

GENERAL  
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## On the Tube Microstructure of Recent Spirorbids (Annelida, Polychaeta)

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Calcareous tubes are unique for polychaetan families Spirorbidae, Serpulidae, and some forms of Sabellidae. Literature sources on the tube microstructure of spirorbids are scarce [5–7], whereas serpulids are known slightly better. The lack of data results in attribution of fossils of uncertain affinity with calcareous tubes [1, 4, 8] to worms. The assignment of convergently similar fossils with a different microstructure of tubes [6, 7] to spirorbids leads to an incorrect conclusion that the group is phylogenetically old, which is an important argument in phylogenetic reconstructions [3]. Study of the diversity of tube microstructure in recent spirorbids may provide the basis for species and genus identification based on tubes, and, in the long run, may appear useful in studies on paleontological material.

### MATERIALS AND METHODS

Tube microstructures of spirorbids belonging to 62 species of 21 genera and subgenera from all six subfamilies (Paralaeospirinae, Romanchellinae, Spirorbinae, Circeinae, Januinae, and Pileolariinae), i.e., about 40% of recent species, were studied using a Camscan scanning electron microscope. The microstructure of tube walls was studied on the surfaces of longitudinal cracks without etching. Whenever possible, several specimens of the same species were studied to estimate variability.

### RESULTS AND DISCUSSION

The tubes of adult spirorbids are small (the coil diameter is 1.5–4; less frequently, it reaches 8 mm), have a planospiral shape with three or four closed, or,

less frequently, unclosed coils. As a rule, they are white opaque with a chalky (matte) or, less frequently, porcelain-like (glossy) surface. The tubes of some species are semitranslucent with a glossy surface or absolutely transparent, vitreous. The surface can be smooth or have longitudinal and transverse ridges and constrictions (alveoli). The wall on the inner side of the coils is usually three to four times thinner than on the external side and is usually accompanied by a reduction of some microstructural layers. The internal surface of the tubes is lined with an organic layer of varying thickness. It is frequently invisible under a binocular microscope, but sometimes it is pigmented and, hence, distinct. Longitudinal cracks of the wall show a characteristic “parabolic” texture reflecting a configuration of elementary growth lines, curved towards the anterior edge of the tube.

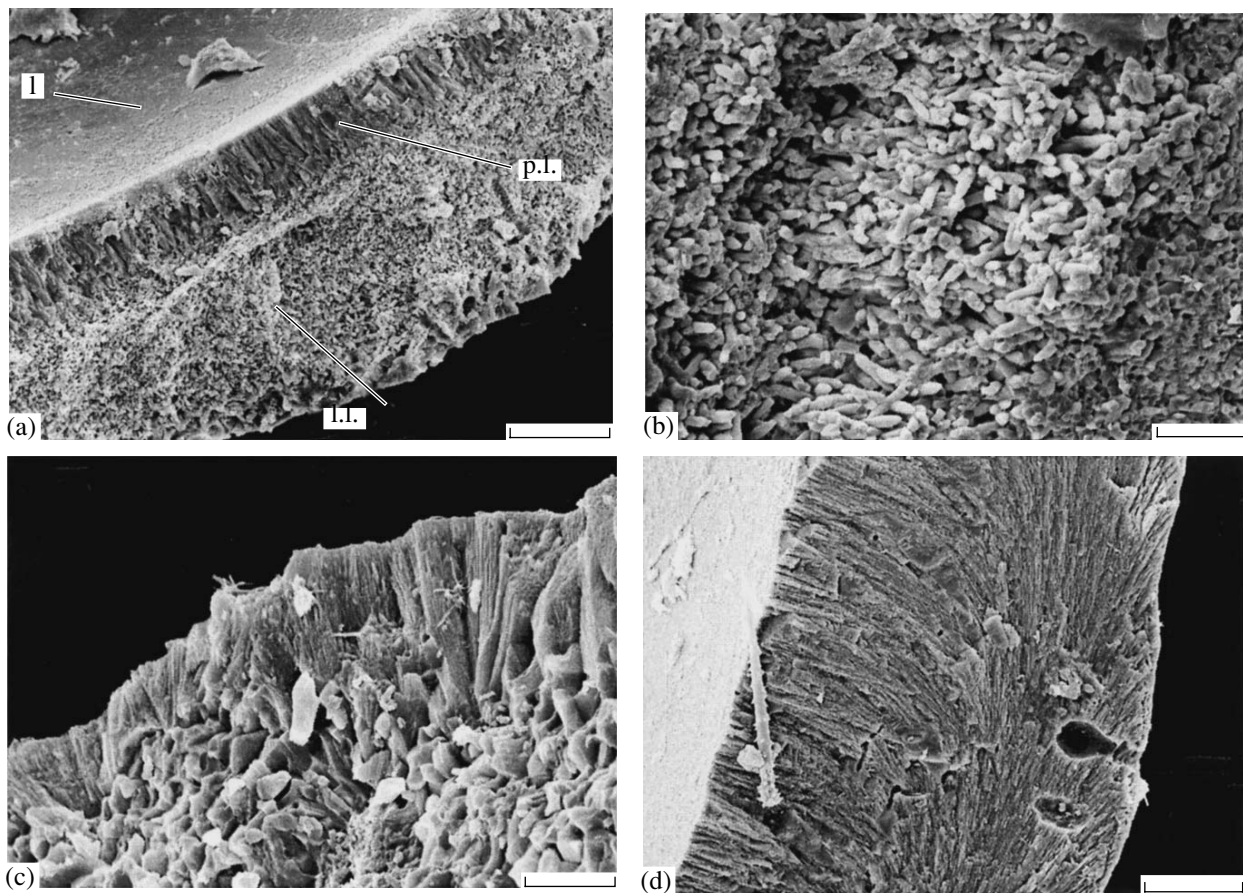
The basic structural elements of the walls (Fig. 1a) are the following.

(1) A layer built of unordered elongated, weakly elongated, and isometric crystals or their combination (Fig. 1b). Elongated crystals are up to 5  $\mu\text{m}$  long and 0.75  $\mu\text{m}$  wide; isometric crystals are 0.5–1  $\mu\text{m}$  (sometimes, up to 2.5–5  $\mu\text{m}$ ) in diameter. In the majority of spirorbids, this layer is the thickest and constitutes the main part of the tube wall. Different parts of this layer contain different types of crystals; in some cases, their shape regularly changes in the direction from internal to external surfaces. This layer usually has a rather loose structure with crystals not cemented to each other.

More elongated crystals usually occur near the inflection areas of parabolic growth lines in the central part of the wall. The central part of the main layer along the growth lines also shows alternating narrow transverse layers built of larger elongated and smaller isometric crystals. Near external and internal surfaces, the tube consists of smaller isometric crystals, frequently cemented to each other. The boundaries of “cemented” zones and the central part are indistinct. When prismatic type crystals are developed at the surface (see below), the size reduction of crystals is not quite appar-

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**Fig. 1.** Microstructure of spirorbid tubes on longitudinal crack surfaces. (a) *Spirorbis rothlisbergi*, a general view of the wall; the scale bar is 30  $\mu\text{m}$ : l, organic lining, p.l., prismatic layer, l.l., main loose layer. (b) The structure of the main layer containing unordered crystals as exemplified by *Protolaeospira ushakovi*; the scale bar is 20  $\mu\text{m}$ . (c) The structure of the prismatic layer (the external surface of *Protolaeospira stalagmia*); the scale bar is 10  $\mu\text{m}$ . (d) *Protolaeospira augeneri*, a general view of the wall completely built of prismatic crystals; the scale bar is 30  $\mu\text{m}$ .

ent. In some cases (some *Bushiella*), crystals at the external surface are larger than in the central parts of the wall, though the reverse situation is more common. In one case (*Protolaeospira stalagmia*), large, slightly elongated crystals form the internal layer of the tube wall.

The internal surface of tubes in many species is lined with a layer of elongated crystals with a length up to 5–6  $\mu\text{m}$  and a width of 0.5  $\mu\text{m}$ , with the long axis parallel to the internal surface of the tube. They form a separate thin layer with a thickness of several microns; in two studied species (*Pileolaria militaris* and *Ampliocaria spiculosa*), its thickness was as much as 10–12  $\mu\text{m}$ . The close similarity in the shape of crystals of this layer and those of the main layer suggests a common pathway of their formation, though the arrangement of crystals and the distinct boundary between the layers suggest that the covering layer is an independent structural unit.

(2) Layers built of oriented, elongated (prismatic or conic) crystals, usually 10–15  $\mu\text{m}$  long (Fig. 1c), with their long axes arranged at the right angle to growth

lines. Crystals of this type merge together to form thin layers (usually, about five or less percent of the overall wall thickness) with the prismatic structure on the internal or external surface of the tube, though many spirorbids have no these layers. Several species (*Helicosiphon platyspira* and *Protolaeospira stalagmia*) show a spherulitic prismatic microstructure at the tube surface, similar to the pattern described in [7]. Its homology to the prismatic layer, of which it is essentially a variant, is obvious because, in some places, spherulites transform into zones with prismatic structure.

In some species, elongated crystals stretch along separate parabolic growth lines inside the main wall layer, sometimes forming a connection between the internal and external prismatic layers, which indicates their common origin. The central part of the wall may contain alternating prismatic layers and zones with the irregular structure typical of the main layer (*Romanchella quadricostalis*). In other species (*Protolaeospira capensis* and *P. lebruni*), the prismatic penetrating layers are rare and apparently mark the periods when the tube growth stopped. In species with a transparent vit-

reous tube (*Protolaeospira augeneri*, *Crozetospira dufresnei*, and the genus *Paradexiospira*), the main layer with unordered crystals (see above) is completely reduced, and the wall is formed by merged, well-developed prismatic crystals arranged transversely to the growth lines (Fig. 1d). Sometimes, massive layers with prismatic structure in the central parts of the wall retain relicts of the main layer with randomly oriented crystals (*Protolaeospira striata*).

It appears that the majority of spirorbids have a loose structure of the inner part of the tube wall and more compact portions at its surfaces. The structure of the marginal zones is apparently strongly influenced by the organic phase of the skeleton functioning as cement. The sculpture of the external surface, often represented by longitudinal ridges and clearly discernible macroscopically, is formed via thickening of the main layer, whereas crystals in the prismatic layer covering the external surface of tubes elongate only slightly.

The spatial combinations and relationships of the two microstructural types apparently formed, as described above, by different secretion modes of the carbonate matter, as well as zoning of the main layer, determine the diversity of microstructures in tubes of spirorbids. The structural characteristics of each layer (the thickness, form of crystals, degree of their homogeneity within layers, and zoning) are specific for most studied species, which leads us to a preliminary conclusion that, in principle, these microstructures can be used for species identification based on tube structure. Further research is necessary to assess the ontogenetic and intraspecific variations of the microstructure.

Hence, it is possible to infer a distinct common pattern of spirorbid tube structure. The study of microstructure may be useful for deciphering the paleontological record of spirorbids and serpulids. Our study

further confirms the conclusion [2, 6, 7] that fossils structurally similar to tubes of spirorbids but distinctly different in the microstructure described from Paleozoic and Triassic deposits do not belong to Spirorbidae, because they fall beyond the variability range of microstructures of recent species.

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