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The Axial Complex of Echinoderms Represents the Kidney and Is Homologous to the Hemichordate Heart-Kidney

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Abstract—The question of the presence of kidneys in echinoderms is a subject of discussion. Many guides state the absence of a special excretory organ in the echinoderms. However, there is a special excretory organ (kidney) in echinoderms. It is the axial complex. The blood network of the axial complex is represented by the system of haemocoelic spaces, which lie between the folds of the coelothelium of axial coelom. This haemocoelic capillary system is an axial organ. Contractions of the heart, which is enclosed into the pericardial coelom on the aboral side of the body, provides directional movement of the blood. The heart accepts the blood from two aboral haemal rings: the gastric ring and the genital ring. Haemocoelic spaces of the axial organ are separated from the axial coelom by the basal lamina. The surface of this basal lamina from the side of coelom is covered by the coelothelial lining, which contains the podocytes and epithelial-muscle cells. The extracellular diaphragms are stretched between the processes of the podocytes. Contractions of the heart and epithelial-muscle cells create the pressure, which provides the ultrafiltration of liquid from the haemocoel to the axial coelom. The coelomic liquid with the products of excretion is removed from the axial coelom to the environment via the pores of madreporic plate. The hemichordate heart-kidney consists of the proboscis coelom, which develops from the left axocoel of tornaria, the pericardium, which develops from the right axocoel, the heart, and the so-called glomerulus, i.e., a network of haemocoelic spaces between the folds of the proboscis coelom. The fluid is filtered from the haemocoelic spaces of the glomerulus through the basal lamina, passes between the finger-like processes of the podocytes, and reaches the proboscis coelom, from which it is excreted to the environment via the coelomoduct. The axial complex of Echinodermata is an undoubted homologue of the heart-kidney of Hemichordata. It is formed from the homologous larval coeloms, has a significant similarity in the structure, and is analogous in function. Probably, the excretory organ based on the dissymmetric preoral coeloms was formed in the common ancestor of hemichordates and echinoderms. It represents the most important synapomorphy of Ambulacraria.

Keywords: axial complex, heart-kidney, ultrafiltration, excretion, Echinodermata, Hemichordata, Ambulacraria

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INTRODUCTION

The question of whether echinoderms have kidneys comparable to those of other invertebrates is a subject of debate. Many textbooks and manuals do not mention the presence of a kidney in these animals at all, and non-specialized structures are believed to be responsible for excretion in echinoderms. For example, in the guide by V.N. Beklemishev "Principles of Comparative Anatomy of Invertebrates" (1964), it is emphasized that echinoderms almost lack separate excretory organs and that their excretion performed by amoebocytes, which are loaded with decay products and then leave the organism, crawling out through the skin surface, gut, respiratory trees (in holothuroids), bursa (in ophiuroids), etc. In the textbook "Zoology of Invertebrates" by Dogel (1975), in the introduction to the chapter "Phylum Echinodermata," it is stated that these animals have no special excretory organs. In the manual "Zoology of Invertebrates" edited by W. Westheide and R. Rieger, in the chapter on echinoderms (Goldschmid, 1996), it is postulated that echinoderms do not have specialized excretory organs, and metabolic products are collected in the coelom and excreted through thin-walled organs (tube feet, skin gills, respiratory trees, thin body wall, and hindgut). Only in the guide by Ruppert et al. (2004), is it mentioned that echinoderms have a specialized excretory organ, namely, an axial blood organ, which, like the gastric haemal tufts, is covered with podocytes and is probably the site of ultrafiltration.

However, D.M. Fedotov (1923, 1924) pointed out the possibility of homology between the axial complex of echinoderms and the heart-kidney complex of hemichordates. This opinion was expressed several times in the literature (see, for example, Cameron, 2000).

In this article, we will attempt to analyze the data in favor of homology between the heart-kidney complex of hemichordates and the axial complex of echinoderms and will discuss the possible function of the latter.

HEART-KIDNEY COMPLEX OF HEMICHORDATA

The heart-kidney complex (HKC) of hemichordates is located along the anteroposterior axis of the body in the proximal part of the proboscis, where the proboscis is connected to the collar by a stalk (Fig. 1a). The central structures of the HKC are the pericardial coelom, the heart, the proboscis coelom, and the proboscis coelomoduct, as well as the glomerulus, which is situated between these two coeloms (Fig. 1b). The pericardial coelom (right protocoel) is a closed sac covering the heart from above and from the sides. The heart lies on the dorsal side of the buccal diverticulum (=stomochord) in its proximal segment (Ezhova and Malakhov, 2010c). The buccal diverticulum protrudes into the proboscis, projecting forwards from the dorsal wall of the animal's pharynx, and consists of large vacuolated cells. The buccal diverticulum, in turn, leans on the skeletal element of the stalk. The structure of the skeletal element differs in members of different taxonomic groups of Hemichordata (Spengel, 1893; Van der Horst, 1939; Ezhova and Malakhov, 2009, 2010a). As a rule, the stalk skeletal element comprises an unpaired lamina underlying the buccal diverticulum from the ventral side, and paired horns extending back into the collar region on the sides of the digestive tube. In its nature, the skeletal element is a layer of dense connective tissue (Ezhova and Malakhov, 2010a, 2010b). The glomerulus encloses the anterior part of the buccal diverticulum as a sleeve (Figs. 1a, 1b). The buccal diverticulum and the skeletal element support the heart, pericardium, and glomerulus. All these parts of the HKC are surrounded by the proboscis coelom (left protocoel), which opens outwards with a coelomoduct to the left of the other parts of the HKC (Fig. 1c). The left and right collar coeloms each have one short coelomoduct, which in Graptolithoidea (Pterobranchia) open immediately into the external environment (Ridewood, 1907; Schepotieff, 1907). In Enteropneusta, coelomoducts of collar coeloms open into the first pair of gill slits (Spengel, 1893; Hyman, 1959; Ezhova and Malakhov, 2015). The trunk coeloms of hemichordates are devoid of permanent coelomoducts. From a morphological point of view, numerous gonoducts are coelomoducts of trunk coeloms. The gonoducts are formed during reproduction and remove gametes from the gonads localized in the trunk coelom.

The glomerulus is a three-dimensional network of haemocoelic spaces between the folds of the coelothelia of the proboscis and pericardial coeloms (Figs. 1b, 1c) (Balser and Ruppert, 1990; Ezhova and Malakhov, 2010d). Thus, the walls of the haemocoelic lacunae of the glomerulus are formed by the basal lamina underlying the coelothelium of the proboscis and pericardial coeloms (Figs. 1b, 1d, 1e). The coelothelial lining in these sites is formed by flagellate epithelial-muscle cells. Myofilaments pass through the basal parts of these cells (Fig. 1e). Ultrastructural studies showed that the basal parts of myoepithelial cells form numerous processes that may contain or not contain myofilaments (Ezhova and Malakhov, 2010d). The processes of both types intertwine and form a multilayer lattice (Fig. 1d). Between adjacent processes, there are diaphragms, membranes formed by non-cellular matter (Fig. 1e). Thus, myoepithelial cells of the coelomic lining are, at the same time, podocytes.

Blood enters the glomerulus from the heart, which in hemichordates is an extension of the dorsal blood vessel. Due to the presence of myofilaments, the network of processes of myoepithelial cells of the coelomic lining can contract and exert pressure on the walls of blood lacunae of the glomerulus, which is important for ultrafiltration. The fluid from the haemocoel of the blood vessels passes through the basal lamina into the narrow spaces between the processes of the podocytes and then into the cavity of the proboscis coelom through the diaphragms (Fig. 1e). When passing between the processes, the ultrafiltrate is modified, after which it enters the cavity of the proboscis coelom, from which it is excreted into the external environment via the proboscis coelomoduct (Fig. 1c). Blood passed through the capillaries of the glomerulus is collected in two efferent arteries, which are connected behind the pharynx into the ventral blood vessel, through which blood flows back to the gill slits, gut, and gonads (Fig. 1c).

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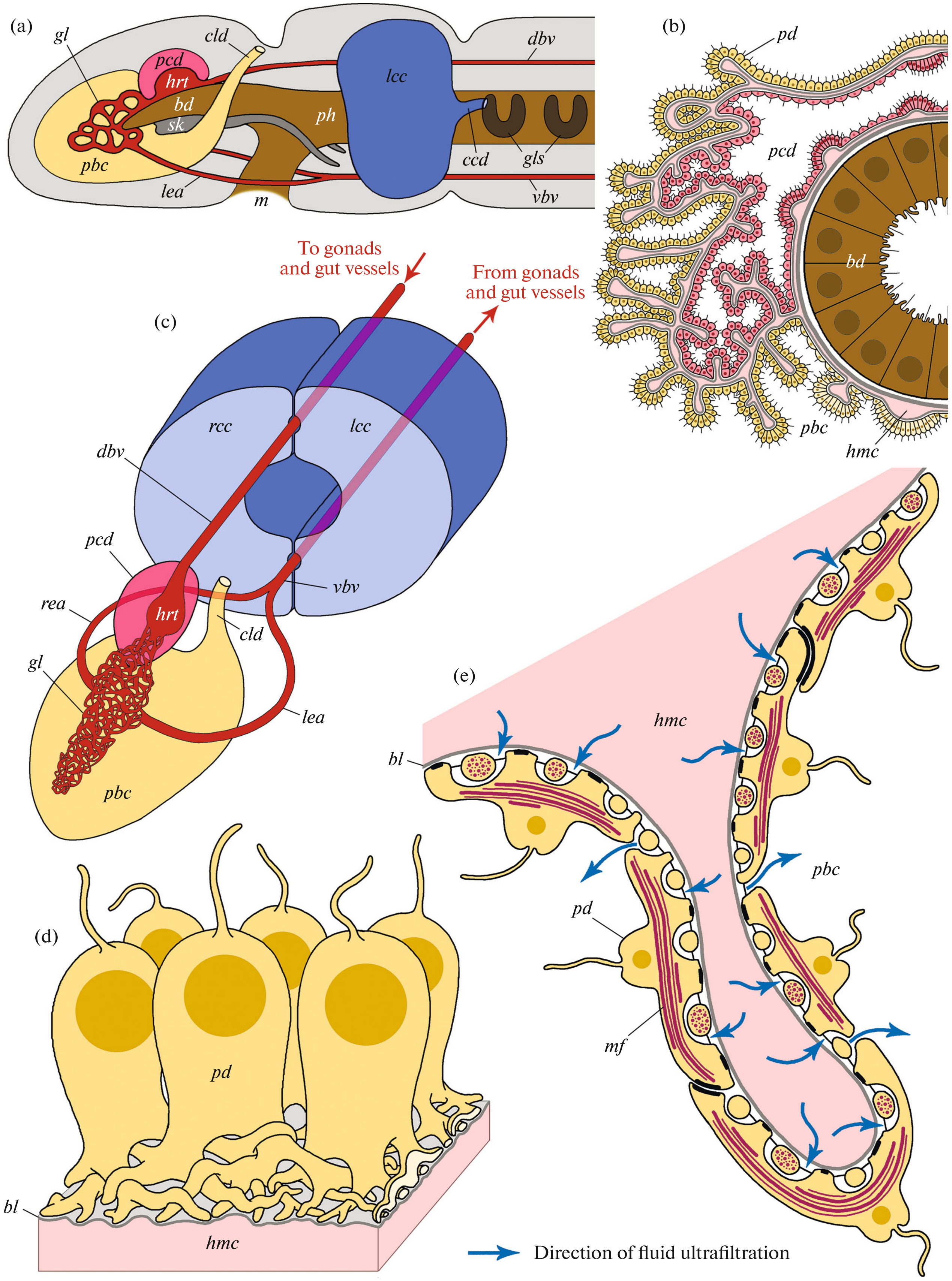
Fig. 1. Heart-kidney complex (HKC) of Hemichordata. (a) Scheme of location of the HKC in *Saccoglossus* and its main structures. (b) Scheme of a cross section through the glomerulus. (c) Scheme of organization of the coelomic and haemal structures of the HKC. (d) Podocytes of the glomerulus. (e) Scheme of the fine structure of podocytes of the glomerulus. Designations: *bd*, buccal diverticulum (stomochord); *bl*, basal lamina; *ccd*, collar coelomoduct; *cld*, proboscis coelomoduct; *dbv*, dorsal blood vessel; *gl*, glomerulus; *gsl*, gill slits; *hmc*, haemocoel; *hrt*, heart; *lcc*, left collar coelom; *lea*, left efferent artery; *m*, mouth; *mf*, myofilaments; *pbc*, proboscis coelom; *pcd*, pericardial coelom; *pd*, podocytes; *ph*, pharynx; *rcc*, right collar coelom; *rea*, right efferent artery; *sk*, stalk skeletal element; *vbv*, ventral blood vessel.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Direction of fluid ultrafiltration

AXIAL COMPLEX OF ECHINODERMATA

Central structures of the axial complex (ACO) of Eleutherozoa[1] echinoderms are located in interradius CD, laterally to the digestive tract, along the oral-aboral axis of the body (Fig. 2a). The central structures of the ACO are: the axial coelom and the madreporic ampulla (derivatives of the left protocoel = left axocoel), the pericardial coelom (right protocoel = right axocoel) and the axial organ (Fig. 2b). The latter stretches along a stone canal, the calcified walls of which serve as a support for the ACO in echinoderms. The axial organ is a network of haemocoelic spaces lying between the folds of the coelothelium. Depending on what type of coelothelium forms these folds, the pericardial and axial parts of the axial organ can be distinguished: the pericardial part passes between the folds of the pericardial coelom (right axocoel), and the axial part passes between the folds of the axial coelom (left axocoel). The pericardial part is usually smaller than the axial one. In the pericardial part, there is a haemocoelic vesicle with muscle walls formed by the myoepithelial cells of the pericardium; in starfish and sea urchins, this vesicle is called the heart (Fig. 2b) (Agassiz, 1873; Perrier, 1875; Gemmill, 1914; Ezhova et al., 2013, 2018). Brittle stars also have a haemocoelic vesicle in the pericardial part, although it is shifted to the oral side together with the pericardium (Ezhova et al., 2015). The pericardial coelom has no excretory ducts. The axial coelom is connected with the madreporic ampulla, which opens into the external environment with one or several madreporic pores (Fig. 2b). The stone canal also opens into the madreporic ampulla cavity. In sea cucumbers, the madreporic ampulla is the only remnant of the axial coelom.

The axial organ is represented by a network of haemocoelic spaces (=blood capillaries), the walls of which are formed by the basal lamina and a layer of coelomic epithelium (Figs. 2c, 2d). Ultrastructural studies of ACO showed the presence of ultrafiltration sites in it (Bargmann, von Hehn, 1968; Holland, 1970; Bachmann and Goldschmid, 1978; Welsch and Rehkämper, 1987; Balser and Ruppert, 1993; Ziegler, 2009; Ezhova et al., 2016). The coelothelium of the axial coelom consists of two types of flagellate cells (Figs. 2c, 2d). Cells of the first type are myoepithelial cells with basal processes containing bundles of muscle fibers (Fig. 2c). The myoepithelial cells are connected to each other through desmosomes (Fig. 2d) and form a three-dimensional contractile network. Cells of the second type are devoid of contractile fibers, i.e., are purely epithelial. These cells can be characterized as podocytes, because their basal processes have numerous fingerlike outgrowths lying in a single layer on the basal lamina (Fig. 2c). The adjacent processes of podocytes are interconnected through diaphragms—thin bridges formed by non-cellular matter (Fig. 2d) (Bargmann and von Hehn, 1968; Welsch and Rehkämper, 1987; Balser and Ruppert, 1993).

The issue of the direction of blood flow in the circulatory system of echinoderms is worth special consideration. Ubaghs (1967) assumed that blood moves from the genital haemal ring through ACO vessels to the oral haemal ring and then into the radial vessels of radii. Goldschmidt (1996) admits that the direction of pulsations of the heart and ACO in general may change; therefore, the direction of the entire blood flow also changes. Ruppert et al. (2004) assumed that a change in the blood flow direction may be widespread in animals with the so-called serial circulation, when the arrangement of organs allows blood to flow sequentially from one organ to another. If blood flowed in only one direction, then some organs would always receive blood rich in nutrients, whereas others would receive depleted blood, and some organs would be supplied with blood with a high oxygen concentration, whereas others would receive blood with a low oxygen concentration. When the blood flow direction changes, the organs located at the end of the blood circuit are at the very beginning and receive blood rich in oxygen and nutrients. Indeed, a periodic change in the blood flow direction has long been known in ascidians. A similar phenomenon can be assumed for echinoderms. However, given that the axial part of the ACO in echinoderms is much larger and stronger than the pericardial one, it can be assumed that the predominant direction of blood flow in echinoderms is from the aboral side of the body to the oral one. Blood enters the heart and the pericardial part of the axial organ from the aboral side, from two circumintestinal haemal rings (genital and gastric) in Asterozoa and from the vessels of the gonads and the intestinal haemal plexus in Echinozoa (Fig. 2b). Then, blood is pushed into the vessels of the axial part of the ACO.

The contraction of the muscle network formed by the processes of myoepithelial cells leads to an increase in pressure in the vessels of the axial organ. Under the influence of this pressure, the fluid from the haemocoelic spaces of the axial organ passes first through the basal lamina and then through the diaphragms between the processes of podocytes (Fig. 2d). The modified ultrafiltrate gets into the cavity of the axial coelom, wherefrom enters the madreporic ampulla and is excreted into the environment via the madreporic pores. An indirect proof of the possible involvement of the axial organ in excretion is the well-developed capillary network, which increases the surface area through which ultrafiltration takes place. The axial coelom is connected to the external environment through the madreporic ampulla, which, there-

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[1] The clade Crinozoa, which is sister to the Eleutherozoa, has many differences in the ACO structure, which deserve special consideration.

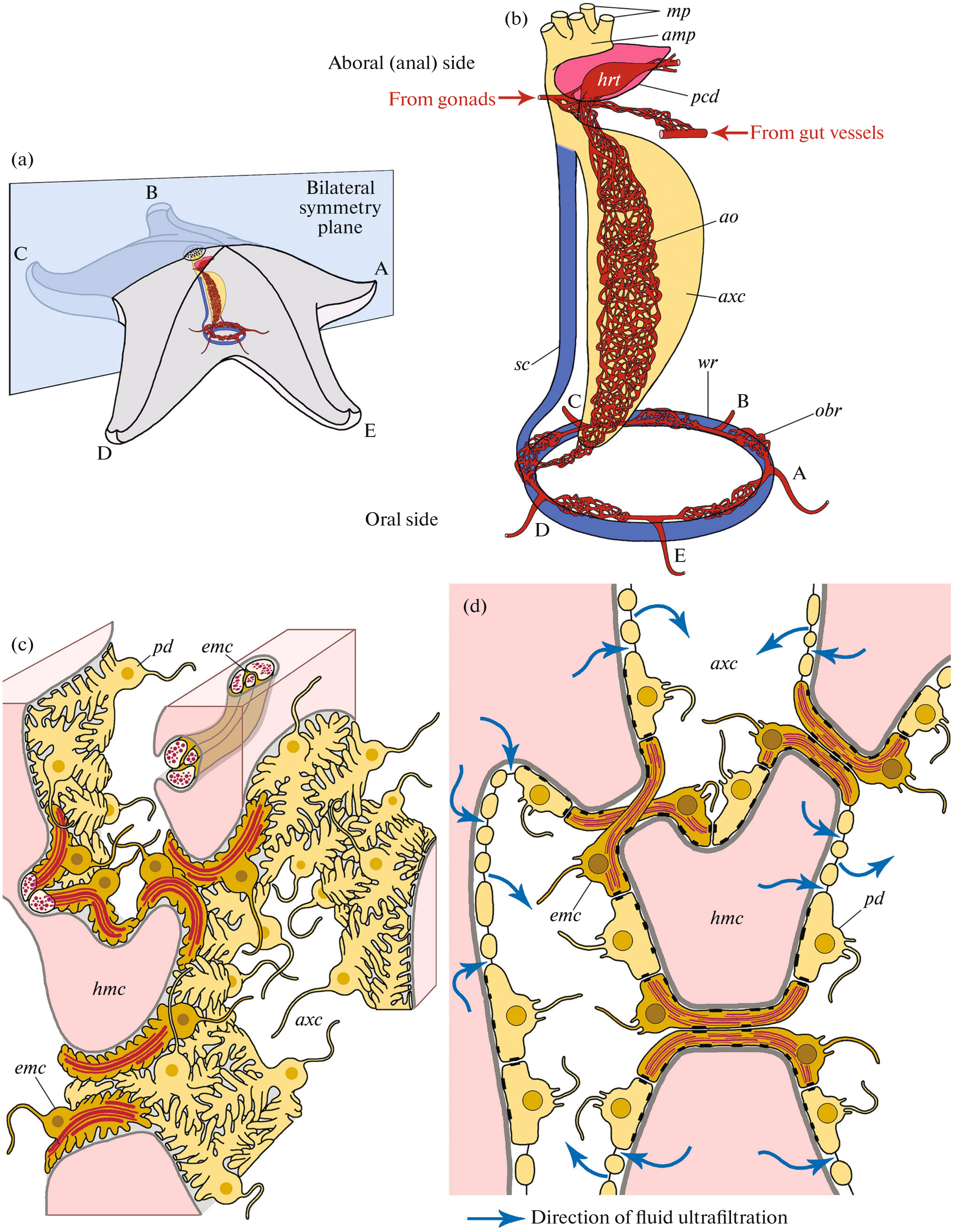

Fig. 2. Axial complex (ACO) of Echinodermata. (a) Scheme of location of ACO in the starfish body. Radii are indicated with capital letters. (b) Scheme of organization of coelomic and haemal structures of ACO. Radii are indicated with capital letters. (c) Podocytes and epithelial-muscle cells in the axial organ. (d) Diagram of the fine structure of the axial organ. Designations: *amp*, madreporic ampulla; *ao*, axial organ (axial part); *axc*, axial coelom; *emc*, epithelial-muscle cells; *hmc*, haemocoel; *hrt*, heart; *mp*, madreporic pores; *obr*, oral haemal ring; *pcd*, pericardial coelom; *pd*, podocytes; *sc*, stone canal; *wr*, water ring.

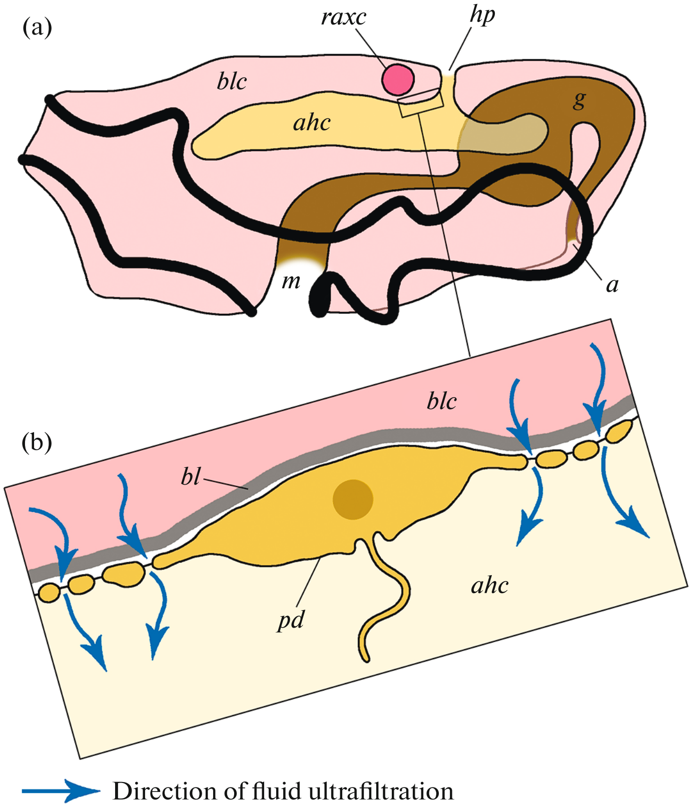

Fig. 3. Ultrafiltration in larva of Echinodermata (by Ruppert and Balser, 1986). (a) Scheme of location and structure of the left and right protocoels (axocoels) of larva. (b) Scheme of the fine structure of the larva ultrafiltration site. Designations: *a*, anus; *ahc*, left axohydrocoel; *bl*, basal plate; *blc*, blastocoel; *g*, gut; *hp*, hydropore; *m*, mouth; *pd*, podocyte; *raxc*, right axocoel.

fore, can function as an excretory opening. Cuénot (1948) injected dye into the axial coelom of adult starfish and observed its excretion into the external environment through the madreporic pores.

HEART-KIDNEY–AXIAL COMPLEX OF ORGANS IS A SYNAPOMORPHY OF THE CLADE AMBULACRARIA

It is known that hemichordates and echinoderms have a typical pelagobenthic life cycle and have ciliary planktotrophic larvae with a common body plan (Metschnikoff, 1869; Heider, 1909; Ubisch, 1913; Gemmill, 1914; Olsen, 1942; Dawydoff, 1948). Earlier, this allowed Metschnikoff (1881) to assume the phylogenetic closeness of echinoderms and hemichordates and combine both groups into the taxon Ambulacraria. Today, the concept of Ambulacraria is supported by molecular phylogenetic data (Wada and Satoh, 1994; Furlong and Holland, 2002; Halanych, 2004). Larvae of Ambulacraria have well-developed coelomic cavities. In particular, the hemichordate tornaria possess an extensive left protocoel, which is connected with the environment via the ciliary canal, which opens with an excretory opening (hydropore) on the dorsal side. The right protocoel is much smaller than the left one and is represented by a small contracting vesicle. In late tornaria, paired mesocoels (rudiments of collar coeloms) and paired metacoels (somatocoels, rudiments of trunk coeloms) are laid (Heider, 1909; Stiasny-Wijnhoff and Stiasny, 1927; Dawydoff, 1948).

Echinoderm larvae of various structures have a developed coelomic apparatus, which includes three pairs of coeloms, namely, protocoels (axocoels), mesocoels (hydrocoels), and metacoels (somatocoels). The coeloms of echinoderm larvae are characterized by dissymmetry of the same type as in the larvae of hemichordates, though more pronounced. The extensive left protocoel (=axocoel) is connected to the left mesocoel (hydrocoel) so that a common axohydrocoel is formed, which is connected to the environment via the ciliary pore canal, which opens with an excretory opening (hydropore) on the dorsal side (Figs. 3a, 4b). The right protocoel (axocoel) is represented by a small vesicle, whereas the right mesocoel (hydrocoel) usually does not develop at all (Selenka, 1876; MacBride, 1903, 1907; Gemmill, 1912, 1914,

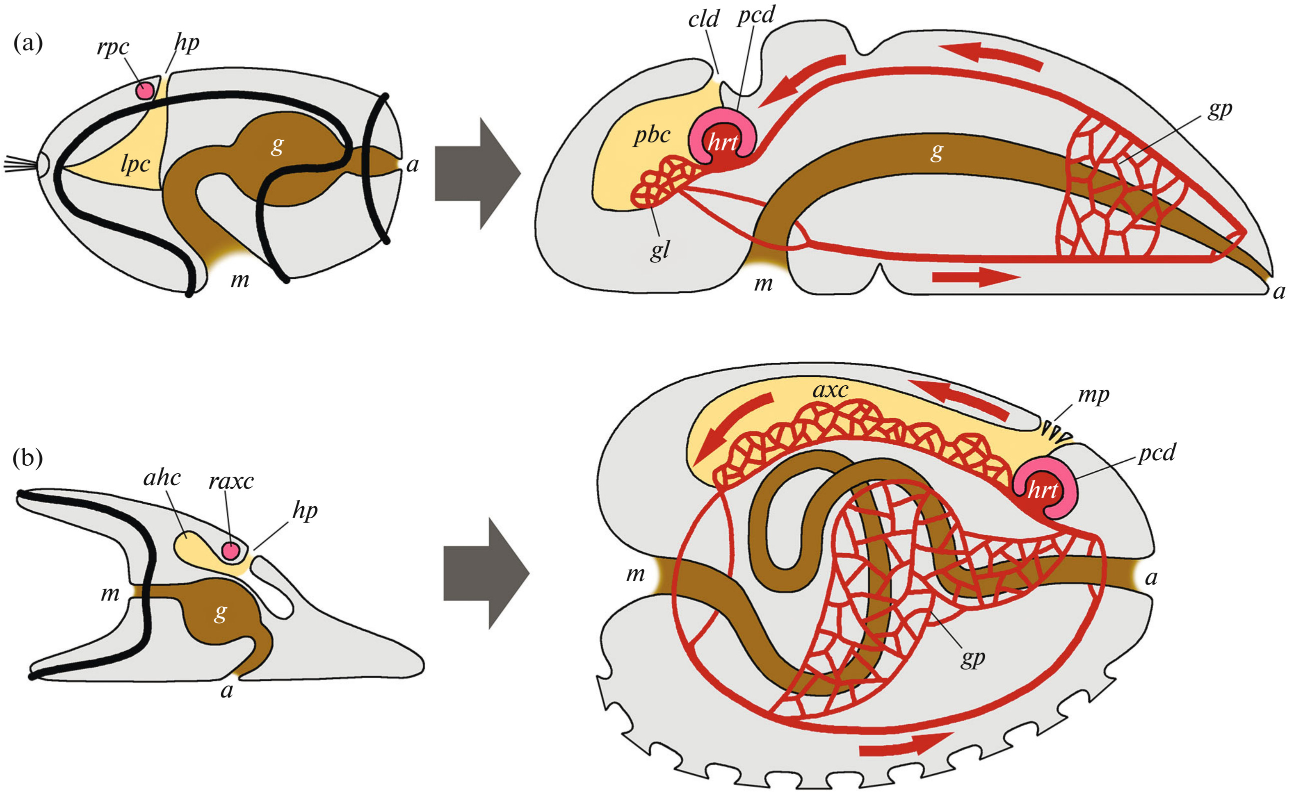

Fig. 4. Comparative anatomical scheme of organization of preoral coeloms of larvae as well as HKC and ACO of adult Hemichordata (a) and Echinodermata (b). The arrows show the direction of blood flow. Designations: *a*, anus; *ahc*, left axohydrocoel; *axc*, axial coelom; *cld*, proboscis coelomoduct; *g*, gut; *gl*, glomerulus; *gp*, gut haemal plexus; *hp*, hydropore; *hrt*, heart; *lpc*, left protocoel; *m*, mouth; *mp*, madreporic pore; *pbc*, proboscis coelom; *pcd*, pericardial coelom; *raxc*, right axocoel; *rpc*, right protocoel.

1920; Runnström, 1927; Hörstadius, 1939; Ivanova-Kazas, 1978; Balser et al., 1993).

Larval coeloms of hemichordates and echinoderms are involved in the excretory function. The walls of larval coeloms are formed by flagellated mesodermal cells lying on the basal lamina, which separates the coelomic cavity of the larva from the blastocoel (Fig. 3b). Coelomic cells that form the coelom wall near the pore canal are formed by podocytes, flagellated cells with processes between which diaphragms are located (Ruppert and Balser, 1986). The fluid from the blastocoel is filtered first through the basal lamina and then through the diaphragms between the processes of podocytes (Fig. 3b). Due to the beating of the flagella of the cells that form the pore canal wall, the ultrafiltrate is evacuated from the coelom of the larva into the external environment. The filtration intensity, calculated on the basis of the speed of fluid movement via the pore canal, is quite significant. Thus, the entire volume of the blastocoelic fluid in the tornaria could be cleared in 50 h, whereas the volume of the blastocoel fluid of the starfish larva could be cleared in only 5 h (Ruppert and Balser, 1986).

Thus, the ciliary larvae of Deuterostomia have a developed excretory system, which with high intensity ensures ultrafiltration of fluid from the primary body cavity, the blastocoel (ontogenetic progenitor of the haemocoel), into the secondary body cavity, the coelom, and then into the external environment via the ciliary coelomoduct. In terms of structure and mechanism of functioning, this excretory system corresponds to metanephridia (see Ruppert and Balser, 1986; Ruppert and Smith, 1988). This clearly distinguishes the larvae of Deuterostomia from the ciliated larvae of Lophotrochozoa, which have protonephridia.

During metamorphosis, the excretory organs of hemichordates and echinoderms are formed on the basis of the same coelomic structures that provide the excretory function in larvae. The formation of the HKC of hemichordates involves the proboscis coelom, originating from the left protocoel of the larva, and the pericardial coelom, originating from the right protocoel (Fig. 4a). In echinoderms, the formation of the ACO involves the left axocoel, which gives rise to the axial coelom and the madreporic ampulla, and the pericardial coelom, which originates from the right axocoel of the larva (Fig. 4b).

The axial organ of echinoderms is an undoubted homologue of the heart-kidney of hemichordates. It is formed from homologous coeloms of the larva, has a significant similarity in structure, and retains the continuity of function. Probably, the excretory organ based on dissymmetric preoral coeloms, one of which (right) took over the function of the pericardium, and the other (left) took over the function of the excretory cavity, formed in the common ancestor of hemichordates and echinoderms and represents the key synapomorphy of the clade Ambulacraria. It cannot be ruled out that the formation of dissymetry of protocoels, which is a common feature of the clade Ambulacraria, is associated with this division of functions between the preoral coeloms. Subsequently, due to this previous dissymmetry in the ancestors of Echinodermata (in which the mesocoel=hydrocoel is drained via a common pore with the protocoel=axocoel rather than separately, as in hemichordates), a more profound coelomic dissymmetry arose, which encompasses both protocoels and mesocoels.

CONCLUSIONS

The features of microscopic anatomy and fine structure led us to conclude that the axial complex of echinoderms is an excretory organ—a kidney of echinoderms. The sites of ultrafiltration are the walls of the blood capillaries of the axial organ. The fluid from the blood capillaries is filtered through the basal lamina, and then through the diaphragms between the processes of podocytes. The pressure required for filtration is created by the contractions of the heart and myoepithelial cells, which form the coelomic lining along with podocytes. The modified ultrafiltrate gets to the cavity of the axial coelom and is excreted from there via the madreporic pores, which thus play the role of an excretory opening. The axial organ of echinoderms is formed from the same larval coeloms as the heart-kidney of hemichordates, namely, from the left axocoel, which becomes the axial coelom of the ACO, and from the right axocoel, which becomes the pericardium. This allowed us to conclude that the progenitor of the heart-kidney and the axial complex formed in the common ancestor of hemichordates and echinoderms. Thus, the ACO of echinoderms is formed from the homologous larval coeloms, shows significant similarity in structure, retains the continuity of function, and is a homologue of the HKC of hemichordates. Probably, the excretory organ based on dissymmetric preoral coeloms was formed even in the common ancestor of hemichordates and echinoderms and represents the most important synapomorphy of the clade Ambulacraria.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

REFERENCES

Adoutte, A., Balavoine, G., Lartillot, N., Lespinet, O., Prud'homme, B., and de Rosa, R., The new animal phylogeny: reliability and implications, *Proc. Natl. Acad. Sci. U. S. A.*, 2000, vol. 97, no. 9, pp. 4453–4456.

Agassiz, A., Revision of the Echini, *Mem. Mus. Comp. Zool. Harvard*, 1873, vol. 3, pp. 383–628.

Bachmann, S. and Goldschmid, A., Fine structure of the axial complex of *Sphaerechinus granularis* (Lam.) (Echinodermata: Echinoidea), *Cell Tiss. Res.*, 1978, no. 193, pp. 107–123.

Balser, E.J. and Ruppert, E.E., Structure, ultrastructure, and function of the preoral heart-kidney in *Saccoglossus kowalevskii* (Hemichordata, Enteropneusta) including new data on the stomochord, *Acta Zool.* (Stockholm), 1990, no. 71, pp. 235–249.

Balser, E.J. and Ruppert, E.E., Ultrastructure of axial vascular and coelomic organs in comasterid featherstars (Echinodermata: Crinoidea), *Acta Zool. (Stockholm)*, 1993, vol. 74, no. 2, pp. 87–101.

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.

Bargmann, W. and von Hehn, G., Über das Axialorgan ("mysterious gland") von *Asterias rubens* L., *Z. Zellforsch. Mikrosk. Anat. Histochem.*, 1968, vol. 88, pp. 262–277.

Beklemishev, V.N., *Osnovy sravnitel'noi anatomii bespozvonochnykh* (Principles of Comparative Anatomy of Invertebrates), vol. 2: *Organologiya* (Organology), Moscow: Nauka, 1964.

Cameron, C.B.*, The phylogeny of the Hemichordata and ecology of two new enteropneust species from Barkley Sound.* Diss. Dr of Philosophy. Edmonton: Alberta Fall, 2000, p. 178.

Cuénot, L., Anatomie, éthologie et systématique des Échinodermes, dans *Traité de Zoologie*, Paris: Masson et Cie Éditeurs, 1948, vol. 11, pp. 1–275.

Dawydoff, C., Embranchement des Stomocordés, dans *Traité de Zoologie*, Grassé, P.P., Ed., Paris: Masson et Cie, 1948, vol. 11, pp. 367–532.

Dogel, V.A., *Zoologiya bespozvonochnykh* (Zoology of Invertebrates), Moscow: Vysshaya shkola, 1975.

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.*, 2016, vol. 468, pp. 129–132.

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

Ezhova, O.V. and Malakhov, V.V., Three-dimensional structure of the skeleton and buccal diverticulum of an acorn worm *Saccoglossus mereschkowskii* Wagner, 1885 (Hemichordata, Enteropneusta), *Invertebr. Zool.*, 2009, vol. 6, no. 2, pp. 103–116.

Ezhova, O.V. and Malakhov, V.V., Microscopic anatomy and fine structure of the skeleton—heart-kidney complex in *Saccoglossus mereschkowskii* (Hemichordata, Enteropneusta): 1. Stalk skeleton, Biol. Bull. (Moscow), 2010a, vol. 37, no. 8, pp. 795–806.

Ezhova, O.V. and Malakhov, V.V., Microscopic anatomy and fine structure of the skeleton—heart-kidney complex in *Saccoglossus mereschkowskii* (Hemichordata, Enteropneusta): 2. Buccal diverticulum, *Zool. Zh.*, 2010b, vol. 89, no. 6, pp. 643–662.

Ezhova, O.V. and Malakhov, V.V., Microscopic anatomy and fine structure of the skeleton—heart-kidney complex in *Saccoglossus mereschkowskii* (Hemichordata, Enteropneusta): 3. Heart and blood vessels, *Zool. Zh.*, 2010c, vol. 89, no. 7, pp. 771–785.

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, *Zool. Zh.*, 2010d, vol. 89, no. 8, pp. 899–923.

Ezhova, O.V. and Malakhov, V.V., The nephridial hypothesis of the gill slit origin, *J. Exp. Zool., B: Mol. Dev. Evol.*, 2015, vol. 324, no. 8, 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.

Fedotov, D.M., On the problem of the homology of coeloms of Echinodermata, Enteropneusta, and Chordata, *Izv. Biol. Naucno-Issled. Inst. Perm. Univ.*, 1923, vol. 2, no. 1, pp. 1–11.

Fedotov, D.M., Zur Morphologie des axialen Organkomplexes der Echinodermen, *Z. Wiss. Zool.*, 1924, no. 123, pp. 209–304.

Furlong, R.F. and Holland, P.W.H., Bayesian phylogenetic analysis supports monophyly of Ambulacraria and of Cyclostomes, *Zool. Sci.*, 2002, vol. 19, no. 5, pp. 593–599.

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, Phil. Trans. R. Soc. Lond.*, 1914, no. 205, pp. 213–294.

Gemmill, J.F., The development of the starfish *Crossaster papposus* Muller and Troschel, *Quart. J. Microscop. Sci.*, 1920, vol. 64, no. 2, pp. 155–189.

Goldschmid, A., Echinodermata, in *Spezielle Zoologie*, Teil 1: *Einzeller und Wirbellose Tiere*, Westheide, W. and Rieger, R., Eds., Stuttgart: Gustav Fischer Verlag, 1996, pp. 778–834.

Halanych, K.M., The new view of animal phylogeny, *Annu. Rev. Ecol. Evol. Syst.*, 2004, vol. 35, pp. 229–56.

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

Holland, N.D., The fine structure of the axial organ of the feather star *Nemaster rubiginosa* (Echinodermata: Crinoidea), *Tissue Cell*, 1970, vol. 2, no. 4, pp. 625–636.

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

Hyman, L.H., Smaller coelomate groups. Phylum Hemichordata, in *The Invertebrates*, New York: McGraw-Hill, 1959, vol. 5, pp. 72–154.

Ivanova-Kazas, O.M., *Sravnitel'naya embriologiya bespozvonochnykh: iglokozhie i polukhordovye* (Comparative Embryology of Invertebrates: Echinoderms and Hemichordates), Moscow: Nauka, 1978.

MacBride, E.W., The development of *Echinus esculentus* together with some points in the development of *E. miliaris* and *E. acutus, Phil. Trans. R. Soc. London*, 1903, vol. 195, pp. 285–327.

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

Metschnikoff, E.E., Studien über die Entwickelung der Echinodermen und Nemertinen, *Memoires L'Academie Imperial des Sciences de St.-Petersbourg*, VII Serie, St. Petersbourg, 1869, vol. 14, no. 8.

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

Olsen, H., The development of the brittle-star *Ophiopholis aculeata* with a short report on the outer hyaline layer, *Bergens Mus. Arbok. Naturvitenskap*, 1942, vol. 6, pp. 1–107.

Perrier, E., L'appareil circulatoire des Oursins, *Arch. Zool. Exp. Gén. Ser.*, 1875, vol. 4, pp. 605–643.

Ridewood, W., Pterobranchia: Cephalodiscus, *Natl. Antarctic Exped. Nat. Hist., Zool.*, 1907, vol. 2, pp. 1–67.

Runnström, S., Über die Entwicklung von *Leptosynapta inhaerens* (O.Fr. Müller), *Bergens 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. and Smith, P.R., The functional organization of filtration nephridia, *Biol. Rev.*, 1988, no. 171, pp. 231–258.

Ruppert, E.E., Fox, R.S., and Barnes, R.D., *Invertebrate Zoology*, Belmont: Thomson Brooks/Cole, 2004.

Schepotieff, A., Knospungsprozess und Gehäuse von *Rhabdopleura, Zool. Jahrb. Abt. Anat.*, 1907, vol. 24, pp. 193–238.

Selenka, E., Zur Entwicklung der Holothurien (*Holothuria tubulosa* und *Cucumaria doliolum*), Ein Beitrag zur Keimblättertheorie, *Zeit. Wissenschaft. Zool.*, 1876, vol. 27, no. 2, pp. 155–178.

Spengel, J.W., Die Enteropneusten des Golfes von Neapel, in *Fauna und Flora des Golfes von Neapel*, Herausgegeben von der Zoologischen Station zu Neapel, Monograph, 1893, no. 18, pp. 1–757.

Stiasny-Wijnhoff, G. and Stiasny, G., Die Tornarien. Kritik der Beschreibungen und Vergleich samlicher bekannter Enteropiieustenlarren, *Ergebn. Fortschr. Zool.*, 1927, vol. 7, pp. 38–192.

Ubaghs, G., General characters of Echinodermata, in *Treatise on Invertebrate Paleontology*, Part S: *Echinodermata 1*, The University of Kansas and The Geological Society of America, 1967, pp. 3–60.

Ubisch, L., Die Entwicklung von *Strongylocentrotus lividus* (*Echinus microtuberculatus, Arbacia pustulosa*), *Z. Wiss. Zool.*, 1913, no. 106, pp. 409–448.

Van der Horst, C.J., Hemichordata, in *Klassen und Ordnungen des Tierreichs*, Bronns, H.G., Ed., Leipzig: Leipzig Akademische Verlagsgesellschaft M. B. H., 1939.

Wada, H. and Satoh, N., Details of the evolutionary history from invertebrates to vertebrates, as deduced from the sequences of 18s rDNA, *Proc. Natl. Acad. Sci. U. S. A.*, 1994, vol. 91, pp. 1801–1804.

Welsch, U. and Rehkamper, G., Podocytes in the axial organ of echinoderms, *J. Zool. London*, 1987, vol. 213, pp. 45–50.

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. 10, pp. 1–31.

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