REVIEW

Invertebrate Zoology

The Morphology of the Axial Complex and Associated Structures in Asterozoa (Asteroidea, Echinoidea, Ophiuroidea)

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Received September 19, 2013

Abstract—The representatives of Asterozoa (Asteroidea, Echinoidea, and Ophiuroidea) have a similar structural plan of the axial complex with minor differences within each class; this structural scheme substantially differs from that in Crinozoa and Holothurozoa. The axial complex consists of the coelomic organs and the haemocoel (blood) structures, which are morphologically and functionally integral. The coelomic organs are the stone canal, axial coelom, perihaemal coeloms (axocoel perihaemal ring and somatocoel perihaemal ring), water ring, and pericardial and genital coeloms. These organs are closely associated with the epigastric and hypogastric coeloms and with the perioral coelomic ring. The haemocoel structures of the axial complex include the oral haemal ring, heart, axial organ, genital haemal ring, and gastric haemal ring. The epineural canals of echinoids and ophiuroids are of a noncoelomic nature. They are formed by the invagination of the ectoneural cord and closing of the epidermis above it. The possible functions of the axial complex in Asterozoa are blood circulation and excretion.

The most striking feature of the structural organization of echinoderms is the axial complex of organs that occur in all representatives of this type. The structure of the axial complex in different groups of echinoderms has attracted the attention of researchers for more than a century. The homology of the axial complex in representatives of different echinoderm classes has been vividly discussed in numerous papers [2–7, 13, 24, 25, 30, 39, 40, 57, 66]. Unfortunately, all the reports and manuals describe the structure of the axial complex in very different ways; the terms used by researchers are not consistent. This makes the descriptions of the axial complex organization uncomprehensive and creates many problems in establishing homologies between its parts in different groups of echinoderms.

The present work is devoted to a comparative analysis of the microscopic anatomy of the axial complex and associated structures in the subtype Asterozoa, which comprises three classes: Asteroidea, Echinoidea, and Ophiuroidea.

CLASS ASTEROIDEA

The structure of the axial complex in Asteroidea has been described in a number of works for the families Acanthasteridae [21], Asteriidae [2, 19, 21, 27, 28, 33, 53], Asterinidae [21, 32, 46], Astropectinidae [21, 38], Echinasteridae [36], Ophidiasteridae [21], Solasteridae [26, 29], Stichasteridae [21], and Xyloplacidae [9, 41, 56].

The central structures of the axial complex concentrate in the interradius CD. A stone canal that is formed as a tubular organ with partially calcified walls runs there from the madreporite in the oral direction. On the oral side of the starfish, the stone canal opens into the coelomic water ring. In the aboral end, the stone canal is connected with the axial coelom and opens into the madreporic ampulla (Fig. 1a). Five radial ambulacral coelomic processes, one per each radius, exit from the water ring (Fig. 1b). The water ring with its radial canals derives from the left hydrocoel (mesocoel).

The axial coelom (left axocoel or protocoel) is a sac extended in the oral-aboral direction; it envelopes the stone canal along its entire length, mainly from outside (i.e., from the side of the interradius CD). On the aboral side, the axial coelom forms a process, skirting the stone canal and communicating with it. Thus, the stone canal, which is connected both with the axial coelom (on the aboral side) and with the water ring (on the oral side) (Figs. 1a and 2a) is a coelomoduct.

The perihaemal system includes two ring coeloms separated by a mesentery. On the oral side, the axial coelom opens into the axocoel (internal by its position) coelomic ring of the perihaemal system (Figs. 1a
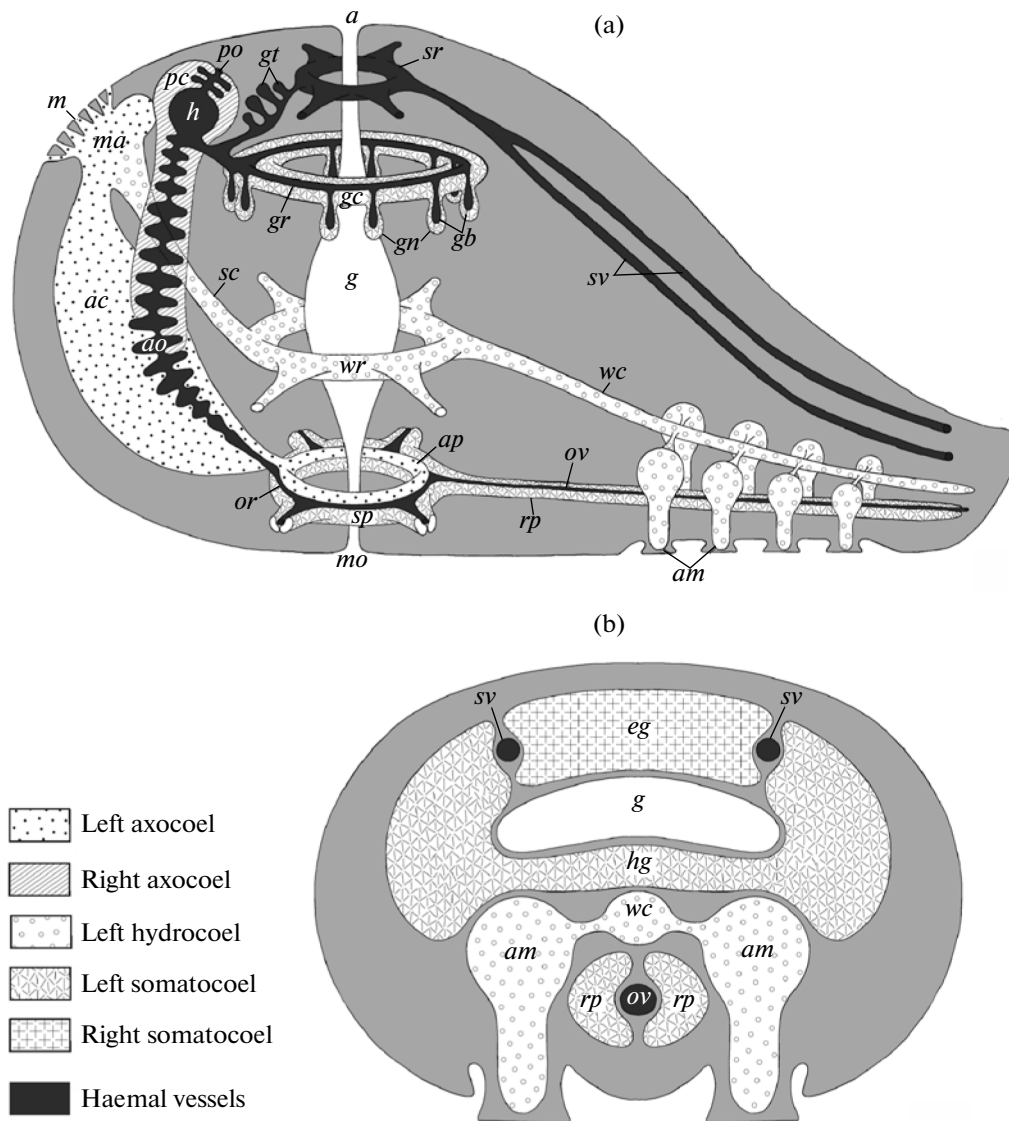
Fig. 1. The axial complex of organs and associated structures in Asteroidea based on the example of the sea star *Asterias rubens*. (a) Generalized scheme; right somatocoel (epigastric coelom) not shown; (b) scheme of a section through the starfish ray. Symbols: *a*, anus; *ac*, axial coelom; *am*, ampullae of ambulacral podia; *ao*, axial part of the axial organ; *ap*, axocoel perihaemal coelom; *eg*, epigastric coelom; *g*, gut; *gb*, gonadal blood lacuna; *gc*, genital coelom; *gn*, gonad; *gr*, genital haemal ring; *gt*, gastric haemal tufts; *h*, heart; *hg*, hypogastric coelom; *m*, madreporite; *ma*, madreporic ampulla; *mo*, mouth; *or*, oral haemal ring; *ov*, radial blood vessel from the oral ring; *pc*, pericardial coelom; *po*, pericardial part of the axial organ; *rp*, radial processes of the perihaemal coelom; *sc*, stone canal; *sp*, somatocoel perihaemal coelom; *sr*, gastric haemal ring; *sv*, radial blood vessel from the gastric ring; *wc*, radial water coelomic process; *wr*, water ring.

and 2a). The axocoel perihaemal coelomic ring is a continuation of the left axocoel (of the left protocoel). The somatocoel perihaemal coelomic ring (external in its position) in *Asterias rubens* (L., 1758) [27, 28] and in some other starfish, for example in *Crossaster papposus* (L., 1767) [29], develops in ontogenesis as a derivative of the left somatocoel (metacoel). In other Asteroidea species, viz., *Asterina gibbosa* (Pennant, 1777), *Solaster endeca* (L., 1771), *Leptasterias hexactis* (Stimpson, 1862), *Astropecten aurantiacus* (L., 1758), one of the five anlagen of the somatocoel perihaemal coelomic ring, namely the one lying in the interradius

CD, derives from the left axocoel, while the others arise from the left somatocoel [19, 26, 32, 38, 46, 53]. In adult starfish, the somatocoel coelomic ring of the perihaemal system is a closed coelomic cavity that is not connected in any way with the axocoel or the somatocoel.

Thus, starfish possess three coelomic rings around the mouth: the ambulacral (or water ring, where the stone canal opens), axocoel perihaemal (connected with the axial coelom) and somatocoel perihaemal rings (Fig. 2a). Moreover, some Asteroidea have an anlage of the perioral coelom derived from the left
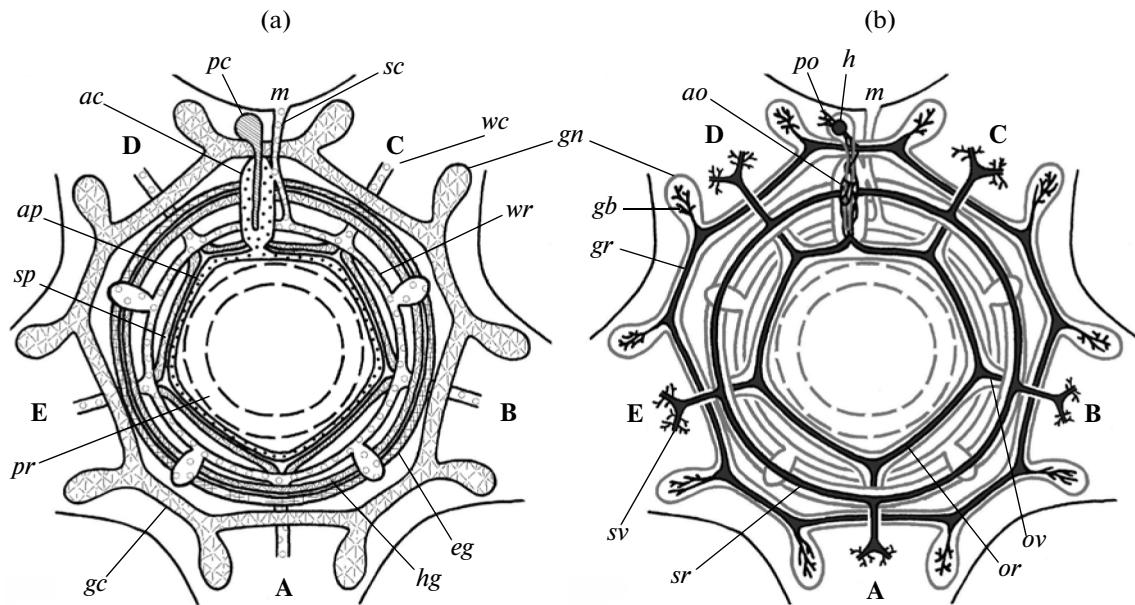
Fig. 2. Coelomic and haemocoelic (blood circulatory) structures of the axial complex of organs in Asteroidea. Aboral view. (a) Diagram of coeloms; blood vessels not shown; (b) diagram of blood circulatory (haemocoelic) structures; outlines of the coeloms are shown with light-gray lines. Symbols: *ac*, axial coelom; *ao*, axial part of the axial organ; *ap*, axocoel perihaemal coelom; *eg*, epigastric coelom; *gb*, gonadal blood lacuna; *gc*, genital coelom; *gn*, gonad; *gr*, genital haemal ring; *h*, heart; *hg*, hypogastric coelom; *m*, madreporite; *or*, oral haemal ring; *ov*, radial blood vessel from the oral ring; *pc*, pericardial coelom; *po*, pericardial part of the axial organ; *pr*, perioral coelom; *sc*, stone canal; *sp*, somatocoel perihaemal coelom; *sr*, gastric haemal ring; *sv*, radial blood vessel of the gastric ring; *wc*, radial water coelomic process; *wr*, water ring. The perioral coelom is shown with a dotted line; absent in *Asterias rubens*.

somatocoel [26, 29], i.e., a fourth perioral coelomic ring (Fig. 2a). In relation to the water ring, the perihaemal coeloms are shifted orally [2]. In the mesentery, the oral haemal ring is found among perihaemal coeloms (Figs. 1a and 2b). the haemal net of the axial organ enters in this ring in the interradius CD. The somatocoel perihaemal ring sends paired processes in each ray of the starfish; the mesentery between these paired processes includes a radial blood vessel (Figs. 1a and 2b) that originates from the oral haemal ring.

The pericardial coelom of *A. rubens* is a closed coelomic cavity derived from the right axocoel (right protocoel). The pericardial coelom is situated on the aboral side, adjoining the madreporic ampulla (Figs. 1a and 2a), and sends a branched process into the axial coelom; the vessels of the haemal system of the axial organ run among these branches [2]. The coelothelium of the pericardial coelom builds the walls of the heart and the vessels in the pericardial part of the axial organ. The heart is formed as an elongated vesicle and divides the axial organ into a smaller pericardial (aboral in position) and a bigger axial (oral in position) parts (Figs. 1a and 2b). The heart is connected with the haemocoel of the body wall of the starfish through the vessels of the pericardial part of the axial organ [2].

The axial organ has a spindle-like structure formed by a plexus of blood vessels; it stretches in the oral-aboral direction from the pericardial coelom through the axial coelom to the perihaemal coelomic rings

(Figs. 1a and 2b). the vessels of the axial organ are formed as haemocoel spaces among the basal plates of the coelomic epithelia of the pericardial and axial coeloms.

The smaller paricardial part of the axial organ lies entirely in the pericardial coelom. The per se axial part of the axial organ is situated mostly in the axial coelom, but protrudes in the aboral portion as well in the pericardial coelom. The most oral segment of the axial organ connects with the haemocoel space within the mesentery between the perihaemal coeloms, namely with the oral ring vessel.

In the vicinity of the axial complex, we observe the ring genital coelom (Figs. 1a and 2a), or rather, its part located in the interradius CD. This is a separate coelomic cavity, which lies aborally around the hindgut and does not communicate with other coeloms [2]. The genital coelom is a derivative of the left somatocoel (left metacoel). Ontogenetically, its formation starts in the interradius CD: the left somatocoel develops a tubular projection aborally to form a ring around the hindgut [26, 27, 29, 46]. A genital rachis is differentiated within the genital ring coelom; it is a cord of germinal epithelium covered with the celothelium and has a cavity in the center of each gonad. This cavity of the germinal epithelium receives mature sex products. Thus, the cavity of the genital coelom is limited from one side by the coelothelium of the genital coelom,

and from the other side by the coelothelium of the genital rachis [2].

Gonads are formed as interradial protrusions of the genital rachis. Typically, Asteroidea form five interradial gonads; each is divided into two branches (Figs. 1a and 2a). a genital haemal ring from which the gonadal haemal lacunae depart in the oral direction, is differentiated between the germinal epithelium and the surrounding coelothelium of the genital coelom [33]. In the interradius CD, the gonadal haemal lacuna joins with the vessels of the axial organ where its axial part exits from the heart (Figs. 1a and 2b).

A gastric haemal ring runs in the horizontal mesentery that separates the epigastric coelom (derivative of the right somatocoel) and the hypogastric coelom (derivative of the left somatocoel) (Figs. 1 and 2b). In adult starfish, coelothelia of these coeloms diverge and thus form swellings on the horizontal mesentery ("gastric haemal tufts," [39]) with blood lacunae inside. The gastric haemal ring enters the axial organ in the interradius CD together with the gonadal blood lacuna (Figs. 1a and 2b) [2]. The gastric haemal ring sends a radial blood vessel into each radius, which bifurcate into two vessels. These vessels run in the mesentery between the epigastric and hypogastric coeloms (Fig. 1b).

The genus *Xyloplax* has been described relatively recently; two species of the genus were primarily assigned to a separate class of echinoderms—Concentricycloidea [9, 56]. Later, *Xyloplax* was moved closer to starfish [1, 41, 60]. The axial complex of these very peculiar echinoderms is simplified and represented merely by a stone canal that connects the environment with the water ring [41, 56]. The water ring extends five short radial processes that enter the second (external) coelomic ring, connected with coeloms of the ambulacral podia. The external coelomic ring of *Xyloplax* has no homologues in the coelomic system of typical starfish. In *Xyloplax*, no axial organ, or axial coelom, or perihaemal rings have ever been found [41, 56]. Probably, we shall regard the absence of these structures in *Xyloplax* as a result of simplification caused by the tiny sizes of these animals. As to some elements of the architecture of the axial complex, there is an opinion that adult *Xyloplax* retains its larval structure. This is true, for example, for madreporite, which looks in *Xyloplax* like a larval hydropore [41, 56].

Very rarely, some representatives of starfish possess more than one madreporite plate. The presence of several madreporites and axial complexes is associated either with mutation (e.g., *Acanthaster echinites* (Ellis et Solander, 1786) possesses from 13 to 20 rays and from 5 to 16 madreporites), or with preparation to asexual reproduction through division at the early stages of ontogenesis. Thus, *Coscinasterias tenuispina* (Lamarck, 1816) has, as a rule, seven rays and up to five (but not always five) madreporites [20], and a majority (79%) of *Coscinasterias acutispina* (Stimp-

son, 1862) individuals have eight rays and four madreporites [65]. Representatives of the genus *Linckia* have usually four to eight arms and nearly always two madreporites, or rarely one, three, four, or five madreporites [24]. *Allostichaster polyplax* (Müller et Troschel, 1844) is characterized by numerous madreporites; this is expressed in its species name [21]. The question of which coelomic anlagen participate in the formation of the great number of axial complexes remains open.

CLASS ECHINOIDEA

In sea urchins, the axial complex of the organs has been studied in detail for Arbaciidae [63, 66], Aspidodiadematidae [66], Cidaridae [43, 66], Diadematidae [66], Echinidae [8, 14, 18, 34, 42, 43, 47, 54, 63, 66], Echinothuriidae [66], Parechinidae [66], Pedinidae [66], Phormosomatidae [66], Saleniidae [66], Spatangidae [34, 42, 66], Strongylocentrotidae [63, 66], Schizasteridae [42], and Toxopneustidae [50]. The old studies that were devoted to the morphology of the axial complex in sea urchins do not present any image of an axial coelom around the axial organ [18, 34, 43]. This led Hyman [39] to the conclusion that, unlike starfish, Echinoidea have no axial coelom. However, according to more recent data of other authors [24, 30, 66], the axial coelom is present in sea urchins, it is but a relatively narrow tubule and probably therefore was not noticed before. Nearly the entire volume of the axial coelom is occupied by the circulatory system of the axial organ, while the left axocoel is in fact its thin wall.

In general, the morphology of the axial complex in sea urchins is similar to that in starfish (Figs. 3 and 4). In sea urchins, the mouth is surrounded by coelomic rings (Figs. 3a and 4a): the water ring (left hydrocoel, i.e., mesocoel) and perihaemal ring [23, 34]. Sea urchins have only one perihaemal ring, which derives from the left somatocoel [47, 63]. Based on this observation, we can conclude that the single perihaemal ring of sea urchins is a homologue of the somatocoel (external) perihaemal coelomic ring of starfish. The vertical mesentery, which separates the paired radial processes of the somatocoel perihaemal coelomic ring in starfish, is not found in sea urchins. The somatocoel coelomic ring in sea urchins extends five unpaired radial processes. The radial blood vessel runs in the vertical mesentery in starfish and in the mesentery, separating the radial process of the perihaemal coelomic ring and the radial process of the water coelomic ring, in sea urchins (Fig. 3b). Moreover, Echinoidea have a perioral ring coelom that is also derived from the left somatocoel [47, 63]. This coelom surrounds water, perihaemal, and epineural (see below) rings.

As Ziegler et al. showed [66], the axial coelom of sea urchins is blindly closed at its oral end and does not communicate here with any coelomic cavity (Figs. 3a and 4a). in sea urchins, this is apparently related to the
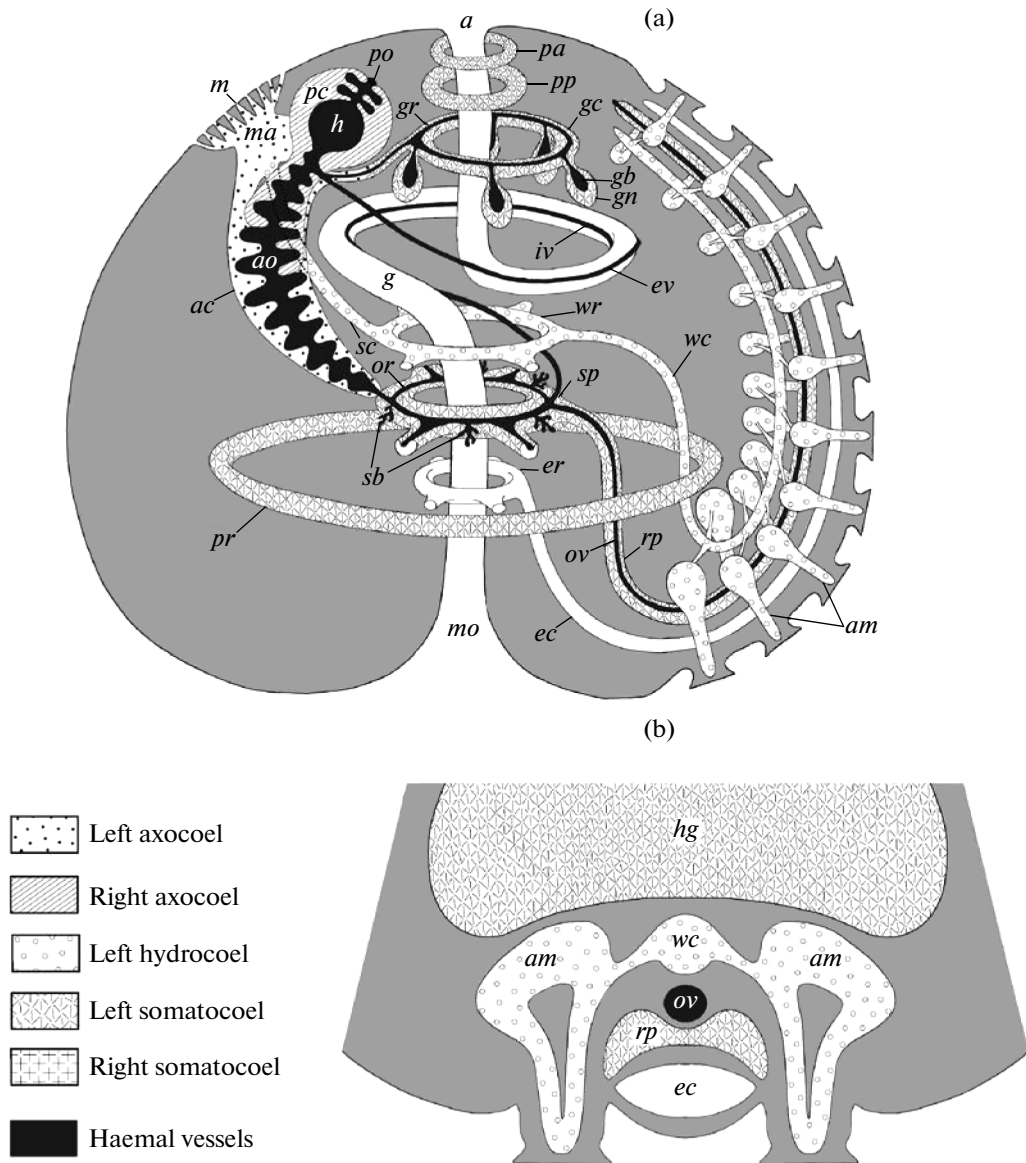
Fig. 3. The axial complex of organs and associated structures in Echinoidea. (a) Generalized scheme; right somatocoel (epigastric coelom) not shown; (b) scheme of a section through the radius of the sea urchin. Symbols: *a*, anus; *ac*, axial coelom; *am*, ampulla of ambulacral podia; *ao*, axial part of the axial organ; *ec*, epineural radial canal; *er*, epineural ring canal; *ev*, external marginal vessel; *g*, gut; *gb*, gonadal blood lacuna; *gc*, genital coelom; *gn*, gonad; *gr*, genital haemal ring; *h*, heart; *hg*, hypogastric coelom; *iv*, internal marginal vessel; *m*, madreporite; *ma*, madreporic ampulla; *mo*, mouth; *or*, oral haemal ring; *ov*, radial blood vessel from the oral ring; *pa*, perianal coelom; *pc*, pericardial coelom; *po*, paricardial part of the axial organ; *pp*, periproctal coelom; *pr*, perioral coelom; *rp*, radial processes of the perihaemal coelom; *sb*, spongy body; *sc*, stone canal; *sp*, perihaemal coelom; *wc*, radial water coelomic process; *wr*, water ring.

absence of a perihaemal ring, which is a homologue to the axocoel (internal) perihaemal ring of the starfish. The axial coelom on the aboral end in Echinoidea, as in Asteroidea, communicates with the madreporic ampulla and the stone canal [23, 24, 34, 66]. In sea urchins, the genital ring coelom also opens into the axial coelom in its aboral part (Figs. 3a and 4a). Among other things, this distinguishes the coelomic system of sea urchins from that of the starfish, whose genital coelom is not connected with other coeloms.

The haemocoelic structures of the axial complex in sea urchins have a number of peculiarities. The oral haemal ring sends, in addition to five radial vessels into each radius, five interradial branches (Figs. 3a and 4b), one per each spongy body (Polian vesicles of the water ring) [23].

Another distinguishing feature of the axial complex of the sea urchins from that of the starfish is the absence in Echinoidea of the gastric ring that is so well
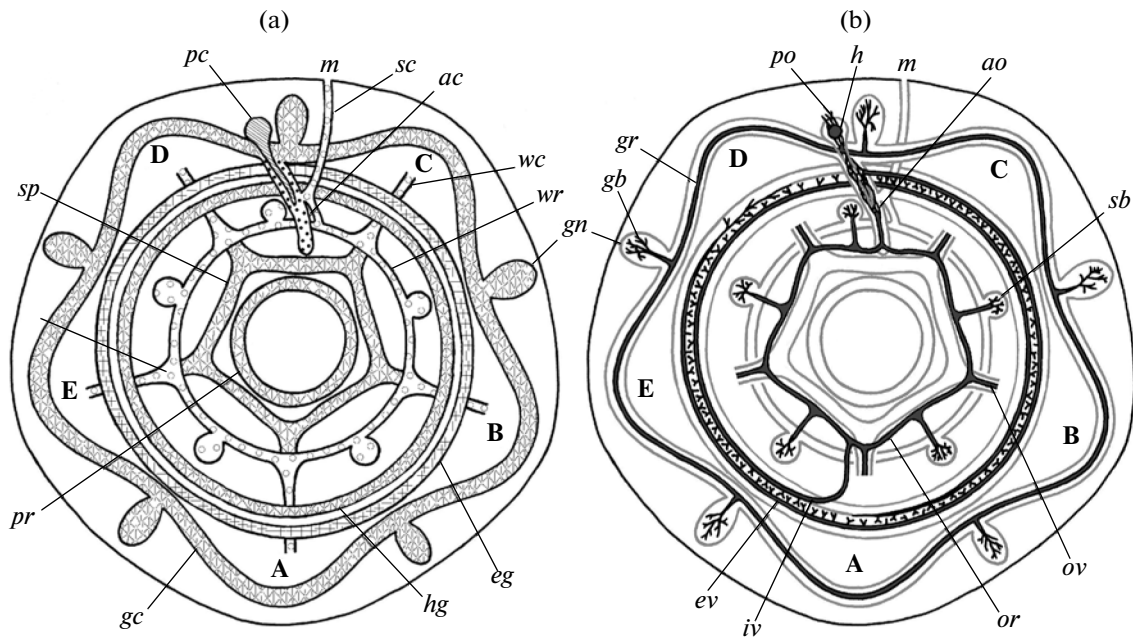
Fig. 4. Coelomic and haemocoelic (blood circulatory) structures of the axial complex of organs in Echinoidea. Aboral view. Perianal and periproctal coelomic rings not shown. (a) Diagram of coeloms, blood vessels not shown. (b) diagram of blood circulatory (haemocoelic) structures, the outlines of coeloms are shown with light-gray lines. Symbols: *ac*, axial coelom; *ao*, axial part of the axial organ; *eg*, epigastric coelom; *ev*, external marginal vessel; *gb*, gonadal blood lacuna; *gc*, genital coelom; *gn*, gonad; *gr*, genital haemal ring; *h*, heart; *hg*, hypogastric coelom; *iv*, internal marginal vessel; *m*, madreporite; *or*, oral haemal ring; *ov*, radial blood vessel from the oral ring; *pc*, pericardial coelom; *po*, pericardial part of the axial organ; *pr*, perioral coelom; *sb*, spongy body; *sc*, stone canal; *sp*, perihaemal coelom; *wc*, radial water coelomic process; *wr*, water ring.

pronounced in starfish. Instead, they possess a complex blood circulatory network that is developed in the mesenteries along the intestine [14, 42, 54]. The network originates from the oral haemal ring and includes two large marginal (or boundary) vessels, viz., the internal (ventral) and the external (dorsal) ones (Figs. 3a and 4b). The internal vessel ascends from the oral ring and runs along the intestine from the internal side, abundantly branching in the intestinal wall. The external vessel, along with the vessels of the axial organ, extends from the same canal, abundantly ramifies, gradually thins out, and disappears. The vessels of the intestinal network run in the so-called horizontal mesentery separating the hypogastric (left somatocoel) and the epigastric (right somatocoel) coeloms. The vessels of the axial organ and large lacunae of the intestinal network pulsate. Some researchers [8, 54] have reported for Echinoidea the presence of the heart in the aboral portion of the axial organ (Fig. 3a).

As noted above for sea urchins, the blood vessels that extend from the oral haemal ring into the radii are located in the mesentery between the radial processes of the ambulacral and perihaemal coeloms. However, in contrast to starfish, one more canal, the so-called epineural canal, lies in every radius of Echinoidea (Fig. 3b). It runs more orally of the perihaemal coelom and accompanies the epineural nerve cord. Interestingly, early studies suggested a coelomic nature of the epineural canal [34]. Later, the coelomic nature of the

epineural canal was rejected, because it forms during ontogenesis through immersion of the ectoneural cord with closure of the epidermis above it [47, 63]. The radial epineural canals enter the ring epineural canal which is located more orally of the perihaemal coelomic ring (Fig. 3a).

In the sea urchins of the group Regularia, the five interradial gonads do not divide into paired branches but are represented by cluster-shaped structures extending along the interradii on the aboral side of the animal [50]. In the group Irregularia, the gonad number is, as a rule, reduced to four owing to the absence of the gonad in the interradius AB because of the displacement of the periproct with the anal opening into this interradius. Some Spatangoida (Irregularia) species belonging to the genera *Abatus, Schizaster*, and *Lovenia*, retain only three gonads, because they lost a gonad in the interradius CD. Finally, the sea urchin *Schizaster canaliferus* (Lamarck, 1816) retains only two gonads because of disappearance of the gonad in the interradius DE [42].

CLASS OPHIUROIDEA

The axial complex of ophiuroids has been studied in representatives of the families Euryalidae [22, 44], Gorgonocephalidae [22, 25, 44], Ophiactidae [52], Ophiocomidae [51, 55], Ophionereididae [22], Ophiotrichidae [48, 61], and Ophiuridae [16, 35]. In

all the brittle stars that have been studied, the madreporite openings are shifted orally, and, correspondingly, the axial complexes of the organs are turned orally. Most brittle stars have a single axial complex located in the interradius CD. The stone canal can open through a single pore, but this is not characteristic of all brittle stars. *Ophionereis annulata* (Le Conte, 1851) possesses eight pores and pore canals [22], and *Ophiopsila annulosa* (Sars, 1859), has from 3 to 12 pores [55], while *Gorgonocephalus* has developed a true madreporite with up to 250 pores [44].

In brittle stars with a single axial complex of organs, a curved stone canal runs from the madreporic ampulla into the water ring, surrounding the mouth. Moreover, the ophiuran mouth is surrounded by three other coelomic rings. Two of these are the somatocoel and axocoel perihaemal rings. The axocoel perihaemal ring develops from the left axocoel [16, 48]. The somatocoel perihaemal ring forms from five coelomic anlagen; four of these are interradial protrusions of the left somatocoel, while the fifth one separates from the left axocoel in the interradius CD [16, 48]. However, in some other brittle stars all five anlagens of the somatocoel perihaemal coelom derive from the left somatocoel [51]. Unlike that of starfish, the ophiuran somatocoel perihaemal ring has an internal position, while the axocoelic ring is external (Figs. 5a and 6a). brittle stars, as well as some starfish, possess a perioral coelomic ring derived from the left somatocoel. The perioral coelomic ring is situated aborally of the perihaemal system [22]. Thus, ophiurans have four coelomic rings around the mouth, viz., the water ring, the somatocoel perihaemal ring, axocoel perihaemal, and perioral rings (Figs. 5a and 6a).

The oral haemal ring is situated in brittle stars between the somatocoelic and the axocoelic perihaemal coelomic rings (Figs. 5a and 6b). Five radial blood vessels, lying within the mesenteries among paired processes of the somatocoel perihaemal ring, exit from the oral haemal ring and run into the radii, similarly to the arrangement in the starfish arms (Fig. 5b). From the aboral side, radial processes of the ambulacral coelom extend over these processes of the perihaemal coelom and the blood vessel that is enclosed between them [35].

The axial coelom of Ophiuroidea (the left axocoel), which is extended in the oral-aboral direction, opens, as in starfish, on the oral end into the axocoel ring of the perihaemal system [25]. On the aboral end (which is located more orally than the water ring because of the shift of the madreporite to the oral side), the axial coelom enters into the madreporic ampulla and communicates with the stone canal [25, 61].

The axial organ of Ophiuroidea, as in representatives of two other Asterozoa classes, is stretched along the stone canal and enclosed in the cavity of the pericardial coelom, which is covered from outside by the axial coelom (Figs. 5a and 6a). These coeloms are rel-

atively narrow tubes, so that the axial organ occupies almost their entire volume [22, 61]. Essentially, the axial organ separates the axial and the pericardial coeloms derived from the left and the right larval axocoels [25, 61]. In general, this situation corresponds to that observed in other Asterozoa.

The axial organ of brittle stars consists of two sections. The first wider section is an axial part of the axial organ; it looks darker in histological sections [61]. This part of the axial organ is homologous to the axial part of the axial organ in Asteroidea and Echinoidea; however, in brittle stars it lies more aborally owing to the turn of the axial complex of organs. The second portion is narrow, oblong, and lighter in histological sections [61]. It is homologous to the pericardial part of the axial organ in Asterozoa, but lies more orally in brittle stars. The literature does not mention the presence of a heart in the brittle stars [24, 30, 39, 57].

According to Fedotov [25], the axial coelom of brittle stars communicates on the aboral side not only with the madreporic ampulla, but also with the genital coelom (Figs. 5a and 6a). The same author reports that the pericardial part of the organ receives the genital haemal ring running between coelothelia of the genital coelom and the genital rachis. The genital coelom and the genital haemal ring surround the jaw apparatus of Ophiuroidea and lie more orally than all other components of the axial complex because of the shift of the madreporite. However, in radii, the tubular genital coelom ascends arcuately to form five loops, one loop per each radius [45]. These loops of the genital coelom encircle radial processes of the perihaemal and ambulacral coeloms from the aboral side. Thus, the genital coelomic ring itself remains aboral, as in other Asterozoa, and only its interradial parts descend to the oral side of the animal to follow the shift of the madreporite and the axial organ (Fig. 5a).

The epigastric and hypogastric coeloms in brittle stars partially merge to form a perivisceral coelom (Fig. 6b) [45, 52]. The mesentery between the epigastric and hypogastric coeloms is fragmentary. The remains of the mesentery are penetrated by the intestinal capillary network. They fuse to form gastric vessels, which enter the genital haemal ring in every radius. The question of whether a gastric haemal ring (which occurs in starfish) is present in brittle stars remains open. According to our unpublished data, the gastric haemal ring is present in *Ophiura robusta* (Ayres, 1854).

The gonads of brittle stars lie in interradii; their number and sizes can strongly vary from one or two large gonads in each interradius up to multiple tiny gonads forming clusters or rows [35].

The radii of brittle stars include not only processes of the ambulacral and the somatocoel perihaemal coeloms, but also an epineural canal (Fig. 5). This canal forms in the same way as that of sea urchins, i.e., through immersion of the ectoneural cord and closure
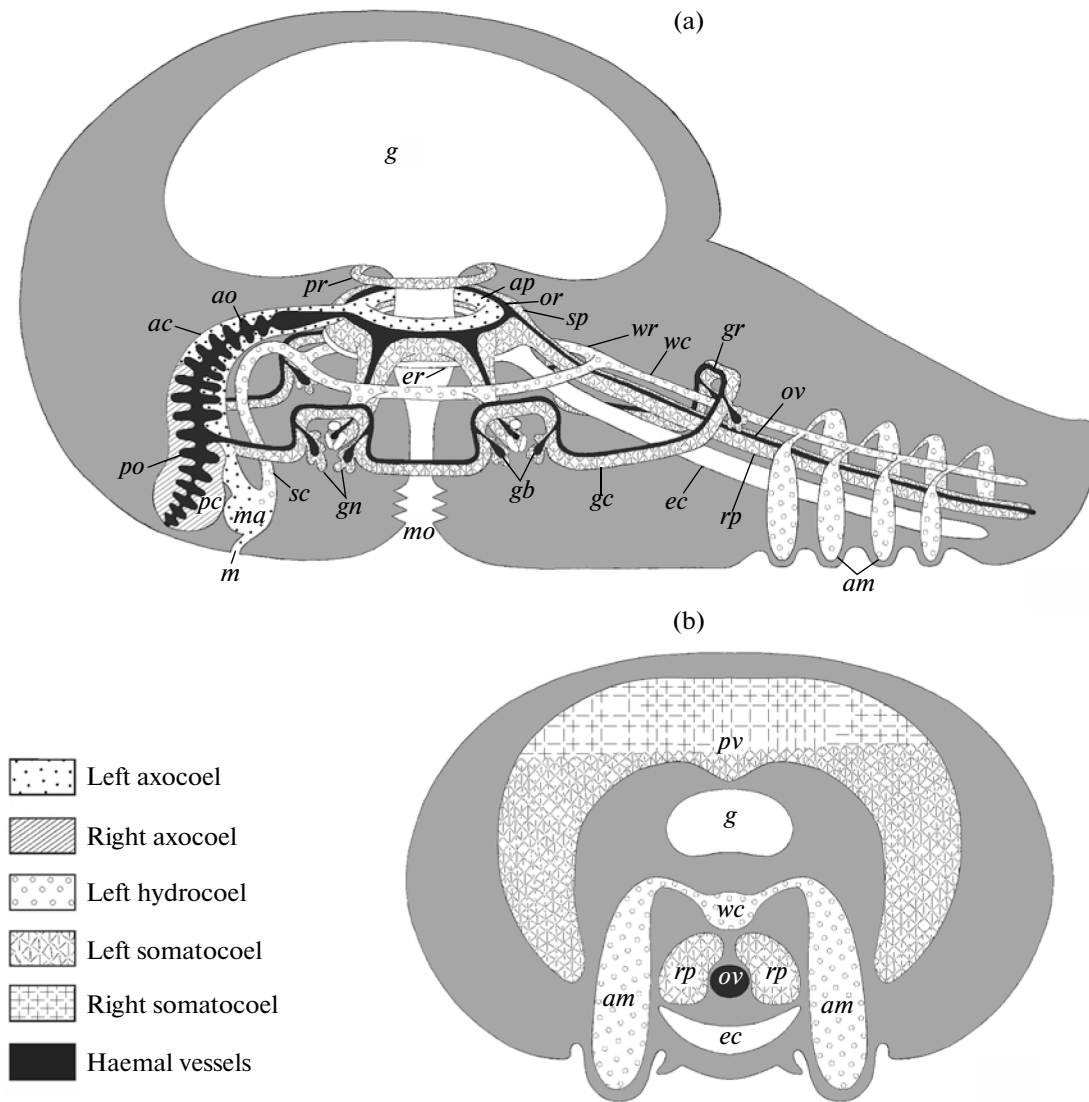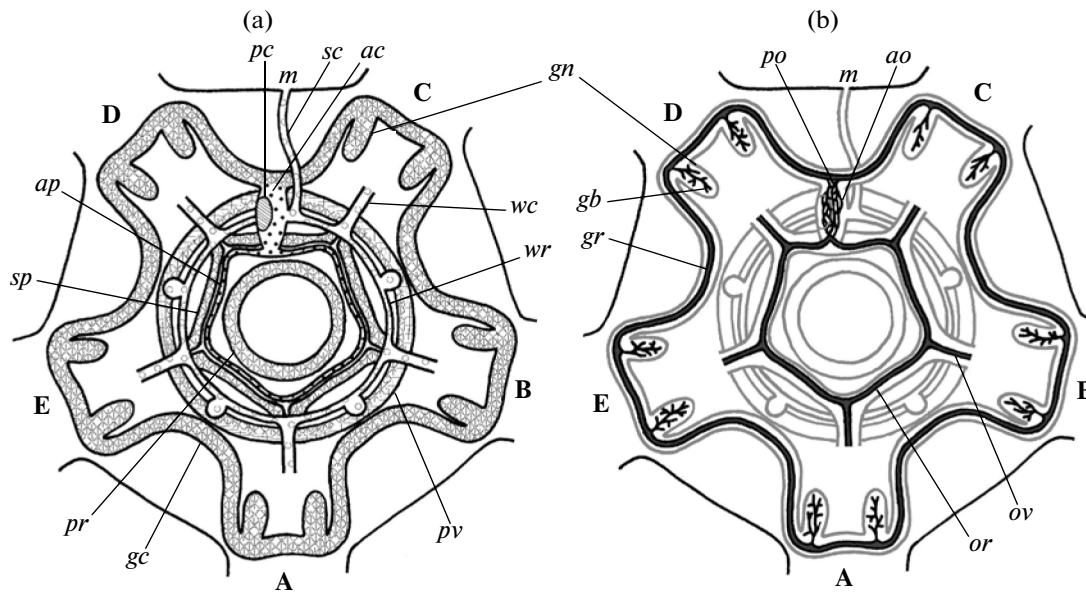
Fig. 5. Axial complex of organs and associated structures in Ophiuroidea. Interposition of the axocoelic and somatocoelic perihaemal coelomic rings is shown schematically (for explanations see the text). (a) Generalized scheme, right somatocoel (epigastric coelom) not shown; (b) scheme of a section through the ophiuran ray. Symbols: *ac*, axial coelom; *am*, ampulla of ambulacral podia; *ao*, axial part of the axial organ; *ap*, axocoel perihaemal coelom; *ec*, epineural radial canal; *er*, epineural ring canal; *g*, gut; *gb*, gonadal blood lacuna; *gc*, genital coelom; *gn*, gonad; *gr*, genital haemal ring; *m*, madreporite; *ma*, madreporic ampulla; *mo*, mouth; *or*, oral haemal ring; *ov*, radial blood vessel from the oral ring; *pc*, pericardial coelom; *po*, pericardial part of the axial organ; *pr*, perioral coelom; *pv*, perivisceral coelom; *rp*, radial processes of the perihaemal coelom; *sc*, stone canal; *sp*, somatocoel perihaemal coelom; *wc*, radial water coelomic process; *wr*, water ring.

of the epidermis above it [22, 35, 45]. The radial epineural canals enter the epineural perioral ring surrounding from outside the rings of the perihaemal system [22].

All the above said is true for ophiuran species with one axial complex. However, this class of echinoderms also includes forms with several axial complexes. Thus, *Ophiactis virens* (Sars, 1857) has up to five (but not always five) axial complexes and madreporite plates. Initially, this species has only one stone canal

and one madreporite, and an increase in their number is associated with preparation to asexual reproduction through division [59]. In *Trichaster elegans* (Ludwig, 1878) [44], every interradius has an axial complex and each of them opens into the external medium through a simple pore. Five axial complexes are characteristic of representatives of the genus *Astrophyton*, where five true madereporite plates are described, but each of them is penetrated by 15—20 pores [22, 44]. Unfortunately, it is still not clear which coelomic anlagen participate in formation of the multiple axial complexes.

Fig. 6. Coelomic and haemocoelic (blood circulatory) structures of the axial complex of organs in Ophiuroidea. Interposition of the axocoelic and somatocoelic perihaemal coelomic rings is shown schematically (for explanations see the text). Aboral view. (a) Diagram of coeloms, blood vessels not shown. (b) Diagram of blood circulatory (haemocoelic) structures, the outlines of coeloms are shown with light-gray lines. Symbols: *ac*, axial coelom; *ao*, axial part of the axial organ; *ap*, axocoel perihaemal coelom; *gb*, gonadal blood lacuna; *gc*, genital coelom; *gn*, gonad; *gr*, genital haemal ring; *m*, madreporite; *or*, oral haemal ring; *ov*, radial blood vessel from the oral ring; *pc*, pericardial coelom; *po*, pericardial part of the axial organ; *pr*, perioral coelom; *pv*, perivisceral coelom; *sc*, stone canal; *sp*, somatocoel perihaemal coelom; *wc*, radial water coelomic process; *wr*, water ring.

DISCUSSION

Asterozoa possess some structures that are common for all three classes, this suggests the existence of a general plan of the arrangement of the axial complex of organs. Actually, the axial part of the system is the stone canal of the ambulacral system, which is extended in the oral-aboral direction and communicates with the water ring (left hydrocoel) on the oral side and opens into the madreporic ampulla on the aboral side. The stone canal adjoins the axial coelom (left axocoel), and the pericardial coelom (right axocoel) adjoins the madreporic ampulla. Among the coelothelial walls of the axial and pericardial coeloms, along the stone canal, the axial organ runs, viz., the haemal network, which is connected with the oral haemal ring on the oral side and with the genital haemal ring on the aboral side.

The oral haemal ring enters the mesentery formed with participation of the ring perihaemal coelom, which is derived from the left somatocoel. In Asteroidea and Ophiuroidea, this mesentery is located between the somatocoel perihaemal ring (derived from the left somatocoel) and axocoel perihaemal ring (derived from the left axocoel). In Echinoidea, this mesentery is located between the perihaemal ring (derived from the left somatocoel) and the water ring (derived from the left hydrocoel). A radial blood vessel protrudes from the oral haemal ring into every radius. This vessel lies in the mesentery formed by radial processes of the coeloms surrounding the oral haemal ring. The radial blood vessel runs in the mesentery between processes of the somatocoel perihaemal ring in starfish and brittle stars and between the process of the somatocoel perihaemal ring and the process of the water ring in sea urchins.

The genital haemal ring in representatives of all three classes runs within the genital coelom (derived from the left somatocoel) among its coelothelium and the coelothelium of the genital rachis. The latter is a germinative epithelium of the gonad. The interradial blood lacunae of gonads branch from the genital haemal ring.

The ambulacral coelomic ring in Asteroidea and Echinoidea is located between the perihaemal coelomic rings (two in starfish and one in sea urchins) from the oral side and the genital coelom from the aboral side. In Ophiuroidea, the ambulacral coelomic ring is also located between the perihaemal rings and the genital coelom, but because of the turning of the axial complex of organs, the perihaemal coelomic rings are detected on the aboral side, while the genital coelom is found more orally. The water ring extends radial coelomic processes.

We emphasize that the structures that are associated with the axial complex of organs are arranged relative each other in a similar way in all the Asterozoa. Even in brittle stars, in spite of the shift of the madreporite and the ampulla towards the oral side and the turning of the axial complex of organs, the genital coelom remains aboral, runs in radii over the ambulac-

ral coelom, and descends to the oral side only in interradial sites (Fig. 5a).

At the same time, the structures of the axial complex in representatives of the three Asterozoa classes have a number of important differences. First of all, this is true for the perigastric coelomic rings. Starfish and brittle stars possess a axocoel perihaemal coelomic ring that is derived from the left axocoel and communicates with the axial coelom (it has not been described for sea urchins). The perioral coelom is present in all the studied Echinoidea and Ophiuroidea, but not in all species of the class Asteroidea, e.g. it is not found in *Asterias rubens* [2]. The absence of the perioral coelom in some starfish species is probably a secondary phenomenon. In *Asterias pallida* [54], the perioral coelom separates from the dorsal process of the left somatocoel and merges further with the hypogastric coelom [31].

On the aboral side of Echinoidea, two other small coelomic rings, periproctal and perianal, separate from the left somatocoel (Fig. 3a). Thus, the total number of the coelomic rings in different classes of Asterozoa (excluding the epigastric and hypogastric coeloms) is four or five (axocoelic perihaemal, somatocoelic perihaemal, water or ambulacral, genital, and, in some cases, perioral) in Asterioidea; six (somatocoelic perihaemal, perioral, ambulacral, genital, periproctal, and perianal) in Echinoidea, and five (axocoelic perihaemal, somatocoelic perihaemal, perioral, ambulacral, and genital) in Ophiuroidea. In addition, sea urchins and brittle stars have a developed epineural ring of a non-coelomic structure; this sends its canals into the radii.

Differences were also found in the organization of the haemal structures of the axial complex in Asterozoa; these were mostly associated with the gastric vessels. In Asteroidea, the horizontal mesentery between the hypogastric and epigastric coeloms includes the gastric haemal ring, which sends a radial vessel into each ray; the vessel ramifies along the ray length into two branches, each of these also ramifies over and over again to form a capillary network. In starfish, the gastric haemal ring, along with the genital haemal ring, is connected with the axial organ in its aboral region. Here swellings with haemal lacunae develop, the "gastric haemal tufts." In Echinoidea, instead of a ring, two large marginal vessels, the internal and the external ones, develop in the horizontal mesentery; these give rise to the capillaries of the intestinal haemal network. In Ophiuroidea, no ring haemal structures of the stomach have been yet described, except for *Ophiura robusta* (our unpublished data). The radial gastric vessels extend from the genital haemal ring and disintegrate into a capillary network in the remains of the horizontal mesentery.

The axial organ of all Asterozoa is divided into the pericardial and axial parts. However, in Echinoidea and Asteroidea, the heart is located between these parts. For Ophiuroidea, the heart has not been described, although the axial organ consists of compartments that are homologous to the pericardial and axial portions of the axial organ in other Asterozoa.

Finally, representatives of the three classes differ in the number of gonads: initially, ten gonads in Ophiuroidea, typically five paired gonads in Asteroidea, and from five to two single gonads in Echinoidea.

A separate question is that of what the functions of the axial complex are. It was previously suggested that the axial complex is of no use at all, since the animals continue to live for a few months after resection of the complex [11, 58]. One of possible functions of the axial complex is to ensure blood circulation. It is known that the heart of echinoderms is capable of periodic pulsations [27, 57]. For example, in *Asterias forbesi* (Desor, 1848) these pulsations at 25°C occur at a rate of about six beats per minute [57]. Slow pulsations are also typical of the entire axial organ [15, 17, 49]. The coelomic epithelium of the axial organ walls is made of epithelial-muscular cells, including nerve elements [12, 37, 64].

The question of the direction in which the blood moves in echinoderms is more complicated. Ubaghs [62] suggested that blood moves from the genital haemal ring through the vessels of the axial organ to the oral ring and further into the radial vessels of the rays. Goldschmid [30] assumed that the direction of pulsations of the heart and the axial organ can vary, and, consequently, the direction of the entire blood circulation also changes. Ruppert et al. [57] suggested that changes in the direction of the blood flow may be very common among animals with the so-called sequential blood circulation, whereby the organs are arranged so that the blood flows sequentially from one organ to another. If the blood moved only in one direction some organs would always get nutrient-rich blood, and others only nutrient-poor blood; thus some organs would be provided with blood with a high oxygen concentration and others with blood of a low oxygen concentration. With a change of the direction of the blood flow, the organs at the end of the blood circulation ring appear to be at the very beginning and are the first to obtain blood rich in oxygen and nutrients. In fact, a periodic change of the blood flow direction has been known for a long time for ascidians. We can admit the possibility of such a phenomenon only for echinoderms. However, considering that the axial part of the axial organ in these animals is significantly larger and more powerful than in the pericardium, we can suggest that the predominant direction of the blood flow in echinoderms is from the aboral side of the body towards the oral part.

The second probable function of the axial complex is excretion. Many authors have detected podocytes in the composition of the coelomic epithelium that form the blood vessel wall of the axial organ of echinoderms [1, 12, 37, 64, 66]. These data allow us to suggest that

the axial organ performs the function of ultrafiltration from the blood vessels into the axial coelom. Indirect evidence of the possible involvement of the axial organ in excretion is the powerful development of the capillary network, which significantly increases the surface of the area of ultrafiltration. The axial coelom is connected with the external medium through the ampulla of the madreporite plate, which can thus function as an excretion opening. In larval starfish, the hydropore actually exerts the function of an excretory pore; it has even been estimated for the bipinnaria *Asterias forbesi* that axocoel podocytes filter 14% of the blastocoel fluid per hour, which is then excreted through a hydropore [30]. Cuénot injected dyes into the axial coelom of adult starfish and observed its excretion into the external medium through the madreporite [24].

As noted above, it is very difficult to conduct a comparative analysis of the structure of the axial complex and the related structures in Asterozoa using the data from different authors because of the considerable inconsistency in terminology and descriptions.

We find it necessary to conduct original research on different representatives of Asterozoa using the latest techniques in order to remove the inconsistencies and inaccuracies that exist presently in the literature.

ACKNOWLEDGMENTS

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Translated by I. Barsegova