

Coelomic System of the Sea Urchin *Strongylocentrotus pallidus* (Echinodermata, Echinoidea) and the Issue of Coelomic Metamery in Echinoderms

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Abstract—The representatives of the main phylogenetic clades of Bilateria are characterized by metamery. In Deuterostomia, metamery is presented in hemichordates and chordates. Sea urchins have 7 metameric coelomic rings located along the oral-aboral axis of the body. A similar coelomic metamery is also a sign of representatives of other classes of echinoderms. We hypothesize that the metameric coelomic rings in echinoderms are inherent of the common ancestor of Deuterostomia. Asymmetry in the structure of echinoderm coeloms is the result of ancestral forms lying on the right side of the body, which led to a reduction of the coeloms on the right side. During the sedentary lifestyle, the left-side coeloms formed metameric coelomic rings.

Keywords: metamery, coeloms, asymmetry, origin of echinoderms

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In the modern system of the kingdom Animalia, there are four main groups of bilaterally symmetric animals: Trochozoa, Lophophorata, Ecdysozoa, and Deuterostomia [1, 2]. Coelomic metamery is present in the representatives of all four Bilateria branches, which suggests that the common ancestor of Bilateria was a segmented organism [2–4]. Among Deuterostomia, chordates (Chordata) have undoubted metamery. Metamery of Hemichordata is expressed as metameric gill slits and gill pores, their origin is probably associated with metamery of metanephridia and endodermal intestinal pockets [5]. All this allows us to discuss whether metamery is preserved in echinoderms (Echinodermata). Metameric structures are known in echinoderms, but this metamery affects body appendages, i.e., the metameric arrangement of sclerites in the stalk of sea lilies, metameric vertebrae in the hands of ophiurs, etc. The issue of presence of the coelomic metamery in echinoderms, like that in the vertebrates, was discussed from the standpoint of the theory of primary heteronomous metamery presented by Ivanov [6]. According to Svetlov and Ivanova-Kazas [7, 8], three pairs of coeloms in dipleurula are considered as larval segments, while in chordates not only larval, but also post-larval segments (trunk somites) are developed [9]. Here, we try to answer the question of whether echinoderms retain the remains of somatocoelous coelomic segments comparable to

metameric trunk somites of chordates. It is possible that echinoderms retain remnants of metamery, which was possessed by the common ancestor of Deuterostomia, and, probably, by the common ancestor of Bilateria. A new study of the coelomic organization of a typical representative of echinoderms, the sea urchin *Strongylocentrotus pallidus* (Sars, G.O. 1871), was performed using modern 3D reconstruction methods in order to obtain an objective idea of the relative position of the coelomic compartments.

Seven specimens of *S. pallidus* (Echinoidea), collected in the vicinity of the Dalnie Zelentsy Biological Station (Murmansk Marine Biological Institute, the Barents Sea) were collected from a depth of 20–30 m. The diameter of the collected specimens was approximately 10 mm. The material was fixed in Bouin's solution and then transferred for conservation in 70% ethyl alcohol. EDTA solution (Trilon B, Helaton-3) was used for decalcification. Standard histological methods of material dehydration in alcohols of ascending concentration, Paraplast mounting, and preparing a series of 5 µm thick slides using a Leica RM 2125 microtome were applied. Sections were stained with Caracci's hematoxylin. The slides were examined under a Mikmed-6 microscope (LOMO, St. Petersburg, Russia, 2018) with a mounted MC-12 digital camera. Detailed 3D reconstruction of the coelomic system was carried out for a series of histological sections using the AMIRA software, version 6.5.0. In total, 240 slides of oral-aboral series were used for reconstruction.

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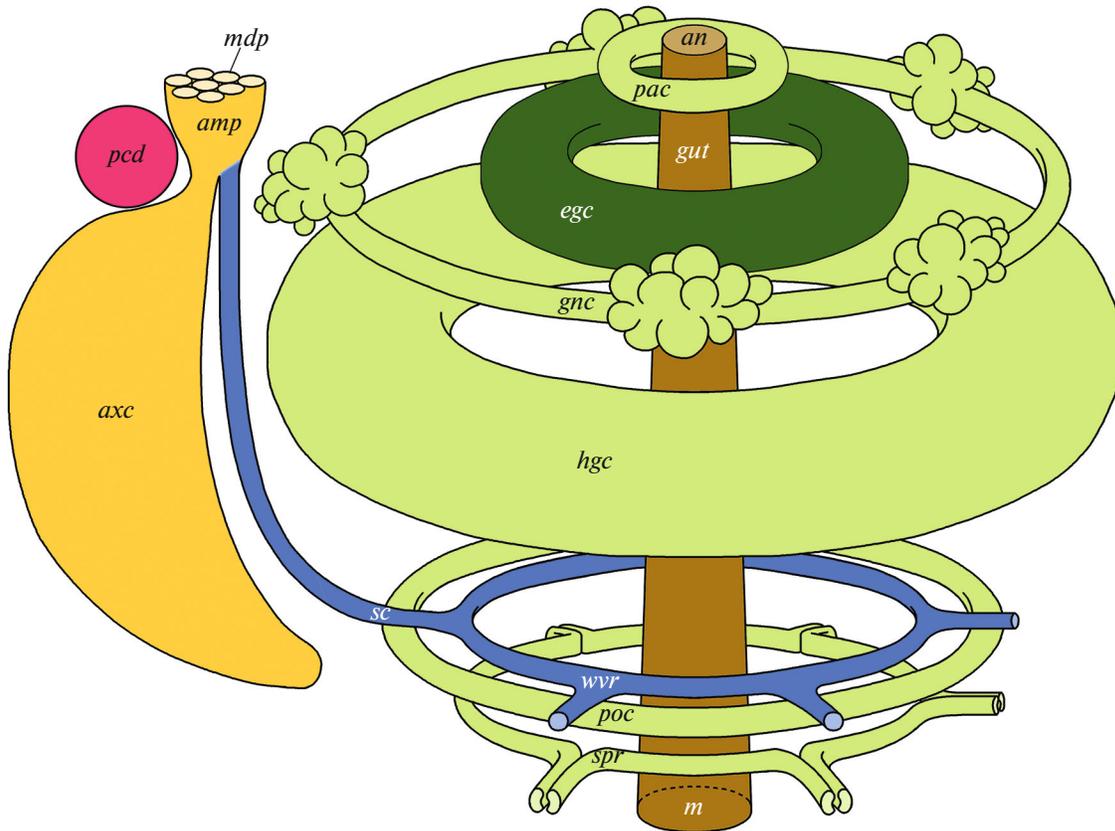


Fig. 1. Structure of the coelomic system of *Strongylocentrotus pallidus*: *amp*, madreporic ampulla; *an*, anus; *axc*, axial coelom; *egc*, epigastric coelom; *gnc*, genital coelom; *gut*, gut; *hgc*, hypogastric coelom; *m*, mouth; *mdp*, madreporic plate; *pac*, perianal coelom; *pcd*, pericardial coelom; *poc*, perial coelom; *sc*, stone canal; *spr*, somatocoelomic perihaemal ring; *wvr*, ambulacral ring.

The ambulacral ring (water ring) of *S. pallidus* (a derivative of the left hydrocoel) lies in the middle part of the body and surrounds the pharynx above Aristotle's lantern (Figs. 1, 2, *wvr*). It appears to be inserted between two other coelomic rings: the perivisceral coelom (Fig. 1, *hgc*), which represents the main coelom of the sea urchin, and an extensive perial coelom (Fig. 1, *poc*), which surrounds the jaw apparatus. There is an oral blood ring between the coelothelia of all three coelomic rings (ambulacral, perivisceral, and perial).

The stone canal (Fig. 1, *sc*) is located in the upper, aboral half of the body of *S. pallidus*, and at its oral end flows into the ambulacral ring (Fig. 1, *wvr*). The aboral end of the stone canal opens into the madreporic ampulla (Fig. 1, *amp*), which is a very flattened coelomic cistern (a derivative of the left axocoel). The madreporic ampulla communicates with the external environment through a multitude of thin pore channels (up to 200 in the specimens studied) that penetrate through the madreporic plate (Fig. 1, *mdp*). From the side of radius D, a stone canal (Fig. 1, *sc*) and an axial coelom (a derivative of the left axocoel) both open from below into the madreporic ampulla (Fig. 1, *axc*).

The axial coelom of *S. pallidus* (Fig. 1, *axc*) is extended along a stone canal, to which it adjoins closely from the side of radius C. On the aboral side, the axial coelom looks like an extensive cavity, clearly visible on histological sections. In other areas, the cavity of the axial coelom is practically displaced by an overgrown axial organ and, therefore, is represented by narrow slit-like spaces. On the aboral side, the axial coelom communicates with the madreporic ampulla (Fig. 1, *amp*), on the oral side, it ends with no opening at the confluence of the stone canal into the ambulacral ring. The axial coelom of *S. pallidus* does not form axocoelomic perihaemal coelomic ring.

The pericardial coelom of *S. pallidus* (a derivative of the right axocoel) (Fig. 1, *pcd*) is a disc-shaped coelomic compartment that does not communicate with any other coelomic cavities. On the aboral side, the pericardium is bordered by the madreporic ampulla (Fig. 1, *amp*). On the oral side, from the side of radius C, the pericardium is adjacent to the axial coelom (Fig. 1, *axc*) and the genital coelom (Fig. 1, *gnc*), and from the side of radius D, to the perivisceral coelom (Fig. 1, *hgc*).

The genital coelom (a derivative of the left somatocoel) (Figs. 1, 2, *gnc*) is a coelomic ring adjacent to the

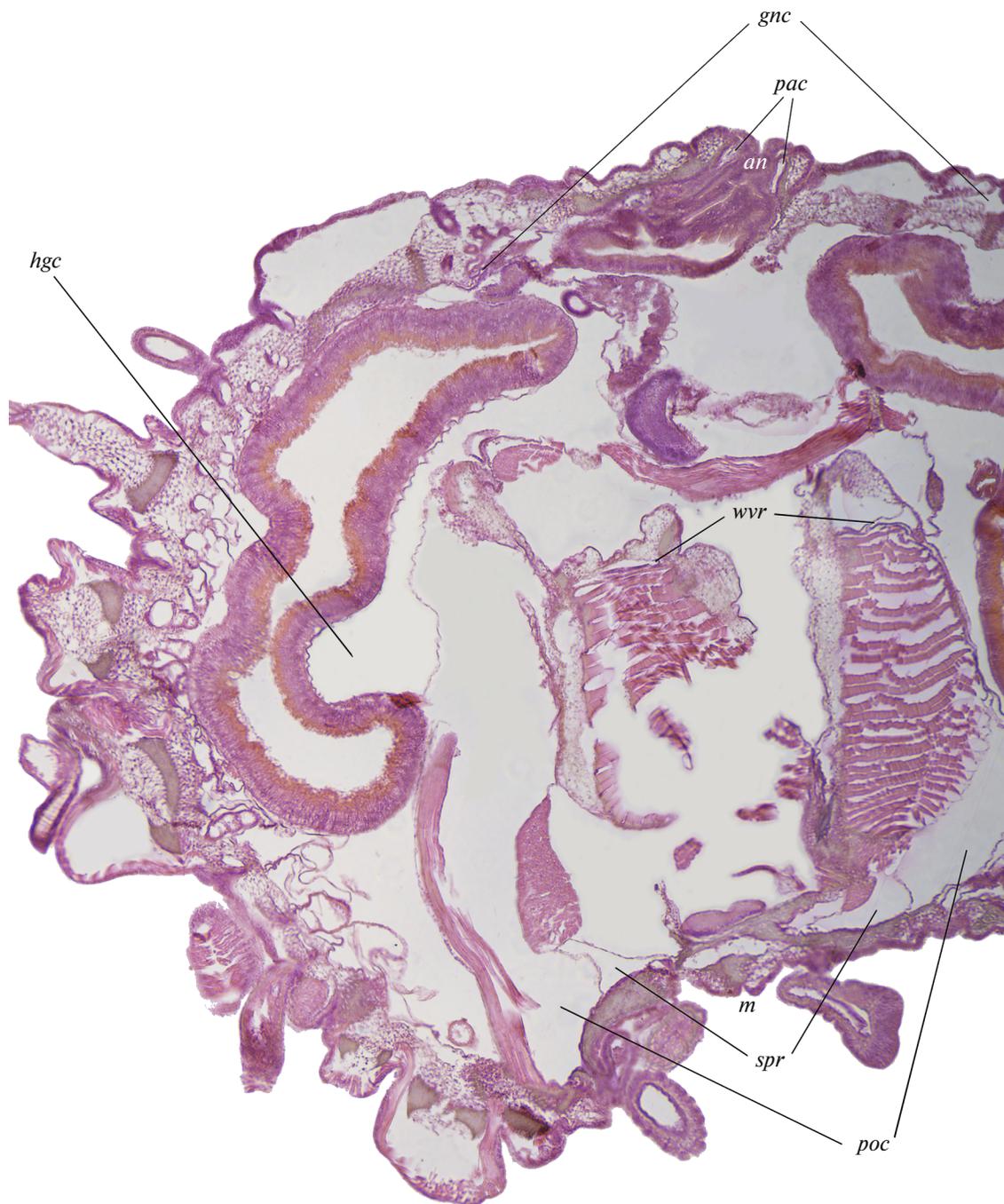


Fig. 2. Derivatives of the left somatocoel of *Strongylocentrotus pallidus* at the sagittal transect in the CD-interradius area: *an*, anus; *gnc*, genital coelom; *hgc*, perivisceral coelom formed by fusion of hypogastric and epigastric coeloms; *m*, mouth; *pac*, perianal coelom; *poc*, perioral coelom; *spr*, somatocoelomic perihæmal ring; *wvr*, ambulacral ring.

aboral body wall of the *S. pallidus* and surrounding the hindgut. The genital blood ring runs in the mesentery between the genital coelom and the perivisceral coelom.

In the most aboral part of the body of *S. pallidus*, there is a small coelomic ring surrounding the hindgut. This is the perianal ring (Figs. 1, 2, *pac*), originating

from the left somatocoel. It adjoins the vast perivisceral coelom.

The perivisceral coelom (Fig. 2, *hgc*) is the next coelomic ring surrounding the intestine. It is formed as a result of the fusion of two coelomic cavities: one of the derivatives of the left somatocoel (hypogastric coelomic ring) (Fig. 1, *hgc*) and the only derivative of the

right somatocoel (epigastric coelomic ring) (Fig. 1, *egc*).

The perioral (or peripharyngeal) coelomic ring of *S. pallidus* (Figs. 1, 2, *poc*) is located in the oral side of the body and surrounds the pharynx. It has a very complex shape, since it penetrates into the inner grooves of the pyramids, into the spaces between the pyramids themselves, encloses the teeth, i.e., “enveloping” the numerous calcareous elements of the Aristotle’s lantern. The perioral coelom is surrounded by the perivisceral coelom laterally and from the aboral side. In the circumoral mesentery, the oral blood ring passes between the perivisceral and perioral coeloms.

The somatocoelomic periaemal ring of *S. pallidus* (a derivative of the left somatocoel) (Figs. 1, 2, *spr*) is located in the most oral part of the body. Here, it surrounds the jaw apparatus and adjoins the perioral coelom. A pair of coelomic outgrowths extend from the somatocoel periaemal ring in each radius.

Therefore, the coeloms of *S. pallidus*, with the exception of the axial and pericardial ones, form a series of 7 circum-intestinal rings located along the oral–aboral axis of the body. A similar arrangement of coelomic rings is typical for other groups of echinoderms. In particular, in different species of sea stars, it is possible to find 6 to 7 rings; in ophiurids, 7; in sea cucumbers, 4; and in sea lilies, 4 [10–12].

The presence of metameric coelomic rings in Echinodermata suggests that metamery of echinoderms occurs from metamery characteristic of the common ancestors of Deuterostomia (Fig. 3). Metamery of Hemichordata has several elements: (1) the pre-oral segment carrying asymmetrical left (proboscis) and right (pericardial) coeloms, (2) the perioral segment carrying symmetrical collar coeloms, and (3) the trunk coelom, where dissepiments are not preserved, but metamery of the trunk is evident in the metamery of the gill pores, gill slits, and intestinal diverticula. In Chordata, metamery is expressed by premandibular, mandibular, and trunk somites. This suggests that the common ancestor of Deuterostomia had metamery similar to that of Annelida or Arthropoda embryos, i.e. possessed a pre-oral segment, a perioral segment, and a metameric body. Each segment contained a pair of coelomic sacs. In Hemichordata and Cephalochordata, there is an asymmetry in the coelom structure of the pre-oral region. It is known that echinoderms have a much more pronounced asymmetry of coeloms than all other Deuterostomia. In echinoderms, only the left hydrocoel is retained (homologue of the left collar coelom). According to our study and other researchers [10–12], the structure of the trunk coeloms is also asymmetric. In particular, *S. pallidus* has five coelomic rings originating from the left somatocoel of the larva, and only one originating from the right somatocoel. The same ratio is typical for sea stars, ophiurs, sea cucumbers, and sea lilies.

In order to explain the asymmetric organization of echinoderms, there were hypotheses stating the probable ancestors of echinoderms were facing the substrate with the right side of the body, which resulted in asymmetry of the coeloms [13, 14]. At the same time, the tentacular apparatus of the left side of the body and the left hydrocoel were preserved, while the tentacular apparatus on the right side and the corresponding right hydrocoel reduced completely [13, 14]. It can be assumed that in this case the majority of metameric somatocoelous coeloms of the right side also underwent reduction (Fig. 3).

On the other hand, Holland [15] suggests that the reduction of the right anterior and medial coeloms is explained by lying on the left side. Subsequently, the ancestors of echinoderms switched to sedentary life; as a result, secondary radial symmetry was formed, and the preserved left coeloms of the collar and trunk areas formed the circum-intestinal coelomic rings (Fig. 3). It is curious that in Echinodermata even the arrangement of the coelomic rings corresponds to the order in which the metameric coeloms are located in hemichordates and chordates. The axocoel periaemal ring (which is absent in sea urchins) corresponds to the anterior proboscis coelom of hemichordates (premandibular somites of chordates), followed by an ambulacral ring homologous to the left collar coelom of hemichordates (left mandibular somite of chordates), followed by the somatocoelomic periaemal coelom, perioral coelom, hypogastric coelom, and genital coelom, which correspond to the left trunk somites of chordates. The epigastric coelom, originating from the right somatocoel of the larva, probably corresponds to the stalk of the possible ancestor, which was used as an anchoring organ. In the framework of the proposed hypothesis, the ancestors of echinoderms were anchored in the substrate by a modified posterior end of the body; hence, the stalk of sedentary representatives of this phylum was formed on its basis. At first glance, the latter assumption is contradicted by the fact that the larvae of modern sea lilies attach to the substrate by the pre-oral part of the body. This fact is usually interpreted as evidence that the stalk of sea lilies is derived from the pre-oral lobe of the larva. However, if this had been true, then in the stalk of sea lilies there would have been derivatives of the axocoel (preoral coelom). However, in the stalk of sea lilies, there are derivatives of the right somatocoel (chambered organ). In our opinion, two processes are reflected in the ontogeny of sea lilies: 1) the crawling of ancestral forms on the pre-oral lobe, similar to what is now taking place in the pterobranch hemichordates (Graptolithoidea, formerly Pterobranchia); and 2) attachment to the substrate by the posterior end of the body, usual for young Enteropneusta.

Undoubtedly, the proposed hypothesis needs to be substantiated by the data of modern developmental biology and supported by paleontological material.

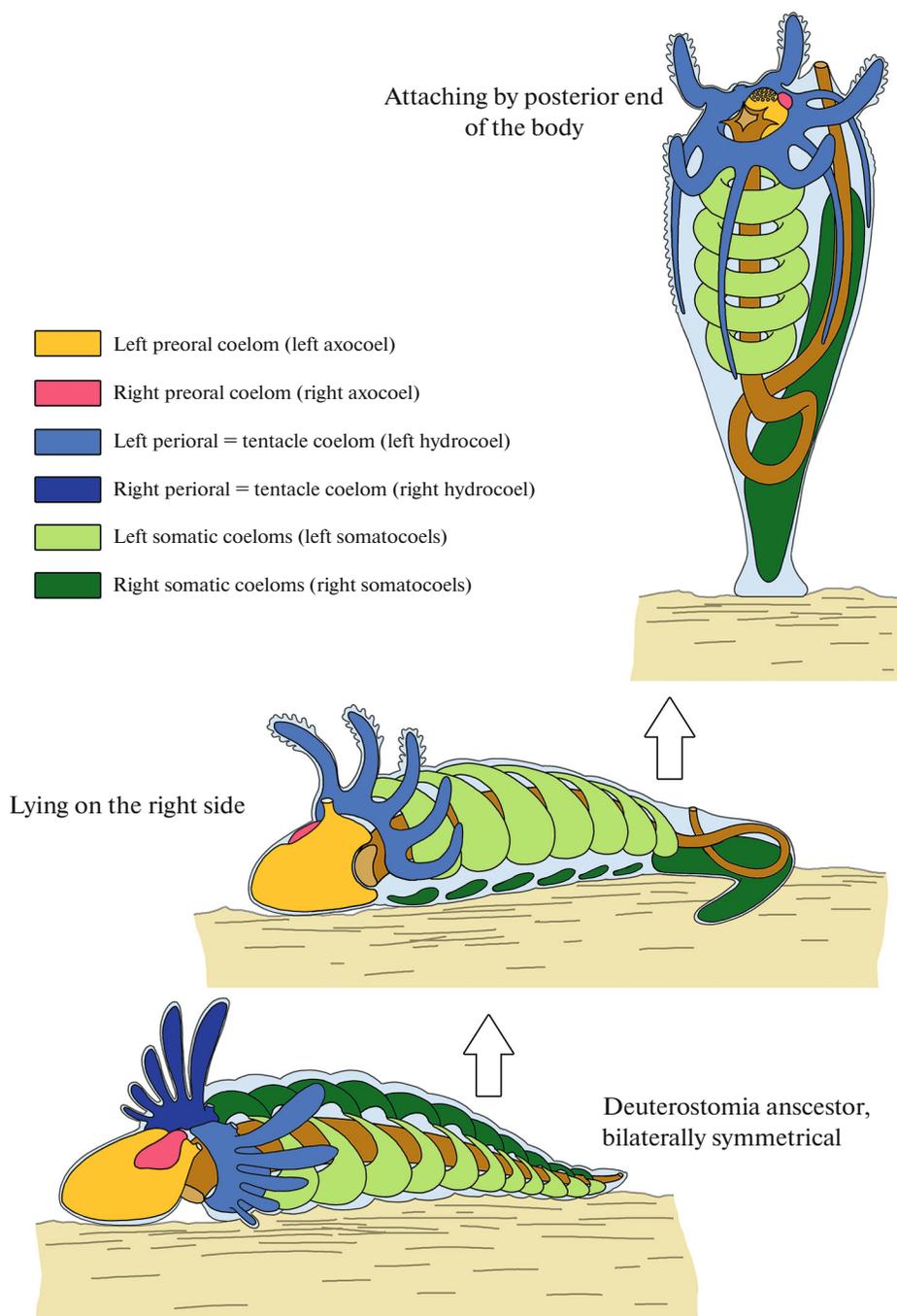


Fig. 3. Reconstruction of the possible evolution of the coelomic system of Echinodermata.

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COMPLIANCE WITH ETHICAL STANDARDS

All applicable international, national and institutional guidelines for the use of animals have been followed.

CONFLICT OF INTEREST

The authors have no financial or any other conflicts of interest. All authors have read the final version of the manuscript.

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