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GENERAL BIOLOGY

Musculo-Epithelial Cells in the Intestine of the Representative of Hemichordates *Saccoglossus mereschkowskii* (Hemichordata, Enteropneusta)

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Hemichordates (the phylum Hemichordata) are a small taxon of marine invertebrates considered to be phylogenetically close to the ancestors of chordates. Enteropneusta is a class of Hemichordata whose representatives are burrowing animals living in sea bottom sediments. The microscopic anatomy of Enteropneusta has been described in several classic works [3, 5]. However, this class has not been studied in sufficient detail with the use of up-to-date methods. The ultrastructural studies that have been performed to date [2, 4, 6] have not encompassed all systems of organs.

We studied the intestinal epithelium of the pharyngeal region of *Saccoglossus mereschkowskii* Wagner, 1885, a representative of Enteropneusta. The material was collected near the White Sea Biological Station of Moscow State University located on Kandalaksha Bay of the White Sea (Primorskii village, Loukhskii raion, Karelian Republic, Russia). The animals were found on silty grounds at a depth of 5–10 m. Fragments of the animals were fixed in a 2.5% glutaraldehyde solution in 0.1 M sucrose buffered with 0.1 M sodium cacodylate (pH 7.35). Postfixation was performed in 1% osmium tetroxide buffered with 0.1 M sucrose buffered with sodium cacodylate (pH 7.36). Ultrathin sections were contrasted with uranyl acetate and lead citrate. The sections were examined under a JEOM-1011 transmission electron microscope.

The intestinal epithelium of the *S. mereschkowskii* pharynx consisted of columnar cells about 30 μm in height. Microscopic examination of the apical regions of cells showed the following characteristics of their ultrastructure. Intestinal epithelium cells were ciliate, each cell bearing about 80 cilia. The basal bodies of cilia were located in the surface layer of the cytoplasm; two striated radices began from each basal body: a long radix oriented in the apical–basal direction and a short (lateral) one, which was parallel to the apical surface of the cell (Fig. 1). The apical surface of the cells bore microvilli about 1 μm in height and 0.1–0.12 μm in

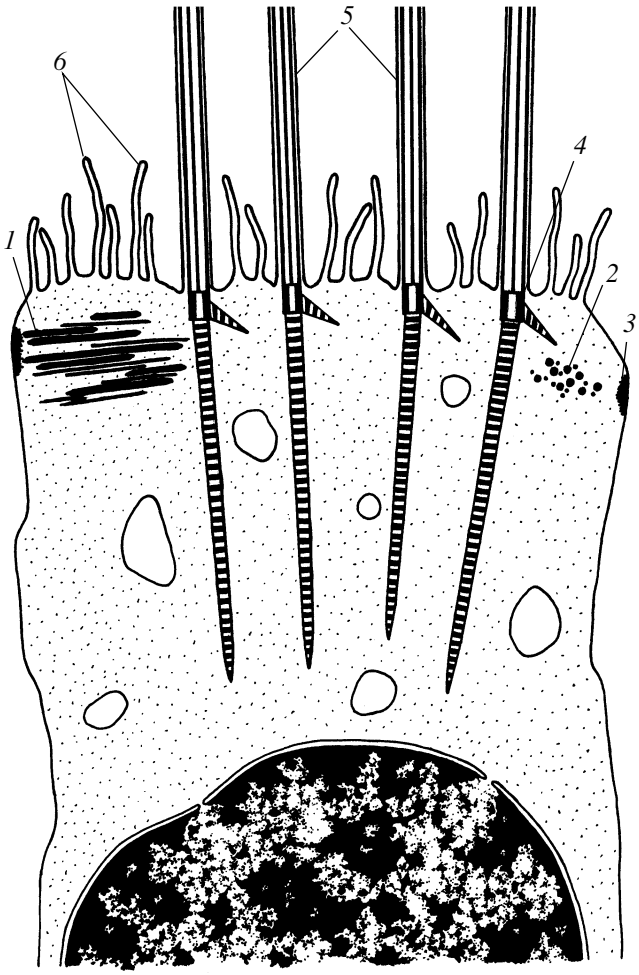

Fig. 1. A schematic diagram of the apical region of an intestinal epithelial cell of the *S. mereschkowskii* pharynx. Here and in Figs. 2–4: *1*, muscle filaments cut longitudinally; *2*, the same, cut transversally; *3*, circular adherence contacts; *4*, the basal body of a cilium; *5*, cilia; *6*, microvilli.

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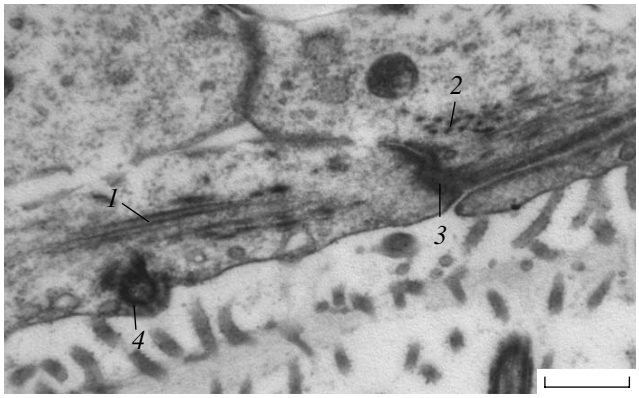

Fig. 2. A longitudinal section of the apical region of the intestinal epithelium of the *S. mereschkowskii* pharynx. Scale bar, 0.5 μm.

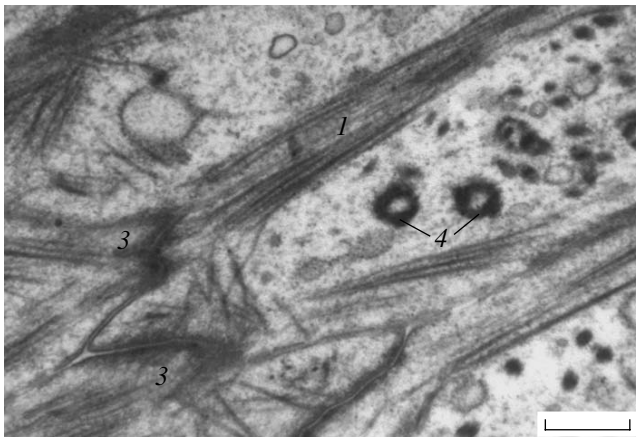

Fig. 3. A tangential section of the apical region of the intestinal epithelium of the *S. mereschkowskii* pharynx. Scale bar, 0.5 μm.

diameter. The cells were connected with one another via circular adherence junctions, which looked like aggregations of dark material adjacent to the inner surface of the membrane in the apical regions of the cells (Fig. 2).

In apical regions of the cytoplasm of intestinal epithelial cells, we observed bundles of filaments similar to muscle filaments with respect to their organization (Figs. 2, 3). Thick and thin filaments were discernible in the bundles. The thick (presumably myosin) and thin (presumably actin) filaments were about 25 and 7–8 nm in diameter, respectively. The muscle bundles were parallel to the apical surface of the cells and located along the cell perimeter (Fig. 4). In some sections, the bundles were clearly seen to begin in dense material associated with the circular adherence junctions (Fig. 3).

Contractile filaments were earlier found in vacuolated stomochord cells of another species of Enteropneusta, *S. kowalevskii* [2]. Muscle filaments in stomochord cells are oriented in the apical–basal direction, as well is in the circular direction in the basal regions of the cell. The stomochord is a preoral diverticulum of the intestine of Enteropneusta; stomochord cells belong to a specialized type of entodermal cells. We found muscle filaments in a typical intestinal epithelium of the pharyngeal region of Enteropneusta.

Another example of Bilateria whose intestinal epithelial cells contain muscle filaments is the relict group Phoronida [1]. In these animals, muscle filaments are located in the basal regions of intestinal cells and are circularly oriented (perpendicular to the axis of the intestinal tube). These filaments are functional substitute of the circular muscles of the intestinal tube in Phoronida, because musculo-epithelial cells of the celomic lining of the intestinal surface are oriented longitudinally [1].

The muscle filaments of the Enteropneusta intestine are located in apical portions of cells, forming a subsurface contractile layer along the cell perimeter (Fig. 4). When they contract, the apical surface of the cells shrinks. In this case, the inner surface of the intestinal tube must form folds and creases. It is conceivable that the formation of these folds affects the direction of water flows within the intestinal tube. This may play a role in the suspension type of feeding characteristic of

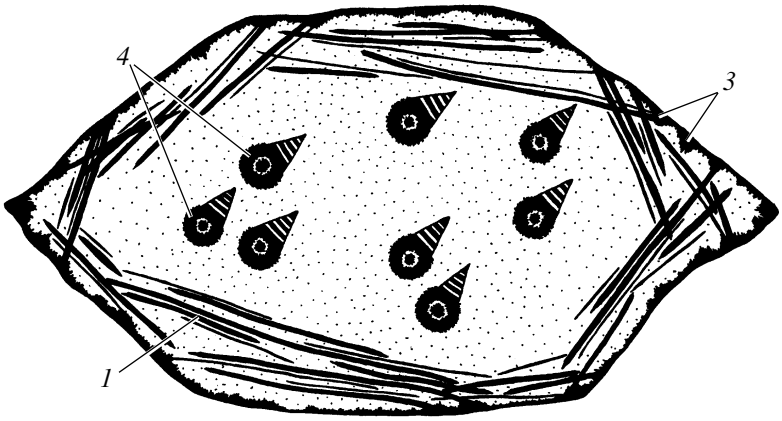

Fig. 4. A schematic diagram of the tangential section of the apical region of an intestinal epithelial cell of the *S. mereschkowskii* pharynx (basal bodies of cilia are fewer than in reality).

Enteropneusta and the control of water flow through the gill slits.

The finding of muscle elements in the intestine of hemichordates has important phylogenetic implications. Musculo-epithelial cells are known to be characteristic of the intestinal epithelium of stinging Cnidaria. The intestinal epithelium of most Bilateria lacks muscle elements. They are usually left in cells of the celomic lining that forms the muscle layer of the intestinal tube wall. Muscle elements in the intestinal epithelium of bilaterally symmetric are an extremely rare phenomenon. The muscle filaments that have been preserved in the entodermal epithelium of Phoronida and Hemichordata may be regarded as evidence for the basic positions of these phyla in the phylogenetic tree of Bilateria.

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