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The Nephridial Hypothesis of the Gill Slit Origin

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ABSTRACT

Metameric gill slits are mysterious structures, unique for Chordata and Hemichordata, and also, perhaps, for the extinct Cambrian Calcichordata. There is a discussed hypothesis of the gill slits origin from the metameric nephridia. According to the hypothesis, the hypothetical metameric deuterostome ancestor had in each segment a pair of coelomoducts and a pair of intestinal pockets. In the anterior segments, the coelomoducts have fused with the intestinal pockets. As a result, each nephridium opened both into the gut and into the environment. Then the dissepiments and funnels reduced in all segments except the collar one. Thus, in recent enteropneusts, only the first pair of gill slits keeps the ancestral arrangement communicating at the same time with the gut, with the environment, and with the coelom of the preceding (collar) segment. In the anterior part of the branchio-genital trunk region of enteropneusts, the metameric intestinal pockets remained, as well as the metameric coelomoducts functioning as the ducts of the metameric gonads, i.e., as the gonoducts. The consequence of the hypothesis is that the metameric gill pores originate from the metameric excreting pores, and the metameric branchial sacs originate from the metameric endodermal pockets of the gut fused with the coelomoducts. The metameric gill slits by themselves correspond with metameric openings connecting the gut with metameric intestinal pockets. *J. Exp. Zool. (Mol. Dev. Evol.) 324B:647–652, 2015.* © 2015 Wiley Periodicals, Inc.

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The metameric gill slits are mysterious structures unique for representatives of two animal phyla—Chordata and Hemichordata, which belong to deuterostomes. Deuterostomia also include the phylum Echinodermata, which is considered as a sister group of Hemichordata in the clade Ambulacralia (Echinodermata + Hemichordata) (Bromham and Degnan, ’99; Lowe et al., 2015). Although all recent echinoderms lack gill slits, according to Jefferies’ theory (Jefferies, ’68, ’81; Gee, ’96), the Cambrian Calcichordata had one row of the metameric gill slits located on the upper side of the animal which were homologous to the left-sided gill slits of Hemichordata and Chordata (Fig. 1). It is important that in Enteropneusta and lower Chordata, the gill slits open to the exterior not directly, but through the branchial sacs or the common peribranchial cavity connecting with the environment by pores. The shape of these pores differs from the shape of gill slits (see Fig. 1).

The connection of the gut with the exterior similar to the gill slits is almost never found outside deuterostome animals. In Macrodasyidae (Gastrotricha), there is a pair of pharyngeal pores (Remane, ’27), but these pores are not metameric and the macrodasyid pharyngeal pores lead to the exterior from the ectodermal pharynx, not from the endodermal gut. Also, they have no respiratory function. The deuterostome gill slits are certainly metameric and play a respiratory role. Based on classical and modern data, it is firmly established that the gill slits connect the exterior with an endodermal pharynx, not

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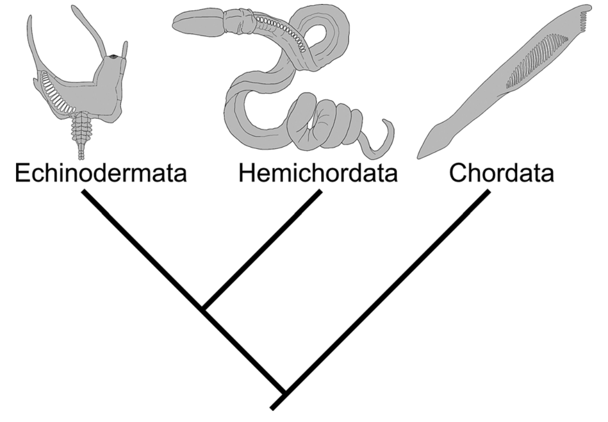

Figure 1. Metameric gill pores of the representatives of extinct Echinodermata (after Jefferies, '81), Chordata (after Ruppert, 2004), and Hemichordata. The modern phylogenetic tree is taken from Cameron (2005).

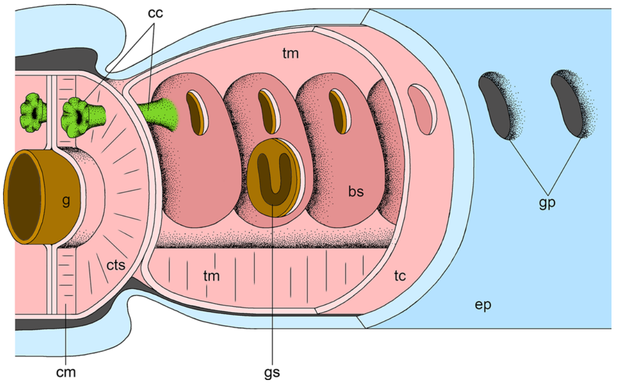

Figure 2. Reconstructed model of the typical enteropneust branchial apparatus (based upon Benito and Pardos, 1997, highly modified). bs, branchial sac; cc, collar coelomoduct; cm, collar mesenterium; cts, collar-trunk septum; ep, epidermis; g, gut; gp, gill pores; gs, gill slit; tc, coelothelium of the trunk coelom; tm, trunk mesenterium.

ectodermal (Hyman, '59; Ivanova-Kazas, '78; Benito and Pardos, 1997; Kaul-Strehlow and Stach, 2013).

Thus, the gill slits possibly represent a synapomorphy of Deuterostomia, lost in extant echinoderms. This synapomorphy requires explanation. It is difficult to imagine from the evolutionary viewpoint how the symmetrical lateral rows of the numerous metameric paired openings leading from the gut to the exterior could form in the trunk of the general ancestor of Deuterostomia.

BRANCHIAL APPARATUS OF MODERN ENTEROPNEUSTA

In Enteropneusta, the dorsal body-side in the branchial region of the trunk just behind the collar is pierced by two, right and left, rows of openings—gill pores. The dorsal wall of the gut in this region is in turn pierced by two rows of U-shaped gill slits, which communicate with the environment through the gill pores (Fig. 2). Typically each gill slit has its own gill pore, and between the ”gill slit in the pharyngeal wall and the gill pore in the epidermis there is a branchial sac, individual for each gill slit (Hyman, '59). However, in some enteropneust species, there is a fusing of the first branchial sacs (Fig. 3). In *Glossobalanus hedleyi* (Ptychoderidae) (see Hill, 1897), the first and the second gill slits lead to a common branchial sac. In *Willeyia bisulcata* (Spengelidae), three anterior branchial sacs are joined together and open to the exterior by a common pore between the collar and the trunk (Punnett, '03). In *Balanoglossus misakiensis* and *Glossobalanus ruficollis* (Ptychoderidae), the first four sacs on each side unite and open into the environment by a single common pore (Kuwano, '02; Horst, '39; Dawydoff, '48). Bateson in his classic work (Bateson, 1886, Plate XXXIII, 14) depicted the horizontal section of a young *“Balanoglossus kowalevskii*“ (=*Saccoglossus kowalevskii*), where the collar coelomoduct opened into the branchial sac. According to the cited figure, the first and second gill slits also opened into this branchial sac. Another variant is described for *Stereobalanus canadensis* (Harrimaniidae): all branchial sacs on each side are fused and open by a single deep longitudinal slit (Reinhard, '42) (Fig. 3).

In the embryogenesis, the rudiments of the gill slits develop as paired evaginations of the endodermal wall of the gut. The endoderm of these evaginations grows to the ectoderm, contacts with the epidermis, and opens into the exterior, forming circular-shaped gill pores (Ivanova-Kazas, '78; Kaul-Strehlow and Stach, 2013).

Even though the organization of the anterior branchial sacs in some enteropneust species can vary, in all acorn worms the first pair of gill slits has a peculiar arrangement. The coelomoduct of the collar coelom opens into the first gill slit of each body-side[1] (Fig. 4). In other words, the paired collar coelomoducts do not communicate directly with the environment, but penetrate the septum between the collar and the trunk and lead from the collar coelom to the branchial sacs of the first pair of gill slits (Figs. 2, and 4B and C). Thus, each gill slit of the first pair has a double function: it functions as a respiratory organ as the other gill slits, and also it is a nephridium. Such fusion of the coelomoducts and the first gill slits in enteropneusts gives us reason to discuss the hypothesis of the metameric gill slit origin from the metameric excretory nephridia located in each segment.

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[1] Collar coelomoducts seem to be lacking in the genus *Stereobalanus* (Hyman, '59).

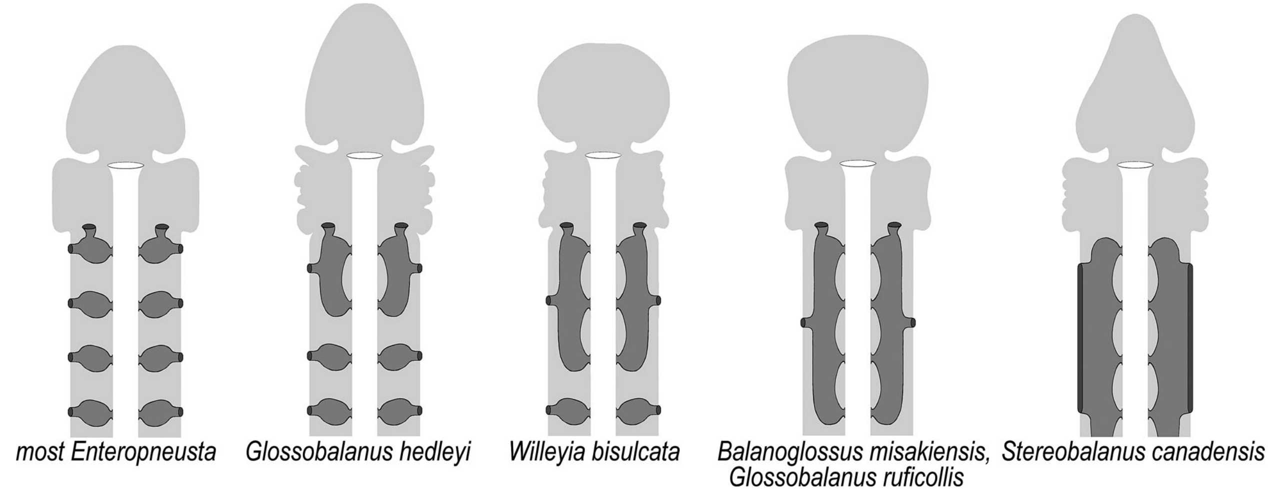

Figure 3. Different variants of the communication between the first branchial sacs and the environment in different Enteropneusta.

THE NEPHRIDIAL HYPOTHESIS OF THE GILL SLIT ORIGIN

An important initial issue of the hypothesis is the recognition of the metamerism of the hypothetical deuterostome ancestor. In each segment, there was a pair of the intestinal pockets. In modern Enteropneusta, there are metameric hepatic sacculations in the hepatic region of the gut following the branchial region (Horst, '37). Each segment contained a pair of coelomoducts, whose funnels opened into the coelomic cavity of the preceding anterior segment. The ducts, penetrating the dissepiment, ran backward and opened latero-dorsally into the exterior (Fig. 5A). This case exactly is observed in recent enteropneusts in the arrangement of the collar coelomoducts, whose funnels open into the collar coelom, and the coelomoducts pierce the dissepiment between the collar and the trunk regions, run backward and open into the first pair of branchial sacs (Figs. 2 and 4).

According to the hypothesis, in anterior segments, the coelomoducts have fused with the intestinal pockets (Fig. 5B). As a result of such fusing, each metameric nephridium had an opening into the gut and a pore into the environment. The products of metabolism could be excreted into the exterior (when the animal poked out of the ground) or into the gut (when the animal buried in the sediment). The next step is the reduction of dissepiments and nephridial funnels in all segments except the collar one (Fig. 5C). Thus, in recent enteropneusts, only the first pair of gill slits keeps the ancestral arrangement and communicates at the same time with the gut, with the environment, and with the coelom of the preceding (collar) segment. The assumed fusing of the coelomoducts with the intestinal pockets took place only in the anterior segments, the number of which corresponds with the number of gill slits. In the posterior segments, the metameric intestinal pockets have remained, as well as the metameric coelomoducts which function as ducts of the metameric gonads, i.e., as the gonoducts (Spengel, 1893; Horst, '39).

The discussed hypothesis is not completely new. In the 19th century, similar ideas were formulated by Anton Dohrn (1875), who attempted to derive the vertebrates from the annelids. Dohrn wrote: "Stellen wir uns nun vor, dass an verschiedenen Punkten die inneren Mündungen der Segmental-Organe mit der Darmwand verschmelzen . . . – so ist die postulirte Verbindung des Darms mit dem äusseren Medium, unabhängig von Mund- und Afteröffnung, geschehen" (Dohrn, 1875, S.10) and later: "Durch die schon oben angenommene Communication der Segmental-Organe mit dem Darme, – die vielleicht durch Divertikelbildung des Darms veranlasst. . ." (Dohrn, 1875, S.16–17)[2]. Unfortunately, the Dohrn's ideas were not illustrated and therefore they were almost forgotten.

From the proposed hypothesis, it follows that the metameric gill pores originate from the metameric excreting pores, and the metameric branchial sacs originate from the metameric endodermal pockets of the gut fused with coelomoducts. The metameric gill slits by themselves correspond with metameric openings connecting the gut with metameric intestinal pockets. It is interesting that the original excreting function of the

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[2] "Let us now imagine that at various points the inner orifices of the segmental organs fuse with the walls of the gut . . . – then the postulated connection has occurred between the gut and the external medium, independently of the mouth and anus"; "Via the above-hypothesized communication of the segmental organs with the gut – which perhaps was brought about by formation of gut diverticula. . ." (Ghiselin, '94).

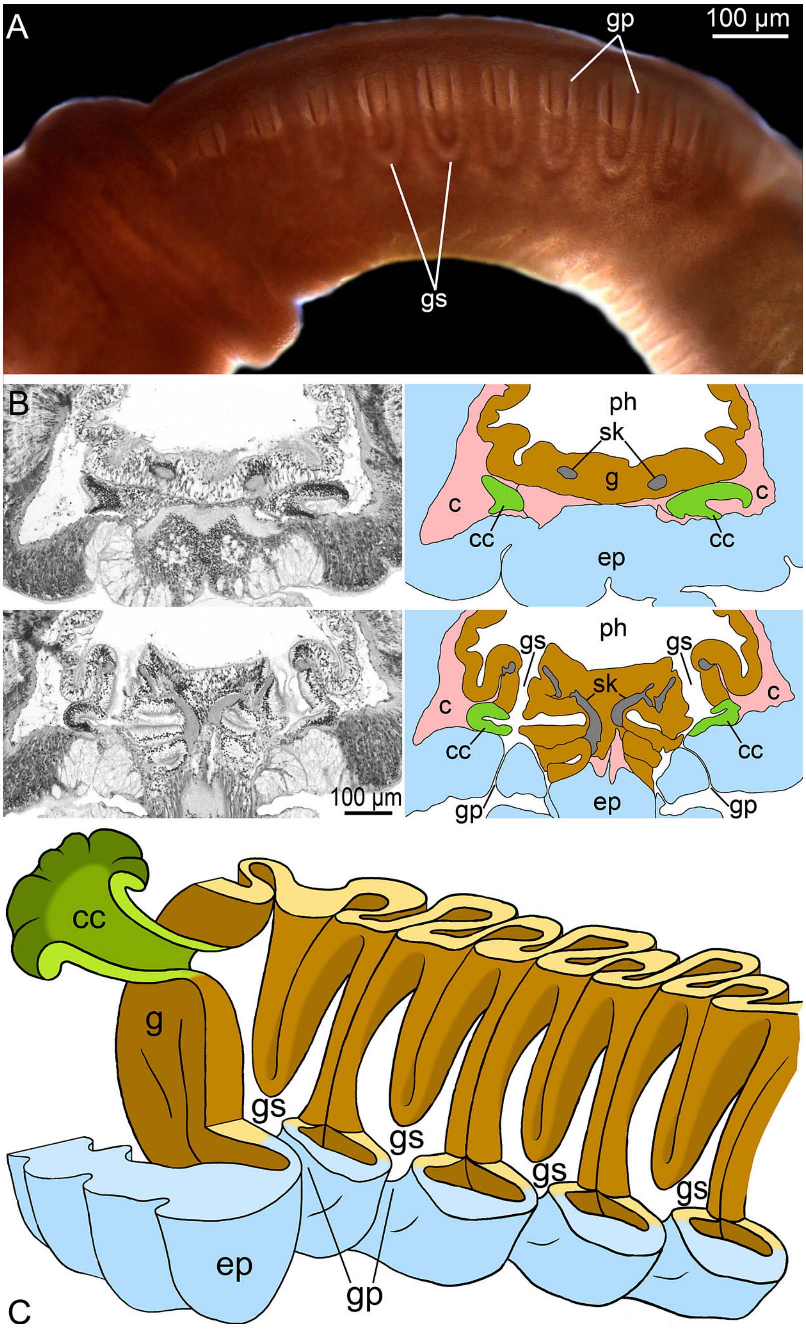

Figure 4. The branchial apparatus of the acorn worm *Saccoglossus mereschkowskii.* A: Outward appearance of the gill pores and gill slits. B: The communication of the collar coelomoducts with the first gill slits. Frontal sections, more dorsal (above) and more ventral (below), and the schemes of these sections (right). C: Reconstructed model of the branchial apparatus. c, collar coelom; cc, collar coelomoduct; ep, epidermis; g, gut; gp, gill pores; gs, gill slit; ph, pharynx; sk, gill skeleton.

hypothesized complex “coelomoduct + intestinal pocket” partly remains in the modern branchial sacs. It is known that the branchial sacs from the coelom-side are lined by specialized podocytes and perform excretory function (Pardos and Benito, 1988). Furthermore, the idea that the collar coelomoducts might function as the excretory sites was introduced (Lester et al, ’85).

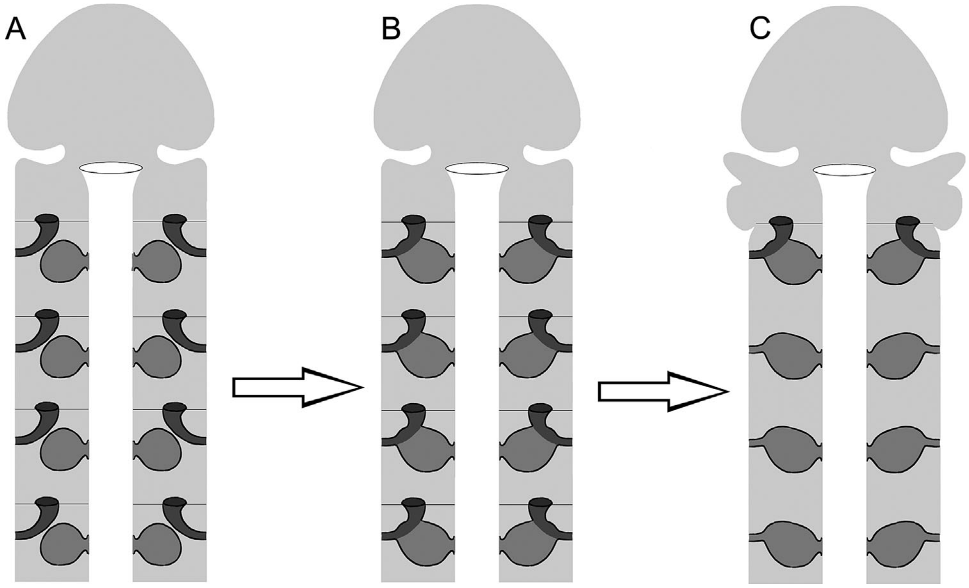

Figure 5. Possible evolutionary transformations leading from ancestor with metameric coelomoducts and intestinal pockets to modern condition in branchial apparatus. A: Ancestral organism with separated metameric segments; each segment contains a pair of the nephridial funnels and ducts to the exterior, and a pair of the independent intestinal pockets. B: Intermediate variant after fusing of coelomoducts and intestinal pockets in each segment still separated by dissepiments. C: Modern condition in recent Enteropneusta, where the collar coelomoduct runs through the septum into the first gill slit, and in other segments the coelomoduct funnels and dissepiments have disappeared.

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