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Origin of Echinodermata

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Abstract—The common ancestor of Ambulacraria was a mobile bilaterally symmetrical organism. Its body was subdivided into a preoral (proboscis) region, a perioral (collar) region with ciliated tentacles, and a trunk region with a metameric coelom and metameric gill slits. Like in other Bilateria, the preoral and tentacular regions of Ambulacraria are free of *Hox* gene expression, which begins in the area of the first pair of gill slits in compliance with the colinearity. The axial complex is a synapomorphy of the Ambulacraria clade. A bilaterally symmetrical ancestor of Echinodermata lay on its dorsal side, so its anus was shifted to the ventral side as in present-day echinoderm larvae. This stage of evolution corresponds to the Early Paleozoic bilaterally symmetrical forms, such as *Protocinctus, Ctenocystis*, and *Ctenoimbricata*. The common ancestor of echinoderms had a symmetrical tentacular apparatus consisting of five ciliated tentacles on each side of a collar. At the next stage, the ancestors of echinoderms lay on the right side that resulted in the reduction of the tentacles on the right side and the right hydrocoel. This evolution stage includes various Early Paleozoic forms (*Cothurnocystis*, *Dendrocystoides*, *Syringocrinus*, *Castericystis*, *Coleicarpus*, *Rhenocystis*, etc.). The next stage is related to the sedentary lifestyle. During this stage, the mouth and tentacles occupied an apical position, the anus has shifted up, and thus an intestinal loop was formed. The five primary tentacles of the left side of the ancestor of Ambulacraria predestined the formation of pentaradial symmetry of echinoderms. The primary tentacles remained only in Holothuroidea. The secondary ciliary grooves were formed between the primary tentacles. These grooves were accompanied by hydrocoelic canals, which gave rise to the water-vascular (ambulacral) system. The present-day echinoderms are characterized by several metameric rings formed by the derivatives of the left somatocoel. They derive from the coelomic segments of the left side of the trunk of the ambulacrarian ancestor and, thus, the echinoderms retain coelomic metamerism. The attachment of the crinoid larvae by the preoral lobe reflects the ancient method of locomotion of deuterostomes using the proboscis, but, in reality, the Pelmatozoa stalk is homologous to the Pterobranchia stalk, i.e., the posterior end of the body, because the right somatocoel grows into it. During metamorphosis, the internal coelomic complex of the larva is inverted by 180°. The significance of this inversion for the translocation of the anterior genes of the *Hox* cluster is discussed. The ancestors of Eleutherozoa began to crawl on the oral surface, which led to a shift of the anus to the aboral side. Thus, the ontogeny and phylogeny of echinoderms exhibits a change from bilateral symmetry to dissymmetry, and then the development of pentameric symmetry.

Keywords: Echinodermata, Ambulacraria, Deuterostomia, comparative anatomy, paleontology, phylogeny, larvae evolution, dissymmetry, coeloms, axial complex, *Hox* cluster, metamerism

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INTRODUCTION

Echinodermata is one of most morphologically enigmatic animal groups. Perhaps, there is no other animal phylum with such complex and confused anatomical organization. For most bilaterally symmetrical animals, it is easy to determine the anterior and posterior parts of the body or the dorsal and ventral sides, unlike Echinodermata. “Echinoderms could be variations on celestial stars that fell to the Earth as extraterrestrials, so extraordinary is their form and function”: such an emotional observation in a present-day zoological textbook results from the specific anatomical organization of representatives of this animal phylum (Ruppert et al., 2004, p. 873).

Most hypotheses on the origin of Echinodermata were formulated as early as the end of the 19th–the beginning of the 20th centuries (see Semon, 1888; Bury, 1895; MacBride, 1896; Bather, 1900; Heider, 1912, 1913; Fedotov, 1923; Grobben, 1923). The authors of these hypotheses derive Echinodermata from a bilaterally symmetrical dipleuruloid ancestor (the organization of which is more or less recapitulated by the early echinoderm larvae), which became sedentary having attached to the substrate by the preoral lobe. The authors of these hypotheses suggested that, after the attachment, the primary bilateral symmetry was completely lost and changed by pentaradial symmetry in spite of different viewpoints on the formation of anatomical organization of the present-day echinoderms (see Semon, 1888; Bury, 1895; Bather, 1900; Grobben, 1923). These ideas were included in most reviews and tutorials published in the second half of the 20th–the beginning of the 21st centuries (Hyman, 1955; Beklemishev, 1964; Ubaghs, 1967; Ivanova-Kasas, 1978a; Brusca, R.C. and Brusca, G.J., 2003; Ruppert et al., 2004).

Recent decades yielded new studies of embryonic and larval evolution and expression of regulatory genes in the evolution of echinoderms, as well as refined data on comparative anatomical analysis of present-day echinoderms (Lacalli and West, 2000; Fröbius et al., 2008; Ezhova and Malakhov, 2021a, 2021b; Bakalenko et al., 2013; Ezhova et al., 2013, 2014, 2015, 2017, 2018, 2020; Kaul-Strehlow and Stach, 2013; Janssen et al., 2014; Dolmatov et al., 2016; Maletz and Cameron, 2016; Martin et al., 2016; Gaunt, 2018; Rakaj et al., 2019; Gąsiorowski and Hejnol, 2020; etc.). New groups of fossil Echinodermata are described (Rahman and Zamora, 2009; Zamora et al., 2012, 2013; Rahman et al., 2015a, 2015b, 2019). Application of molecular phylogenetics significantly changed the ideas on the system and phylogeny of animals in general. All this allows us to once again consider the problem of the origin of echinoderms. In this work, we provide an original concept, which is mostly based on comparative morphology of present-day echinoderms, evolutionary biology, molecular phylogenetics, and new paleontological discoveries. Our concept does not answer all the questions and is open for criticism, but by publishing this material, we would like to offer it up to open a new stage of the discussion of the problem of the origin of echinoderms.

POSITION OF DEUTEROSTOMIA IN BILATERIA

For the entire 20th century, biology was influenced by dominant ideas on the system and phylogeny of bilaterally symmetrical animals elaborated by the Austrian zoologist K. Grobben (Grobben, 1908). The studies of the last decades have significantly changed ideas on the systematics of bilaterians (Aguinaldo et al., 1997; Rosa et al., 1999; Balavoine et al., 2002; Halanych, 2004; Dunn et al., 2008, 2014; Malakhov, 2009, 2010; Telford, 2013; Giribet, 2016; Laumer et al., 2019). According to the current phylogenetic concepts, Bilateria comprises three large groups of organisms: Lophotrochozoa (Trochozoa and Lophophorata), Ecdysozoa (Arthropoda, Lobopoda, Nematoda, Priapulida, Kinorhyncha, Loricifera, and Nematomorpha), and Deuterostomia (Chordata, Hemichordata, and Echinodermata) (Fig. 1). In spite of a dramatic reconstruction of the Bilateria system, the new system sustains the subdivision into Protostomia and Deuterostomia suggested by Grobben (1908). In the new system, the Deuterostomia includes the same three groups (Chordata, Hemichordata, and Echinodermata) that were included in the structure of this taxon by Grobben (1908). There are suggestions, however, that the turbellarian-shaped organisms Xenoturbellida, Nemertodermatida, and Acoela should be included in the structure of Deuterostomia (see Bourlat et al., 2006; Philippe et al., 2011, 2019). These suggestions are based exclusively on molecular phylogenetic data and are not supported by morphological or embryonic studies. Based on the analysis of all molecular phylogenetic data, other authors consider Xenoacoelamorpha (Xenoturbellida and Nemertodermatida + Acoela) a group of primitive multicellular organisms, which is a sister group to true bilaterally symmetrical organisms (Jondelius et al., 2002, 2019; Hejnol et al., 2009; Ax, 2012; Achatz et al., 2013; Cannon et al., 2016; Hejnol and Pang, 2016; Rouse et al., 2016; Ruiz-Trillo and Paps, 2016). In the last case, Deuterostomia, Ecdysozoa, and Lophotrochozoa represent a monophyletic group. Two names have been suggested for this group. The name Nephrozoa Jondelius et al., 2002 is based on the presence of specific excretory organs of true bilaterians: metanephridia and protonephridia (in the apomorphic groups, they can be reduced and replaced by other specific excretory organs, e.g., a Malpighian tubules, etc.), whereas Xenoturbellida, Nemertodermatida, and Acoela are devoid of specific excretory organs. Later, Ax (2012) used the name Eubilateria Ax, 2012 for the same monophyletic group. The problem of Xenoacoelomorpha requires additional discussion, which is beyond the scope of our work.

As for the origin of the true bilaterians (Nephrozoa = Eubilateria), the analysis of the morphological features of Lophotrochozoa, Ecdysozoa, and Deuterostomia shows that all three groups share basic features, e.g., the presence of a through intestine, a coelomic cavity, metamerism, and metameric limbs (see Malakhov, 2009, 2010, 2013; Malakhov and Bogomolova, 2016). Because it is difficult to assume that these features appeared independently in three groups Nephrozoa–Eubilateria, we should accept that the last common ancestor of Eubilateria–Nephrozoa had a complex morphological organization, i.e., it had a through intestine, a metameric coelom, and even metameric limbs (Malakhov, 2009, 2010, 2013).

Coelomic metamerism and metameric limbs are found in the basal representatives of all main four clades of true bilaterians: Ecdysozoa, Lophophorata, Trochozoa, and Deuterostomia (Fig. 2) (Ezhova and Malakhov, 2021b). The coelomic metamerism of Protostomia corresponds to metamerism of coelomoducts, the funnels of which lie on dissepiments as in the typical case of Annelida. The primary coelomic metamerism of the primitive mollusks Monoplacophora includes six pairs of coelomoducts (Lemche and Wingstrand, 1959; Warén and Hain, 1992). Brachiopoda contains two pairs of lateral mesenteries with nephridial funnels; suggesting that brachiopods have three trunk segments (Malakhov and Kuzmina, 2006).

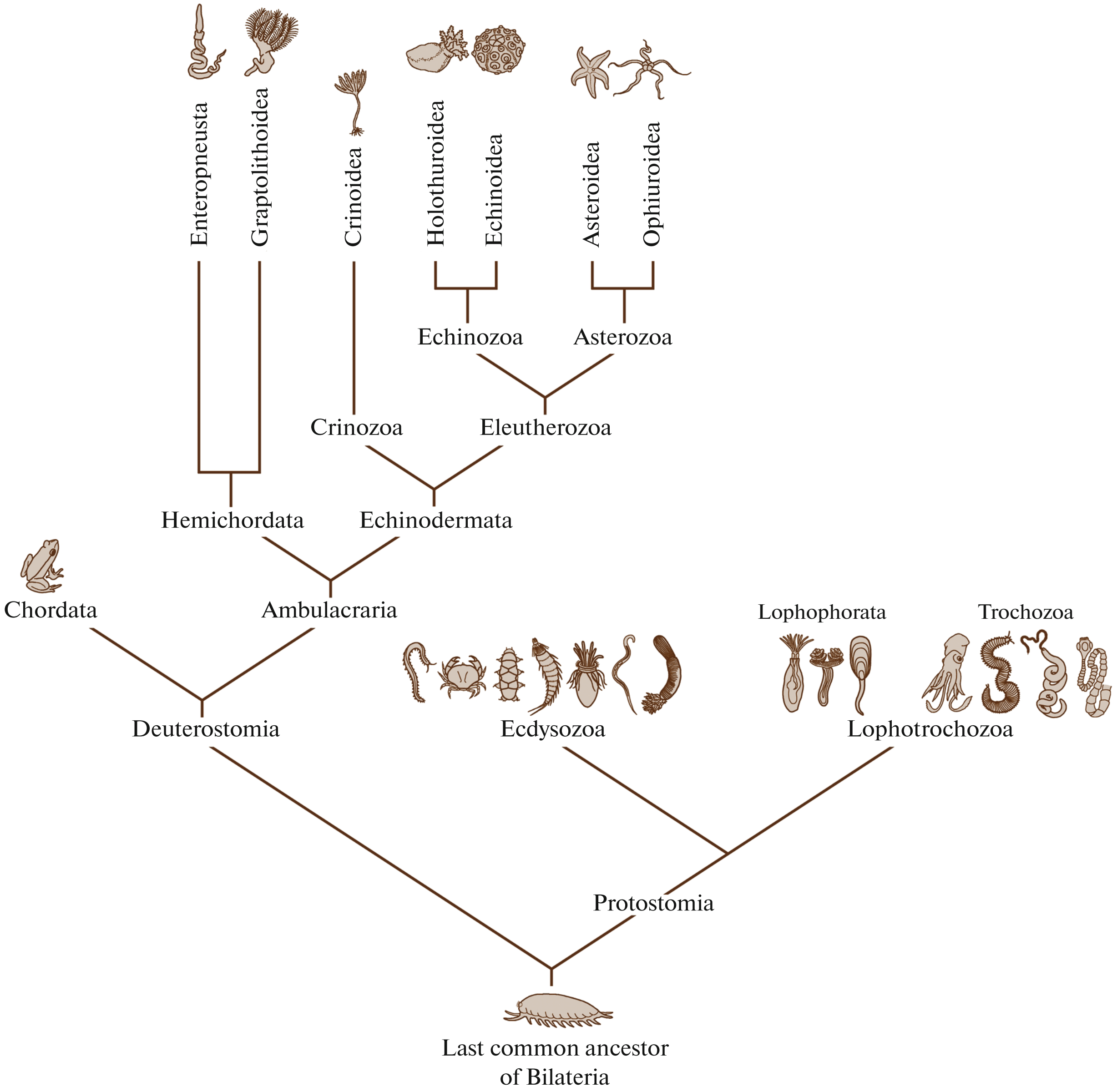


Fig. 1. Position of Deuterostomia on a phylogenetic tree of Bilateria (after Dunn et al., 2014; Telford et al., 2015) and phylogenetic interrelations between various phyla of Deuterostomia and various classes of Ambulacraria (Smith, 1984; Littlewood et al., 1997; Bromham and Degnan, 1999; Ax, 2001; Reich et al., 2015).

This is in agreement with data on the larval evolution of Craniida, which have three pairs of dorsal setal bundles (Nielsen, 1991). The presence of one pair of lateral mesenteries with nephridial funnels of Phoronida suggests that phoronids have two trunk segments (Temereva and Malakhov, 2011). Thus, at least two groups of Lophophorata have relics of metamerism. A common ancestor of Lophotrochozoa was probably a metameric organism and this metamerism was typical exactly of the coelom. Among Ecdysozoa, metamerism is characteristic of arthropods and related groups, such as Onychophora and Tardigrada; among Cycloneuralia, metamerism is characteristic of kinorhynchs. Traces of metamerism can be found in some loricifers (e.g., *Pliciloricus*), the cuticle of which is divided on 11 rings (Higgins and Kristensen, 1986). It is noteworthy that this number coincides with the number of segments (zonites) of kinorhynchs (Adrianov et al., 1989; Malakhov and Adrianov, 1995). Probably, metamerism is characteristic of the common ancestor of Ecdysozoa; and some groups of Cycloneuralia lost metameric limbs and other metameric features due to their burrowing lifestyle (Malakhov, 2009, 2010, 2013).

In the phylogenetic schemes corresponding to new phylogenic concepts of Nephrozoa—Eubilateria (see

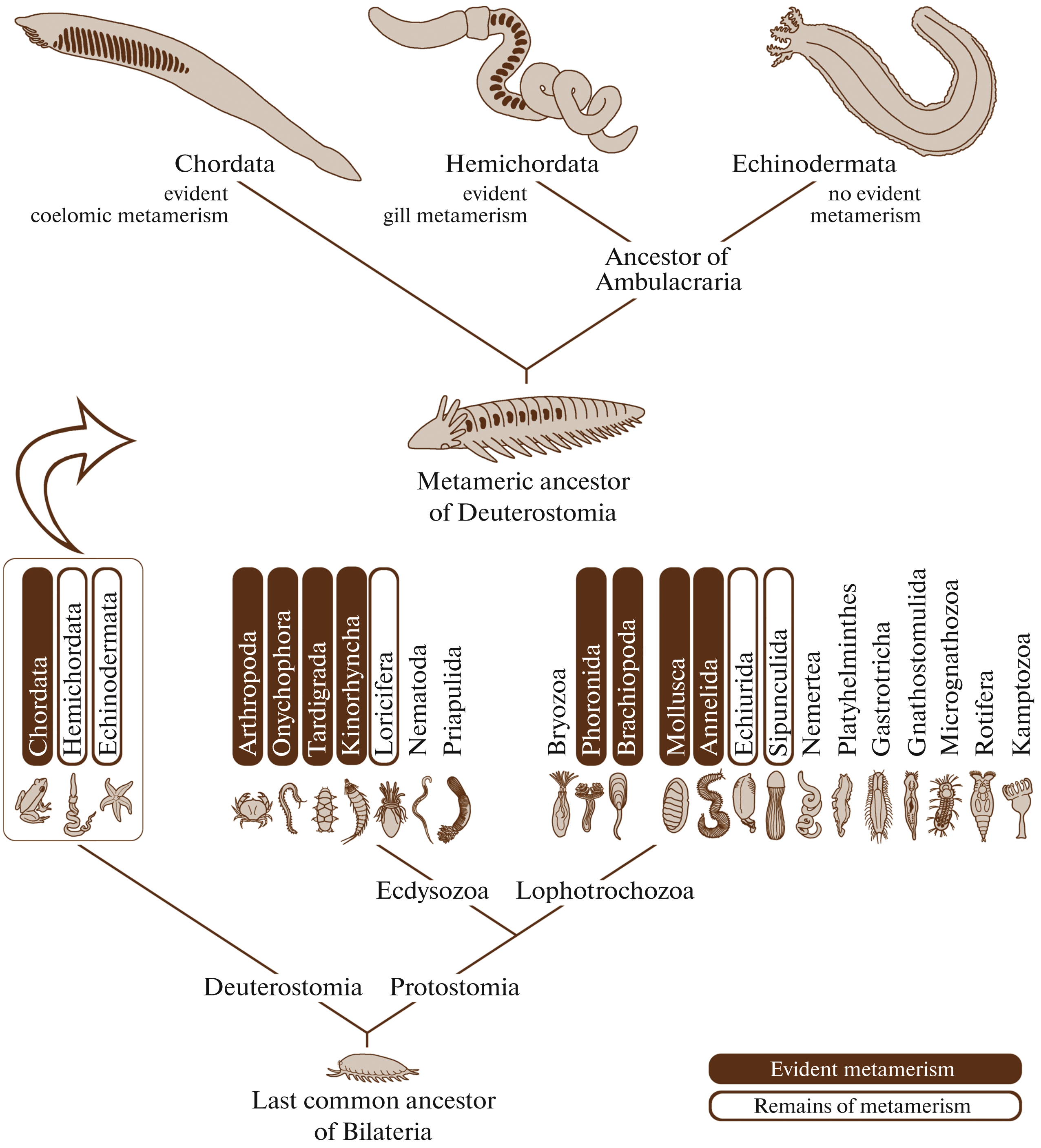


Fig. 2. Coelomic metamerism and its traces in the representatives of main branches of bilaterally symmetrical animals and in various phyla of deuterostome animals.

above), deuterostomes are positioned as a basal group, which was separated early from the common clade of true bilaterians (Fig. 1). Thus, the common ancestor of Deuterostomia should have coelomic metamerism. Among deuterostomes, coelomic metamerism is evidently characteristic of chordate animals (Fig. 2). This is metamerism of the coelomic sacs (somites), which have enterocoelous origin to the left and to the right from the gut (Hatschek, 1881, 1893; MacBride, 1898; Dohrn, 1901; Conklin, 1932; Ivanov, 1937; Ivanova-Kazas, 1978b; Holland et al., 2008b; Onai et al., 2017). Traces of coelomic metamerism are also typical of Hemichordata: the presence of metameric gill slits and gill pores, the origin of which is probably related to the primary metamerism of coelomic nephridia and endodermal intestinal pockets (Dohrn, 1875; Ezhova and Malakhov, 2015).

In addition to metamerism of coelomic rudiments inherited from the common ancestor of Bilateria, the common ancestor of deuterostomes was also characterized by symmetrical gill slits, which communicate the endodermal pharynx with the environment. While the coelomic metamerism is a feature common for all Bilateria, the metameric gill slits are unique for Deuterostomia and occur in no other animal groups. Outside deuterostomes, similar organs are extremely rare. Only one example can be provided: this is the pharynx pores of gastrotrichs Macrodasyida (see Remane, 1927), which represent two symmetrical canals connecting the ectodermal pharynx with the environment. The pharynx pores of Macrodasyida are nonhomologous and are not even similar to the gill slits of deuterostomes. The pharynx pores of the gastrotrichs are formed by ectodermal part of the digestive system, these are not metameric structures, and their function is still unclear (they do not operate as breathing structures), whereas the gill slits of deuterostomes connect the entodermal pharynx with the environment rather than ectodermal one (Hyman, 1959; Ivanova-Kazas, 1978a; Benito and Pardos, 1997; Kaul-Strehlow and Stach, 2013) and they are always metameric and are necessary for breathing.

At present, only two phyla of deuterostome animals have metameric gill slits (Chordata and Hemichordata). According to the current concepts, Hemichordata is a sister group of Echinodermata and together they form the clade Ambulacraria (Figs. 1, 2) (Smith, 1984; Littlewood et al., 1997; Bromham and Degnan, 1999; Ax, 2001; Dunn et al., 2014; Reich et al., 2015; Telford et al., 2015). No present-day echinoderms have the gill slits. Some Cambrian echinoderms of the extinct group Stylophora (Homalozoa, or Carpozoa)—*Cothurnocystis elizae*, *C. (Nevadaecystis) americana*, *Scotiaecystis curvata*, and *Ceratocystis perneri*, however, have one row of metameric gill holes located on the upper side of the animal (Bather, 1913; Ubaghs, 1963; Jefferies, 1969). According to Jefferies (1968, 1981), these holes are homologous to the left row of gill slits of Hemichordata and Chordata (Jefferies, 1968, 1981; Gee, 1996). The bilaterally symmetrical (in contrast to asymmetric Stylophora) *Jaekelocarpus oklahomensis* belonging to the echinoderm group was described for late Carboniferous Mitrata with two (left and right) internal symmetrical rows of gill slits found using computer X-ray tomography (Dominguez et al., 2002). Thus, metameric gill slits evidently represent the most important synapomorphy of deuterostomes, lost by the present-day echinoderms (Figs. 2, 3). The origin of this synapomorphy requires explanations. From an evolutionary viewpoint, it is hard to imagine the formation of symmetrical lateral rows of numerous metameric paired holes connecting the intestine with the environment in the trunk of the common ancestor of the deuterostome animals.

We suggested a nephridial hypothesis, which explains the origin of gill slits of deuterostomes on the basis of two structural features of the present-day Enteropneusta (see Ezhova and Malakhov, 2015). The first feature is the presence of the metameric hepatic pockets in a hepatic region of the intestine located beyond the branchial region (Horst, 1939). The second feature is related to the fact that the paired collar coelomoducts of all known acorn worms do not directly communicate with the environment but penetrate the septa between the collar and the trunk and are the paths from the collar coelom to the gill sacs of the first pair of gill slits (excluding the representatives of the genus *Stereobalanus* without collar coelomoducts) (Hyman, 1959). According to our hypothesis, the ancestor of deuterostomes hosted a pair of the intestinal pockets in each metameric trunk segment (Fig. 3). In addition, each segment was characterized by a pair of nephridia (coelomoducts), the funnels of which opened to the cavity of the anterior segment, and the canals penetrated the dissepiment to the posterior side and laterally—dorsally opened outside (Fig. 3). Exactly the same is observed in the structure of the collar coelomoducts of the present-day acorn worms. Later in evolution, the canals of coelomoducts in the anterior segments merged with intestinal pockets (Fig. 3). This led to the formation of an aperture to both the intestine and the environment in each metameric nephridium. If this hypothetical ancestor organism was a deposit feeder, then its metabolic products could be released outside (if the animal protruded from sediments) or to the intestine (if the animal occurred inside sediments). The next stage is the reduction of the dissepiments, as well as nephridial funnels, in all segments except for the collar one (Fig. 3). This leads to the formation of two rows of metameric canals leading from the endodermal pharynx to the environment. The metameric gill pores originate from metameric excretory pores; the metameric gill sacs derive from metameric endodermal intestinal pockets merged with coelomoducts; and the metameric gill slits correspond to the metameric apertures connecting the intestine and metameric intestinal pockets. Thus, the metamerism of the gill slits originates from primary (for deuterostomes and, probably, for all Eubilateria) coelomic metamerism, although the gill slits are an undoubted synapomorphy of Deuterostomia. Only the first pair of gill slits of the present-day acorn worms retains the ancestral organization communicating simultaneously with intestine, the environment, and the coelom of the previous (collar) segment. The suggested merging of the coelomoducts and intestinal pockets occurred only in the anterior segments. The posterior segments retained the metameric intestinal pocket and metameric coelomoducts, which operates as the ducts of the meta-

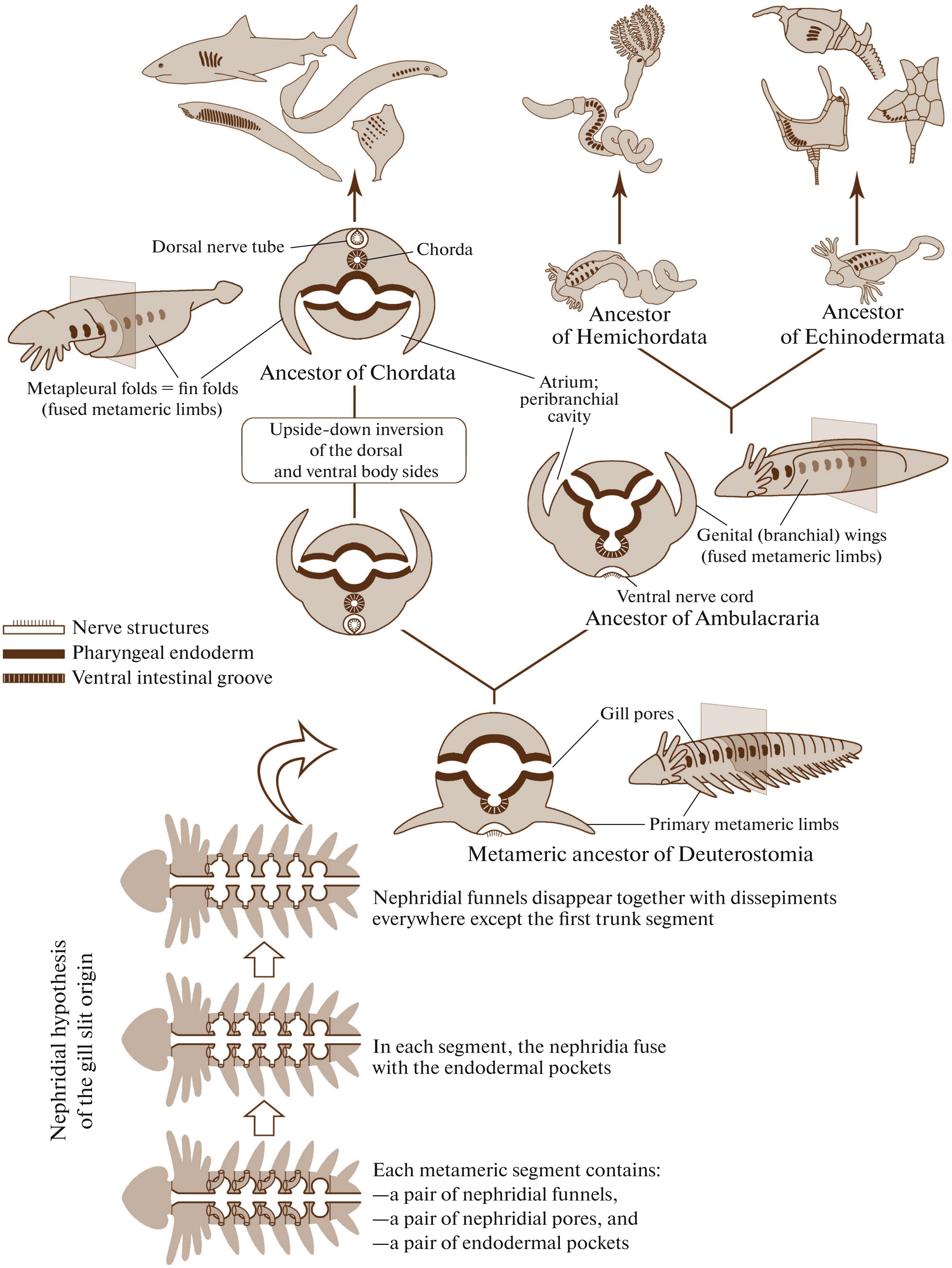


Fig. 3. Formation of the gill apparatus of Deuterostomia.

meric gonads (gonoducts) of present-day acorn worms (Spengel, 1893; Horst, 1939).

The metameric common ancestor of Deuterostomia was also probably characterized by metameric paired limbs on the ventral side in addition to the metameric gill slits and pores located closer to the dorsal side of the body (Fig. 3). During evolution, these limbs merged in left and right extended folds along the sides of the body. These folds could arch, meeting but not merging over the dorsal side of the animal and, therefore, form a peribranchial cavity (atrium) protecting the gill slits from contamination in sediments. The ancestors of Hemichordata retain these folds as the genital wings of the acorn worms containing the metameric gonads. Taking into account the inversion of the sides of the body, these folds of chordate animals form metapleural folds of Cephalochordata (also containing metameric gonads), the homologs of which are probably the fin folds of lower vertebrates transiting to the paired fins and limbs of Tetrapoda (Fig. 3).

COMMON ANCESTOR OF AMBULACRARIA

It can be concluded from the aforesaid that the possible ancestor of Ambulacraria was (i) a bilaterally symmetrical organism, (ii) had the left and right rows of metameric gill slits and gill pores, and (iii) had an evolved coelom organized as metameric coelomic sacs, which are located along the through digestive system. Two anterior segments (preoral and perioral) of most Eubilateria are differentiated specifically and differ from other body segments, which is caused, among other things, by a specific character of the expression of regulatory genes (see below). The preoral segment of the ancestors of Ambulacraria is differentiated as the proboscis region and the perioral segment is a collar region, whereas all other segments comprise the third trunk region of the body. In accordance with this division, the coelomic sacs were also reorganized with position of the paired protocoels (axocoels) in the preoral segment of the body, paired mesocoels (hydrocoels) in the perioral region, and several or many pairs of metameric metacoel sacs (somatocoels) in the trunk region.

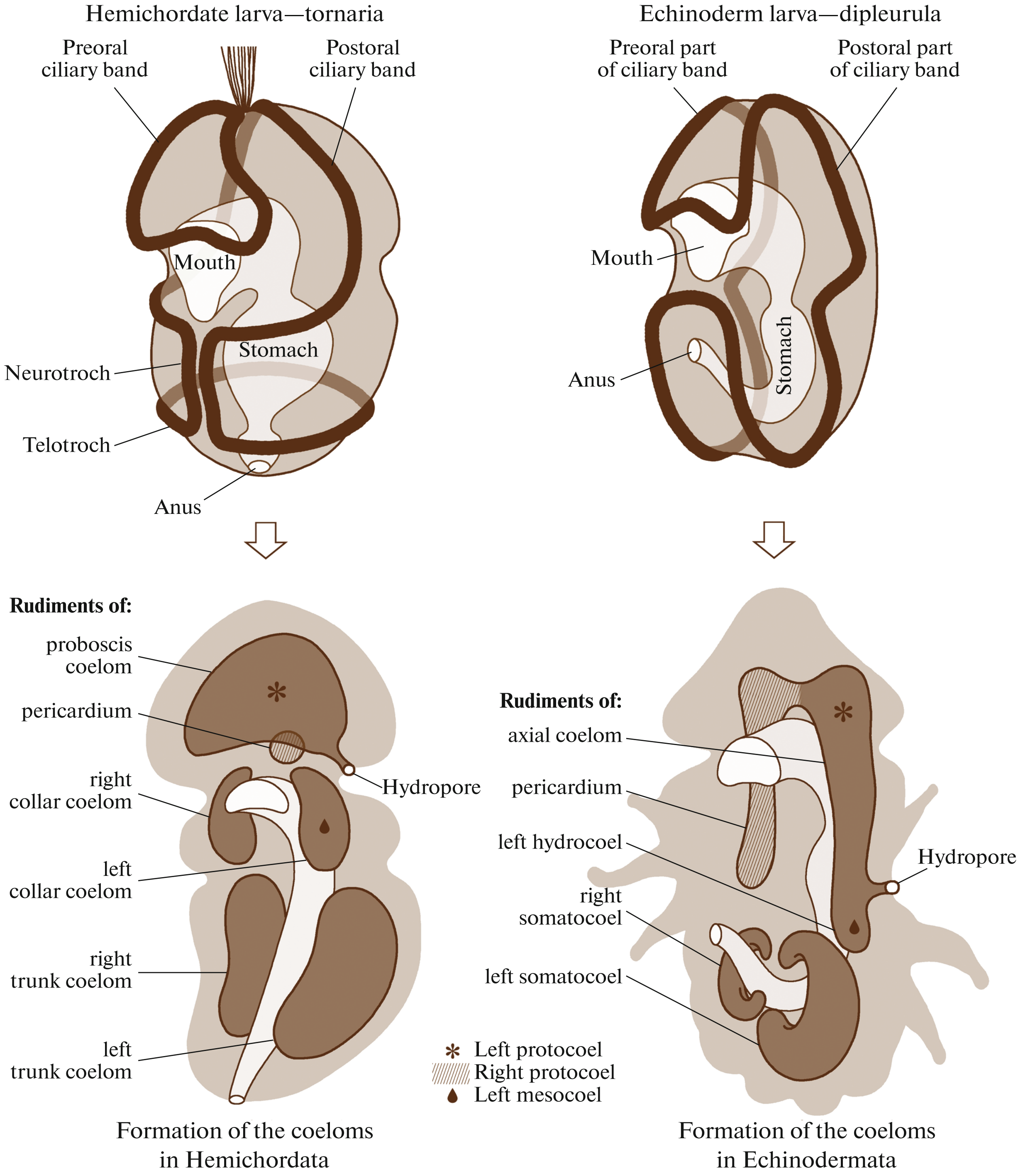
This subdivision of coelomic regions of the ancestor of Ambulacraria is evident from the ontogeny of the present-day Hemichordata and Echinodermata and morphology of their larvae that is so similar (Fig. 4), that it allowed I.I. Metschnikoff to combine these two phyla of deuterostomes into the clade Ambulacraria (Metschnikoff, 1881). The similar formation of the coelomic rudiments of hemichordates and echinoderms and their homologous state (Fig. 4) were mentioned in classical works (MacBride, 1898; Fedotov, 1923, 1924; Svetlov, 1957; Beklemishev, 1964).

During the larval development of the juveniles of Hemichordata, three pairs of coelomic rudiments form: (i) the anterior preoral protocoels, (ii) the perioral mesocoels, and (iii) the posterior metacoels (Bateson, 1884; MacBride, 1898; Davis, 1908; Stiasny, 1914a, 1914b; Stiasny-Wijnhoff and Stiasny, 1926, 1927; Rao, 1953; Kaul-Strehlow and Stach, 2013). The left protocoel of the hemichordate larva is much larger than the right protocoel and is open to the environment by an aperture (hydropore) from the left side of the larva (Fig. 4) (Bateson, 1885; Spengel, 1893; Horst, 1939; Ruppert and Balser, 1986; Kaul-Strehlow and Stach, 2013). The mesocoels evolve symmetrically forming the left and right collar coeloms (Fig. 4). The metacoels also evolve symmetrically; however, the left gill pore originates earlier than the right one during the formation of the first pair of gill pores (Kaul-Strehlow and Stach, 2013).

Three pairs of coelomic rudiments are also characterized for the larvae of Echinodermata: (i) the anterior axocoels (protocoels), (ii) the intermediate hydrocoels (mesocoels), and (iii) the posterior somatocoels (metacoels). The asymmetry of echinoderm coeloms with a dominant left side, however, is more pronounced relatively to hemichordates (Fig. 4). The common axohydrocoel rudiment of many echinoderms remains undivided for a long time; it communicates with the environment by a hydropore from the left side. Further, the axohydrocoel is divided into two parts: a large left axocoel merged with the left hydrocoel and still opened outside by the hydropore and a small right axocoel not connected with the environment. Often, no right hydrocoel forms (Field, 1892; Bury, 1895; MacBride, 1903, 1907; Gemmill, 1914; Ohshima, 1921; Narasimhamurti, 1933; Olsen, 1942; Ivanova-Kazas, 1978a; Ruppert and Balser, 1986; Malakhov and Cherkasova, 1991; Balser et al., 1993). The right somatocoel is small and either forms one small ring around the gut or merges with the left somatocoel, whereas the left somatocoel occupies a significantly large volume in the body of the juvenile echinoderm than the right somatocoel and also forms several (3–6) independent rings around the gut (Selenka, 1867; Ludwig, 1880; Hamann, 1887; Bury, 1888, 1895; Cuénot, 1888, 1891; Hérouard, 1889; MacBride, 1896, 1903, 1907; Goto, 1897; Clark, 1898; Brooks and Grave, 1899; Reichensperger, 1905; Gemmill, 1912, 1914, 1915, 1920; Ubisch, 1913; Osterud, 1918; Runnström, 1927; Narasimhamurti, 1933; Hörstadius, 1939; Olsen, 1942; Chia, 1968; Malakhov and Cherkasova, 1992; Ezhova et al., 2013, 2014, 2015, 2017, 2018, 2020).

Preoral Region of the Body and the Protocoel

The preoral region of the body (proboscis) was probably used for locomotion (Fig. 5). For many present-day hemichordate acorn worms (Enteropneusta: Harrimaniidae, Ptychoderidae), it is a main locomo-


Hemichordate larva—tornaria

Echinoderm larva—dipleurula

Formation of the coeloms in Hemichordata

Formation of the coeloms in Echinodermata

Fig. 4. Structure of larvae of Hemichordata and Echinodermata (based on Heider, 1909; Gemmill, 1914; Stiasny-Wijnhoff and Stiasny, 1926, 1927; Malakhov and Cherkasova, 1991) and formation of their coelomic rudiments.

tory organ with an evolved musculature, which is formed by epithelial-muscular cells organized into several layers (see Ezhova and Malakhov, 2010). The proboscis is used for burrowing sediments by peristaltic contractions, whereas the trunk is pulled following the proboscis along the path produced (Knight-Jones, 1952; Rao, 1954; Hyman, 1959). Pterobranchia (Graptolithoidea) inhabit tubes or cavities of the coenecium and their preoral region is the main locomotory organ. This is a discoid glandular shield, which functions as a crawling foot (Johnston and Muirhead, 1951; Hyman, 1959; Lester, 1985; Ruppert et al., 2004). Adults of extant echinoderms contain no evident preoral region. Nonetheless, at the end of the

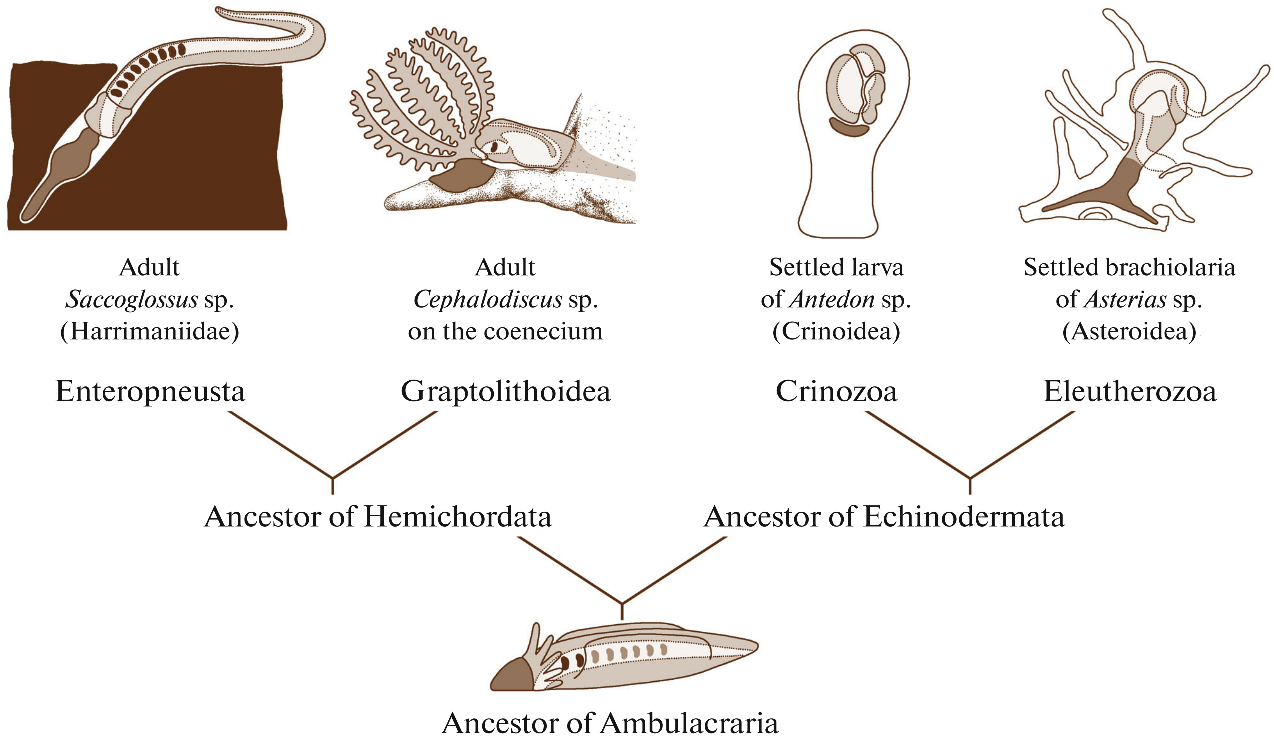


Fig. 5. Locomotory function of the preoral region (darker) of the body of Ambulacraria. Based on Enteropneusta (Knight-Jones, 1952), Graptolithoidea (Pterobranchia) (Schepotieff, 1907b; Lester, 1985), Crinoidea (Thompson, 1865; Seeliger, 1892; Engle, 2012), and Asteroidea (Goto, 1897; Gemmill, 1914; Ivanova-Kazas, 1978a).

pelagic stage, the planktotrophic larvae of sea stars (Echinodermata: Asteroidea) are characterized by the formation of three brachiolar arms (adhesive arms) on the preoral lobe, which contain the diverticules of the preoral coelomic region and a sucker-like organ is developed between the brachiolar arms. The brachiolar arms are supplied by glands producing a glue-like secretion and are necessary for temporary attachment of the larva to various underwater objects, whereas a larva uses a muscular sucker-like organ for long-term attachment to the substrate before metamorphosis (Goto, 1897; Gemmill, 1914; Ivanova-Kazas, 1978a). Other classes of Eleutherozoa exhibit metamorphosis without attachment, thus their preoral lobe is unclear (Ivanova-Kazas, 1978a). The lecithotrophic larvae of crinoids (Echinodermata: Crinoidea), a sister group to other present-day echinoderms (Fig. 1), however, settle on the substrate after 2–3 days of swimming and are attached by the anterior end (Thompson, 1865; Ivanova-Kazas, 1978a; Engle, 2012). At this moment, the rudiment of the protocoel faces the anterior end of the larva. During metamorphosis, when the anterior end of the larva is elongated and transformed into a stalk, the coelomic larval complex is inverted and the rudiment of the right metacoel (right somatocoel) comes to face the stalk. Exactly from the right metacoel the five growths grow, which further form a chambered organ (Barrois, 1888; Seeliger, 1892; Mortensen, 1920).

The most important synapomorphy of Ambulacraria (axial complex or “heart-kidney”) is related to the coelomic rudiments of the preoral region (left and right protocoels) (Fig. 6). The axial complex is the kidney of hemichordates and echinoderms (Ruppert and Balser, 1986; Ruppert and Smith, 1988; Mayer and Bartolomaeus, 2003; Cameron, 2005; Swalla and Smith, 2008; Ziegler et al., 2009; Kaul-Strehlow and Stach, 2013; Ezhova et al., 2016b; Ezhova and Malakhov, 2016a, 2021a). The central structures of the axial complex are: (i) the axial or proboscis coelom (a derivative of the left protocoel) and its coelomoduct, (ii) the pericardial coelom (a derivative of the right protocoel), and (iii) the axial organ or glomerulus (a system of haemal capillaries between the folds of the coelothelia of the aforesaid coeloms) (Fig. 6). The pericardial coelom embraces the heart and, due to contraction of mioepithelial cells of pericardium, blood from the heart is pushed to the capillaries of the axial organ. Outside, the walls of the capillaries are covered by podocytes (cells with an excretory function). The axial organ provides ultrafiltration of the liquid from the haemal capillaries to the cavity of the axial coelom through the basal lamina. Passing between the podocyte processes, the primary urine is modified into secondary urine, which contains meta-

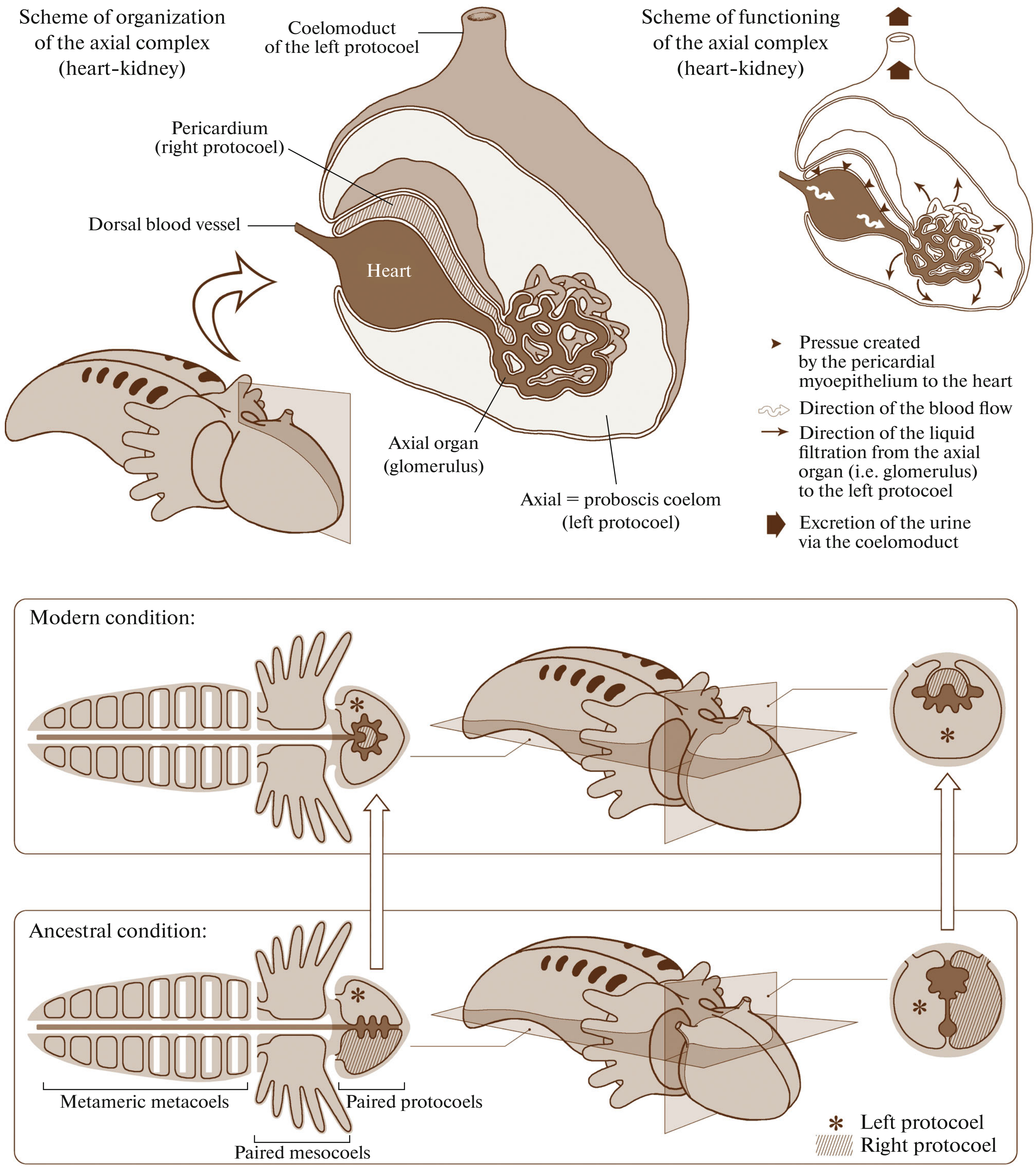


Fig. 6. Axial or "heart-kidney" complex of Ambulacraria and evolutionary transformations of its forming protocoels.

bolic products and is evacuated through the coelomoduct (Fig. 6; see details in Ezhova and Malakhov, 2021a).

The left and right protocoels of the bilaterally symmetrical ancestor of deuterostomes were most likely equally developed and each of them opened into the environment by its coelomoduct (Fig. 6) (the echinoderms could be characterized by a typical atavism with formation of two (rather than one) hydropores: left and right; see Ivanova-Kazas, 1978a). The ancestors of Ambulacraria, which were characterized by burrowing or tubular lifestyle (evident from the presence of

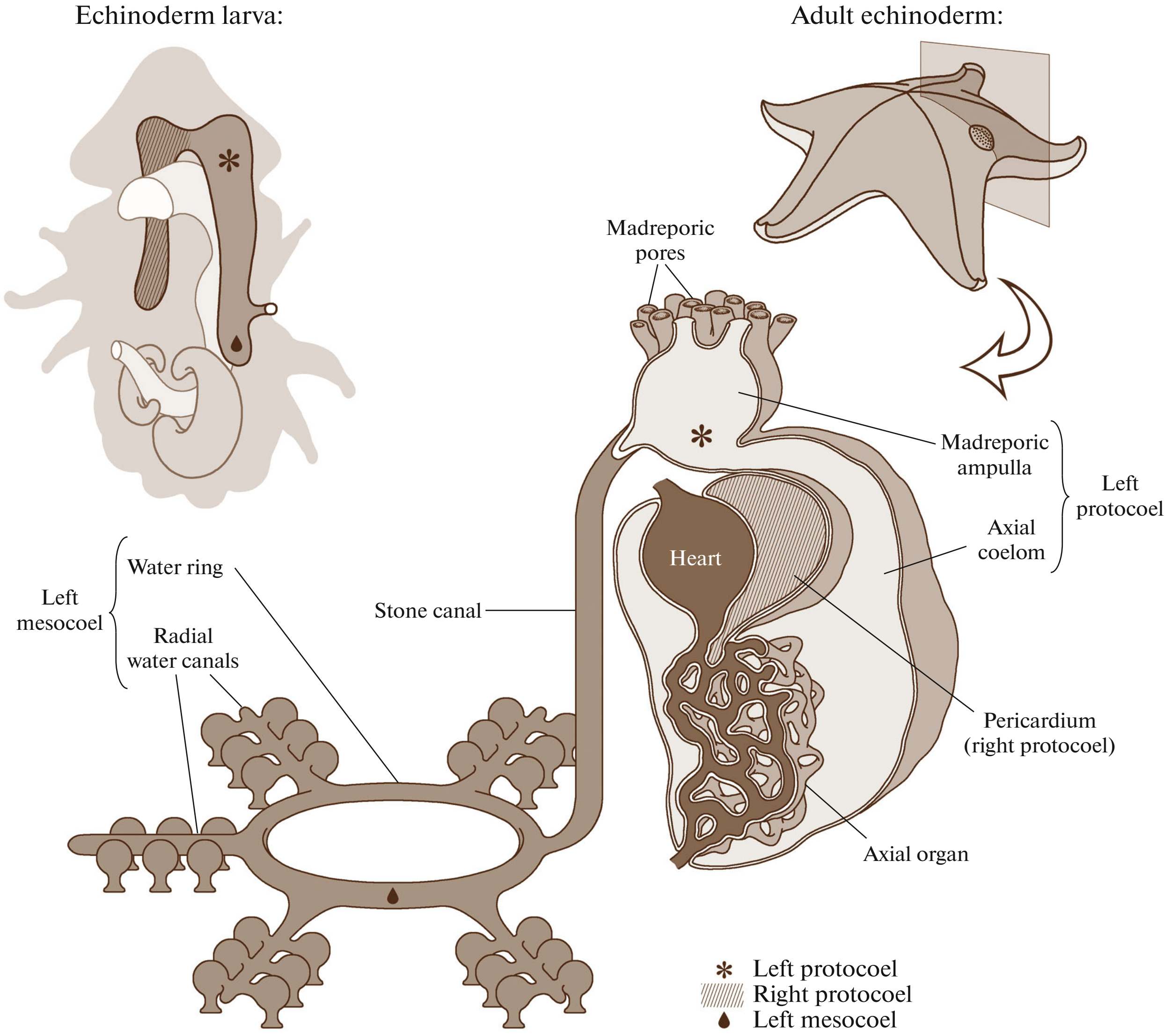


Fig. 7. Structure of the derivatives of the left and right protocoels (axocoels) and left mesocoel (hydrocoel) of Echinodermata: an axial complex and ambulacral (water-vascular) system.

the genital wings protecting the gill slits) exposed only the anterior end of the body to the water column. Thus, the excretory function, which was primarily distributed between numerous metameric coelomoducts, became focused in coelomoducts of the very anterior coeloms: the proboscis and the collar. A similar event (i.e., oligomerization of the amount of coelomoducts and specialization of the anterior pair of coelomoducts) is typical, e.g., for tube-dwelling annelids: Sabellidae, Oweniidae, and Siboglinidae (Claparède, 1873; Meyer, 1887; Fauvel, 1959; Ivanov, 1960; Land and Nørrevang, 1977; Malakhov et al., 1996; Karaseva et al., 2012; Rimskaya-Korsakova et al., 2020).

Dissymmetry of the protocoels of Ambulacraria is related to the transformation of one of the protocoels (right one) to the pulsatory organ. This led to the reduction of the right coelomoduct and hypertrophy of the left protocoel and left coelomoduct (Fig. 6). It can be suggested that the choice of the right protocoel as the pericardium and the left protocoel as the excretory coelom (rather than vice versa) could be an occasional evolutionary event (similar to torsion leading to the fundamental dissymmetry of gastropods, which could have occurred clockwise or counterclockwise, but occurred counterclockwise in reality; see Naef, 1911). Dissymmetry of the protocoels (Figs. 4, 6, 7), which originated as a result of extreme oligomerization of excretory organs of the common ancestor of Ambulacraria (only this dissymmetry is typical in Hemichordata), was responsible, to a certain degree, for the direction of dissymmetry of Echinodermata.

Perioral Region of the Body and the Mesocoel

The representatives of the three phyla from the taxon Deuterostomia are characterized by perioral ciliated tentacles, which are used for collection of small food particles by means of mucociliary transport. Among chordates, hemichordates, and echinoderms, these tentacles are characteristic of Cephalochordata, Pterobranchia, and Holothuroidea, respectively. In all cases, ciliated tentacles are the appendages of the perioral (collar) segment and are supplied by coelomic canals from the second pair of coeloms. It is unlikely that the ciliated tentacles, which were supplied by coelomic cavities from the collar coeloms, appeared independently in three branches of Deuterostomia. It is possible that the common ancestor of Deuterostomia had ciliated tentacles on the perioral segment, but they only remained in a few present-day groups. Moreover, there are grounds to believe that perioral ciliated tentacles were typical of the common ancestor of Eubilateria (see Malakhov et al., 2019).

Thus, the presence of tentacles is not a synapomorphy of the Ambulacraria clade in contrast to the number of tentacles. The ancestor of Ambulacraria probably had two tentacle groups: five tentacles from each side of the collar region. The same number of tentacles (pinnate arms) occur from each side of representatives of the pterobranchs *Cephalodiscus* (see Andersson, 1907; Ridewood, 1907; Schepotieff, 1907b, 1907c, 1908; Hyman, 1959; Lester, 1985; Benito and Pardos, 1997; Maletz and Cameron, 2016). Because of the small sizes, another present-day representative of the pterobranchs *Rhabdopleura* has simpler organization (in particular, without gill slits) and possesses only a pair of pinnate arms (by one from each side) (Schepotieff, 1904, 1906, 1907a, 1907c; Hyman, 1959; Lester, 1985; Dilly, 1985; Halanych, 1993).

In two classes of Hemichordata, the collar region is organized with considerable differences (Fig. 8). Pterobranchia retain the tentacles, which collect the food particles from the water column using up-stream filtration (Halanych, 1993). The deposit feeders Enteropneusta are characterized by reduced tentacles, and they collect food by ciliated epithelium of the proboscis and the collar, which move the mucus-food cords with organic particles toward the mouth (Barrington, 1940; Knight-Jones, 1953; Burdon-Jones, 1962; Thomas, 1972; Cameron, 2009; Gonzalez and Cameron, 2009). The deep-water acorn worms of the family Torquaratoridae exhibit a secondary epibenthic lifestyle and collect food particles from a bottom water layer and a surface sediment coat. They collect food particles using wide lips of the collar region (Fig. 8), which thus functionally replace the lost ciliated tentacles (Holland et al., 2005; Osborn et al., 2012; Priede et al., 2012; Jones et al., 2013).

During metamorphosis, Holothuroidea possesses five ciliated tentacles around the mouth. They are supplied by coelomic canals only from the left hydrocoel, which loops the esophagus in a horseshoe shape (Selenka, 1876; Semon, 1888; Inaba, 1930; Chia and Buchanan, 1969; Smiley, 1986; Malakhov and Cherkasova, 1992; Dolmatov and Yushin, 1993). In the subsequent stages of metamorphosis, five radial canals of the water-vascular system are formed in the metamorphosing holothuroids between the five coelomic canals extending into the ciliated tentacles. These five radial canals grow from the hydrocoel ring in the aboral direction (Selenka, 1876; Becher, 1907; Edwards, 1909; Runnström, 1927; Inaba, 1930; Malakhov and Cherkasova, 1992; Dolmatov and Yushin, 1993; Dolmatov et al., 2016). The presence of five primary tentacles (inherited from the common ancestors of Ambulacraria) of the ancestors of echinoderms predetermined the formation of five radial canals and in this way it predetermined the formation of the pentaradial symmetry, which is dominant in organization of Holothurozoa, Crinozoa, and other echinoderms (Fig. 8).

Trunk Region of the Body and the Metacoel

The trunk region of Enteropneusta is characterized by features of metamerism primary for Deuterostomia (Fig. 9): the metameric gill slits, metameric hepatic sacculations, and gonads. Enteropneusta contain no dissepiments, which divide the trunk coelom into metameric compartments. The reduction of the dissepiments is typical of burrowing forms because the dissepiments prevent from the movement of the coelomic liquid during peristaltic locomotion inside the sediment, e.g., for echiurids and sipunculids, the metameric origin of which is proven (see Hessling, 2002; Struck et al., 2007; Kristof et al., 2008; Wanninger et al., 2009; Goto et al., 2020). It is possible that an atypical radial musculature across the coelom of the trunk region of Enteropneusta (see Spengel, 1893; Horst, 1939; Hyman, 1959; Benito and Pardos, 1997) is a rudiment of the musculature of the reduced dissepiments.

As for echinoderms, the aforementioned dissymmetry of the protocoels and mesocoels is also typical of the metacoels (somatocoels). The left metacoel forms three to six circumintestinal rings, whereas the right metacoel forms only one ring around the gut in the aboral part of the body (Fig. 9). In Eleutherozoa, this ring of the right metacoel communicates or even merges with the largest left metacoel ring, thus forming a common perivisceral coelom. The right metacoel of Crinoidea is divided into five compartments and form a chambered organ in the aboral part of the body, which passes into the attaching stalk of sea lilies (Barrois, 1888; Seeliger, 1892; Mortensen, 1920). We suggest that these rings of the left somatocoel, which follow each other along the gut, represent a remnant of the primary coelomic metamerism of the common ancestor of Bilateria (Fig. 9; for details, see Ezhova and Malakhov, 2021b).

The comparison of expression of genes of the *Hox* cluster of the present-day Hemichordata and Echinodermata can reveal the organization of the metacoelo-

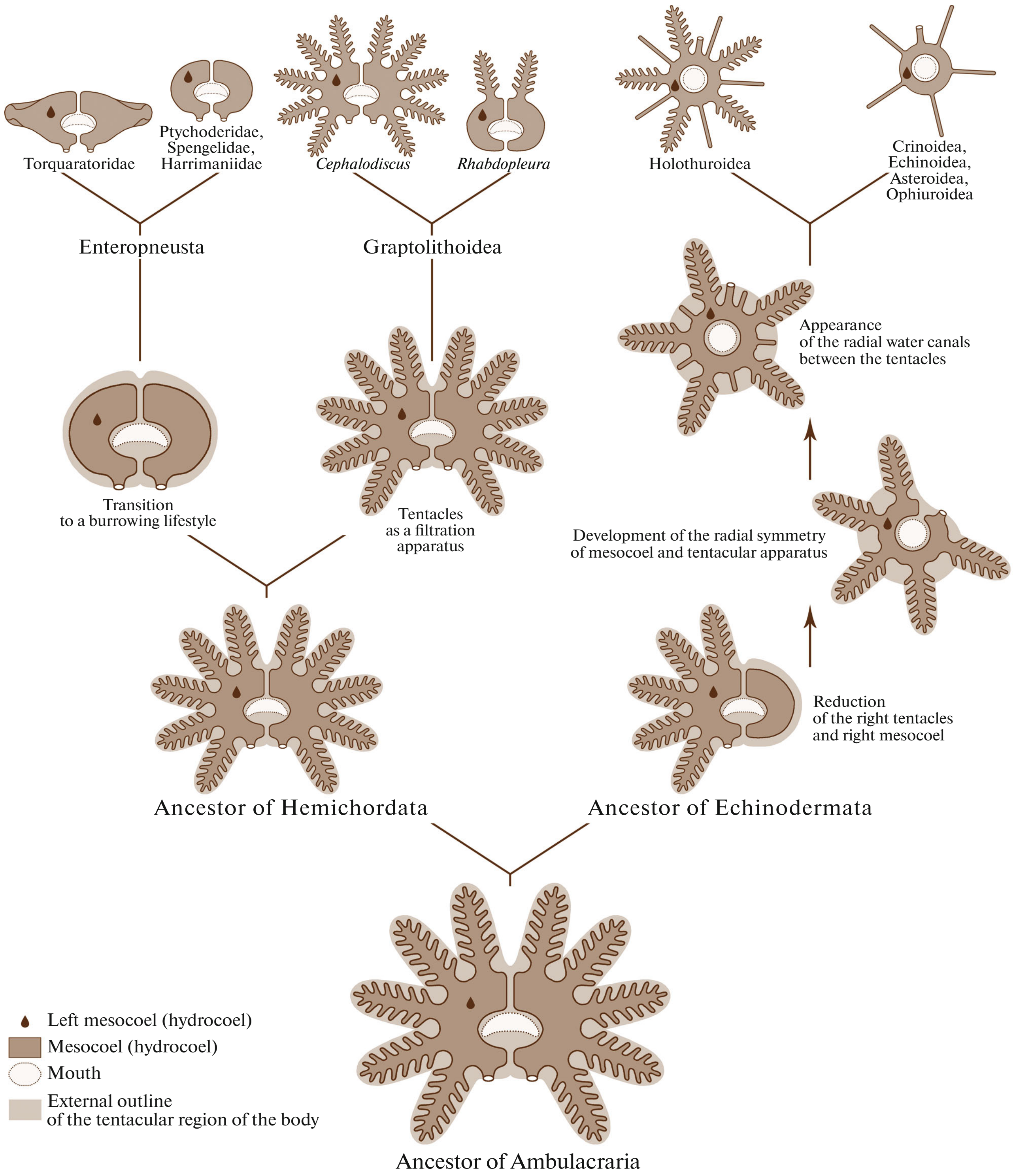


Fig. 8. Evolution of the mesocoel (hydrocoel) of Ambulacraria.

mic region of the ancestors of Ambulacraria and possible metamerism of the left metacoel of echinoderms. The *Hox* genes regulate the formation of the regions of the Bilateria body along the anterior-posterior axis. The preoral and tentacle regions of the body of most present-day Bilateria are free of expression of *Hox* genes; their expression begins beyond the tentacle region enhancing from the anterior end to the posterior one (Fig. 10) (Fröbius et al., 2008; Bakalenko et al., 2013; Janssen et al., 2014; Martin et al., 2016;

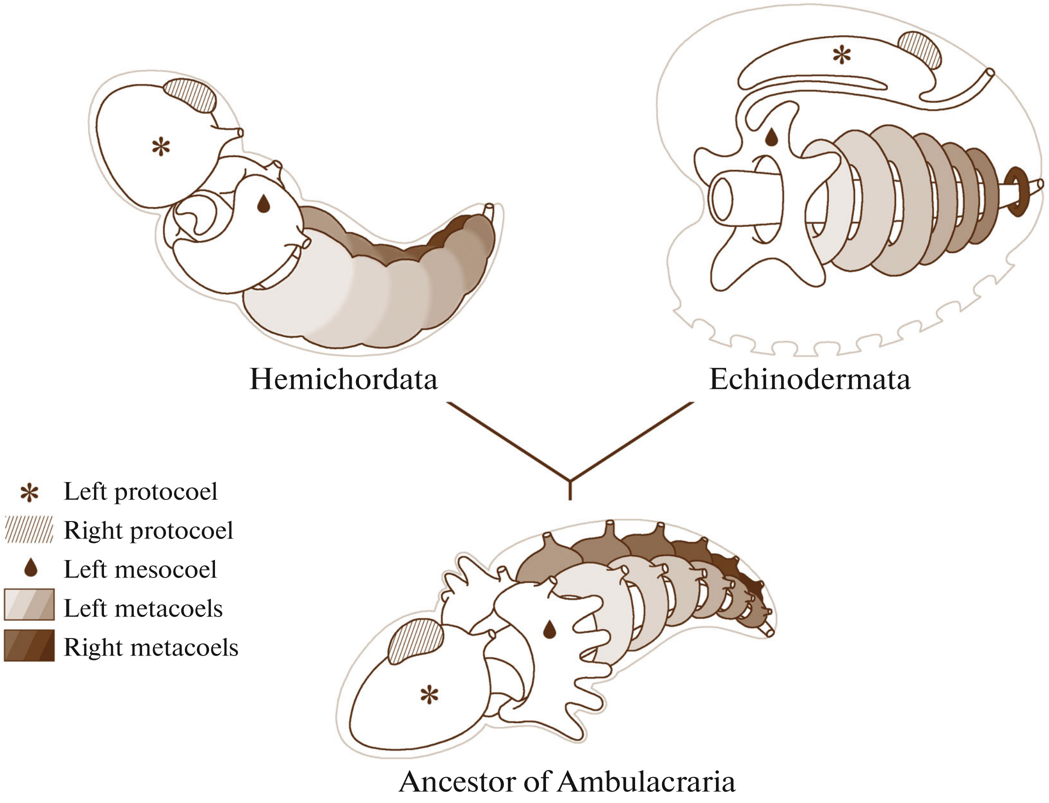


Fig. 9. Metamerism of metacoels (somatocoels) of the ancestors of Ambulacraria and its traces in present-day hemichordates and echinoderms.

Gaunt, 2018; Gąsiorowski and Hejnol, 2020). In present-day Enteropneusta, *Hox* genes are also expressed only in the trunk (metacoelic) region (Aronowicz and Lowe, 2006; Cannon et al., 2009b; Urata et al., 2009; Freeman et al., 2012; David and Mooi, 2014; Gonzalez et al., 2017). They are located following each other in a cluster in a strong order and are expressed in the ectoderm in compliance with the colinearity (Fig. 11). It is evident that this is the ancestral organization of the *Hox* cluster (Freeman et al., 2012; Gaunt, 2018) and the expression of *Hox* genes of the ancestor of Ambulacraria also began in the area of the first pair of gill slits in compliance with the colinearity similarly to the present-day acorn worms.

Present-day echinoderms are characterized by striking rearrangements of the *Hox* cluster and considerable violations of the colinearity (Fig. 11). Sea cucumbers and sea urchins even exhibit translocation of the anterior *Hox* genes (*Hox1*, *Hox2*, *Hox3*) to the end of the cluster and inversion of the direction of its transcription. One more difference between two phyla of Ambulacraria is related to the expression of *Hox* genes. In hemichordates, it occurs mostly in the ectoderm, whereas most *Hox* genes of echinoderms are expressed in the mesoderm (Table 1) and not only in the metacoels but also in the mesocoel. Thus, in contrast to most Bilateria, the expression of *Hox* genes is partly propagated to the tentacle region.

These changes in location and expression of *Hox* genes are probably a result of complex morphological transformations which affected echinoderms during their evolution (Rozhnov, 2012). Similar events can be observed in other groups of Eubilateria, which are characterized by significant transformations of the structure plan. For example, the violations in the organization of *Hox* genes and colinearity are also registered for Tunicata (Fig. 11) (David and Mooi, 2014). The *Hox* cluster of Ascidiacea is divided into several parts (Ikuta et al., 2004) and *Hox10* occurs between *Hox4* and *Hox5* (Caputi et al., 2008). The *Hox* cluster of Appendicularia is "atomized" decomposing on individual genes (Seo et al., 2004), which is probably related to a strongly dominant few-celled developmental type. During the development of the representatives of the basal mollusk group Polyplacophora, the *Hox* genes are expressed in compliance with colinearity (Fritsch et al., 2015), but this principle in expression of *Hox* genes is significantly violated in a series Scaphopoda–Cephalopoda–Gastropoda (Wollesen et al., 2018) as if parallel with more complex changes in the structural plan of these mollusk groups. The mollusks also exhibit a "shift" of the area of expression of *Hox* genes (Gąsiorowski and Hejnol, 2020) similar

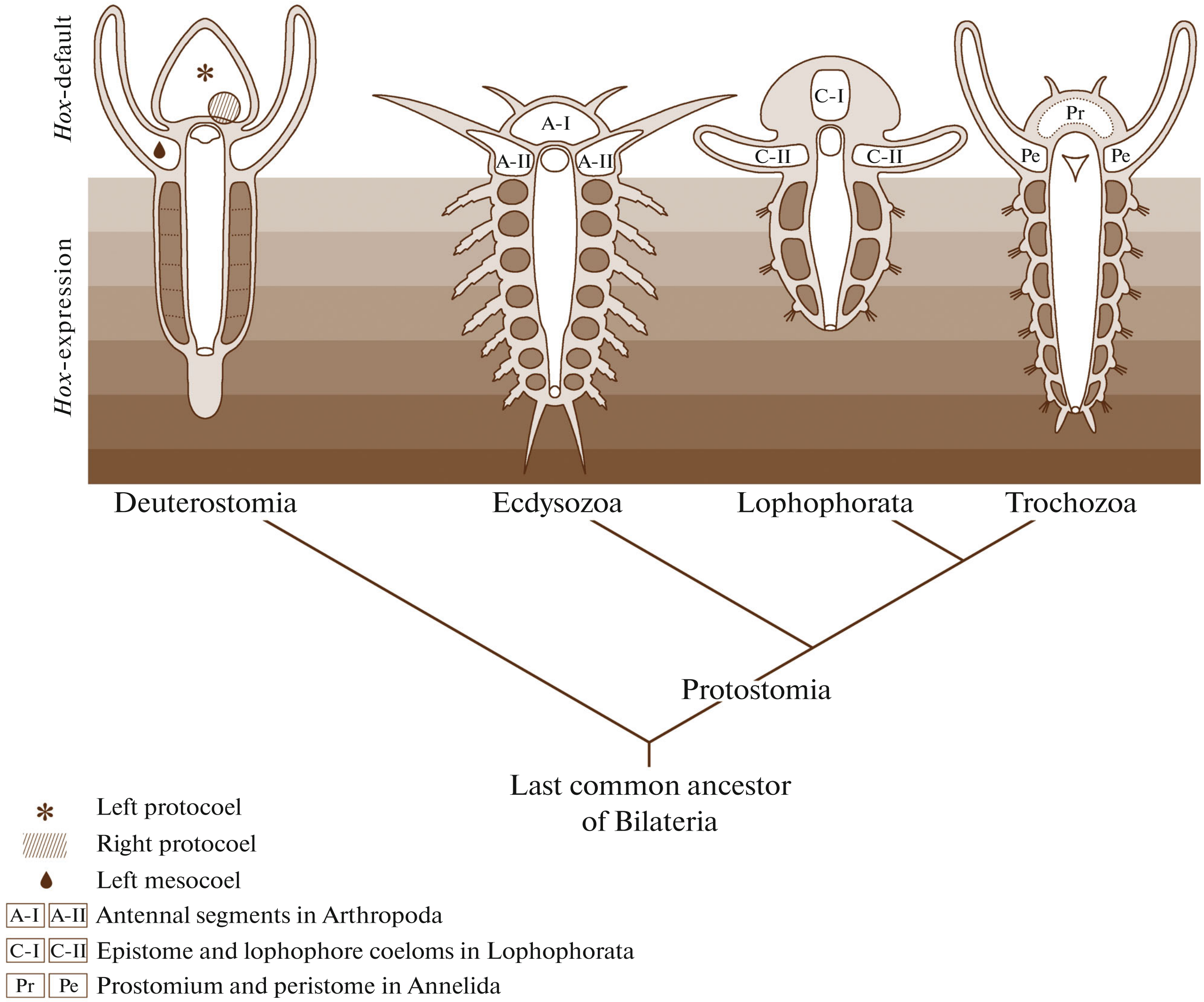


Fig. 10. Expression of *Hox* genes in four main branches of Bilateria (based on Bakalenko et al., 2013; Martin et al., 2016; Gaunt, 2018; Gąsiorowski and Hejnol, 2020).

to that observed in Ambulacraria (Table 1). If most *Hox* genes of Annelida and Brachiopoda are expressed in the ectoderm and only some *Hox* genes (in addition to ectoderm) are expressed in the mesoderm, than all ten *Hox* genes of Polyplacophora are expressed in the mesoderm and only five of ten genes are additionally expressed in the ectoderm. Gastropoda, which underwent the most complex rearrangement, exhibits a nearly complete “shift” of the expression of *Hox* genes from the ectoderm.

The comparison of the character of spatial expression of *Hox* genes of Ambulacraria and animals with evident segmentation (Cephalochordata (Deuterostomia), Annelida, and Arthropoda (Protostomia)) is noteworthy. These groups are characterized by segment-by-segment expression of *Hox* genes typically with a step of one or two segments (Fig. 12). The expression of *Hox* genes of Echinodermata is “shifted” to the metacoels (Table 1), but nonetheless, it remains segment-by-segment as for true metameric animals (Fig. 12). The solution of this problem requires additional studies focused on the localization of *Hox* gene expression not only in echinoderm larvae, but also in juvenile stages with the metacoel already divided on the metameric coelomic rings.

Types of Larvae and Life Cycle

A pelagic-benthic life cycle with planktotrophic larvae arranged by a common plan is initial for Ambulacraria. Metschnikoff (1870) found that tornaria, which was previously mistaken for an echinoderm larva, is a stage of the development of hemichordates. On the basis of this observation, Metschnikoff (1881) suggested a new taxon Ambulacraria Metschnikoff, 1881 including Echinodermata and Hemichordata.

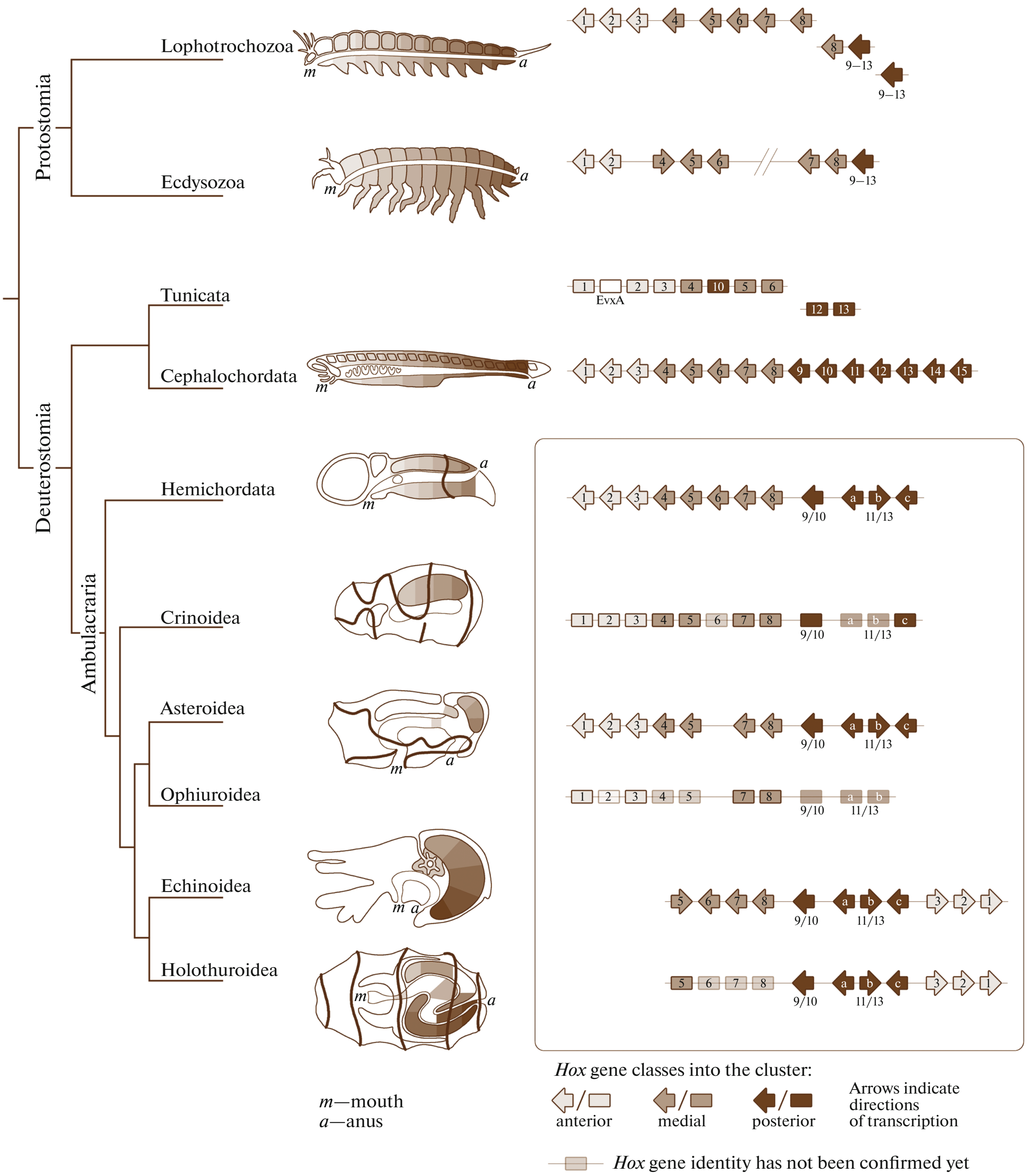


Fig. 11. Organization of *Hox* cluster and expression of *Hox* genes of segmented animals and Ambulacraria. The gradients do not mean the precise homology of segments. Based on Lophotrochozoa (Polychaeta) (Fröbius et al., 2008; Bakalenko et al., 2013), Ecdysozoa (Crustacea) (Lemons and McGinnis, 2006; Martin et al., 2016), Tunicata (Ikuta et al., 2004; Caputi et al., 2008; David and Mooi, 2014), Cephalochordata (Wada et al., 1999; Holland et al., 2008a), Hemichordata (Aronowicz and Lowe, 2006; Urata et al., 2009; Freeman et al., 2012), Crinoidea (Hara et al., 2006; Byrne et al., 2016), Asteroidea (Cisternas and Byrne, 2009; David and Mooi, 2014), Ophiuroidea (Mito and Endo, 2000; David and Mooi, 2014; Byrne et al., 2016), Echinoidea (Arenas-Mena et al., 2000; Byrne et al., 2016), and Holothuroidea (Kikuchi et al., 2015); in general part—David and Mooi, 2014; Byrne et al., 2016; Gaunt, 2018; figures of animals are based on the following works (Delage and Hérouard, 1898; MacBride, 1898; Cuénot, 1948; Ivanova-Kazas, 1978a; Ruppert and Balser, 1986; Malakhov and Cherkasova, 1992; Arenas-Mena et al., 2000; Aronowicz and Lowe, 2006; Holland et al., 2008a; Amemiya et al., 2015; Kikuchi et al., 2015; Martin et al., 2016).

Table 1. Expression of *Hox* genes of various species of Ambulacraria

Species	Group	Reference	*Hox* genes											
			Hox1	*Hox2*	*Hox3*	*Hox4*	*Hox5*	*Hox6*	*Hox7*	*Hox8*	*Hox9/10*	*Hox11/13a*	*Hox11/13b*	*Hox11/13c*
Saccoglossus kowalevskii	Hemichordata, Enteropneusta, Harrimaniidae	Aronowicz and Lowe, 2006; Freeman et al., 2012	Ectoderm, entoderm	Ectoderm, entoderm	Ectoderm	Ectoderm	Ectoderm	Ectoderm	Ectoderm	Ectoderm	Ectoderm	Ectoderm	Ectoderm, entoderm	Ectoderm, entoderm
Schizocardium californicum	Hemichordata, Enteropneusta, Spengelidae	Gonzalez et al, 2017	Ectoderm		Ectoderm	Ectoderm	Ectoderm	Ectoderm	Ectoderm		Ectoderm, entoderm	Ectoderm	Ectoderm	Ectoderm
Metacrinus rotundus	Echinodermata, Crinoidea	Hara et al., 2006					Metacoels		Ectoderm, archenteron, metacoels	Archenteron, metacoels	Metacoels			
Asterias rubens	Echinodermata, Asteroidea, Forcipulatida	Thorndyke et al., 2001	Nerves											
Parvulastra exigua	Echinodermata, Asteroidea, Valvatida	Cisternas and Byrne, 2009				Archenteron, protocoel, mesocoel, metacoels								
Strongylocentrotus purpuratus	Echinodermata, Echinoidea, Carinacea	Arenas-Mena et al., 1998, 2000		Metacoels	Metacoels	–			Ectoderm, nerves, mesenchyme, metacoels	Metacoels	Metacoels	Spines, metacoels	Spines, entoderm, metacoels	
Holopneustes purpurascens	Echinodermata, Echinoidea, Carinacea	Morris and Byrne, 2005, 2014; Byrne et al., 2016			Mesocoel, metacoels	–	Mesocoel, left metacoel					Archenteron, mesocoel	Archenteron, mesocoel	Archenteron, mesocoel
Peronella japonica	Echinodermata, Echinoidea, Irregularia	Tsuchimoto and Yamaguchi, 2014; Byrne et al., 2016	Ectoderm		Spines, metacoels	–	Ectoderm, left metacoel	Center of imaginal disk (rudiment)	Left metacoel	Left metacoel	Metacoels	Left metacoel	Ectoderm, entoderm, left metacoel	
Apostichopus japonicus	Echinodermata, Holothuroidea	Kikuchi et al., 2015	Ectoderm, entoderm, mesenchyme				Metacoels		Ectoderm, archenteron, entoderm,	Archenteron, entoderm, metacoels	Mesocoel, metacoels	Entoderm, metacoels	Archenteron, entoderm, mesenchyme, metacoels	Entoderm, metacoels

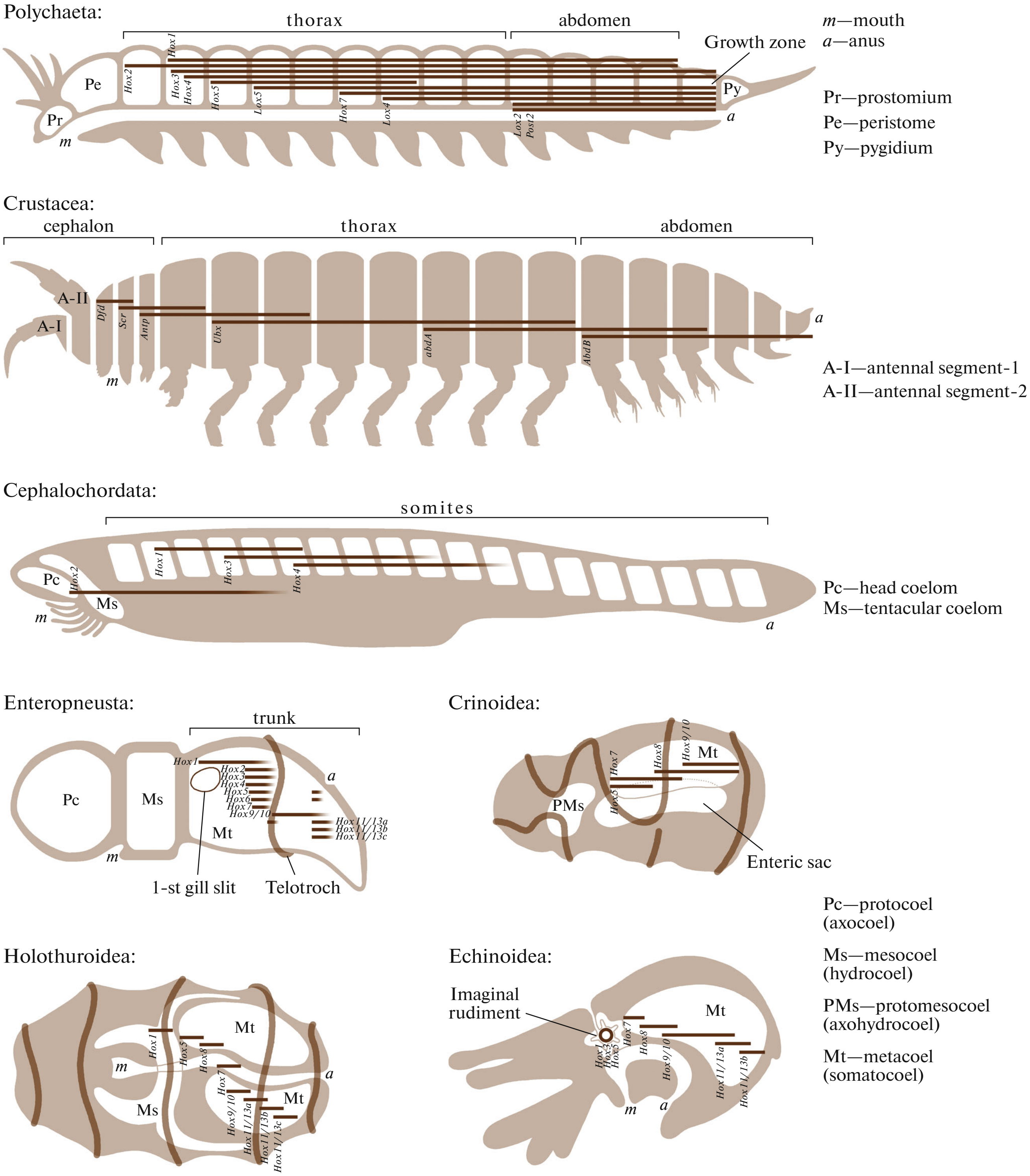


Fig. 12. Segment-by-segment expression of *Hox* genes of animals with striking metamerism of coeloms and limbs (Polychaeta, Crustacea, Cephalochordata) and representatives of Ambulacraria (based on Wada et al., 1999; Arenas-Mena et al., 2000; Aronowicz and Lowe, 2006; Hara et al., 2006; Bakalenko et al., 2013; Tsuchimoto and Yamaguchi, 2014; Kikuchi et al., 2015; Martin et al., 2016; Gaunt, 2018).

This suggestion was not recognized by contemporaries and was not adopted for a long time. Only nowadays, due to successes in molecular phylogenetics, his idea has been brought back to life, and the taxon Ambulacraria became firmly established in zoological literature (Furlong and Holland, 2002; Dohle, 2004;

Peterson, 2004; Bourlat et al., 2006; Cannon et al., 2009a; Hejnol et al., 2009; Edgecombe et al., 2011; Perseke et al., 2011, 2013; Freeman et al., 2012; Tarver et al., 2013; Kaul-Strehlow and Röttinger, 2015; Kaul-Strehlow et al., 2015; Ezhova and Malakhov, 2016a, 2016b; Peterson and Eernisse, 2016; Formery et al., 2019).

The blastula and gastrula stages of Enteropneusta occur below the egg cover, but the cells of the ectodermal epithelium at the gastrula stage become ciliated and the embryo begins to spin actively (see Tagawa et al., 1998; Urata and Yamaguchi, 2004; Urata et al., 2014). After hatching, the secondary mouth appears on the ventral side of the larva following by the formation of the ciliary bands and the larva starts active feeding (Figs. 4, 13). The ciliary ornament of tornaria is well known from classical and present-day works (Agassiz, 1872; Bateson, 1884; Morgan, 1891, 1894; Spengel, 1893; Heider, 1909; Stiasny, 1914a; Stiasny-Wijnhoff and Stiasny, 1926, 1927; Dawydoff, 1948; Jägersten, 1972; Urata and Yamaguchi, 2004; Miyamoto and Saito, 2007; Nielsen and Hay-Schmidt, 2007; Lin et al., 2016; Gonzalez et al., 2018). It includes an adoral ciliary zone rimmed by preoral and postoral ciliary bands, a neurotroch (a ciliary band along the middle line of the ventral side), and a ring telotroch around the anus on the posterior end of the larva, which plays an important role in locomotion (Fig. 4).

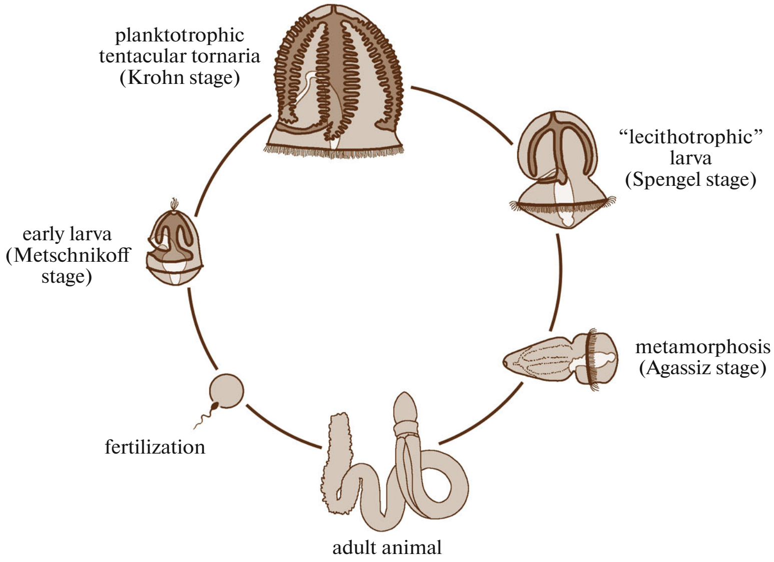
The comparative analysis shows that the elements of the ciliary ornament of tornaria could be compared with ciliary structures of the trochophore larvae: the preoral and postoral ciliary bands of tornaria could be homologous with a prototroch and a metatroch, respectively, whereas the neurotroch of the trochophore and the telotroch of the trochophore correspond to the neurotroch of tornaria and telotroch of tornaria, respectively (Malakhov et al., 2019). Within the hypothesis of the cited work, the bilaterally symmetrical larvae of Eubilateria originate from the bottom-dwelling juvenile individuals, which were uplifted into the water column as a result of prolongation of the pelagic stage of life cycle. The ciliated tentacles of the bottom-dwelling individuals gave rise to the adoral ciliary zone of the larvae rimmed by ciliary bands (Fig. 14). The suggested common ancestor of Eubilateria used these tentacles to collect food particles by mucociliary transport, and this function is preserved by the larvae (Malakhov et al., 2019). The larvae of the deuterostome animals use up-stream collecting of food particles, when the cilia of ciliary bands beat away in opposite directions providing an inflow of water in the adoral ciliary zone and food particles fall to this zone due to reversal of the action of cilia (Strathman, 1971, 1975; Strathmann and Bonar, 1976; Gilmour, 1985, 1986, 1988; Hart, 1991; Lacalli, 1993; Riisgård and Larsen, 2010).

The form of the adoral ciliary zone and ciliary bands of the planktotrophic tornariae can be very intricate. At Metschnikoff stage, the preoral and postoral bands form loops (Fig. 13) (Metschnikoff, 1870; Morgan, 1891, 1894; Spengel, 1893; Stiasny-Wijnhoff and Stiasny, 1926, 1927). The large tornariae exhibit a more complex structure of the ciliary bands. At Krohn stages, the tentacle-like processes form along the course of the preoral and postoral ciliary bands (Fig. 13) (Krohn, 1854; Morgan, 1891; Stiasny-Wijnhoff and Stiasny, 1927; Damas and Stiasny, 1961; Hadfield, 1975; Strathmann and Bonar, 1976; Nielsen and Hay-Schmidt, 2007). The planktotrophic larvae of Enteropneusta reach 9 mm in size and swim in the water column for up to five months (Kaul-Strehlow and Röttinger, 2015). At the next developmental stage (Spengel stage), the larva significantly decreases in sizes, the tentacle-like processes are reduced, and the configuration of the ciliary band is simplified (Spengel, 1893; Morgan, 1894; Stiasny, 1914b). This larva swims in the water column but does not feed, using the reserves accumulated at the previous planktotrophic stage (Fig. 13). During metamorphosis (Agassiz stage), the larva loses all ciliary bands except the telotroch (Fig. 13), falls down onto the seabed, and its body is subdivided into the proboscis, collar, and trunk regions (Agassiz, 1873; Morgan, 1891, 1894; Stiasny-Wijnhoff and Stiasny, 1926, 1927; Dawydoff, 1948; Jägersten, 1972; Urata and Yamaguchi, 2004; Miyamoto and Saito, 2007; Nielsen and Hay-Schmidt, 2007; Lin et al., 2016; Gonzalez et al., 2018).

In the development of the acorn worms of the family Harrimaniidae, a lecithotrophic larva corresponding to Agassiz stage is hatched from an egg and swims for a short period of time in the bottom water layer before its metamorphosis (Bateson, 1885, 1886; Burdon-Jones, 1952; Stach and Kaul, 2012). The development of present-day Graptolithoidea (Pterobranchia) is also lacks planktotrophic larvae. In pterobranchs, a planuliform larva with ciliated epithelium is released from the egg, and it immediately settles the metamorphosis (Stebbing, 1970; Dilly, 1973, 2013; Lester, 1988a, 1988b; Sato et al., 2008). Development with planktotrophic larvae (Fig. 13) can be considered initial for Hemichordata, whereas the transition to the lecithotrophic development is an apomorphic feature, which independently appeared in various phylogenetic branches of this phylum.

The planktotrophic development of Echinodermata is also considered a primary feature of the life cycle (Arnone et al., 2015). Development with planktotrophic larvae is typical of all classes of Eleutherozoa (although all classes include forms with lecithotrophic development). The representatives of the class Crinoidea include only development with lecithotrophic larvae (Fig. 15). Echinoderms with planktotrophic development (Fig. 13) demonstrate hatching ciliary blastula ready for free living (Selenka, 1876; Field, 1892; Grave, 1899a; Boveri, 1901; Ubish, 1913; Holland, 1981;

Life cycle of Enteropneusta (Hemichordata):



Life cycle of Holothuroidea (Echinodermata):

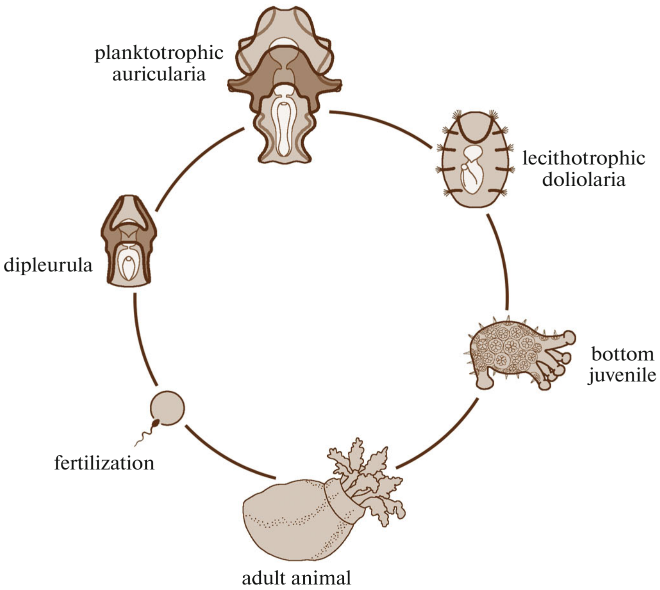
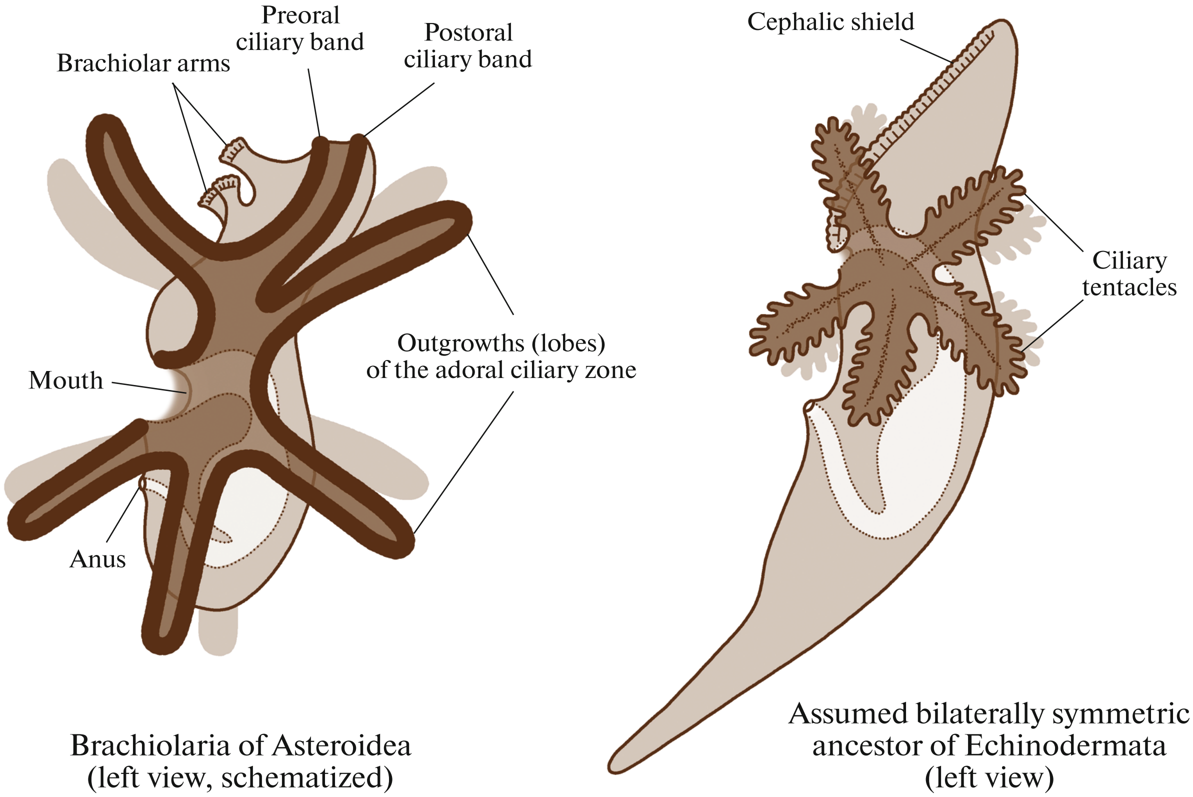


Fig. 13. Life cycle of most Enteropneusta (Hemichordata) (see Heider, 1909; Stiasny, 1914a, 1914b; Stiasny-Wijnhoff and Stiasny, 1926; Burdon-Jones, 1952; Gonzalez et al., 2017, 2018) and life cycle of Echinodermata using the example of Holothuroidea (Metschnikoff, 1869; Semon, 1888; Bury, 1895; Smiley, 1986; Malakhov and Cherkasova, 1991, 1992; Lacalli, 1993; Lacalli and West, 2000; Dolmatov et al., 2016; Rakaj et al., 2019).

Malakhov and Cherkasova, 1991). All further developmental stages occur in the water column. The early release of larvae from eggs at the ciliary blastula stage should be considered an archaic feature, which emphasizes the basal position of deuterostomes on the phylogenetic tree of Eubilateria.

The early larvae of the representatives of various classes of echinoderms (dipleurula larvae) have a similar structure. The echinoderm larvae are evidently similar to the tornariae of the acorn worms, but they differ in several important features (Fig. 4). The secondary mouth of the hemichordate larvae is opened on the ventral side, whereas the anus evolving instead of the blastopore, remains at the posterior end of the larva. The mouth of the echinoderm larvae also appears on the ventral side, whereas the anus, which is



Brachiolaria of Asteroidea (left view, schematized)

Assumed bilaterally symmetric ancestor of Echinodermata (left view)

Fig. 14. Structure of the adoral ciliary zone and intestine of sea star larva and reconstruction of the tentacle apparatus and digestive system of the suggested ancestor of echinoderms.

a derivative of the blastopore, is shifted to the ventral side (Fig. 4). Thus, the intestine of the planktotrophic larvae of echinoderms forms a specific loop, as a result of which the mouth and the anus become approached on the ventral side. It is likely that this feature is related to the absence of a circumanal ciliary ring (telotroch) of the echinoderm larvae. The adoral ciliary zone rimmed by preoral and postoral ciliary bands acquires the intricate configuration, which differs in the representatives of various echinoderm classes. The preoral and postoral ciliary bands of larvae of sea cucumbers, sea urchins, and brittle stars transit into each other forming a common circumoral ciliary band, whereas the preoral and postoral bands of the larvae of sea stars are divided in the area of the anterior larval end (Fig. 14) (Müller, 1853; MacBride, 1896, 1903; Dawydoff, 1928; Ivanova-Kazas, 1978a). It is noteworthy that the adoral ciliary zone of the developed sea star larvae (late bipinnaria and brachiolaria) forms five processes on each body side (Fig. 14). The traces of this pentameric organization of the adoral ciliary zone can be found in the position of auricules of the ciliary band of the holothuroid larvae or arms of pluteus of sea urchins (Lacalli, 1993). If we accept a hypothesis that the circumoral larval zone rimmed by the ciliary band is the perioral ciliary tentacles transformed to the larval stage (see Malakhov et al., 2019), it can be suggested that the five processes of the adoral ciliary zone of the larvae correspond to the five perioral ciliated tentacles (from each side) of the common ancestor of Ambulacraria (Fig. 14). It is noteworthy that, on the oral side, the Early Silurian ophiocistoid *Sollasina cthulhu* had five bundles of probably tube feet, which were located radially symmetrically around the mouth rimmed by the ambulacral ring (Sollas, 1899; Rahman et al., 2019). The structural plan of ophiocistoids is considered a possible ancestral scenario of the organization of the first holothuroids (Smith and Reich, 2013), although the presence of an Aristotle's lantern brings the ophiocistoids closer to ancient sea urchins (Reich and Smith, 2009).

The ciliary bands of the echinoderm larvae perform the locomotory and feeding functions at the same time. Like hemichordates, the planktotrophic larvae of echinoderms collect food particles using up-stream filtration (Strathman, 1971, 1975; Gilmour, 1985, 1986, 1988; Hart, 1991; Lacalli, 1993; Riisgård and Larsen, 2010).

There are two planktonic larvae in the life cycle of echinoderms with planktotrophic development similarly to the acorn worms: the feeding stage with complexly organized ciliary bands and short-lived nonfeeding stage with simplified ciliary structures (Fig. 13). Two larval stages are better expressed in the

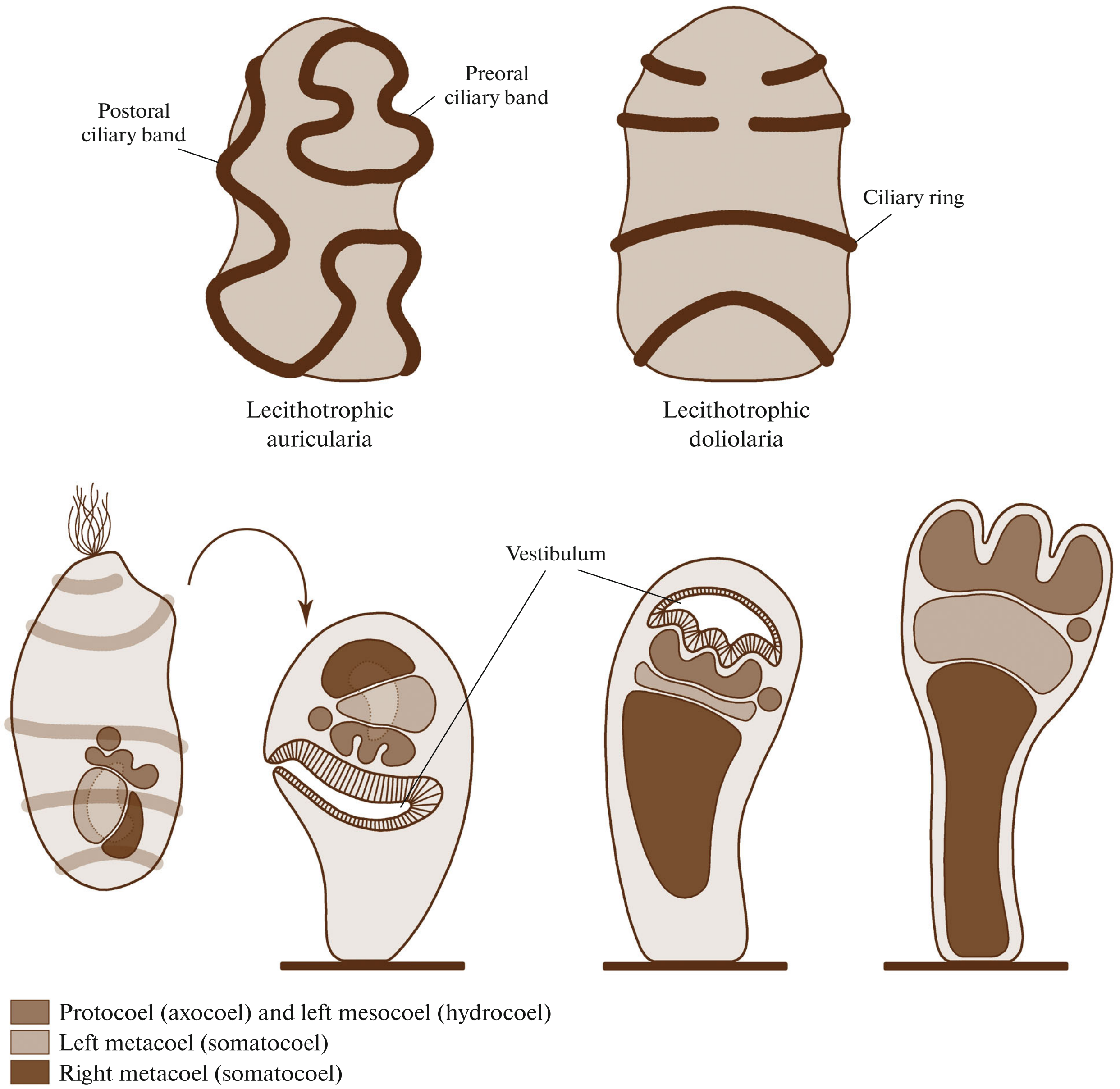


Fig. 15. Details of the larval development of Crinoidea: auricularia and doliolaria of sea lilies after (Nakano et al., 2003) and position of coelomic rudiments in the attached crinoid *Antedon*, (modified after Barrois, 1888; Seeliger, 1892).

development of the holothuroids (Metschnikoff, 1869; Semon, 1888; Bury, 1895; Smiley, 1986; Malakhov and Cherkasova, 1992; Lacalli, 1993; Lacalli and West, 2000; Dolmatov et al., 2016; Rakaj et al., 2019). The planktotrophic larva of the holothuroids (auricularia) has a complex configuration of the ciliary band, which forms the auricular ('ear-shaped') processes (Fig. 13). The auricularia swims in the water column for 2–3 weeks reaching 0.7–1.7 mm in size. The next stage larva in the development of the holothuroids (doliolaria) (Fig. 13) does not feed and uses resources accumulated by the auricularia. During the transition to doliolaria, the larval size decreases to 40–50%, and the body becomes barrel-shaped. The continuous ciliary band of the auricularia decomposes to five pairs of incomplete ciliary arches (Metschnikoff, 1869; Semon, 1888; Bury, 1895; Smiley, 1986; Malakhov and Cherkasova, 1992; Lacalli, 1993; Lacalli and West, 2000; Dolmatov et al., 2016; Rakai et al., 2018). The duration of the doliolaria stage of various species varies from 1–2 to 8–9 days. After that, the larva loses the ciliary rings, settles on the seabed, and undergoes metamorphosis transforming into a bottom-living juvenile stage (pentactula) (Fig. 13).

There are two trends in the evolution of ontogenesis of echinoderms. The life cycle of sea stars, sea urchins, and brittle stars, as a rule, is characterized by the presence of a planktotrophic larva with ciliary bands, which is transformed into a bottom-living juve-

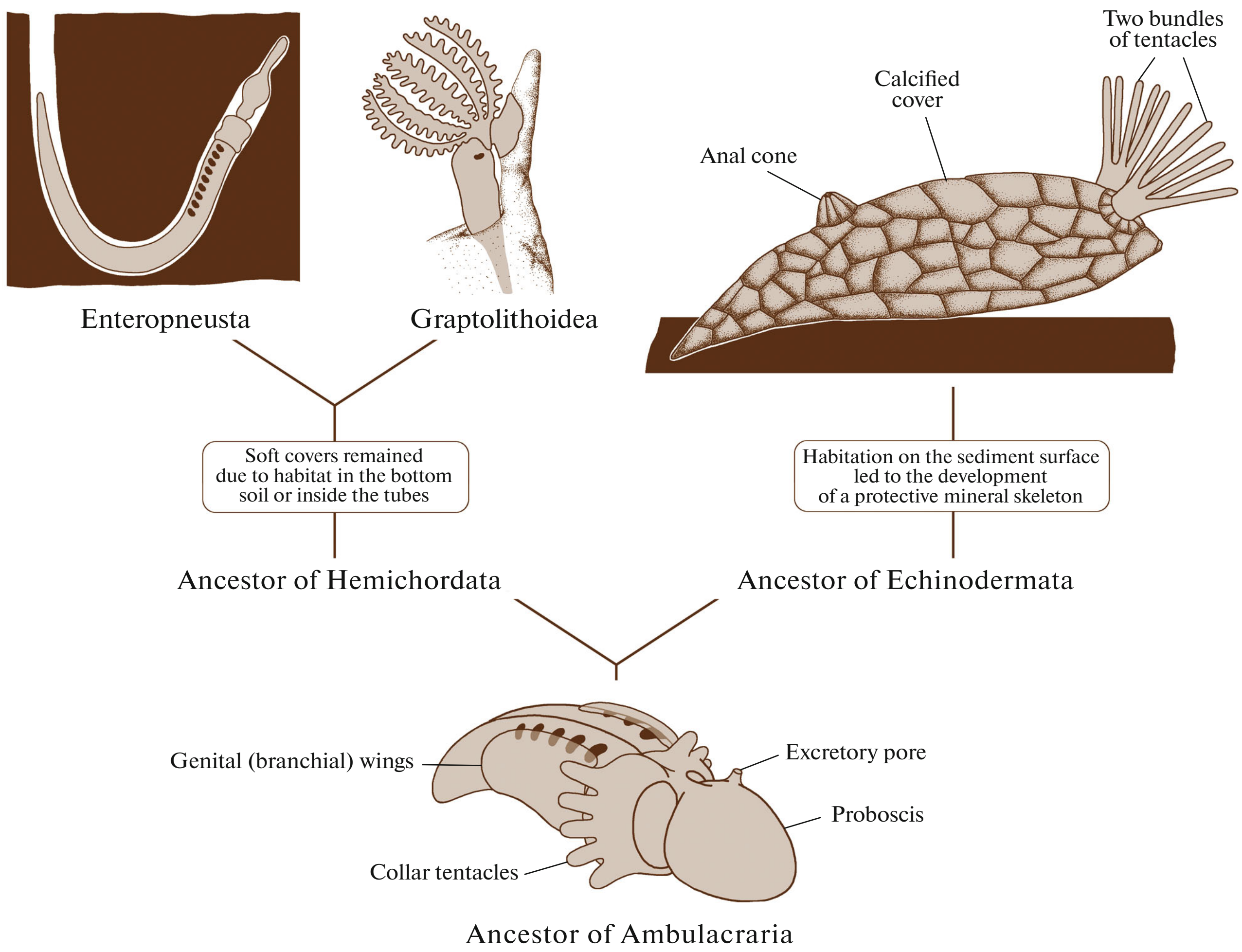


Fig. 16. Influence of living conditions on development of calcified covers of ancestors of echinoderms and primary (bilaterally symmetrical) stage of the formation of the echinoderm body plan: the shift of the anus to the ventral side due to burrowing in sediment by the posterior end of the body.

nile stage without doliolaria stage during the metamorphosis. On the other hand, most present-day crinoids have no planktotrophic larva and the barrel-shaped doliolaria is released from the egg (Fig. 15). There are grounds to believe that both these simplified scenarios of the life cycle formed from a more complex life cycle, which includes both planktotrophic larva with ciliary bands and non-feeding larva with ciliary rings. The development of some sea urchins and brittle stars prior to metamorphosis is characterized by the formation of the barrel-shaped stages with several ciliary rings that can be considered the evidence of the presence of doliolaria in ancestors of these groups (Grave, 1899b, 1903). On the other hand, the doliolarian stage in the ontogenesis of the sea lilies follows the lecithotrophic auricularia stage, which is similar to the planktotrophic auricularia of the holothuroids (Fig. 15). The continuous ciliary band of the auricularia of the crinoids decomposes into separate fragments, which give rise to incomplete ciliary rings of the doliolaria, similar to the development of the holothuroids (Lacalli, 2003; Nakano et al., 2003). All this suggests that initially the life cycle of Ambulacraria included two larval stages: the planktotrophic larva with a complex configuration of the ciliary band and a non-feeding larva with a simplified organization of ciliary stuctures. This developmental type is still characteristic of representatives of Enteropneusta among hemichordates and in Holothuroidea and stalked Crinoidea among echinoderms.

FORMATION OF THE ECHINODERM BODY PLAN

The origin of echinoderms can be subdivided into several stages.

(1) The common ancestor of Ambulacraria was an epibenthic mobile organism, which, probably, inhabited the soft sediment and could burrow the surface sediment layer leaving a symmetrical tentacle apparatus in the water column (Fig. 16). It had a differentiated preoral (proboscis) region, a perioral (collar)

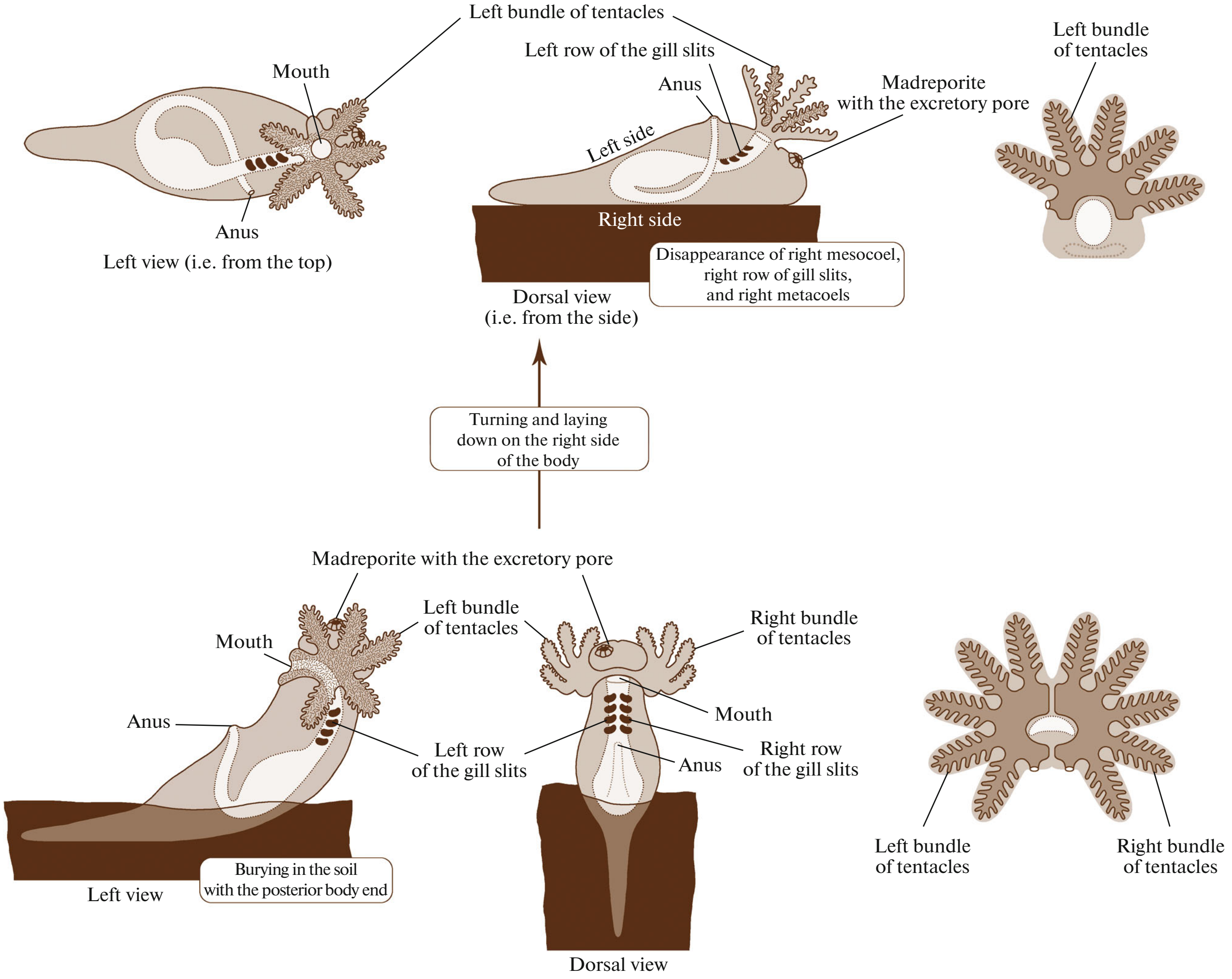


Fig. 17. Second (dissymmetric) stage of the formation of the echinoderm body plan: transition to lying on the right side of the body resulted in the disappearance of the right bundle of tentacles, right mesocoel, right row of gill slits, and a significant reduction of the right metacoel.

region with ciliated tentacles, and a trunk region with metameric gill slits and gill pores protected from contamination by genital wings curved to the dorsal side. The common ancestor of Ambulacraria, probably, partially retained the metamerism of the trunk coeloms, but the excretory function has already been focused only on the anterior coeloms like other burrowing animals (see above). Further evolution of Hemichordata was related to living in deep burrows in the sediments (Enteropneusta) or in tubes of coenecium (Graptolithoidea). This allowed Hemichordata to keep the soft covers but led to the reduction of the coelomic metamerism of the trunk region (Figs. 9, 16). The ancestors of Echinodermata probably lived in the uppermost sedimentary layer or on the substrate surface, thus they acquired the rigid covers, which were formed by skeletal plates of the connective tissue (Fig. 16). The common ancestor of Ambulacraria was generally a bilaterally symmetrical organism with dissymmetry only in the preoral (proboscis) coeloms and the position of an excretory pore (on the left side of the body) (Fig. 16), which was related to intensified excretory function.

(2) The organization of the early larvae of Echinodermata (dipleurula) indicates that the common ancestor of echinoderms was also a bilaterally symmetrical organism. The shift of the anus of the larvae to the ventral side suggests that the common ancestor of echinoderms lived in the sediment with the dorsal side partly buried (Fig. 16). The anus of Hemichordata, which are temporarily (as in juvenile *Saccoglossus*) or permanently attached by the posterior end of the body, is shifted to the dorsal side and this shift is especially striking in tubicolous Graptolithoidea (Pterobranchia).

Beginning from the Early Cambrian to the Devonian, bilaterally symmetrical animals, which are assumed to be echinoderms are known from the fossil

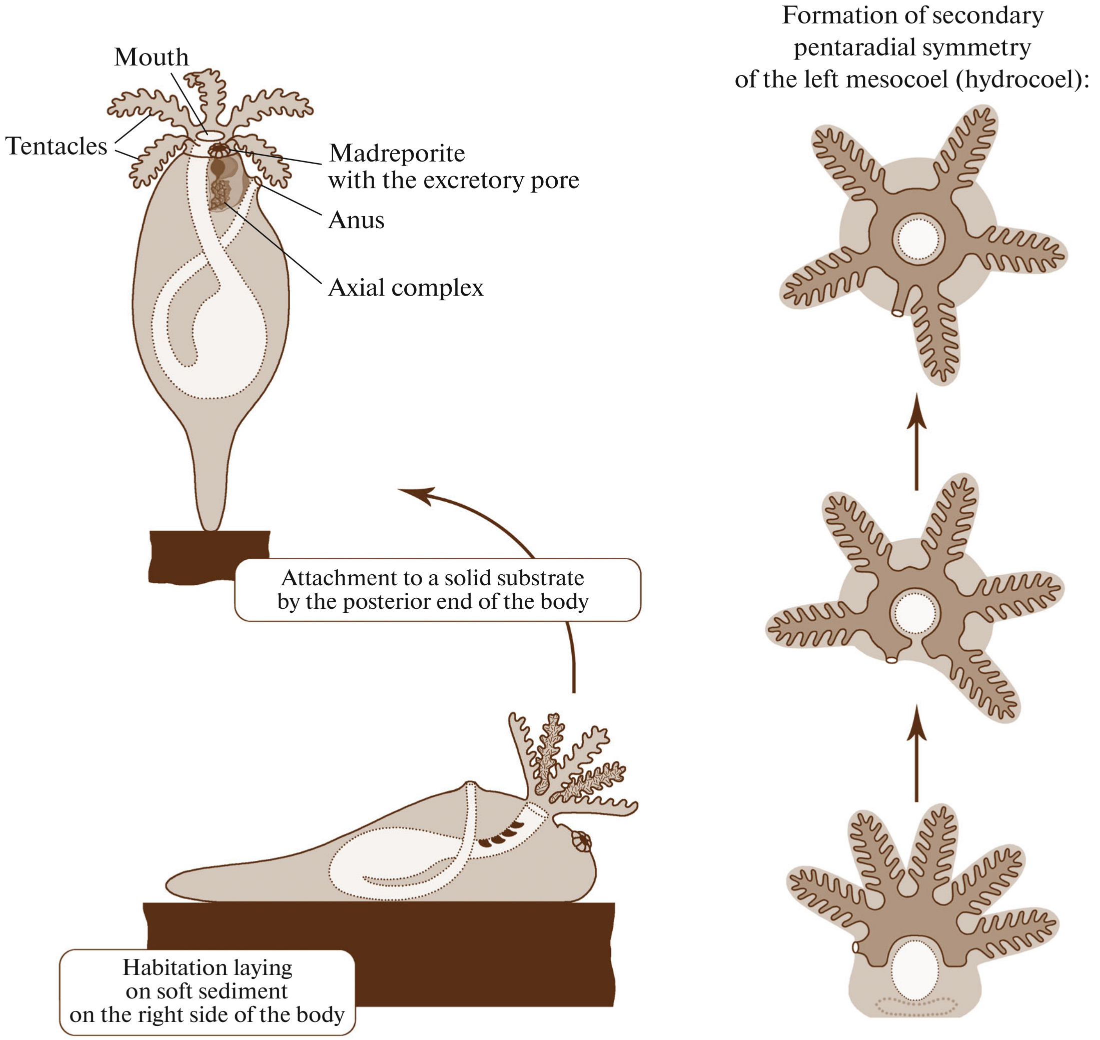


Fig. 18. Third stage of evolution of the echinoderm body plan: transition to sedentary lifestyle due to attachment by the posterior end of the body and formation of secondary radial symmetry.

record, e.g., *Protocinctus*, *Ctenocystis*, and *Ctenoimbricata* (see Robison and Sprinkle, 1969; Rahman and Clausen, 2009; Rahman and Zamora, 2009; Zamora et al., 2012; Rahman et al., 2015a). Many of them had a segmented mobile stalk, which, as suggested, was used for burrowing into the soft sediment or even for movement. The common ancestor of echinoderms was characterized by a symmetrical tentacle apparatus composed of five ciliated tentacles from each side (Figs. 16, 17), which were used to collect the food particles by mucociliary transport of the up-stream filtration type. This evolutionary stage is reflected in the development of five symmetrical processes of the adoral ciliary zone from each side of the larvae of some echinoderms (e.g., sea stars) (Fig. 14). Cambrian Edrioasteroidea also preserved bilateral symmetry at early ontogenic stages (Zamora et al., 2013).

(3) The next stage of the morphological evolution of Echinodermata is a transition from bilaterally symmetrical structure to dissymmetrical organization. In the ontogenesis of echinoderms, this stage is reflected in a complete reduction of the right hydrocoel and greatest development of the left somatocoel in comparison with the right somatocoel (Figs. 4, 8, 9). The reduction of the right hydrocoel (as well as right half of the tentacle apparatus) and the preferential development of the left somatocoel mean that the ancestor of the present-day echinoderms started to rest on the right side at a certain evolutionary stage (Fig. 17) (Malakhov, 1989; Jefferies et al., 1996). This position of the organism on the substrate surface could be preferred, because, in this case, the excretory pore (madreporite) located from the left was at the top and was open to the water column (Fig. 17). Thus, the dissymmetry of the protocoels, which originated as a result of intensification of the excretory function, could be a trigger for the choice of a dissymmetry sign, i.e., which side of the ancestor of the present-

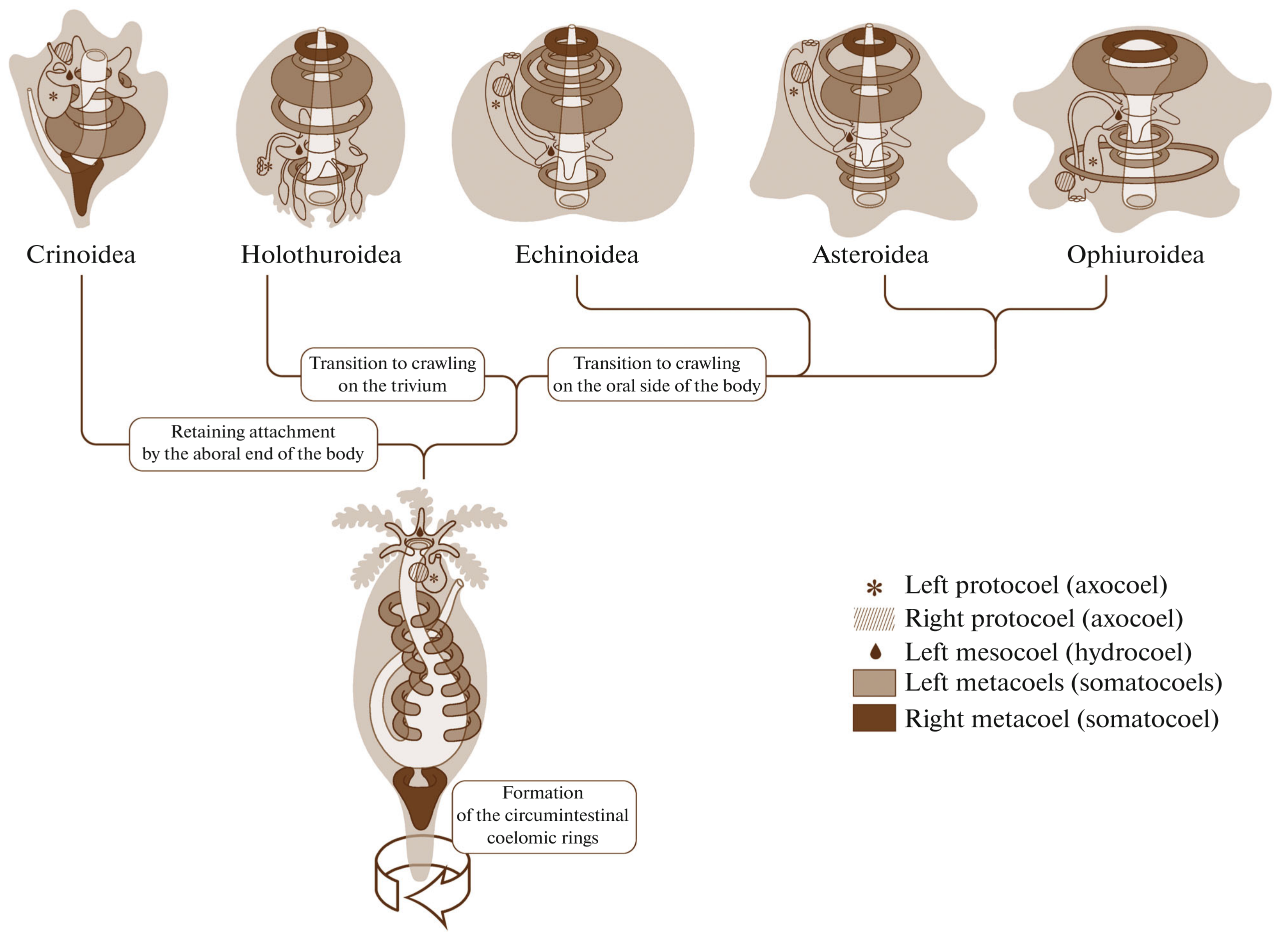


Fig. 19. Metamerism in structure of the left somatocoel of the present-day echinoderms.

day echinoderm was chosen for the settlement in the sediment.

This stage of the morphological evolution of echinoderms includes a large diversity of Early Paleozoic forms with dissymmetrical organization (see Ubaghs, 1968). The substrate-facing (probably, right) side was flat or even concave in contrast to the opposite (left) convex side as was shown, e.g., for *Syringocrinus* (see Gill and Caster, 1960; Ubaghs and Caster, 1967; Jefferies, 1986). The convex side of some forms is characterized by a row of metameric holes (probably, gill slits), the anal cone or madreporite (e.g., *Cothurnocystis*; see Bather, 1913; Ubaghs, 1963; Jefferies, 1969). A stalk, as can be suggested, served for anchoring and movement in the soft sediment (see Jefferies, 1972; Kolata et al., 1991, Jefferies et al., 1996; Sutcliffe et al., 2000; Lefebvre, 2003).

(4) The next stage of the evolutionary formation of Echinodermata is a transition to the sedentary lifestyle on the solid substrate (Fig. 18). At this stage, the ancestors of echinoderms were attached by the posterior end of the body. The mouth and surrounding tentacles became apical and the anus (as in many sedentary forms) was also shifted up, resulting in the formation of a typical intestinal loop. The lying Cambrian Cincta were characterized by a short stele at the posterior end, whereas the anal cone was already shifted laterally and forward closer to the mouth that indicates the formation of the intestinal loop (Zamora et al., 2012; Rahman et al., 2015b). The stele of Ordovician Soluta was used for attachment to solid substrates (Zamora et al., 2017).

The formation of secondary radial symmetry related to a sedentary lifestyle is accepted in most concepts of the origin of echinoderms (see Semon, 1888; Bury, 1895; Bather, 1900; Grobben, 1923; Hyman, 1955; Beklemishev, 1964; Ubaghs, 1967). This symmetry is pentaradial, which is probably because the common ancestor of echinoderms (probably, the common ancestor of Ambulacraria) was characterized by five tentacles from each side of the collar region (Fig. 18). The ancestor of Pelmatozoa+Eleutherozoa retained only five tentacles on the left side supplied by coelomic canals from the left hydrocoel (Fig. 18). The left hydrocoel forms a ring around the esophagus. In addition, present-day echinoderms contain several metameric rings formed by the derivatives of the left

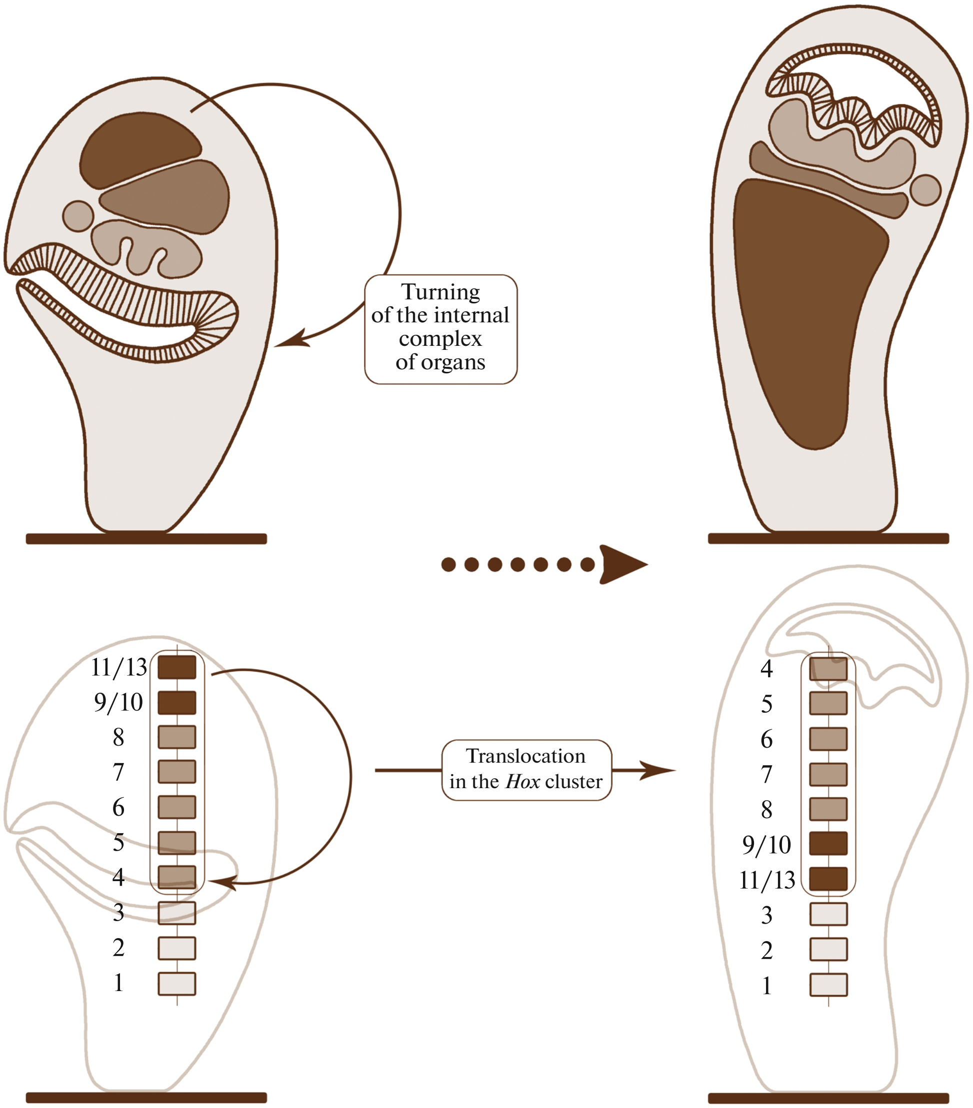


Fig. 20. Hypothesis explaining the translocation to the end of the *Hox* cluster and inversion of the direction of transcription of the anterior *Hox* genes (*Hox1*, *Hox2*, *Hox3*) of present-day Echinozoa by rotation of the embryonic coelomic complex occurred during the attachment of larval ancestral forms to the substrate.

somatocoel (Fig. 19). Taking into account that the common ancestor of Ambulacraria was a metameric organism, it is logical to suggest that these rings corresponded to the left metamers of the trunk coelom (Figs. 9, 19). The right somatocoel forms one ring, which probably corresponds to one of the posterior coelomic segments of the right side (Figs. 9, 19). The right metacoel (right somatocoel) is preserved because the derivatives of this coelomic segment formed a coelom of the stalk of attached echinoderms. During the metamorphosis of present-day Crinoidea, the right metacoel embraces the gut and, further, gives rise to five tubular diverticula growing to the stalk and forming a chambered organ (a coelomic system of the stalk) (Mortensen, 1920; Ivanova-Kazas, 1978a).

This circumstance raises a question on the origin of the attaching stalk of Pelmatozoa. In most concepts of the origin of echinoderms, it is suggested that the attaching stalk of Pelmatozoa originates at the expense of the preoral lobe, i.e., the proboscis region (Semon, 1888; Bury, 1895; Bather, 1900; Grobben, 1923; Hyman, 1955; Beklemishev, 1964; Ubaghs, 1967). This opinion originated because, during metamorphosis, the crinoid larvae are attached to the substrate by the ventral side of the anterior end of the body, which later gives rise to the stalk (Thompson, 1865; Barrois, 1888; Bury, 1888; Seeliger, 1892; MacBride, 1896). Temporary attachment by the preoral lobe is typical of the metamorphosing larvae of sea stars (Fig. 5) (Goto, 1897; Gemmil, 1914). If we consider this process as a recapitulation of the transformation of the preoral lobe into the stalk of ancient echinoderms, then the presence of the coelomic cavity of the protocoel (i.e., proboscis coelom) within the stalk should be expected. The chambered organ in the stalk of Crinoidea, however, originates from the right somatocoel rather than from the proboscis coelom (Barrois, 1888; Mortensen, 1920). The metamorphosis of Crinoidea reflects two stages of their evolution. The attachment to the substrate by the preoral lobe (which is also observed in the larvae of sea stars) reflects the ancient locomotion of deuterostomes using the proboscis region of the body (Fig. 5). Graptolithoidea (Pterobranchia) can crawl on the cephalic shield, which is a preoral lobe, and adult acorn worms use the proboscis region as the main burrowing organ. It is likely that the ancestors of echinoderms used the preoral lobe for crawling or temporary attachment. However, during the sedentary lifestyle, the ancestors of echinoderms were attached to the substrate by morphologically adjusted posterior end of the body (stalk), in a similar way to pterobranchs and some juvenile representatives of acorn worms, e.g., *Saccoglossus*.

During metamorphosis, the crinoid larva attaches to the substrate by the anterior end of the body and the vestibulum closes. After that, the inner complex of organs is rotated so that the right larval somatocoel in the posterior end becomes positioned in front of the attachment area (future stalk) (Figs. 15, 20). It is likely that these processes in the larval evolution of the echinoderm ancestors are responsible for the violation of the colinearity in location of *Hox* genes of the present-day Echinozoa, namely, translocation of genes *Hox1–Hox3* to the posterior end of the *Hox* cluster (Figs. 11, 20).

The sedentary lifestyle changed the structure of the tentacle apparatus, which is associated with the left hydrocoel (Fig. 8). The food-collecting grooves underlain by coelomic canals originated from the left hydrocoel were formed between the primary tentacles. These collecting grooves gave rise to the ambulacral (water-vascular) system: synapomorphy of the Pelmatozoa + Eleutherozoa clade. Exactly this new system of most echinoderms replaces the tentacle apparatus (Fig. 8). Primary tentacles, which are characteristic of the common ancestor of both Ambulacraria and Deuterostomia (possibly even the common ancestors of Eubilateria), are retained only in Holothuroidea.

(5) The last large evolutionary stage of echinoderms is related to the formation of the Eleutherozoa clade. In classical concepts (see Semon, 1888; Bury, 1895; Bather, 1900; Grobben, 1923; Hyman, 1955; Beklemishev, 1964; Ubaghs, 1967), the origin of Eleutherozoa is related to the transition to a mobile lifestyle: crawling on the oral surface. This lifestyle led to a shift of the anus (as well as the madreporite) to the aboral side (Fig. 19). The reverse displacement of the madreporite to the oral side was typical of Ophiuroidea, and is reflected in their larval evolution (see MacBride, 1907; Ezhova et al., 2015, 2016a).

Numerous traces of these stages of the evolution of Echinodermata in the structure and ontogenesis of present-day echinoderms need to be considered in detail in further work.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interests.

REFERENCES

Achatz, J.G., Chiodin, M., Salvenmoser, W., et al., The Acoela: on their kind and kinships, especially with nemertodermatids and xenoturbellids (Bilateria incertae sedis), *Org. Div. Evol.*, 2013, vol. 13, pp. 267–286.

Adrianov A.V., Malakhov V.V., and Yushin V.V., Loriciferans—a new taxon of marine invertebrates, *Biol. Morya*, 1989, no. 2, p. 70–72.

Agassiz, A., Tornaria, the young stage of *Balanoglossus, Am. Nat.*, 1872, vol. 6, pp. 636–637.

Agassiz, A., The history of *Balanoglossus* and *Tornaria, Mem. Am. Acad. Arts Sci.*, 1873, vol. 9, no. 2, pp. 421–436.

Aguinaldo, A.M.A., Turbeville, J.M., Linford, L.S., et al., Evidence for a clade of nematodes, arthropods and other moulting animals, *Nature*, 1997, vol. 387, pp. 489–493.

Amemiya, S., Hibino, T., Nakano, H., et al., Development of ciliary bands in larvae of the living isocrinid sea lily *Metacrinus rotundus, Acta Zool.*, 2015, vol. 96, no. 1, pp. 36–43.

Andersson, K.A., Die Pterobranchier der Schwedischen Südpolar-Expedition, 1901–1903, *Wiss. Erg. Schwed. Sudpolar-Exp. Stockh*, 1907, vol. 5, pp. 1–122.

Arenas-Mena, C., Cameron, A.R., and Davidson, E.H., Spatial expression of *Hox* cluster genes in the ontogeny of a sea urchin, *Development*, 2000, vol. 127, pp. 4631–4643.

Arenas-Mena, C., Martinez, P., Cameron, R.A., et al., Expression of the *Hox* gene complex in the indirect development of a sea urchin, *Proc. Natl. Acad. Sci. USA*, 1998, vol. 95, pp. 13062–13067.

Arnone, M.I., Byrne, M., and Martinez, P., Echinodermata, *Evolutionary Developmental Biology of Invertebrates*, vol. 6, Wien: Springer, 2005, pp. 1–57.

Aronowicz, J. and Lowe, C.J., *Hox* gene expression in the hemichordate *Saccoglossus kowalevskii* and the evolution of deuterostome nervous systems, *Integr. Comp. Biol.*, 2006, vol. 46, pp. 890–901.

Ax, P., *Das System der Metazoa III: Ein Lehrbuch der Phylogenetischen Systematik.* Heidelberg: Spektrum Akad., 2001.

Ax, P., *Multicellular Animals*, Berlin: Springer Sci. Bus. Media, 2012.

Bakalenko, N.I., Novikova, E.L., Nesterenko, A.Y., et al., *Hox* gene expression during postlarval development of the polychaete *Alitta virens, EvoDevo*, 2013, vol. 4, no. 13.

Balavoine, G., de Rosa, R., and Adouette, A., *Hox* clusters and bilaterian phylogeny, *Mol. Phyl. Evol.*, 2002, vol. 24, pp. 366–373.

Balser, E.J., Ruppert, E.E., and Jaeckle, W.B., Ultrastructure of auricularia larval coeloms: evidence for the presence of an axocoel, *Biol. Bull.*, 1993, vol. 185, no. 1, pp. 86–96.

Barrington, E.J.W., Observations on feeding and digestion in *Glossobalanus minutes, Quart. J. Micr. Sci.*, 1940, vol. 82, pp. 227–260.

Barrois, J., Recherches sur le Développement de la Comatule (*C. mediterranea*), *Rec. Zool. Suisse*, 1888, no. 4, pp. 545–651.

Bateson, W., The early stages in the development of *Balanoglossus, Q. J. Microsc. Sci.*, 1884, vol. 24, pp. 208–236.

Bateson, W., The later stages in the development of *Balanoglossus kowalevskii*, with a suggestion on the affinities of the Enteropneusta, *Q. J. Microsc. Sci.*, 1885, vol. 25, pp. 81–128.

Bateson, W., Continued account of the later stages in the development of *Balanoglossus kowalevskii*, and the morphology of the Enteropneusta, *Q. J. Microsc. Sci.*, 1886, vol. 26, pp. 511–533.

Bather, F.A., *The Echinoderma. A Treatise on Zoology*, pt. 3, London: Adam & Charles Black, 1900.

Bather, F.A., Caradocian Cystidea from Girvan, *Trans. Roy. Soc. Edin.*, 1913, no. 49, pp. 359–529.

Becher, S., *Rhabdomolgus ruber* Keferstein und die Stammform der Holothurien, *Z. Wiss. Zool.*, 1907, vol. 88, pp. 545–689.

Beklemishev V.N., *Osnovy sravnitel'noi anatomii bespozvonochnykh. T. 1. Promorfologiya. T. 2. Organologiya* (Fundamentals of Comparative Anatomy of Invertebrates, vol. 1. Promorphology, vol. 2, Organology). Moscow: Nauka, 1964.

Benito, J. and Pardos, F., *Hemichordata, Microscopic Anatomy of Invertebrates.* New York: Wiley-Liss, 1997, pp. 15–101.

Bourlat, S.J., Juliusdottir, T., Lowe, C.J., et al., Deuterostome phylogeny reveals monophyletic chordates and the new phylum Xenoturbellida, *Nature*, 2006, vol. 444, pp. 85–88.

Boveri, T., Die Polaritat der Oocyte, Ei und Larve der *Strongylocentrotus lividus, Zool. Jahrb. Abt. Anat. Ont. Tiere*, 1901, vol. 14, pp. 630–651.

Bromham, L.D. and Degnan, B.M., Hemichordates and deuterostome evolution: robust molecular phylogenetic support for a hemichordate+echinoderm clade, *Evol. Dev.*, 1999, vol. 1, no. 3, pp. 166–171.

Brooks, W.K. and Grave, C., *Ophiura brevispina*, *Mem. Nat. Acad. Sci. Wash.*, 1899, vol. 5, pp. 79–100.

Brusca, R.C. and Brusca, G.J., *Invertebrates*, Sunderland, Massachusetts: Sinauer Associates, 2003.

Burdon-Jones, C., Development and biology of the larva of *Saccoglossus horsti* (Enteropneusta), *Philos. Trans. R. Soc., B*, 1952, vol. 236, no. 639, pp. 553–590.

Burdon-Jones, C., The feeding mechanism of *Balanoglossus gigas, Mar. Sci. Lab. Univ. Wales*, 1962, no. 261, Zool. 24, pp. 255–280.

Bury, H., The early stages in the development of *Antedon rosacea, Philos. Trans. R. Soc., B*, 1888, vol. 179, pp. 257–301.

Bury, H., Metamorphosis of Echinoderms, *Quart. J. Micr. Sci.*, 1895, vol. 38, pp. 45–137.

Byrne, M., Martinez, P., and Morris, V., Evolution of a pentameral body plan was not linked to translocation of anterior *Hox* genes: the echinoderm HOX cluster revisited, *Evol. Dev.*, 2016, vol. 18, no. 2, pp. 137–143.

Cameron, C.B., A phylogeny of the hemichordates based on morphological characters, *Can. J. Zool.*, 2005, vol. 83, pp. 196–215.

Cameron, C.B., Particle retention and flow in the pharynx of the Enteropneust worm *Harrimania planktophilus*: the filter-feeding pharynx may have evolved before the chordates, *Biol. J. Linn. Soc.*, 2009, vol. 98, pp. 898–906.

Cannon, J.T., Rychel, A.L., Eccleston, H., et al., Molecular phylogeny of hemichordata, with updated status of deep-sea enteropneusts, *Mol. Phyl. Evol.*, 2009a, vol. 52, pp. 17–24.

Cannon, J.T., Rychel, A.L., Swalla, B.J., et al., Hemichordate evolution: Derived body plans and suspect families, *Int. Comp. Biol.*, 2009b, vol. 49, pp. E27–E27.

Cannon, J.T., Vellutini, B.C., Smith, J., et al., Xenacoelomorpha is the sister group to Nephrozoa, *Nature*, 2016, vol. 530, pp. 89–93.

Caputi, L., Borra, M., Andreakis, N., et al., SNPs and *Hox* gene mapping in *Ciona intestinalis, BMC Genomics*, 2008, vol. 9, no. 39.

Chia, F.-S., The embryology of a brooding starfish *Leptasterias hexactis* Stimpson, *Acta Zool.*, 1968, vol. 49, no. 3, pp. 321–364.

Chia, F.-S. and Buchanan, J.B., Larval development of *Cucumaria elongata* (Echinodermata: Holothuroidea), *J. Mar. Biol. Ass. UK*, 1969, vol. 49, pp. 151–159.

Cisternas, P. and Byrne, M., Expression of *Hox4* during development of the pentamerous juvenile sea star, *Parvulastra exigua, Dev. Gen. Evol.*, 2009, vol. 219, pp. 613–618.

Claparède, É., Recherches sur la structure des Annélides sédentaires, *Mem. Soc. Phys. Hist. Nat. Gen.*, 1873, vol. 20, pp. 1–200.

Clark, H.L., *Synapta vivipara*, a contribution of the morphology of Echinoderms, *Mem. Boston Soc. Nat. Hist.*, 1898, vol. 5, pp. 53–88.

Conklin, E.G., The embryology of *Amphioxus, J. Morphol.*, 1932, vol. 54, pp. 69–151.

Cuénot, L., Études anatomiques et morphologiques sur les ophiures, *Arch. Zool. Exp. Gen. Ser.*, 1888, vol. 6, pp. 33–82.

Cuénot, L., Études morphologiques sur les echinoderms, *Arch. Biol.*, 1891, vol. 11, pp. 313–680.

Cuénot, L., Anatomie, éthologie et systématique des Échinodermes, in *Traité de Zoologie*, Paris: Masson et C-ie Editeurs, 1948, vol. 11, pp. 933–935.

Damas, D. and Stiasny, G., Les larves planctoniques d'enteropneustes (tornaria et planctosphaera), *Verh. K. Vlaam. Acad. Wet.* (KI. Wetenschappen), 1961, vol. 15, pp. 1–68.

David, B. and Mooi, R., How *Hox* genes can shed light on the place of echinoderms among the deuterostomes, *EvoDevo*, 2014, vol. 5, p. 22.

Davis, B.M., The early life-history of *Dolichoglossus pusillus* Ritter, *Univ. Calif. Pub. Zool.*, 1908, vol. 4, pp. 187–226.

Dawydoff, C., 1928. *Traite d'Embryologie Comparee des Invertebres*, Paris: Masson, 1928.

Dawydoff, C., Classe des Enteropneustes + Classe des Pterobranches, in *Traité de Zoologie*, Paris: Masson, 1948, vol. 2, pp. 369–489.

Delage, Y. and Hérouard, E.J.É., *Traité de Zoologie concrète: Les Procordés*, Paris: Schleicher Freres et Cie, 1898, vol. 8.

Dilly, P.N., The larva of *Rhabdopleura compacta* (Hemichordata), *Mar. Biol.* (Berlin), 1973, vol. 18, pp. 69–86.

Dilly, P.N., The habitat and behaviour of *Cephalodiscus gracilis* (Pterobranchia, Hemichordata) from Bermuda, *J. Zool.*, 1985, vol. 207, pp. 223–239.

Dilly, P.N., *Cephalodiscus* reproductive biology (Pterobranchia, Hemichordata), *Acta Zool.*, 2013, vol. 95, pp. 111–124.

Dohle, W., Die Verwandtschaftsbeziehungen der Grossgruppen der Deuterostomier: Alternative hypothesen und ihre begründungen, *Sitz. Ges. Nat. Fr. Berlin*, 2004, vol. 43, pp. 123–162.

Dohrn, A., *Der Ursprung der Wirbelthiere und das Princip des Functionswechsels. Genealogische Skizzen*, Leipzig: Verlag von Wilhelm Engelmann, 1875, pp. 10–17.

Dohrn, A., Studien zur urgeschichte des Wirbelthierkorpers, *Mitt. Zool. St. Neap.*, 1901, vol. 15, pp. 1–279.

Dolmatov, I.Yu., Ginanova, T.T., and Frolova, L.T., Metamorphosis and definitive organogenesis in the holothurians *Apostichopus japonicus, Zoomorphology*, 2016, vol. 135, pp. 173–188.

Dolmatov, I.Y. and Yushin, V.V., Larval development of *Eupentacta fraudatrix* (Holothuroidea, Dendrochirota), *As. Mar. Biol.*, 1993, vol. 10, pp. 125–134.

Dominguez, P., Jacobson, A.G., and Jefferies, R.P.S., Paired gill slits in a fossil with a calcite skeleton, *Nature*, 2002, vol. 417, pp. 841–844.

Dunn, C.W., Giribet, G., Edgecombe, G.D., et al., Animal phylogeny and its evolutionary implications, *Ann. Rev. Ecol. Evol. Syst.*, 2014, vol. 45, pp. 371–395.

Dunn, C.W., Hejnol, A., Matus, D.Q., et al., Broad phylogenomic sampling improves resolution of the animal tree of life, *Nature*, 2008, vol. 452, pp. 745–750.

Edgecombe, G., Giribet, G., Dunn, C., et al., Higher-level metazoan relationships: recent progress and remaining questions, *Org. Div. Evol.*, 2011, vol. 11, pp. 151–172.

Edwards, C.L., The development of *Holothuria floridana* pourtales with especial reference to the ambulacral appendages, *J. Morphol.*, 1909, vol. 20, pp. 211–230.

Engle, S., Ultrastructure and development of the body cavities in *Antedon bifida* (Pennant, 1777) (Comatulida, Crinoida), PhD Thesis, Berlin, 2012.

Ezhova, O.V., Egorova, E.A., and Malakhov, V.V., Transformations of the ophiuroid axial complex as a result of the shifting of the madreporite to the oral side, *Biol. Bull.*, 2016a, vol. 43, no. 6., pp. 494–502.

Ezhova, O.V., Egorova, E.A., and Malakhov, V.V., Ultrastructural evidence of the excretory function in the asteroid axial organ (Asteroidea, Echinodermata), *Dokl. Biol. Sci.*, 2016b, vol. 468, pp. 129–132.

Ezhova, O.V., Ershova, N.A., and Malakhov, V.V., Microscopic anatomy of the axial complex and associated structures in the sea cucumber *Chiridota laevis* Fabricius, 1780 (Echinodermata, Holothuroidea), *Zoomorphology*, 2017, vol. 136, no. 2, pp. 205–217.

Ezhova, O.V., Lavrova, E.A., Ershova, N.A., et al., Microscopic anatomy of the axial complex and associated structures in the brittle star *Ophiura robusta* Ayres, 1854 (Echinodermata, Ophiuroidea), *Zoomorphology*, 2015, vol. 134, no. 2, pp. 247–258.

Ezhova, O.V., Lavrova, E.A., and Malakhov, V.V., Microscopic anatomy of the of the axial complex in the starfish *Asterias rubens* (Echinodermata, Asteroidea), *Biol. Bull.*, 2013, vol. 40, no. 8, pp. 643–653.

Ezhova, O.V., Lavrova, E.A., and Malakhov, V.V., The morphology of the axial complex and associated structures in Asterozoa (Asteroidea, Echinoidea, Ophiuroidea), *Rus. J. Mar. Biol.*, 2014, vol. 40, no. 3, pp. 153–164.

Ezhova, O.V. and Malakhov, V.V., Axial complex of Crinoidea: comparison with other Ambulacraria, *J. Morphol.*, 2020, vol. 281, no. 11, pp. 1456–1475.

Ezhova, O.V. and Malakhov, V.V., Are there the kidneys of echinoderms? *Priroda*, 2016a, no. 7, pp. 22–29.

Ezhova, O.V. and Malakhov, V.V., How did the gill slits originate? *Priroda*, 2016b, no. 10, pp. 9–15.

Ezhova, O.V. and Malakhov, V.V., Microscopic anatomy and fine structure of the Skeleton–Heart–Kidney complex in *Saccoglossus mereschkowskii* (Hemichordata, Enteropneusta). 4. Glomerulus, proboscis coelom, and proboscis coelomoduct, *Rus. J. Zool.*, 2010, vol. 89, no. 8, pp. 899–923.

Ezhova, O.V. and Malakhov, V.V., The axial complex of Echinoderms represents the kidney and is homologous to the Hemichordate heart-kidney, *Paleontol. J.*, 2021a, vol. 55, pp. 1029–1038.

Ezhova, O.V. and Malakhov, V.V., Coelom metamerism in Echinodermata, *Paleontol. J.*, 2021b, vol. 55, pp. 1073–1083.

Ezhova, O.V. and Malakhov, V.V., The nephridial hypothesis of the gill slit origin, *J. Exp. Zool., Part B*, 2015, no. 324B, pp. 647–652.

Ezhova, O.V., Malakhov, V.V., and Egorova, E.A., Axial complex and associated structures of the sea urchin *Strongylocentrotus pallidus* (Sars, G.O. 1871) (Echinodermata: Echinoidea), *J. Morphol.*, 2018, vol. 279, no. 6, pp. 792–808.

Fauvel, P., Classe des Annelides Polychetes, in *Traite de Zoologie*, Paris: Masson et Cie, 1959, vol. 5, no. 1, pp. 13–200.

Fedotov, D.M., To the problem of homology of coeloms of echinoderms, enteropneustes, and chordates, *Izv. Perm. Nauch.-Issled. Biol. Inst.*, 1923, vol. 2, no. 1, pp. 1–11.

Fedotov, D.M., Zur morphologie des axialen organkomplexes der Echinodermen, *Z. Wiss. Zool.*, 1924, vol. 123, pp. 209–304.

Field, G.W., The larva of *Asterias vulgaris, Q. J. Microsc. Sci.*, 1892, vol. 34, pp. 105–128.

Formery, L., Schubert, M., and Croce, J.C., Ambulacrarians and the ancestry of deuterostome nervous systems, in *Evo-Devo: Non-model Species in Cell and Developmental Biology. Results and Problems in Cell Differentiation*. Springer, Cham, 2019, vol. 68, pp. 31–59.

Freeman, R., Ikuta, T., Wu, M., et al., Identical genomic organization of two hemichordate *Hox* clusters, *Curr. Biol.*, 2012, vol. 22, pp. 2053–2058.

Fritsch, M., Wollesen, T., de Oliveira, A.L., et al., Unexpected co-linearity of *Hox* gene expression in an aculiferan mollusk, *BMC Evol. Biol.*, 2015, vol. 15, no. 151.

Fröbius, A.C., Matus, D.Q., and Seaver, E.C., Genomic organization and expression demonstrate spatial and temporal *Hox* gene colinearity in the lophotrochozoan *Capitella sp., PLoS One*, 2008, vol. 3, no. 12, e4004.

Furlong, R.F. and Holland, P.W.H., Bayesian phylogenetic analysis supports monophyly of Ambulacraria and of Cyclostomes, *Zool. Sci.*, 2002, vol. 19, pp. 593–599.

Gasiorowski, L. and Hejnol, A., *Hox* gene expression during development of the phoronid *Phoronopsis harmeri, EvoDevo*, 2020, vol. 11, no. 2.

Gaunt, S.J., *Hox* cluster genes and collinearities throughout the tree of animal life, *Int. J. Dev. Biol.*, 2018, vol. 62, nos. 11–12, pp. 673–683.

Gee, H., *Before the Backbone*, Suffolk: Chapman & Hall, 1996, pp. 201–286.

Gemmill, J.F., The development of the starfish *Solaster endeca* Fobes, *Trans. Zool. Soc.*, 1912, vol. 20, no. 1, pp. 1–71.

Gemmill, J.F., The development and certain points in the adult structure of the starfish *Asterias rubens* L., *Philos. Trans. R. Soc., B*, 1914, vol. 205, pp. 213–294.

Gemmill, J.F., Double hydrocoele in the development and metamorphosis in the larva of *Asterias rubens* L., *Q. J. Microsc. Sci.*, 1915, no. 61, pp. 51–80.

Gemmill, J.F., The development of the starfish *Crossaster papposus* Müller and Troschel, *Q. J. Microsc. Sci.*, 1920, no. 64, pp. 155–189.

Gill, E.D. and Caster, K.E., Carpoid echinoderms from the Silurian and Devonian of Australia, *Bull. Am. Paleontol.*, 1960, vol. 41, pp. 1–71.

Gilmour, T.H.J., An analysis of videotape recording of larval feeding in the sea urchin *Lytechinus pictus* (Verril), *Can. J. Zool.*, 1985, vol. 63, pp. 1354–1359.

Gilmour, T.H.J., Streamline and particles paths in the feeding mechanisms of larvae of the sea urchin *Lytechinus pictus* Verril, *J. Exp. Mar. Biol. Ecol.*, 1986, vol. 5, pp. 27–36.

Gilmour, T.H.J., Feeding behavior of holothurians larvae, *Am. Zool.*, 1988, vol. 28, p. 67.

Giribet, G., New animal phylogeny: future challenges for animal phylogeny in the age of phylogenomics, *Org. Div. Evol.*, 2016, vol. 16, pp. 419–426.

Gonzalez, P. and Cameron, C.B., The gill slits and pre-oral ciliary organ of *Protoglossus* (Hemichordata: Enteropneusta) are filter-feeding structures, *Biol. J. Linn. Soc.*, 2009, vol. 98, pp. 898–906.

Gonzalez, P., Jiang, J.Z., and Lowe, C.J., The development and metamorphosis of the indirect developing acorn worm *Schizocardium californicum* (Enteropneusta: Spengelidae), *Front. Zool.*, 2018, vol. 15, p. 26.

Gonzalez, P., Uhlinger, K.R., and Lowe, C.J., The adult body plan of indirect developing hemichordates develops by adding a *Hox*-patterned trunk to an anterior larval territory, *Curr. Biol.*, 2017, vol. 27, no. 1, pp. 87–95.

Goto, S., The metamorphosis of *Asterias pallida* with special reference to the fate of the body cavities, *J. Coll. Sci., Imp. Univ. Tokyo*, 1897, no. 10, pp. 239–278.

Goto, R.E., Monnington, J., Sciberras, M., et al., Phylogeny of Echiura updated, with a revised taxonomy to reflect their placement in Annelida as sister group to Capitellidae, *Invertebr. Syst.*, 2020, vol. 34, pp. 101–111.

Grave, C., Embryology of *Ophiocoma echinata*, Agassiz. (Preliminary note.), *Ann. Mag. Nat. Hist. Ser.*, 1899a, vol. 3, pp. 456–461.

Grave, C., *Ophiura brevispina*, *Mem. Nat. Acad. Sci.*, 1899b, vol. 8, pp. 1–166.

Grave, C., On the occurrence among echinoderms of larvae with cilia arranged in transverse rings, with a suggestion as to their significance, *Biol. Bull.*, 1903, vol. 5, pp. 169–186.

Grobben, K., Die systematische Einteilung des Tierreiches, *Verh. Kais. Zool.-Bot. Ges.*, Wien, 1908, vol. 58, pp. 491–511.

Grobben, K., Theoretische erorterungen betreffend die phylogenetische Ableitung der Echinodermen, *Sitz. Akad. Wiss. Wien*, 1923, vol. 132, pt. 1, pp. 263–290.

Hadfield, M., Hemichordata, in *Reproduction of Marine Invertebrates*, New York: Acad. Press, 1975, pp. 185–240.

Halanych, K.M., Suspension feeding by the lophophore-like apparatus of the pterobranch hemichordate *Rhabdopleura normani, Biol. Bull.*, 1993, vol. 185, pp. 417–427.

Halanych, K.M., The new view of animal phylogeny, *Ann. Rev. Ecol. Evol. Syst.*, 2004, vol. 35, pp. 229–256.

Hamann, O., *Beiträge zur Histologie der Echinodermen. Heft 3. Die Anatomie und Histologie der Echiniden und Spatangiden*, Jena: G. Fischer, 1887.

Hara, Y., Yamaguchi, M., Akasaka, K., et al., Expression patterns of *Hox* genes in larvae of the sea lily *Metacrinus rotundus, Dev. Gen. Evol.*, 2006, vol. 216, pp. 797–809.

Hart, M.W., Particle captures and the method of suspension feeding by echinoderm larvae, *Biol. Bull.*, 1991, vol. 180, pp. 12–27.

Hatschek, B., Studien über Entwicklung des *Amphioxus, Arb. Zool. Inst. Univ. Wien Zool. Stn. Triest*, 1881, vol. 4, pp. 1–88.

Hatschek, B., *The Amphioxus and its Development*, London: Swan Sonnenschein, 1893.

Heider, K., Zur Entwicklung von *Balanoglossus clavigerus, Zool. Anz.*, 1909, vol. 34, pp. 695–704.

Heider, K., Über Organverlagerungen bei der Echinodermen-Metamorphose, *Verh. Dtsch. Zool. Ges.*, 1912, vol. 22, pp. 239–251.

Heider, K., Entwicklungsgeschichte und Morphologie der Wirbellosen, *Kultur Ggw.*, 1913, vol. 2, no. 4.

Hejnol, A., Obst, M., Stamatakis, A., et al., Assessing the root of bilaterian animals with scalable phylogenomic methods, *Proc. R. Soc. B*, 2009, vol. 276, pp. 4261–4270.

Hejnol, A. and Pang, K., Xenacoelomorpha's significance for understanding bilaterian evolution, *Curr. Opin. Genet. Dev.*, 2016, vol. 39, pp. 48–54.

Hérouard, E., Recherches sur les holothuries des côtes de France, *Arch. Zool. Exp. Gen.*, 1889, vol. 7, pp. 573–704.

Hessling, R., Metameric organisation of the nervous system in developmental stages of *Urechis caupo* (Echiura) and its phylogenetic implications, *Zoomorphology*, 2002, vol. 121, pp. 221–234.

Higgins, R.P. and Kristensen, R.M., *New Loricifera from southeastern United States coastal waters*, Smithson. Contrib. Zool., 438, Washington, DC: Smithson. Inst. Press, 1986.

Holland, N.D., Electron microscopic study of development in a sea cucumber, *Stichopus tremulus* (Holothuroidea), from unfertilized egg through hatched blastula, *Acta Zool.*, 1981, vol. 62, pp. 89–111.

Holland, L.Z., Albalat, R., Azumi, K., et al., The amphioxus genome illuminates vertebrate origins and cephalochordate biology, *Genet. Res.*, 2008a, vol. 18, pp. 1100–1111.

Holland, N.D., Clague, D.A., Gordon, D.P., et al., 'Lophenteropneust' hypothesis refuted by collection and photos of new deep-sea hemichordates, *Nature*, 2005, vol. 434, pp. 374–376.

Holland, L.Z., Holland, N.D., and Gilland, E., *Amphioxus* and the evolution of head segmentation, *Int. Comp. Biol.*, 2008b, vol. 48, pp. 630–646.

Horst, C.J., van der, Hemichordata, in *Klassen und Ordnungen des Tierreichs*, Leipzig: Leipzig Akad. Verlagsgesellschaft M.B.H., 1939.

Horstadius, S., Über die Entwicklung von *Astropecten aurantiacus* L., *Pubbl. Staz. Zool. Napoli*, 1939, vol. 17, no. 2, pp. 221–312.

Hyman, L.H., *Echinodermata*, in *The Invertebrates, Vol. 4*, New York: McGraw-Hill Book Comp., 1955.

Hyman, L.H., Phylum Hemichordata, in *The Invertebrates: Smaller Coelomate Groups*. New York: McGraw-Hill Book Comp., 1959, pp. 72–207.

Ikuta, T., Yoshida, N., Satoh, N., et al., *Ciona intestinalis Hox* gene cluster: Its dispersed structure and residual colinear expression in development, *Proc. Natl. Acad. Sci. U.S.A.*, 2004, vol. 101, no. 42, pp. 15118–15123.

Inaba, D., Notes on the development of a holothurian, *Caudina chilensis* (J. Muller), *Sci. Rep. Tohoku Univ. Fourth Ser. (Biol.)*, 1930, vol. 5, pp. 215–248.

Ivanov, A.V., *Pogonofory. Fauna SSSR. Novaya seriya* (Pogonophors. Fauna of the USSR. New Ser.), Moscow–Leningrad: Izd. Akad. Nauk SSSR, 1960. no. 75.

Ivanov, P.P., *Obshchaya i sravnitel'naya embriologiya* (General and Comparative Embryology), Moscow–Leningrad: Biomedgiz, 1937.

Ivanova-Kazas, O.M., *Sravnitel'naya embriologiya bespozvonochnykh zhivotnykh. T. 3. Iglokozhie i polukhordovye* (Comparative Embryology of Invertebrate Animals. Vol. 3. Echinoderms and Hemichordates), Moscow: Nauka, 1978a.

Ivanova-Kazas, O.M., *Sravnitel'naya embriologiya bespozvonochnykh zhivotnykh. T. 4. Nizshie khordovye* (Comparative Embryology of Invertebrate Animals. Vol. 4. Lower Chordates), Moscow: Nauka, 1978b.

Jägersten, G., *Evolution of the Metazoan Life Cycle: a Comprehensive Theory*, L., N.-Y.: Acad. Press, 1972.

Janssen, R., Eriksson, B.J., Tait, N.N., et al., Onychophoran *Hox* genes and the evolution of arthropod *Hox* gene expression, *Front. Zool.*, 2014, vol. 11.

Jefferies, R.P.S., The subphylum Calcichordata (Jefferies, 1967)—primitive fossil chordates with echinoderm affinities, *Bull. Br. Mus. (Nat. Hist.), Geol.*, 1968, no. 16, pp. 243–339.

Jefferies, R.P.S., *Ceratocystis perneri*—a Middle Cambrian chordate with echinoderm affinities, *Palaeontology*, 1969, no. 12, pp. 494–535.

Jefferies, R.P.S., A new calcichordate from the Ordovician of Bohemia and its anatomy, adaptations and relationships, *Biol. J. Linn. Soc.*, 1972, no. 4, pp. 69–115.

Jefferies, R.P.S., In defence of the calcichordates, *Zool. J. Linn. Soc.*, 1981, no. 73, pp. 351–396.

Jefferies, R.P.S., *The ancestry of the Vertebrates*, London: British Museum (Natural History), 1986.

Jefferies, R.P.S., Brown, N.A., and Daley, P.E.J., The early phylogeny of chordates and echinoderms and the origin of chordate left-right asymmetry and bilateral symmetry, *Acta Zool. (Stockh)*, 1996, vol. 77, pp. 101–122.

Johnston, T. and Muirhead, N., *Cephalodiscus*, *Rep. Brit. Austr. New Zeal. Ant. Exp. Ser. B*, 1951, vol. 1, pp. 91–120.

Jondelius, U., Raikova, O.I., and Martinez, P., Xenacoelomorpha, a key group to understand Bilaterian evolution: morphological and molecular perspectives, in *Evolution, Origin of Life, Concepts and Methods*, Springer. Marseille: Aix-Marseille Univ., 2019, ch. 14, pp. 287–316.

Jondelius, U., Ruiz-Trillo, I., Baguna, J., et al., The Nemertodermatida are basal bilaterians and not members of the Platyhelminthes, *Zool. Scripta*, 2002, vol. 31, pp. 201–215.

Jones, D.O.B., Alt, C.H.S., Priede, I.G., et al., Deep-sea surface-dwelling enteropneusts from the Mid-Atlantic Ridge: their ecology, distribution and mode of life, *Deep-Sea Res.*, 2013, vol. II, no. 98, pp. 374–387.

Karaseva, N.P., Malakhov, V.V., and Galkin, S.V., The morphology and anatomy of the vestimentiferan worm *Oasisia alvinae* Jones, 1985 (Annelida: Siboglinidae). iii. Coelomic cavity, trophosome and blood, excretory and reproductive systems, *Rus. J. Mar. Biol.*, 2012, vol. 38, pp. 122–138.

Kaul-Strehlow, S. and Rottinger, E., Hemichordata. vol. 6. Deuterostomia, in *Evolutionary Developmental Biology of Invertebrates*, Wien: Springer, 2015, pp. 59–89.

Kaul-Strehlow, S. and Stach, T., A detailed description of the development of the hemichordate *Saccoglossus kowalevskii* using SEM, TEM, histology and 3D-reconstructions, *Front. Zool.*, 2013, vol. 10, no. 1.

Kaul-Strehlow, S., Urata, M., Minokawa, T., et al., Neurogenesis in directly and indirectly developing enteropneusts: of nets and cords, *Org. Div. Evol.*, 2015, vol. 15, pp. 405–422.

Kikuchi, M., Omori, A., Kurokawa, D., et al., Patterning of anteroposterior body axis displayed in the expression of *Hox* genes in sea cucumber *Apostichopus japonicus*, *Dev. Gen. Evol.*, 2015, vol. 225, no. 5, pp. 275–286.

Knight-Jones, E.W., On the nervous system of *Saccoglossus cambrensis* (Enteropneusta), *Philos. Trans. R. Soc., B*, 1952, vol. 236, pp. 315–354.

Knight-Jones, E.W., Feeding in *Saccoglossus* (Enteropneusta), *Proc. Zool. Soc. London*, 1953, vol. 123, pp. 637–658.

Kolata, D.R., Frest, T.J., and Mapes, R.H., The youngest Carpoid: occurrence, affinities, and life mode of a Pennsylvanian (Morrowan) mitrate from Oklahoma, *J. Paleont.*, 1991, vol. 65, no. 5, pp. 844–855.

Kristof, A., Wollesen, T., and Wanninger, A., Segmental mode of neural patterning in Sipuncula, *Curr. Biol.*, 2008, vol. 18, pp. 1129–1132.

Krohn, A., Beobachtungen über Echinodermenlarven, *Arch. Anat. Phys. Wiss. Med.*, 1854, pp. 208–213.

Lacalli, T.C., Ciliary bands in echinoderm larvae: evidence for structural homologies and a common plan, *Acta Zool. (Stockh.)*, 1993, vol. 74, pp. 127–133.

Lacalli, T.C., A larval revelation, *Nature*, 2003, vol. 421, pp. 120–121.

Lacalli, T.C. and West, J.E., The auricularia-to-doliolaria transformation in two aspidochirote holothurians, *Holothuria mexicana* and *Stichopus californicus, Invert. Biol.*, 2000, vol. 119, pp. 421–432.

Land, J., van der, and Nørrevang A., Structure and relationship of Lamellibranchia (Annelida, Vestimentifera), *K. Danske Vidensk. Selsk. Skr.,* 1977, vol. 21, pp. 1–102.

Laumer, C.E., Fernandez, R., Lemer, S., et al., Revisiting metazoan phylogeny with genomic sampling of all phyla, *Philos. Trans. R. Soc., B*, 2019, p. 20190831.

Lefebvre, B., Functional morphology of stylophoran echinoderms, *Palaeontol.*, 2003, vol. 46, pp. 511–555.

Lemche, H. and Wingstrand, K.G., The anatomy of *Neopilina galatheae* Lemche, 1957 (Mollusca, Tryblidiacea), *Galathea Report*, 1959, no. 3, pp. 9–72.

Lemons, D. and McGinnis, W., Genomic evolution of *Hox* gene clusters, *Science*, 2006, vol. 313, pp. 1918–1922.

Lester, S.M., *Cephalodiscus* sp. (Hemichordata: Pterobranchia): observations of functional morphology, behavior and occurrence in shallow water around Bermuda, *Mar. Biol.*, 1985, vol. 85, pp. 263–268.

Lester, S.M., Ultrastructure of adult gonads and development and structure of the larva of *Rhabdopleura normani* (Hemichordata: Pterobranchia), *Acta Zool.*, 1988a, vol. 69, pp. 95–109.

Lester, S.M., Settlement and metamorphosis of *Rhabdopleura normani* (Hemichordata: Pterobranchia), *Acta Zool.*, 1988b, vol. 69, pp. 111–120.

Lin, C.-Y., Tung, C.-H., Yu, J.-K., et al., Reproductive periodicity, spawning induction, and larval metamorphosis of the hemichordate acorn worm *Ptychodera flava, J. Exp. Zool., Part B*, 2016, vol. 326B, pp. 47–60.

Littlewood, D.T.J., Smith, A.B., Clough, K.A., et al., The interrelationships of the echinoderm classes: morphological and molecular evidence, *Biol. J. Linn. Soc.*, 1997, no. 61, pp. 409–438.

Ludwig, H., Neue Beiträge zur Anatomie der Ophiuren, *Z. Wiss. Zool.*, 1880, vol. 34, pp. 57–89.

MacBride, E.W., The development of *Asterina gibbosa, Q. J. Microsc. Sci.*, 1896, vol. 38, pp. 339–411.

MacBride, E.W., The development of *Echinus esculentus, Phil. Trans. R. Soc.*, 1903, vol. 195, pp. 285–327.

MacBride, E.W., The development of *Ophiothrix fragilis, Q. J. Microsc. Sci.*, 1907, vol. 51, pp. 557–606.

MacBride, E.W., The early development of *Amphioxus, Q. J. Microsc. Sci.*, 1898, vol. 40, pp. 589–612.

Malakhov, V.V., A new system of Bilateria, *Vest. Russ. Acad. Sci.*, 2010, vol. 80, no. 1, pp. 27–44.

Malakhov, V.V., Problem of origin of echinoderm according to their embryonic evolution, in *Problems of Study of Fossil and Present-Day Echinoderms*, Tallinn: Akad. Nauk Estonskoi SSR. Inst. Geol., 1989, pp. 14–23.

Malakhov V.V. A revolution in zoology: a new system of Bilateria, *Priroda*, 2009, no. 3, pp. 40–54.

Malakhov, V.V., A revolution in zoology: New concepts of the metazoan system and phylogeny, *Herald Russ. Acad. Sci.*, 2013, vol. 83, no. 2, pp. 123–127.

Malakhov, V.V. and Adrianov, A.V., *Golovokhobotnye (Cephalorhyncha)—novyi tip zhivotnogo tsarstva* (Cephalorhyncha—a New Phylum of the Animal Kingdom), Moscow: KMK Sci. Press, 1995.

Malakhov, V.V. and Bogomolova, E.V., New glance at the structure and origin of the body cavity of multicellular organisms, *Priroda*, 2016, no. 2, pp. 12–27.

Malakhov, V.V., Bogomolova, E.V., Kuzmina, T.V., et al., Evolution of metazoan life cycles and the origin of pelagic larvae, *Rus. J. Dev. Biol.*, 2019, vol. 50, no. 6, pp. 303–316.

Malakhov, V.V. and Cherkasova, I.V., Embryonic and early larval evolution of holothurian *Stichopus japonicus* var. Armatus (Aspidochirota, Stichopodidae), *Zool. Zh.*, 1991, vol. 70, no. 4, pp. 55–67.

Malakhov, V.V. and Cherkasova, I.V., Metamorphosis of holothurian *Stichopus japonicus* (Aspidochirota, Stichopodidae), *Zool. Zh.*, 1992, vol. 71, no. 9, pp. 11–21.

Malakhov, V.V. and Kuzmina, T.V., Metameric origin of lateral mesenteries in Brachiopoda, *Dokl. Biol. Sci.*, 2006, vol. 409, pp. 340–342.

Malakhov, V.V., Popelyaev, I.S., and Galkin, S.V., Microscopic anatomy of *Ridgeia phaeophiale* Jones, 1985 (Pogonophora, Vestimentifera) and the problem of the position of vestimentifera in the system of the animal kingdom. IV. Excretory and reproductive systems and coelom, *Rus. J. Mar. Biol.*, 1996, vol. 22, no. 5, pp. 249–261.

Maletz, J. and Cameron, C., Introduction to the class Pterobranchia Lankester, 1877, *Treatise OnLine*, 2016, no. 82, p. 2.

Martin, A., Serano, J.M., Jarvis, E., et al., CRISPR/Cas9 mutagenesis reveals versatile roles of *Hox* genes in crustacean limb specification and evolution, *Curr. Biol.*, 2016, vol. 26, pp. 14–26.

Mayer, G. and Bartolomaeus, T., Ultrastructure of the stomochord and the heart-glomerulus complex in *Rhabdopleura compacta* (Pterobranchia): phylogenetic implications, *Zoomorphology*, 2003, vol. 122, pp. 125–133.

Metschnikoff, E., Studien über die Entwicklung der Echinodermen und Nemertinen, *Mem. Acad. Sci. St.-Petersburg*, Ser. 7, 1869, vol. 14, pp. 1–73.

Metschnikoff, E.E., Untersuchungen über die Metamorphose einiger Seethiere. Über Tornaria, *Z. Wiss. Zool.*, 1870, vol. 20, pp. 131–144.

Metschnikoff, E.E., Über die Systematische Stellung von *Balanoglossus, Zool. Anz.*, 1881, vol. 4, pp. 153–157.

Meyer, E., Studien über den Körperbau der Anneliden, *Mitt. Zool. Stat. Neapel*, 1887, vol. 7, pp. 592–741.

Mito, T. and Endo, K., PCR survey of *Hox* genes in the crinoid and ophiuroid: evidence for anterior conservation and posterior expansion in the echinoderm *Hox* gene cluster, *Mol. Phyl. Evol.*, 2000, vol. 14, no. 3, pp. 375–388.

Miyamoto, N. and Saito, Y., Morphology and development of a new species of *Balanoglossus* (Hemichordata: Enteropneusta: Ptychoderidae) from Shimoda, Japan, *Zool. Sci.*, 2007, vol. 24, pp. 1278–1285.

Morgan, T.H., Growth and metamorphosis of tornaria, *J. Morphol.*, 1891, vol. 5, pp. 407–458.

Morgan, T.H., The development of *Balanoglossus, J. Morphol.*, 1894, vol. 9, pp. 1–86.

Morris, V.B. and Byrne, M., Involvement of two *Hox* genes and *Otx* in echinoderm body-plan morphogenesis in the sea urchin *Holopneustes purpurescens, J. Exp. Zool., Part B.*, 2005, vol. 304, pp. 456–467.

Morris, V.B. and Byrne, M., Oral–aboral identity displayed in the expression of *HpHox3* and *HpHox11/13* in the adult rudiment of the sea urchin *Holopneustes purpurescens, Dev. Gen. Evol.*, 2014, vol. 224, pp. 1–11.

Mortensen, T., Studies in the development of Crinoids, *Pap. Dep. Mar. Biol. Carnegie Inst. Washington,* 1920, vol. 16, pp. 1–94.

Müller, J., Über den allgemeinen Plan in der Entwickelung der Echinodermen*, Abh. Konig. Akad. Wiss. Berlin (Physik)*, 1853, pp. 25–65.

Naef, A., Studien zur generellen Morphologie der Mollusken 1. Teil: Über Torsion und Asymmetrie der Gastropoden, in *Ergebnisse und Fortschritte der Zoologie*, Jena: Gustav Fisher, 1911, vol. 3, no. 2, pp. 73–164.

Nakano, H., Hibino, T., Oji, T., et al., Larval stages of a living sea lily (stalked crinoid echinoderm), *Nature*, 2003, vol. 421, pp. 158–160.

Narasimhamurti, N., The development of *Ophiocoma nigra, Quart. J. Micr. Sci.*, 1933, vol. 76, pp. 63–88.

Nielsen, C., The development of the brachiopod *Crania (Neocrania) anomala* (O. F. Müller) and its phylogenetic significance, *Acta Zool. (Stockh.)*, 1991, no. 72, pp. 7–28.

Nielsen, C. and Hay-Schmidt, A., Development of the enteropneust *Ptychodera flava*: ciliary bands and nervous system, *J. Morphol.*, 2007, vol. 268, pp. 551–570.

Ohshima, H., On the development of *Cucumaria echinata* v. Marenzeller, *Q. J. Microsc. Sci.*, 1921, vol. 65, pp. 173–246.

Olsen, H., The development of the brittle-star *Ophiopholis aculeata* with a short report on the outer hyaline layer, *Berg. Mus. Årb.*, 1942, no. 6, pp. 1–107.

Onai, T., Adachi, N., and Kuratani, S., Metamerism in cephalochordates and the problem of the vertebrate head, *J. Dev. Biol.*, 2017, vol. 621–632.

Osborn, K.J., Kuhnz, L.A., Priede, I.G., et al., Diversification of acorn worms (Hemichordata, Enteropneusta) revealed in the deep sea, *Philos. Trans. R. Soc., B*, 2012, vol. 279, pp. 1646–1654.

Osterud, H.L., Preliminary observations on the development of *Leptasterias hexactis, Publ. Puget Sound Biol. St.*, 1918, vol. 2, pp. 1–15.

Perseke, M., Golombek, A., Schlegel, M., et al., The impact of mitochondrial genome analyses on the understanding of deuterostome phylogeny, *Mol. Phyl. Evol.*, 2013, vol. 66, pp. 898–905.

Perseke, M., Hetmank, J., Bernt, M., et al., The enigmatic mitochondrial genome of *Rhabdopleura compacta* (Pterobranchia) reveals insights into selection of an efficient tRNA system and supports monophyly of Ambulacraria, *BMC Evol. Biol.*, 2011, vol. 11, p. 134.

Peterson, K.J., Isolation of *Hox* and *Parahox* genes in the hemichordate *Ptychodera flava* and the evolution of deuterostome *Hox* genes, *Mol. Phyl. Evol.*, 2004, vol. 31, pp. 1208–1215.

Peterson, K.J. and Eernisse, D.J., The phylogeny, evolutionary developmental biology, and paleobiology of the Deuterostomia: 25 years of new techniques, new discoveries, and new ideas, *Org. Div. Evol.*, 2016, vol. 16, pp. 401–418.

Philippe, H., Brinkmann, H., Copley, R.R., et al., Acoelomorph flatworms are deuterostomes related to *Xenoturbella, Nature*, 2011, vol. 470, no. 7333, pp. 255–258.

Philippe, H., Poustka, A.J., Chiodin, M., et al., Mitigating anticipated effects of systematic errors supports sister-group relationship between Xenacoelomorpha and Smbulacraria, *Curr. Biol.*, 2019, vol. 29, pp. 1–9.

Priede, I.G., Osborn, K.J., Gebruk, A.V., et al., Observations on torquaratorid acorn worms (Hemichordata, Enteropneusta) from the North Atlantic with descriptions of a new genus and three new species, *Invert. Biol.*, 2012, vol. 131, no. 3, pp. 244–257.

Rahman, I.A. and Clausen, S., Re-evaluating the palaeobiology and affinities of the Ctenocystoidea (Echinodermata), *J. Syst. Palaeont.*, 2009, vol. 7, pp. 413–426.

Rahman, I.A., Stewart, S.E., and Zamora, S., The youngest ctenocystoids from the Upper Ordovician of the United Kingdom and the evolution of the bilateral body plan in echinoderms, *Acta Palaeont. Pol.*, 2015a, vol. 60, pp. 39–48.

Rahman, I.A., Thompson, J.R., Briggs, D.E.G., et al., A new ophiocistioid with soft-tissue preservation from the Silurian Herefordshire Lagerstätte, and the evolution of the holothurian body plan, *Proc. R. Soc., B*, 2019, vol. 286.

Rahman, I.A. and Zamora, S., The oldest cinctan carpoid (stem-group Echinodermata), and the evolution of the water vascular system, *Zool. J. Linn. Soc.*, 2009, vol. 157, pp. 420–432.

Rahman, I.A., Zamora, S., Falkingham, P.L., et al., Cambrian cinctan echinoderms shed light on feeding in the ancestral deuterostome, *Proc. R. Soc. B*, 2015b, vol. 282.

Rakaj, A., Fianchini, A., Boncagni, P., et al., Artificial reproduction of *Holothuria polii*: a new candidate for aquaculture, *Aquaculture*, 2019, vol. 498, pp. 444–453.

Rao, K.P., The development of *Glandiceps* (Enteropneusta; Spengelidae), *J. Morphol.*, 1953, vol. 93, pp. 1–18.

Rao, K.P., Bionomics of *Ptychodera flava* Eschscholtz (Enteropneusta)*, J. Madras Univ.*, 1954.

Reich, A., Dunn, C., Akasaka, K., et al., Phylogenomic analyses of Echinodermata support the sister groups of Asterozoa and Echinozoa, *PLoS ONE*, 2015, vol. 10, no. 3.

Reich, M. and Smith, A.B., Origins and biomechanical evolution of teeth in echinoids and their relatives, *Palaeontol.*, 2009, vol. 52, pp. 1149–1168.

Reichensperger, A., Zur Anatomie von *Pentacrinus decorus, Z. Wiss. Zool.*, 1905, vol. 80, pp. 22–55.

Remane, A., Beiträge zur Systematik der Süsswassergastrotrichen, *Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tiere*, 1927, no. 53, pp. 269–320.

Ridewood, W., Pterobranchia: *Cephalodiscus, Nat. Ant. Exp. Nat. Hist. Rep. Zool.*, 1907, vol. 2, no. 5, pp. 1–67.

Riisgård, H.U. and Larsen, P.S., Particle capture mechanisms in suspension-feeding invertebrates, *Mar. Ecol. Proc. Ser.*, 2010, vol. 418, pp. 255–293.

Rimskaya-Korsakova, N., Dyachuk, V., and Temereva, E., Parapodial glandular organs in *Owenia borealis* (Annelida: Oweniidae) and their possible relationship with nephridia, *J. Exp. Zool., Part B*, 2020, vol. 334, no. 2, pp. 88–99.

Robison, R.A. and Sprinkle, J., Ctenocystoidea: new class of primitive echinoderms, *Science*, 1969, vol. 166, no. 3912, pp. 1512–1514.

Rosa, R., Grenier, J.K., Andreeva, T., et al., HOX genes in brachiopods and priapulids and protostome evolution, *Nature*, 1999, vol. 399, pp. 772–776.

Rouse, G.W., Wilson, N.G., Carvajal, J.I., et al., New deep-sea species of *Xenoturbella* and the position of Xenacoelomorpha, *Nature*, 2016, vol. 530, pp. 94–97.

Rozhnov, S.V., The anteroposterior axis in echinoderms and displacement of the mouth in their phylogeny and ontogeny, *Biol. Bull.*, 2012, vol. 39, pp. 162–171.

Ruiz-Trillo, I. and Paps, J., Acoelomorpha: earliest branching bilaterians or deuterostomes? *Org. Div. Evol.*, 2016, vol. 16, pp. 391–399.

Runnström, S., Über die Entwicklung von *Leptosynapta inhaerens* (O.Fr. Müller), *Berg. Mus. Årb.*, 1927, no. 1, pp. 1–80.

Ruppert, E.E. and Balser, E.J., Nephridia in the larvae of hemichordates and echinoderms, *Biol. Bull.*, 1986, no. 171, pp. 188–196.

Ruppert, E.E., Barnes, R.D., and Fox, R.S., *Hemichordata*, *Fox Invertebrate Zoology*, Belmont: Thomson Brooks/Cole, 2004, vol. 27, pp. 857–929.

Ruppert, E.E. and Smith, P.R., The functional organization of filtration nephridia, *Biol. Rev.*, 1988, no. 171, pp. 231–258.

Sato, A., Bishop, J.D.D., and Holland, P.W.H., Developmental biology of pterobranch hemichordates: history and perspectives, *Genesis*, 2008, vol. 46, pp. 587–591.

Schepotieff, A., Zur Organisation von Rhabdopleura*, Vorl. Mitt. Berg. Mus. Årb.*, 1904, p. 1–21.

Schepotieff, A., Die Pterobranchier. Anatomische und histologische Untersuchungen über *Rhabdopleura normanii* Allman und *Cephalodiscus dodecalophus* M'Int. 1. Teil. *Rhabdopleura normanii* Allman. Die Anatomie von *Rhabdopleura, Zool. Jahrb. Abt. Anat. Ont. Tiere*, 1906, vol. 23, pp. 463–534.

Schepotieff, A., Die Pterobranchier. Anatomische und histologische Untersuchungen über *Rhabdopleura normanii* Allman und *Cephalodiscus dodecalophus* M'Int. 1. Teil. *Rhabdopleura normanii* Allman. 2. Abschnitt. Knospungsprozess und Gehäuse von Rhabdopleura, *Zool. Jahrb. Abt. Anat. Ont. Tiere*, 1907a, vol. 24, pp. 193–238.

Schepotieff, A., Die Pterobranchier. Anatomische und histologische Untersuchungen über *Rhabdopleura normanii* Allman und *Cephalodiscus dodecalophus* M'Int. 2. Teil. *Cephalodiscus dodecalophus* M'Int. 1. Abschnitt. Die Anatomie von Cephalodiscus, *Zool. Jahrb. Abt. Anat. Ont. Tiere*, 1907b, vol. 25, pp. 553–608.

Schepotieff, A.M., *Pterobranchia*, St. Petersburg, 1907c.

Schepotieff, A., Die Pterobranchier. Anatomische und histologische Untersuchungen über *Rhabdopleura normanii* Allman und *Cephalodiscus dodecalophus* M'Int. 2. Teil. *Cephalodiscus dodecalophus* M'Int. 2. Abschnitt. Knospungsprozess von Cephalodiscus, *Zool. Jahrb. Abt. Anat. Ont. Tiere*, 1908, vol. 25, pp. 404–494.

Seeliger, O., Studien zur Entwicklungsgeschichte der Crinoiden (*Antedon rosacea*), *Zool. Jahrb. Abt. Anat. Ont. Tiere*, 1892, vol. 6, pp. 161–444.

Selenka, E., Beiträge zur Anatomie und Systematik der Holothurien, *Zeit. wiss. Zool.*, 1867, vol. 17, pp. 291–374.

Selenka, E., Zur Entwicklung der Holothurien *Holothuria tubulosa* und *Cucumaria doliolum, Z. Wiss. Zool.*, 1876, vol. 27, pp. 155–187.

Semon, R., Die Entwickelung der *Synapta digitata* und ihre Bedeutung für die Phylogenie der Echinodermen, *Jena. Z. Naturwiss.*, 1888, vol. 22, pp. 175–309.

Seo, H.C., Edvardsen, R.B., Maeland, A.D., et al., *Hox* cluster disintegration with persistent anteroposterior order of expression in *Oikopleura dioica, Nature*, 2004, vol. 431, pp. 67–71.

Smiley, S., Metamorphosis of *Stichopus californicus* (Echinodermata: Holothuroidea) and its phylogenetic implications, *Biol. Bull.*, 1986, vol. 171, pp. 611–631.

Smith, A.B., Classification of the Echinodermata, *Paleontology*, 1984, vol. 27, no. 3, pp. 431–459.

Smith, A.B. and Reich, M., Tracing the evolution of holothurian body plan through stem-group fossils, *Biol. J. Linn. Soc.*, 2013, vol. 109, pp. 670–681.

Sollas, W.J., Fossils in the University Museum, Oxford: I. On Silurian Echinoidea and Ophiuroidea, *Quart. J. Geol. Soc. London*, 1899, vol. 55.

Spengel, J.W., Die Enteropneusten des Golfes von Neapel und der angrenzenden Meeres-Abschnitte, in *Fauna und Flora des Golfes von Neapel. Herausg. Zool. St. Neap. 18. Monograph*, Berlin: Verlag von R. Friedländer Sohn, 1893.

Stach, T. and Kaul, S., The postanal tail of the enteropneust *Saccoglossus kowalevskii* is a ciliary creeping organ without distinct similarities to the chordate tail, *Acta Zool.*, 2012, vol. 92, pp. 150–160.

Stebbing, A.R.D., Aspects of the reproduction and life cycle of *Rhabdopleura compacta* (Hemichordata), *Mar. Biol. (Berlin)*, 1970, vol. 5, pp. 205–212.

Stiasny, G., Studien über die Entwicklung des *Balanoglossus clavigerus*. Delle Chiaje. I. Die Entwicklung der Tornaria, *Mitt. Zool. Stat. Neapel*, 1914a, vol. 22, pp. 255–290.

Stiasny, G., Studien über die Entwicklung des *Balanoglossus clavigerus*. Delle Chiaje. II. Darstellung der weiteren Entwicklung bis zur Metamorphose, *Mitt. Zool. Stat. Neapel*, 1914b, vol. 22, pp. 255–290.

Stiasny-Wijnhoff, G. and Stiasny, G., Über Tornarien-Typen und ihre Beziehung zur Systematik der Enteropneusten, *Zool. Anz.*, 1926, vol. 68, pp. 159–165.

Stiasny-Wijnhoff, G. and Stiasny, G., Die Tornarien. Kritik der Beschreibungen und Vergleich sämtlicher bekannter Enteropneustenlarven, *Erg. Fort. Zool. (Stuttgart)*, 1927, vol. 7, pp. 38–208.

Strathmann, R.R., The behavior of planktotrophic echinodermlarvae: mechanisms, regulation, and rates of suspension feeding, *J. Exp. Mar. Biol. Ecol.*, 1971, vol. 6, pp. 109–160.

Strathmann, R.R., Larval feeding in echinoderms, *Am. Zool.*, 1975, vol. 5, pp. 717–730.

Strathmann, R. and Bonar, D., Ciliary feeding of tornaria larvae of *Ptychodera flava* (Hemichordata: Enteropneusta), *Mar. Biol. (Berlin)*, 1976, vol. 34, pp. 317–324.

Struck, T., Schult, N., Kusen, T., et al., Annelid phylogeny and the status of Sipuncula and Echiura, *BMC Evol. Biol.*, 2007, vol. 7, p. 57.

Sutcliffe, O.E., Sudkamp, W.H., and Jefferies, R.P.S., Ichnological evidence on the behaviour of mitrates: two trails associated with the Devonian mitrate *Rhenocystis, Lethaia*, 2000, vol. 33, pp. 1–12.

Svetlov, P.G., Primary heteronomy of the body structure of vertebrates, *Arkh. Anat. Gist. Embr.*, 1957, vol. 34, no. 2, pp. 4–16.

Swalla, B.J. and Smith, A.B., Deciphering deuterostome phylogeny: molecular, morphological and palaeontological perspectives, *Philos. Trans. R. Soc., B*, 2008, vol. 363, pp. 1557–1568.

Tagawa, K., Nishino, A., Humphreys, T., et al., The spawning and early development of the Hawaiian acorn worm (Hemichordate), *Ptychodera flava*, *Zool. Sci.*, 1998, vol. 15, pp. 85–91.

Tarver, J.E., Sperling, E.A., Nailor, A., et al., miRNAs: small genes with big potential in metazoan phylogenetics, *Mol. Biol. Evol.*, 2013, vol. 30, pp. 2369–2382.

Telford, M.J., The animal tree of life, *Science*, 2013, vol. 339, pp. 764–766.

Telford, M.J., Budd, G.E., and Herve, P., Phylogenomic insights into animal evolution, *Curr. Biol.*, 2015, no. 25, pp. R876–R887.

Temereva, E.N. and Malakhov, V.V., The evidence of metamery in adult brachiopods and phoronids, *Invertebr. Zool.*, 2011, vol. 8, no. 2, pp. 91–112.

Thomas, I.M., Action of the gut in *Saccoglossus otagoensis* (Hemichordata: Enteropneusta), *N. Z. J. Mar. Freshwater Res.*, 1972, vol. 6, pp. 560–569.

Thompson, W., On the embryology of *Antedon rosaceus, Philos. Trans. R. Soc., B*, 1865, vol. 155, pp. 513–544.

Thorndyke, M.C., Chen W.-C., Beesley, P.W., et al., Molecular approach to echinoderm regeneration, *Micr. Res. Techn.*, 2001, vol. 55, pp. 474–485.

Tsuchimoto, J. and Yamaguchi, M., *Hox* expression in the direct-type developing sand dollar *Peronella japonica, Dev. Dynamics*, 2014, vol. 243, pp. 1020–1029.

Ubaghs, G., *Cothurnocystis* Bather, *Phyllocystis* Thoral and an undetermined member of the order Soluta (Echinodermata, Carpoidea) in the Uppermost Cambrian of Nevada, *J. Paleont.*, 1963, vol. 37, no. 6, pp. 1133–1142.

Ubaghs, G., General characters of Echinodermata, in *Treatise on Invertebrate Paleontology. Part S. Echinodermata 1,* Lawrence: Univ. Kansas Press, 1967, pp. 3–60.

Ubaghs, G., Stylophora, in *Treatise on Invertebrate Paleontology. Part S, Echinodemata. V. 1(2)*, Lawrence: Univ. Kansas Press, 1968, pp. S495–S565.

Ubaghs, G. and Caster, K.E., Homalozoans, in *Treatise on Invertebrate Paleontology*, Lawrence: Univ. Kansas Press, 1967, pp. 495–627.

Ubisch, L., Die Entwicklung von *Strongylocentrotus lividus* (*Echinus microtuberculatus, Arbacia pustulosa*), *Zeit. wiss. Zool.*, 1913, vol. 106, pp. 409–448.

Urata, M., Iwasaki, S., Ohtsuka, S., et al., Development of the swimming acorn worm *Glandiceps hacksi*: similarity to holothuroids, *Evol. Dev.*, 2014, vol. 16, pp. 49–154.

Urata, M., Tsuchimoto, J., Yasui, K., et al., The *Hox8* of the hemichordate *Balanoglossus misakiensis, Dev. Gen. Evol.*, 2009, vol. 219, pp. 377–382.

Urata, M. and Yamaguchi, M., The development of the enteropneust hemichordate *Balanoglossus misakiensis* Kuwano, *Zool. Sci.*, 2004, vol. 21, pp. 533–540.

Wada, H., Garcia-Fernandez, J., and Holland, P.W.H., Colinear and segmental expression of amphioxus *Hox* genes, *Dev. Biol.*, 1999, vol. 213, pp. 131–141.

Wanninger, A., Kristof, A., and Brinkmann, N., Sipunculans and segmentation, *Comm. Int. Biol.*, 2009, vol. 2, no. 1, pp. 56–59.

Waren, A. and Hain, S., *Laevipilina antarctica* and *Micropilina arntzi*, two new monoplacophorans from the Antarctic, *Veliger*, 1992, vol. 35, pp. 165–176.

Wollesen, T., Rodriguez Monje, S.V., Luiz de Oliveira, A., et al., Staggered *Hox* expression is more widespread among molluscs than previously appreciated, *Proc. R. Soc. B*, 2018, vol. 285, 20181513.

Zamora, S., Deline, B., Álvaro, J.J., et al., The Cambrian substrate revolution and the early evolution of attachment in suspension-feeding echinoderms, *Earth-Sci. Rev.*, 2017, vol. 171, pp. 478–491.

Zamora, S., Rahman, I.A., and Smith, A.B., Plated Cambrian bilaterians reveal the earliest stages of echinoderm evolution, *PLoS ONE*, 2012, vol. 7, no. 6, e38296.

Zamora, S., Sumrall, C.D., and Vizcaïno, D., Morphology and ontogeny of the Cambrian edrioasteroid echinoderm *Cambraster cannati* from western Gondwana, *Acta Palaeontol. Polon.*, 2013, vol. 58, pp. 545–559.

Ziegler, A., Faber, C., and Bartolomaeus, T., Comparative morphology of the axial complex and interdependence of internal organ systems in sea urchins (Echinodermata: Echinoidea), *Front. Zool.*, 2009, vol. 6, no. 1, pp. 10–31.

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