ISSN 1062-3590, Biology Bulletin, 2016, Vol. 43, No. 6, pp. 494–502. © Pleiades Publishing, Inc., 2016.
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CONFERENCE MATERIALS

Transformations of the Axial Complex of Ophiuroids as a Result of Shifting of the Madreporite to the Oral Side

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Received March 15, 2016

Abstract—In comparison with Asteroidea, the axial complex of ophiuroids has some important features, which are the result of shifting of the madreporite from the aboral side to the oral side. In contrast to Asteroidea, the stone canal of ophiuroids connects with the water ring from the outside, not from the inside. In Ophiuroidea, the somatocoelomic perihaemal coelom is closer to the mouth than the axocoelomic ring. The water ring of ophiuroids is shifted to the oral side relative to the perihaemal coelomic rings. The genital coelom and gastric haemal ring are located on the outer side of the axial complex, whereas in Asteroidea, they are located on the inner side. The pericardial part of the axial organ is situated on the oral side. The interradial sections of the genital coelom and genital haemal ring are descended to the oral side. Our hypothesis considers that the ancestors of ophiuroids turned the aboral side of the animal to the substratum. It caused shifting of the madreporite to the oral side and closing of the anus.

DOI: 10.1134/S1062359016060091

INTRODUCTION

Several hypotheses on the phylogenetic relationships between extant classes of echinoderms have been discussed in works on the taxonomy and phylogeny of Echinodermata over the past two decades (Littlewood et al., 1997; Janies, 2001) (Fig. 1). The two hypotheses that most often compete with each other are the following: the Asterozoa–Echinozoa hypothesis and the Cryptosyringida hypothesis (Janies et al., 2011; O'Hara et al., 2014). According to the first hypothesis, the Eleutherozoa classes are divided into two clades: Asteroidea + Ophiuroidea and Echinoidea + Holothuroidea (Smith, 1984; Mooi and David, 2000). According to the second hypothesis, the ophiuroids are included in the group Cryptosyringida, which includes all Eleutherozoa, except for sea stars (Smith, 1984). Another phylogenetic scheme is also popular, in which Ophiuroidea are located at the base of the Eleutherozoa tree (Perseke et al., 2010; Smith and Reich, 2013). However, in all these cases, brittle stars and starfish are the closest groups (Fig. 1).

The axial complex of organs is the most important synapomorphy of echinoderms, and its structural features in different groups represent the stages of evolution of this structure within the type. The question arises of how important the differences in the organization of the axial complex in Asteroidea and Ophiuroidea are. We use the results of original studies of the microscopic anatomy of the axial complex in *Asterias rubens* Linnaeus, 1758 (see Ezhova et al., 2013) and *Ophiura robusta* Ayres, 1854 (see Ezhova et al., 2015), as well as the data of other authors (Ludwig, 1878, 1880; Cuénot, 1888; Hamann, 1889; Mac Bride, 1896, 1907; Goto, 1898; Brooks and Grave, 1899; Reichensperger, 1908; Gemmill, 1912, 1914, 1915, 1920; Osterud, 1918; Fedotov, 1924; Narasimhamurti, 1933; Hörstadius, 1939; Smith, 1940; Olsen, 1942; Chia, 1968).

There is no terminological unity in the descriptions of the structures that are part of the axial complex of organs. Various authors describe the same axial complex structures under different names, making it very difficult to homologize the parts of the axial complex in various echinoderms. An analysis of the original and summarizing works on the structure of the coelomic and haemal systems of starfish and brittle stars allows us to homologize the structures that constitute the axial complex of organs and to propose a common terminology (Table 1).

THE AXIAL COMPLEX STRUCTURE IN ASTEROIDS

The central structures of the axial complex of sea stars are concentrated in the CD interradius. Here, the madreporite pierced by numerous pores is located on the aboral side (Fig. 2a). The pores lead to the madreporic ampulla. The stone canal originates here, extending to the oral side, where it bends and enters

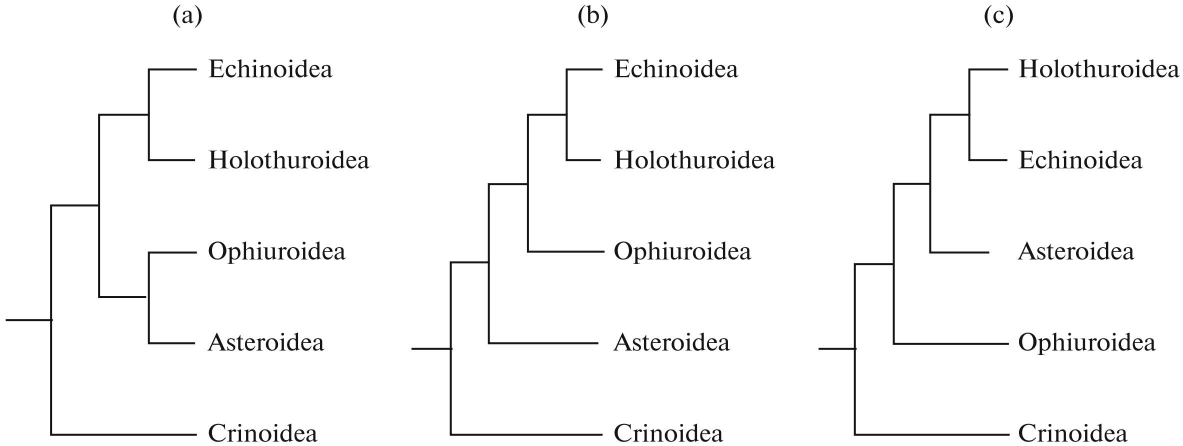

Fig. 1. Various hypotheses of the phylogenetic relationships of the extant classes of Echinodermata. (a) The Asterozoa–Echinozoa hypothesis; (b) the Cryptosyringida hypothesis; (c) the hypothesis of basality of Ophiuroidea.

the water ring from the proximal side. The radial ambulacral processes extend into the radii from the water ring.

The stone canal is enclosed with the axial coelom, which has the shape of a horseshoe in cross section. On the aboral side, the axial coelom communicates with the madreporic ampulla, and on the oral side, with the axocoelomic perihaemal coelom (Fig. 2a). The madreporic ampulla is adjoined by the pericardial coelom, which is a small closed coelomic pouch (Fig. 2a). The coelothelia of the axial and pericardial coeloms in the areas of contact with each other, as well as the coelothelium of the axial coelom near the stone canal, form numerous folds and bulges. The haemocoelic lacunae of these bulges constitute the blood system of the axial organ. Depending on the location and belonging of the forming coelothelia, the axial organ can be divided into the pericardial and axial parts, which lie in the pericardial and axial coeloms, respectively (Fig. 2b). On its aboral side, the pericardial part of the axial organ opens to the common haemocoel of the body wall, and, on the oral side, the axial part of the axial organ communicates with the oral haemal ring (Fig. 2b).

The axocoelomic perihaemal coelom is covered by a larger somacoelomic perihaemal ring on the distal side (Fig. 2a). An oral haemal ring passes between their coelothelia (Fig. 2b). The perioral coelom was described for some sea stars (Gemmill, 1912, 1920), but, for example, in *A. rubens*, it is missing (Ezhova et al., 2013). From the somacoelomic perihaemal ring, paired processes extend into the radii and between them pass the radial haemal vessels (Fig. 2).

On the aboral side of the animal, the genital ring coelom develops (Fig. 2a). Its plot in the CD interradius is located in close proximity to the pericardial coelom and the madreporic ampulla, on the proximal side of the axial structures of the complex. The genital coelom is a closed tube that does not communicate with anything, inside which runs another coelomic tube: the genital rachis. The coelothelium of the genital rachis is a germinal epithelium: gametes are formed here. Between the coelothelia of the genital coelom and the genital rachis, a genital haemal ring that supplies blood to the gonads is located. In the section between the pericardial and the axial parts of the axial organ, the genital haemal ring communicates with the axial organ (Fig. 2b).

In the same section, two tufts of blood capillaries extend proximally from the axial organ. They are formed by folds and swellings of the coelothelia, which form the horizontal mesentery between the hypogastric and epigastric coeloms. Via these gastric haemal tufts, the blood system of the axial organ communicates with the gastric haaemal ring extending in the horizontal mesentery (Fig. 2b).

THE AXIAL COMPLEX STRUCTURE IN OPHIUROIDS

In all ophiuroids, the madreporite is shifted to the oral side and, accordingly, the axial complex of the organs is turned orally (Fig. 3). A single pore canal passes in the madreporite of the majority of ophiuroids, which opens outside with a single pore on the side of the D radius. However, this situation is not inherent to all brittle stars. In *Ophionereis annulata* (Le Conte, 1851), there are 8 pores and pore canals (Cuénot, 1888), in *Ophiopsila annulosa* (M. Sars, 1859), from 3 to 12 pores (Reichensperger, 1908), and *Gorgonocephalus* developed a real madreporite with up to 250 pores (Ludwig, 1878). In all ophiuroids, the pore canals communicate with the madreporic ampulla where the stone canal and axial coelom open (Fig. 3a).

The stone canal rises to the aboral side and enters the water ring on the distal side (Fig. 3a). The radial

Table 1. The terms used for designation of the homologous structures of the axial complex in Asteroidea and Ophiuroidea

Terms used in paper	Terms used in other papers (original language)								
	MacBride, 1892, 1907	Narasimhamurti, 1933	Smith, 1940	Cuénot, 1948	Hyman, 1955	Ivanova-Kazas, 1978	Ivanov et al., 1985	Goldschmid, 1996	Ruppert et al., 2004
Stone canal	Stone-canal	Stone canal	Stone canal	Tube aquifère	Stone canal	Stone canal	Stone canal	Steinkanal	Stone canal
Pore canal	Pore-canal	Pore canal	Pore canal	Pore aquifère	Pore canal	Pore canal	Pore canal	Hydroporus-kanal	Pore canal
Axial coelom	Ampulla = sinus *c*; axial sinus = sinus *b*	Ampulla of the stone canal	Left axial sinus	Sinus glandulaire; sinus entérocœlien	Axial sinus	Left axocoel; axial sinus; ampulla of the stone canal	Left axial sinus	Axocoel	Axial canal (sinus)
Perihaemal coeloms	Perihæmal system	Perihaemal system of cavities	–	Anneau périhémal oral; "pentagone oral"; anneau péristomien; sinus hyponeural	Hyponeural ring sinus; oral ring (haemal) sinus; oral perihaemal ring	Oral perihaemal system; oral perihaemal rings	Pharyngeal perihaemal ring; perihaemal canals	Hyponeural-kanal	Hyponeural canal (coelom)
axocoelomic perihaemal coelom	Perihæmal space = sinus *b*	–	–	–	–	Inner perihaemal ring	–	Ringkanal des Axocoel	–
somatocoelomic perihaemal coelom	Perihæmal cavities	–	–	Sinus hyponeural	Hyponeural ring canal (sinus)	Outer perihaemal ring	–	Hyponeural-kanal (Somatocoel) Ringkanal	–
Perioral coelom	Peri-oral cœlom	Peri-oral coelom	–	Espace périœsophagienne; cavité péristomienne	Peristomial ring sinus	Perioral coelom	–	–	–

Table 1. (Contd.)

Terms used in paper	Terms used in other papers (original language)								
	MacBride, 1892, 1907	Narasimhamurti, 1933	Smith, 1940	Cuénot, 1948	Hyman, 1955	Ivanova-Kazas, 1978	Ivanov et al., 1985	Goldschmid, 1996	Ruppert et al., 2004
Pericardial coelom	Right hydrocœle; axial sinus = sinus *b*	Pericardial vesicle	Madreporic vesicle; right axial sinus	Sinus terminal; sac dorsal	Dorsal sac; terminal sac; madreporic vesicle; right part of the axial sinus	Right axocoel; pericardium; madreporic vesicle	Right axial sinus	Dorsalblase	Pericardial cavity; dorsal sac
Axial organ	Ovoid gland	–	Axial organ	Glande brune	Axial gland	Axial gland	Axial organ	Axialorgan	Axial organ; axial hemal vessel (gland)
axial part of axial organ	–	–	Left axial organ	Glande brune	Darker thicker aboral part	–	Oral part	–	–
pericardial part of axial organ	–	–	Right axial organ	Extrémité ventrale de la gland brune; processus terminal	Lighter slender oral part; head (terminal) process	–	Aboral part	Fortsatzsinus	–
Genital coelom	Aboral sinus = sinus *a*	–	Genital sinus	Anneau périhémal aboral; sinus ondulé; sinus gonadique; sinus périgénital; "pentagone aboral"	Aboral (coelomic) sinus; genital sinus	Aboral perihaemal ring; genital sinus	Genital sinus	Aboraler Genitalkanal; Genitalcoelom; Aboraler Somatocoelring	Genital coelom
Genital rachis	Genital rachis	Genital rachis	Genital rachis	Cordon génital	Genital rachis	Genital cord	Genital stolon (cord)	Genitalrhachis; Genitalstrang	–

* "–" means the structure is not indicated in the paper.

ambulacral processes extend from the water ring. The axial coelom also rises up to the aboral side and opens to the axocoelomic perihaemal ring (Fig. 3a). The axocoelomic perihaemal ring encloses the somatocoelomic perihaemal ring on the distal side. From the latter, paired processes extend into the radii. Between the axocoelomic and somatocoelomic perihaemal rings, the oral haemal ring passes, and between the radial processes of the somatocoelomic perihaemal coelom, radial haemal vessels extend (Fig. 3b). In addition, ophiuroids have a perioral coelom.

Near the madreporic ampulla, the pericardial coelom is located. It is not connected with anything and is a closed coelomic cavity (Fig. 3a). The mutual interdigitations of the coelothelia of the pericardial and axial coeloms form a network of blood lacunae of the axial organ. Accordingly, the pericardial and axial parts can be identified in the axial organ (Fig. 3b). The pericardial part of the axial organ opens to the haemocoel of the body wall, and the axial part of the axial organ on the aboral side communicates with the oral haemal ring (Ezhova et al., 2015).

On the oral side, the genital coelom is located, through which the genital rachis runs. However, unlike starfish, in ophiuroids, the genital coelom is adjacent to the axial structures of the complex not on the proximal but on the distal side (Fig. 3a). The genital haemal ring is in communication with the axial organ in the area between the pericardial and the axial parts (Fig. 3b). In the same section, a pair of capillary tufts extends from the axial organ to the gastric haemal ring. However, they are also located not on the proximal but on the distal side of the axial components of the complex.

It should be noted that, despite the oral location of the genital structures in the CD interradius (and in other interradii), the radial sections of the genital coelom and the genital haemal ring retain their aboral position, skirting the radial outgrowths of the ambulacral and somatocoelomic perihaemal coeloms in an arclike manner (Fig. 3).

POSSIBLE WAYS OF EVOLUTION

The axial complex structures can be divided into coelomic and haemocoelic, i.e., haemal. At the same time, the structures of the axial complex of the organs of Asteroidea and Ophiuroidea can be divided into the axial ones located in the CD interradius and the circular ones extending in the central disk, enclosing the digestive tube and sometimes sending processes into the radii (Table 2).

Note that (Figs. 2, 3) the organization of the axial complexes of organs in asteroids and ophiuroids differs only due to the fact that in ophiuroids the madreporite is located not on the aboral but on the oral side. Direct embryological observations indicate that such a shift of the madreporite really occurred in the ontogenesis

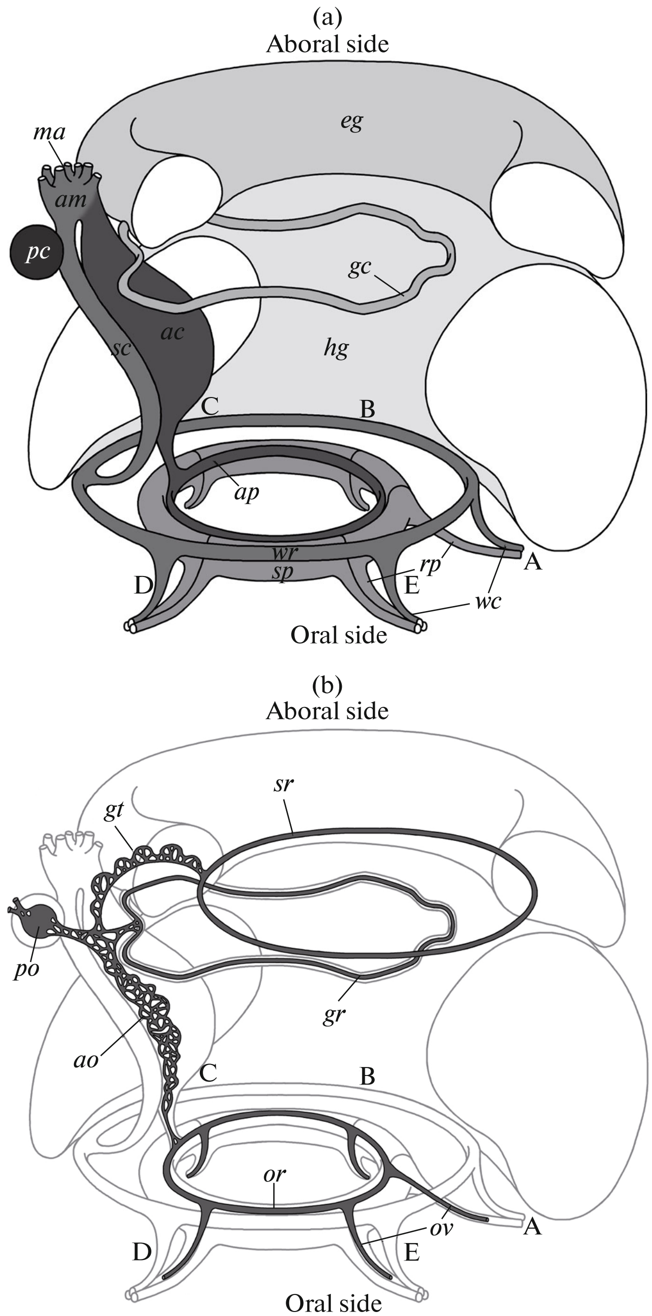

Fig. 2. The schemes of (a) the coelomic and (b) the haemal systems of Asteroidea (the perioral coelom is not shown). (*wr*) Water ring, (*am*) madreporic ampulla, (*ao*) the axial part of the axial organ, (*ap*) axocoelomic perihaemal coelom, (*wc*) radial water coelom, (*hg*) hypogastric coelom, (*gr*) genital haemal ring, (*gt*) gastric haemal tufts, (*gc*) genital coelom, (*sr*) gastric (stomach) haemal ring, (*sc*) stone canal, (*ma*) madreporite, (*or*) oral haemal ring, (*ac*) axial coelom, (*pc*) pericardial coelom, (*po*) pericardial part of the axial organ, (*ov*) radial haemal vessel from the oral ring, (*sp*) somatocoelomic perihaemal coelom, (*rp*) radial perihaemal coelom, and (*eg*) epigastric coelom. The letters A, B, C, D, and E denote the radii; for Figs. 2 and 3.

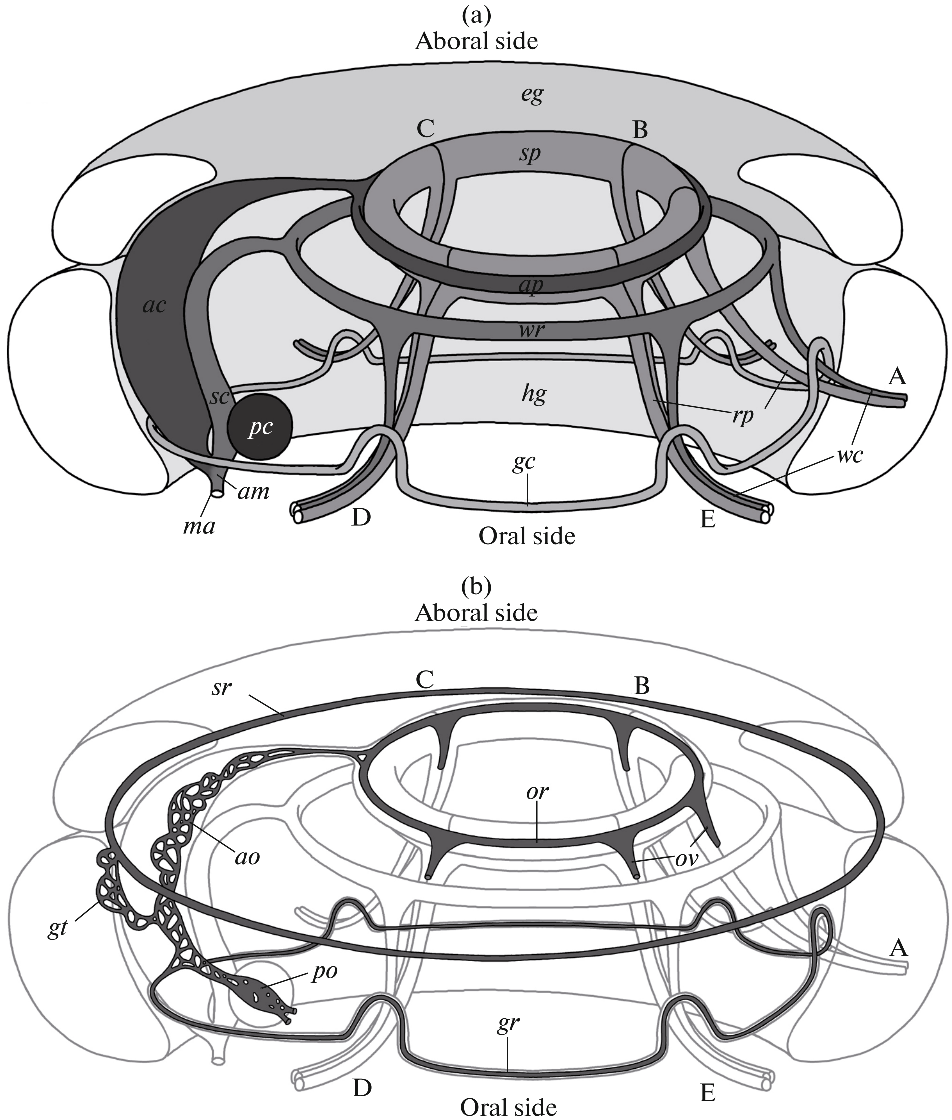

Fig. 3. The schemes of (a) the coelomic and (b) the haemal systems of Ophiuroidea (the perioral coelom is not shown).

of the ophiuroids (Mac Bride, 1907). We can assume that the shift of the madreporite in the ontogenesis of ophiuroids reflects the phylogenetic process of moving of the madreporite from the aboral side of the body to the oral side.

The moving of the madreporite to the oral side leads to changes in the topography of other structures of the axial complex of organs, namely, the following:

—the stone canal of ophiuroids opens into the water ring on the outside rather than the inside, as in starfish;

—the axocoelomic perihaemal coelom in ophiuroids is located outside the somatocoelomic perihaemal coelom, whereas in starfish, it is the opposite;

—the water ring in ophiuroids is shifted to the oral side relative to the perihaemal coelomic rings, and in starfish, the ambulacral coelomic ring is shifted toward the aboral side relative to the perihaemal coelomic rings;

—the genital coelom in ophiuroids embraces the axial coelom on the outside, and in starfish the genital coelom is adjacent to the axial coelom on the inside;

—the gastric haemal ring in ophiuroids extends from the outer side of the axial complex, and in starfish, from the inner side;

—the pericardial part of the axial organ of ophiuroids is located on the oral side, whereas in starfish, it lies on the aboral side. The pericardial part of the axial organ retains all connections, namely with the genital haemal ring, with the haemocoel of the body wall, with the axial part of the axial organ, and with the gastric haemal ring;

Table 2. Organs and structures of the axial complex in Asteroidea and Ophiuroidea

Axial complex structures	Coelomic	Haemocoelic
Axial	Pericardial coelom*	Pericardial part of axial organ
	Axial coelom**	Axial part of axial organ
	Madreporic ampulla**	
	Madreporite and pore canals**,***	
	Stone canal**,***	
Circular	Water ring***	
	Axocoelomic perihaemal coelom**	Oral haemal ring
	Somatocoelomic perihaemal coelom****	
	Perioral coelom****	
	Genital coelom****	Genital haemal ring
	Genital rachis****	
		Gastric haemal ring

The haemocoelic structures are on the level of its location between the coelomic derivations.
* Derivations of the right axocoel (protocoel).
** Derivations of the left axocoel (protocoel).
*** Derivations of the left hydrocoel (mesocoel).
**** Derivations of the left somatocoel (metacoel).

—the interradial areas of the genital coelom and the genital haemal ring descend to the oral side and are located here more orally than all other structures of the axial complex, in contrast to starfish, the genital coelom of which is located on the aboral side of the body. The radial portions of the genital coelom and the genital haemal ring form five loops in the radii. Paired radial processes of the somatocoelomic perihaemal coelom (with a blood vessel in the mesentery between them) and a radial process of the ambulacral coelom pass under each loop.

What could have caused the shifting of the madreporite from the aboral side to the oral side in ancestor ophiuroids? We offer a hypothesis explaining this process (Fig. 4): as is known, starfish crawl on the oral side, collecting food with the mouth. The anus is

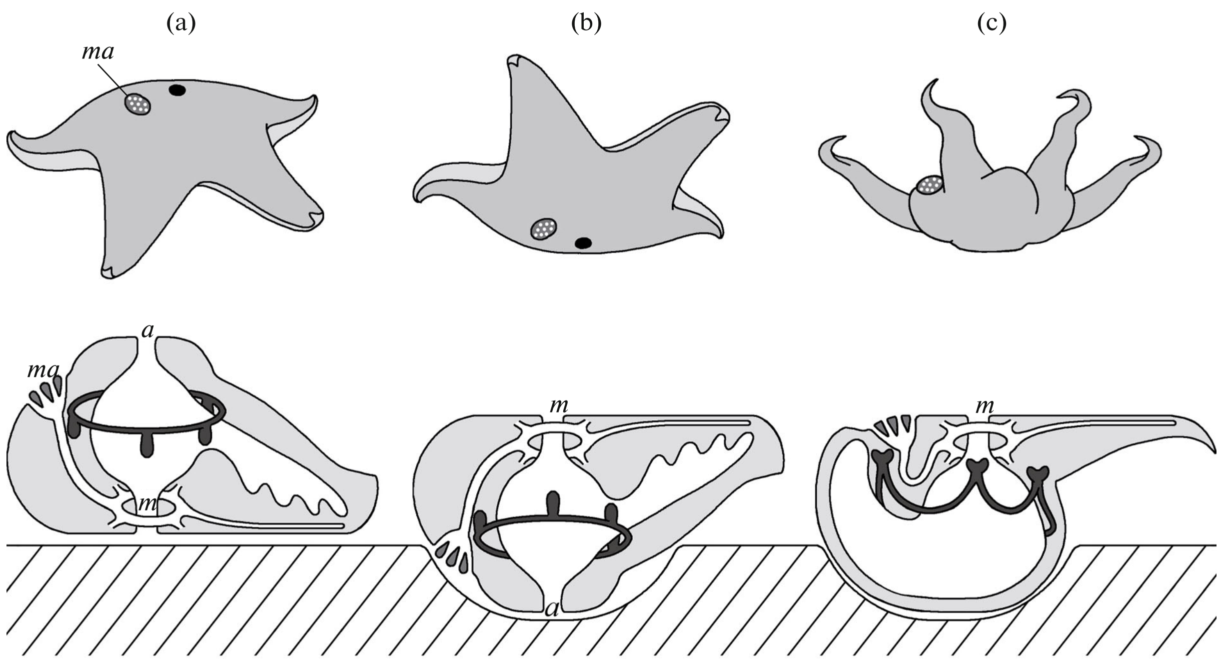

Fig. 4. (a) The turnover of the ancestors of ophiuroids that had a madreporite and anus to the oral side: (b) as a result of which the aboral side was turned to the substrate, (c) which, in turn, led to the shift of the madreporite to the oral side and closure of anus. (*a*) Anus, (*ma*) madreporite, and (*m*) mouth.

located on the opposite (aboral) side, as is the madreporite. Owing to this, both the undigested remnants from the intestine and products of the excretion from the cavity of the axial coelom can easily be disposed of into the environment.

Ophiuroids can crawl on the oral side, but spend the greater part of time turned over on the aboral side and raising their arms in order to catch food (Hyman, 1955; Litvinova, 1979, 1980; Ruppert et al., 2004). In this case, the aboral side with the anus and madreporite initially located thereon is facing the substrate. This factor could have led to the closure of the anus and the formation of the secondary sacciform intestine, in which the mouth functions both for taking food and defecation. The madreporite is a coelomoduct pore through which the products of metabolism are excreted, which enter the axial coelom from the blood by ultrafiltration in the axial organ (Cuénot, 1948; Ziegler et al., 2009 Ezhova et al., 2013, 2014, 2015). The madreporic pore in ophiuroids is preserved, but shifted to the oral side (Fig. 4), causing the movement of other structures connected with the madreporite in one way or another.

ACKNOWLEDGMENTS

This work was supported by the Russian Science Foundation, grant no. 14-50-00034.

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Translated by N. Smolina