure in the median zone of parabolic growth lamellae; H — general view of the longitudinal section of contact of the whorls at earlier growth stage, showing unilayered SP structure of the internal wall and three-layered external wall, with continuous IOP structure of the middle layer.

layer has SPHP structure and is about 5–6 µm thick. The outer layer probably also has SPHP structure, but it cannot be visually separated from the wall of the internal side of the next whorl, having the same SPHP structure. The middle layer is represented by fine (0.25–0.5 µm long) isometric crystals forming the RHC structure. This kind of structure in juveniles is similar to that observed for some juvenile Spirorbini (Ippolitov, Rzhavsky, 2015a).

***Protolaeospira (Protolaeospira) tricostalis*
(de Lamarck, 1818)**

Fig. 11A–I.

For descriptions see Vine, 1977: 30–32, figs 12c, 16, 17a (as “*Protolaeospira lebruni* (Caullery et Mesnil, 1897)”; Knight-Jones P., 1973: 239–242, fig. 3a–m (as “*Protolaeospira (Protolaeospira) canina*”); Knight-Jones P., Knight-Jones E.W., 1991: 681–582, 585, fig. 2A, B.

MATERIAL EXAMINED. Two specimens (IPEE No. 1/2400, South Sandwich Islands, South Atlantic, depth 370 m) were analysed with SEM in longitudinal sections. Mineralogy was analysed using fragments of two tubes taken from the same sample. External tube morphology was illustrated by paratype of *Protolaeospira (Protolaeospira) canina* P. Knight-Jones, 1973 (=junior synonym of *P. (P.) tricostalis*) deposited in AMRI (W.4475, Cape du Couedic, Kangaroo Island, South Australia; on stones in mid-littoral pools) and several additional figures from the publications.

TUBE MORPHOLOGY. Unfortunately, the external tube morphology of our specimens was not described before they were destroyed for mineralogical composition analysis. According to (Vine, 1977), tubes are sinistral, with coil diameter up to 2 (rarely 2.5) mm; tube walls are thick, hard, white and slightly porcellaneous. According to Harris (1969; as “*lebruni*”), tubes are unsculptured, but P. Knight-

Jones (1973) and Vine (1977) report two keels — see also Remarks. Our tubes were also sculptured with two or three keels. The paratype of “*canina*” (AMRI W.4475; Fig. 11A) has two keels located on the inner and outer margins of the upper side. According to P. Knight-Jones (1973), the inner keel is more prominent than the outer one.

TUBE ULTRASTRUCTURES. The wall is two to three-layered (Fig. 11E, H). The inner layer is composed of irregularly shaped spherulites, unevenly oriented perpendicular to the lumen surface (SPHP structure; Fig. 11E). This layer is about 10–12 µm thick, while the corresponding wall thickness is 90 µm. The main layer making up the middle and inner parts of the wall is composed of elongated crystals (up to 6–7 µm long and 2–2.5 µm wide) with smaller irregular isometric varieties (1.5–2 µm), together forming IOP structure (Fig. 11E, G, H). In certain areas, one type of fabric may predominate. The outer SPHP layer, similar to the inner one, was found only in some of the studied sections near the growth stops, where SPHP crystals running along growth lines connect the inner layer with the outer one (Fig. 11H, I). The width of the SPHP layer at such growth stops increases to 20 µm. The outer SPHP layer has irregular distribution and may locally disappear.

Inner organic lining was not observed.

TUBE MINERALOGY. 100% calcite ($I_{calc} = 129$).

DISTRIBUTION. The Atlantic and Pacific coasts of South America from the subtropical waters to Cape Horn; the Antarctic Peninsula; New Zealand and south-western Australia; the Falkland Islands (South Atlantic), Kerguelen and Heard Islands (South Indian Ocean) (see Knight-Jones P., Knight-Jones E.W., 1984, 1991; Vine, 1977). Also recorded from the South Sandwich Islands (South Atlantic) (Rzhavsky, unpubl.).

ECOLOGY. According to the literature data (Caullery, Mesnil, 1897; Fauvel, 1916; Monro, 1939;

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

Рис. 10. *Protolaeospira (Protolaeospira) pedalis* (A–D) и *P. (P.) striata* (E–H): детали строения трубок и их ультраструктуры. A–D — *P. (P.) pedalis*: A — трубка (из Knight-Jones P., Knight-Jones E.W., 1994: fig. 3A); B–D — ультраструктуры трубок (изображения получены из россыпи фрагментов, и могут относиться к одному, 2 или 3 экземплярам): B — общий вид продольного сечения; C — участок внутренней части стенки, на котором хорошо виден тонкий слой с простой призматической (SP) структурой; D — область смыкания ранних оборотов. E–H — *P. (P.) striata*. E, F — трубки; G — общий вид продольного сечения последнего оборота, на фоне основной сферулитовой призматической (SPHP) / простой призматической (SP) структуры в осевой части параболических линий роста хорошо видны участки остаточной структуры из хаотически ориентированных призматических кристаллов (IOP); H — общий вид продольного сечения соприкасающихся оборотов на ранней стадии роста, хорошо видна однослойная стенка с простой призматической структурой на внутренней стороне оборота, и трехслойное строение стенки на внешней стороне с выдержанным средним слоем, имеющим структуру хаотически ориентированных призматических кристаллов (IOP).

Обозначения: is — внутренняя поверхность; we — стенка наружной стороны раннего оборота; os — наружная поверхность; wi — стенка внутренней стороны позднего оборота. Большие стрелки показывают направление роста трубки.

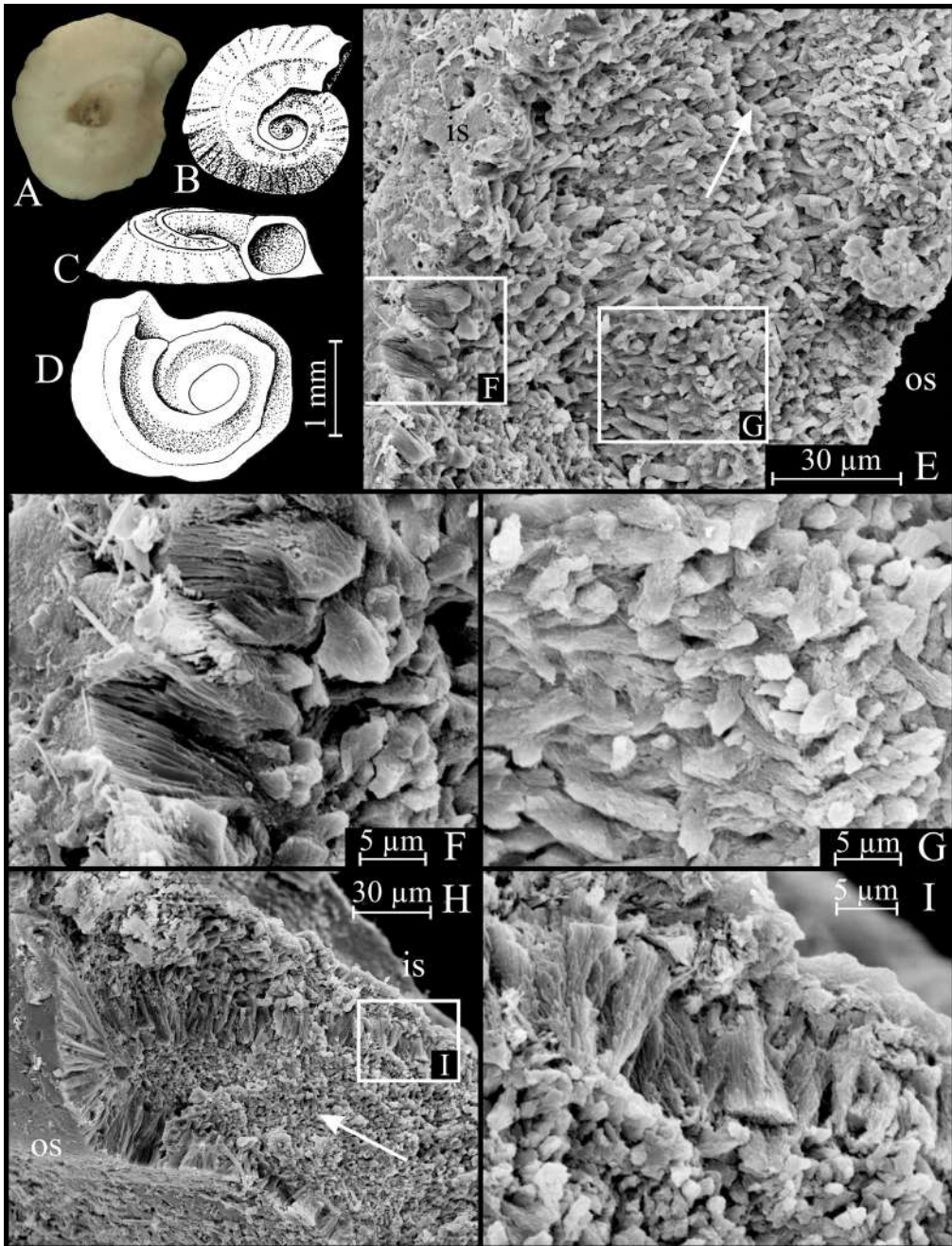


Fig. 11. *Protolaeospira* (*Protolaeospira*) *tricostalis*: details of tube morphology and ultrastructures. A–D — tubes; A — paratype of *P. (P.) canina* (junior subjective synonym of *P. (P.) tricostalis*; B, C — a single tube with a pair of longitudinal keels (from Knight-Jones P., 1973: fig. 3A, B); D — variation with massive keels (from Vine, 1977: fig. 16A; as “*lebruni*”); E–I — tube ultrastructures (all from one specimen): E — general view of the longitudinal section; F — details of the inner zone of the tube, showing unevenly oriented spherulites of SPHP structure; G — central zone of the wall showing details of prismatic crystals forming IOP structure; H — longitudinal section across the peristome, showing SPHP structure penetrating across the wall along growth lamellae; I — details of SPHP layer at the inner side of the wall.

Harris, 1969; Vine, 1977; Knight-Jones P., 1973; Knight-Jones P., Knight-Jones E.W., 1991), this species can be found at depths of 0–16 m, settling on the undersides of stones, algae, bivalve and gastropod shells, and sea urchin *Austrocidaris canaliculata* (Agassiz, 1863). Our material was collected much deeper, from a depth of 370 m.

REMARKS. *Protolaeospira* (*P.*) *tricostalis* was originally described by de Lamarck (1818; as *Spirorbis tricostalis*) from Port King George area, Western Australia, while its presumed junior synonym *Protolaeospira* (*Protolaeospira*) *lebruni* (Caullery et Mesnil, 1897) was described from Cape Horn, South America (as “*Spirorbis* (*Paralaeospira*) *lebruni*”). The original description of “*tricostalis*” was very brief and not supported by illustrations, while the description of “*lebruni*” included figures of the operculum and is more substantial. Probably for this reason, the specific name introduced by Lamarck was ignored for a long time, and numerous specimens from the Southern Hemisphere were recorded as “*lebruni*” (see Vine, 1977: 30–31), while P. Knight-Jones (1973) described a third nominal species, *P.* (*P.*) *canina*, from Australia. After a long obliteration, Lamarck’s “*tricostalis*” was mentioned by P. Knight-Jones and Fordy (1979), who considered “*tricostalis*,” “*lebruni*,” and “*canina*” to be separate species. However, while describing the distribution of spirorbins in the Southern Hemisphere, P. Knight-Jones and E.W. Knight-Jones (1984) synonymised all three names without any explanations. In our opinion, synonymising these species names is not justified. The specific name “*tricostalis*” suggests the presence of three keels on the tube, while according to Vine (1977) and P. Knight-Jones (1973), the tubes have only two keels, and according to the figure by Harris (1969), the tube is unsculptured. Such variability of sculpture can be intraspecific (Rzhavsky, 1994), but more frequently it is not. As resolving the status of these three nominal species is outside the scope of this paper, here we follow the latest classifications by P. Knight-Jones and E.W. Knight-Jones (1984, 1991).

Subgenus *Dextralia* P. Knight-Jones in P. Knight-Jones et Walker, 1972

TYPE SPECIES: *Protolaeospira* (*Dextralia*) *falklandica* (Pixell, 1913).

DIAGNOSIS. Tubes are dextral (anticlockwise).

COMPOSITION. 2 species, one described below.

REMARKS. The subgenus *Dextralia* is frequently considered to be established by P. Knight-Jones (1973) — such authorship was claimed in Fauchald (1977) and Vine (1977) and at present cited in several important web sources (Integrated Taxonomic Information System — <https://www.gbif.org/uk/species/7086>; Wikipedia — <https://en.wikipedia.org/wiki/Serpulidae>). However, the subgenus was first mentioned in P. Knight-Jones and Walker (1972), who refer to “Knight-Jones, 1972b”, which indeed points to the afore-mentioned paper published in 1973. This is likely this is a result of a publication delay (see “Notes” in Read, Fauchald, 2024). The paper by P. Knight-Jones and Walker (1972) contains both the subgeneric diagnosis and the indication of the type species; however, this taxon was not certainly indicated as new. However, such an indication became obligatory only after 1999 (International Code of Zoological Nomenclature, 1999, art. 16.1); thus, we amend the authorship of the subgenus to “P. Knight-Jones in P. Knight-Jones et Walker, 1972”.

Protolaeospira (*Dextralia*) *stalagmia* P. Knight-Jones et Walker, 1972

Fig. 12A–J.

For description see Knight-Jones P., Walker, 1972: 37–38, fig. 2a–n.

MATERIAL EXAMINED. Two specimens (IPEE No. 1/2523, Signy Island, the South Atlantic; British Antarctic Survey, St. 403) were studied with SEM in longitudinal sections. Mineralogy was analysed using tube fragments from the same sample. External tube morphology was illustrated using specimens IPEE No. 2/2523 (King George Island of

Abbreviations: is — inner surface; os — outer surface. Large arrows indicate the direction of tube growth.

Рис. 11. *Protolaeospira* (*Protolaeospira*) *tricostalis*: детали строения трубок и их ультраструктуры. А–D — трубки; А — паратип of *P.* (*P.*) *canina* (младший субъективный синоним *P.* (*P.*) *tricostalis*); В, С — трубка с двумя тонкими выдержанными киями (из Knight-Jones P., 1973: fig. 3А, В); D — разновидность с массивными киями (из Vine, 1977: fig. 16А, как “*lebruni*”); Е–I — ультраструктуры трубок (все фотографии получены с одного экземпляра): Е — общий вид продольного сечения; F — детали строения внутренней части трубки со сферулитовой призматической структурой (SPHP), видна невыдержанность ориентировки сферулитов; G — центральная часть стенки, видны детали строения призматических кристаллов, имеющих хаотическую ориентировку (структура IOP); H — продольное сечение перистома, видна сферулитовая призматическая структура (SPHP) покровного слоя, протягивающаяся через всю стенку вдоль параболических линий роста; I — детали строения сферулитового призматического слоя близ внутренней поверхности трубки.

Обозначения: is — внутренняя поверхность; os — наружная поверхность. Большие стрелки показывают направление роста трубки.

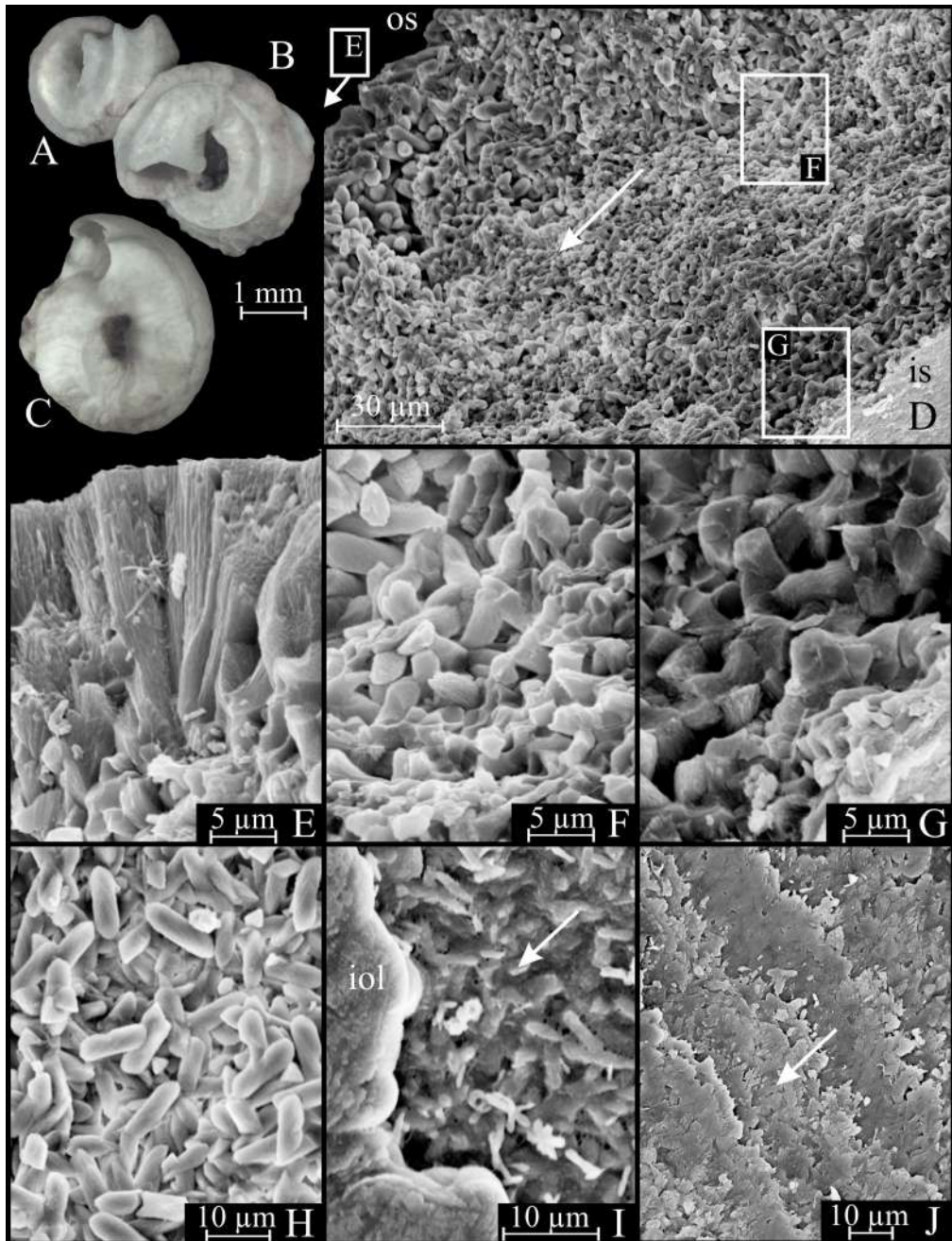


Fig. 12. *Protolaeospira (Dextralia) stalagmia*: details of tube morphology and ultrastructures. A–C — tubes: A, B — variety with three massive keels; C — variety with a single median keel; D–I — tube ultrastructures (all from specimen 1): D — general view of the longitudinal section; E — details of outer zone, showing SPHP covering layer; F — details of the central zone of the wall, showing IOP structure; G — details of the innermost part of the wall showing SIOP structure; H — peanut-shaped prismatic crystals of the outer part of the main layer; horizontal section of the wall; I — inner side of the wall, organic lining is partly detached uncovering small prismatic crystals; J — growth lines on the tube outer surface (specimen 2). Abbreviations: is — inner surface; os — outer surface. Large arrows indicate the direction of tube growth.

the South Shetland Islands, on rocks and stones in a low intertidal zone).

TUBE MORPHOLOGY. Tubes (Fig. 12A–C) are dextral, usually planospiral, but sometimes the last whorl may slightly overlap the previous ones. Coil diameter is up to 6 mm. Adults usually have three (Fig. 12A, B), rarely one (Fig. 12C) smooth longitudinal keels terminating as short teeth over the mouth. Juvenile tubes are unsculptured or bear only a single median keel. Tube walls are thick, hard to break, white, and slightly porcellaneous. This species often forms aggregations resulting from the selective settlement of larvae on the conspecific adult tubes.

TUBE ULTRASTRUCTURES. The tube wall is two-layered at first glance (Fig. 12D) but shows a more complex structure if one looks deeper. The outer layer (Fig. 12E) has irregular SPHP structure typical for the genus, consisting of pyramidal and irregular spherulites oriented more or less perpendicular to the surface. The width of the outer layer does not exceed 10 µm, locally up to 15 µm (corresponding wall thickness is ~150 µm). The main layer has a transitional IOP to SIOP structure and a very complex substructure. The outer part underlying the spherulites of the outer SPHP layer is represented by irregularly oriented spherulites, forming SIOP structure with a slight transition to the outer layer (Fig. 12E). The thickness of this zone is 15–20 µm. Then, spherulites are gradually replaced by distinct peanut-shaped prismatic crystals with rounded ends (Fig. 12F, H), which are 8–10 µm long and 2.5–3 µm wide (locally smaller). Towards the central part of the wall, these crystals decrease in size by 1.5–2 times, and near the lumen, they become larger again (Fig. 12G). In the innermost part of the wall, the peanut-shaped spherulites are oriented more or less along the lumen. Immediately under the inner organic lining, we observed a very thin inner layer made of numerous scattered elongated prismatic crystals with rounded ends, like those typical for Spirorbini (see Ippolitov, Rzhavsky, 2015a) — 3–4 µm long, 1 µm wide (Fig. 12I).

Inner organic lining is less than 1 µm thick (Fig. 12I).

TUBE MINERALOGY. 100% calcite ($I_{\text{calc}}=405$).

DISTRIBUTION. *Protolaeospira (D.) stalagmia* is recorded from the South Orkney Islands in the Atlantic sector of the Southern Ocean (Knight-Jones P., Walker, 1972; Knight-Jones P., Knight-Jones E.W., 1994) and from the King George Island of the South Shetland Islands (Rzhavsky, unpubl.).

ECOLOGY. This species was recorded from the littoral zone down to 30 m deep; occupying limpet, brachiopod, and gastropod shells, crustaceans, empty serpulid tubes, as well as rocks and stones.

REMARKS. The external tube surface is consolidated by micritic matter and shows distinct growth increments evenly spaced at ~20 µm (Fig. 12J).

Genus *Romanchella* Caullery et Mesnil, 1897
(see also description in Kupriyanova *et al.*, 2020: 264)

TYPE SPECIES: *Spirorbis (Romanchella) perrieri* Caullery et Mesnil, 1897

DIAGNOSIS. Tubes are usually sinistral (clockwise) or, more rarely, dextral (anticlockwise); margins of collar and thoracic membranes are fused over thoracic groove; large collar chaetae are bent and not modified; sickle chaetae present in 3rd fascicle; there are three thoracic chaetigers.

COMPOSITION. The genus includes 8 extant species, 5 of which are described below, and 3 were not covered in the present study.

DISTRIBUTION. *Romanchella* is known from all oceans of the Southern Hemisphere, ranging from the Antarctic coast to subtropical waters.

REMARKS. The real number of species in the genus may be higher as some materials remain undescribed.

***Romanchella perrieri* Caullery et Mesnil, 1897**

Fig. 13A–H.

For description see Caullery, Mesnil, 1897: 208–210, pl. VIII, pl. IX, figs 15a–c; 16a–b, 17 (as “*Spirorbis (Romanchella) perrieri*”); Vine, 1977: 34–37, figs 19a–m, 20a, 21.

MATERIAL EXAMINED. Two specimens (IPEE No. 1/2524, Crozet Islands, 45°59.2'S,

Рис. 12. *Protolaeospira (Dextralia) stalagmia*: детали строения трубок и их ультраструктуры. А–С — трубки: А, В — разновидность с тремя массивными килями; С — разновидность с единственным медианным килем; D–I — ультраструктуры трубок (все — экземпляр №1): D — общий вид продольного сечения; E — внешняя часть стенки, на которой виден слой со сферулитовой призматической структурой (SPHP); F — детали строения центральной части стенки, имеющей структуру хаотически ориентированных призматических кристаллов (IOP); G — детали строения внутренней части стенки, имеющей структуру из хаотически ориентированных сферулитов (SIOP); H — призматические кристаллы, имеющие характерную форму арахиса, во внешней зоне основного слоя; горизонтальное сечение трубки; I — внутренняя поверхность трубки с частично удаленной органической мембраной, видны мелкие призматические кристаллы; J — линии роста на поверхности трубки (экземпляр №2). Обозначения: is — внутренняя поверхность; os — наружная поверхность. Большие стрелки показывают направление роста трубки.

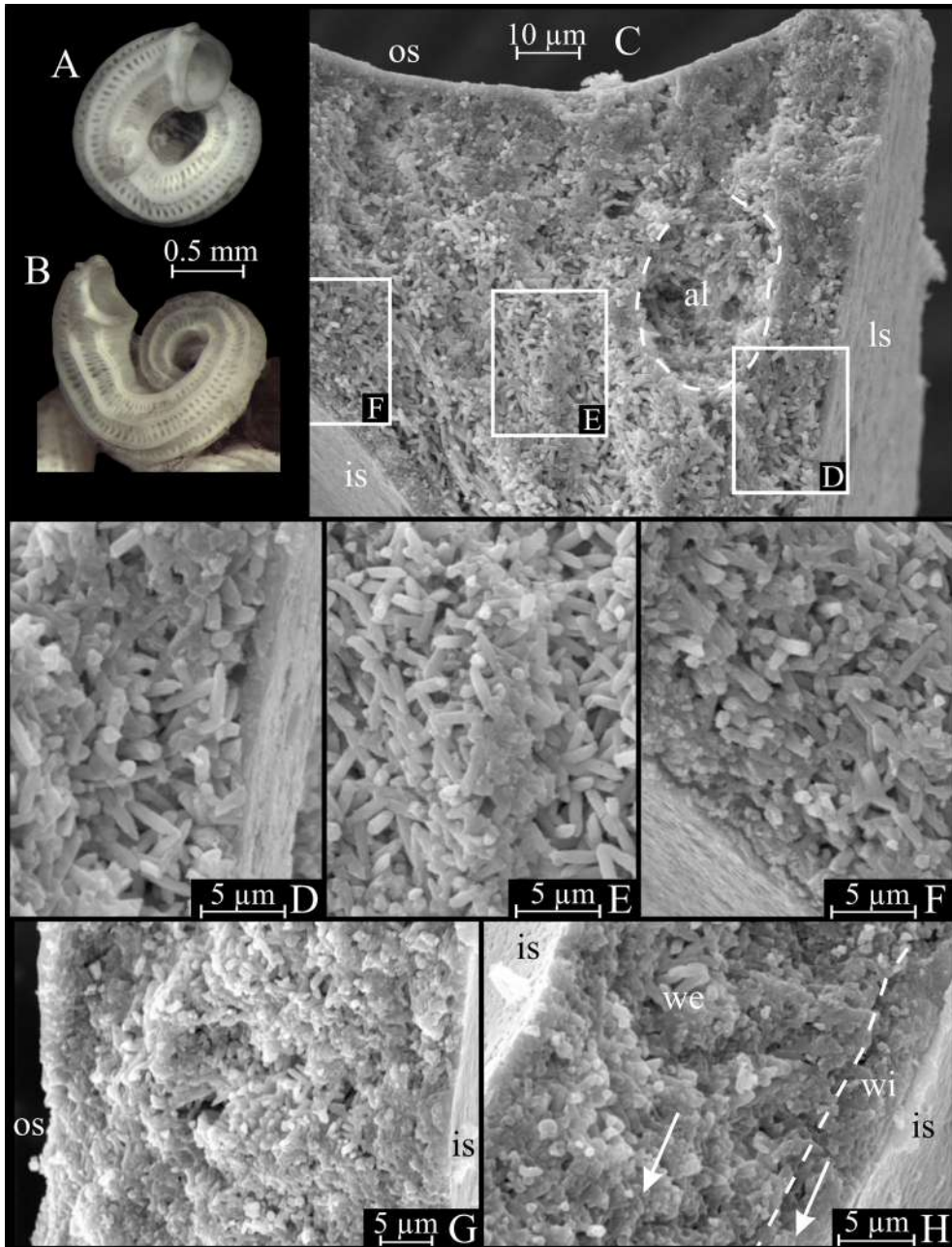


Fig. 13. *Romanchella perrieri*: details of tube morphology and ultrastructures. A, B — tubes, note somewhat evolute coiling in both specimens; C–I — tube ultrastructures (C–F: specimen 1; G, H: specimen 2): C — general view of the transverse section, tube base area, note unilayered IOP structure and the alveolus visible within the wall; D — details of attachment zone; E — details of the central part of the wall, F — details of the innermost zone of the wall; G — general view of the longitudinal section in another specimen; H — whorls contact at earlier growth stage, showing unilayered IOP structure in both external and internal walls. Abbreviations: al — alveolus; is — inner surface; ls — lower surface; os — outer surface; we — tube wall on the external side of the next-to-last whorl; wi — tube wall on the internal side of the last whorl. Large arrow indicates the direction of tube growth.

50°28.8'E, on hydrozoans, depth 115 m) were examined with SEM in longitudinal and transverse sections. Mineralogy was analysed using several tubes from the same sample. External tube morphology was illustrated using specimens from the same sample as used for SEM.

TUBE MORPHOLOGY. Tubes (Fig. 13A, B) are sinistral, planospiral or with last whorls ascending upwards and sometimes slightly overlapping previous ones. Coil diameter is up to 1.5 mm. The sculpture is represented by three longitudinal keels, and an additional fourth keel runs on the tube periphery in the lower part of the outer lateral side (Fig. 13B). The keels are sharp and well-defined. In between the keels, numerous transverse oblong indentations (alveoli) form transverse rows. These alveoli can be distinct or rudimentary and may also perforate the median and, sometimes, lateral keels. Tube walls are thin, fragile, white, somewhat porcellaneous.

TUBE ULTRASTRUCTURES. The wall is unilayered, with IOP structure (Fig. 13C). Crystals are up to 5 µm long and 1 µm wide, with rounded or blunt ends. Crystal shapes are clearly seen only locally (e.g., near the attachment area, Fig. 13D, and in some areas inside the wall, Fig. 13G), while most part of the IOP layer is densely cemented with abundant micritic matter concealing the shape of isolated crystals (Fig. 13G). Below the inner organic lining, individual crystals are consolidated by micrite and become completely indistinguishable (Fig. 13F). Near the inner side of the wall, crystals can be roughly oriented along growth lamellae (Fig. 13F). Early ontogenetic stages show a high amount of micritic matter (Fig. 13H). The wall structure at the inner side of the whorl does not differ significantly from that at the outer side (Fig. 13H); in the area of connecting whorls, visual separation of neighbouring whorls' walls is hardly possible.

Inner organic lining is thin (~1 µm).

TUBE MINERALOGY. 100% calcite ($I_{calc} = 66$).

DISTRIBUTION. *Romanchella perrieri* is widely distributed in the Southern Hemisphere. It was recorded from New Zealand (Vine, 1977), numerous islands of the Pacific, Indian and Atlantic Oceans, and some localities off the Antarctic shores (Knight-Jones

P., Knight-Jones E.W., 1984; Rzhavsky, 1998). It is also recorded from Cape Town, South Africa (Knight-Jones P., Knight-Jones E.W., 1974, 1984) and from the Magellan Strait to about 40°S in the Pacific and Atlantic (Knight-Jones P., Knight Jones E.W., 1984; 1991). *Romanchella perrieri* is also plotted on the generalised Romanchellini distribution map for the south coast of Australia (Knight-Jones P., Knight-Jones E.W. 1984: fig. 5) but is absent on a similar map describing Australian spirorbins (Knight-Jones P., Knight-Jones E.W., 1984: fig. 2).

ECOLOGY. This species was recorded from depths of 5–140 m and a variety of substrates such as laminarians and other algae, bryozoans, hydroids, sea urchin spines, and bivalve shells.

Romanchella pustulata P. Knight-Jones, 1978

Fig. 14A–F.

For description see Knight-Jones P., 1978: 231–232, fig. 17A–J.

MATERIAL EXAMINED. Four specimens (IPEE No. 1/2520, Castro, Chile) were studied with SEM in longitudinal and transverse sections. Mineralogy was analysed using a set of tube fragments from the same sample. External tube morphology was illustrated using a figure from P. Knight-Jones (1978: fig. 17A).

TUBE MORPHOLOGY. Tubes (Fig. 14A) are sinistral and planospiral, with coil diameters up to 4 mm, typically having a distinct median keel (rarely three keels) or unsculptured. Specimens from branching bryozoans may be “spiralling away” (Knight-Jones P., Knight-Jones E.W., 1991: 583). The tube wall is thick, white (and probably non-porcellaneous).

TUBE ULTRASTRUCTURES. The wall is two-layered (Fig. 14B). The outer layer is extremely thin (2–3 µm; corresponding tube wall ~45 µm) and has SPHP structure. This layer was observed only in one out of four studied specimens. The main layer is composed of small (1 µm long and 0.3–0.5 µm wide) prismatic crystals, lying loosely in the wall and unoriented, and therefore, forming IOP structure (Fig. 14B–D). Crystals do not change their appearance throughout the wall, but locally, they can be smaller and

Рис. 13. *Romanchella perrieri*: детали строения трубок и их ультраструктуры. А, В — трубки, хорошо заметно раскручивание оборотов у обоих экземпляров; С–I — ультраструктуры трубок (С–F: экземпляр №1; G, H: экземпляр №2): С — общий вид поперечного сечения в области основания трубки, хорошо видно, что трубка имеет однослойное строение (структура хаотически ориентированных призматических кристаллов, IOP), также видна альвеоля; D — детали строения зоны прикрепления к субстрату; E — центральная часть стенки, F — внутренняя часть стенки; G — общий вид продольного сечения другого экземпляра (№2); H — смыкание оборотов на ранней стадии роста, хорошо видно, что и на внешней, и на внутренней стороне стенка имеет однослойное строение со структурой хаотически ориентированных призматических кристаллов.

Обозначения: al — альвеоля; is — внутренняя поверхность трубки; ls — нижняя поверхность трубки; os — наружная поверхность; we — стенка наружной стороны раннего оборота; wi — стенка внутренней стороны позднего оборота. Большая стрелка показывает направление роста трубки.

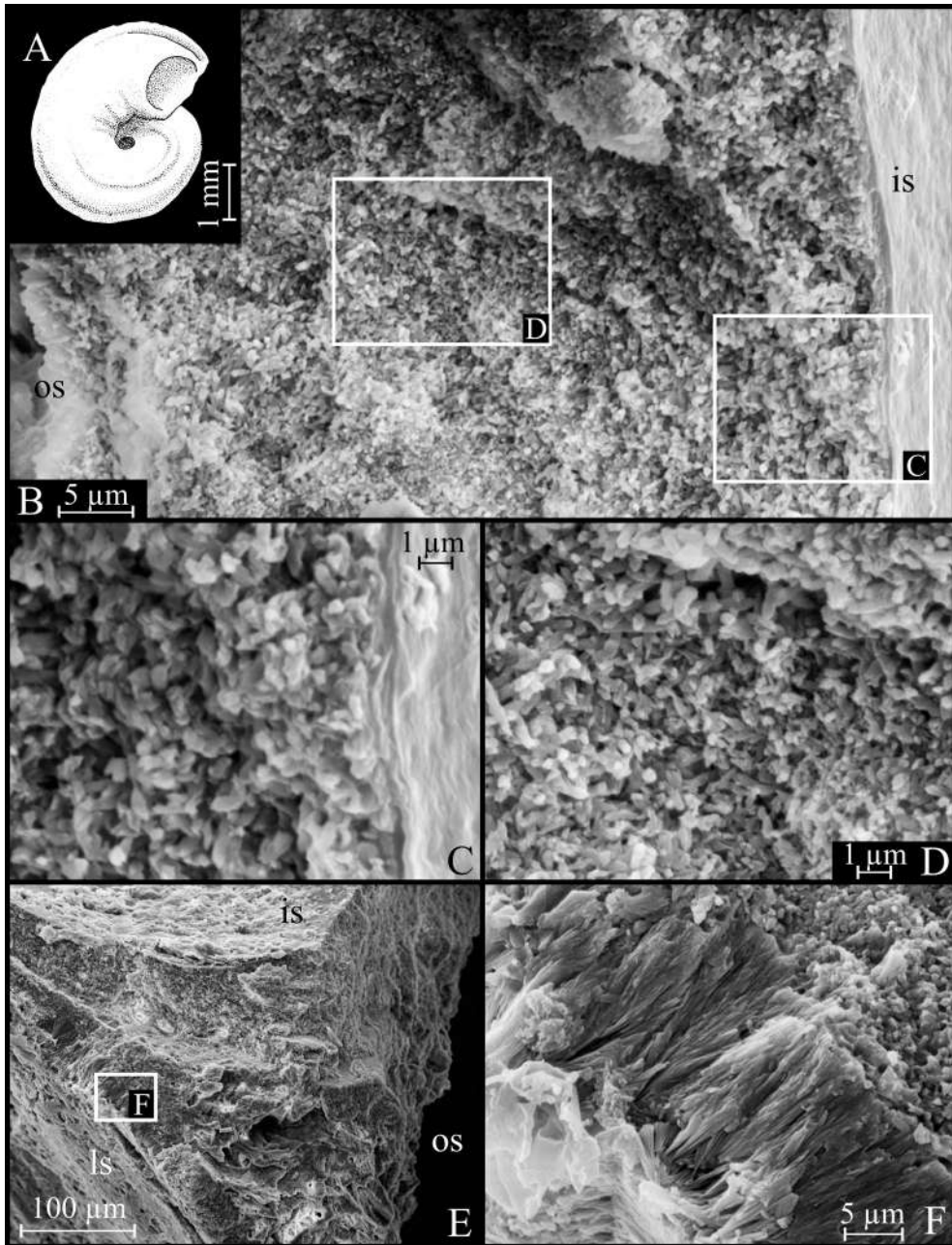


Fig. 14. *Romanchella pustulata*: details of tube morphology and ultrastructures. A — tube (from Knight-Jones P., 1978: fig. 17A); B–F — tube ultrastructures (B–D: specimen 1; E, F: specimen 2): B — general view of the longitudinal section, showing unilayered IOP structure composed of enormously small crystals; C — details of the innermost zone with inner organic lining, slightly distorted by SEM artefact; D — details of the central zone of the wall; E — basal part of the tube wall at the outer side of the whorl, F — details of attachment plate having SPHP structure.

Abbreviations: is — inner surface; ls — lower side; os — outer surface.

Рис. 14. *Romanchella pustulata*: детали строения трубок и их ультраструктуры. А — трубка (из Knight-Jones P., 1978: fig. 17A); В–F — ультраструктуры трубок (В–D: экземпляр № 1; Е, F: экземпляр № 2):

occasionally can be consolidated by micritic matter. The attachment area has a different ultrastructure with an unevenly distributed but sometimes thick SPHP layer (up to 18 μm wide; Fig. 14E, F) with narrow ends of sectorial spherulites turned to the substrate.

Inner organic lining is thin, ~ 0.5 μm or less (Fig. 14C).

TUBE MINERALOGY. 100% high-Mg calcite ($I_{\text{calc}}=41$), average data reliability.

DISTRIBUTION. *Romanchella pustulata* is known only from the Pacific and Atlantic coasts of South America, from the Magellan Strait to about 40°S latitude (Knight-Jones P., 1978; Knight-Jones P., Knight-Jones E.W., 1984, 1991).

ECOLOGY. In her original description, P. Knight-Jones (1978) reported that worms settle on decapods, bivalves, and gastropods but did not indicate the depth. According to P. Knight-Jones and E.W. Knight-Jones (1991), *R. pustulata* can be found in shallow-water habitats down to 18 m deep, attached to rocks, shells, bryozoans or, rarely, red algae.

***Romanchella quadricostalis* P. Knight-Jones, 1973**
Fig. 15A–G.

For description, see Knight-Jones P., 1973: 243–245, fig. 4a–s.

MATERIAL EXAMINED. One specimen (IPEE No. 2/2566, Kangaroo Island, South Australia, littoral, on algae) was studied with SEM in a longitudinal section. Mineralogy was analysed using two tubes from the same sample. External tube morphology illustrated using a specimen from AMRI collection (W.46247; off Middle Point near Cape Northumberland, South Australia, 38°4'S, 140°38'E, depth 13 m, on algae).

TUBE MORPHOLOGY. Tubes (Fig. 15A, B) are sinistral, with coil diameter up to 2.5 mm, planospiral or irregularly coiled, bearing four or five high smooth keels, all located in the upper part of the tube and forming prominent protruding teeth at its mouth. Tube walls are thick, hard to break, white porcellaneous.

TUBE ULTRASTRUCTURES. The wall is unilayered to locally three-layered, having a complex structure. The standard longitudinal section of the last whorl (wall thickness 130 μm) shows a single layer consisting of two different ultrastructural types, intercalating along parabolic growth lines (Fig. 15C). The first type is simple prismatic (SP) structure (Fig. 15D), the second is represented by fine (0.5–1 μm in

diameter) isometric crystals with some micritic matter, which can be classified as rounded homogenous crystal (RHC) structure *sensu* Vinn *et al.* (2008; but “HRC” in Vinn, 2013) (Fig. 15E). In another longitudinal section (Fig. 15G) made through early ontogenetic stages of the same specimen (wall thickness of ~ 20 μm), there is a thin, but well-defined external SP layer (2–3 μm), and the intercalation in the middle part of the wall is not regular. Finally, the third section (Fig. 15F) shows only RHC structure in the main layer, combined with a thin (2 μm) inner SP layer. So, at least locally, crystals of SP structure form well-defined inner and (or) outer layers. The internal side of the whorl, observed in one section (Fig. 15G), is thin (5 μm), unilayered, and has RHC structure.

Inner organic lining was not observed.

TUBE MINERALOGY. 100% high-Mg calcite ($I_{\text{calc}}=72$).

DISTRIBUTION. *Romanchella quadricostalis* is known only from South Australia (Knight-Jones P., Knight-Jones E.W., 1984).

ECOLOGY. Recorded only from the low littoral zone being attached to various (usually red) algae.

REMARKS. The observed RHC ultrastructure has no clear analogues in other Romanchellini, except maybe for small prismatic crystals in *R. pustulata*.

***Romanchella scoresbyi* (Harris, 1969)**
Fig. 16A, B.

For descriptions see Harris, 1969: 167–168, fig. 18a–m (as “*Spirorbis scoresbyi*”); Knight-Jones P., Knight-Jones E.W., 1991: fig. 2E.

MATERIAL EXAMINED. Two specimens were studied with SEM in longitudinal sections (IPEE No. 1/2578, Possession Island of the Crozet Islands, the South Indian Ocean; low littoral zone on rhizoids of *Durvillea* sp.). External tube morphology was illustrated using a figure from the original description (Harris, 1969, fig. 18a).

TUBE MORPHOLOGY. Tubes are sinistral, planospiral, with coil diameter not exceeding 1.5 mm; unsculptured (Fig. 16A). The walls are fragile, white opaque, probably non-porcellaneous.

TUBE ULTRASTRUCTURES. The wall is two-layered, with the main layer having an IOP structure (Fig. 16B). Crystals are represented by mostly elongated forms with irregular ends (up to 4 μm long, 1.5 μm wide), freely lying in the wall and chaotically oriented. The material is poorly sorted

В — общий вид продольного сечения, видно, что стенка сложена хаотически ориентированными призматическими кристаллами (структура IOP) очень мелкого размера; С — внутренняя часть стенки и органическая мембрана, изображение слегка искажено дефектом при съемке; D — центральная часть стенки; E — основание трубки на внешней стороне оборота, F — детали строения пластинки прикрепления, имеющей сферулитовую призматическую структуру.

Обозначения: is — внутренняя поверхность; ls — нижняя сторона трубки; os — наружная поверхность.

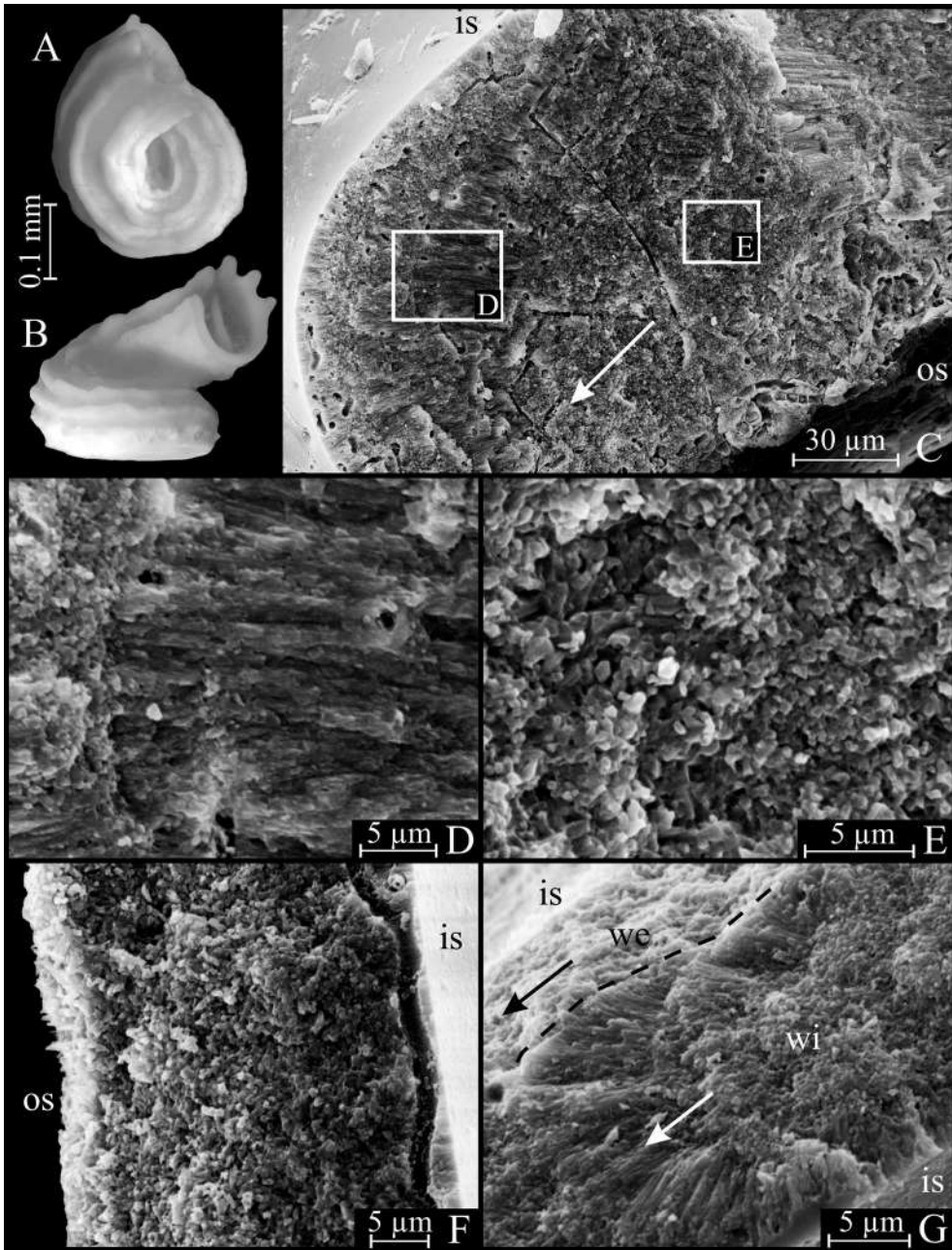


Fig. 15. *Romanchella quadricostalis*: details of tube morphology and ultrastructures. A, B — tube of the same specimen from different sides, note 5 teeth over the mouth; C–G — tube ultrastructures: C — general view of the longitudinal section at the mouth area, showing interbedding parabolic sections with SP and RHC structures; D — details of SP structure; E — details of RHC structure; F — general view of the longitudinal section of a younger specimen showing RHC structure with thin inner covering SP layer; G — general view of the longitudinal section across the whorl contact at in early growth stage, showing RHC structure of the internal wall.

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

by size and shape, and there is a huge number of smaller rice grain-like crystals, as well as isometric ones with irregular shapes. Near the inner surface, crystals lie more or less parallel to the lumen and are strongly consolidated with micritic matter. The outer SPHP layer was observed only in one specimen. It is very thin (~3 µm) and consists of spherulites (Fig. 16B), oriented either chaotically or perpendicular to the surface.

Inner organic lining is thin, but the details were not established clearly.

TUBE MINERALOGY. Not studied due to insufficient amount of material.

DISTRIBUTION. This species was recorded from the Atlantic coast of South America, ranging from Golfo San Jose to Puerto Deseado, Argentina, and the Tristan de Cunha Islands in the South Atlantic. It is also known from the Marion Island of the Prince Edward Islands and the Crozet Islands, the southern part of the Indian Ocean (Harris, 1969; Knight-Jones P., Knight-Jones E.W., 1984; 1991; Rzhavsky, 1998).

ECOLOGY. Can be found from the littoral zone to some unknown depth (no data available), being attached to various algae (most typically, to *Macrocystis* sp., including its surface-swimming parts).

Romanchella sepicula Rzhavsky, 1997

Fig. 16C–H.

For description see Rzhavsky, 1997: 239–242, fig. 3A–L.

MATERIAL EXAMINED. Two specimens and multiple fragments (IPEE No. 2/2526, Marion Island, Indian Ocean, 46°55.7'S, 37°54.1'E, on bryozoans, depth 95 m) were studied with SEM in longitudinal and transverse sections. External tube morphology was illustrated using specimens from the aforementioned sample and IPEE No. 1/2525 (Marion Island, Indian Ocean, 46°46.2'S, 38°03.2'E, on hydrozoans or bryozoans, 190 m) and figures from the original description.

TUBE MORPHOLOGY. Tubes are sinistral, usually planospiral in juveniles and sometimes in adults (Fig. 16D). Adult tubes are often loosely coiled (Fig. 16C, D) or tower-shaped (Fig. 16F). The diameter of the largest whorls of these specimens is ~0.7

mm, while the height of tower-shaped specimens is ~1–1.5 mm. Tube walls are thin and fragile. Sculpture is typically absent (Fig. 16C–E), or there is a single low sharp keel running along the whorl periphery (Fig. 16F). Tube mouth is round, but in the tower-shaped specimens, the adjacent upper surface bounded by the sharp peripheral ridge is almost flat (Fig. 16F). Tubes are white opaque.

TUBE ULTRASTRUCTURES. The wall is unilayered (Fig. 16G, H) with IOP structure composed of elongated cylindrical crystals shaped like rice grains (1–2 µm long and 0.4–0.5 µm wide), cemented with dense micritic matter. In the central zone of the wall, crystals are larger and stouter. In the inner third, they are smaller and intermixed with small isometric crystals. The outer and inner sides of the wall are consolidated with abundant micritic matter.

Inner organic lining is thin, less than 1 µm.

TUBE MINERALOGY. Not studied due to insufficient amount of material.

DISTRIBUTION. The Crozet Islands and Marion Island of the Prince Edward Islands, the southern part of the Indian Ocean (Rzhavsky, 1997).

ECOLOGY. Specimens were collected from 75–195 m depth, found on hydrozoans and bryozoans *Idmidronea* sp. and *Caberea darwinii* Busk, 1884.

Tube morphology of species not covered with the SEM study

Nine species of the tribe Romanchellini were not covered in the present study (Fig. 17). These are: one species of *Eulaeospira* (*E. arguta* (Bush in Moore et Bush, 1904)), five species of *Protolaeospira* (*P. (P.) calypso* (Zibrowius, 1970); *P. (P.) cavata* P. Knight-Jones et E.W. Knight-Jones, 1994; *P. (P.) gracei* Vine, 1977; *P. (P.) triflabellis* P. Knight-Jones, 1973 and *P. (Dextralia) falklandica* (Pixell, 1913)), and three species of *Romanchella* (*R. bicava* P. Knight-Jones, 1978; *R. inventis* (Harris, 1969) and *R. solea* Vine, 1977).

Рис. 15. *Romanchella quadricostalis*: детали строения трубок и их ультраструктуры. А, В — трубка одного экземпляра, изображенная с разных сторон, хорошо заметны 5 зубцов над устьем, образованные продолжением 5 продольных килей; С–G — ультраструктуры трубок: С — общий вид продольного сечения в устьевой части трубки, на котором выявляется переслаивание секторов роста с простой призматической (SP) структурой и структурой округлых изометричных кристаллов (RHC); D — детали строения простой призматической структуры (SP); E — детали строения структуры округлых изометричных кристаллов (RHC); F — общий вид продольного сечения молодого экземпляра, у которого видна RHC-структура в основной части стенки и тонкий слой простой призматической (SP) структуры на внутренней стороне; G — общий вид продольного сечения через зону смыкания оборотов на ранней стадии, хорошо видно, что стенка на внутренней стороне оборота имеет однослойное строение (структура округлых изометричных кристаллов, RHC).

Обозначения: is — внутренняя поверхность; os — наружная поверхность; we — стенка наружной стороны раннего оборота; wi — стенка внутренней стороны позднего оборота. Большие стрелки показывают направление роста трубки.

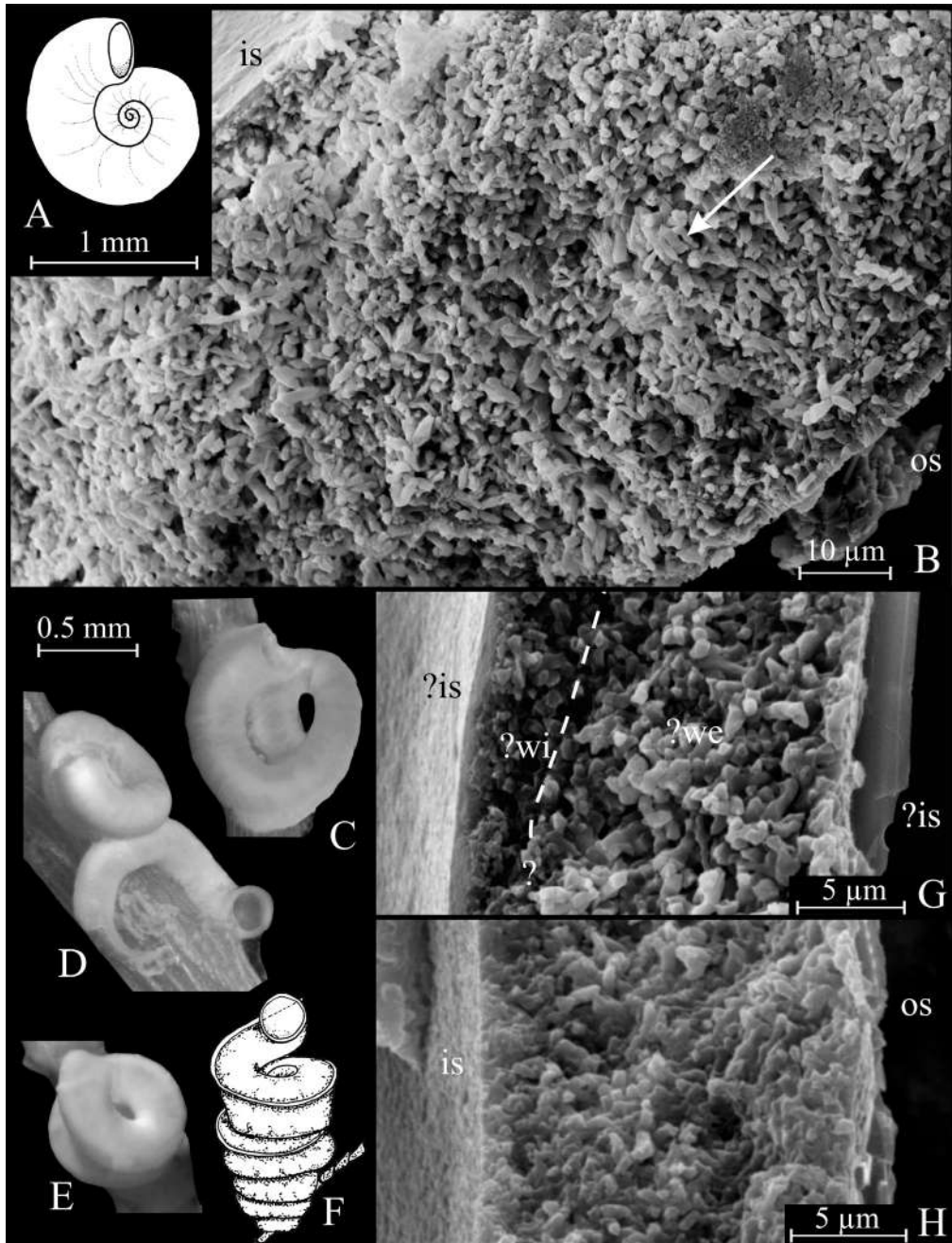


Fig. 16. *Romanchella scorebyi* (A, B) and *Romanchella sepicula* (C–H): details of tube morphology and ultrastructures. A, B — *Romanchella scorebyi*: A — tube (from Harris, 1969: fig. 18a); B — general view of the longitudinal section showing IOP structure with large crystals and thin outer covering layer with SPHP structure. C–H — *Romanchella sepicula*: C–F — tubes, C–E — unsculptured (typical) variation (C, D — IPEE No. 1/2525; E — IPEE No. 2/2526); F — tower-shaped variety with a single keel running along the periphery of the whorl (from Rzhavsky, 1997: fig. 3A); G, H — general view of the longitudinal sections in two specimens, showing IOP structure with large-sized crystals (Fig. 16G probably represents the area of whorls contact).

Eulaeospira arguta (Fig. 17A) has a small planospiral and thin-walled white tube, ~1 mm in coil diameter. The tubes show a single keel on the upper side of the tube, running along most of its length except for the terminal part, which is often smooth with the mouth part growing upwards from the substrate (Pillai, 1960). The presence of a median keel clearly differentiates *E. arguta* from *E. convexis* described above.

All five species of the genus *Protolaeospira* not covered here are known only from their original descriptions. The tubes of the subgenus *Protolaeospira* s.str. are quite variable in external morphology. However, they are always sinistral (coiled clockwise) and are usually thick-walled and hard to break.

Protolaeospira (P.) calypso, according to Zibrowius' (1970) description, has planospiral unsculptured white tubes with coil diameters up to 2.5 mm, but the tubes have never been illustrated. Tubes of *Protolaeospira (P.) cavata* (Fig. 17B, C) were originally described as "sinistral, round in cross-section, with a single median ridge, coiled in one plane, or with successive whorls one upon the other forming a tower" (Knight-Jones P., Knight-Jones E. W., 1994). The coil diameter of the tower-shaped modification, judging from the figures, is about 2 mm. Tubes of *P. (P.) gracei* (Fig. 17D) were characterised by Vine (1977) as planospiral with coil diameter up to 2.8 mm, bearing a single median keel, with white and somewhat porcellaneous walls, hard to break. *Protolaeospira (P.) triflabellis* (Fig. 17E, F) has planospiral tubes with coil diameters up to 4 mm and frequent regularly spaced transverse ridges; tube walls are "thick and hard, but in no way translucent" (Knight-Jones P., 1973). By its remarkable transverse sculpture, this species is

indistinguishable from the sculptured variety of *P. (P.) eximia*, described above.

The tube morphology of *P. (D.) falklandica* (Fig. 17G) falls within the described intraspecific variability of *P. (D.) stalagmia*, described above (see Knight-Jones P., Walker, 1972). The original description lacks tube illustrations, but Harris (1969) provided them using the type material.

Tubes of *Romanchella* spp. are also variable in their external morphology, and all three species not covered in the present study are known only from their original descriptions.

Romanchella bicava (Fig. 17H) is the only species of the genus showing dextral (anticlockwise) coiling. According to P. Knight-Jones (1978), the tube is planospiral with a coil diameter of up to 1.8 mm, three distinct keels (however, four are seen on her drawing) and thick tube walls. No data are available on the tube colour and transparency, but based on the ultrastructures of studied *Romanchella* species, it is expected to be white opaque because SPHP/SP structures that result in transparency (Ippolitov, Rzhavsky, 2008, 2015b) are relatively poorly developed in *Romanchella*. Tubes of *R. inventis* (Fig. 17I) were initially described and figured by Harris (1969) as planospiral with coil diameter up to 1 mm, white opaque and unsculptured. *Romanchella solea* (Fig. 17J, K), according to Vine (1977), has planospiral tubes with coil diameters up to 2 mm and three or four keels; its walls are thick, white and porcellaneous.

Discussion

Remarks to fossil *Romanchellini*, described in the literature. There are two unequivocal records of fossil romanchellins, closely related

Abbreviations: is — inner surface; os — outer surface; ?we — questionable tube wall on the external side of the next-to-last whorl; ?wi — questionable tube wall on the internal side of the last whorl. Large arrow indicates the direction of tube growth. Рис. 16. *Romanchella scorebyi* (A, B) и *Romanchella sepicula* (C–H): детали строения трубок и их ультраструктуры. A, B — *Romanchella scorebyi*: A — трубка (из Harris, 1969: fig. 18a); B — общий вид продольного сечения, на котором видна структура хаотически ориентированных призматических кристаллов (ИОР) и тонкий внешний слой со сферулитовой призматической (SPHP) структурой. C–H — *Romanchella sepicula*: C–F — трубки, C–E — нескульптированная (наиболее типичная) разновидность (C, D — ИРЕЕ № 1/2525; E — ИРЕЕ № 2/2526); F — башенковидная разновидность с продольным килем на внешней стороне оборота (из Rzhavsky, 1997: fig. 3A); G, H — общий вид продольных сечений в двух различных экземплярах, показывающий структуру хаотических ориентированных призматических кристаллов (ИОР), сформированную крупными элементами (Рис. 16G, по-видимому, показывает смыкающиеся обороты).

Обозначения: is — внутренняя поверхность; os — наружная поверхность; ?we — вероятно, стенка наружной стороны раннего оборота; ?wi — вероятно, стенка внутренней стороны позднего оборота. Большая стрелка показывает направление роста трубки.

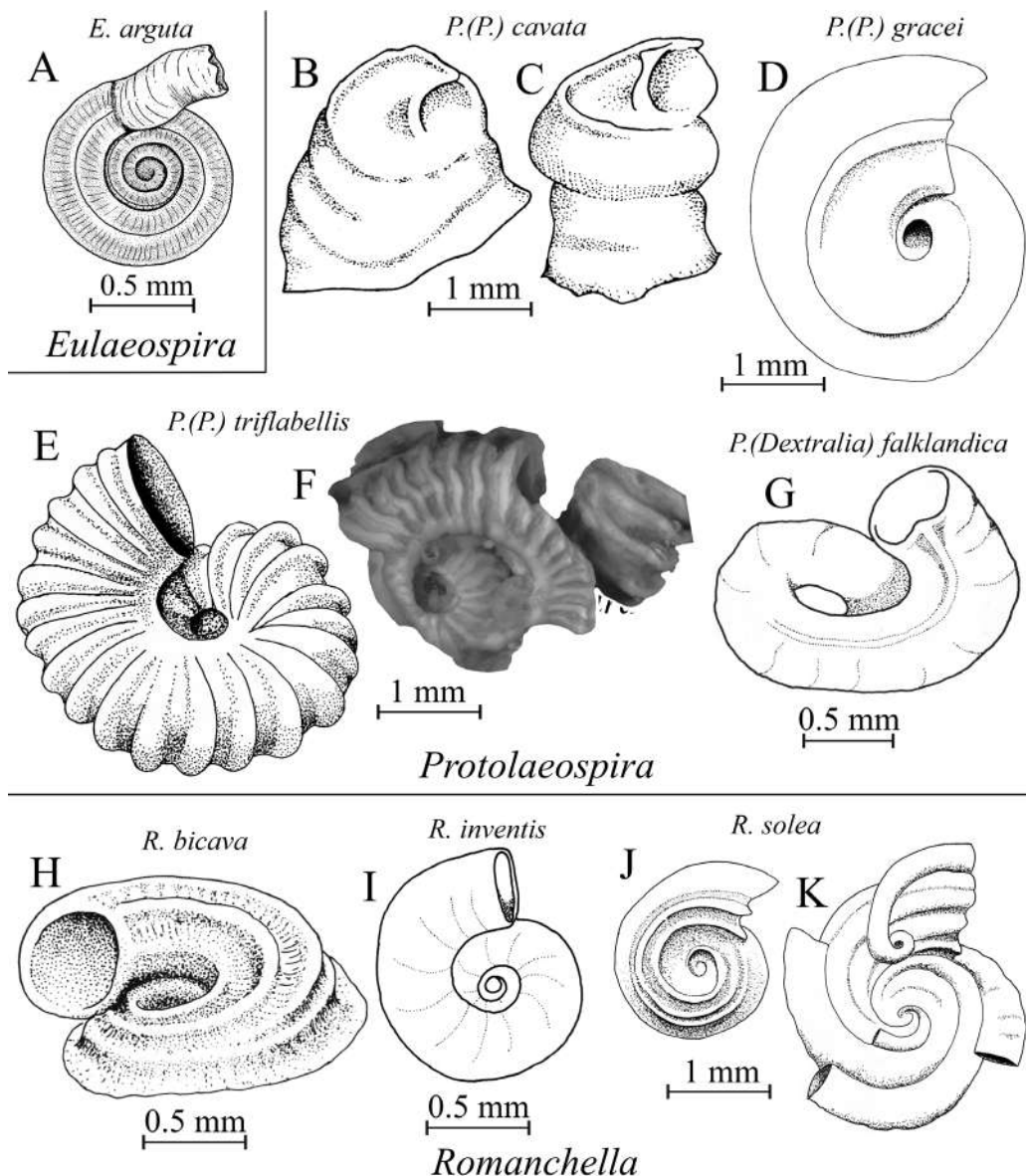


Fig. 17. Tubes of Romanchellini species not covered in the present study. A — *Eulaeospira arguta* (from Pillai, 1960: fig. 14D; as “*Spirorbis (Laeospira) orientalis*”); B, C — *Protolaeospira (Protolaeospira) cavata* (from Knight-Jones P., Knight-Jones E.W., 1994: fig. 4A, B); D — *Protolaeospira (Protolaeospira) gracei* (from Vine, 1977: fig. 15A); E, F — *Protolaeospira (Protolaeospira) triflabellis*: E — (from Knight-Jones P., 1973: fig. 2a); F — paratype AMRI W.4474; G — *Protolaeospira (Dextralia) falklandica* (from Harris, 1969: text-fig. 6a); H — *Romanchella bicava* (from Knight-Jones P., 1978: fig. 16A); I — *Romanchella inventis* (from Harris, 1969: text-fig. 10a); J, K — *Romanchella solea* (from Vine, 1977: fig. 22a, b): J — solitary tube; K — adult tube overgrown by *Paralaeospira levinseni* Caullery et Mesnil, 1897.

Рис. 17. Трубки представителей трибы Romanchellini species не изученные в ходе настоящего исследования. А — *Eulaeospira arguta* (из Pillai, 1960: fig. 14D; как “*Spirorbis (Laeospira) orientalis*”); В, С — *Protolaeospira (Protolaeospira) cavata* (из Knight-Jones P., Knight-Jones E.W., 1994: fig. 4A, B); D — *Protolaeospira (Protolaeospira) gracei* (из Vine, 1977: fig. 15A); E, F — *Protolaeospira (Protolaeo-*

to extant species as can be recognised by their characteristic tubes (cf. *Romanchella perrieri* from the Castlecliffian of New Zealand (Pleistocene, 1.63–0.34 Ma), see Vine in Fleming, 1974 and the original record by Fleming, 1972; and *Helicosiphon biscoeensis* from the Holocene strata of the Antarctic coast, see Pickard, 1985). Besides, there are two more ancient records of potential romanchellins, which can now be re-interpreted at least from the point of their tube morphologies — while the data on well-preserved tube ultrastructure in these fossils, similar to those introduced by Kočí *et al.* (2022), are still lacking.

“*Spirorbis* sp. B” from the Altonian of New Zealand (lower Miocene; 18.7–15.9 Ma) figured by Fleming (1972), was compared both to extant species *Pileolaria militaris* Claparède, 1870 (tribe Pileolariini) and to *Protolaeospira* by Vine (in Fleming, 1974), with a preference to the former option. The examination of Fleming’s originals, kept in GNS Science (Lower Hutt, New Zealand) revealed that they have porcellaneous tube surface, not typical for *Pileolaria* at all (see descriptions in Rzhavsky *et al.*, 2014, 2018; Ippolitov, Rzhavsky, unpubl.). In our opinion, these fossils are best compatible with *Protolaeospira* because of their size (3.5 mm in coil diameter of largest specimens vs 2, rarely 3 mm in most *Pileolaria* spp. — see Knight-Jones *P. et al.*, 1979; while the largest *Protolaeospira* species, *P. (P.) eximia* and *P. (D.) stalagma*, may attain 5 and 6 mm, respectively) and characteristic transversely rugose surface, which can be observed in many *Protolaeospira* species (see Figs 8A, B; 10F, F; 11B–C, 12A–C in the present paper). The latter feature differentiates “*Spirorbis* sp. B” from another large-sized romanchellin genus, *Helicosiphon*, which has more or less smooth tube surfaces (see Figs 2A, B; 3A, B in the present paper).

More ancient *Metalaespira pileiformis* Lommerzheim, 1981 from the Palaeocene (Selandian–Thanetian, Globorotalia pseudomenardii Zone, 60.75–57.1 Ma) of the NW Pacific Emperor Seamount chain falls far aside from the known geographical range of extant *Metalaespira*,

confined only to the middle and high latitudes of the Southern Hemisphere, and does not belong to this genus. It is hardly compatible with any known extant spirorbin due to its very multiple (5–7, according to Lommerzheim, 1981) longitudinal keels and the massive opercular cap.

Patterns and variations. Romanchellini are very uniform in having 100% calcitic tubes (except *Metalaespira pixelli*, in which 3% aragonite content was registered — and this may result from some alien carbonate skeleton attached to the analysed tube). However, Romanchellini demonstrate an outstanding ultrastructural variability spectrum compared to that previously observed for tribes Paralaespirini, Spirorbini and Circeini altogether (Ippolitov, Rzhavsky, 2014, 2015a, b). By the shape of crystals within the central part of the wall, three main types of fabric constituting oriented prismatic (IOP) structure may be distinguished:

IOP₁ — prismatic crystals of regular rice grain shape, with rounded blunt ends (e.g., Fig. 1C);

IOP₂ — crystals of irregular angular shape poorly sorted by size. Both micro-spherulites and prismatic crystals are intermixed (e.g., Fig. 8E);

IOP₃ — large crystals of a regular peanut-like shape (peanut-like spherulites) that can penetrate each other (e.g., Figs 9F, 11F, 12H). This variety is an example of a gradual transition to spherulitic irregularly oriented prismatic (SIOP) structure (cf. Figs 3I, 12G).

It should be noted, that within a single tube, any number of varieties listed above can be present.

Eulaespira convexis and *Romanchella perrieri* clearly stand out from the observed diversity of romanchellin structures. Both have unilayered tubes with IOP₁ structures and no traces of SPHP/SP structures, but further details differ. *Eulaespira convexis* differs from most Romanchellini by a high Mg content in calcite (main peak at $d=3.010$ Å vs 3.018–3.044 Å in most romanchellins, except *P. (P.) tricostalis* and *P. (P.) striata*). *Romanchella perrieri* differs from other Romanchellini not only by its unilayered IOP₁ tube, but also by having alveoli, resembling

spira triflabellis: E — (из Knight-Jones P., 1973: fig. 2a); F — паратип, AMRI W.4474; G — *Protolaeospira (Dextralia) falklandica* (из Harris, 1969: text-fig. 6a); H — *Romanchella bicava* (из Knight-Jones P., 1978: fig. 16A); I — *Romanchella inventis* (из Harris, 1969: text-fig. 10a); J, K — *Romanchella solea* (из Vine, 1977: fig. 22a, b); J — одиночная трубка; K — взрослая трубка, обросшая спирорбинами другого вида, *Paralaespira levinseni* Caullery et Mesnil, 1897.

those of Januini (comparison to be provided in the Part V of the present series).

The other Romanchellini may be subdivided into 4 groups (Table S1), based on the shape of crystals making IOP structure of the main layer and the presence/absence of SPHP layers along the inner and outer wall surfaces.

Group A includes all *Helicosiphon*, *Metalaeospira*, and *Protolaeospira* (*Dextralia*) *stalagmia* and is characterised by a well-developed outer SPHP layer with spherulites' characteristic irregular orientation and by the presence of IOP₂/IOP₃ crystals in the main layer, where they can be intermixed with each other and with IOP₁ crystals.

Group B includes most of the studied *Protolaeospira* species, except for *P. (D.) stalagmia* (→Group A) and *P. (P.) pedalis* (→Group C). The essential characteristic of Group B is the presence of SPHP/SP layers along both the inner and outer wall surfaces. Extensive development of SPHP structures leads to a full or partial reduction of the main IOP layer in *Protolaeospira* (*P. augeneri* and *P. (P.) striata*, respectively, making the tube vitreous. Macroscopically, members of Group B typically have well-developed transverse sculpture, represented by irregular flaring peristomes or modified into regular transverse ridges (as in *P. (P.) eximia*, and questionably, *P. (P.) triflabellis*).

Group C includes *P. (P.) pedalis* and two *Romanchella* species (*R. scoresbyi* and *R. sepicula*). The close phylogenetic relationship between the members of this small group with unilayered tubes is not confident. In fact, such an interpretation is based on the assumption that the observed tube structure is derived from those typical for Groups A or B via reduction of outer (and, questionably, inner) SPHP layers, but such a process could occur independently in different lineages. Among members of the group, *R. sepicula* does not show traces of SP/SPHP structures, while the other two show residual inner SP layers. The IOP₂ crystals of the central part of the wall in all three species are similar to those observed in Groups A and B.

Group D includes *Romanchella pustulata* and *R. quadricostalis*, which demonstrate the presence of a unique rounded homogeneous crystal (RHC) structure made of tiny isometric crystals. In *R. quadricostalis*, this type of structure is interbedded with SP structure along chevron-shaped growth lamellae. This structure seems

to be a secondary derivate of IOP_{1/2} structures combined with the presence of the inner/outer SPHP layers (see “Phylogenetic significance” below).

The proposed groups correlate well with the taxonomic classification: Group A includes all *Helicosiphon* and *Metalaeospira*; Group B — most of *Protolaeospira*; Group C — most of *Romanchella*, while Group D includes species within *Romanchella*. Using ultrastructures for precise generic attribution is mostly impossible. However, two ultrastructural types (unilayered SPHP/SP wall with reduced main IOP layer and three-layered tubes with well-developed both inner and outer SPHP/SP layers) always characterise subgenus *Protolaeospira* s. str. that can also be recognised by its tendency to have transverse sculpture. Also, it should be noted that species of the genus *Protolaeospira* are incorporated into three different groups (B, C and D), which may be explained by the possible polyphyletic nature of this genus (see also Rouse *et al.*, 2024: figs 3, 4). Another pair of taxa, *Metalaeospira* and *Helicosiphon*, which have similar ultrastructures of the tube and both belong to the Romanchellini Group A, are not likely to be closely related (Rouse *et al.*, 2024: figs 2–4).

To conclude, among Romanchellini, there is no one tube character that could be interpreted as a clear synapomorphy for all the species included in the tribe: the only common feature is the absence of aragonite (=100% calcitic composition). However, such a mineralogical composition is common for other spirorbini tribes (see Ippolitov, Rzhavsky, 2014, 2015a, b) and for many serpulins and filogranins as well (see Vinn *et al.*, 2008; Smith *et al.*, 2013).

Comparison with other Spirorbinae. Variability in tube ultrastructures within Romanchellini makes tribe-to-tribe comparison problematic since Romanchellini do not demonstrate a clear common pattern that would characterise the entire tribe. So below, we compare previously studied tribes with ultrastructural groups A–D of Romanchellini (see above).

Paralaeospirini (see Ippolitov, Rzhavsky, 2014) have unilayered tubes with IOP₁ structure, which are comparable among Romanchellini only to that found in *Romanchella perrieri* and *Eulaeospira convexis*. However, in the former species, the presence of the alveoli makes confu-

sion with Paralaeospirini impossible. The second species, *Eulaeospira convexis*, is indistinguishable from Paralaeospirini both by tube ultrastructure and tube morphology, thus suggesting that the original placement of *Eulaeospira* within Paralaeospirini (Knight-Jones P., Fordy, 1979), which was recently re-established in Rouse *et al.* (2024), is likely to be correct. However, IOP₁ structure is extremely widespread not only among other Spirorbinae (Ippolitov, Rzhavsky, 2015a) but also among non-spirorbin Serpulidae (Vinn *et al.*, 2008; Ippolitov, unpubl.). Other members of Romanchellini cannot be confused with Paralaeospirini. Members of groups A and B usually have well-developed SPHP layers that are absent in Paralaeospirini. Romanchellini Group C has unlayered tubes with IOP₂ fabric, not IOP₁ as in Paralaeospirini, while Group D is distinct because of its recognisable RHC structure and local presence of SP/SPHP layers. *Paralaeospira aadeonella* Day, 1963 attributed to the tribe Paralaeospirini, has a transparent tube, thus it probably has SP wall structure. However, its taxonomic position requires revision — this species may belong to *Protolaeospira* s. str., judging from the presence of regular transverse sculpture characteristic for romanchellin Group B (see Ippolitov, Rzhavsky, 2014: 308).

Spirorbini (see Ippolitov, Rzhavsky, 2015a) usually have IOP₁ fabric of the main layer, sometimes combined with an unevenly developed SPHP outer layer. Such an architecture makes Spirorbini comparable with certain romanchellin species — *Eulaeospira convexis*, *Romanchella perrieri* and members of Group A. *Eulaeospira convexis* and *Romanchella perrieri* are characterised by the absence of SPHP layer in standard section. They are indistinguishable by ultrastructure from those of Spirorbini, which lack SPHP layers (=“Spirorbini group A” *sensu* Ippolitov, Rzhavsky, 2015a). Members of Romanchellini Group A are typically characterised by the presence of the IOP₂ fabric, which differs from the IOP₁ of Spirorbini. An ultrastructurally unique member of Spirorbini, *Spirorbis rothlisbergi* P. Knight-Jones, 1978, has a three-layered tube comparable to the members of romanchellin Group B. However, the IOP₁ fabric of the main layer in *S. rothlisbergi* is incompatible with the IOP₂ fabric of romanchellin Group B. Therefore, only *Eulaeospira convexis* and *Romanchella perrieri* can be confused with Spirorbini.

Circeini (see Ippolitov, Rzhavsky, 2015b) are characterised by two main ultrastructural types: three-layered tubes with well-developed SP/SPHP outer and inner layers in *Circeis* de Saint-Joseph, 1894 and unlayered SP tubes in *Paradexiospira* Caullery et Mesnil, 1897. Both these architectures were found in Romanchellini (in particular, in Group B, which includes most *Protolaeospira* s.str.). However, the coiling direction, strictly sinistral in Romanchellini Group B and predominantly dextral in Circeini, provides a reliable recognition criterion. The second important point of difference is the axis of parabolic growth lamellae, which is strongly displaced to the outer side in *Protolaeospira* and only slightly in Circeini. The transitions from three-layered white porcellaneous (SPHP–IOP–SPHP) to unlayered transparent (SP to SPHP) tubes in both tribes are apparently convergent, as ‘transitional’ taxa in both tribes demonstrate different structures. In Circeini, *Circeis spirillum* (Linnaeus, 1758) shows the reduction of the main layer via its gradual transformation into SIO structure coupled with thickening of inner and outer SPHP layers, while in the romanchellin *Protolaeospira striata* transition to SP structure appears to be a result of numerous growth stops, each causing the development of thick SP/SPHP layer running along growth lamellae and locking original IOP structure in ‘pockets’ between these stops (cf. Fig. 10H). A similar intercalation of ultrastructures was described for longitudinal internal sculpture (so-called “internal tube structures”, or ITS) of the serpulid genus *Spiraserpula* Regenhardt, 1961 (see Vinn, 2007: fig. 4.6).

Comparison with extant Januini and Pileolariiini will be provided in subsequent parts of the present study.

Phylogenetic significance. In their recent phylogenetic analysis of Spirorbinae based on both molecular and morphological datasets, Rouse *et al.* (2024) analysed six species of Romanchellini — *Metalaeospira tenuis*, *Helicosiphon biscoeensis*, *Protolaeospira* cf. *capensis*, *P.* cf. *eximia*, *P.* cf. *tricastalis* and *Romanchella quadricostalis*. All these nominal species were covered in the present study. According to Rouse *et al.* (2024), *M. tenuis* is the sister group to the rest of their studied taxa. Therefore, its ultrastructures (thick main IOP layer with outer

SPHP layer, often distributed irregularly and with spherulites often not strictly aligning the tube surface; Group A) can be expected to be plesiomorphic relative to other members of the tribe. Therefore, the development of strongly consolidated tubes with developed SP/SPHP layers, and especially with missing main IOP layer in *Protolaeospira* s. str. having entirely transparent tubes (*P. (P.) augeneri* and *P. (P.) striata*; both Group B), is an apomorphic state. We also observed a transition from the three-layered tube SPHP-IOP-SPHP to the unilayered SP/SPHP wall in the ontogeny of *P. (P.) striata*. The assumption of the apomorphic nature of the unilayered SP/SPHP wall is in agreement with our previous observations on Circeini, which show a comparable ultrastructural variety (Ippolitov, Rzhavsky, 2015b).

The transitions between different types of IOP fabric within the studied tribe are still hypothetical. IOP₁ looks to be a basic state, as this kind of fabric is common not only among Spirorbinae (including Paralaespirini, Spirorbini, Januini — see Ippolitov, Rzhavsky, 2014, 2015a, and unpubl.) but also among non-spirorbin Serpulidae (see Vinn *et al.*, 2008). Besides, in *Metalaespira pixelli*, we observed the ontogenetic transition from IOP₁ fabric in the early whorls to IOP₂ fabric in the last whorl.

RHC structure found in two rather specialised species (*Romanchella pustulata* and *R. quadricostalis*), was previously known in a single non-spirorbin serpulid species *Pomatostegus stellatus* (Abildgaard, 1789) (see Vinn *et al.*, 2008), which is close to the filogranin/spirorbin divergence node in serpulid phylogeny (Kupriyanova *et al.*, 2023). However, in Romanchellini, RHC structures are found in members of the genus *Romanchella*, which do not seem to be the least specialised among the tribe, as it follows from the phylogeny of Rouse *et al.* (2024); besides, all Romanchellini have advanced brooding scheme. Therefore, RHC structure in spirorbins is likely to be an apomorphic feature relative to IOP structure rather than a plesiomorphic character occasionally preserved in a few taxa.

Ecological implications. In summary, Romanchellini show a wide variation of wall ultrastructures ranging from arguably plesiomorphic types (unilayered IOP) to highly complex and specialised types (three-layered SPHP–

IOP–SPHP and unilayered SP/SPHP). Like in Spirorbini and Circeini (see Ippolitov, Rzhavsky, 2015a, b), some groups of Romanchellini show a clear trend towards consolidation of the outer and inner zones of the walls by strongly developed SPHP layers and their further transformation into unilayered SP structure. The extensive diversification of oriented structures (SPHP, SP), as well as a tendency to consolidate the main layer of the tube (transition from IOP₁ to IOP₃ type), can be a result of adaptation to habitats in environments with stronger hydrodynamics and sand abrasion. Notably, *Protolaeospira* spp. typically selecting stones and shell debris as the preferred type of substrate are characterised by the thickest tubes within the tribe. On the contrary, thin-walled *Metalaespira* spp. most typically attach to algae; their relatively loose microstructure may be due to the selective advantage of having lightweight tubes in such conditions. The adaptation to rocky environments in *Protolaeospira* is an example of a reverse ecological transition within Spirorbinae, basically diverging from other serpulids because of their adaptation to the settlement of flexible and ephemeral substrates (Ippolitov *et al.*, 2014).

Supplementary data. The following materials are available online.

Table S1. Main tube characters for studied Romanchellini and subdivision into Groups A–C. Abbreviations: arag — aragonite; calc — calcite; D — dextral (anticlockwise) coiling; S — sinistral (clockwise) coiling.

Acknowledgements. We thank L.T. Protasevich, A.V. Kravtsev, R.A. Rakitov (Office of Instrumental Analytics, PIN RAS), V.L. Kosorukov (Laboratory of Lithology and Facies analysis, Geological Faculty of Moscow State University) and Sue Lindsay (AMRI) for their kind help with the technical part of the study. The material was partly processed in the Joint Usage Center “Instrumental Methods in Ecology” at the IPEE RAS with the help of A.N. Nekrasov, A.N. Neretina, and late N.N. Surovenkova. We also thank specialists who donated materials to the collection of A.V. Rzhavsky (see Ippolitov, Rzhavsky, 2014). Our special thanks are due to E.K. Kupriyanova (AMRI), who not only reviewed the manuscript and provided invaluable remarks and suggestions, significantly improving the paper, but also motivated us to finalise this work. A.V. Rzhavsky spirorbin investigation was also supported by the Japan Society for the Promotion of Science (JSPS) Short-Term Fellowship and KAKENHI grant in aid (No. 22510100) in 2000 and

Geddes visiting collection fellowship of AMRI in 2013. For A.P. Ippolitov, this paper has been supported by the Kazan Federal University Strategic Academic Leadership Program (PRIORITY-2030) and by the subsidy allocated to Kazan Federal University for the state assignment project No. FZSM-2023-0023.

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Responsible editors: I.A. Jirkov, E.N. Temereva

Table S1. Main tube characters for studied Romanchellini and subdivision into Groups A–D. Abbreviations: arag — aragonite; calc — calcite; D — dextral (anticlockwise) coiling; S — sinistral (clockwise) coiling.

Таблица S1. Основные черты строения трубок изученных видов Romanchellini и их разделение на группы A–D. 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	Transverse sculpture	Transparency	Surface	Arag/calc ratio	Mg content in calcite	Dense outer layer	Main layer and crystal size (µm)	Dense inner layer	micrite	additional
untypica	<i>E. convexis</i>	1	S	0	irregular infrequent peristomes	opaque	porcellaneous	0/100	High	–	IOP ₁ 3	–	low	
	<i>R. perrieri</i>	1.5	S	4	alveoli	opaque	porcellaneous	0/100	average	–	IOP ₁ 5	–	low to high	
A	<i>H. biscoeensis</i>	n/a	S	1*	–	opaque	non-porcellaneous	0/100	low	irregular SPHP	IOP _{1,2} 5–6	–	average	locally OF structure was observed
	<i>H. platyspira</i>	5	S	0	–	opaque	non-porcellaneous	0/100	average	irregular SPHP	IOP _{1,2} 5	–	average	
	<i>M. armiger</i>	3	S	3	–	opaque	porcellaneous	0/100	average	irregular SPHP	IOP _{2,3} to SIOP 4–5	–	low	
	<i>M. clansmani</i>	3	S	0	–	opaque	porcellaneous	0/100 **	low	uneven SPHP	IOP _{1,2, 23} 1.5–2	–	high to average	peripheral flange is formed by extensions of the outer SPHP layer
	<i>M. pixelli</i>	3(4?)	S	0–1	–	semivitreous	porcellaneous	3/97	low	irregular SPHP	IOP _{1,2} 3	–	low	
	<i>M. tenuis</i>	3	S	0–1	–	semivitreous	porcellaneous	?	?	SPHP	IOP _{2,3} 1.5–2.5	–	low to medium	
	<i>P. (D.) stalagma</i>	6	D	(1) 3	–	opaque	porcellaneous	0/100	average	uneven SPHP	IOP _{1,2,3} to SIOP up to 8–10	–	low	
B	<i>P. (P.) augeneri</i>	2.5	S	0 (2)	irregular infrequent peristomes	vitreous/semivitreous	–	0/100	low	SP/SPHP	– (reduced)	SP/SPHP	–	SIOP attachment area
	<i>P. (P.) capensis</i>	2	S	0–1	indistinct irregular peristomes	vitreous/semivitreous thin bands	porcellaneous (background)	0/100	average	SPHP	IOP ₂ 2–4	uneven SPHP	low	
	<i>P. (P.) eximia</i>	5	S	0	regular ridges	opaque	porcellaneous	0/100	low	SPHP	IOP _{1,2,3} to SIOP 6–8	SPHP	low	
					irregular peristomes	vitreous brownish	–	not studied						
	<i>P. (P.) tricostalis</i>	2–2.5	S	0 (2)	–	opaque	porcellaneous	0/100	low	uneven SPHP	IOP ₂ 6–7	SPHP	low	locally, IOP may transform into SIOP
	<i>P. (P.) striata</i>	3	S	0	regular/ irregular ridges	vitreous	–	not studied		SP/SPHP	reduced (locally IOP ₂)	SP/SPHP	medium	In early growth stages, the middle layer has IOP ₁ structure
C	<i>P. (P.) pedalis</i>	2	S	0 (3)	–	opaque	?	0/100	low	–	IOP ₂ 2.5 (up to 5)	(residual SPHP)	low	
	<i>R. scoresbyi</i>	1.5	S	0	–	opaque	?non-porcellaneous	not studied		–	IOP ₂ 4	(residual SP)	low	
	<i>R. sepicula</i>	0.7	S	0–1	–	opaque	porcellaneous	not studied		–	IOP _{1,2} 1.5–2	–	high	
D	<i>R. pustulata</i>	4	S	0	–	opaque	?non-porcellaneous	0/100	high	–	RHC to IOP ₁ 1	–	high	SPHP basal plate
	<i>R. quadricostalis</i>	2.5	S	4–5	–	opaque	porcellaneous	0/100	high	intercalation of growth lamellae with RHC (0.5–1) and SP structure			high	in adults
SP										RHC 0.5–1	SP	in juveniles		

*ascending portion of the tube may demonstrate angular cross-section with 4 indistinct keels (приподнимающаяся вверх от субстрата часть трубки имеет неправильно-угловатое сечение, иногда с 4 гранями)

**doubtful (shifted) aragonite peak was registered (зафиксирован сомнительный смещенный пик, который может указывать на присутствие арагонита).