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Microscopic Anatomy of the Axial Complex in the Starfish *Asterias rubens* (Echinodermata, Asteroidea)

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Abstract—The axial complex is one of the most characteristic features of echinoderms. Descriptions of it in classic papers are contradictory. The present paper provides data on the microscopic anatomy of the axial complex in the starfish *Asterias rubens* restudied using histological techniques. The axial complex is located in the wall of the interradius CD; it is elongated in the oral–aboral direction. The stone canal in its aboral end communicates with the axial coelom; in its oral end, it communicates with the water-vascular ring canal. The axial coelom opens to the madreporic ampulla of the stone canal on its aboral end and to the axocoel perihemal coelom on the oral end. The axial organ is formed by the blood vessel network between the basal laminae of the pericardial, axial, and perihemal coelothelia. In *Asterias rubens*, the heart is a part of the axial organ, which divides the latter into the true axial and pericardial parts. The extensive axial (oral) part of the axial organ opens to the oral blood ring, which is situated in the mesentery between the perihemal coeloms. The smaller, pericardial (aboral), part of the axial organ opens to the hemocoel of the body wall. The genital coelom represents an integral part of the axial complex since one of the five gonad blood lacunae located in the interradius CD communicates with the heart and axial organ vessels. The mistakes and inaccuracies extant in the scientific literature about the anatomy of the asteroid axial complex are discussed. The blood circulation into the axial organ occurs predominantly from the aboral side to the oral side of starfish.

Keywords: axial complex, starfishes, echinoderms, microscopic anatomy, Asteroidea, Echinodermata
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INTRODUCTION

The axial complex is one of the most characteristic features of organization in echinoderms. Its structure, the homology of its parts with the organs of other Deuterostomia, and the phylogenetic importance of these homologies have discussed intensively for more than one hundred years (see Bather, 1900; Fedotov, 1923, 1951, 1966; Fedotov, 1924; Cuénot, 1948; Hyman, 1955; Ivanova-Kazas, 1978; Ivanov et al.,1985; Ruppert and Balser, 1986; Chia and Koss, 1994; Tagawa et al., 1998; Peterson et al., 1999a, 1999b; Shoguchi et al., 1999; Cameron, 2000; Janies, 2001; Ruppert et al., 2004; Westhide and Rieger, 2006). The organization of the axial complex in starfishes in described in the original papers by several authors (Hamann, 1885; Cuénot, 1887; Pietschmann, 1906; Chadwick, 1923; Hayashi, 1935; Bargmann and von Hehn, 1968; Warnau and Jangoux, 1992). However, a few problems concerning the anatomy of the axial complex of organs are still unclear. As a result, the reconstructions of this organ are not in agreement in various publications and the homologization of the complex as a whole and of its parts is still problematic. An analysis of the published papers shows that even the books that have served for many decades as the main source of information about the organization of echinoderms give different descriptions of the structure of the axial organ (see Cuénot, 1948; Hyman, 1955; Ubaghs, 1967; Ivanov et al., 1985; Goldschmid, 1996; Ruppert et al., 2004). This disagreement hampers correct understanding of the axial complex of organs and analysis of its structure in the comparative morphological and functional aspects, as well as its description in educational courses. All the information noted above has stimulated us to re-investigate the organization of the axial complex of organs in starfish *Asterias rubens* Linnaeus 1758 (fam. Asteriidae; order Forcipulatida).

MATERIALS AND METHODS

Sexually immature specimens of *A. rubens* (5 mm to 2 cm in size) collected in summer (July–August 2009) in Kandalakshskii Bay of the White Sea near Pertsov Belomorskaya Biological Station of Moscow State University (Primorskii Settlement, Loukhskii raion, Karelian Republic) were used for this study. The animals were collected at depths of 2 m to 10 m on stony ground in thickets of kelp and red algae. Small

specimens (to 1 cm) were used for histological studies; only disks without the rays were used in larger animals.

For histological study the animals were preserved in Boin's solution followed by transfer for conservation in 70% ethanol. To prepare the materials for histological processing, the tissues were decalcificated following either of the following methods: in nitric acid according to the standard practice or using EDTA solution (Trilon B, Chelaton-3) (Valovaya and Kavtaradze, 1993). To study the microscopic anatomy, the standard technique was used: dehydration in alcohols in ascending concentrations, impregnation with Paraplast, and sectioning to 5 μm cross sections. In total, seven specimens were studied at the light microscopy level with preparation of seven cross sections of the disks in the region of the axial complex: three series in the madreporic plane and four series in the in the "plane of the star," i.e., perpendicularly to the oral–aboral axis. The histological cross sections were photographed using a Zeiss Axioplan 2 Imaging Photomicroscope.

RESULTS

The axial complex in *A. rubens* is situated in the CD interradius and is prolonged in the oral-aboral direction (Fig. 1). The complex consists of the following organs: stone canal, axial coelom (axocoel), perihemal coeloms, pericardial coelom, heart, axial organ, and genital coelom.

The stone canal is a tubular organ with partially calcified walls. The internal lumen of the stone canal is more or less rounded; the larger specimens have an epithelial ridge protruding to the stone canal lumen from the D radius side (Fig. 2b). The aboral end of the stone canal opens into the madreporic ampulla (Fig. 2a). On the oral side, the stone canal bends at almost a right angle and opens into the ambulacral coelomic ring from the inner side (Fig. 2c).

The axial coelom (left axocoel) is a sack elongated in the oral-aboral direction which envelops the stone canal along the whole length predominantly from the outer side (i.e., from the side of the CD interradius) (Fig. 3). The coelothelium of the axial coelom is represented by a flat monociliary epithelium. On the aboral side, the axial coelom forms the process enveloping the stone canal protruding to the D radius side (Fig. 3). This process opens directly to the stone canal from the C radius side (Fig. 2a).

Thus, the stone canal is connected both to the axial coelom (on the aboral side) and to the ambulacral ring (on the oral side) (Fig. 2c). On the oral side, the axial coelom opens into the axocoel coelomic ring of the perihemal system (Fig. 3). It is known that the perihemal system includes two ring coeloms: (somatocoel (outer) and axocoel (inner) divided by the mesenterium. The axocoel perihemal coelom is a prolongation of the axocoel (i.e., of the left protocoel). The somatocoel perihemal coelom is connected neither to the axocoel nor to the somatocoel (although in ontogenesis it develops as a derivative of the left somatocoel; see Ivanova-Kazas, 1978). Thus, there are three coelomic rings around the *A. rubens* mouth: ambulacral (into which the stone canal opens), axocoel perihemal (connected with the axial coelom), and somatocoel perihemal (Fig. 4). The perihemal coeloms are shifted relative to the ambulacral ring towards the oral side of the animal. The oral circular blood vessel is situated in the mesenterium (Fig. 2c). From one side its wall is formed by the coelothelium of the axocoel perihemal ring (the derivative of the left axocoel), while from the other side it is formed by the coelothelium of the somatocoel perihemal coelom (the derivative of the left somatocoel). The vessel's wall formed by the coelothelium of the axocoel perihemal coelom is invaginated into it so that the vessel in fact runs inside this coelom. The circulatory network of the axial organ opens into the oral circulatory ring in the CD interradius (Fig. 3).

The pericardial coelom (derivative of the right axocoel) in *A. rubens* is a closed coelomic cavity of 125–175 μm in diameter (in the 5 mm starfishes) situated on the aboral side adjoining the ampula (Figs. 3, 4a).The shape of the pericardial coelom is oval, the coelom has a process protruding into the axial coelom, and the blood vessels of the circulatory system of axial organ run between the processes. The monociliar coelomic epithelium of the pericardial coelom forms the walls of the heart and vessels of the pericardial part of axial organ (Fig. 2a). The heart is an oblong vesicle of about 120 μm long and about 45 μm wide (in 5 mm starfishes). The heart is stretched slantwise between the opposite walls of the pericardial coelom in the direction from the D radius (on the aboral side) to the C radius (on the oral side). On its aboral side, the heart is connected with the vessels of the pericardial part of axial organ though which it connects to the joined hemocoel of the starfish (Figs. 2a, 3). In the smallest studied specimens, the pericardial part of the axial organ is almost not developed and represents a simple short tube; in the larger animals, it is a plicate organ having complicated morphology. The heart divides the axial organ into the smaller pericardial (aboral) and bigger true axial (oral) parts.

The axial organ is a spindle-shaped structure formed by a plexus of blood vessels stretched in the oral–aboral direction from the pericardial coelom through the axial coelom to the perihemal coeloms. The vessels of the axial organ represent hemocoel spaces between the basal laminae of the coelomic epithelia (Fig. 5a). The walls of the pericardial and axial coeloms participate in the formation of the axial organ vessels. The hemocoel spaces limited by the basal laminae of the coelothelia build a three-dimensional system of blood vessels of the axial organ. The diameter of the vessel measured at the cross sections through the axial organ fluctuate between 5 μm to 10 μm (in 5 mm starfishes).

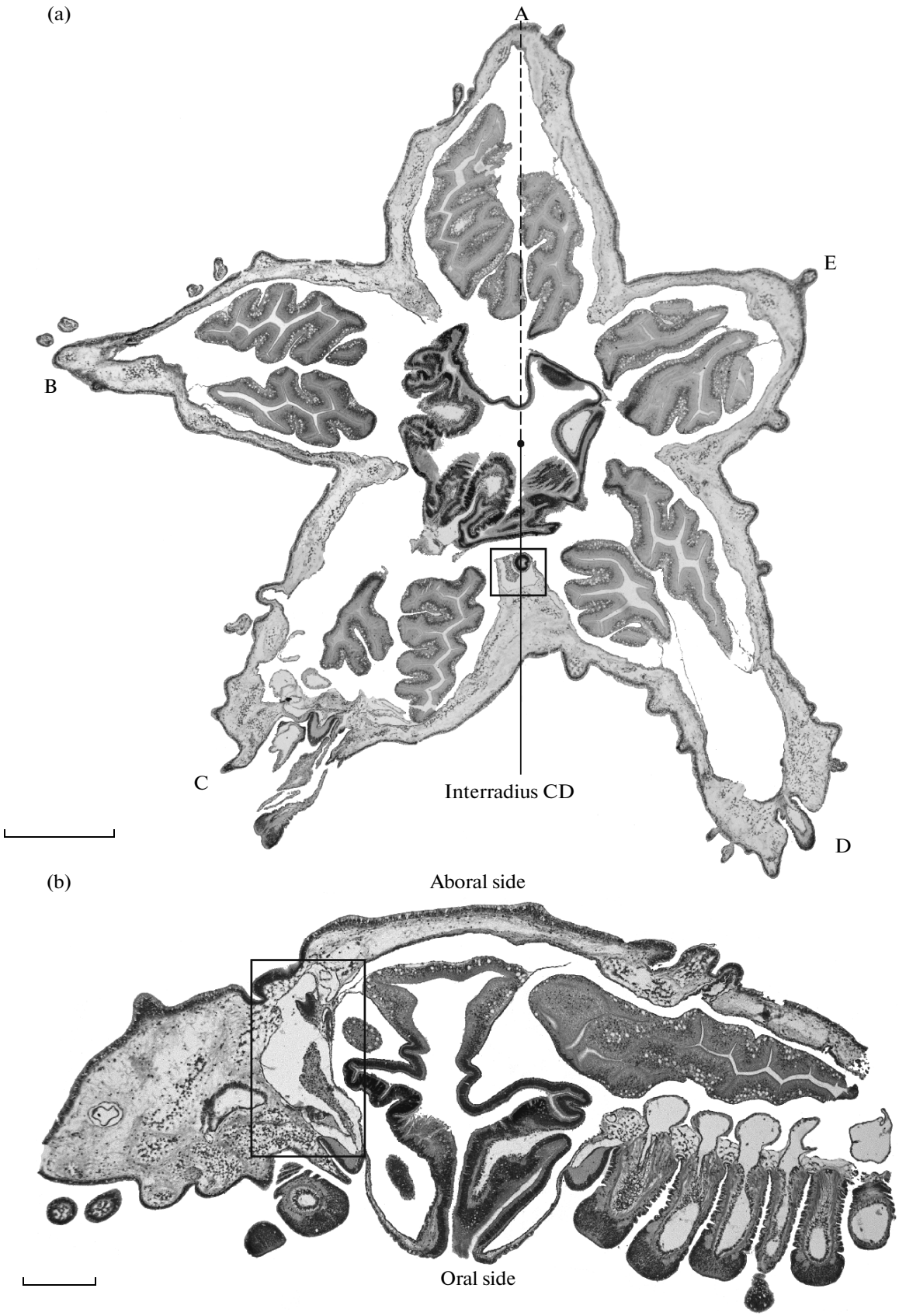


Fig. 1. Position of the axial complex (separated by the rectangular frame) in the body of *A. rubens*. (a) cross section perpendicular to the oral–aboral axis; (b) cross section in the madreporic plats along the line of the noted interradius. Scale (μm): (a) 500; (b) 200.

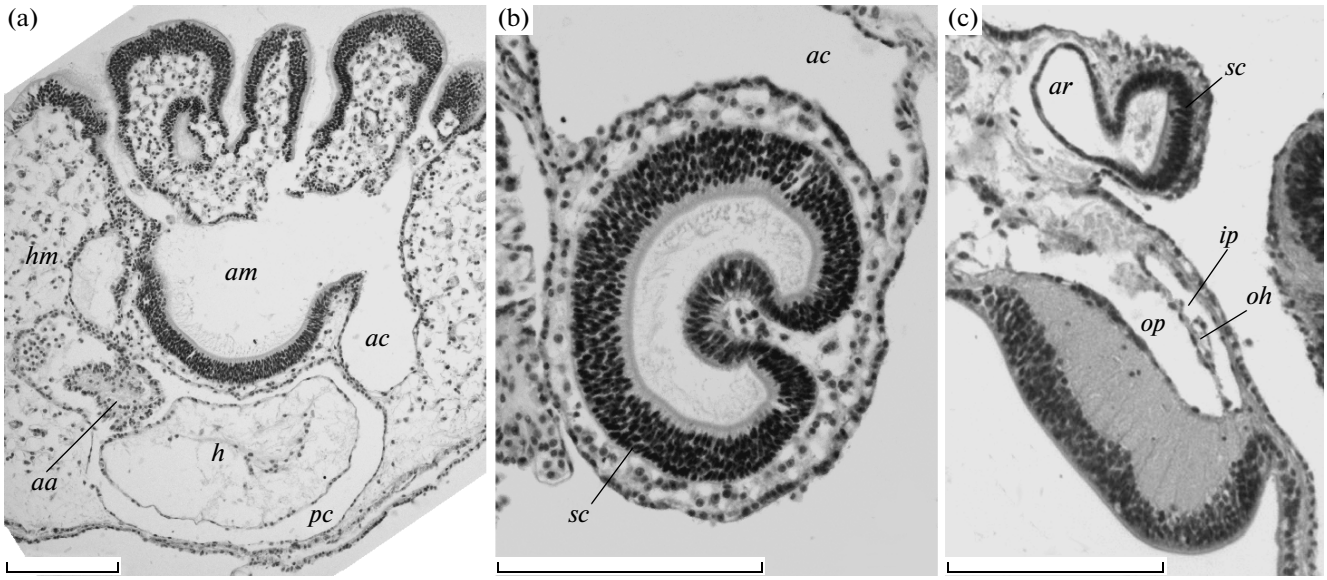


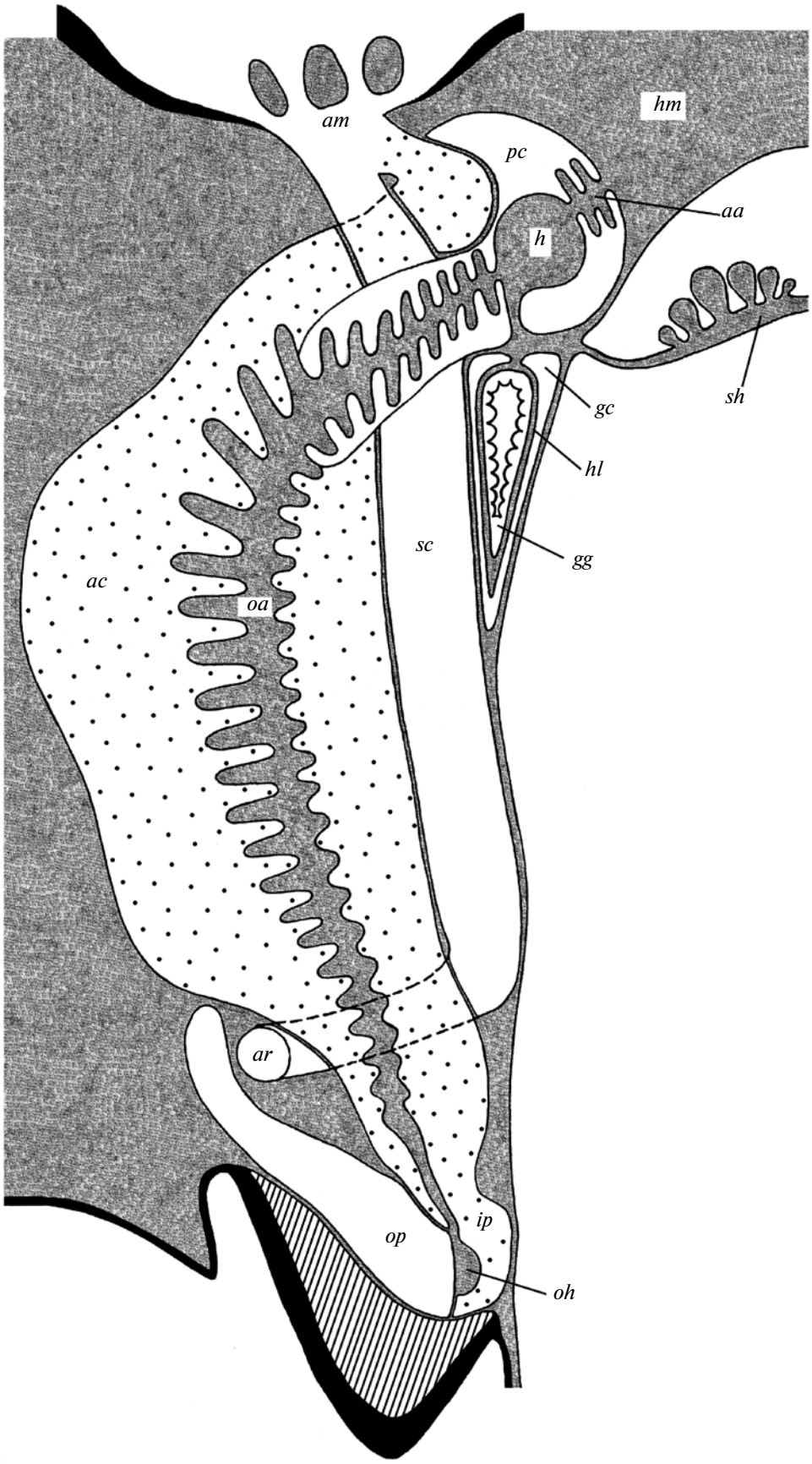
Fig. 2. Stone canal of *A. rubens*. (a) The place of connection of the stone canal with madreporite ampulla and axial coelom, the cross section perpendicular to the oral–aboral axis; (b) central part of the stone canal, the cross section perpendicular to the oral–aboral axis; (c) the place of connections of the stone canal with the abulacral ring, cross section in the madreporite plain. Scale: 100 μm. Designations of letter symbols in Figs. 2–5: *ac*—ambulacral ring, *am*—ampoule madreporita, *aa*—aboral part of the axial body, *ip*—internal perihemal coelom, *h*—haemocoel, *gg*—germ of gonad, *gc*—genital coelom, *s*—stomach, *sh*—stomach hemal ring, *hl*—hemal lacuna of gonad, *sc*—stone channel, *op*—outside perihemal coelom, *oh*—oral hemal ring, *oa*—oral part of the axial organ, *ac*—axial coelom, *pc*—pericardial coelom, *h*—heart.

The smaller in size pericardial part of the axial organ lies fully in the pericardial coelom (Figs. 3, 4b). From the oral side, it is connected with the heart; on the aboral side, with the hemocoel of the body wall, i.e., with the space between basal laminae of the integumentary epithelium and the coelothelium of the somatocoel. The true axial part of the axial organ is situated mostly in the axial coelom, but partially (in the aboral section itself) penetrates into the pericardial coelom as well. The "oral-most" section of the axial organ (as was noted above) is connected with the hemocoel space within the mesenterium between the perihemal coeloms, i.e., with the oral ring vessel. Thus, the vessels of the axial organ are connected with the hemocoel of the body wall (in the pericardial part), with the heart (dividing the pericardial and true axial parts of the axial organ), and with the oral circulatory ring (in the true axial part) composing integration with the structures listed above.

The so-called "genital coelom" (or more precisely its part that is situated in the CD interradius) is situated in direct proximity of the axial complex of organs (Figs. 3; 5b, 5c). The genital coelom represents a ring in the aboral part of the starfish. This is separate coelomic cavity not connected with other coeloms. It is situated aborally around the posterior gut, covered with a flat monociliar epithelium, and is contained inside the epithelial strand of large, rounded sexual cells (the so-called "genital rachis") (Figs. 5b, 5c). In each interradius the genital coelom produces a process in the oral direction; a pair of branches originates from such a process: one branch per ray. These processes and their paired branches contain germs of the gonads—evaginations of the genital rachis in the interradial processes of the genital coelom (Figs. 5b, 5c). The gonadal ring hemal lacuna runs within the genital ring with the hemal lacunas of gonads stretching from the former lacuna in the oral direction. In the CD interradius, the gonadal circulatory lacuna is connected with the vessels of the axial organ at the point where the true axial part of the axial organ deviates from the heart (Fig. 5c).

The horizontal mesenterium dividing the epigastric coelom (derivative of the right somatocoel) and hypogastric coelom (derivative of the left somatocoel) contains the gastric circulatory ring. In the adult starfish, the coelothelia of the coeloms are separated. As a result, the swellings ("gastric haemal tuffs," see Ruppert et al., 2004) are formed on the horizontal coelom. The hemal lacunas run within these swellings. The histological structure of these swellings is similar to that of the axial organ (Fig. 5d). The gastric circulatory ring

Fig. 3. The scheme of the generalized cross section through the axial complex of *A. rubens.* The black color corresponds to the integumentary epithelium; dark-grey, to hemocoel and hemocoel structures; white, to coelomic structures; and dots, to the axial and axocoel perihemal coeloms.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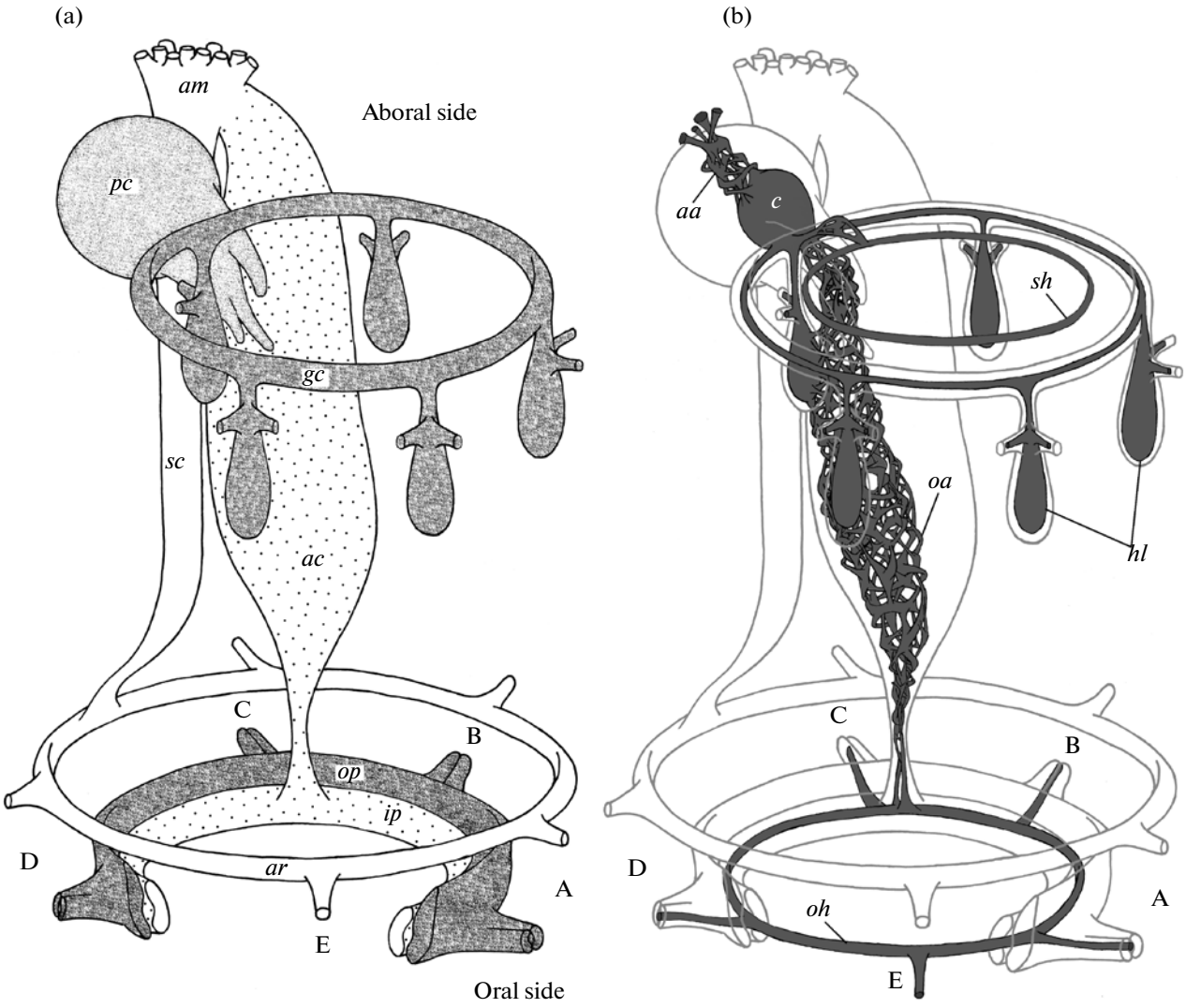

Fig. 4. Interrelations of various coeloms (a) and circulatory (hemal) structures (b) in the axial complex of *A. rubens.*

together with the gonadal hemal lacuna fuses with the axial organ in the CD interradius (Figs. 3, 5d).

DISCUSSION

It is believed that the microscopic anatomy of starfish has been well studied and has been the subject of practical studies for many generations of students. In spite of this history, there are still many uncertainties and controversies concerning the understanding of the structure of the axial complex in Asteroidea. Discussions on the anatomic structure of the axial complex in echinoderms are hampered, since different terms for descriptions of the same structures are used in different papers. Thus, we consider it reasonable to give a generalized table of the terms used in published papers for the designations of the organs that we included in the assemblage of the axial complex (table).

In addition to the terminological differences, there are many factual discrepancies in the description of the axial complex in various publications. Even classical textbooks used for many decades by students in zoology give controversial information. In *Bol'shoi praktikum po zoologii pozvonochnykh* (Ivanov et al., 1985), it is stated that for *A. rubens* particularly the axial ceolom is split into the left and right halves: left and right sinuses of which the "right sinus is slightly offset to the top compared to the left one" (Ivanov et al., 1985, p. 293). In this book the left sinus is understood as the axial coelom itself that opens into the near-throat perihemal ring and originates from the left front coelom of larva. The term "right axial sinus" is used for the pericardial coelom originating from the right front coelom of larva. It is not stated clearly if the latter is fully separated from the "left sinus," i.e., if the axial coelom communicates with that one. However,

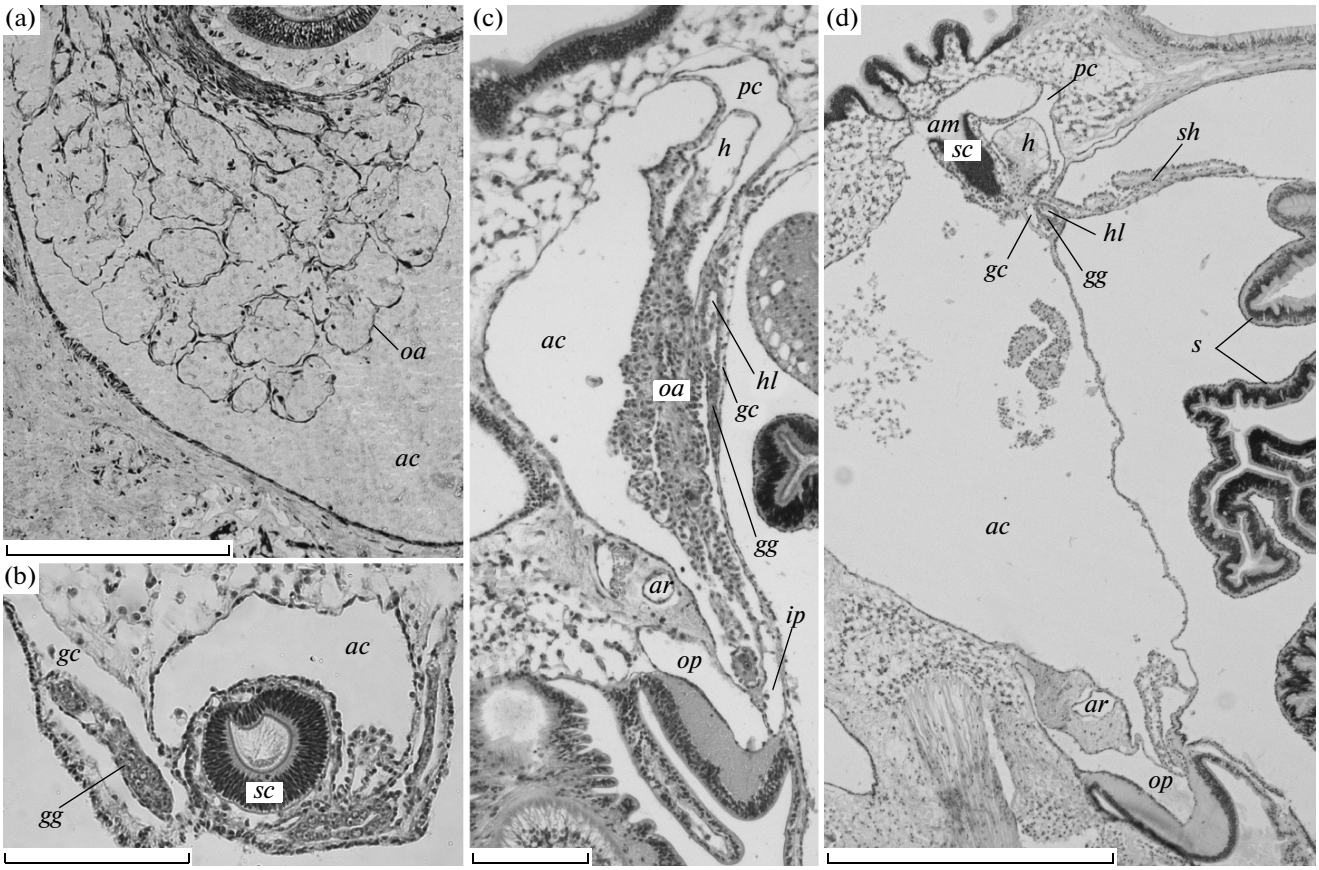

Fig. 5. The axial organ, genital coelom, and gonads in *A. rubens*: (a) histological structure of the axial organ, cross section perpendicular to the oral–aboral axis; (b) genital coelom, genital rachis, and germs of gonads, cross section perpendicular to the oral–aboral axis; (c) germ of gonad in the CD interradius, cross section in the madreporic cavity; (d) swellings with hemal lacunae of the gastric hemal ring in the horizontal mesenterium of the somatocoel. Scale (μm): (a–c) 100, (d) 500.

in the description of the axial complex in the basket stars, it is written that "the cavity of the axial complex is divided by a partition into the right and left sinuses" (Ivanov et al., 1985, p. 318). The axial organ is described as loose connective-tissue mass without an indication of the coelothelia forming this organ. The authors define the oral and aboral parts of the organ according to their positions in the left or right sinus. However, the heart is not mentioned; in spite, it is written that the aboral (pericardial) part of the axial organ pulses. Nothing is said about the connection of the axial coelom with the stone canal ampulla. The genital rachis is described as "the process of the aboral part of the axial organ" (Ivanov et al., 1985, p. 294) which is not really true: the genital part of the axial complex is connected with the axial organ via the system of blood vessels, not via the genital rachis. It is indicated for starfish that the genital coelom communicates with neither of the coelomic cavities of the axial complex (Ivanov et al., 1985, p. 294). At the same time, it is indicated for basket stars that the sexual coelom deviates from the right axial sinus (Ivanov et al., 1985, p. 318), i.e., from the pericardium.

Ivanova-Kazas (1978) also did not mention the heart. Instead, she gives several hypotheses on the origin of the so-called "madreporic vesicle" proposed by various authors and reports that the madreporic vesicle in *A. rubens* starts to pulse on the 35th day of development. In addition, it is said that the wall of the madreporic vesicle "adjacent to the axial sinus invaginates in the form of a fold penetrated by the prolongations of the axial gland and genital rachis" (Ivanova-Kazas, 1978, p. 23). It is likely that by the term "madreporic vesicle" what is meant is the pericardial coelom, which really includes the pericardial part of the axial organ, although according to our observations the genital rachis has no direct connection to the pericardium. Ivanova-Kazas (1978, p. 23) indicates that the "internal oral ring of the perihemal system is formed by the axocoel and remains connected to the axial sinus." It is noted in the cited paper that in many starfish the genital rachis penetrates into the pericardial part of the axial organ. However, our present study disproves this notion.

Hyman (1955) on basis of the original studies of various starfishes (Hamann, 1885; Hayashi, 1935) reports that the stone canal and the axial organ ("axial

The terms used for designation of the organs in the axial complex

The terms used in the present paper	The terms used in other papers (original languages)								
	Domestic papers		Foreign papers						
	Ivanov et al., 1985	Ivanova-Kazas, 1978	Hyman, 1955	Cuénot, 1948	Ubaghs, 1967	Chia and Koss, 1994	Goldschmid, 1996	Ruppert et al., 2004	Ziegler et al., 2009*
Stone canal	Stone canal	Stone canal	Stone canal	Tube aquifère	Stone canal	Stone canal	Steinkanal	Stone canal	Stone canal
Axial coelom (axocoel)	Left axial sinus	Axial sinus; left axocoel	Axial sinus	Sinus glandulaire	Axial sinus	Axial sinus	Axocoel	Axial canal (sinus)	Axial coelom
Perihemal coeloms (perihemal system)	Peripharyngeal perihemal ring	Oral perihemal rings	Hyponeural ring sinus; oral ring (haemal) sinus	Anneau périhémal oral; anneau péristomien; “pentagone oral”	Hyponeural ring sinus; hyponeural sinus system	Hyponeural pair of cavities	Ringkanal, Hyponeuralkanal (Somatocoel) und Ringkanal des Axocoels;	Hyponeural coelom; hyponeural ring canals (sinuses); perihemal coelom	–
Pericardial coelom (pericardium)	Right axial sinus	Madreporic vesicle	Dorsal sac; terminal sac; madreporic vesicle	Sinus terminal; sac dorsal	Dorsal sac; madreporic vesicle	Dorsal sac	Dorsalblase	Pericardial cavity; dorsal sac	Dorsal sac
Heart	–	–	–	–	–	–	Herz	Heart; central blood sinus	–
Axial organ	Axial organ	Axial gland	Axial gland	Glande brune	Axial (ovoid, brown) gland	Axial organ	Axialorgan	Axial hemal vessel (gland)	Axial organ
—True axial part —Pericardial part	Oral part (sector) Aboral part (sector)		Head (terminal) process	Processus terminal	Head process		Fortsatzsinus; Herz		Head process
Genital coelom	Genital sinus	Aboral perihemal ring; genital sinus	Aboral sinus; genital sinus	Anneau périhémal aboral; sinus gonadique; “pentagone aboral”	Genital sinus	Genital sinus; perihemal sinus; aboral coelomic sinus	Genitalcoelom; Aboraler Somatocoelring	Genital coelom	–
Genital rachis	Genital cord (stolon)	Genital cord	–	Cordon génital	–	Germinal epithelium (layer)	Genitalrhachis; Genitalstrang	–	–

* The terms used in this paper relate to sea urchins (Echinoidea).

gland") that runs along it are enveloped in the axial coelom, which is connected with the ampulla of madreporite at the aboral end. In reality, the axial coelom envelopes as a horseshoe-like structure the stone canal and axial organ from the side of the CD interradius. According to Hymans' description (Hyman, 1955), the axial coelom opens into the genital coelom: "a tubular sinus in the form of a pentagon" (Hyman, 1955, pp. 275, 283). According to our data, the axial and genital coeloms in *A. rubens* are fully separated. Hyman (1955) indicates that the genital coelom is not closed to a ring but has a gap in the region of the stone canal. According to our data (although it concerns only very young specimens), the genital coelom has no gap in this region. Other differences between the data by Hyman (1955) and our present study may be treated as terminological. Hyman (1955) calls the axocoel ring of the perihemal system the "hyponeural ring sinus" (Hyman, 1955, p. 285). According to Hyman's description (Hyman, 1955, p. 285), at the oral end the axial organ "terminates in the septum that subdivides the hyponeural ring sinus" or, in other words, protrudes into the perioral circulatory ring (according to our terminology). At the aboral end, the so-called "terminal process" enclosed in the coelomic cavity (the "dorsal sac" or madreporic vesicle) and able to contract deviates from the axial organ (Hyman, 1955, p. 285). It is likely this is how the pericardial coelom is designated here. Hyman (1955) does not mention the heart itself but noted about the contractions of the "terminal process" of the axial organ and of the aboral circulatory ring as well as of the so-called "gastric circulatory bundles."

For starfishes in general, Cuénot (Cuénot, 1948, p. 225) confirms the presence of the connection of the axial coelom ("le sinus glandulaire") with the stone canal ampulla ("le tube aquifère") and reports that the "stained liquid [injected into the axial coelom] exits from the madreporite." It is said further that the stain penetrates into the genital coelom and stains the gonads (for *Asterina gibbosa, Asterias rubens*, and *Astropecten irregularis*). As was noted above, according to our data there is no connection between the genital and axial coeloms. At the same time, this author indicates for *Asterias glacialis* Linnaeus 1758 (? = *Marthasterias glacialis* (Linnaeus 1758)) that the genital coelom ("le pentagone aboral") "runs near the axial coelom without connection with the latter" (Cuénot, 1948, p. 226). The genital coelom is depicted as an open-loop, but the gap in it is situated not in the CD interradius as indicated by Hyman (see above) but on the opposite side, in the region of the A radius (Cuénot, 1948, p. 225, Fig. 257, *3*). At the same time, another picture (Cuénot, 1948, p. 229, Fig. 259) shows that the genital coelom is locked into a ring and the axial coelom opens into it on the aboral side. According to our data, the genital coelom has no gaps along its whole length and is not connected with the axial coelom. Concerning the perihemal coeloms, Cuénot (Cuénot, 1948, pp. 226–227) reports that they represent a ring divided "by an oblique partition into two rings embedded into one another connected ... by the apertures." According to our data, no connection between the somatocoel and axocoel perihemal coeloms exists. The description of the perihemal coeloms and their connection with the axial coelom given by Cuénot (Cuénot, 1948) contains obvious contradictions. Figure 257, *2* in the cited paper shows that the axial coelom opens into the "upper" ("partie superieure ou dorsale de l'anneau perihemal oral") perihemal ring while the perihemal branches into the rays originate from the "lower" ("partie inferieure ou ventrale de l'anneau perihemal oral") perihemal ring (which conforms to our data). At the same time as is shown in other figures (Cuénot, 1948, p. 225, Fig. 257, *1*; p. 229, Fig. 259), the branches to the radii originate from the same ring into which the axial coelom opens. This is not true. It is written in the text that the lower (dorsal) ring opens into the axial coelom and is connected with it by the common origin while the upper (ventral) ring originates from the hypogastric cavity, i.e., from the somatocoel and is branched to the radii. In this case the "upper" and "lower' rings are mixed up. In the composition of the axial, organ Cuénot (Cuénot, 1948) defines the aboral "terminal process" as embedded into the closed "terminal sinus" or "dorsal sac," i.e., into the pericardial coelom. It is also noted that the "terminal process" and pericardium are able to contract rhythmically but the heart is not described.

In the description of starfishes in the handbook *Treatise on Invertebrate Paleontology* (Ubaghs, 1967), several mistakes are repeated following Hyman (Hyman, 1955); e.g., the images show that the axial and genital coeloms are connected to each other (Ubaghs, 1967, p. 19, Fig. 5). The perihemal coeloms ("hyponeural sinuses") are described as paired, and it is noted that the internal perihemal coelom is connected with the axocoel; however, in the figures the hyponeural sinus is shown as a single structure with the oral hemal ring situated within it ("periesophagial hemal ring") (Ubaghs, 1967, p. 19, Fig. 5, *2*; p. 20, Fig. 6). The heart is not described but the picture of the "head process of the axial gland" (which could be identified as the pericardial part of the axial organ) situated in the closed coelomic sac, i.e., the madreporic vesicle with contracting walls, is given (Ubaghs, 1967, p. 25).

In the description of the hemal system of starfishes given in the book *Microscopic Anatomy of Invertebrates* (the chapter devoted to Asteroidea), it is written that "the oral hemal system is connected to ... the axial organ, ... the hemal system of the gut, and the aboral hemal ring, and, eventually terminates in a blind sac" (Chia and Koss, 1994, p. 206). This description contains two inaccuracies: (1) the axial organ is not connected directly with the stone canal (the axial coelom

but not the axial organ opens into the stone canal); (2) the pericardial part of the axial organ does not "terminates" in the pericardium but opens into the hemocoel on the aboral part of the pericardial coelom. Then, it is reported that the axial organ and the aboral hemal ring are suspended on the perforated mesenteria inside the axial coelom. This may be understood as the genital coelom containing the aboral hemal rings, which represents the prolongation of the axial coelom. However, this is not true: the genital and axial coeloms are not interconnected. It is likely that the coelothelium of the axial coelom is meant. The heart is not noted. Concerning the structure of gonads, it is written that they include two tubular sinuses and the genital coelomic sinus. Thus, the term "perihemal" is used for the aboral (but not oral) coelomic ring of the axial complex.

In the handbook *Zoology of Invertebrates* edited by Westheide and Rieger (Westheide and Rieger, 2008), the generalized scheme of the structure of a starfish is given. In this scheme the stone canal is shown to be enclosed in the axial coelom along with the axial organ. However, in reality the axial coelom just closely adjoins the stone canal enveloping the latter from three sides but not enclosing it fully. In the same figure, the genital coelom is depicted as a closed ring having no gaps either in the CD interradius region or in the region of the A radius but connected with the axial coelom. In reality, no direct connection between the genital and axial coeloms exists. The aboral part of the axial organ is also shown as blindly closed in the pericardial coelom (Goldschmid, 1996, p. 787, Fig. 1082; Westheide and Rieger, 2008) while in reality it is connected with the hemocoel. As is shown in the cited figure, the pericardium communicates with the axial coelom, which is not correct: the processes of the pericardium penetrate the axial coelom, but the cavities of these coeloms do not communicate with each other. It is also noted in the cited handbook that the axial organ is divided into the oral and aboral parts ("accessory sinus") entering the dorsal vesicle. The "slow pulsations of alternating directions" are noted for the "accessory sinus." This is why the "accessory sinus" (the pericardial part of the axial organ) is also defined as the heart (Westheide and Rieger, 2008, p. 819).

Our original data are closest to the description of the axial complex in starfishes given by Ruppert et al. (Ruppert et al., 2004, 2008). The following correct points are presented in this handbook: the presence of the communication of the axial coelom with the stone canal ampulla and perihemal coelom, the communication of the axocoel particularly with the inner (axocoel) perihemal coelomic ring, the vascular nature of the axial organ, the genital coelom opens into neither coelomic cavity and the heart is positioned at the top of the axial organ. Ruppert et al. (Ruppert et al., 2004, 2008) use the term "heart" for the whole assemblage of structures: the myocardium including the heart opening, pericardial cavity, and dorsal sac, i.e., the pericardium, which does not connect with any other coelom. However, the pericardial part of the axial organ is still depicted as a blindly ending structure and its communication with the common hemocoel of the starfish is not noted (Ruppert et al., 2004, p. 883, Fig. 28-15; Ruppert et al., 2008).

The question whether the hemal system of starfishes is closed or not is still debatable, as is the question on the functions of the axial complex. It is known that the heart in echinoderms is able to pulsate periodically (Gemmill, 1919; Ruppert et al., 2004). In *Asterias forbesi* the frequency of these pulsations is about 6 beats per minute at 25°C (Ruppert et al., 2004). In addition slow pulsations are characteristic of the whole axial organ (Burton, 1964; Boolootian et al., 1965; Millott, 1966). It was found that the walls of both parts (true axial and pericardial) of the axial organ contain the epithelial-muscular cells and nervous elements along with podocytes (Bargmann and von Hehn, 1968; Holland, 1970; Welsch and Rehkämper, 1987). Thus, the axial organ participates in hemal circulation of starfishes; however, the direction in which the blood flows has not yet been studied. Goldschmid (1996) concedes that the direction of pulsations of the heart and the oral part of the axial organ may change. The phenomenon of alternating direction of blood flow among Deuterostomia has been known for a long time in ascidia. Ruppert et al. (2004) give the following explanations of this phenomenon. The organs and tissues in these animals are organized in such a manner that if the blood had moved from the heart to only one side, then the supply of organs by nutrients would have been irregular. This is why in ascidia every few minutes the pulsations of the heart stop and then restart in the opposite direction. In this way the organs and tissues that before were at the end of the circulation ring, after the direction of hemal flow changes are positioned at its very beginning. The hemal network of the axial organ is situated on both sides of the heart (i.e., from the aboral and oral sides). This suggests that the above-mentioned inversion of the hemal flow may take place in starfish as well. However, since the true axial part of the axial organ is much bigger and more powerful than the pericardial one, we assume that the prevailing direction of the blood flow is from the aboral part of the body to the oral one. Obviously this problem needs to be studied using experimental methods.

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