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GENERAL BIOLOGY

Metameric Origin of Lateral Mesenteries in Brachiopoda

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Brachiopoda are a group of marine invertebrates with an unclear taxonomic position. In most modern textbooks, Brachiopoda are considered to be close to Phoronida and Bryozoa, the three groups being combined into the superphylum Lophophorata. The position of Lophophorata in general and Brachiopoda in particular in the total system of the animal kingdom is actively discussed. Lophophorata were traditionally regarded as a group intermediate between Protostomia and Deuterostomia [1–3]. Recent evidence indicates that Lophophorata should be combined with trochophore animals into the taxon Lophotrochozoa [4, 5]. As early as in the 19th century, Kovalevskii [6] noted that Brachiopoda were taxonomically close to Annelida, typically trochophore animals. Metamerism of the larva of the primitive brachiopod *Novocrania anomala* was found recently [7]. According to these data, the larva of *N. anomala* has an anterior lobe, three pairs of the bundles of setae, and four pairs of coelomic sacs. One pair may be considered to belong to the anterior lobe, and three more pairs are located in the trunk and correspond to the three pairs of the bundles of setae. More recent studies confirmed the existence of metameric bundles of setae but disproved complex segmentation of the larval coelom [8]. The organization of adult brachiopods lacks any distinct signs of metamerism.

The purpose of this study was to reconstruct the coelomic cavities of *Hemithyris psittacea,* a representative of articulated brachiopods. The material was collected in August 2002 and July 2004 in Kandalaksha Bay of the White Sea, near the White Sea Biological Station of Moscow State University, at a depth of 9 m. To study the microscopic anatomy, the material was fixed with Boin's liquid, embedded in paraplast, and divided into 8-μm slices by the standard method. Series of slices were used to reconstruct the coelomic cavities and the location of mesenteries. In addition, the material was anatomized manually, for which the animals were fixed with 4% formaldehyde dissolved in seawater.

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The coelomic system of *H. psittacea* consists of the large perivisceral coelom projecting into mantles, lophophore cavities, and periesophageal coelom. For the purpose of our study, the organization of the perivisceral coelom is of special importance. We will consider it here in more detail. The perivisceral coelom contains the main organs of the animal and is crossed with dorsoventral and lateral mesenteries. The dorsoventral mesentery of brachiopods, as well as that of other coelomic animals, is located in the sagittal plane and attaches the digestive tract to the body wall. In the species studied (as in most brachiopods), it is incomplete, i.e., it consists of separate bands, the coeloms of the right and left sides of the body communicating with each other through the gaps between the bands.

Lateral mesenteries are specific for brachiopods. Most brachiopods have two lateral mesenteries, the gastroparietal and ileoparietal ones (Fig. 1). The gastroparietal mesentery runs along the dorsal side of the stomach and continues along both sides of the digestive tract, attaching it to the sides of the body. The ileoparietal mesentery runs along the dorsal side of the intestine (in the region where the stomach transits into the hindgut) and continues on both sides of the digestive tract, attaching to the lateral walls of the body. The gastroparietal and ileoparietal mesenteries are linked with each other by lateral membranes running along the stomach symmetrically on the right and on the left.

The gastroparietal mesentery is attached to the stomach at the lower edge and to the lateral and dorsal walls of the body on the right and on the left. The ileoparietal mesentery is bound to the anterior portion of the hindgut, it runs at a sharp angle to the intestine.

The species studied has two pairs of metanephridia, the dorsal and ventral ones. The fornices of the dorsal pair are located on the gastroparietal mesentery where it touches the lateral walls of the body. The fornices of the ventral pair are located on the ileoparietal mesentery also in the regions where it is in contact with the body wall. The reconstruction of the positions of lateral mesenteries based on the series of slices has led to the conclusion that they are located at a sharp angle to each other. The plane of the gastroparietal mesentery is perpendicular to the stomach surface and almost parallel to the dorsal valve. The ileoparietal mesentery is located

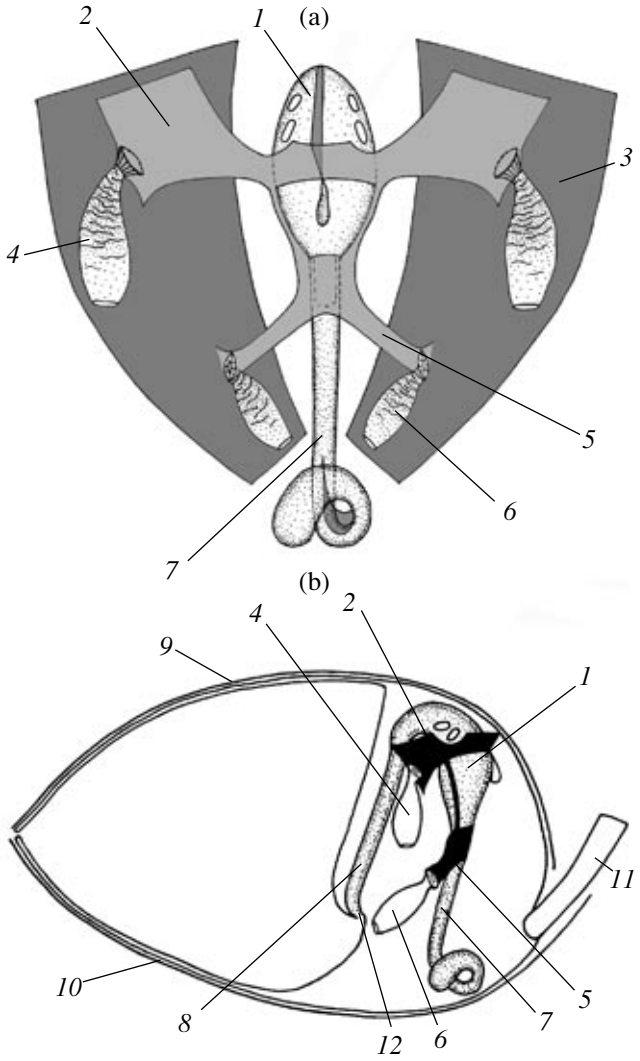

Fig. 1. Lateral mesenteries of *H. psittacea.* The arrangement of lateral mesenteries, (a) dorsal view and (b) side view: *1*, stomach; *2*, gastroparietal mesentery; *3*, lateral wall of the body; *4*, dorsal metanephridium; *5*, ileoparietal mesentery; *6*, ventral metanephridium; *7*, hindgut; *8*, esophagus; *9*, dorsal (brachial) valve; *10*, ventral (pedicle) valve; *11*, pedicle; *12*, mouth.

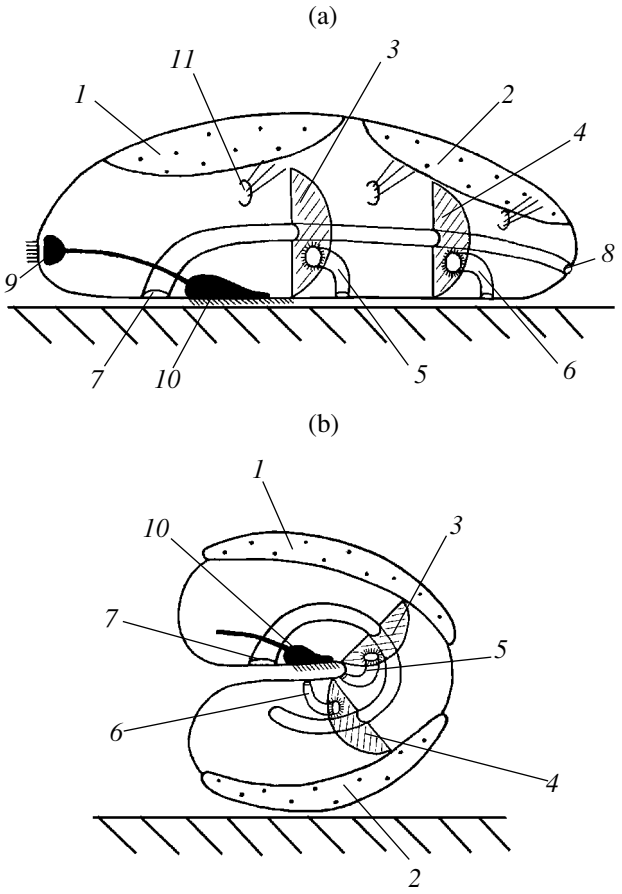

Fig. 2. The origin of the structural pattern of brachiopods (the lophophore is not shown): (a) the structural pattern of the ancestor of brachiopods; (b) the same after folding. *1*, anterior (brachial) valve; *2*, posterior (pedicle) valve; *3,* anterior dissepiment (gastroparietal mesentery); *4*, posterior dissepiment (ileoparietal mesentery); *5*, anterior (dorsal) metanephridium; *6*, posterior (ventral) metanephridium; *7*, mouth; *8*, anus; *9*, apical ganglion; *10*, ventral (subpharyngeal ganglion); *11*, bundle of setae.

at a sharp angle to the hindgut, the mesentery plane crossing both valves (Fig. 1b).

These results are very interesting in terms of the new views on the general structural pattern of brachiopods. The larva of *N. anomala* has proved to fold to the abdominal side during metamorphosis. The anterior part of the dorsal side of the larva gives rise to the so-called dorsal (brachial) valve; and the posterior part of the dorsal side, to the ventral (pedicle) valve. These processes are believed to reflect the phylogeny of the structural pattern of brachiopods [7, 8–11]. If the assumption on body folding is true for articulated brachiopods, this explains the existence of two lateral mesenteries. They correspond to two sequential dissepiments that divided the body of brachiopods' ancestors into three segments (Fig. 2). When the body folded, the anterior dissepiment turned into the gastroparietal coelom, and the posterior one, into the ileoparietal coelom. The segmentary nature of lateral mesenteries is emphasized by the fact that, at least in representatives of the order Rhynchonellida, a pair of metanephridia is connected with each of them. Some representatives of the order Lingulida (*Discinisca*) have two pairs of gonads, each of which is connected with the corresponding lateral mesentery [1]. All this indicates that brachiopods retain the segmentary organization in the adult state; however, metamerism is hidden by the curvature of the primary front–back axis. In fact, Gutmann et al. [12] were the first to put forward the idea of the metameric structure of the body in brachiopods. However, nothing was known in that time about the folding of the larva to the abdominal side; therefore, Gutmann et al. presumed that the front–back axis of the annelid

ancestor of brachiopods has transited into the apical–basal axis of brachiopods without curvature.

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