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Axial complex of Crinoidea: Comparison with other Ambulacraria

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Abstract

The anatomy of Crinoidea differs from that of the other modern echinoderms. In order to see, whether such differences extend to the axial complex as well, we studied the axial complex of *Himerometra robustipinna* (Himerometridae, Comatulida) and compared it with modern Eleutherozoa. The axial coelom is represented by narrow spaces lined with squamous coelothelium, and surrounds the extracellular haemocoelic lacunae of the axial organ. The latter is located, for the most part, along the central oral-aboral axis of the body. The axial organ can be divided into the lacunar and tubular region. The tubular coelomic canals penetrating the thickness of the axial organ have cuboidal epithelial lining, and end blindly both on the oral and aboral sides. The axial coelom, perihaemal coelom, and genital coelom are clearly visible, but they connect with the general perivisceral coelom and with each other via numerous openings. The haemocoelic spaces of the oral haemal ring pass between the clefts of the perihaemal coelom, and connect with the axial organ. In addition, the axial organ connects with intestinal haemal vessels and with the genital haemal lacuna. Numerous thin stone canaliculi pierce the spongy tissue of the oral haemal ring. They do not connect with the environment. On the oral side, each stone canaliculus opens into the water ring. The numerous slender tegmenal pores penetrate the oral epidermis of the calyx and open to the environment. Tegmenal canaliculi lead into bubbles of the perivisceral coelom. Some structures of the crinoid axial complex (stone canaliculi, communication between different coeloms) are numerous whereas in other echinoderms these structures are fewer or only one. The arrangement of the circumoral complex of Crinoidea is most similar to Holothuroidea. The anatomical structure and histology of the axial complex of Crinoidea resembles the “heart-kidney” of Hemichordata in some aspects.

KEYWORDS
axial organ, circumoral complex, coelom, haemal system, pericardial coelom

1 | INTRODUCTION

Crinoids is the sister group to all other echinoderms, which are united into the group Eleutherozoa (Ax, 2001; Littlewood, Smith, Clough, & Emson, 1997; Reich, Dunn, Akasaka, & Wessel, 2015; Smith, 1984). Crinoidea diverged from their common ancestor with other echinoderms approximately 500 million years ago (Ivanova-Kazas, 1978; Ubaghs, 1967; Wright, 2017) and they possibly retain numerous characters inherited from the last common ancestor of Echinodermata; however, the crown groups of echinoderm classes are considerably younger than this age (Rouse et al., 2013), and the morphological form in extant crinoids differs in many important ways from

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stem group crinoids (Heinzeller & Fechter, 1995; Wright, Ausich, Cole, Peter, & Rhenberg, 2017).

Crinoids clearly differ from Eleutherozoa by a number of features. They are sedentary animals. Their oral side faces up, not down. They lack a madreporic plate, per se, and almost the entire oral side of the calyx is pierced by numerous pores. The CD interradius is identified by the so-called anal cone, on the top of which the anus opens (the larval hydropore opens in the same interradius; Hamann, 1889; Reichensperger, 1905). The right (aboral) somatocoel of crinoids is developed to a much greater extent than the left (oral) somatocoel (Breimer, 1978; Ivanov, Polyanskii, & Strelkov, 1985; Ivanova-Kazas, 1978). However, according to other authors, it is just the other way around and the left somatocoel is developed to a greater extent than the right somatocoel (e.g., Cuénot, 1948). Some researchers point out that the prevalence of one somatocoel over the other is still unclear (Heinzeller & Welsch, 1994). In accordance to the pentameric symmetry, five outgrowths extend from the right somatocoel to the aboral side, which form the so-called chambered organ (Bury, 1888; Seeliger, 1892).

The axial complex of Eleutherozoa (except Holothuroidea) consists of the following main organs: axial coelom + madreporic ampulla (derivatives of the left axocoel), pericardial coelom (derivative of the right axocoel), axial organ, which consists of an axial part (a mesh of the haemocoelic spaces between the folds of the coelothelium of the axial coelom) and a pericardial part including a heart (a haemocoelic vesicle and capillaries surrounded by the coelothelium of the pericardial coelom), and calcareous stone canal, which supports the soft organs of the axial complex and communicates with the water ring at the oral end and with the madreporic ampulla and the environment at the aboral end. The axial complex is morphologically and functionally associated with the gonads and genital haemal ring, with the perihaemal coeloms and the oral haemal ring, with the intestinal vessels, with the perioral coelom, and with the nerve structures associated with the perihaemal coeloms and epineural canals (Cuénot, 1948; Erber, 1983a, 1983b; Ezhova, Ershova, & Malakhov, 2017; Ezhova, Lavrova, Ershova, & Malakhov, 2015; Ezhova, Lavrova, & Malakhov, 2013, 2014; Ezhova, Malakhov, & Egorova, 2018; Hyman, 1955; Ivanov et al., 1985; Ziegler, Faber, & Bartolomaeus, 2009). In Holothuroidea, the left and right axocoels are reduced, so the axial complex retains only the madreporic ampulla and the stone canal surrounded by the haemal lacuna, which connects with the genital haemal lacuna, with the oral haemal ring, and with the intestinal vessels (Balser, Ruppert, & Jaeckle, 1993; Erber, 1983a, 1983b; Ezhova et al., 2017).

Focusing on the central structures of the crinoid axial complex, it can be noted that adult crinoids lack, for example, a single stone canal. In Eleutherozoa, the stone canal acts as the supporting axis for the central structures of the axial complex and develops from the larval coelomoduct connecting the left axocoel with the left hydrocoel (Gemmill, 1914; MacBride, 1907; Narasimhamurti, 1933; Ubisch, 1913). As shown in the crinoid *Antedon*, the stone canal of attached juveniles forms in close proximity with the axial organ and connects the water ring with the axocoelomic ampulla, which opens to the exterior through a pore canal ending in a hydropore (Barrois, 1888; Bury, 1888; Chadwick, 1907; Hyman, 1955). However, during metamorphosis the primary stone canal and pore canal are reduced and replaced by multiple secondary stone canaliculi (Chadwick, 1907; Ivanov et al., 1985); Balser and Ruppert (1989) suppose that developmentally the primary stone canal and its hydropore divide to give rise to the multiple tegmenal ducts (secondary stone canaliculi) and pores found in the adult.

In general, the crinoid axial complex is so different from the axial complex of all other modern echinoderms, that it has been suggested that the axial organ of Crinoidea is not homologous to the axial organ of Eleutherozoa (Cuénot, 1948). Some authors (Ivanov et al., 1985) suggest that the axial organ of Crinoidea is homologous to the pericardial part of the axial organ of Asteroidea, Ophiuroidea, and Echinoidea, which is surrounded in these groups by the right axocoel, that is, pericardium. Balser and Ruppert (1993) investigated the microscopic anatomy of the axial organ of several species of Crinoidea, but concluded that the clarification of homology between the crinoid axial coelom and that of Asteroidea, Ophiuroidea, and Echinoidea needs additional ontogenetic research (Balser, 1994; Balser & Ruppert, 1993).

We decided to re-investigate in detail the microscopic anatomy of the axial complex of Crinoidea to compare it with the axial complex of Eleutherozoa. Extant crinoids are commonly grouped into two informal groups: the sea lilies (that retain the stalk in the adult) and feather stars (that lose the stem during postlarval development and do not possess a stalk as adult). However, there may be more common features between the feather stars and sea. For example, the stalkless state in feather stars was hypothetically evolved by modifications of the isocrinoid-type stalk growth mechanism (Nakano, 2001; Nakano, Hibino, Hara, Oji, & Amemiya, 2004). That is why we tried to discuss in this work not only feather stars, but all crinoids, even though we have chosen the feather star *Himerometra robustipinna* (Carpenter, 1881) from the family Himerometridae, order Comatulida (formerly Comasteridae, see Summers, Messing, & Rouse, 2014) as the study object. The members of Comatulidae are among the most diverse and ecologically abundant crinoids. Some of them possess several key anatomical differences from *H. robustipinna* and other feather stars. However, these differences relate to a digestive system, such as a marginal mouth and a central anal opening, which results in a unique configuration of the gut (see Messing, Hoggett, Vail, Rouse, & Rowe, 2017), and do not affect the axial complex.

2 | MATERIALS AND METHODS

Mature specimens of *H. robustipinna* (Carpenter, 1881) with a calyx diameter of 10–12 mm were collected in 2014 from Nha Trang Bay (South China Sea). Animals were collected by scuba divers. For histological studies, the animals were fixed in 4% regular formaldehyde in seawater. The animals were fixed for 2 months until processing. Prior to histological processing, the material was preserved in 70% ethanol. To decalcify the samples we used 7% nitric acid for 48 hours

TABLE 1 Characteristics of the material used for the work

Collection no	Species	Fixation	Section direction	Section thickness	Figures
2014-HR-01	*Himerometra robustipinna*	4% regular formaldehyde in seawater	Sagittal	8 μm	2–7, 9, 10, 12
2014-HR-03	*Himerometra robustipinna*	4% regular formaldehyde in seawater	Transverse	10 μm	2–10, 13
2014-Hsp.-02	*Henricia* sp.	4% regular formaldehyde in seawater	Transverse	8 μm	13
2014-Hsp.-03	*Henricia* sp.	4% regular formaldehyde in seawater	Sagittal	8 μm	12
2014-OA-01	*Ophiopholis aculeata*	4% regular formaldehyde in seawater	Sagittal	10 μm	12
2016-SP-31	*Strongylocentrotus pallidus*	Bouin's fluid	Sagittal	5 μm	12
2013-CL-02	*Chiridota laevis*	4% regular formaldehyde in seawater	Sagittal	8 μm	12
2006-SM-06	*Saccoglossus mereschkowskii*	Bouin's fluid	Transverse	7 μm	13

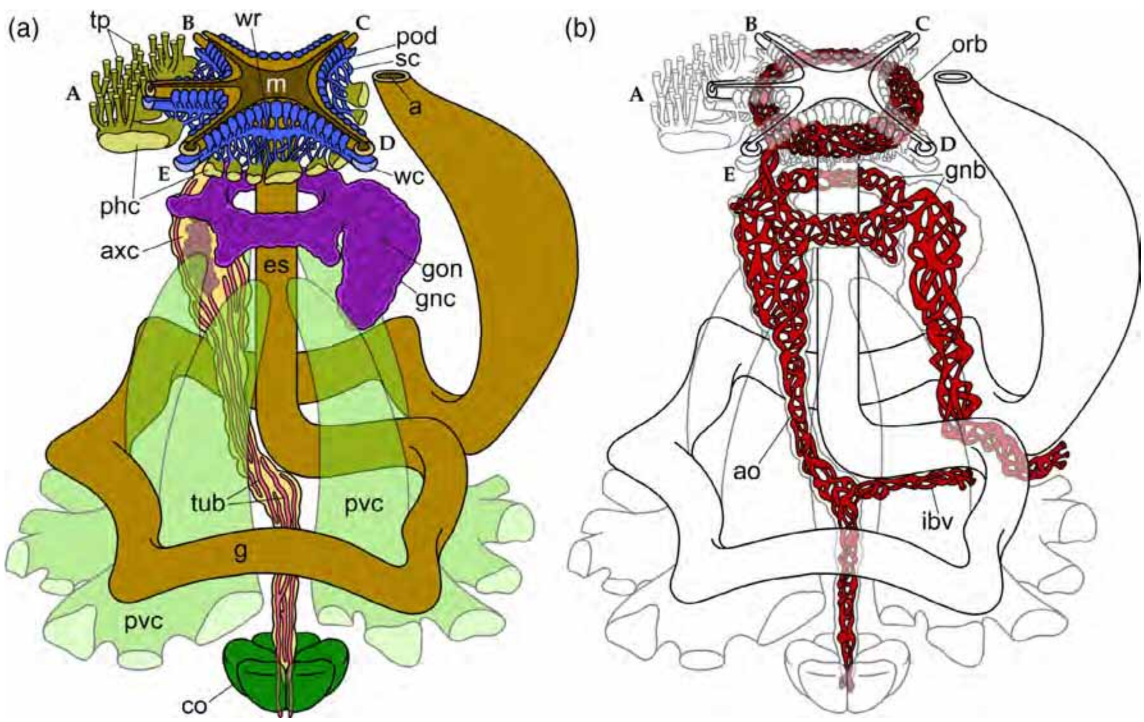

FIGURE 1 *Himerometra robustipinna*. Interrelations between the coeloms (a) and haemocoel structures (b) in the axial complex with relation to the gut. Capital letters indicate the radii. The perivisceral coelom (fusion of left and right somatocoels) is shown very simplified. a, anus; ao, axial organ; axc, axial coelom; co, chambered organ; es, esophagus; g, gut; gnb, genital haemal lacuna; gnc, genital coelom; gon, gonad; ibv, intestinal haemal vessels; m, mouth; orb, oral haemal ring; phc, (clefts of) perihaemal coelomic ring; pod, podia; pvc, perivisceral coelom; sc, stone canaliculi; tp, tegmenal pores; tub, tubules of axial organ; wc, radial water canal; wr, water ring

(Valovaya & Kavtaradze, 1993). The samples were then dehydrated through increasing series of ethanol, embedded in paraplast and sectioned into sections 8 μm thick (sagittal sections) and 10 μm thick (transverse sections). The sections were then stained with hematoxylin following standard procedures (Valovaya & Kavtaradze, 1993). The material is deposited in a collection of the Student Laboratory of Evolutionary Morphology of Animals (www.evolmorphan.ru), Department of Invertebrate Zoology, Biological Faculty of Lomonosov Moscow State University; the collection numbers are 2014-HR-01 and 2014-HR-03 (Table 1). In total, two specimens were studied using light microscopy (one series of sections in the sagittal plane and one series perpendicular to the oral-aboral axis, that is, transverse sections). Photographs of histological sections were made using a Micmed-6 microscope ("LOMO", Saint-Petersburg, Russia, 2018) with a digital camera MC-12.

For comparative purpose we used additional slides from the collections of the Student Laboratory of Evolutionary Morphology of Animals (www.evolmorphan.ru), Department of Invertebrate Zoology, Biological Faculty of Lomonosov Moscow State University. The collection numbers and characteristics of the material are shown in Table 1.

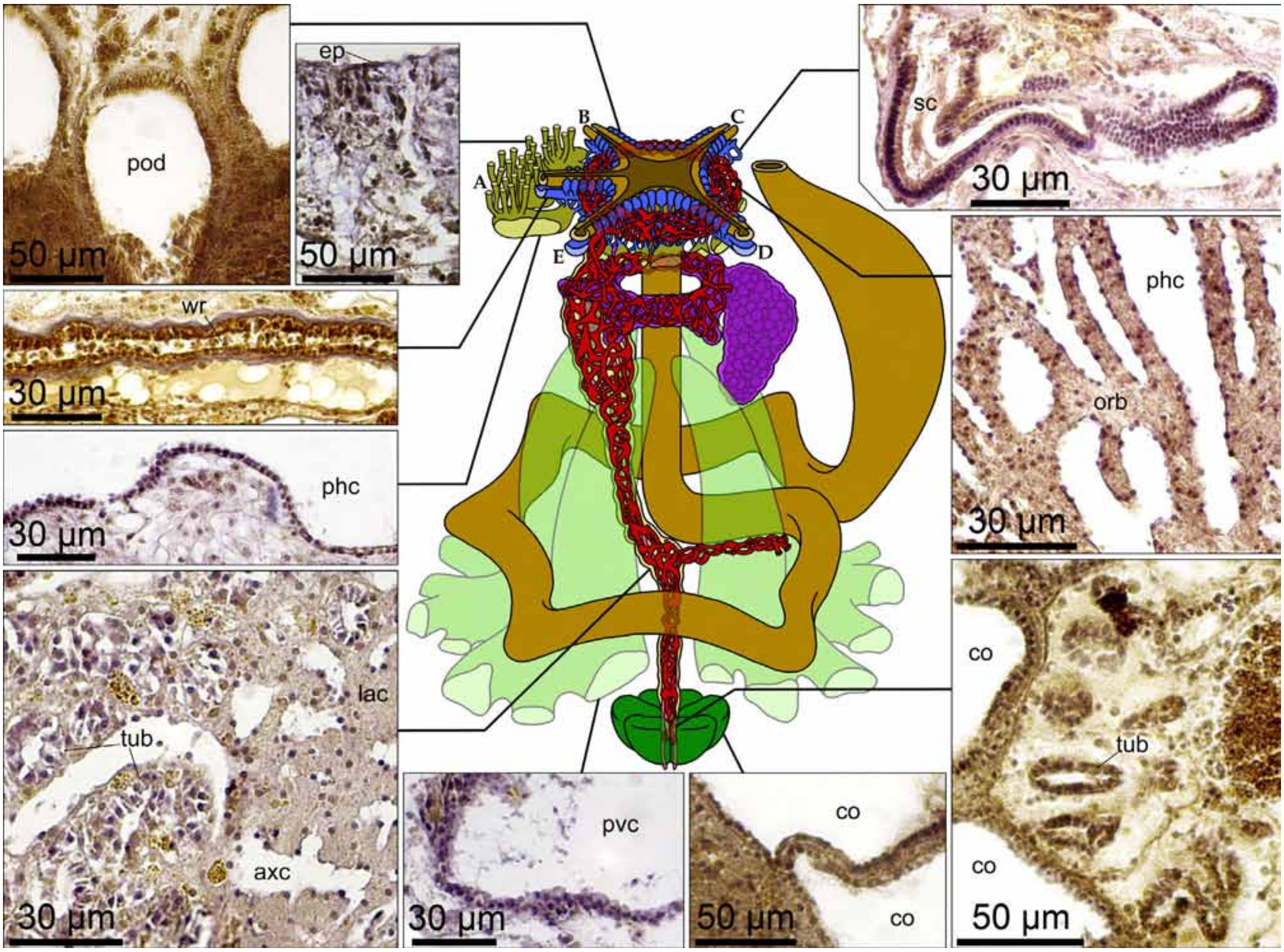

FIGURE 2 *Himerometra robustipinna*. Histological structure (high magnification histological photos and schemes) of the epithelia and different coelothelial lining in the axial complex. Dark gray lines indicate the basal laminae; a light gray area indicates the haemocoel (primary body cavity). ao, aboral (tubular) region of axial organ; axc, axial coelom; co, chambered organ; ep, epidermis with tegmenal pores; lac, lacunar region of axial organ; orb, oral haemal ring; phc, perihaemal coelom; pod, podia; pvc, perivisceral coelom; sc, stone canaliculus; tub, tubules within the tubular region of the axial organ; wr, water ring

3 | RESULTS

The axial organ of *H. robustipinna* is an elongated fusiform haemocoelic organ, which is surrounded by the coelothelium of a narrow coelomic cavity (i.e., axial coelom, see below; Figures 1 and 2). The axial organ is located, for the most part, along the central oral-aboral axis of the body (Figures 1b and 3a,b). The oral part of the axial organ passes along the esophagus on the side of the AB interradius (Figures 1b and 3c,d), deviating from the central axis of the body.

The axial organ of *H. robustipinna* can be divided into a broader oral part (the maximum width in the studied specimens is 1 mm) and a narrow elongated aboral part (the width does not exceed 400 μm; Figure 4). In the broad (oral) part of the axial organ (Figures 4c and 5) we can differentiate a central region (we refer to it as “lacunar”; Figure 5e) and a peripheral region, which is filled by numerous coelomic tubules (we refer to it as “tubular”). The tubules end blindly and are lined with cuboidal epithelium (Figure 5c). The epithelial cells of these tubules sit on the basal lamina (Figures 2 and 5c). From the oral side, a part of the gonad reaches into the thickness of the axial organ (Figures 1 and 5d). The lacunar region of the axial organ consists of a mesh of haemocoelic lacunae, which lie between the numerous folds of the squamous coelothelium (Figures 2 and 5e). Small, but well noticeable coelomic cavities between the lacunae of the axial organ make the consistency of lacunar region quite loose. The peripheral tubular region of the axial organ is denser, although the slit-like coelomic cavities lined with squamous, not cuboidal, epithelium lining also occur between the tubules (Figure 5c). Both the lacunar region and spaces between the tubules of the tubular region of the axial organ, contain small, but dense congregations of extracellular spherical granules, which are stained amber-yellow or dark-brown in the sections (Figure 5f).

The lacunar region is mostly absent in the narrow aboral part of the axial organ. The coelomic tubules with the cuboidal epithelium lining are packed closely and almost have no between them the coelomic cavities lined with squamous epithelium (Figures 2, 4a,d, and 6a–c). The tubules are not located randomly, but are organized into

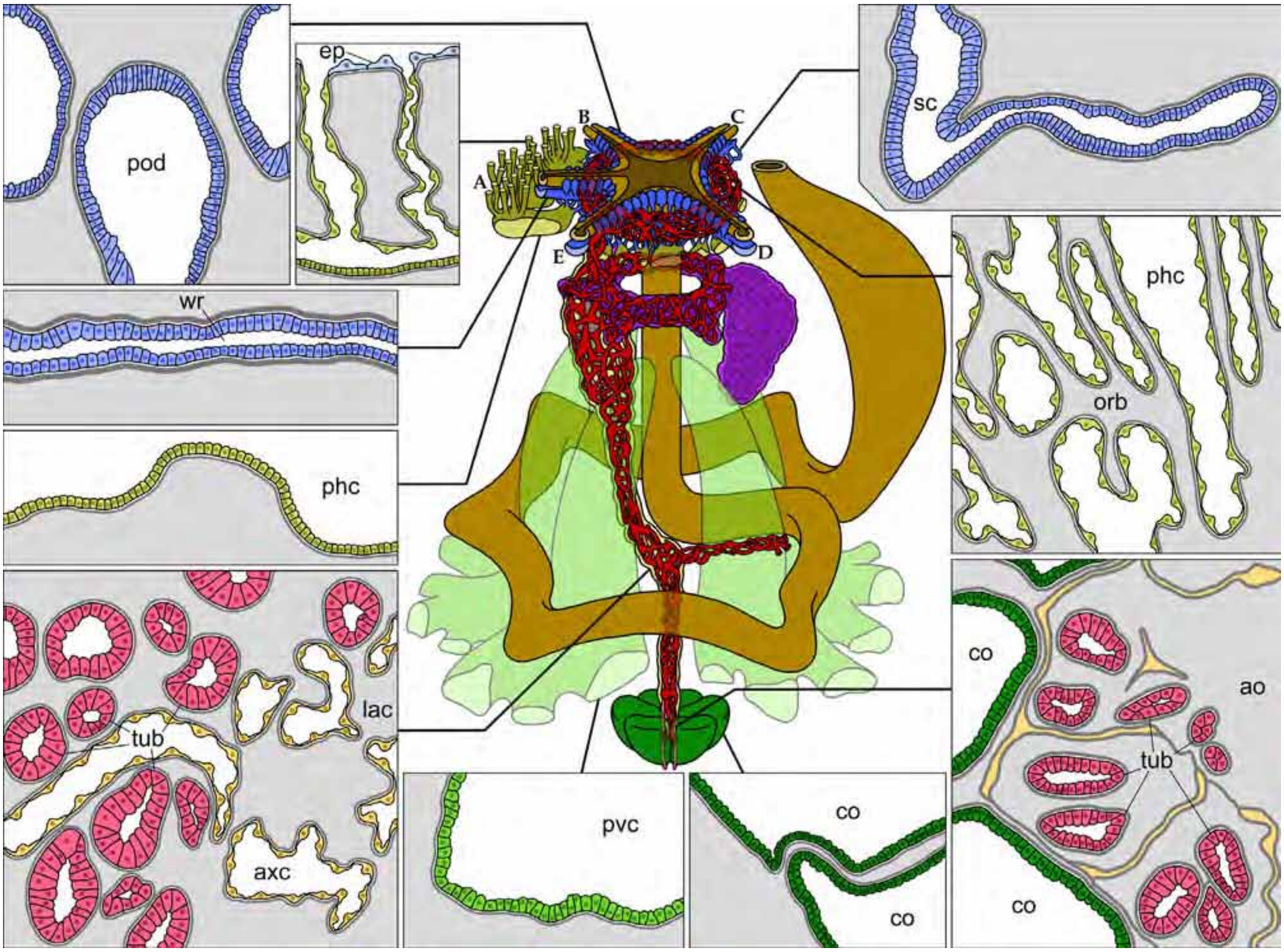

FIGURE 2 (Continued)

bundles or rows. Compartments of such bundles are separated by thin partitions that lie within the haemocoel surrounding the tubules (Figures 4d,e and 6b,c). These partitions consist of narrow, practically fused coelomic slits with squamous epithelial lining. The entire axial organ in this part can be distinguished by several characteristics from the surrounding haemocoelic bridges, which stretch between the somatocoelomic bubbles. First, the haemocoelic component of the axial organ is much lighter. Second, the dark partition, which surrounds the entire axial organ on the periphery, is visible (Figures 4e, 6c, and 7c). This dark partition consists of the coelothelia of the axial coelom, which are fused here.

The axial organ becomes thinner at its aboral end in the thickness of a centrodorsal plate, and enters into the haemocoelic central axis between the five compartments of the chambered organ (see below; Figure 4a,f). Here, the tubules, which penetrate the tubular region of the axial organ, end blindly within the thickness of the aboral nervous center under the chambered organ (Figure 7a,d) and do not connect with the coelomic compartments of the chambered organ.

On the oral side, the haemocoelic lacunae of the axial organ connect with the oral haemal ring (Figures 1b and 4a), with the haemal system of the gut, where the esophagus turns and becomes the midgut (Figures 1b, 3a, and 6e), and with the genital haemal lacuna in radius B (Figures 1b, 5a, and 6d).

The axial coelom (left axocoel) of *H. robustipinna* is a narrow coelomic cavity, adjacent and enclosing the axial organ (Figures 1, 2, 4a,c, d, 5a,b and 6a). The axial coelom is also elongated in oral-aboral direction. Its narrow spaces surround the periphery of the oral part of the axial organ. These spaces are crossed by mesenteric bridges, on which the axial organ is suspended (Figures 5b and 6a,e). Other supporting structures for the axial organ are absent in crinoids. In the aboral part, these peripheric spaces become thin and slit like, and on the aboral side only closely spaced or fused basal laminae of the coelothelium of the axial coelom remain and form the partitions, which separate the compartments of the tubules (see above).

The oral haemal ring of *H. robustipinna* is surrounded by the cavity of the perihaemal ring coelom (Figures 1, 2, 8, and 9). This perihaemal coelomic ring widely connects with the genital coelom ring. In the oral region, the axial coelom also communicates with the genital coelom (Figures 3c and 5a). Additionally, the axial coelom connects throughout its length with the surrounding clefts of the perivisceral coelom (Figures 4a, 5a,b, and 6a,e).

The chambered organ of *H. robustipinna* is located on the aboral side in the base of the centrodorsal plate (Figures 1a and 4a). It is

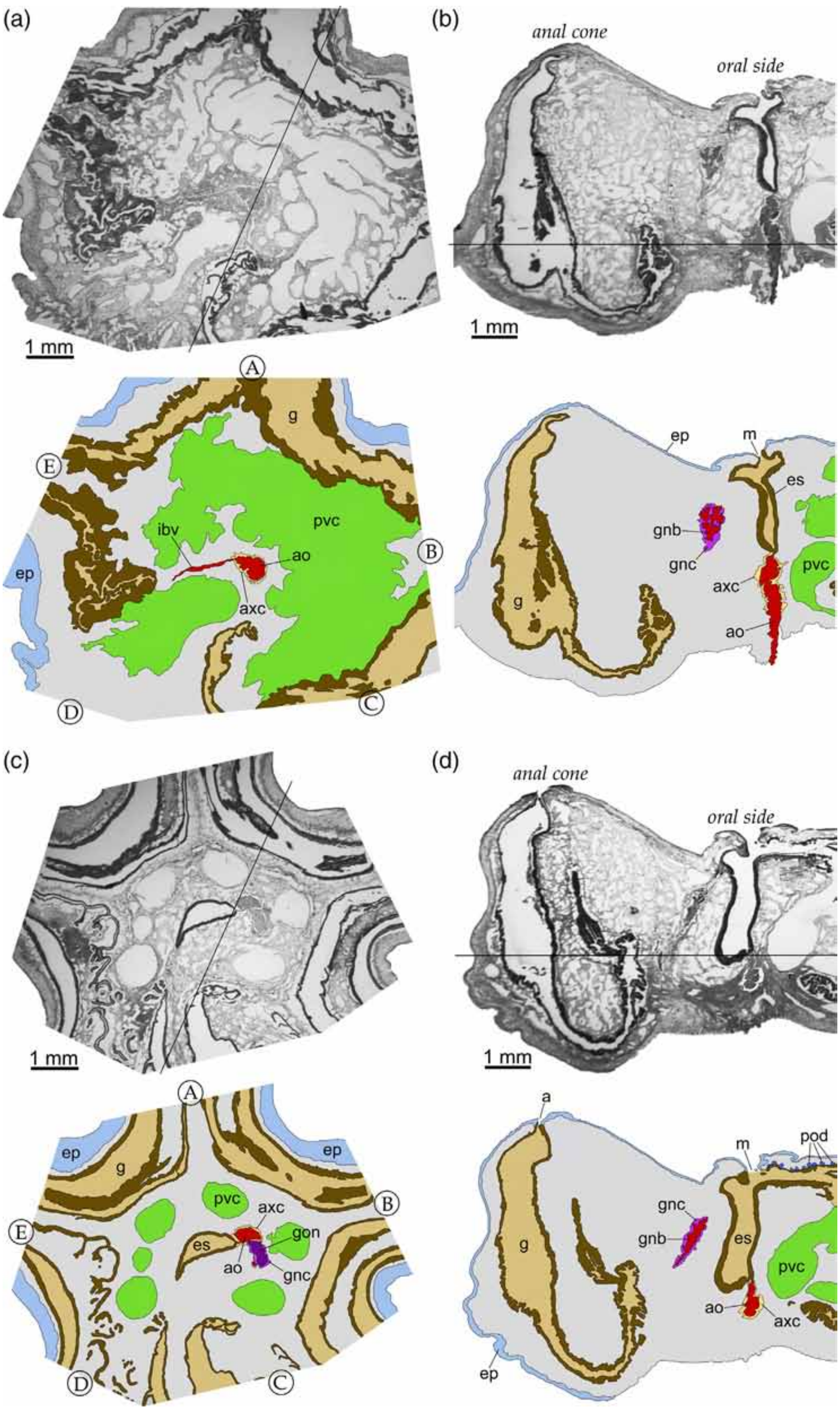

FIGURE 3 *Himerometra robustipinna*. Transverse (a,c) and sagittal (b,d) sections of the disc closer to the aboral side (a,b) and to the oral side (c,d). Lines on the transverse sections (a,c) indicate the corresponding sections in the sagittal plane (b,d). Lines on the sagittal sections (b,d) indicate the corresponding sections in the transverse plane (a,c). Capital letters indicate the radii. Gray area on the schemes shows a mesh of clefts of perivisceral coelom and haemocoelic lacuna. a, anus; ao, axial organ; axc, axial coelom; ep, epidermis; es, esophagus; g, gut; gnb, genital haemal lacuna; gnc, genital coelom; ibv, intestinal haemal vessels; m, mouth; pod, podia; pvc, perivisceral coelom

small in size in comparison with other structures of the axial complex (in the studied specimens the dimensions were 250 μm in height and more than 650 μm in diameter). The chambered organ possesses an ideal five-ray symmetry (Figure 7b). The chambered organ is formed by five radial coelomic compartments, which are separated by thin interradial partitions (Figures 1a and 7b). The central axis of the chambered organ is formed by the aboral end of the tubular region of the axial organ (Figures 1a, 4a, and 7). From the aboral side, the chambered organ is submerged into the thickness of the nerve tissue of the aboral nervous center (Figures 4a and 7a,d).

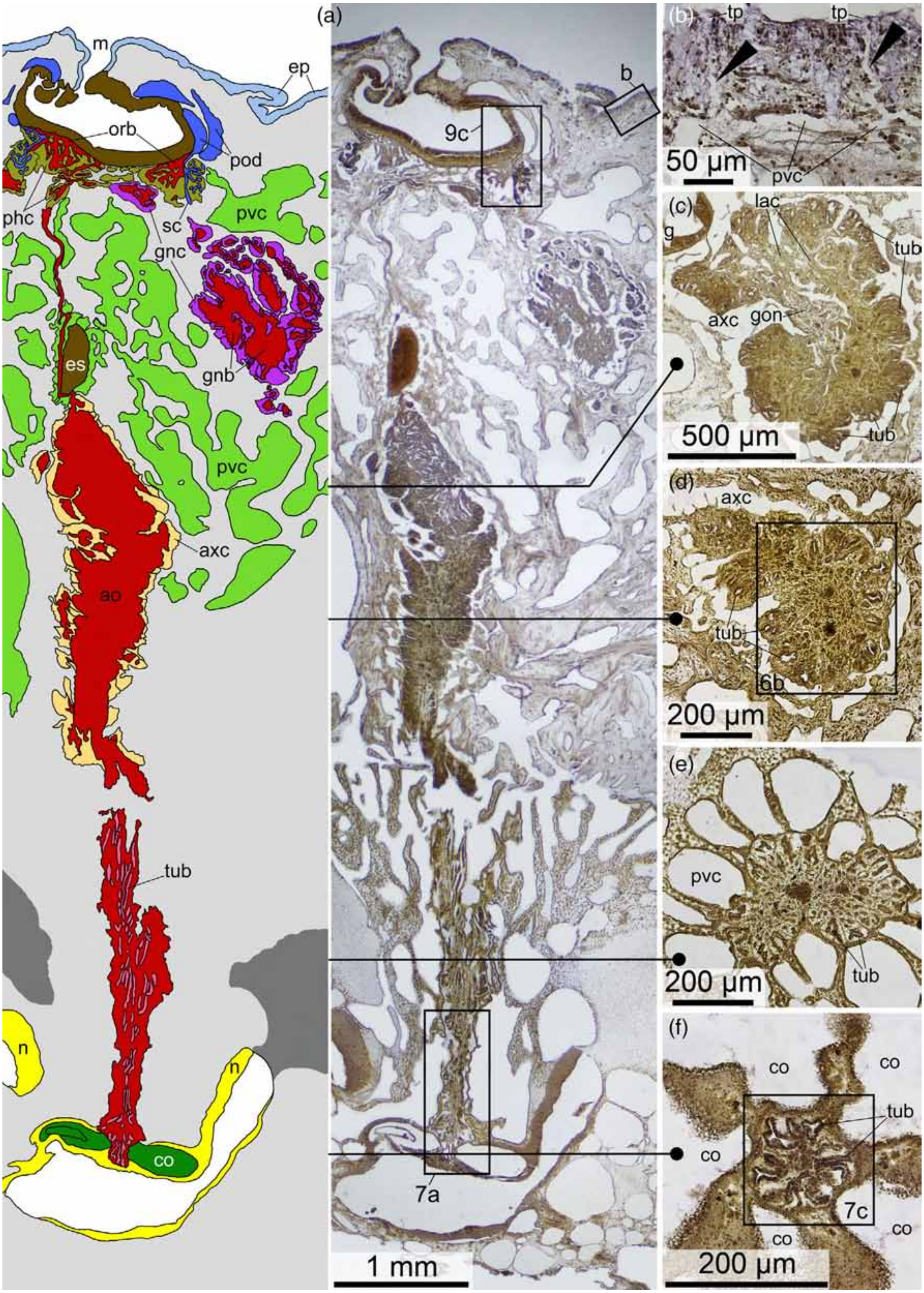

FIGURE 4 Legend on next page.

The gonad of *H. robustipinna* lies in the oral part of the calyx. It encircles the esophagus immediately under the oral haemal ring and the perihaemal coelomic ring (Figure 8). The gonad is enclosed in a cavity of the genital coelom, filling it almost entirely. Like the axial coelom, the genital coelom is crossed by numerous mesenteric bridges, which support the gonad (Figures 8 and 10b,c).

The gonad of *H. robustipinna* has a spongy structure and consists of a band that is folded multiple times. The gonad is covered by squamous coelothelium with individual oogonia, which are distinguished by a larger size (Figures 5a,d, 8, and 10b,c,e). The folds of this band are filled inside by haemocoelic material.

The gonad is tangled and pierced by haemocoelic vessels, which form an extensive three-dimensional network (Figures 3, 4a, and 8). The capillaries of this network are covered on the outside (from the side of genital coelom, perihaemal coelomic ring, and axial coelom) with squamous coelothelium, which consists of small cells and forms numerous folds (Figures 5d and 10b,c). We call this haemocoelic network the "genital haemal lacuna". The capillaries of this network continue into the capillaries of the same folded oral haemal ring, which is pierced by numerous stone canaliculi (Figures 8, 9, and 10a,b). The genital haemal lacuna with the capillaries of the oral haemal ring is often referred to as "spongy body" in various descriptions (Balser & Ruppert, 1993; Heinzeller & Welsch, 1994; Hyman, 1955; Ruppert, Fox, & Barnes, 2004). In the interradius AB, the gonad is immersed into the thickness of the axial organ (Figures 1, 3c, and 5b). The genital haemal lacuna accompanies the gonad and widely connects with the "lacunar" region of the axial organ (Figure 5d). However, most of the volume of the gonad and the genital haemal lacuna is located in the CD interradius (Figures 1 and 10d). On the aboral side, the genital haemal lacuna connects with the intestinal haemal vessels (Figures 1b and 10d).

The oral haemal ring of *H. robustipinna* surrounds the mouth and the oral part of the esophagus (Figures 1b, 4a, 5a, 8, 9, and 10a). From the oral side, the oral haemal ring is closely adjoint to the water ring. Here, the oral haemal ring walls are not folded (Figure 9a). From the aboral side, the oral haemal ring has a spongy structure and forms numerous lacunae between the folds of the squamous coelothelium of the perihaemal coelomic ring (Figures 2 and 9c-e). The capillaries of this "spongy" part of the oral haemal ring communicate with the genital haemal lacuna (Figure 10a). The "spongy" part of the oral haemal ring is pierced by numerous stone canaliculi (Figures 4a, 5a, 8, and 9), which act as the main support structures for the extensive lacunar system of the oral haemal ring.

The stone canaliculi and the water ring of *H. robustipinna* are the central structures of the crinoid water-vascular system (Figures 1 and 8). Numerous thin stone canaliculi extend in the oral-aboral direction, and can be slightly curved (Figures 2 and 9b–e). Their height in the studied specimens was approximately 300 μm, diameter was 25 μm, diameter of the lumen was 10–12 μm. The walls of the stone canaliculi are formed by a monociliar cuboidal epithelium (Figures 2 and 9d,e).

Stone canaliculi, as mentioned above, pierce the oral haemal ring and together with it surround the esophagus, forming the circumoral ring of the stone canaliculi (Figures 1, 4a, 5a, 8, 9, and 10a). A minimum 4–5 cut stone canaliculi can be seen on each transverse section of the ring. On the aboral side, each stone canaliculus opens into the perihaemal coelomic ring (Figures 1 and 9), which has numerous connections with the clefts of the perivisceral coelom. On the oral side, each stone canaliculus opens into the water ring (Figures 1 and 9). The stone canaliculi do not communicate with the external environment. Instead, numerous thin tegmenal pores and pore canaliculi pierce the epidermis of the oral side of the calyx and open into the environment (Figure 4b). The pore canaliculi of the tegmenal pores lead into the clefts of the perivisceral coelom.

The water ring of *H. robustipinna* (Figure 8a,b) lies directly under the columnar epithelium of the mouth cavity. From the internal side (i.e., from the side of oral-aboral axis of the body), the oral haemal ring is adjoint to the water ring (Figure 9a,c–e). The cells of the coelothelial lining of the water ring are more loosely arranged than in the stone canaliculi, but more densely packed than in the squamous coelothelium of the perihaemal coelom, axial coelom, and genital coelom (Figures 2 and 9a,c–e).

Thin canaliculi originate from the water ring and lead to numerous coelomic sacs, labial podia, which surround the mouth (Figures 1a, 8a, and 9b,c). One canaliculus leads into each coelomic sac of the podia.

Thus, the gonad, the oral haemal ring, the water ring, and the ring of stone canaliculi of *H. robustipinna* form a single circumoral complex. All structures of this complex continue into the radii; as a result, the circumoral part takes the form of a pentagon on the transverse sections through the calyx of feather star (Figure 8).

FIGURE 4 *Himerometra robustipinna*. Axial organ: general view on the sagittal section (a) with detailed view of the epidermis (b) and transverse sections through the different regions (c–f). (a) General view of axial organ (ao) and its location in the body. Lines indicate the location of the corresponding transverse sections. The frames indicate the structures shown on (4b), (7a), and (9c). Light gray area on the scheme shows a mesh of clefts of perivisceral coelom and haemocoelic lacuna; dark gray area shows the calcareous structures. (b) Tegmenal pores (tp) in the epidermis. Arrows indicate the tegmenal canals. (c) Oral part with lacunar and tubular regions and the gonad outgrowth (gon) in the centre. (d) The oral portion of the tubular region. The frame indicates the structures shown on (6b). (e) The aboral portion of the tubular region. (f) The central axis of the chambered organ (co). The frame indicates the structures shown on (7c). ao, axial organ; axc, axial coelom; co, chambers of the chambered organ; ep, epidermis; es, esophagus; gnb, genital haemal lacuna; gnc, genital coelom; gon, gonad; lac, lacunar region of axial organ; m, mouth; n, nerves; orb, oral haemal ring; phc, (clefts of) perihaemal coelomic ring; pod, podia; pvc, (some clefts of) perivisceral coelom; sc, stone canaliculi; tp, tegmenal pores; tub, tubules of axial organ (tubular region of axial organ)

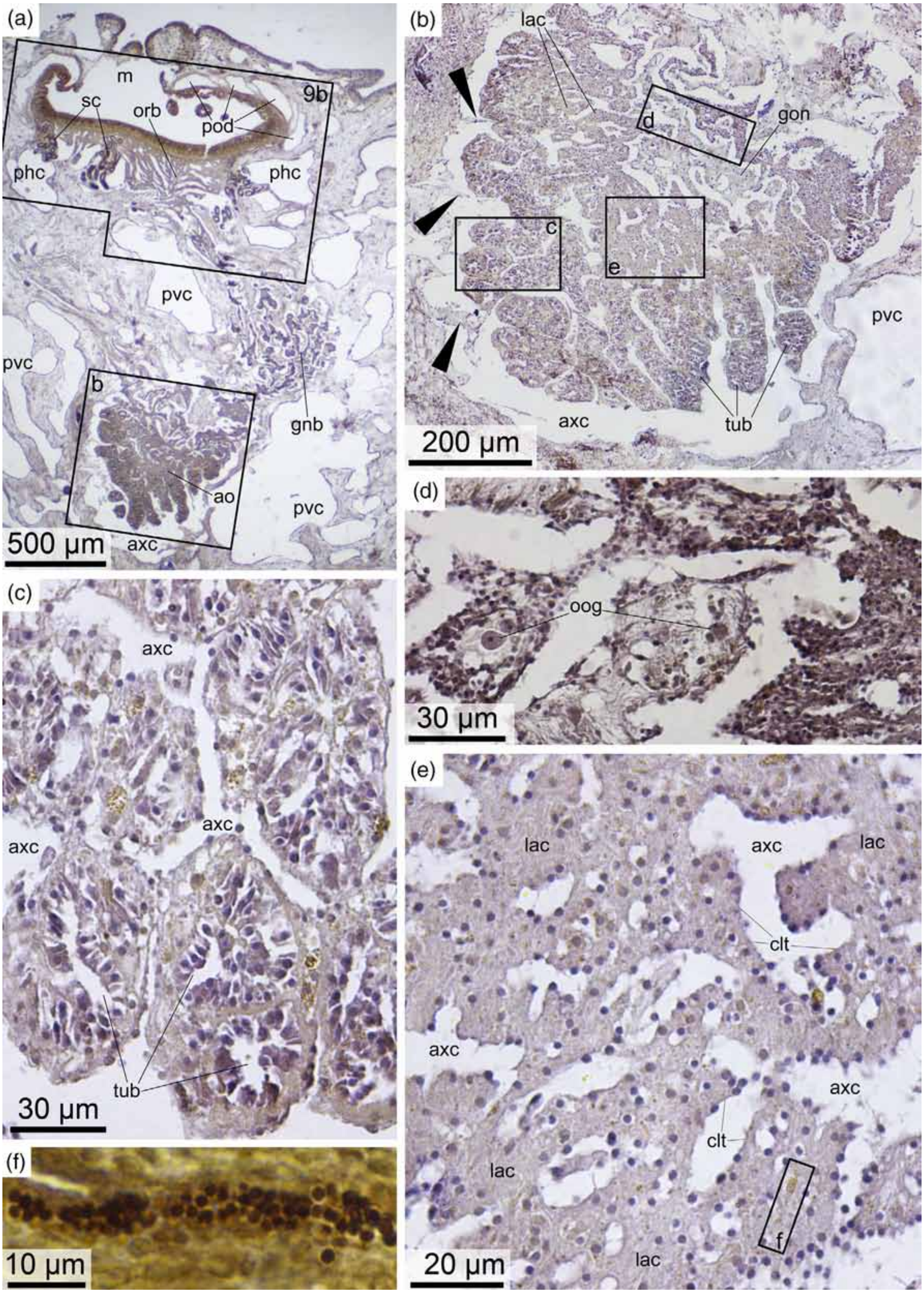

FIGURE 5 *Himerometra robustipinna*. Histological structure of the oral part of axial organ. Sagittal (a–e) and transverse (f) sections. (a) General view in the body. The frames indicate the structures shown on (5b) and (9b). (b) Axial organ surrounded by the axial coelom (axc). The frames indicate the structures shown on (5c–e); the (5d) shows the marked area from one of the adjacent slices. Arrows indicate the mesenteric bridges. (c) Peripheral tubular region. (d) Gonad outgrowth in the centre. (e) Central lacunar region. The frame indicates the structures shown on (5f). (f) Granules. ao, axial organ; axc, axial coelom; clt, coelothelium of the axial coelom; gnb, genital haemal lacuna; gon, gonad; lac, haemocoelic lacunae of the lacunar region of axial organ; m, mouth; oog, oogonia; orb, oral haemal ring; phc, (clefts of) perihaemal coelomic ring; pod, podia; pvc, perivisceral coelom; sc, stone canaliculi; tub, tubules of axial organ (tubular region of axial organ)

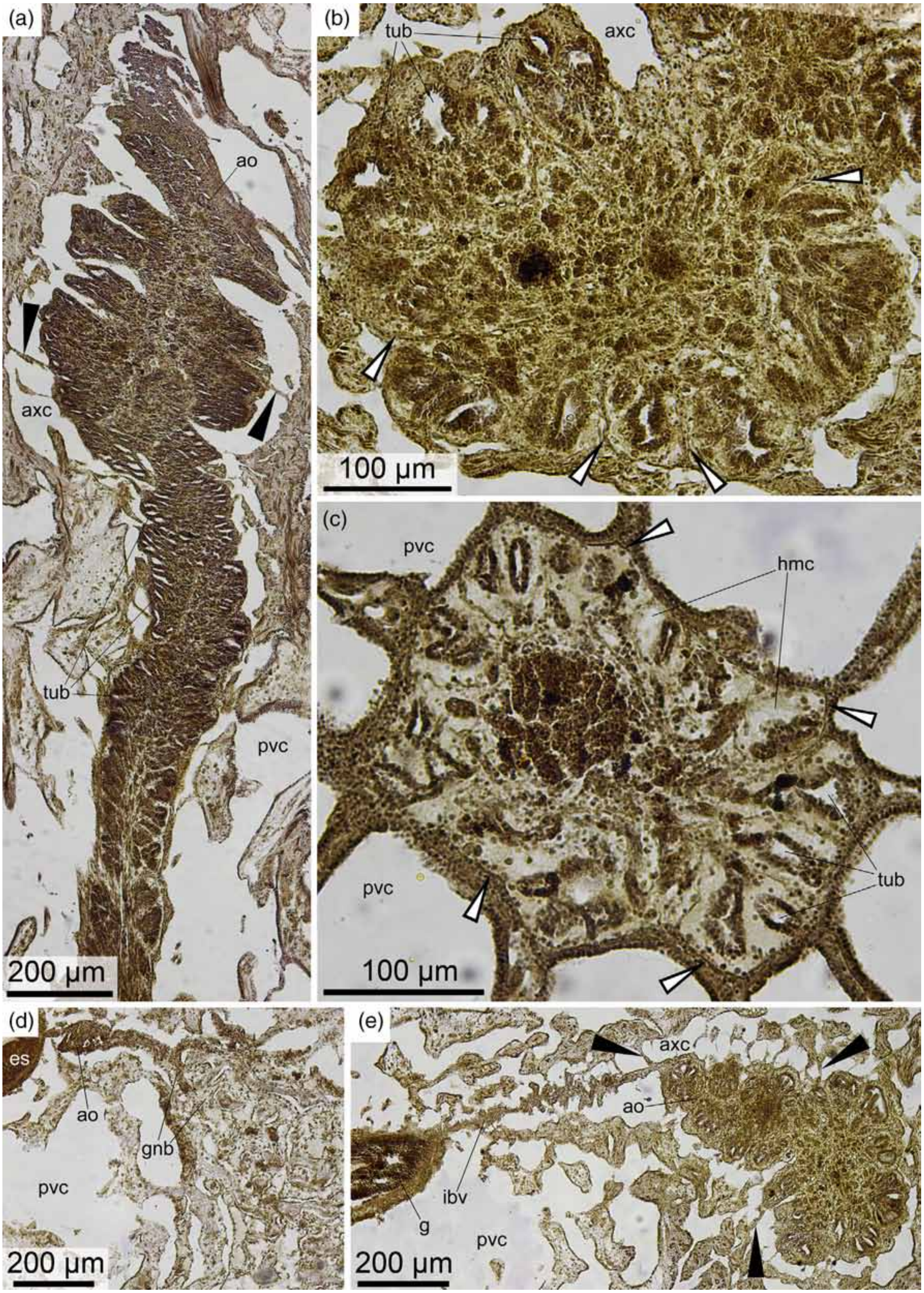

FIGURE 6 *Himerometra robustipinna*. Different features of the axial organ on sagittal (a) and transverse (b-e) sections. (a) Closely packed tubules (tub) in the oral and central parts of axial organ (ao). (b) Compartments of the coelomic tubules (tub) and connective tissue (haemocoel) surrounded by thin partitions (are shown by black-white arrows) in the central part of axial organ. (c) Compartments with the coelomic tubules (tub) and light haemocoel spaces (hmc) divided by thin partitions of the basal laminae (are shown by arrows) in the aboral part of axial organ. (d) Connection of gonad haemal plexus (gnb) with the very beginning of axial organ (ao) on the oral side. (e) Connection of the axial organ (ao) with the intestinal haemal plexus (ibv). Black arrows indicate the mesenteric bridges. ao, axial organ; axc, axial coelom; es, esophagus; g, gut; gnb, genital haemal plexus; hmc, haemocoel spaces; ibv, intestinal haemal vessels; pvc, perivisceral coelom; tub, tubules of axial organ

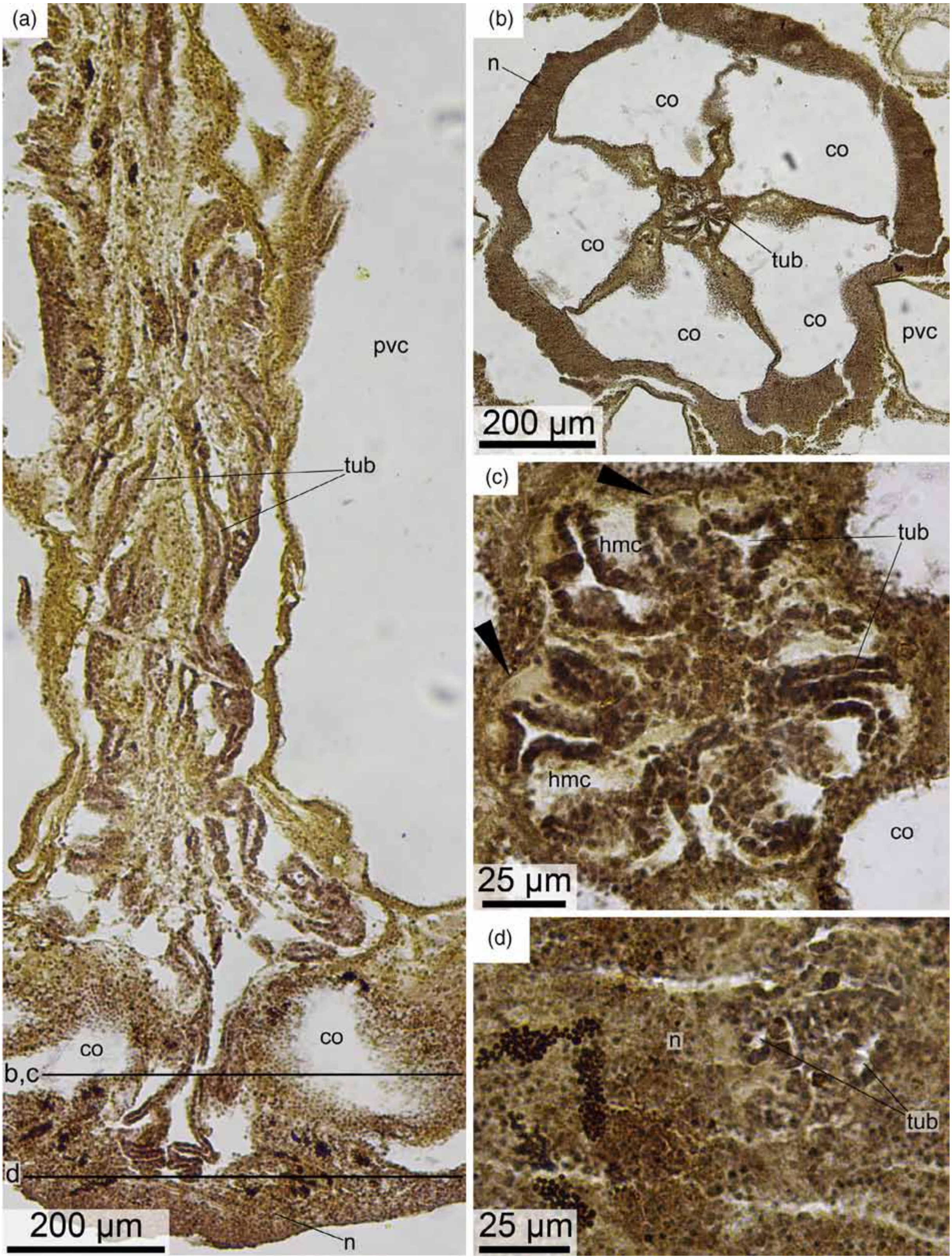

FIGURE 7 *Himerometra robustipinna*. Aboral part of the axial organ and chambered organ on sagittal (a) and transverse (b-d) sections. (a) Histological structure of the aboral part of the axial organ. Horizontal lines indicate the position of transverse sections from (7b,c) and (7d). (b) General view of chambered organ. (c) Tubules (tub) of the most aboral part of the axial organ entering the central axis of the chambered organ (co). Arrows indicate the basal laminae. (d) Tubules (tub) of the axial organ penetrating the aboral nerve mass (n) under the chambered organ. co, chambers of the chambered organ; hmc, haemocoel spaces; n, nerves; pvc, perivisceral coelom; tub, tubules of axial organ

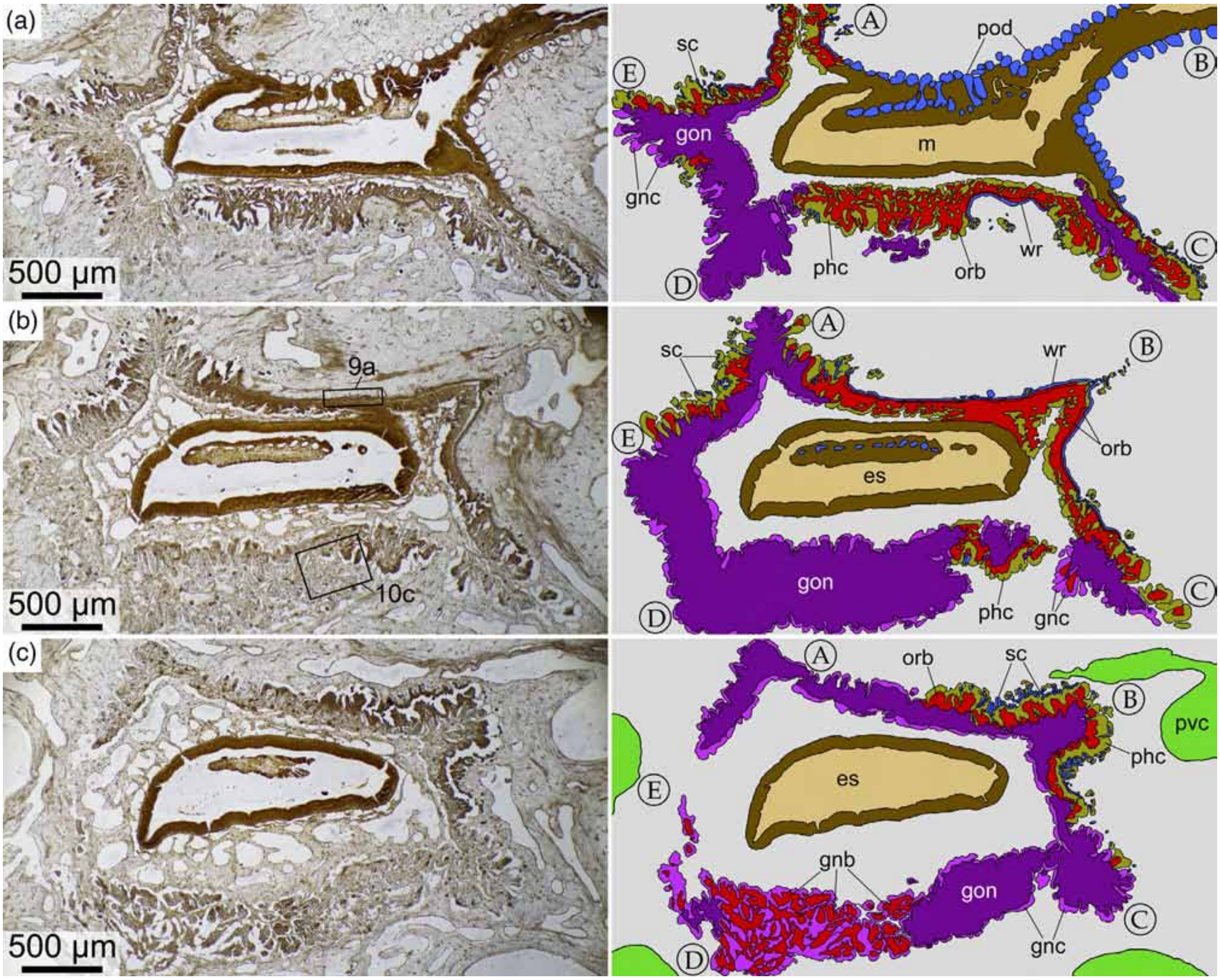

FIGURE 8 *Himerometra robustipinna*. Topography of the circumoral structures on consecutive transverse sections from the most oral section (a) to the deeper one (c). Capital letters indicate the radii. Gray area on the schemes shows a mesh of clefts of the perivisceral coelom and haemocoelic lacunae. (a) Podia (pod) surrounding the mouth (m); water ring (wr), perihaemal coelomic ring (phc), and oral haemal ring (orb) in the radii A, C, E and interradius CD; gonad (gon) in the radii C–E. (b) Water ring (wr), perihaemal coelomic ring (phc), and oral haemal ring (orb) in the radii A–C; gonad (gon) in the radii A, C–E. The frames indicate the structures shown on (9a) and (10c). (c) Gonad (gon) in the radii A–D and genital haemal lacuna (gnb) in interradius CD. es, esophagus; gnb, genital haemal lacuna; gnc, genital coelom; gon, gonad; m, mouth; orb, oral haemal ring; phc, perihaemal coelomic ring; pod, podia; pvc, perivisceral coelom; sc, stone canaliculi; wr, water ring

4 | DISCUSSION

Comparing the axial complex of Crinoidea with that of other Echinodermata, the multiplicity of some structures and features is obvious. This applies not only to numerous stone canaliculi, but also to the numerous connections of the coelom with the environment, and to the numerous connections between different coeloms (Figure 11). The axial coelom, the perivisceral coelom, and the genital coelom of crinoids are in a wide communication with each other, and with the water-vascular system (Balser & Ruppert, 1993; Grimmer & Holland, 1979; Hyman, 1955). Balser and Ruppert (1993, p. 93, 95), referring to other sources (Bury, 1888; Ferguson & Walker, 1991; Gemmill, 1914; Grimmer & Holland, 1979; Hyman, 1955; Ludwig, 1877; Mortensen, 1920), concluded that the stone canals, tegmental pores, and their canals, as well as a coelom, through which they communicate with each other, are morphologically and developmentally similar to the stone canal, madreporic plate, and ampulla of the axial coelom in other echinoderms. According to Heinzeller & Welsch (1994, p. 66), only the tegmental pores may be considered the remains of the axocoel in crinoids and they “are equivalent to madreporic canals”. The coelomic cavity, into which the stone canals open, and the coelom, which surrounds the axial organ, are considered to be the somatocoel, and not the axocoel (Heinzeller & Welsch, 1994, p. 68, p. 73). However, Mortensen (1920, p. 66) in the work on larval development of crinoids notes that disappearance of primary hydropore and formation of new hydropore during the ontogenesis does not prove that “madreporic pores … of Crinoids are not homologous with those of the madreporic system of other Echinoderms.” In any case,

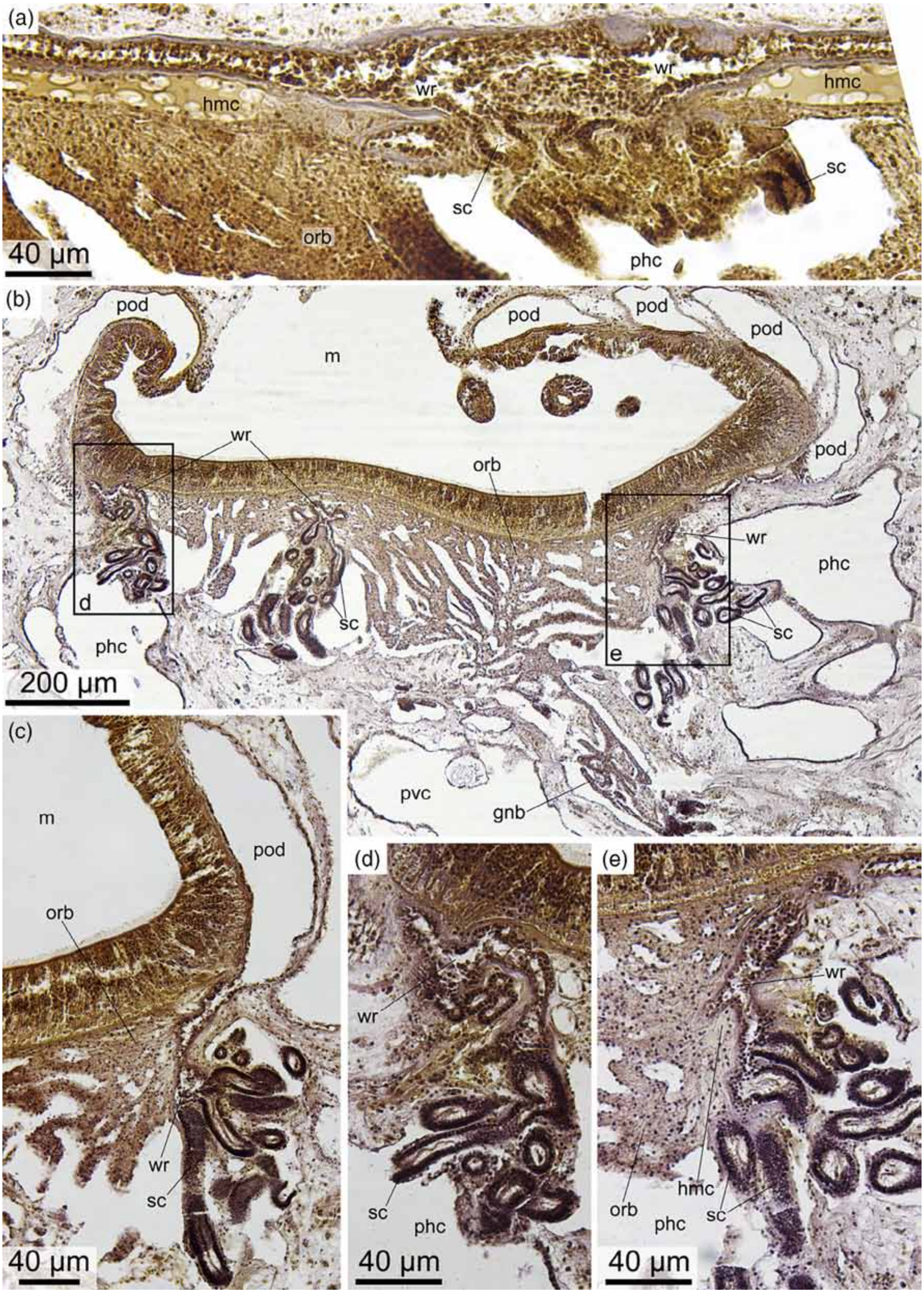

FIGURE 9 *Himerometra robustipinna*. Morphology of the circumoral structures on transverse (a) and sagittal (b–e) sections. (a) Communication of the stone canaliculi (sc) with the water ring (wr) and perihaemal coelomic ring (phc); different parts of the oral haemal ring (hmc, orb). (b) Stone canaliculi (sc) pierce the mesh of the oral haemal ring (orb). Communication of the oral haemal ring (orb) with the genital haemal lacuna (gnb). The frames indicate the structures shown on (d, e). (c) Communication of the stone canaliculus (sc) and water ring (wr) with the cavity of podium (pod). (d) Communication of the stone canaliculus (sc) with the cavity of perihaemal coelomic ring (phc). (e) Histological structure of the oral haemal ring (hmc, orb). gnb, genital haemal lacuna; hmc, part of oral haemal ring without the folded walls; m, mouth; orb, folded part of oral haemal ring; phc, perihaemal coelomic ring; pod, podia; pvc, perivisceral coelom; sc, stone canaliculi; wr, water ring

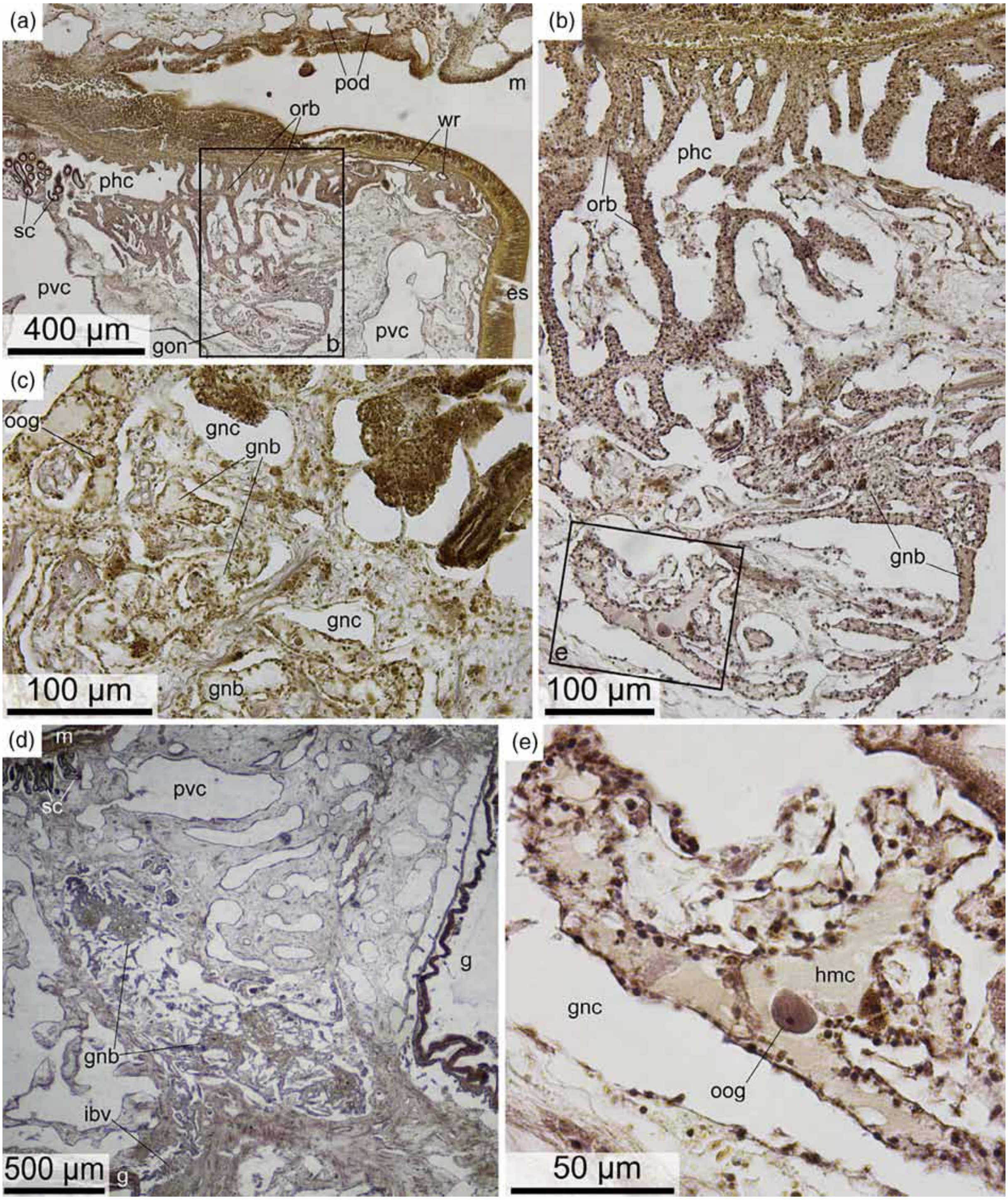

FIGURE 10 *Himerometra robustipinna*. Topography and morphology of the gonads on sagittal (a,b,d,e) and transverse (c) sections. (a) Interrelationship between the gonad (gon), oral haemal ring (orb), perihaemal coelomic ring (phc), and stone canaliculi (sc). The frame indicates the structures shown on (b). (b) Communication of the genital haemal lacuna (gnb) with the oral haemal ring (orb). The frame indicates the structures shown on (d). (c) Histological structure of the gonad, genital coelom (gnc), and genital haemal lacuna (gnb). (d) Communication of the genital haemal lacuna (gnb) with the haemal plexus of the gut (ibv). (e) Oogonium (oog) into the haemocoel (hmc) of the genital haemal lacuna. es, esophagus; g, gut; gnb, genital haemal lacuna; gnc, genital coelom; gon, gonad; hmc, haemocoelic spaces of the genital haemal lacuna; ibv, intestinal haemal vessels; m, mouth; oog, oogonium; orb, oral haemal ring; phc, perihaemal coelomic ring; pod, podia; pvc, perivisceral coelom; sc, stone canaliculi; wr, water ring

the coeloms of Crinoidea communicate with each other in many sites and connect with the environment via many pores on the entire oral surface of the calyx. This situation rather differs from most other echinoderms (Figure 11). Eleutherozoans have the only connection of the hydrocoel (water-vascular system) with the derivative of the left axocoel (madreporic ampulla and axial coelom; Figure 11). Multiple

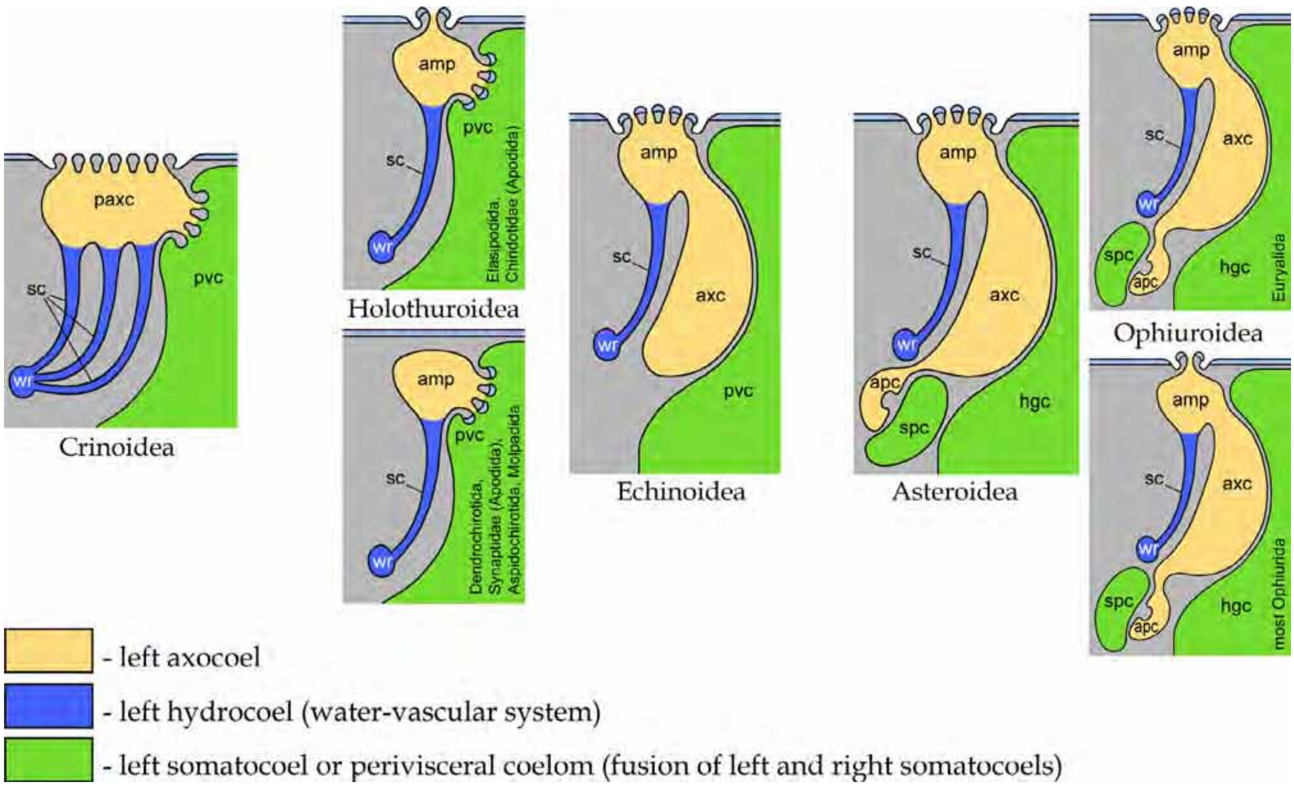

FIGURE 11 Organization of the madreporic plate, madreporic ampulla (left axocoel), stone canal, water ring, and left somatocoel in different classes of echinoderms (Hayashi, 1935; Cuénot, 1948; Hyman, 1955; Ivanova-Kazas, 1978; Erber, 1983a, 1983b; Ivanov et al., 1985; Balser & Ruppert,1993; Ziegler et al., 2009; Ezhova et al., 2013, 2014, 2015, 2017, 2018; Ezhova, Malakhov, & Martynov, 2016). amp, madreporic ampulla; apc, axocoelomic perihaemal ring; axc, axial coelom; hgc, hypogastric coelom (left somatocoel); paxc, perihaemal axocoelomic ring; pvc, perivisceral coelom; sc, stone canals; spc, somatocoelomic perihaemal ring; wr, water ring

connections of the axocoelomic cavities with the derivatives of somatocoels (perivisceral coelom) are present in Holothuroidea. In this aspect, the morphology of Crinoidea is closest to the organization of Holothuroidea: in most holothuroids, the pore canals of the madreporic plate depart from the madreporic ampulla, but do not communicate with the environment and open into the perivisceral coelom (which is formed as a result of fusing of the somatocoels). Thus, in Holothuroidea, the left axocoel (madreporic ampulla) is partially fused with the somatocoels (perivisceral coelom), though they remain more or less separated from each other (Figure 11). In Asteroidea, Ophiuroidea, and Echinoidea, there is no communication between the derivatives of the left axocoel and the somatocoels (Figure 11).

The same applies to the connection with the environment: the area of such a communication is reduced in most Eleutherozoa to the madreporic plate in the CD-interradius. The number of pores in the madreporic plate ranges from several to hundreds. In some Asteroidea (*Allostichaster polyplax*, *Coscinasterias tenuispina*, *C. acutispina*, *Acanthaster echinites*, and genius *Linckia*), there are several madreporic plates. In asteroids, it is often associated either with mutation, or with preparation to asexual reproduction through division at the early stages of ontogenesis (Crozier, 1920; Cuénot, 1887, 1948; Ezhova et al., 2014; Yamazi, 1950). Ophiuroids usually have a single madreporic pore (Figure 11). In some Ophiuroidea, there is the madreporic plate in each interradius: *Trichaster elegans* has several madreporic plates with a simple pore in each of them. For the genus *Astrophyton* five true madereporic plates are described and each of them is penetrated by 15–20 pores (Cuénot, 1888; Ludwig, 1878). *Ophiactis virens* has up to five madreporic plates. Initially, this species has only one stone canal and one madreporic plate, and an increase in their number is associated with preparation to asexual reproduction through division (Simroth, 1877). *Asteroschema inornatum*, *Euryale aspera*, *Ophiologimus* cf., *secundus*, *Ophiolimna perfida*, *Ophiopsila bispinosa*, and *Ophiostriatus* sp. have the madreporic plate with 1–3 pores in each interradius (Ezhova et al., 2016). In most holothuroids, the coeloms have no openings to the environment. The primary stone canal during the larval development of holothuroids communicates with the environment via the hydropore (Dolmatov & Yushin, 1993; Malakhov & Cherkasova, 1992; Mashanov & Dolmatov, 2000; McEuen & Chia, 1991), but in adult holothuroids this communication is lost in most cases. The adult representatives of only two orders (Elasipodida and Apodidae) retain the single pore in the CD-interradius (Erber, 1983a, 1983b; Ezhova et al., 2017). Sometimes, the number of the stone canals may secondarily increase during the ontogenesis of holothuroids (Ivanova-Kazas, 1978). According to some paleontological data (Haugh, 1973; Haugh & Bell, 1980), in fossil camerate crinoids, "function and morphology of the water vascular

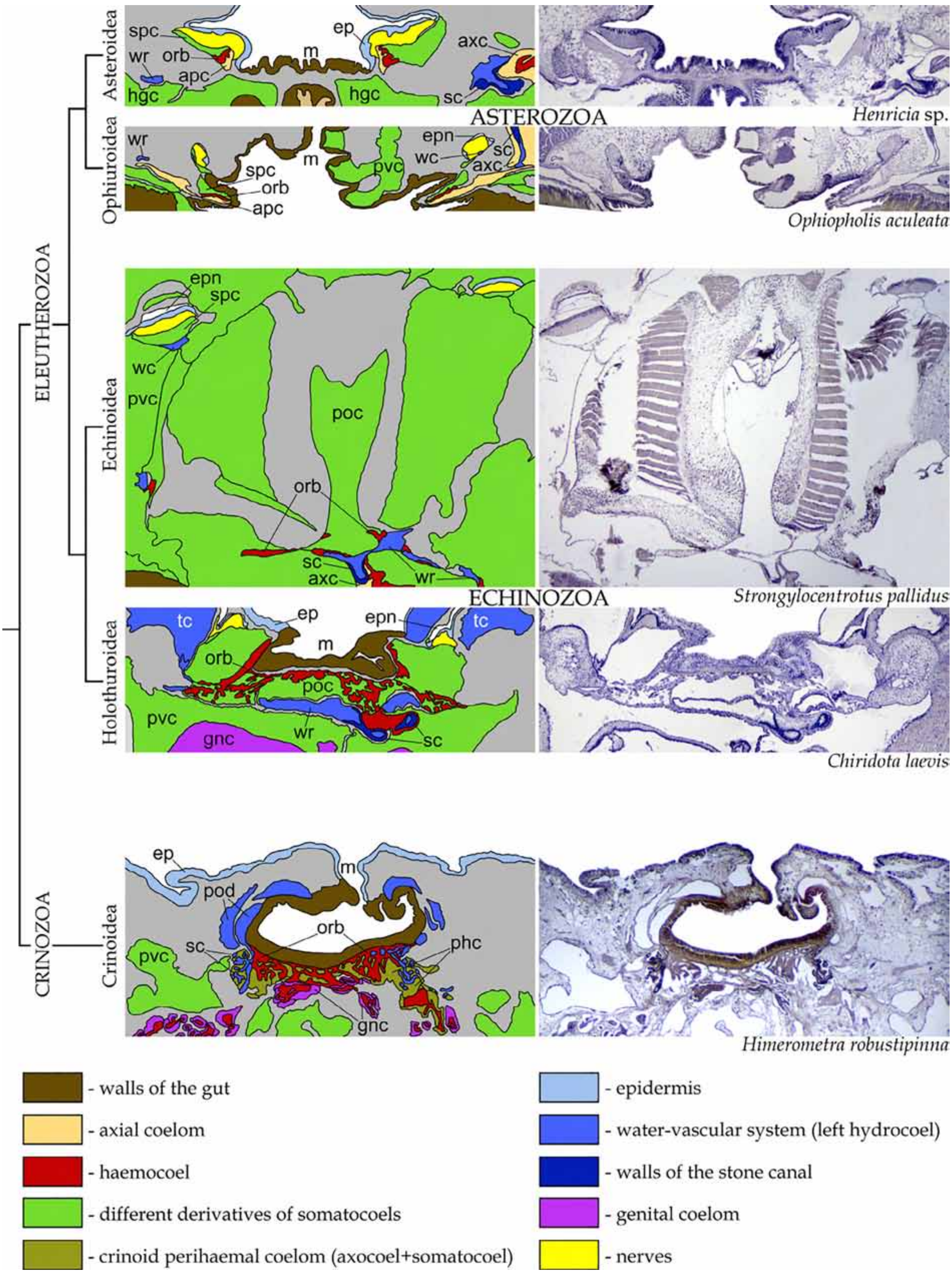

FIGURE 12 Circumoral complex in different classes of modern echinoderms. Oral surface is overhand on all schemes and photos. Gray area on the schemes shows a mesh of calcareous structures and haemocoelic lacunae. Taxonomic scheme is based on Janies, Voight, & Daly, 2011. apc, axocoelomic perihaemal ring; axc, axial coelom; ep, epidermis; epn, epineural canal; gnc, genital coelom; hgc, hypogastric coelom; m, mouth; orb, oral haemal ring; phc, perihaemal coelomic ring; poc, perioral coelom; pod, podia; pvc, perivisceral coelom; sc, stone canals; spc, somatocoelomic perihaemal ring; tc, tentacular coelom; wc, radial water canal; wr, water ring

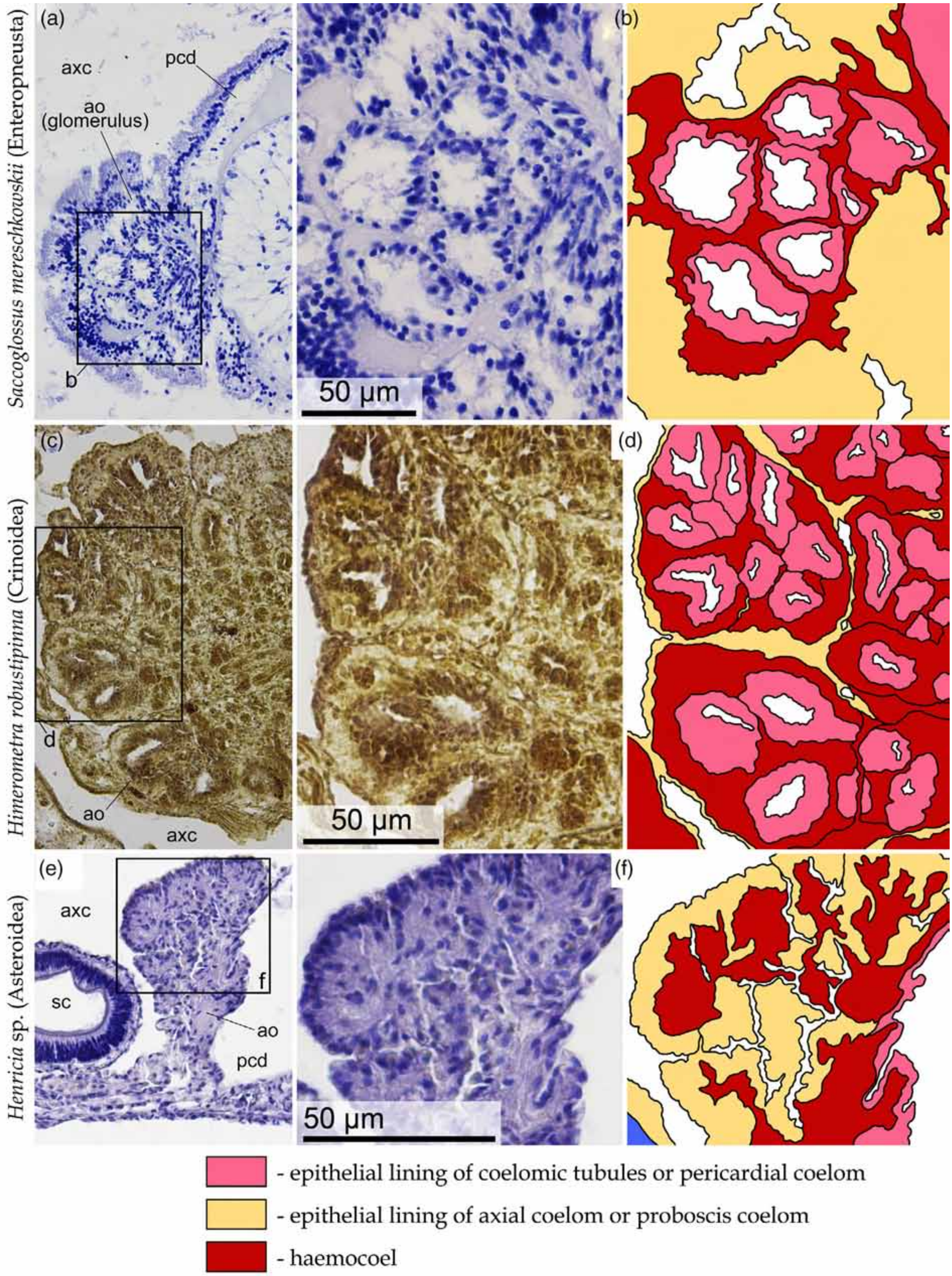

FIGURE 13 (a,b) *Saccoglossus mereschkowskii*. Histological structure of enteropneust glomerulus (Ezhova & Malakhov, 2010a, p. 772, fig. 1E; Ezhova & Malakhov, 2010b, p. 900, fig. 1A, p. 920, fig. 18). (c,d) *Himerometra robustipinna*. Histological structure of the crinoid axial organ. (e,f) *Henricia* sp. Histological structure of the asteroid axial organ. Comparison of the histological structure of the enteropneust glomerulus with the echinoderm axial organ. ao, axial organ or glomerulus; axc, axial or proboscis coelom; pcd, pericardial coelom; sc, stone canal

system more closely resembles that of living holothurians than any other living group of echinoderms" (Haugh, 1973). Additionally, Mortensen (1920, p. 68), based on the development of the primary gonad of crinoids in the interradius CD, indicates the similarity of Crinoidea and Holothuroidea, and supposes that the ancestors of crinoids had a single gonad in the interradius CD, as is the case in modern holothuroids.

Speaking about the arrangement of the circumoral complex, it is important to note first of all that its arrangement in Asterozoa differs from Echinozoa (Ezhova et al., 2018, p. 805, Figure 9): the oral haemal ring of Echinozoa lies between the water ring (left hydrocoel) and the perioral coelomic ring (one of derivatives of the left somatocoel), and in Asterozoa, the oral haemal ring lies between the special perihaemal rings, axocoelomic and somatocoelomic (i.e., the derivatives of the left axocoel and the left somatocoel). The water ring and the perioral ring in Asterozoa do not closely adjoin to each other like in Echinozoa, but lie at a distance from each other. The arrangement of the circumoral complex of Crinoidea is again closest to Holothuroidea (Figure 12): the oral haemal ring is located directly under the mouth and, from the other side, the water ring and the somatocoelomic cavity are adjacent to it. However, in holothuroids, the oral haemal ring lies along the perioral coelom, which originates from the left somatocoel; in crinoids, the oral haemal ring lies either in the left axocoel (Balser & Ruppert, 1993), in the cavity, which is formed by fusion of the left axocoel and the somatocoels, or in the somatocoel (according to Heinzeller & Welsch, 1994). In the latter case, the similarity of the circumoral complex of Crinoidea and Holothuroidea becomes even more obvious (Figure 12). Most likely, the axocoelomic perihaemal coelom in Crinoidea is actually fused with the oral part of the perivisceral coelom (left somatocoel). Then, the cavity which surrounds the oral haemal ring is the result of this fusion, but is not the axocoel or somatocoel in its pure form.

Another interesting similarity was found in the comparison of the histological structure of the axial organ of *H. robustipinna* with the axial organ of the acorn worm *Saccoglossus mereschkowskii* (Hemichordata, Enteropneusta). The haemocoel of crinoid axial organ in its tubular region is pierced by the elongated tufts of coelomic tubules lined with the cuboidal coelothelium (Figure 13c,d). These tubules end blindly on both sides, without any connection with other coeloms or with the environment. The "glandular tubules" within the axial organ were described for *Nemaster rubiginosa* (see Holland, 1970), and for other crinoids (Heinzeller & Welsch, 1994; Welsch, Heinzeller, & Holland, 1994). Engle (2013) in her dissertation also describes these tubules within the thickness of the axial organ: "in the oral half of the glandular axial organ, there are further tubular entities … The tubules are formed by an epithelium of cuboidal to columnar monociliated cells, whose apical surfaces are directed toward the tubule's center and which are underlain by a continuous basal lamina on the tubules' outside, toward the glandular axial organ's hemal space." Similar tubules lined by the cuboidal coelothelium fill the haemocoelic thickness in the glomerulus of *S. mereschkowskii* (Ezhova & Malakhov, 2010a, 2010b). These tubules represent the numerous canals of the pericardial coelom (right protocoel) of *S. mereschkowskii*, which pass between the haemocoelic lacunae, and this entire system is surrounded by the left protocoel (proboscis coelom; Figure 13a,b). The enteropneust pericardial coelom has no openings to the environment and does not communicate with any other coelom (Balser & Ruppert, 1990; Benito & Pardos, 1997; Cameron, 2000; Ezhova & Malakhov, 2010a, 2010b; Fedotov, 1923, 1924; Hyman, 1959). According to different authors (Barrois, 1888; Dawydoff, 1948; Seeliger, 1892), during the larval development of crinoids, the right axocoel (future pericardial coelom) does not appear at all; "the common rudiment of unpaired axo- and hydrocoel is separated" from the anterior bubble of the archenteron (Ivanova-Kazas, 1978, p. 97). Balser and Ruppert (1993, p. 89) mention that "a pericardium, or dorsal sac, is likewise as yet unidentified" in crinoids. Engle (2013, p. 75) does not mention the pericardium or right axocoel for *Antedon bifida*, but she describes a "small ventral coelom", which "can be found … at the aboral end of the axocoel". In most echinoderms (Asteroidea, Ophiuroidea, and Echinoidea), the haemocoelic lacunae of the axial organ lie between the folds of the coelothelium of mostly the left protocoel (left axocoel, i.e., the axial coelom) and partly the right protocoel (right axocoel, that is, pericardial coelom; Figure 13e,f). We did not find such tufts of coelomic tubules, between which lie the haemocoelomic lacunae, during our earlier studies of eleutherozoan axial complexes. From this point of view, the axial complex of crinoids is closer in its histological structure to the "heart-kidney" of hemichordates (Ezhova & Malakhov, 2010a, p. 772, fig. 1E; Ezhova & Malakhov, 2010b, p. 900, fig. 1A, p. 920, fig. 18) than to the axial complex of other echinoderms.

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AUTHOR CONTRIBUTIONS

Olga Ezhova: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; supervision; validation; visualization; writing-original draft; writing-review and editing. **Vladimir Malakhov:** Conceptualization; data curation; formal analysis; funding acquisition; methodology; project administration; supervision; validation.

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 article.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon the request.

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