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The ultrastructure of calcareous cirratulid (Polychaeta, Annelida) tubes

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Abstract. The entire tube wall of *Dodecaceria caulleryi* and *D. coralii* is composed of thin calcareous lamellae with a spherulitic prismatic ultrastructure. In *Diplochaetetes mexicanus* the tube ultrastructure is similar, but contains also some lamellae with a homogeneous structure. The biomineralization system of cirratulids has not evolved since the appearance of calcareous tubes in the Oligocene. The tube ultrastructure of cirratulids shows the strongest similarity to that of sabellids.

Key words: Cirratulidae, ultrastructure, biomineralization, Oligocene, Recent.

INTRODUCTION

Among annelids, calcareous tubes occur in the families of Serpulidae, Sabellidae, and Cirratulidae. The skeletons of serpulids are exclusively calcareous in contrast to a single recent calcareous sabellid species (*Glomerula piloseta* (Perkins, 1991)) and a few recent calcareous cirratulid species (e.g. *Dodecaceria coralii* (Leidi, 1855), *D. fistulicola* Ehlers, 1901, and *D. caulleryi* Dehorne, 1933) (Fischer et al. 2000; Vinn 2005). The earliest calcareous tubes in cirratulids (*Diplochaetetes mexicanus* Wilson, 1986) are known from the Oligocene of Mexico (Fischer et al. 2000). The tube structure and ultrastructure is relatively well known in serpulids (Sanfilippo 1996; Vinn 2007, 2008; Vinn et al. 2008a, 2008b, 2008c, 2008d) and sabellids (Vinn et al. 2008c), based on the scanning electronmicroscopy (SEM) studies of ample recent and fossil material. The tube microstructure of cirratulids, however, has been studied recently by mainly using the optical light microscopy (Wilson 1986; Fischer et al. 1989, 2000). According to Fischer et al. (2000), cirratulid tubes are composed of micritic peloidal lamellae. They form a stromatolitic fabric with intercalated lenses of fibrous calcite/aragonite (Fischer et al. 2000). In their study of cirratulid biomineralization Fischer et al. (2000) hypothesized that these worms precipitate their hard parts by a method, hitherto unknown in eumetazoan animals. They recognized two mechanisms: (1) outside the soft tissue within a Ca^{2+} binding mucus, excreted by an exotissue (basal layer), from which calcified lamellae are produced; (2) calcification of remains of biofilms and bacterial rods, which is not controlled by the animal itself. The last mechanism produces fibrous cement rims and peloidal aggregates (Fischer et al. 2000). The ultrastructure of such unusual biomineralization is not known and detailed SEM studies of cirratulid skeletal ultrastructures are necessary for proper comparison with the structures of serpulids and sabellids as well as of other invertebrates.

The aim of the paper is (1) to find structural support for the supposed unique biomineralization system of cirratulids, (2) to compare cirratulid skeletal structures with phylogenetically close sabellids and serpulids in order to find similarities, and (3) to find whether the skeletal ultrastructures of cirratulids have evolved since the Oligocene. The collection is housed at the Zoological Museum, University of Amsterdam (ZMA), and at the Museum of Natural History, University of Tartu (TUG).

MATERIAL AND METHODS

Three cirratulid species (*Diplochaetetes mexicanus*, *Dodecaceria coralii*, and *D. caulleryi*) and one sabellid species (*Glomerula piloseta*) were selected for the study of their skeletal ultrastructures (Table 1). Cirratulid tubes were cut using a small electrical saw. A piece of worm colonies of each species with the size of 10 mm × 10 mm was then oriented and mounted in Canada balsam for grinding. A tube fragment of *G. piloseta* was also cut in longitudinal section in Canada balsam. Sections of tubes were polished and treated with a 1 : 1 mixture of 25% glutaraldehyde and 1% acetic acid, to which alcian blue was added (Mutvei solution) before performing the SEM study (Schöne et al. 2005). All preparations were gold-sputtered prior to SEM investigation. The SEM studies were performed on a Hitachi S-4300 SEM, equipped with an Inca EDX system, at the Swedish Museum of Natural History, Stockholm.

Table 1. Age and locality information of the samples studied

Species	Collection number	Age, locality
Diplochaetetes mexicanus	ZMA.V.Pol. 3808	Oligocene, Baja California, Mexico
Dodecaceria coralii	ZMA.V.Pol. 3803	Recent, Mexico, Yucatan, Chicxulub Puerto
Dodecaceria caulleryi	TUG 1232-3	Recent, Atlantic coast of South Africa
Glomerula piloseta	ZMA.V.Pol. 3744	Recent, Australia, Queensland, Lizard Island; paratypes

RESULTS

Tube structure and ultrastructure are similar in Recent *Dodecaceria* and Oligocene *Diplochaetetes*. The entire tube wall of *Dodecaceria caulleryi* and *D. coralii* is composed of numerous thin calcareous lamellae (1.5–3.0 µm) with a spherulitic prismatic ultrastructure (Fig. 1A–E). In some parts of the tube wall the boundaries between the calcareous lamellae are more heavily calcified than the interior of the lamellae in *D. caulleryi* (Fig. 1C). The calcareous spherulitic prisms in *D. caulleryi* and *D. coralii* are not epitaxially continuous through several growth lamellae. In *Diplochaetetes mexicanus* the tube structure is also lamellar and mostly with a spherulitic prismatic ultrastructure (Fig. 1F, H). However, there are also lamellae with a homogeneous structure composed of unoriented calcareous rods in the tube wall of *Dip. mexicanus* (Fig. 1F, G). In *Dip. mexicanus* spherulitic prisms can be epitaxially continuous through several growth lamellae (Fig. 1F, H). Spherulites were occasionally found in the tube walls of all studied species. However, they do not form distinct layers but occur within the lamellae of a spherulitic prismatic structure (Fig. 1I). The lithic fragments were found trapped in the tube walls in *D. caulleryi*, as described and figured in Fischer et al. (2000) for cirratulids. Tabulae in *D. caulleryi* have a spherulitic prismatic ultrastructure similar to the ultrastructure of the tube wall (Fig. 1D). The lamellar tube walls of cirratulids with a spherulitic prismatic ultrastructure are not unique among polychaetes and invertebrates in general.

DISCUSSION AND CONCLUSIONS

It is difficult to estimate whether the biomineralization process of cirratulids is unique only on the basis of the studied SEM preparations. The spherulitic prismatic structure occurs also in other calcareous polychaetes (Vinn 2007; Vinn et al. 2008c, 2008d; e.g. sabellids and serpulids) and molluscs (Mutvei 1989). Spherulites form an external tube layer in *Glomerula piloseta* (Sabellidae). They occur in serpulids too, but similarly to cirratulids, they do not form distinct layers. However, the tube ultrastructure of cirratulids shows the strongest similarity to that of sabellids. The tube wall of cirratulids and *G. piloseta* is lamellar, with lamellae differing from chevron-shaped lamellae of serpulids. Spherulitic prisms are oriented perpendicular to the growth lamellae, separated by organic films both in sabellids (Fig. 1J) and cirratulids (Fig. 1A–F, H). Spherulitic prisms can be epitaxially continuous through several growth lamellae both in *Diplochaetetes mexicanus* and *G. piloseta*. The epitaxially continuous spherulitic prismatic sectors are directed towards the tubes lumen both in *Dip. mexicanus* (Fig. 1F, H) and *G. piloseta* (Fig. 1J), indicating a similar accretion direction of the shell material. Based on the above listed similarities in the tube ultrastructure of these polychaetes, I hypothesize that biomineralization systems of sabellids and cirratulids are similar. Thus, the secretion process in tube formation of sabellids (Vinn et al. 2008c) and probably also in cirratulids resembles the one seen in molluscs and many other invertebrate phyla, in which the skeleton is formed by extracellular mineralization, mediated and controlled by an organic matrix that is secreted together with calcium ions by a secretory epithelium (Addadi & Weiner 1992). However, the homogeneous structure composed of irregularly oriented calcareous rods in *Dip. mexicanus* does not have exact analogy in other calcareous polychaetes. Fischer et al. (2000) hypothesized that some cirratulid structures can be formed due to calcification of bacterial rods, not controlled by the worm itself. If this presumption is correct, then the homogeneous structure of *Dip. mexicanus* can be the one formed of calcified bacterial rods.

The biomineralization system of serpulids is most evolved among annelids (Vinn et al. 2008d). Their earliest representatives are known from the Middle Triassic. Recent serpulids possess the diverse fabrics of complex oriented tube ultrastructures which appeared presumably already in the Cretaceous or in the Early Cenozoic at the latest (Vinn 2008; Vinn & Furrer 2008). In contrast to serpulids, the biomineralization system of cirratulids has not evolved since the appearance of calcareous tubes in the Oligocene. In this respect cirratulids are also similar to sabellids, in which the tube structures have remained unchanged from the Early Jurassic when they first began to calcify (Vinn et al. 2008c).

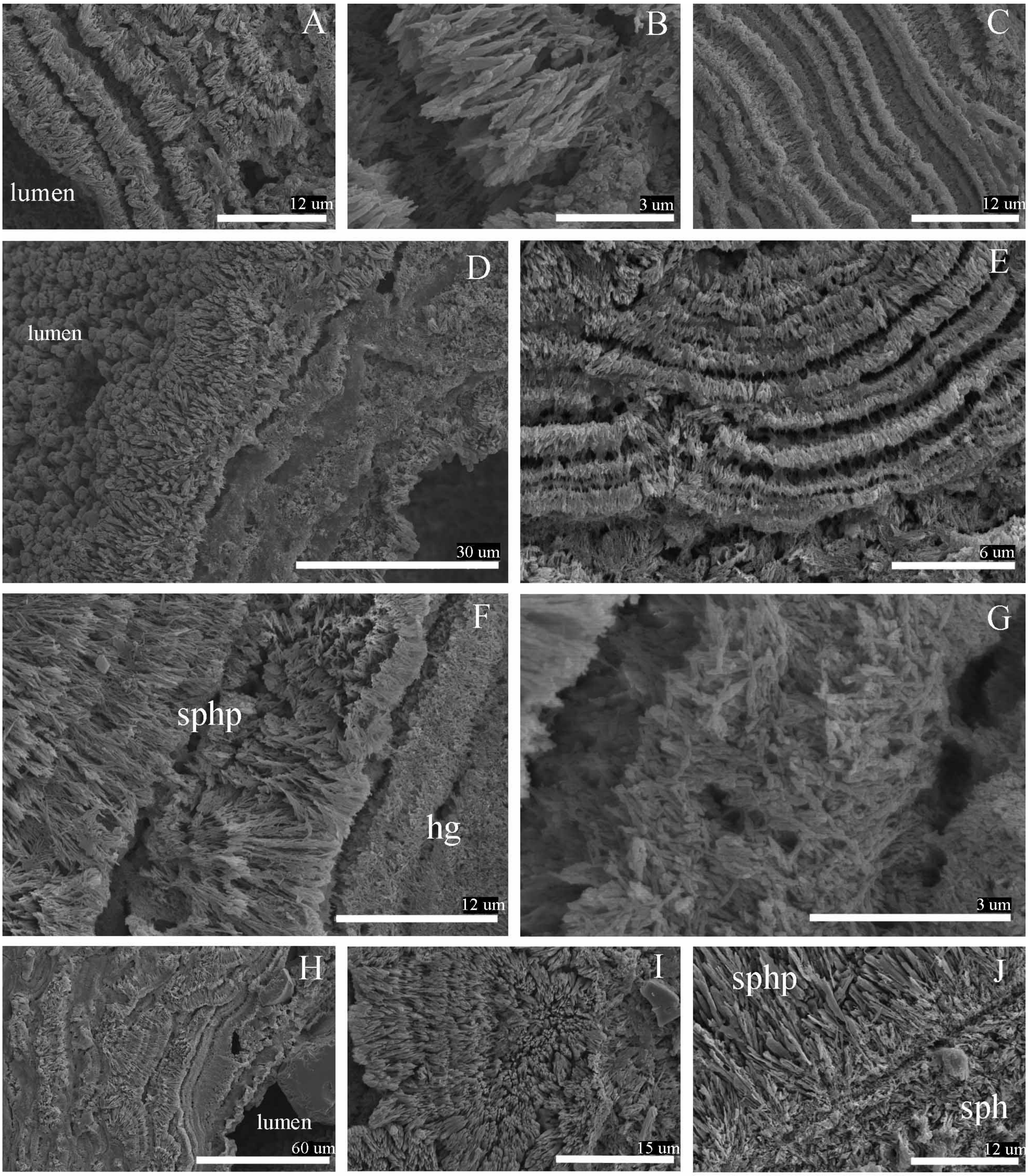

Fig. 1. A–D, *Dodecaceria caulleryi*, longitudinal section, Recent, Atlantic coast of South Africa, TUG 1232-3. A, growth lamellae with spherulitic prismatic structure. B, detail of spherulitic prismatic structure. C, growth lamellae with spherulitic prismatic structure; note the strongly calcified boundaries of lamellae. D, detail of a tabula composed of lamellae with spherulitic prismatic structure. **E**, *Dodecaceria coralii*, longitudinal section, Recent, Mexico, Yucatan, Chicxulub Puerto, ZMA.V.Pol. 3803. **F–I**, *Diplochaetetes mexicanus*, longitudinal section, Oligocene, Baja California, Mexico, ZMA.V.Pol. 3808. F, spherulitic prismatic structure (sphp) and homogeneous structure (hg) composed of irregularly oriented calcareous rods. G, detail of homogeneous structure. H, growth lamellae with spherulitic prismatic structure. I, a spherulite. **J**, *Glomerula piloseta*, longitudinal section of outer spherulitic (sphp) and inner spherulitic prismatic layer (sph), Recent, Australia, Queensland, Lizard Island, ZMA.V.Pol. 3744. All preparations were polished and treated with Mutvei solution for 5 min.

In conclusion, I found that (1) cirratulid ultrastructure is not unique among calcareous polychaetes and invertebrates in general, (2) cirratulid skeletal ultrastructures show the strongest similarity to that of sabellids, and (3) skeletal ultrastructures of cirratulids have not evolved since the appearance of calcareous tubes in the Oligocene.

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Tsirratuliidide (Polychaeta, Annelida) skeleti peenstruktuurid

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Tsirratuliidide lubikojad koosnevad sfäruliitse prismalise struktuuriga lamellidest ja nende koja struktuur on kõige lähedasem sabelliididele. Tsirratuliidide lubikojad tekkisid Oligotseenis ja nende struktuur ei ole sellest ajast alates evolutsioneerunud.