

Coelom Metamerism in Echinodermata

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Abstract—Within all major taxa of Bilateria, there are forms with coelomic metamerism. This suggests that coelomic metamerism was characteristic of the common ancestor of Bilateria. Among deuterostomes, metamerism is clearly expressed in chordates, and elements of metamerism are present in hemichordates. Do echinoderms have remnants of coelomic metamerism that was inherited from the common ancestor of Bilateria? The coelomic system of echinoderms includes several metameric coelomic rings located along the oral-aboral axis, namely: the axocoelomic ring, the hydrocoelomic ring, 2 to 6 coelomic rings originating from the left somatocoel, and one epigastric ring originating from the right somatocoel. Thus, in echinoderms, there is a dissymmetrical metamerism, derived from the original metamerism of the common ancestors of Deuterostomia and, possibly, the common ancestors of Bilateria. The problem of dextiothetism as the cause for the formation of coelomic dissymmetry in echinoderms is discussed.

Keywords: metamerism, dissymmetry, coelomic system, phylogeny, evolution, Echinodermata, Deuterostomia

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INTRODUCTION

In the last two decades, revolutionary transformations have occurred in our understanding of the animal kingdom system. New phylogenetics distinguishes four groups of animals within Bilateria: Trochozoa, Lophophorata, Ecdysozoa, and Deuterostomia (see Halanych et al., 1995; Aguinaldo et al., 1997; De Rosa et al., 1999; Adoutte et al., 2000; Peterson and Eernisse, 2001; Halanych, 2004; Philippe et al., 2005; Bagnà et al., 2008; Dunn et al., 2008, 2014; Malakhov, 2009, 2010, 2013; Smith et al., 2011; Nosenko et al., 2013; Giribet, 2015; Telford et al., 2015; Wanninger, 2016). Each of the four listed large taxa includes metameric forms (i.e., forms in which metamers, or segments with similar structure, are sequentially located along the anteroposterior body axis). Each segment initially has an independent paired coelom; coeloms of adjacent segments are separated by dissepiments. Metamerism appears in the structure of the excretory and circulatory systems, muscles, and nervous system, as well as in the presence of metameric limbs. Since it is unlikely that metamerism occurred independently in three or four phylogenetic branches of bilaterians, it can be assumed that coelomic metamerism was characteristic of the common ancestor of Bilateria (Fig. 1). In a number of classical hypotheses on the origin of Bilateria, it was assumed that the coelomic sacs of the Bilateria ancestors were formed as a result of separation of the gastric pockets of the coelenterate ancestor and, therefore, metamerism (which arose on the basis of cyclomerism of the

coelenteron pockets) is an original feature of bilaterians (Sedgwick, 1884; Van Beneden, 1891; Lameere, 1916; Snodgrass, 1938). The question of the primacy of metamerism in Bilateria is actively discussed today (see De Robertis, 1997, 2008; Davis and Patel, 1999; Balavoine and Adoutte, 2003; Peel and Akam, 2003; Malakhov, 2004, 2009, 2010; Tautz, 2004; Blair, 2008; Couso, 2009; Balavoine, 2014; Minelli, 2017; Arendt, 2018; He et al., 2018).

Among deuterostomes, coelomic metamerism is clearly expressed in chordates. The metameric structure of vertebrates was already evident to naturalists of the late 18th–early 19th centuries. German poet and natural philosopher Johann Wolfgang Goethe came to this idea as early as 1790, although it was only published in 1817 (Goethe, 1817, 1957; Muller, 2015), and the anatomist Lorenz Oken expressed it in his scientific research program after he became a professor in 1807 (Oken, 1807). Modern researchers actively discuss the metamerism of chordates both from the morphological standpoint and from the standpoint of molecular developmental biology (Mazet and Shimeld, 2002; Olsson et al., 2005; Beaster-Jones et al., 2006; Holland et al., 2008; Onai et al., 2015, 2017; Onai, 2018; Yastrebov, 2018). Metamerism of representatives of the phylum Hemichordata appears in the presence of metameric gill pores and gill slits, metameric gonads, as well as metameric hepatic sacculations (Van der Horst, 1939; Hyman, 1959; Benito and Pardos, 1997). Echinoderms have elements of metamerism in the structure of the stem of crinoids,

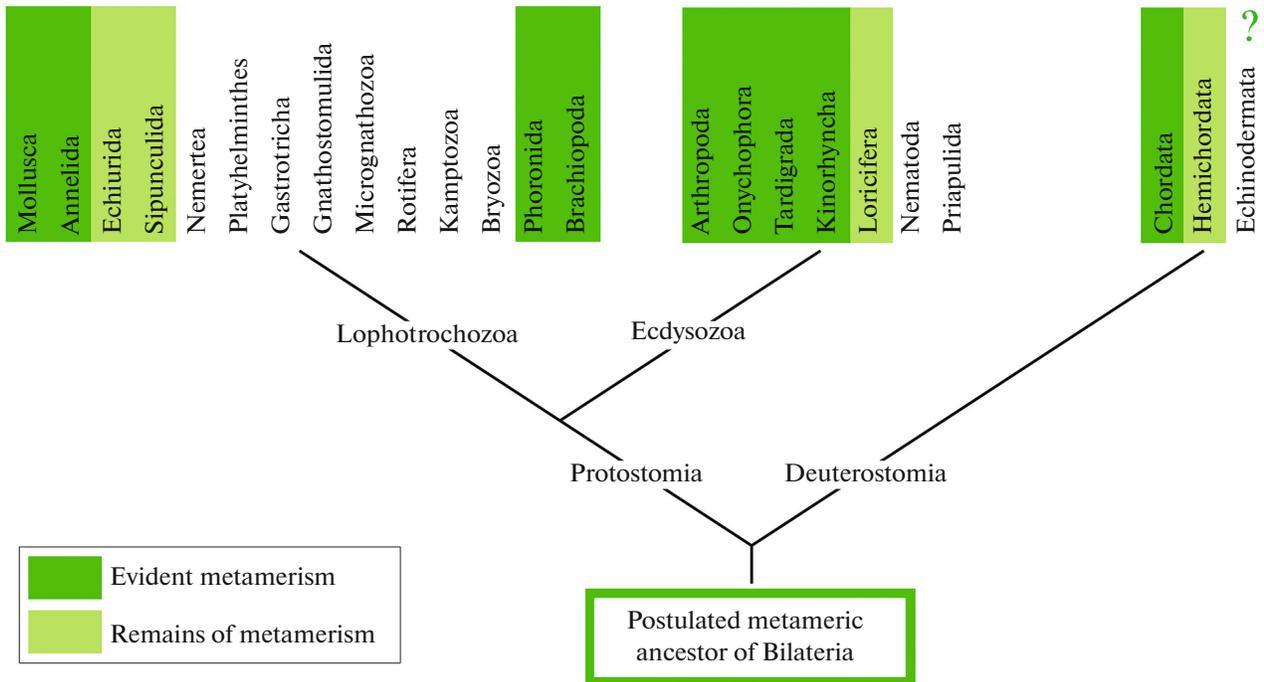


Fig. 1. Presence of metamerism in the main bilaterian clades.

vertebral ossicles in the arms of ophiuroids, and other features of the external structure (Sprinkle, 1973; Rozhnov, 2002). However, in such cases, metamerism is only a tool for increasing the mobility of the corresponding organs, which can be compared with the metameric limbs of arthropods, which occurred for the same purpose. Do echinoderms have remnants of coelomic metamerism, which was characteristic of the common ancestor of Bilateria? Analysis of the expression of *HOX* genes in the development of echinoderms shows that the oral-aboral axis of echinoderms is homologous to the anteroposterior axis of other bilaterians (Cameron et al., 2006; Mooi and David, 2008; Rozhnov, 2013, 2014; David and Mooi, 2014; Kikuchi et al., 2015; Adachi et al., 2018). Analysis of the structure of representatives of various groups of echinoderms showed that the coelomic system of these animals consists of several rings located along the oral-aboral axis (Cuénot, 1888; MacBride, 1896, 1903, 1907; Brooks and Grave, 1899; Gemmill, 1912, 1914, 1920; Ubisch, 1913; Olsen, 1942; Ezhova et al., 2013, 2015, 2017, 2018; Ezhova and Malakhov, 2020). In this article, we attempted to propose an original hypothesis that could explain the presence of these rings from the standpoint of the primary metamerism theory.

COELOMIC SYSTEM OF ECHINODERMATA

It is known that echinoderm larvae have a bilaterally symmetrical external structure (Fig. 2a). In a typical case, three pairs of coelomic rudiments develop in

the larva: protocoels (axocoels), mesocoels (hydrocoels), and metacoels (somatocoels) (Ivanova-Kazas, 1978; Ruppert et al., 2004). During ontogeny, the left coelomic rudiments develop to a much greater extent than the right ones (Figs. 2b, 2c). The right axocoel (future pericardium) is significantly smaller than the left one (future axial coelom). The right hydrocoel disappears completely, and the left hydrocoel after metamorphosis forms the water-vascular system. In adult echinoderms, the right somatocoel is retained; however, it is significantly smaller than the left one (Fig. 2c).

In adult echinoderms, against the background of the reduction of the right coelomic rudiments, partial secondary radial symmetry develops. During this process, the developing coeloms usually close to form rings around the gut (Fig. 2d). The **left axocoel** in asteroids and ophiuroids, in addition to the axial coelom and madreporic ampulla, forms a ring that becomes a component of the periahaemal system (MacBride, 1896, 1907; Brooks and Grave, 1899; Ezhova et al., 2013, 2014, 2015). In echinoids, the left axocoel is represented only by the axial coelom and madreporic ampulla (Ziegler et al., 2009; Ezhova et al., 2018). In holothuroids, the left axocoel is retained only in the form of the madreporic ampulla (Balser et al., 1993; Ezhova et al., 2017). During embryogenesis, the **left hydrocoel** always bends around the intestine and closes in a ring, from which one outgrowth grows in each radius. It should be emphasized that both the left axocoel and the left hydrocoel form only one coelomic ring.

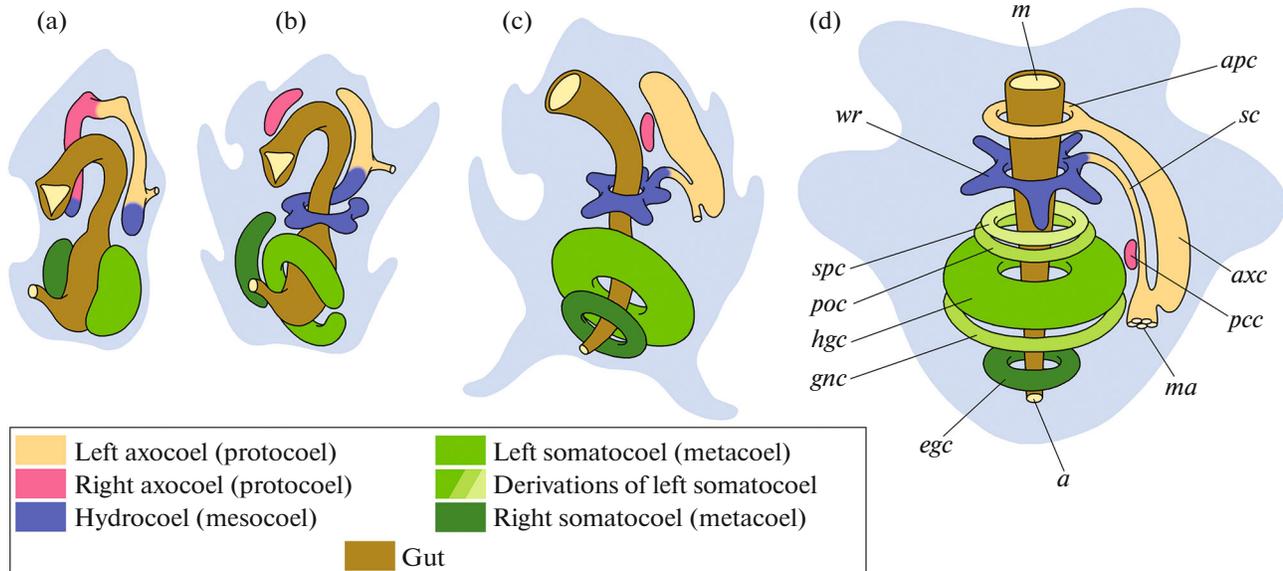


Fig. 2. Scheme of echinoderm coelomic transformations from the larva (a–c) to the adult (d). Based on the development of the coelom in Asterozoa. Designations: *a*, anus; *apc*, axocoelomic periaemal ring; *axc*, axial coelom; *egc*, epigastric coelom; *gnc*, genital coelom; *hgc*, hypogastric coelom; *m*, mouth; *ma*, madreporic ampulla; *pcc*, pericardial coelom; *poc*, perioral coelom; *sc*, stone canal; *spc*, somatocoelomic periaemal ring; *wr*, water coelomic ring.

The fate of the **left somatocoel** should be considered separately (Fig. 3). In Asterozoa, three or four coelomic rings are formed from it: large hypogastric coelom, genital (or “aboral”) coelom, somatocoelomic periaemal coelom, and (in some asteroids) perioral coelom (Fig. 3b) (MacBride, 1896; Goto, 1898; Gemmill, 1912, 1914, 1915, 1920; Osterud, 1918; Hörstadius, 1939; Chia, 1968; Ezhova et al., 2013, 2014, 2016). In Ophiurozoa, the same four coelomic rings develop from the left somatocoel (Fig. 3c) (Ludwig, 1880; Cuénot, 1888; Brooks and Grave, 1899; MacBride, 1907; Narasimhamurti, 1933; Olsen, 1942; Ezhova et al., 2014, 2015, 2016). The somatocoelomic periaemal coelom in representatives of the clade Asterozoa + Ophiurozoa is divided into five horse-shoe-shaped sectors. In Holothurozoa, the left somatocoel gives rise to the ring hypogastric coelom (which fuses with the epigastric coelom to form a common perivisceral cavity), the genital coelom (which is present only in the CD interradius), and the ring perioral and perianal coeloms, i.e., four coelomic compartments (Fig. 3e) (Selenka, 1867; Hérouard, 1889; Bury, 1895; Clark, 1898; Runnström, 1927; Hyman, 1955; Ubaghs, 1967; Malakhov and Cherkasova, 1992; Ezhova et al., 2017). In Echinozoa, six coelomic rings are formed from the left somatocoel: ring hypogastric coelom, genital coelom, somatocoelomic periaemal coelom, perioral (or peripharyngeal) coelom, periproctal coelom, and perianal coelom (Fig. 3d) (Hamann, 1887; Cuénot, 1891; MacBride, 1903; Ubisch, 1913; Ezhova et al., 2014, 2018). Crinozoa have a complete or partial fusion of some of the above-

mentioned coelomic rings. Crinoids have the so-called periaemal coelomic ring, which is connected via tegmenal pores with the external environment and via numerous stone canals with the water ring (Ezhova and Malakhov, 2020). According to Balser and Ruppert (1993), the periaemal coelomic ring corresponds to the axocoel. According to Heinzeller and Welsch (1994), the periaemal coelomic ring is the result of fusion of the axocoel (of which only the tegmenal pores remain) and part of the left somatocoel. In addition, crinoids have two more coelomic rings, which originate from the left somatocoel, namely large ring hypogastric coelom and genital coelom (Fig. 3a).

The **right somatocoel** forms the ring epigastric coelom located in the aboral part of the animal (Figs. 2, 3). In asteroids, this is an isolated coelomic ring, which is separated from the hypogastric coelom by a horizontal mesentery (Ubaghs, 1967; Ezhova et al., 2013). In ophiuroids, the ring epigastric coelom retains autonomy, although the horizontal mesentery is perforated with openings connecting the epigastric and hypogastric coeloms (Ludwig, 1880; Hyman, 1955; Ezhova et al., 2015). In echinoids and holothuroids, initially independent epigastric and hypogastric coeloms during postembryonic organogenesis partially or completely fuse to form a large perivisceral coelom (Smith, 1984; Ivanova-Kazas, 1978). In crinoids, the right somatocoel (a homologue of the epigastric coelom of other echinoderms) forms the coelom of a chambered organ (Bury, 1888; Seeliger, 1892).

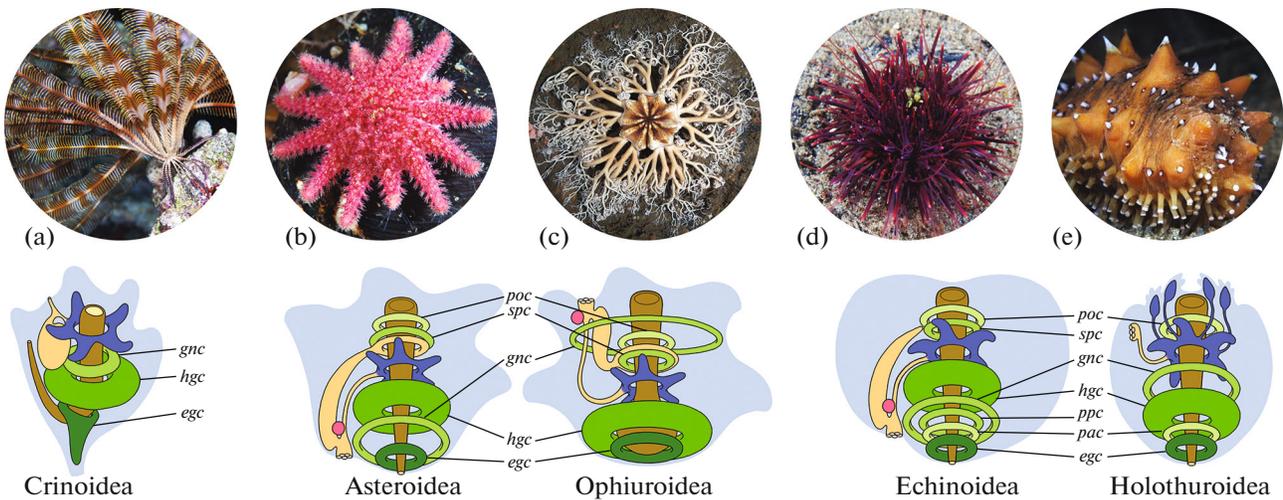


Fig. 3. Scheme of the coelomic organization in extant echinoderm classes. Photos by Alexander Semenov. On the schemes, the animals are shown oral side up. The colors indicate the same structures as in Fig. 2. Designations: *egc*, epigastric coelom; *gnc*, genital coelom; *hgc*, hypogastric coelom; *pac*, perianal coelom; *poc*, perioral coelom; *ppc*, periproctal coelom; *spc*, somato-coelomic periaemal ring.

ORIGIN OF DISSYMMETRICAL METAMERISM OF ECHINODERMS

Above, we noted the signs of metamerism in hemichordates, which appears in the presence of metameric gill slits, gill pores, and gut (hepatic) outgrowths. Earlier, we assumed that the metameric gill apparatus of hemichordates is the result of fusion of metameric nephridia with metameric gut pockets in the segments (Ezhova and Malakhov, 2015). Hemichordata have the left axocoel coelomoduct, as well as a pair of hydrocoel coelomoducts. The latter are represented by funnels that open into the collar coelom (homologue of the hydrocoel of echinoderms), and short coelomoduct channels that extend from the funnels. They penetrate the dissepiment retained between the collar coelom and trunk coelom and open into the first pair of branchial sacs. The dissepiments between the trunk segments in hemichordates were reduced together with the nephridial funnels located on them, the metameric gut pockets gave rise to the branchial sacs, and the nephridial pores gave rise to the metameric openings of the branchial sacs (Ezhova and Malakhov, 2015). Thus, the metamerism of the branchial sacs and their openings is associated in origin with the original coelomic metamerism. The reduction of dissepiments in the trunk region of hemichordates is the result of the burrowing lifestyle and hydraulic locomotion in the sediment. A possible rudiment of the musculature of the hemichordate dissepiments is the slender radial muscle fibers extending from the body wall to the gut (Hyman, 1959). A similar phenomenon—a partial or complete loss of coelomic metamerism in the case of burrowing or tubicolous way of life—is observed in other groups of the animal kingdom. For example,

sedentary annelids living in the bottom or in tubes partially lose their dissepiments; echiurids and sipunculids, which are well adapted to the burrowing or tubicolous way of life, completely lose both coelomic and external metamerism. Nevertheless, the original metamerism of echiurids and sipunculids is traced in the nervous system structure (Hessling and Westheide, 2002; Kristof et al., 2008; Wanniger et al., 2009).

The division of the coelom in Echinodermata larvae is similar to that in hemichordates, which was noted even in classical studies (Fedotov, 1923, 1924). Echinodermata retain the left axocoel. This is an axial coelom, which also forms the axocoelomic periaemal ring in asteroids and ophiuroids (Ezhova et al., 2013, 2015, 2016). The right axocoel in echinoderms is the pericardial coelom. The homologue of the collar coelom is represented by the only coelomic ring derived from the left hydrocoel. In echinoderm larvae, the left axocoel and the left hydrocoel are connected with the environment via the hydropore. In adult animals, both the axial coelom (left axocoel) and the water ring (left hydrocoel) are connected with the environment through a common coelomoduct. The somatocoel is represented by several ring coeloms devoid of coelomoducts: six in echinoids, four in holothuroids, four in ophiuroids, four or three in asteroids, and three in crinoids (Fig. 3). We assume that the presence of several coelomic rings of the somatocoel located along the oral-aboral axis (homologue of the anteroposterior axis of Bilateria) is a rudiment of the coelomic metamerism, which was characteristic of the common ancestor of bilaterally symmetrical animals (Fig. 4).

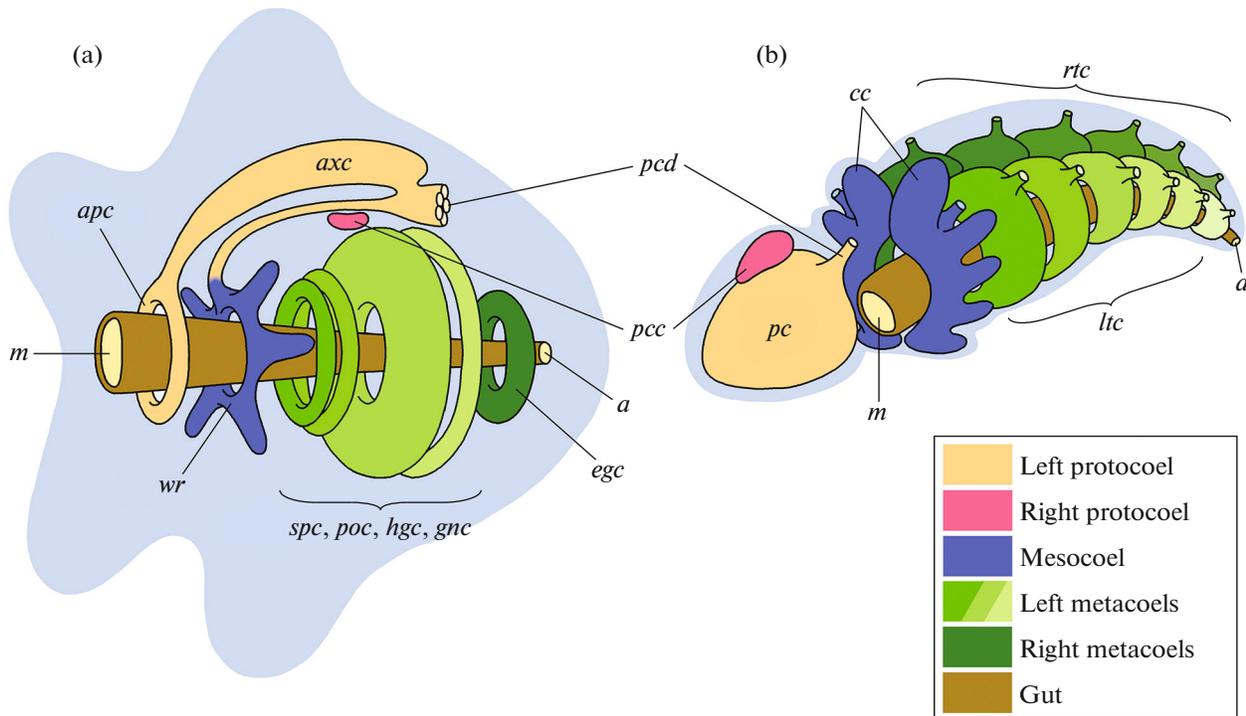


Fig. 4. Comparison of the echinoderm body plan (a) with the hemichordate-like hypothetical ancestor (b). The match of different green tints of separate metacoelomic pouches is schematic and does not indicate individual homology. *a*, anus; *apc*, axocoelomic periaemal ring; *axc*, axial coelom; *cc*, left and right collar coeloms; *egc*, epigastric coelom; *gnc*, genital coelom; *hgc*, hypogastric coelom; *ltc*, left trunk coeloms; *m*, mouth; *pc*, proboscis coelom; *pcc*, pericardial coelom; *pcd*, protoceol coelomoduct; *poc*, perioral coelom; *rtc*, right trunk coeloms; *spc*, somatocoelomic periaemal ring; *wr*, water coelomic ring.

It can be assumed that the ancestor of Ambulacraria was a mobile worm-like organism that had an epibenthic way of life and possessed a symmetrical tentacle apparatus (Fig. 5). This ancestor retained the metamerism characteristic of the common ancestor of Deuterostomia. The body of such an ancestor included the preoral coelom, the perioral coelom with tentacles, and the metameric trunk. The ancestors of Enteropneusta switched to the burrowing lifestyle and lost tentacles (Fig. 5). The tubicolous ancestors of the Graptolithoidea (or Pterobranchia) retained their tentacular apparatus (Fig. 5). Dwelling in burrows in the bottom or in tubes led to a reduction of dissepiments, which, as mentioned above, is typical of burrowing and tubicolous animals.

Echinoderms are characterized by pronounced dissymmetry in the structure of the coelomic apparatus, which appears in the complete reduction of the right hydrocoel and hypertrophied development of the left hydrocoel, which provides the formation of the water-vascular system. The left somatocoel gives rise to several coelomic rings; its volume significantly exceeds the volume of the right somatocoel, which forms the aboral epigastric coelom. We assume that the dissymmetry of the coelomic system of echinoderms was caused by the fact that the ancestor of Echinodermata changed the state typical for the majority of bilateri-

ans, when the ventral side of the body is facing the substrate, to the position in which the substrate is faced by the right side of the body. Lying or crawling on the right side led to a complete reduction of the right tentacular apparatus and the right tentacular coelom (the right hydrocoel). The metamerism coeloms on the right side were also reduced, except for the last one, which presumably grew into the stalk or tail that was used by the ancestors of echinoderms to anchor in the substrate similarly to juvenile Enteropneusta (Burdon-Jones, 1952; Jeffries, 1972; Kolata et al., 1991).

Lying (or moving) on the right side was often used by researchers to explain the dissymmetry in the structure of Deuterostomia (see Bather, 1900; Gislén, 1930; Malakhov, 1977, 1989; Jeffries et al., 1996; Jeffries, 1997). To denote this phenomenon, Jeffries et al. proposed the term dexiothetism (Jeffries et al., 1996; Jeffries, 1997). Indeed, the left–right dissymmetry is more or less characteristic of all deuterostomes. In lower chordates (Cephalochordata), dissymmetry appears at the stages of postembryonic development. The mouth is laid on the left side of the body and migrates to the medioventral position during the development. The primary gill slits are laid on the right side of the body; however, later they migrate to the left side, and the right gill slits are laid in their place (Hatschek, 1881; Lankester and Willey, 1890; Willey,

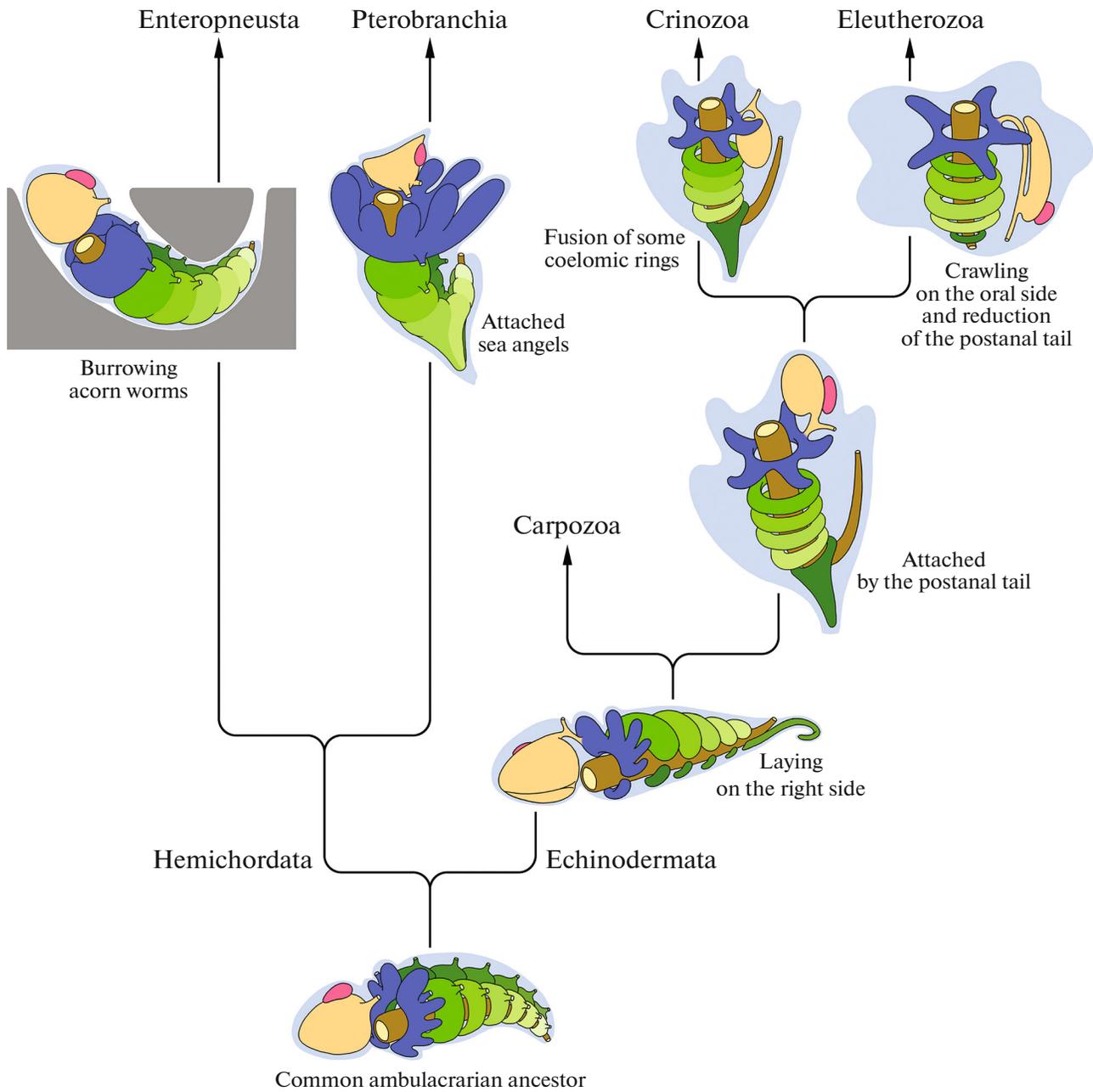


Fig. 5. Hypothesis of echinoderm origin from the hemichordate-like ancestor of Ambulacraria with the retention of coelomic metamerism. The colors indicate the same structures as in Figs. 2–4.

1891; Stokes and Holland, 1995). In adult *Branchiostoma*, the buccal cavity is symmetrical, but it is innervated only by the nerves of the left side (Franz, 1927). The anus in juvenile *Branchiostoma* is laid on the left side, but subsequently migrates to the right side (Stokes and Holland, 1995). In the structure of Cephalochordata, dissymmetry played a major role in the once very popular and still important interpretation of the Lower Paleozoic Carpozoa as members of a spe-

cial group of chordates Calcichordata (see Jefferies, 1972, 1986; Jefferies et al., 1996).

Elements of left–right dissymmetry are also appeared in hemichordates. In extant hemichordates, the right proboscis coelom (homologue of the right axocoel of echinoderms) is represented by the pericardium and is significantly smaller than the left proboscis coelom (homologue of the left axocoel), and only the left proboscis coelom has the coelomduct.

During the development of *Saccoglossus*, the left row of gill slits begins to form earlier than the right one (Kaul-Strehlow and Stach, 2013).

At the present level of our knowledge, it is difficult to speculate on whether the dissymmetry of different groups of Deuterostomia has a common origin. In any way, the left–right dissymmetry in echinoderms is incomparably more pronounced than in all other deuterostomes. For echinoderms, the explanation of their fundamental dissymmetry by the dextrothetism of their ancestors seems quite logical. The next stage in the evolution of echinoderms is the transition to the sedentary lifestyle and attachment to the substrate by the posterior end of the body, i.e. by the same hypothetical stalk, or tail, the coelom of which originates from the right somatocoel (Fig. 5). The anus migrated anteriorly from the site of attachment, and the gut acquired the characteristic loop-like shape.

At first glance, this assumption contradicts to the fact that the larvae of extant crinoids are attached to the substrate by the ventral side of the anterior end of the body (Thompson, 1865; Barrois, 1888; Bury, 1888; Seeliger, 1892; Mortensen, 1920), from which the stem is then formed. Temporary attachment by the preoral lobe is also characteristic of metamorphosing asteroid larvae (Goto, 1898; Gemmill, 1914). If we consider this process as a recapitulation of the transformation of the preoral lobe into the stalk of ancient echinoderms that took place in phylogeny, then we should expect the presence of a coelomic cavity in it, originating from the axocoel (protocoel). However, it is known that crinoids, the only extant group of Crinozoa, have a chambered organ in the stalk, which is a derivative of the right somatocoel, but not the axocoel (Bury, 1888; Seeliger, 1892; Mortensen, 1920; Fedotov, 1951; Ezhova and Malakhov, 2020). In our opinion, the metamorphosis of crinoids reflects two aspects. The attachment to the substrate by the preoral lobe (which is also observed in asteroids) reflects the ancient method of locomotion of deuterostomes with the use of anterior (proboscis, axocoelomic) part of the body. For example, pterobranchs are able to crawl on their cephalic shield (the preoral lobe), and many enteropneusts use the proboscis as the main burrowing organ of an adult animal. Probably, the ancestors of echinoderms also used the preoral lobe for crawling or temporary attachment. However, as an organ of permanent attachment to the substrate, echinoderms, similarly to pterobranchs, used the morphologically posterior end of the body. That is why the derivatives of the trunk pair of coeloms, but not those of the preoral pair of coeloms, got there.

The sedentary lifestyle led to the formation of radial symmetry (Fig. 5), as a result of which metameric coelomic rings formed from the dissymmetrical metameric coeloms. Their location along the oral–aboral axis indicates that the dissymmetric metamer-

ism of extant echinoderms is inherited from the primary metamerism, which is characteristic of the common ancestor of Deuterostomes and, possibly, the common ancestor of Bilateria. The ancestors of Eleutherozoa detached themselves from the substrate and switched to slow crawling on the oral side of the body (Bather, 1900; Beklemishev, 1964). As a result, their stalk was reduced and the anus returned to the aboral side (Fig. 5), although in many forms (e.g., echinoids and holothuroids) the loop-shaped gut is retained. Due to their slow movement, mobile Eleutherozoa did not acquire a new anterior end; as a result, they retain the secondary radial symmetry and dissymmetric metamerism of the coelomic system, acquired by their sedentary ancestors (Fig. 5).

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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