

Axial complex and associated structures of the sea urchin *Strongylocentrotus pallidus* (Sars, G.O. 1871) (Echinodermata: Echinoidea)

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Abstract

Studies of echinoid microscopic anatomy over the last two centuries have created a number of inaccuracies and mistakes that have accumulated in the descriptions of the intricate organization of the coelomic system of Echinoidea. To clarify the situation, we reconstructed the axial complex and radial complex of the echinoid *Strongylocentrotus pallidus*. The water ring is located between the perivisceral coelom and the perioral coelom. The oral haemal ring lies between the coelothelia of the water-vascular, perivisceral, and perioral rings. The axial part of the axial organ communicates with the oral haemal ring in interradius CD, but the axial coelom does not form the axocoelomic periaemal ring. The ventral intestinal haemal vessel originates from the oral haemal ring in radius A, and then branches into a network of capillaries, from which the dorsal intestinal vessel starts. The pericardial coelom envelopes the pericardial part of the axial organ, the lacunae of which communicate with the haemocoel of the body wall and with the axial part of the axial organ. The genital haemal ring and the dorsal intestinal vessel communicate with the axial organ. The genital coelom passes in the CD interradius on the side opposite to the hindgut. There is a somatocoelomic periaemal ring, which sends a pair of coelomic outgrowths into each radius, accompanied by a radial haemal vessel in the oral part. The mistakes and inaccuracies of early descriptions of the echinoid axial complex are listed. The axial complex and associated structures of sea urchins are compared with other eleutherozoans.

KEYWORDS

coelom, Eleutherozoa, haemal system, morphology, radial complex

1 | INTRODUCTION

Sea urchins have been a starting point for the research of Echinodermata in general and were the object of study of many zoologists. A large number of studies is devoted to the morphology of the test and lantern (Hyman, 1955; Ruppert, Fox, & Barnes, 2004). These calcified

structures are well preserved in fossils (Donovan, 1991; Kroh & Nebelsick, 2010) and have attracted the attention of researchers for a long time. Many other studies are devoted to the rich variety of external appendages of sea urchins. Although the structure of the soft internal coelomic organs is not frequently described, it seems to be generally well studied. However, in the course of almost two centuries of the

Abbreviations: aao, axial part of axial organ; amp, madreporic ampulla; ao, axial organ; axc, axial coelom; bw, body wall; cmp, compass of lantern; dbv, dorsal intestinal haemal vessel; dnb, dental haemal vessels; dnt, teeth; ecn, ectoneural radial nerve band; ep, epidermis; eph, epiphysis of the lantern; epn, epineural radial canal; g, pharynx or intestine, or their lumen; gn, gonad; gnb, genital haemal ring; gnc, genital coelom; gnd, gonoduct; gnr, genital rachis; hpc, hyponeural canal; mp, madreporic plate; obv, radial haemal vessel; ooc, oocyte; orb, oral haemal ring; pao, pericardial part of axial organ; pc, pore canals of madreporic plate; pcd, pericardial coelom; poc, perioral coelom; pod, ampullae of podia; pvc, perivisceral coelom; pyr, pyramid of chewing apparatus; rot, rotule of lantern; sb, spongy body; sc, stone canal; spc, somatocoelomic periaemal ring or outgrowths; vbv, ventral intestinal haemal vessel; vm, vertical mesentery; wc, radial water canal; wr, water ring.

study of echinoid microscopic anatomy, many inaccuracies and mistakes have accumulated in the scientific descriptions of the complicated and intricate internal organization of the coelomic system of Echinoidea. Often, different terms are used in different papers to describe the same structures (see Table 1, for example, «Perioral coelom», «Perivisceral coelom», «Genital coelom»). Vice versa, same terms are used for different structures, for example, the hyponeural canals, which are often incorrectly named «perihæmal canals». A number of echinoid coelomic structures are described by some authors, for example, the axial coelom (Cuénot, 1948; Goldschmid, 1996; Ziegler, Faber, & Bartolomæus, 2009), but are absent from other descriptions (Hamann, 1887; Leipoldt, 1893; Chadwick, 1900). The communication of coelomic organs with hæmocoel structures is sometimes mentioned (Hamann, 1887), but based on current knowledge about the nature of the coelom and the hæmocoel, it is difficult to understand how the hæmocoel communicates with the coelom. A clear picture of which coelomic structure of sea urchins corresponds to homologous structures of other eleutherozoans cannot be obtained from the analysis of previous studies.

These inconsistencies in the scientific literature are common not only for sea urchins, but for all modern echinoderm taxa in general. To clarify these inaccuracies, over the last few years we have carried out a series of detailed re-investigations of the axial complex of organs and associated structures in sea stars (Ezhova, Lavrova, & Malakhov, 2013), brittle stars (Ezhova, Lavrova, Ershova, & Malakhov, 2015), and sea cucumbers (Ezhova, Ershova, & Malakhov, 2017). We were faced with the same problem during the analysis of the literature devoted to the morphology of sea urchins, which was a continuation of our work on the study of the microanatomy of the ambulacrarian axial complex. Therefore, we have re-investigated the axial complex of organs in Echinoidea on the example of the sea urchin *Strongylocentrotus pallidus* (Sars, G.O. 1871) from the family Strongylocentrotidae, order Camarodonta, subclass Euechinoidea, group Regularia.

The question may arise: if we emphasize the difficulty of analyzing descriptions of echinoderm anatomy due to different terms being used by different authors, then why do we abandon traditional terms in some cases (Table 1)? This is because we tried to find for each structure of the axial complex from all the existing terms such a name that reflects the topography of this structure and can be used for homologous structures for all echinoderm taxa. An example of this is the somatocoelomic perihæmal coelom: the name for this structure combines the location, which is characteristic in varying degrees for all Eleutherozoa, and its origin from the somatocoel (unlike the axocoelomic perihæmal coelom of sea stars and brittle stars). Additionally, to facilitate the understanding of the difficult organization of echinoid coelomic system, for each coelomic structure we noted in parentheses the larval primordium of the coelom it develops from.

The organs of the echinoid axial complex and the associated structures may be conveniently divided into coelomic and hæmocoelic, and into axial and circumoral parts. The coelomic organs include the axial coelom (left axocoel), pericardial coelom (right axocoel), water-vascular system (left hydrocoel), and the derivatives of the left somatocoel: perioral (or peripharyngeal) coelomic ring, genital coelomic ring with the

genital rachis, and the somatocoelomic perihæmal ring. Additionally, when considering the axial complex, it is important paying attention to the organization of the hypogastric and epigastric coeloms (left and right somatocoels, respectively), which are fused in sea urchins into a common perivisceral cavity. The hæmocoelic structures of the echinoid axial complex include the axial organ, oral hæmal ring and extending from it radial hæmal vessels, the genital hæmal ring and gonad hæmal lacunae, and the so-called marginal intestinal vessels. It is also necessary to consider some features of the radial complex of organs, which, in addition to coelomic and hæmocoelic components, include nerves and epineural canals.

2 | MATERIALS AND METHODS

Mature specimens of *S. pallidus* (Sars, G.O. 1871) 12–15 mm in diameter were collected between 2013 and 2016 near the Pertsov White Sea Biological Station, which is located in the Kandalakshskii Bay (White Sea). Premature specimens near 10 mm in diameter were collected near the Dalnie Zelentsy Biological Station (Barents Sea). Animals were collected at depths from 20 to 30 m from rocky substrates by diving. For histological studies, the animals were fixed in Bouin's fluid. Prior to histological processing, the material was preserved in 70% ethanol. To decalcify the remains of the teeth and pyramids (which the picric acid of the fixative may not reach), and to prepare the material for histological processing, standard decalcification procedures were performed using EDTA solution (Trilon B, Helaton-3) or nitric acid (Valovaya & Kavtaradze, 1993). The standard technique of dehydration of the material in alcohols of increasing concentration was used, followed by the embedding of the material in paraplast and cutting it into sections 5 µm thick. In total, seven specimens were studied using light microscopy. Seven series of sections were made: three series in the sagittal plane and four series perpendicular to the oral–aboral axis (transverse section). Photographs of histological sections were made using an Axioplan 2 photomicroscope («Carl Zeiss Microscopy», Jena, Germany, 2003).

3 | RESULTS

The axial structures of the axial complex of *S. pallidus* are located in the interradius CD (Figure 1), where they are suspended from the vertical mesentery (Figure 2a). This mesentery, on one hand, connects the axial structures with the intestine, and on the other hand, attaches them to the body wall in the aboral area.

In *S. pallidus*, the central structures around which the organs of the axial complex are concentrated are the elements of the water-vascular system (Figures 1 and 2). The water ring (part of the left hydrocoel) surrounds the pharynx and lies in the middle part of the echinoid body above the lantern, approximately halfway between the aboral and oral halves of the body. The water ring is inserted between the perivisceral coelom, which represents the main cavity of the echinoid body, and the vast perioral coelom surrounding the chewing apparatus (Figure 3d). The oral hæmal ring lies between the coelothelia of these

TABLE 1 Terms used for designation of structural elements of the echinoid axial complex

Terms used in the present paper	MacBride (1903)	Cuénot (1948)	Hyman (1955)	Ivanova-Kazas (1978)	Ivanov, Polyanski, and Strelkov (1985)	Ruppert et al. (2004)	Ziegler et al. (2009)
Stone canal	Stone-canal	Tube aquifère	Stone canal	-	Stone canal	Stone canal	Stone canal
Pore canals	Pore-canals	Pores aquifères	Canals through madreporic plate	-	Canaliculi piercing the madreporic plate	-	Madreporic pore canals
Water ring	Left hydrocoel	Anneau ambulacraire oral	Water ring	Ambulacral ring; left hydrocoel; ring of hydrocoel	Ring vessel/canal of ambulacral system	Ring canal of the water-vascular system	Ring canal
Pericardial coelom	Right hydrocoel; madreporic vesicle; «dorsal sac»	Sinus terminal; sac dorsal	Coelomic cavity (right axocoel) in which axial gland terminates	Madreporic vesicle	-	-	Dorsal sac
Axial coelom	Left anterior coelom or ampulla	Sinus glandulaire	Lumen of axial gland	Left axocoel	Axial coelom	-	Axial coelom
Axial organ	-	Glande brune; glande ovotide; organe axial	Axial gland	-	Axial organ	Axial hernal vessel (axial gland); heart-kidney	Axial organ
Axial part of the axial organ	-	Glande brune	Haemal lacunae around axial gland	-	Oral part of axial organ	-	Axial organ
Pericardial part of the axial organ	-	Processus terminal	Terminal process of axial gland	-	Aboral part of axial organ	-	Head process
Somatocoelomic perihæmal coelom	Perihæmal canal; outer perihæmal ring	-	-	-	-	-	-
Hyponeural canal	Perihæmal canal	Sinus hyponeural	Hyponeural sinus; pseudo-hæmal canal; perihæmal canal	Perihæmal system	Radial perihæmal canal	Hyponeural coelom	-
Perioral coelom	Lantern-coelom; dental-sacs	Cavité péripharyngienne; anneau hyponeural	Peripharyngeal coelom; peripharyngeal sinus	Dental sacs	Peripharyngeal sinus	Peripharyngeal (lateral) coelom	-

(Continues)

TABLE 1 (Continued)

Terms used in the present paper	MacBride (1903)	Cuénot (1948)	Hyman (1955)	Ivanova-Kazas (1978)	Ivanov, Polyanski, and Strelkov (1985)	Ruppert et al. (2004)	Ziegler et al. (2009)
		péribuccal					
Perivisceral coelom	-	Vaste cavité, occupant surtout la région centrale	Main coelomic cavity	Hypo- and epigastric coeloms, staying in wide communication to each other	Coelom	Perivisceral coelom	-
Genital coelom	Aboral sinus	Sinus aboral	Aboral coelomic sinus; genital sinus; genital coelom	Genital sinus	-	Genital coelom	-
Genital rachis	Genital rachis	Cordon génital	Genital stolon	Genital stolon; genital cord	-	-	-
Genital haemal ring	-	Anneau lacunaire aboral	Aboral haemal sinus/ ring	-	Ring perianal vessel (sinus)	-	Aboral haemal ring
Oral haemal ring	-	Anneau lacunaire oral	Haemal ring	-	Peripharyngeal ring vessel	-	Perioesophageal haemal ring
Ventral haemal vessel	-	Lacune marginale interne	Inner or ventral marginal sinus	-	Inner intestinal vessel	-	Inner marginal haemal duct
Dorsal haemal vessel	-	Lacune marginale externe	Outer or dorsal marginal sinus	-	Outer intestinal vessel	-	Outer marginal haemal duct
Epineural canal	Epineural canal	Sinus épineural	Epineural sinus	Epineural canal	Epineural canal	Epineural canal	-

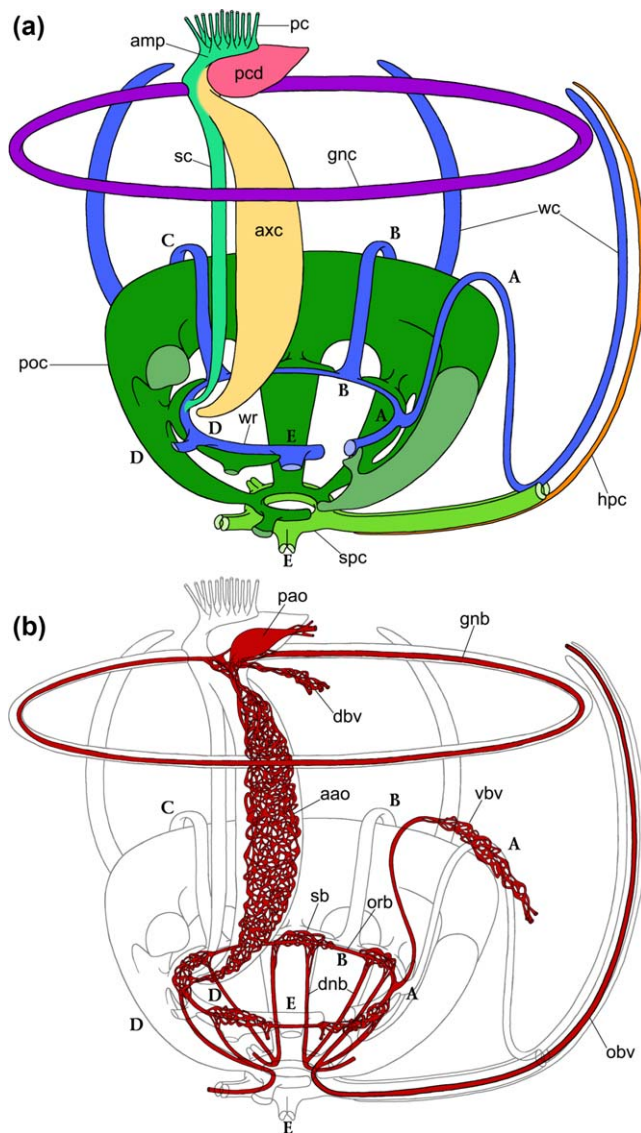


FIGURE 1 Interrelations between different coeloms (a) and haemocoel structures (b) in the axial complex of *S. pallidus*. Capital letters indicate the radii. The perivisceral coelom is not shown. Details of radial complex are shown for radius A. aao, axial part of axial organ; amp, madreporic ampulla; axc, axial coelom; dbv, dorsal haemal vessel; dnb, dental haemal vessels; gnb, genital haemal ring; gnc, genital coelom; hpc, hyponeural canal; obv, radial haemal vessel; orb, oral haemal ring; pao, pericardial part of axial organ; pc, pore canals of madreporic plate; pcd, pericardial coelom; poc, perioral coelom; sb, spongy body; sc, stone canal; spc, somatocoelomic perihemal ring; vbv, ventral intestinal haemal vessel; wc, radial water canal; wr, water ring

three coelomic rings: water ring, perivisceral ring, and perioral ring (Figure 3d).

The water ring expands in the interradii and forms small branched blind pockets, which fill the so-called spongy bodies (Figures 2b and 3d). Outside, these extensions of the water ring are surrounded by an interlacement of haemal lacunae of the oral haemal ring (Figures 2b and 3d).

The water ring gives rise to a wide outgrowth into each of the five radii (Figures 1a and 2c). These radial water canals (another part of the left hydrocoel) continue around the lantern from the aboral side pass under the rotules and above the comminator muscles (interpyramidal muscles). The radial water canals become narrower as they descend to the oral side of the pyramids, where they sharply bend and ascend again to the aboral side along the ambulacra as a part of radial complex (Figures 1a and 3c). Here, the ampullae of the podia branch off from them. The radial water canals end blindly on the aboral side of the animal.

The stone canal (the third part of the left hydrocoel) is located in the upper, aboral half of the body of *S. pallidus*, where it runs in the oral-aboral direction. The oral end of the stone canal fuses with the water ring from the inner side (i.e., from the side of pharynx) (Figures 1a and 3d). The aboral end of the stone canal opens into the madreporic ampulla (part of the left axocoel) (Figures 1a and 3b). The madreporic ampulla of *S. pallidus* is a flattened coelomic cistern adjacent to the madreporic plate from beneath. The madreporic ampulla has a mesh structure: it is not a single cistern, but a set of numerous intersecting horizontal canals merging into each other. Therefore, on the sections the madreporic ampulla does not seem to be a single cavity, but multiple profiles piercing the inferior part of the madreporic plate (Figure 3b). These profiles in their majority contact with the wall of the pericardial coelom, which is adjacent to the madreporic ampulla from the side of radius C (Figures 1a and 3b). The madreporic ampulla communicates with the environment by numerous (up to 200 in studied specimens) thin pore canals, which run vertically and pierce the madreporic plate (Figures 1a and 3a,b). From below the stone canal and the axial coelom open into the madreporic ampulla from the side of radius D (Figures 1a, 3b, and 4a).

The pericardial coelom (the right axocoel) of *S. pallidus* is a discoid coelomic compartment, which does not communicate with any other coelomic cavities (Figures 1a, 3b, and 4a). The pericardial coelothelium adjoins with the coelothelium of the madreporic ampulla from the aboral side. On the oral side, the axial coelom and the genital coelom adjoin to the pericardium from the side of radius C, and the perivisceral coelom from the side of radius D (Figures 1a, 3b, 4a, and 5b,d). The coelothelium of the oral wall of the pericardium forms a swelling, which is the pericardial part of the axial organ, lacunae of which communicate with the haemocoel of the body wall (Figures 1b, 3b, and 4a) and with haemocoelic lacunae of the axial part of the axial organ (Figures 1b and 5b).

The axial coelom (part of the left axocoel) of *S. pallidus* is extended along the stone canal and closely adjoins to it from the side of radius C (Figures 1a, 2a, 3b, and 4b). On the opposite side from the stone canal, the axial part of axial organ extends and submerges into the cavity of the axial coelom in a form of the festooned ridge (Figure 4b,d). The axial part of the axial organ extends along the entire axial coelom and communicates with the oral haemal ring on the oral side (Figures 1b and 3d). In the aboral area the axial coelom constitutes a wide, clearly visible cavity (Figures 3b and 4a). In other parts, the axial part of axial organ expands, partly replacing the coelomic cavity; on histological sections the coelomic cavity is seen as narrow spaces (Figure 4b). On the aboral side the axial coelom connects with the madreporic ampulla (Figure 4a), and on the oral side it ends blindly at the point where the stone

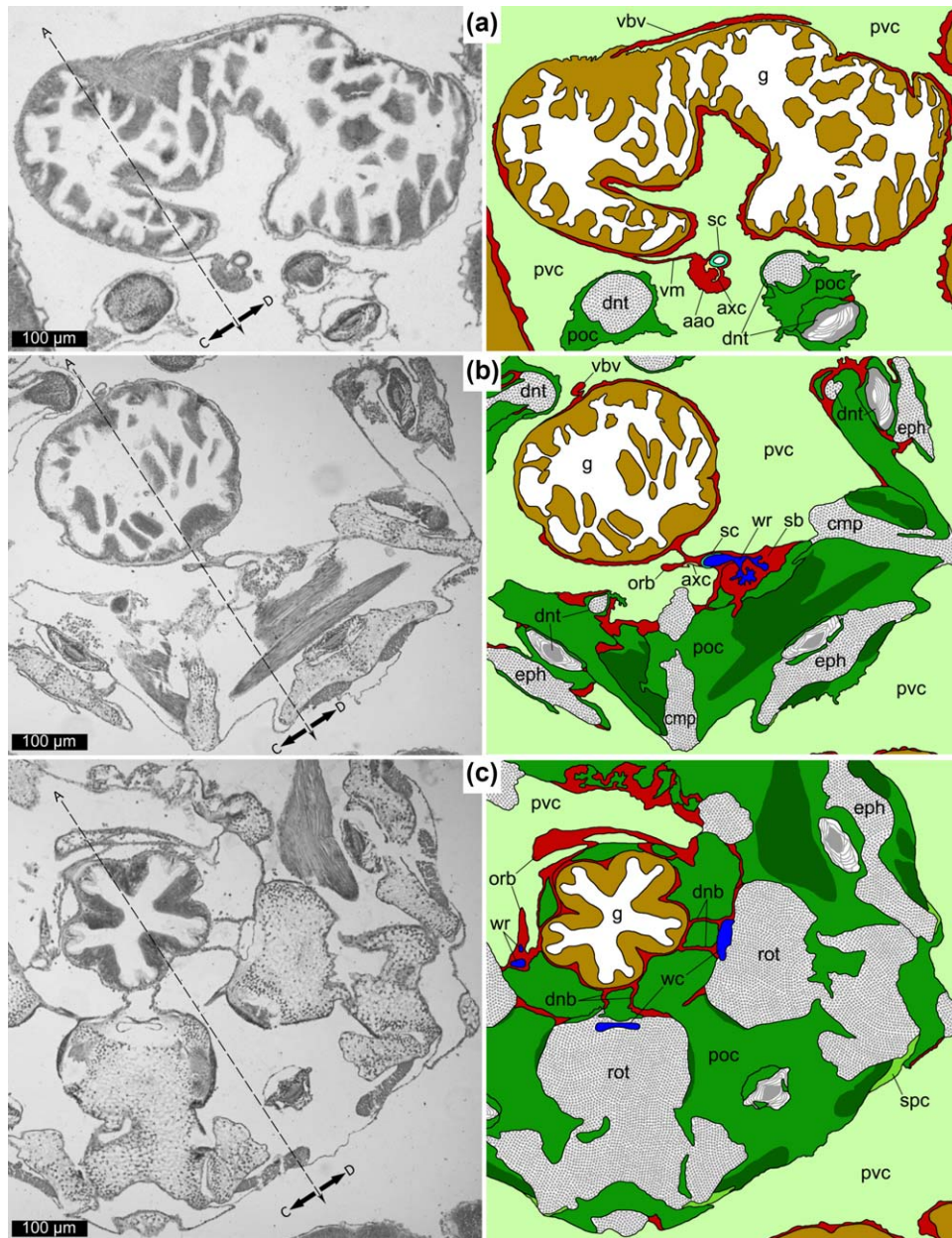


FIGURE 2 Circumoral structures of *S. pallidus*. Sections in the plane perpendicular to oral-aboral axis from the aboral side of the body (a) to oral side (c). The dotted arrow indicates the direction from radius A to interradius CD; the solid arrows indicate the direction to radii C and D. Muscles of the chewing apparatus are colored dark-green. (a) Section on the level of the central area of axial organ; the ventral intestinal haemal vessel (vbw) is visible. (b) Confluence of the stone canal (sc) into the water ring (wr) and continuation of the ventral intestinal haemal vessel (vbw) downwards along the pharynx. (c) Communication of the ventral intestinal haemal vessel (vbw) with the oral haemal ring (orb). aao, axial part of axial organ; cmp, compass of lantern; dnb, dental haemal vessels; dnt, teeth; eph, epiphysis of the lantern; g, lumen of pharynx or intestine; orb, oral haemal ring; poc, perioral coelom; pvc, perivisceral coelom; rot, rotule of lantern; sb, spongy body; sc, stone canal; spc, somatocoelomic periahaemal outgrowth; vbv, ventral intestinal haemal vessel; vm, vertical mesentery; wc, radial water canal; wr, water ring

canal and the water ring connect (Figures 1a and 2a,b). The axocoelomic periahaemal ring does not form from the axial coelom of *S. pallidus*.

Like in other echinoderm taxa, the axial organ is represented by a system of haemocoelic lacunae in the interspaces between the coelothelia of the pericardial, axial, and perivisceral coeloms (Figures 2a, 3b, d, and 4). The axial organ is crossed by thin muscle bundles, which traverse the lacunar spaces. Special investigations of sea stars (Ezhova,

Egorova, & Malakhov, 2016b) show that the muscle bundles of the axial organ are formed by the myoepithelial cells of the coelothelium, which cross the haemocoelic spaces from one wall to the other. The contractions of these muscle bundles provide the blood flow in the axial organ. In fixed specimens, the blood is accumulated in the pericardial part of axial organ. Wide lacunae filled with light content are seen on the sections of this structure. These lacunae are separated from

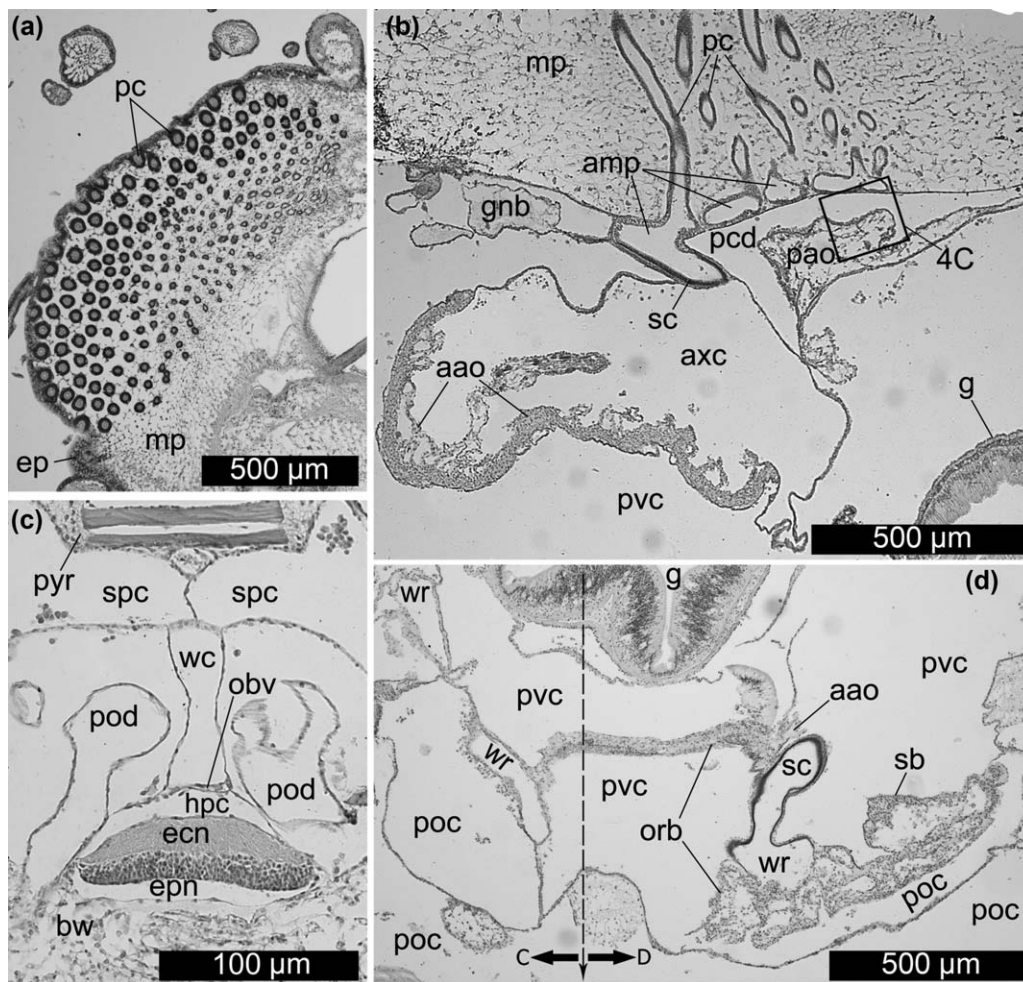


FIGURE 3 Water-vascular system of *S. pallidus*. (a) Pore canals (pc) of the madreporic plate. (b) Communication of the stone canal (sc) with the madreporic ampulla (amp); sagittal section. The frame indicates the structure shown on Figure 4c. (c) Turn of the radial water canal (wc) from the pyramid of lantern (pyr) to the radius; section in the plane perpendicular to oral-aboral axis. (d) Communication of the stone canal (sc) with the water ring (wr); section in the plane perpendicular to oral-aboral axis. The dotted arrow indicates the direction from radius A to interradius CD; the solid arrows indicate the direction to radii C and D. aao, axial part of axial organ; amp, madreporic ampulla; axc, axial coelom; bw, body wall; ecn, ectoneurial radial nerve band; ep, epidermis; epn, epineurial radial canal; g, intestine; gnb, genital haemal ring; hpc, hyponeurial canal; mp, madreporic plate; obv, radial haemal vessel; orb, oral haemal ring; pao, pericardial part of axial organ; pc, pore canals of madreporic plate; pcd, pericardial coelom; poc, perioral coelom; pod, ampullae of podia; pvc, perivisceral coelom; pyr, pyramid of chewing apparatus; sb, spongy body; sc, stone canal; spc, somatocoelomic periaemal outgrowths; wc, radial water canal; wr, water ring

each other by clearly distinguishable bundles of myoepithelial cells (Figure 4c).

The axial part of the axial organ is highly compressed in the fixed specimens, so it looks denser and darker on histological sections compared to the pericardial part (Figure 4d). Small spaces of haemocoelic lacunae are visible only on the periphery of sections of the axial organ (Figures 3b,d and 4a,b). The coelothelium covering the axial organ is different: from the axial coelom the axial part of axial organ is covered by cuboidal coelothelium 10 μm in height (Figure 4b,d), and from the perivisceral coelom it is covered by flat coelothelium of squamous cells with flattened nuclei (Figure 4b).

In addition to the connection of the axial organ with the oral haemal ring (on the oral side) and with the body wall haemocoel (on the aboral side), the haemal lacuna of the axial organ communicates with the genital haemal ring and with the haemal system of the intestine at

the site of the transition of the pericardial part to the axial part (see below).

The genital coelom (one of derivatives of the left somatocoel) is a coelomic ring adjacent to the aboral wall of the sea urchin, which surrounds the hindgut (Figure 1a). On sections perpendicular to the oral-aboral axis of the animal, the genital coelom lies in a way that the axial structures of the axial complex are between the genital coelom and the hindgut, that is, the genital coelom lies in interradius CD on the side opposite to the hindgut (Figure 5a). We note that the location of these structures in similar sections of sea stars is different: the genital coelom is between the gut and the axial structures of the axial complex (Ezhova et al., 2013).

The genital haemal ring passes within the mesentery between the genital coelom and the perivisceral coelom (Figures 1, 3b, 4a, 5b,d, and 7a,b). It communicates with the axial organ in the area between its

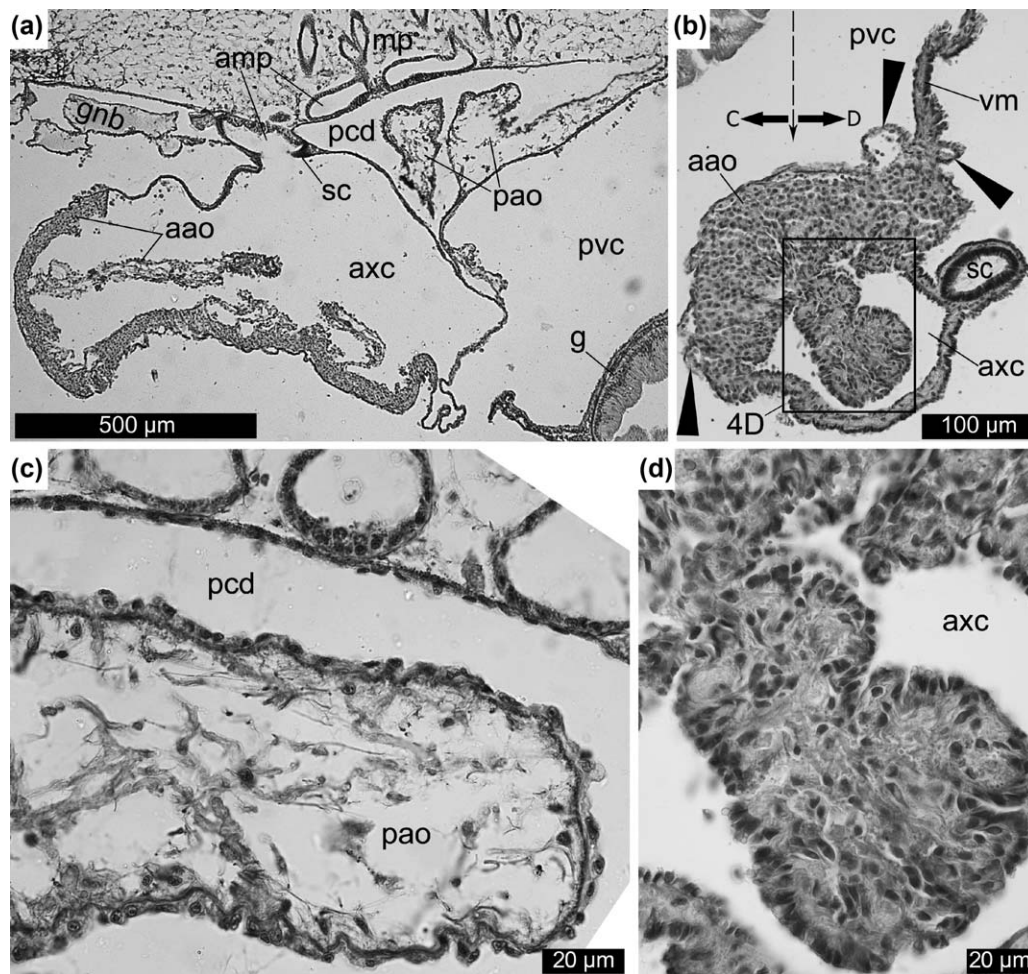


FIGURE 4 Axial coelom and pericardial coelom of *S. pallidus*. (a) Communication of the axial coelom (axc) with the madreporic ampulla (amp); sagittal section. (b) Transverse section through the axial coelom (axc) and the axial part of axial organ (aao) in their central area. The dotted arrow indicates the direction from radius A to terradius CD; the solid arrows indicate the direction to radii C and D. Triangle arrows indicate the transparent haemocoelic lacunae in the periphery of the axial part of axial organ. The frame indicates the structure shown on (d). (c) Histological structure of the pericardial part of axial organ (pao). (d) Histological structure of the axial part of axial organ (aao). aao, axial part of axial organ; amp, madreporic ampulla; axc, axial coelom; g, intestine; gnb, genital haemal ring; mp, madreporic plate; pao, pericardial part of axial organ; pcd, pericardial coelom; pvc, perivisceral coelom; sc, stone canal; vm, vertical mesentery

pericardial part and axial part (Figures 1b and 5b). The dorsal haemal vessel of intestine connects with the axial organ in the same site (Figures 1b, 5a,d, and 6).

The tubular coelomic cord is formed in the cavity of the genital coelom—the genital rachis. The coelomic cavity which lies internally along the axis of the genital rachis represents the derivative of the genital coelom (Figure 7a,c). The coelothelium of the genital rachis represents the germinative epithelium which is 100 µm thick. It consists of gonidia, growing sex cells, and accessory cells which form the vacuolated stroma of the gonad (Figure 7a,c). After maturation, the sex cells move to the cavity of the genital rachis and to the gonoduct (Figures 5b,c and 7), from where they are exit into the environment (Figure 5c). The gonoduct walls consist of tall columnar flagellated cells (Figure 7d,e).

From the outside, the gonad is covered by the coelothelium of the perivisceral coelom. The haemocoelic space of the gonad haemal lacuna is located between the basal membrane of this coelothelium and the basal membrane of the germinative epithelium (Figure 7a–c). It

is filled by blood from the genital haemal ring, which is surrounded by the genital coelom (Figure 7a,b).

The perioral (or peripharyngeal) coelom of *S. pallidus* (another derivative of the left somatocoel) is located in the oral half of the animal's body and surrounds the pharynx. It has an intricate shape; it protrudes into the internal grooves of pyramids, into the spaces between the pyramids, encloses the teeth, that is, envelops the numerous calcareous elements of the lantern (Figures 1a, 2, and 8b–e).

The perioral coelom is surrounded by the perivisceral coelom (fused hypogastric and epigastric coeloms, that is, a part of the left somatocoel and the whole right somatocoel) from the sides and aboral part (Figure 2). On the level of the lantern compasses, the oral haemal ring passes within the circumoral mesentery between the perivisceral and perioral coeloms (Figures 1b, 2b,c, and 3d). The ventral intestinal haemal vessel starts from the oral haemal ring in radius A and ascends along the pharynx to the aboral side of the animal, accompanying the intestine (Figures 1b, 2a,b, and 6) and branching into a network of

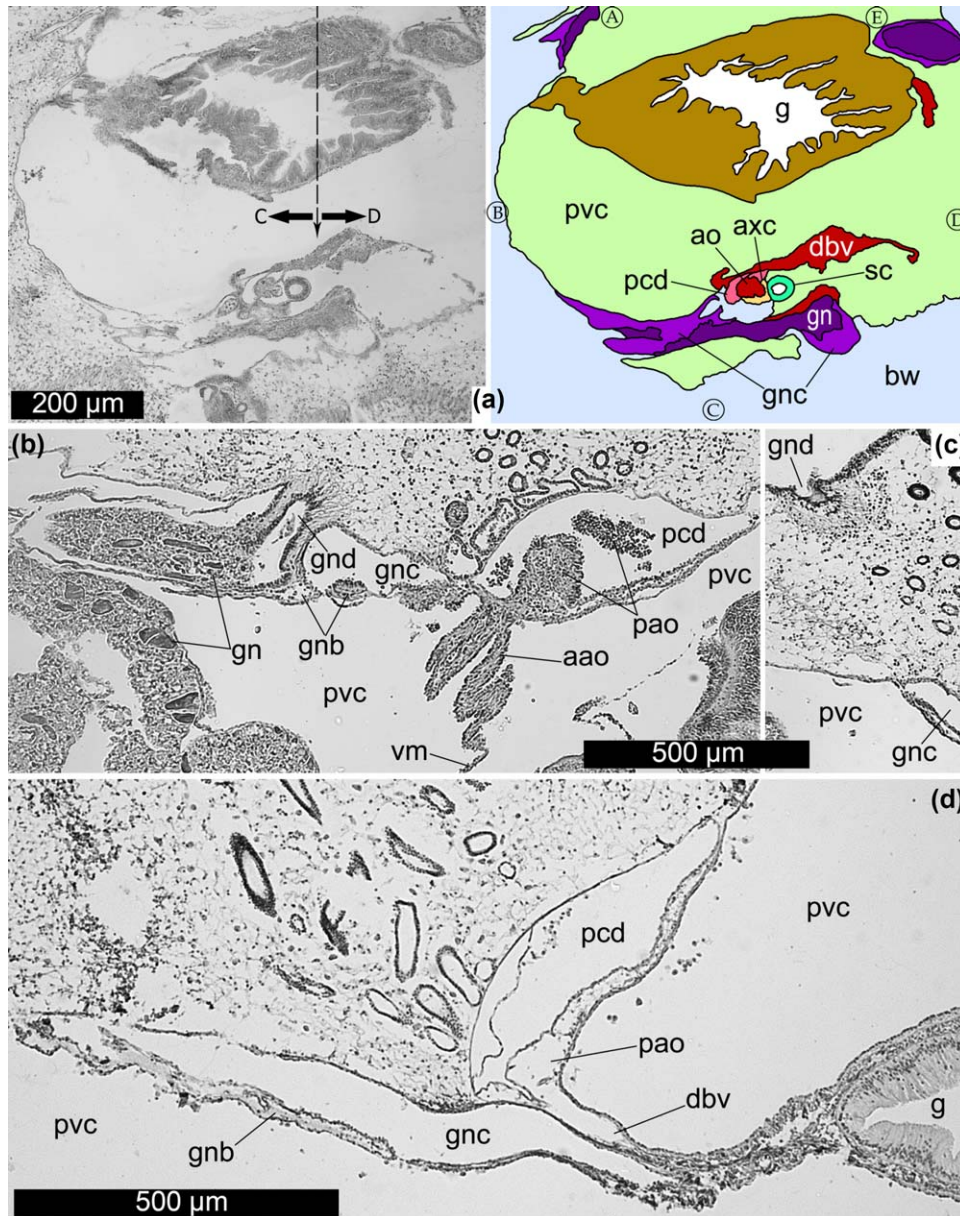


FIGURE 5 Location of the genital coelom and gonads of *S. pallidus*. (a) Relative position of the genital coelom (gnc), axial structures of axial complex, and hindgut (g); section in the plane perpendicular to oral-aboral axis. The dotted arrow indicates the direction from radius A to interradius CD; the solid arrows indicate the direction to radii C and D. Capital letters indicate the radii. (b) Communication of the genital haemal ring (gnb) with the axial organ between its axial part (aao) and pericardial part (pao); sagittal section. (c) Communication of the gonoduct (gnd) with the environment; sagittal section. (d) Communication of the genital haemal ring (gnb) with the pericardial part of axial organ (pao) and the dorsal intestinal haemal vessel (dbv). aao, axial part of axial organ; ao, axial organ; axc, axial coelom; bw, body wall; dbv, dorsal intestinal haemal vessel; g, intestine and hindgut; gn, gonad; gnb, genital haemal ring; gnc, genital coelom; gnd, gonoduct; pao, pericardial part of axial organ; pcd, pericardial coelom; pvc, perivisceral coelom; sc, stone canal; vm, vertical mesentery

intestinal capillaries. The dorsal haemal vessel arises from this network of intestinal capillaries and flows into the axial organ between its axial and pericardial parts (Figures 1b, 5a,d, and 6). The oral haemal ring forms the capillary tufts in each interradius forming the spongy bodies (Figures 1b, 2b, and 3d).

The somatocoelomic periaemal ring of *S. pallidus* (also a derivative of the left somatocoel) lies in the most oral region of the body. Here, it surrounds the chewing apparatus and is adjacent to the perioral coelom (Figures 1a and 8b). A pair of coelomic outgrowths springs from the

comatocoelomic periaemal ring into each radius. They extend in the aboral direction and accompany the radial haemal vessel as part of the radial complex of organs (Figures 1a, 3c, and 8b–g).

The complicated structure of the radial complex of *S. pallidus* is caused by the development of a massive chewing apparatus in sea urchins. The water ring and the somatocoelomic periaemal ring, which both give rise to outgrowths into the radii, are located at a significant distance from each other along the oral–aboral axis of the animal due to the expanded pyramids of the lantern (Figures 1a and 8f).

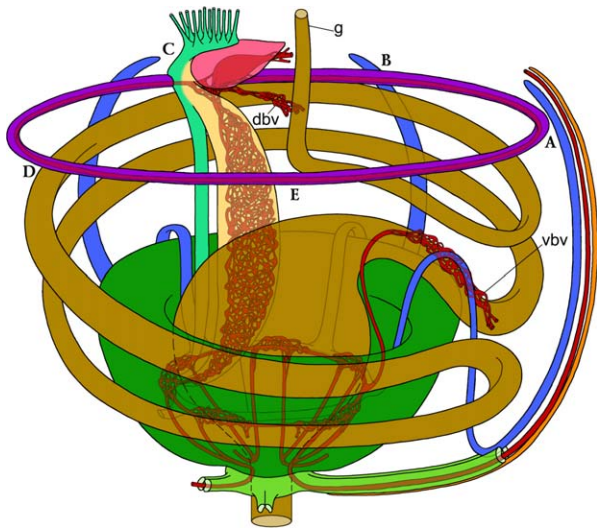


FIGURE 6 Beginning of the ventral intestinal haemal vessel (vbv) in the radius A, and flowing of the dorsal intestinal haemal vessel (dbv) into the axial organ between its pericardial and axial parts. Capital letters indicate the radii. Designations for other structures see on Figure 1. dbv, dorsal intestinal haemal vessel; g, hindgut; vbv, ventral intestinal haemal vessel

Most structures of the radial complex start in the most oral region of the body of *S. pallidus*. Here, one radial nerve continues into each radius, arising from a circumoral nerve ring (Figure 8c,f). The radial nerves (and

the oral nerve ring) are accompanied by epineural canals from the outside (Figure 8a,d,e,g). The epineural canals are parts of the environment that have been enclosed during the ontogenesis (MacBride, 1903; Goldschmid, 1996). On the opposite side, the radial nerve is accompanied by a hyponeural canal (Figure 8a,d–g). There is no hyponeural circumoral ring, and the hyponeural canals are specific only to the radial complex.

The radial nerve of *S. pallidus* includes only an ectoneural band (Figure 8a,g). It is represented by a thickening of the inner wall of the epineural canal. The perikarya of the ectoneural band are concentrated near the lumen of the epineural canal, that is, outwards from the neuropil. The thickness of the neuropil exceeds 20 μm. The hyponeural canal is adjacent to it from the inner side (Figure 8a,f,g). In contrast to sea cucumbers, in which the radial nerve includes both ectoneural and hyponeural bands (Gerould, 1896; Smiley, 1994; Mashanov, Zueva, Heinzeller, & Dolmatov, 2006; Mashanov, Zueva, & García-Arrarás, 2013; Díaz-Balzac, Lázaro-Peña, Vázquez-Figueroa, Díaz-Balzac, & García-Arrarás, 2016; Dolmatov, Ginanova, & Frolova, 2016; Ezhova et al., 2017), there is no radial hyponeural band in sea urchins. The epineural radial canals connect with the circumoral epineural ring adjacent to the oral nerve ring from the inferior (oral) side (Figure 8c).

Each radial nerve and its hyponeural canal is accompanied on the sides by paired outgrowths of the somatocoelomic perihæmal coelom and perivisceral coelom (Figure 8c–g). Within the cavities of the latter, there are coelomic vesicles clearly visible on the histological sections

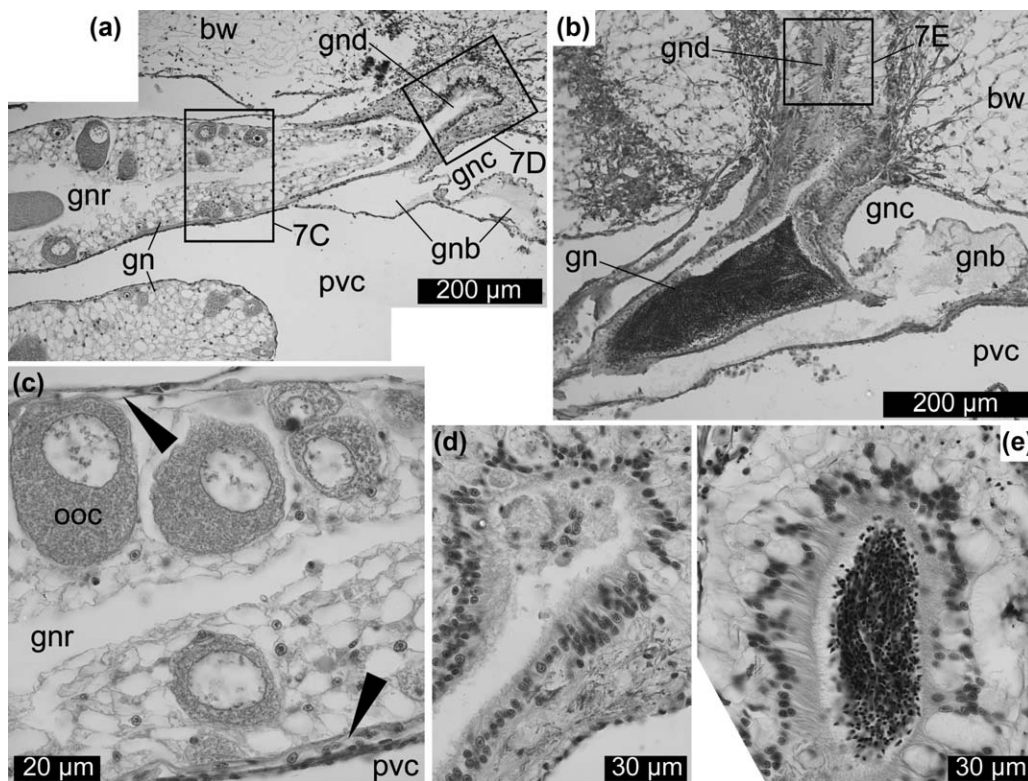


FIGURE 7 Structure of the gonads of *S. pallidus*; sagittal sections. (a) Female gonad. The frames indicate the structure shown on (c,d). (b) Male gonad. The frame indicates the structure shown on (e). (c) Section through the wall of the female gonad. Triangle arrows indicate the haemocoelic space of the gonad haemal lacune. (d) Longitudinal section through the female gonoduct. (e) Longitudinal section through the male gonoduct, within the lumen of which the nuclei of sperms are visible. bw, body wall; gn, gonad; gnb, genital haemal ring; gnc, genital coelom; gnd, gonoduct; gnr, cavity of genital rachis; ooc, oocyte; pvc, perivisceral coelom

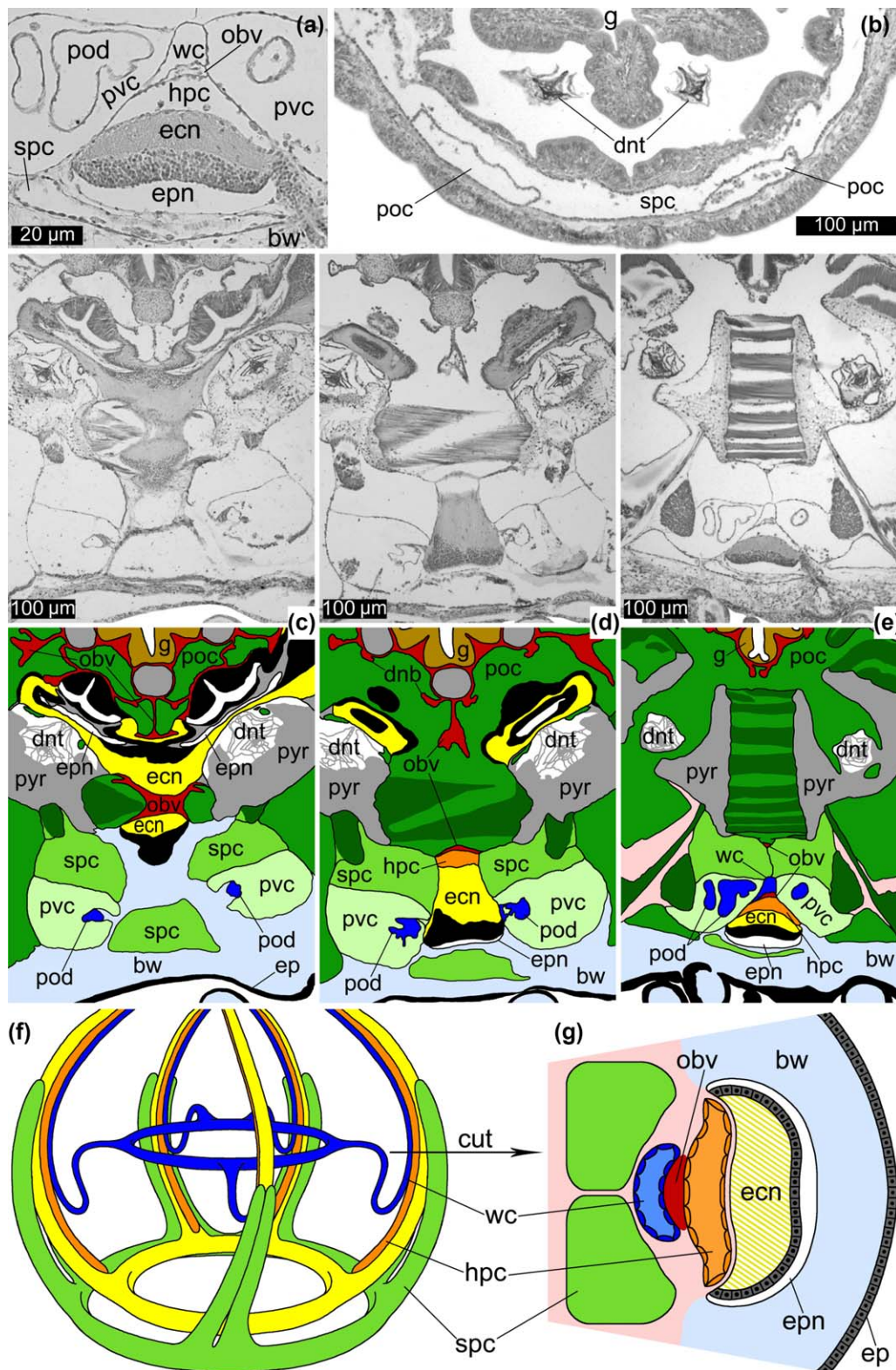


FIGURE 8 Radial complex of *S. pallidus*. (a) Transverse section through the main structures of radial complex (fragment of panel e). (b–e) Section in the plane perpendicular to oral-aboral axis from oral side of the animal to aboral side. Muscles of the chewing apparatus are colored dark-green. (b) Somatocoelomic periahaemal ring (spc) in the most oral area of the animal body. (c) Springing of the radial nerve from the oral nerve ring (ecn) accompanied by the radial haemal vessel (obv). (d) Appearance of the hyponeural canal (hpc). (e) Appearance of the radial water canal (wc). (f, g) Scheme of the relations between the somatocoelomic periahaemal coelom (spc), water ring, nerves, and hyponeural canals (hpc): around the pharynx (f) and in the radius (g). bw, body wall; dnb, dental haemal vessels; dnt, teeth; ecn, oral nerve ring and ectoneural radial nerve band; ep, epidermis; epn, epineural radial and ring canals; g, lumen of pharynx; hpc, hyponeural canal; obv, radial haemal vessel; poc, perioral coelom; pod, ampullae of podia; pvc, outgrowths of the perivisceral coelom; pyr, pyramid of chewing apparatus; spc, somatocoelomic periahaemal ring and its outgrowths; wc, radial water canal

which are ampullae of the podia (Figure 8a,c–e). However, the water radial canal is included in the radial complex more aborally than all other radial structures (Figures 1a, 3c, and 8e,f) as it goes around the pyramids of the lantern from the aboral side. The water radial canal adjoins to the hyponeural canal from the inner side (Figure 8a,e–g).

As noted above, the oral haemal ring is located along the water ring in the middle part of the body of *S. pallidus* (Figure 1). The radial haemal vessels starting from the oral haemal ring do not accompany the radial water canals in their proximal parts but run downward along the teeth (the dental haemal vessels), to the oral nerve ring (Figures 1b, 2c, and 8c–e). Here, they accompany the radial nerves passing between the epithelia of the somatocoelomic periaemal radial outgrowths, perioral coelom, and the hyponeural canal (Figure 8c,d). After the radial water canals become part of the radial complex, the radial haemal vessels lie between them and the hyponeural canals (Figure 8a,d,e,g).

4 | DISCUSSION

4.1 | Inaccuracies and inconsistencies in descriptions of the echinoid axial complex of other authors

Like with the other taxa of Eleutherozoa, some inaccuracies and inconsistencies have accumulated over the past 150 years of studying the anatomy of the sea urchins and persist in descriptions of the echinoid axial complex and associated structures. These inconsistencies complicate the understanding of the results. The terminological inconsistencies are shown in Table 1, and here we largely focus on the actual discrepancies of data from different papers.

Hamann (1887) notes in his histological study, that the «body of (the) axial gland» is covered by a mesh of haemal spaces. Additionally, he indicates that the axial organ communicates with the lumen of the stone canal. However, the coelom cannot communicate with the haemocoel due to the current knowledge about the nature of these two internal cavities. We can only assume that Hamann mistook the axial coelom for the «body of (the) axial gland»: the axial coelom does actually connect with the madreporic ampulla together with the stone canal. The mesh of the haemal spaces mentioned by Hamann, possibly, corresponds to the peripheral lacunae of the axial organ filled with blood, which are sometimes visible on the histological sections (see for example Figures 3b and 4a,b).

MacBride (1903) in his work about the development of *Echinus esculentus* labels a rudiment of the pericardial coelom as the «right hydrocoel» (MacBride, 1903, p. 299). The origin of the pericardial coelom from the right hydrocoel was also proposed by MacBride for sea stars (MacBride, 1896) and for brittle stars (MacBride, 1892, 1907). Other authors, starting with Bury (1895), suggested that the echinoderm pericardial coelom originates from the right axocoel of the larva (Fedotov, 1923, 1924, 1966; Hyman, 1955; Ivanova-Kazas, 1978; etc.).

Hyman (1955), based on the works primarily related to the 19th century (Hamann, 1887; Leipoldt, 1893; Chadwick, 1900) reports, that the axial coelom (left axocoel) is lacking in sea urchins, while there is a well-defined axial organ («axial gland»), «not enclosed in any coelomic cavity», but «containing an extremely irregular cavity that ends blindly

in the oral direction and represents a coelomic cavity, that of the right axocoel» (Hyman, 1955, p. 473). Additionally, she emphasized, that the lumen of the axial organ is lined by a coelomic epithelium. However, the cavity within the axial organ, which Hyman describes, is actually the axial coelom, that is, the derivation of the left axocoel, not the right one. According to our data, it is a relatively narrow tube, which ends blindly on the oral end. The presence of the axial coelom derived from the left axocoel in sea urchins is confirmed by other authors (Cuénot, 1948; Goldschmid, 1996; Ziegler et al. 2009). We assume that the axial coelom has gone unnoticed in the works of some earlier researchers because its cavity is significantly decreased due to the growth of the axial organ.

Cuénot (1948) marks the aboral part in the echinoid axial organ as the «processus terminal», located in a closed coelomic vesicle («le sinus terminal»), which presumably originates from the «right anterior entero-coel» («vésicule entérocoélie (droite antérieure?)») (Cuénot, 1948, p. 155). Hyman, describing «the aboral end of the axial gland», that is, the pericardial part of the axial organ, indicates that it ends blindly within the right axocoel (i.e., within the pericardial coelom). This conclusion is based on the work of Leipoldt (1893). However, according to our data, the pericardial part of the axial organ does not end blindly but opens into the haemocoelic space of the body wall. According to data of Cuénot (1948, pp. 154–155), the aboral (i.e., pericardial) part of axial organ can slowly contract. In opinion of Cuénot, this indicates the role of this structure in echinoid blood («liquide lacunaire») circulation.

MacBride (1903, p. 305) describes five coelomic «dental-sacs» detached from the left somatocoel and that they «correspond in position and origin to the five rudiments of the perihæmal system of canals described ... in the larva of *Asterina gibbosa* (see MacBride, 1896), ... from them are derived the radial perihæmal canals of the adult urchin». These coelomic cavities soon become completely closed. However, on the figure showing the histological section of a young sea urchin (MacBride, 1903, Pl. 15, fig. 54), both hyponeural canals and somatocoelomic perihæmal canals are marked as «perihæmal canals». Possibly, MacBride assumed, that the radial hyponeural canals and somatocoelomic perihæmal coeloms of the sea urchins originate from the same coelomic rudiments, separating from the «dental-sacs», which in turn detach from the left somatocoel. According to our data, in adult sea urchins, the hyponeural canals and the somatocoelomic perihæmal canals represent separate structures that do not communicate with each other. The growing «dental-sacs» form a cavity, which MacBride refers to as the «lantern-coelom» (and we describe as the perioral coelom). MacBride considers the «lantern-coelom» and the «outer perihæmal ring» (i.e., the somatocoelomic perihæmal coelom) of asteroids to be homologous, as these structures form in both sea urchins and sea stars from five separate rudiments detaching from the left somatocoel (MacBride, 1903, p. 314, 318). Ubisch (1913), similarly to MacBride, reported about a single perihæmal ring in sea urchins originating from the left somatocoel and homologous to the somatocoelomic (outer) perihæmal ring of sea stars.

According to our data, both the perioral and the somatocoelomic perihæmal ring are present in adult sea urchins (only one of these two rings, the latter, gives rise to the radial outgrowths). This situation

occurs in some sea stars (Ubaghs, 1967; Ivanova-Kazas, 1978). Only one of these two rings (the somatocoelomic periaemal ring) in asteroids gives rise to the radial outgrowths into the rays. In other sea stars, for example *Asterias rubens*, there is only one coelomic ring (Gemmill, 1914, 1915; Ezhova et al., 2013). As it sends radial outgrowths into the rays, we can consider it to be homologous with the somatocoelomic periaemal ring of sea urchins. The perioral ring of sea stars, according to the data of Goto obtained by studying of *Asteracanthion pallidus* A. Agassiz, 1866 (earlier—*Asterias pallida*, see Goto, 1896), originates during the ontogenesis from the left somatocoel, but after that fuses again with the hypogastric coelom. Incidentally, in the Lang's textbook from the same year, it is indicated that the perioral coelom is lacking in sea stars (Lang, 1896, pp. 441–443).

4.2 | Comparison of organization of the axial complex of organs and associated structures and systems in different sea urchins and other Eleutherozoa

In some clypeasteroids, a single madreporic pore (hydropore) is retained throughout the whole life (Mortensen, 1948), while in the vast majority of sea urchins the number of madreporic pores increases during the life (Hyman, 1955). In brittle stars, on the contrary, a single madreporic pore is characteristic for most families of this taxon. However, in euryalids and in some families of Ophiurida (Ophiuridae—*Ophiocent hastatum* Lyman, 1878; Ophiomyxidae—*Ophioscolex glacialis* Müller & Troschel, 1842; Ophiacanthidae—*Ophiocamax patersoni* Martynov & Litvinova, 2008; Ophionereididae—*Ophionereis schayeri* Müller & Troschel, 1844; Amphiuroidae—*Amphiura diomedea* Lütken & Mortensen, 1899), there are several pores (Ezhova, Malakhov, & Martynov, 2016). In some species of Gorgonocephalidae the number of pores reaches 250 (Ludwig, 1878). In sea cucumbers the madreporite is sunk into the body, and the water-vascular system does not communicate with the environment in most species. In elasipodids and some apodids (Chiridotidae) and molpadids (*Molpadia violacea* Studer, 1876), one pore canal arises from the madreporite and opens into the environment via a single pore (Théel, 1882; Lang, 1896; Hyman, 1955; Erber, 1983b; Ezhova et al., 2017). In *Parastichopus tremulus* (Gunnerus, 1767) from the order Aspidochirota and in *Molpadia oolitica* (Pourtalès, 1851) from the order Molpadida, the madreporic ampulla opens into the environment via several pores (Erber, 1983b, p. 306). The madreporite of Asteroidea bears numerous pores (Lang, 1896; Hyman, 1955); the only exception is the relatively recently described *Xyloplax* (Concentricycloidea), the madreporite of which looks like a larval hydropore (Rowe, Baker, & Clark, 1988; Janies & Mooi, 1998).

A peculiarity of the coelomic system of representatives of the order Cidaroida and the family Echinothuriidae, taxon Echinothurioida, is that the perioral (peripharyngeal) coelom forms five extensive pockets in the radii growing into the perivisceral coelom, which are known as Stewart's organs (Stewart, 1879; Sarasin & Sarasin, 1888). In most Irregularia the perioral coelom is greatly reduced (Hyman, 1955). Perhaps this is due to the reduction of the lantern in Irregularia.

The genital coelomic ring in Irregularia often fuses with other coelomic rings of the aboral side of the body, specifically with the

periproctal and perianal coeloms (Hyman, 1955). In this case, a common coelomic ring is formed, the so-called aboral coelom, which is characteristic only for Irregularia. Such a coelom is absent in Regularia, and three separate coelomic rings correspond to it: the genital ring, periproctal ring, and perianal ring. Thus, the aboral coelomic ring of Irregularia is not to be confused with the «aboral sinus». The term «aboral sinus» is used by some authors (e.g., MacBride, 1903; Cuénot, 1948; Hyman, 1955) to indicate the genital coelom (see Table 1).

In Regularia there are five interradial gonads, extending along the interradial on the aboral side of the animal (Mortensen, 1943). In most Irregularia there are only four gonads, «as the retreat of the periproct along interradius AB usually destroys the gonad of that interradius» (Hyman, 1955). Some species of Spatangoida (Irregularia) belonging to the genera *Abatus*, *Schizaster*, and *Lovenia* have only three gonads, due to the lacking of the gonad in CD interradius. Finally, in *Schizaster canaliciferus* (Lamarck, 1816), only two gonads remain as there is no gonad in the DE interradius (Koehler, 1883).

The oral haemal ring of sea urchins and sea cucumbers (Figure 9) lies between the water ring and the perioral ring (Cuénot, 1948; Ezhova et al., 2017; our data, see Figure 1). In sea stars and brittle stars, the oral haemal ring lies between the special periaemal rings—axocoelomic and somatocoelomic (Hayashi, 1935; Cuénot, 1948; Ezhova et al., 2013; Ezhova, Lavrova, & Malakhov, 2014; Ezhova et al., 2015). The water ring and the perioral ring are also present in sea stars and brittle stars; however, they do not closely adjoin to each other like in sea urchins and sea cucumbers but lie on a significant distance from each other (Figure 9). Therefore, perhaps, the perioral coelom of sea stars and brittle stars is not homologous to the perioral (or peripharyngeal) coelom of sea urchins and sea cucumbers. On the other hand, the topographic differences of the perioral coeloms can be the result of their growth to supply the massive chewing (in Echinoidea) or tentacular (in Holothuroidea) apparatus.

The differences in the coelomic structures associated to the oral haemal ring are related to the differences between the radial complex (Figure 10). In sea stars and brittle stars the radial haemal vessels lie between the paired radial somatocoelomic periaemal outgrowths, which are laterally adjacent to the vessel (Hamann, 1889; Hayashi, 1935; Smith, 1937; Ubaghs, 1967; Ezhova et al., 2013, 2014, 2015). In sea urchins and sea cucumbers, however, each radial haemal vessel lies between the radial water canal and the hyponeural canal, which are adjacent to the vessel from the inside and outside, respectively (Cuénot, 1891; Ubaghs, 1967; Smiley, 1994; Mashanov et al., 2006; Mashanov et al., 2009; Mashanov et al., 2013; Díaz-Balzac et al., 2016; Dolmatov et al., 2016; Ezhova et al., 2017; our data). In sea urchins, the radial haemal vessel lies between the paired somatocoelomic periaemal outgrowths only at the very beginning, where it starts from the oral haemal ring (Figure 1).

Another difference of the haemal system of the axial complex between different Eleutherozoa is the structure of the gastric haemal ring (Figure 11). In sea stars and brittle stars the gastric haemal ring lies within the mesentery between the hypogastric and epigastric coeloms, surrounds the extensive stomach and connects with the axial organ between the pericardial and axial parts via gastric

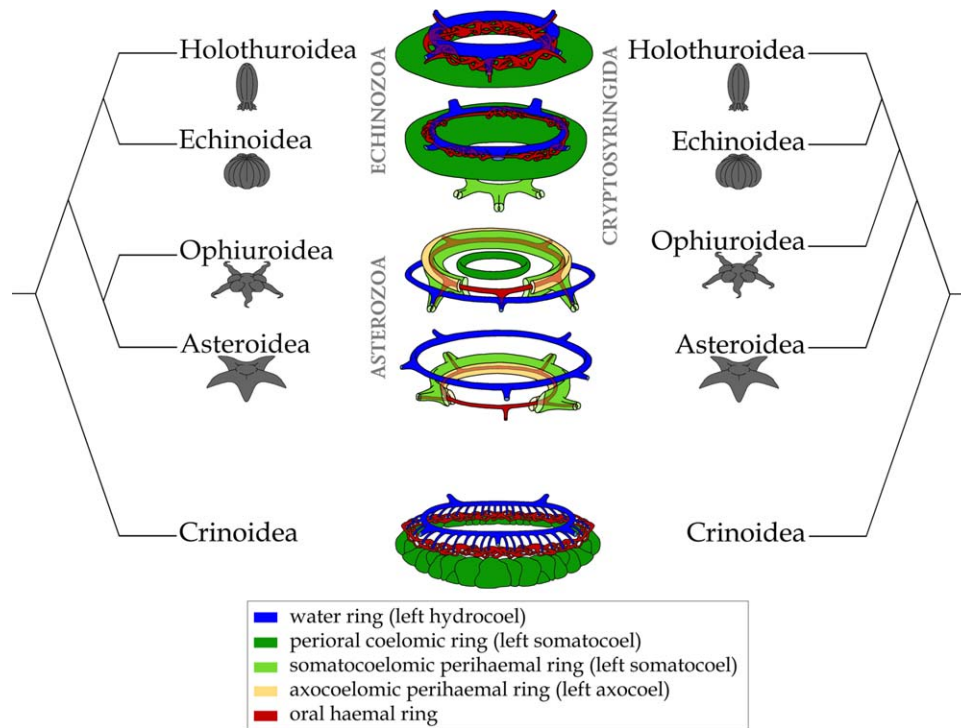


FIGURE 9 Location of the oral hæmal ring in different taxa of Echinodermata. (Two competing hypotheses for the relationships of extant echinoderm classes are from Janies, Voight, and Daly, 2011. The crinoid condition is depicted after Heinzeller & Welsh, 1994, and our unpublished data)

haemal tufts (Cuénot, 1901; Ubaghs, 1967; Ezhova et al., 2013, 2015; Ezhova, Egorova, & Malakhov, 2016a). In sea urchins and sea cucumbers, the gastric hæmal ring itself is missing. The hypogastric

and epigastric coeloms of these animals are fused into a general perivisceral coelom and the continuous mesentery between them does not remain. Also, an extensive stomach does not develop in

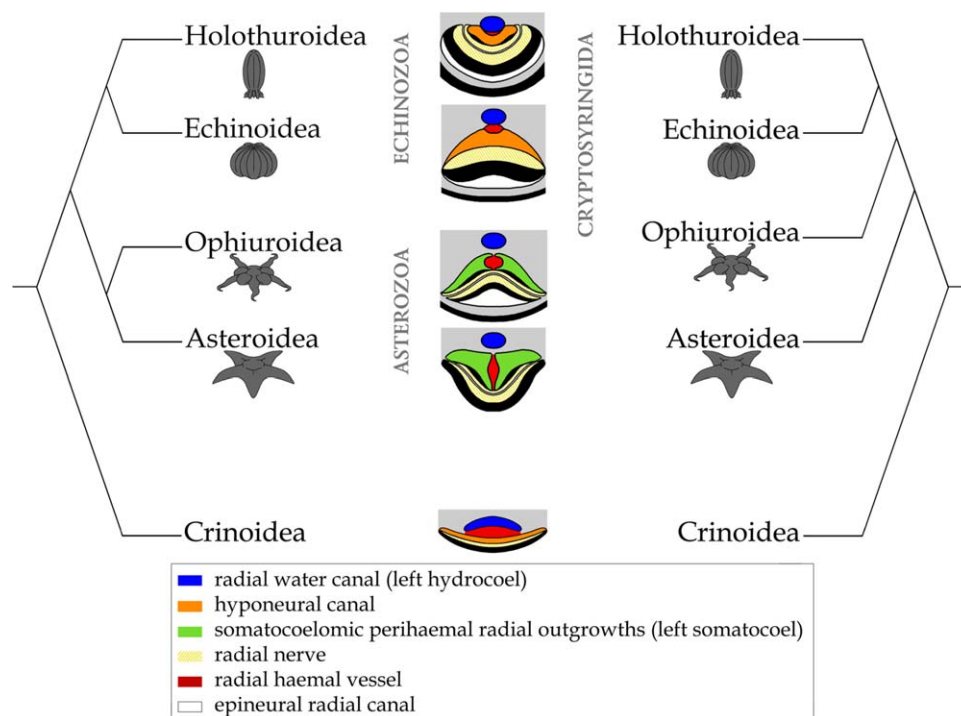


FIGURE 10 Organization of the radial complex in different taxa of Echinodermata—schematic transverse sections through the oral part of the radius (two competing hypotheses for the relationships of extant echinoderm classes are from Janies et al. 2011. The crinoid condition is depicted after Ubaghs, 1967; Heinzeller & Welsh, 1994; Ruppert et al., 2004)

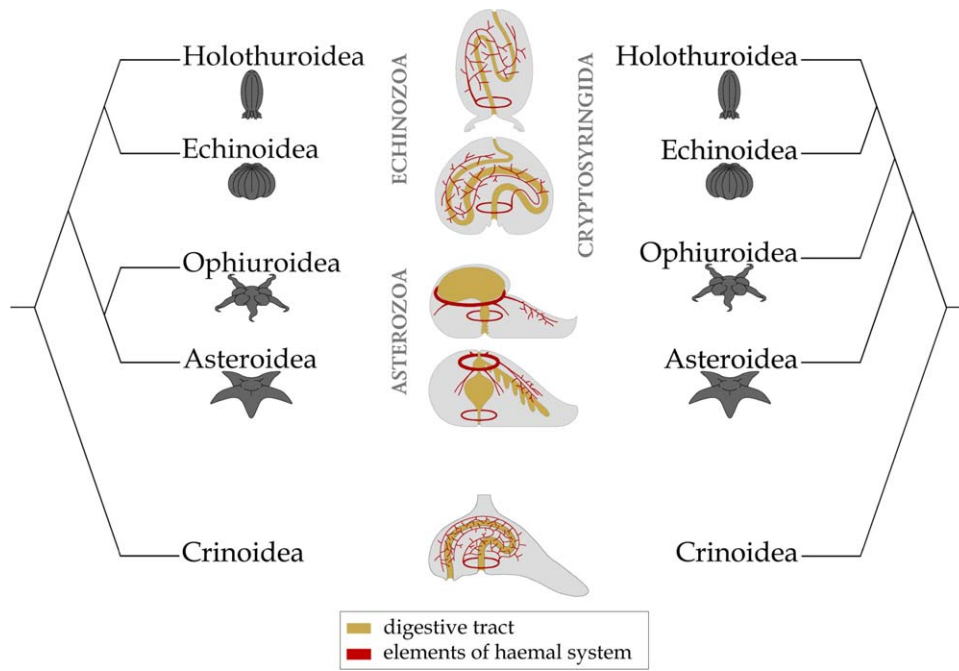


FIGURE 11 Intestinal haemal system in different taxa of Echinodermata (two competing hypotheses for the relationships of extant echinoderm classes are from Janies et al., 2011. The crinoid condition is depicted after Hyman, 1955; Heinzeller & Welsh, 1994; Ruppert et al., 2004)

echinoids and holothuroids. Instead, there is a long, curved intestine. Instead of the gastric haemal vessel, a system of thin haemal capillaries and lacunae develops along the intestine of sea urchins and sea cucumbers—the intestinal haemal plexus, which includes the *rete mirabile* of holothuroids (Ludwig, 1889; Kawamoto, 1927; Sivickis & Domantay, 1928) or the marginal intestinal vessels of sea urchins

(Perrier, 1875; Koehler, 1883; Bonnet, 1925). Additionally, despite the lack of gastric haemal tufts in echinoids and holothuroids, the intestinal haemal plexus communicates with the axial haemal structures of the axial complex. In holothuroids the intestinal haemal vessels are connected through a haemal lacuna of the stone canal and the haemal system of the gonad (Ezhova et al., 2017). In sea

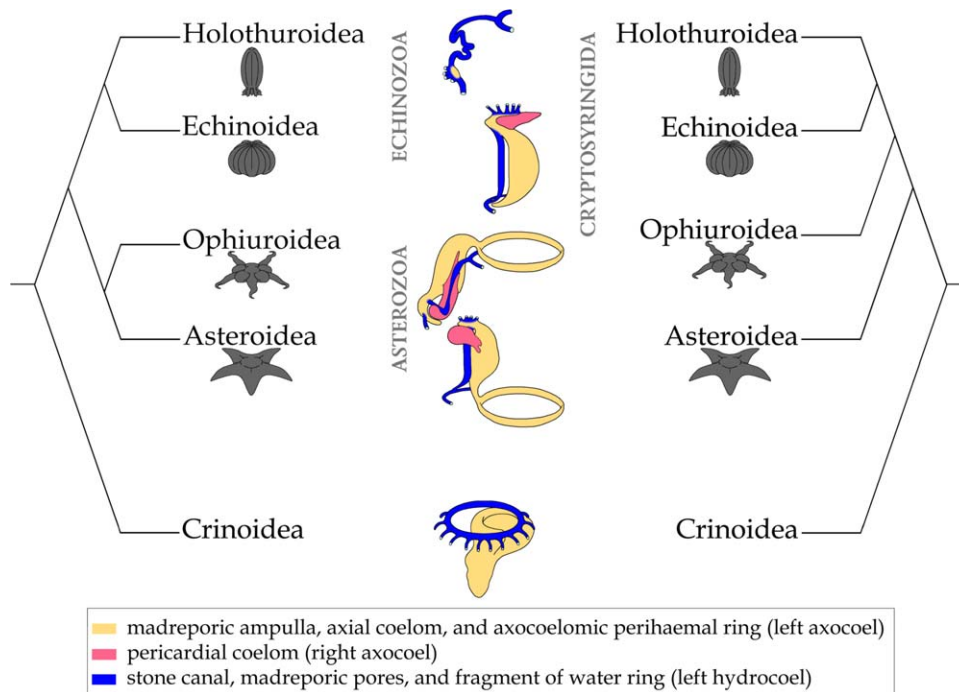


FIGURE 12 The axocoel derivatives in different taxa of Echinodermata (two competing hypotheses for the relationships of extant echinoderm classes are from Janies et al., 2011. The crinoid condition is depicted after Heinzeller & Welsh, 1994; Ruppert et al., 2004; our unpublished data)

urchins, the dorsal haemal vessel opens into the axial organ between its pericardial and axial parts.

In sea stars and brittle stars, the axial coelom gives rise to the axocoelomic perihemal ring (Hayashi, 1935; Cuénot, 1948; Ezhova et al., 2013, 2015, 2016a). In sea urchins and sea cucumbers, the axocoelomic ring is lacking (Figure 12). However, in sea urchins, the axial coelom is present; it descends on the oral side and ends blindly (Cuénot, 1948; Goldschmid, 1996; Ziegler et al., 2009; our data, see Figure 1). In sea cucumbers, its only remnant is the madreporic ampulla (Erber, 1983a,b; Balsler, Ruppert, & Jaekle, 1993). Regarding derivations of the right axocoel (Figure 12), in holothuroids, the pericardial coelom is fully absent. In sea urchins, the pericardial coelom is present, but does not form any interdigitations with the axial coelom, and as a result the pericardial part of axial organ is significantly less developed in sea urchins than in sea stars and brittle stars.

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CONFLICT OF INTEREST

The authors declare that they have no financial or otherwise conflict of interest. All authors read and approved the final manuscript. All the colleagues who are acknowledged as having contributed to the work have agreed to having their names mentioned in the paper.

AUTHOR CONTRIBUTIONS

The author contribution is equal in all aspects of the work.

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