

Innervation of Unpaired Branchial Appendages in the Annelids *Terebellides cf. stroemii* (Trichobrachidae) and *Cossura pygodactylata* (Cossuridae)

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Received March 13, 2017

Abstract—We studied the innervation of unpaired branchial appendages using confocal laser scanning microscopy in two annelid species: *Terebellides cf. stroemii* (Trichobrachidae) and *Cossura pygodactylata* (Cossuridae). The branchial filament was found to be innervated by one unpaired segmental nerve coming from the ventral nerve cord at the level of chaetiger 2 in *C. pygodactylata*. This nerve lies transversally along the body wall and comes laterally to the base of the branchial filament. Such a structure indicates that (1) the branchial filament is unpaired and neither represents merged paired branchiae nor is related in its origin to prostomial appendages or peristomial ones, and (2) the branchial filament is the result of a shift of one of the paired segmental branchiae with parallel reduction of the second branchia in this pair. The branchial organ of *T. cf. stroemii* is innervated by paired segmental nerves from the first and second chaetigers. The segmental nerves are connected by longitudinal nerves going on the lateral sides of the body closer to the dorsum. One nerve on each side proceeds to the anterior part of the branchial stalk, and another nerve proceeds to the posterior part. All these nerves have transversal connections. The anterior stalk nerves come into the anterior branchial lobes, while the posterior nerves come to the posterior lobes. In the branchial lobes, the nerves give rise to thinner nerves, which go to each of the branchial lamellae. The present study confirms that the branchial organ of *Terebellides* has a paired nature and originates from segmental branchiae. Based on the number of innervating segmental nerves, we can conclude that the branchial organ of *T. cf. stroemii* is formed by two pairs of merged branchiae.

Keywords: Annelida, branchiae, buccal tentacles, innervation, cLSM, *Cossura*, *Terebellides*

DOI: 10.1134/S1062359018070166

Unpaired appendages and structures in annelids are mainly located on the prostomium (unpaired antennae). Segmental appendages, including the appendages of the peristomium (palps, tentaculiform antennae, parapods, and branchiae), are usually paired. Some segmental structures can be unpaired, such as, for example, the unpaired nephridial opening on the dorsal side of the body (Sabellidae, Serpulidae, Sabellariidae, and Capitellidae); such openings are considered as two merged structures (Ushakov, 1955; Rouse, Pleijel, 2001). Unpaired branchiae have been found in one species of the family Terebellidae, *Pista unibranchia* Day 1963; one genus of the family Trichobrachidae, *Terebellides*; and in the family of Cossuridae. This is a study of the origin of unpaired branchiae in *Terebellides cf. stroemi* Sars 1835 (Trichobrachidae) and *Cossura pygodactylata* Jones 1956 (Cossuridae).

The branchiae of *Terebellides* consist of a stalk, which has a medial-dorsal position, and four lamellate lobes (Figs. 1c, 1d). The stalk is usually considered as two merged pairs of segmental branchiae (Ushakov, 1955; Holthe, 1986, 1986a; Hutchings, Peart, 2000; Zhirkov, 2001), although the number of segments

involved in the formation of this appendage is unknown (Parapar et al., 2016). According to the data obtained in a study on the morphological and ultrastructural traits of branchiae in *Terebellides stroemi* (Jouin-Toulmond, Hourdez, 2006), the stalk contains two pairs of celomic cavities, which corresponds with the number of branchial lobes, and an unpaired anterior celomic cavity. The authors suggested that this is a rudiment of the third pair of branchiae on the first segment, which was involved in the formation of unpaired branchia. This hypothesis has been criticized by an author who did not perform histological analysis but supposed that the junction of four cylindrical celomic cavities that come to the branchial lobes leads to the formation of a cavity between them, but this cavity is not a rudiment of the anterior pair of branchiae (Muir, 2001). Other species of the family Trichobrachidae have two to four pairs of segmental branchiae. In order to determine the number of segments involved in the formation of unpaired branchia, we investigated the innervation of branchiae in *Terebellides cf. stroemi*. No special studies have been conducted on the structure of the nervous system in *Terebellides cf. stroemi*.

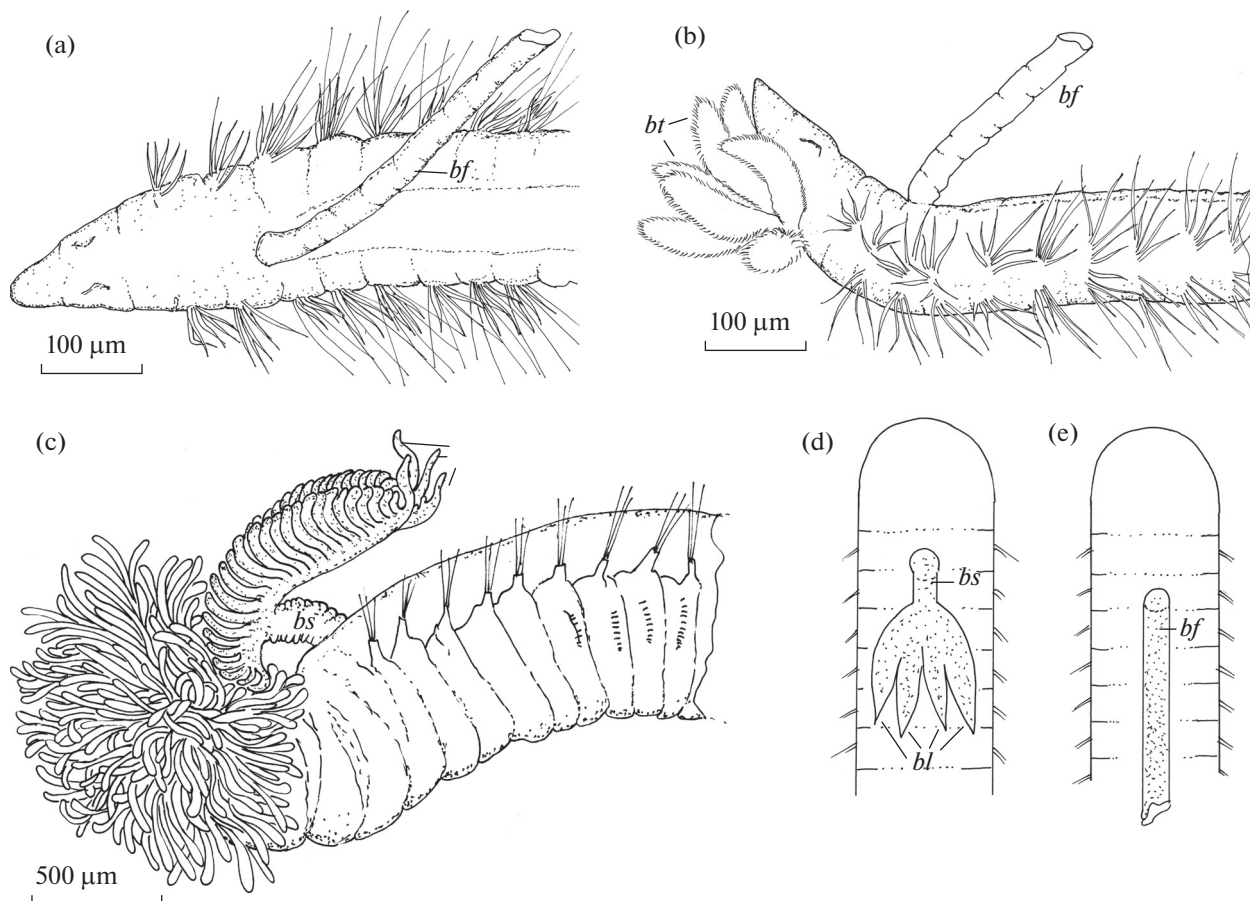


Fig. 1. *Cossura pygodactylata* (a, b, e) and *Terebellides* cf. *stroemii* (c, d): (a) the anterior part of the body, dorsal side; (b, c) the anterior part of the body, lateral side; (d, e) the position of unpaired branchial structures on the dorsal side; bf, branchial filament; bl, branchial lobes; bs, branchial stalk; bt, buccal tentacles.

Cossura is the only genus of the family Cossuridae. All the species of this family have a long unpaired branchial filament on the dorsal side of one of the anterior segments (Figs. 1a, 1b, 1e). The origin of the branchial filament in *Cossura* is unknown. It has no signs of paired nature: it consists of a long cylindrical appendage with a celomic cavity and blood vessels, and its wall contains a small amount of muscle fibers (Fournier, Petersen, 1991; Zhadan et al., 2012, 2014). The phylogenetic position of Cossuridae among other annelids is unknown. The only study based on molecular data showed that this family is probably a sibling taxon with Paraonidae, Fauveliopsidae, and Sternaspidae. None of these taxa has segmental appendages of the anterior segments.

There are several hypotheses about the origin of the branchial filament in Cossuridae:

(1) The branchial filament originates from the junction of paired structures.

(2) The branchial filament originates from the shift of initially paired segmental branchiae to the middle of the dorsal area with parallel reduction of the second segmental branchiae.

(3) The branchial filament was initially an unpaired prostomial or peristomial appendage and then was shifted in the posterior direction.

(4) The branchial filament in Cossuridae is a newly formed structure that does not originate from either the segmental paired organs or the head appendages.

This study was conducted in order to verify these hypotheses by investigating the innervation of unpaired branchial structures in two species of annelids, which have unpaired dorsal organs but belong to two different families, using confocal laser scanning microscopy. This study was based on the assumption that the pattern of innervation is an important parameter for determining the homology of organs and appendages (Gustafson, 1930; Beklemishev, 1944; Remane, 1963; Purschke, 2000; Orrhage, Müller, 2005). For example, the most recent data on the homology of the prostomium in annelids are totally based on the differences in the innervation of palps, antennae, and stomatal tentacles (Orrhage, Müller, 2005). The morphological and ultrastructural parameters of innervation of branchiae are well-defined in the family of Amphinomidae (Purschke et al., 2016). According to the data of these authors, the branchiae are

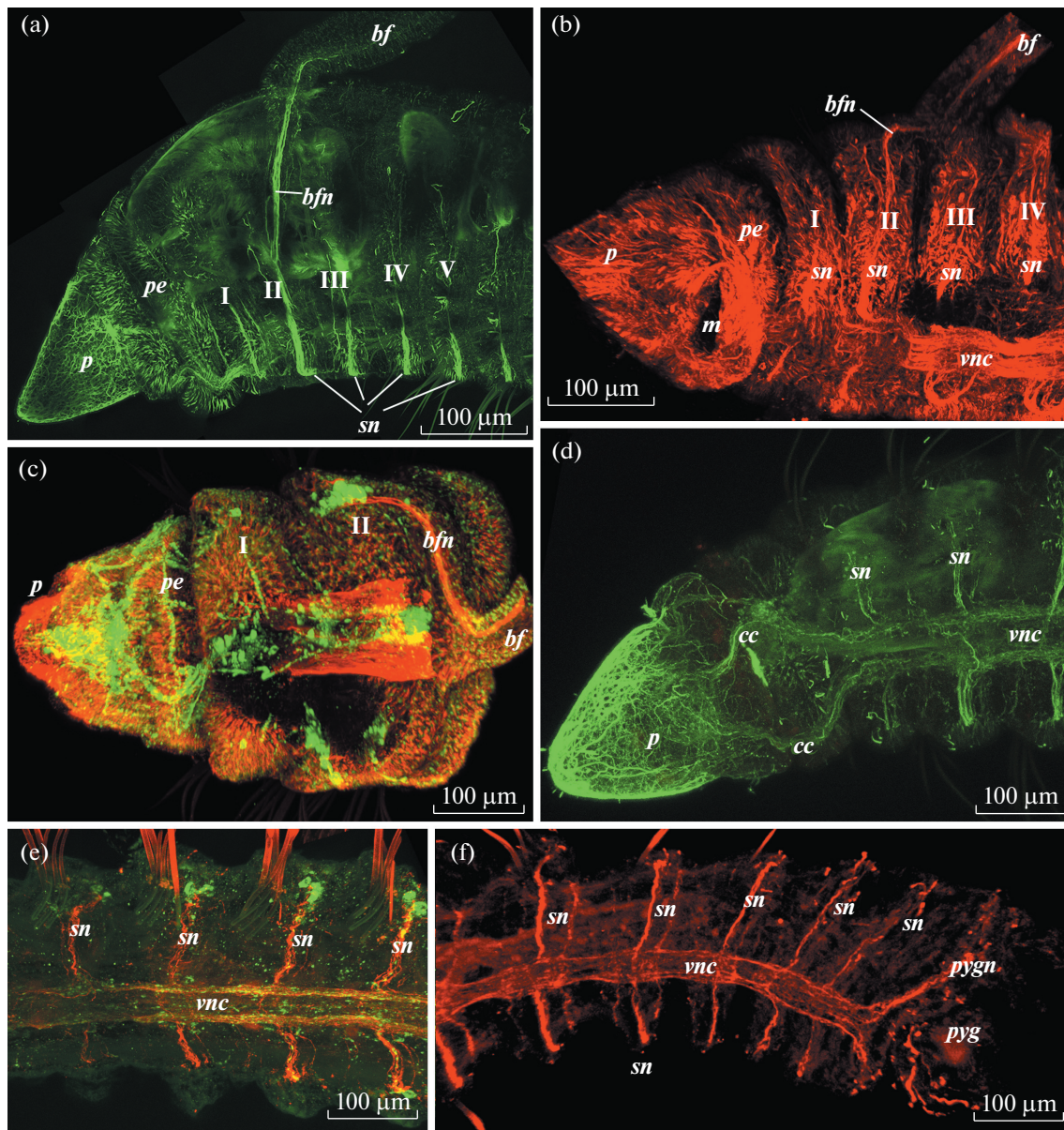


Fig. 2. *Cossura pygodactylata*, cLSM: (a) lateral view, staining for tubulin, the filament nerve to the left; (b) ventral view, staining for tubulin, the filament nerve to the left; (c) dorsal view, staining for tubulin (red) and FMRF-amide (green), the filament nerve to the left; (d) ventral view, staining for tubulin, the innervation of the anterior part, the ventral nerve cord; (e) the anterior part of the body, ventral view; (f) the posterior part of the body, ventral view; I–V are the segment of the body; bf, branchial filament; bfn, nerves of the branchial filament; bt, buccal tentacles; cc, circumpharyngeal connectives; m, mouth; p, prostomium; pe, peristomium; pyg, pygidium; pygn, nerves of pygidium; sn, segmental nerves; vnc, ventral nerve cord.

innervated by segmental nerves that come from the ventral nerve cord in the area of parapodia in each segment.

MATERIALS AND METHODS

The samples of *Cossura pygodactylata* and *Terebellides cf. stroemii* were collected in September 2016 near the Belomorsk Biological Station of Moscow State University in silty soils at a depth of 20–40 m using Ocean sediment samples with a sampling zone area of 0.1 m². The samples were washed on sieves with a

mesh size of 250 and 500 µm; then the animals were selected using a Nikon P-DSL-32 stereomicroscope (Japan).

Three individuals of *C. pygodactylata* were used to investigate the morphological structure in semifine sections. Living individuals were narcotized by magnesium chloride solution isoosmotic to the water of Belomorsk Biological Station (730 mosmol/kg) for 1 h. Then the animals were fixed in 2.5% glutaraldehyde solution with 0.1M phosphate buffer, washed in phosphate buffer three times for 20 min each, and

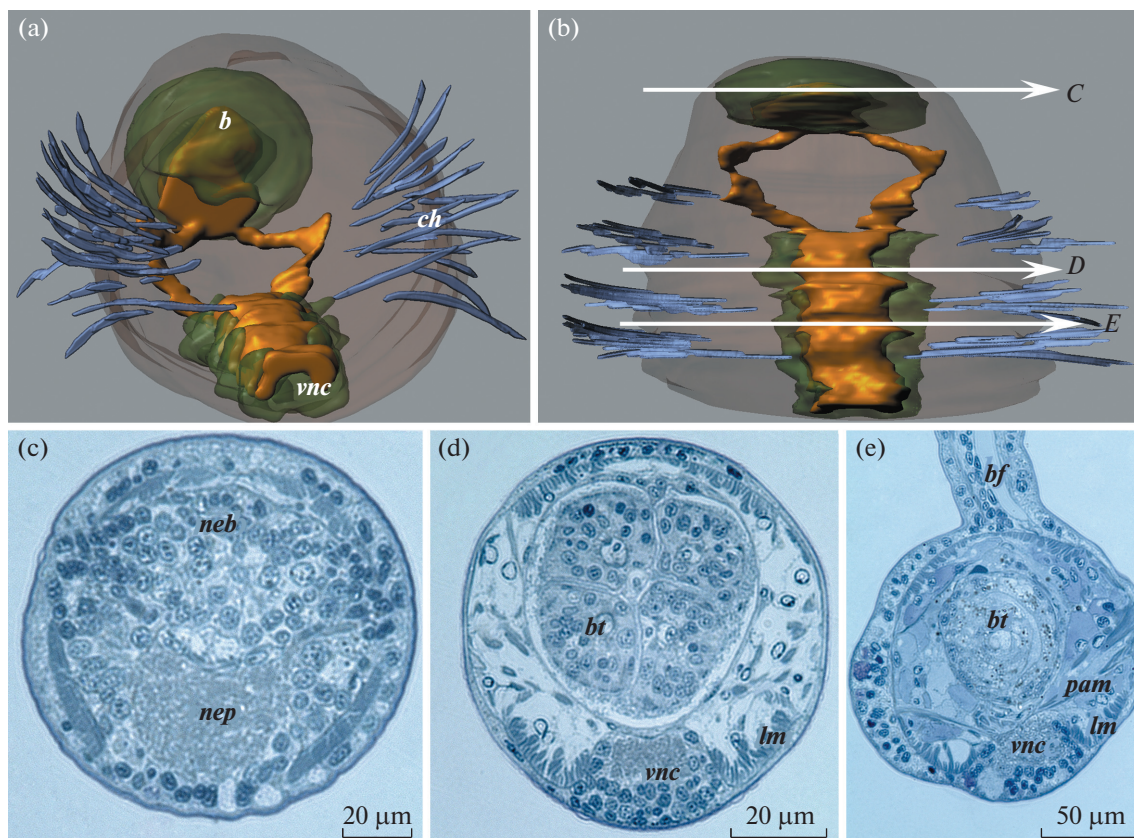


Fig. 3. *Cossura pygodactylata*: (a, b) 3D-reconstruction of the anterior part of the body: (a) posterior view; the bodies of the neuron are shown in green, and the processes (neuropils) are shown in yellow; (b) dorsal view; the section shown in c–e; (c–e) transverse sections of the anterior part of the body: (c) the anterior part of the prostomium and the brain, (d) buccal tentacles (bt), (e) the base of the branchial filament (bf); lm, longitudinal muscles; nep, neuropils; neb, neuron bodies; pam, parapodial muscles; ph, pharynx; vnc, ventral nerve cord.

fixed in 1% osmium tetroxide for 1 h in darkness. Then the animals were washed in 0.1M phosphate buffer and placed in an ascending series of ethanol concentrations up to 70%. For the semifine sections, the objects were placed in an ascending series of ethanol, acetone, and resin solution and mounted in epoxy resin Epon-812. Semifine sections (1 μ m) were made using an ultramicrotome Dupon MT 5000 (United States) with a diamond blade. The sections were stained with a mixture of water solutions of toluidine blue (1%), methylene blue (0.2%), and sodium tetraborate (1%).

One individual of *C. pygodactylata* was used for three-dimensional reconstruction based on the series of semifine sections. The sections were digitized using a Leica DM2500 microscope (Germany) with a digital camera. The series of shoots were joined in stacks using Amira 5.2.2 (United States) and aligned based on the position of sections in the animal body. The three-dimensional models were created using the Imaris 7.0.0 program (Switzerland).

For investigation of the nervous system, we used immunocytochemical staining followed by confocal laser scanning microscopy with the use of a NIKON A1 microscope (Japan). It was rather difficult to stain

the nervous system of *C. pygodactylata*. These worms are very small, and their superficial structure, such as cilia and epithelial nerves, were easily stained, but the deeper components of the nervous system were not stained (more than 20 of our attempts failed). This may result from the presence of a large number of cytoplasmic processes of myocytes in the body cavity. We developed a staining method that provided satisfactory results. Before fixation we cut the upper part of the body right after the branchial filament and removed the buccal tentacles, which were usually inverted through the mouth or the discission. Moreover, the preparations of *C. pygodactylata* were incubated in primary and secondary antibodies for a time interval longer by 1.5–2 times than the preparations of *T. cf. stroemii* and then the standard procedure (see below).

We studied a total of 12 samples of *C. pygodactylata* and five samples of *T. cf. stroemii*. Living worms were narcotized by magnesium chloride solution for 1 h and then fixed in 4% paraformaldehyde with 0.1M phosphate buffer at room temperature for 4 h. Then the worms were washed in 0.1M phosphate buffer twice for 20 min. Before stirring, the primary antibodies were incubated in a blocking solution containing 1% bovine serum albumin, 1% cold-water fish skin gela-

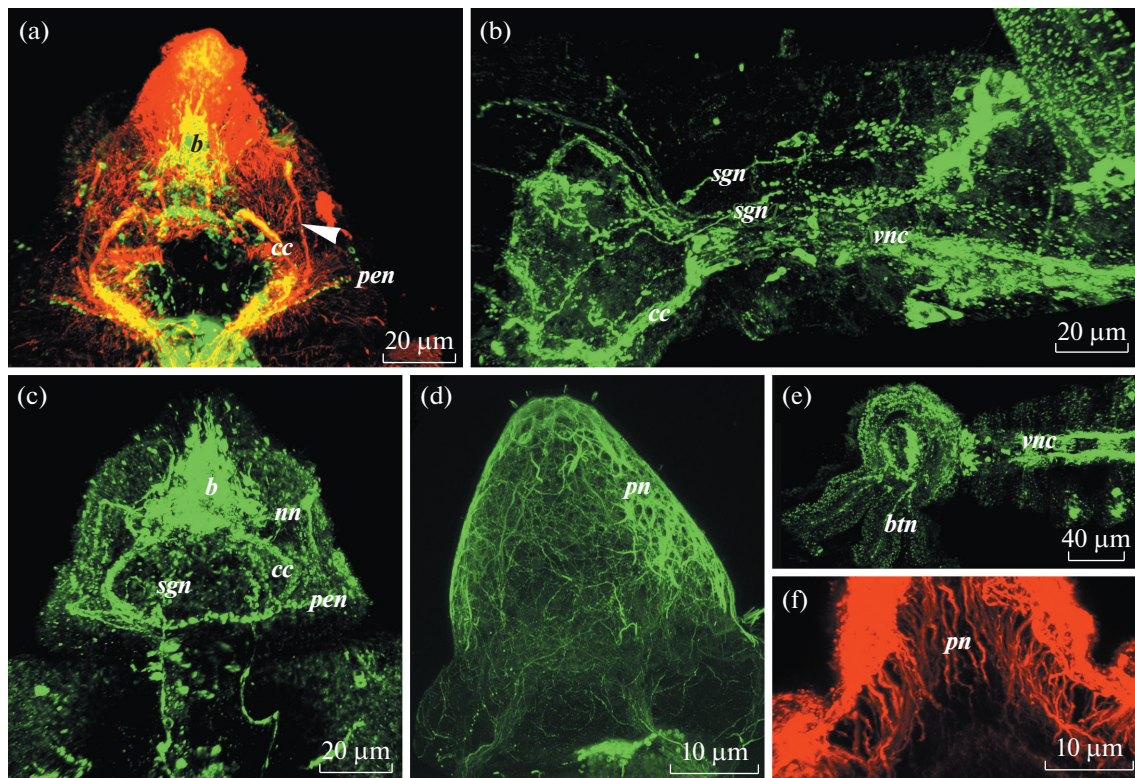


Fig. 4. *Cossura pygodactylata*, cLSM, staining for tubulin (red) and FMRF-amide (green): (a) the anterior part of the body, ventral view; (b) the ventro-lateral view of the ventral nerve cord (vnc); buccal tentacles are removed; a pair of stomatogastric nerves (sgn) starting from the posterior part of the brain; (c) the anterior part of the body, dorsal view; (d) the dorsal view, prostomium nerves (pn); (e) the ventral view, the nerves of buccal tentacles (btn); (f) prostomium nerves (pn); b, brain; cc, circumpharyngeal connectives; nn, nuchal nerves; pen, peristomium nerves; sgn, stomatogastric nerves. The arrows designate nerves that come from the site where the circumpharyngeal connectives are split into nerves to the nuchal organs. Scale: (a–c) 20 μ m; (d, f) 10 μ m; (e) 40 μ m.

tin, 4.5% Triton X100, and 0.4% Tween-20 in phosphate buffer solution. The samples of *T. cf. stroemii* and *C. pygodactylata* were incubated in primary antibodies (anti- α -tubulin Mouse (1:500), anti-tyr-tubulin Mouse (1:500), and anti-FMRF-amide Rabbit (1:1000)) with blocking solution at 4°C for 1 day and 2 days, respectively. Then the samples were washed with blocking solution for 6–8 h. The samples of *T. cf. stroemii* and *C. pygodactylata* were incubated in secondary antibodies (DAM 488 (1:20), DAR (1:20), Alexa) with blocking solution at 4°C for 1 day and 1.5 day, respectively. Some individuals of *T. cf. stroemii* were incubated in Phalloidin 60 (1:70) for 1 h to detect f-actin (the muscular system). The samples were washed in 0.1M phosphate buffer three times for 1 h each. For clarification of the stained samples, they were placed in isopropanol to benzyl benzoate with benzyl alcohol in a 3:1 ratio (Murray Clear). The nervous system was examined by confocal laser scanning microscopy with the use of a NIKON A1 microscope. The three-dimensional models were created using the Imaris 7.0.0 program (Switzerland).

Description of the entire nervous system was not the purpose of this study. However, we described the structure of some element of the nervous system in

addition to the innervation of branchiae whenever possible.

RESULTS

Cossura Pygodactylata

General Organization of the Nervous System. The ventral nerve cord consists of two close cords with a pair of thick and 2 or 3 pairs of thin segmental nerves coming from each segment (Figs. 2a, 2b, 2d–2f). The bodies of neurons lie along the whole nerve cord and do not form ganglia, although there is a small thickening in each segment (Figs. 2b–2f; Figs. 3a–3e). In the posterior part of the body, nerves come from the ventral nerve cord to the pygidium and their processes come to the anal antennae and interantennal appendages of the pygidium (Fig. 2f). Circumpharyngeal connectives start on the border of the peristomium and the first chaetiger, and each nerve of the connectives is divided into two nerves. One pair of nerves comes to the anterior part (to prostomium) and ends up near the nuchal organs (Figs. 4a, 4c; Figs. 5a, 5b). Short nerves come from the nuchal organs to the brain (nuchal nerves; Fig. 4c, nn). Another pair of larger nerves comes to the brain (Figs. 4a, 4c). The nerve cord is not split into dorsal and ventral roots. Another

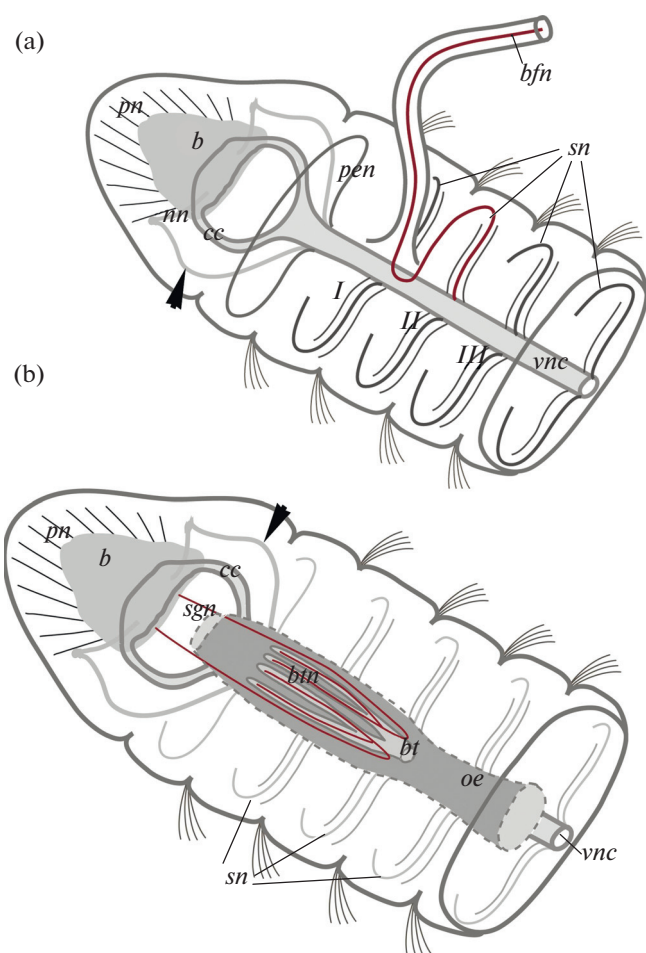


Fig. 5. *Cossura pygodactylata*, the nervous system structure: (a) the innervation of the branchial filament (shown in red); (b) stomatogastric system and the innervation of tentacles (shown in red); I–III are the segments of the body; b, brain; bfn, nerves of the branchial filament; btn, the nerves of the buccal tentacles; cc, circumpharyngeal connectives; oe, esophagus; pn, prostomium nerves; pen, peristomium nerves; sn, segmental nerves; sgn, stomatogastric nerves; vnc, ventral nerve cord. The arrows designate nerves that come from the site where the circumpharyngeal connectives are split into nerves to the nuchal organs.

pair of nerves starts from the site where the circumpharyngeal connectives are split into nerves; these are peristomial segmental nerves (Figs. 4a, 4c, pen). The brain is located in the prostomium and occupies most of its volume (Fig. 2c; Figs. 3a–3c; Figs. 4a, 4c; Figs. 5a, 5b). Numerous thin nerves start in the anterior part of the brain and come to the anterior part of the prostomium, which is covered by nerve endings, especially on its tip, where the nerve endings form a plexus (Fig. 2d; Figs. 4d, 4f; 5). A pair of stomatogastric nerves starts in the posterior part of the brain and innervates the pharynx and buccal tentacles (Figs. 4b, 4c; Fig. 5, sgn). They are split with a dichotomous pattern, and their processes come to each tentacle (Fig. 4e; Fig. 5, btn).

Innervation of the Branchial Filament. One of the segmental nerves that start from the ventral nerve cord

comes along the body wall to the branchial filament and then inside it, supposedly to the end of the filament (Figs. 2a–2c, Fig. 5a, bfn). This nerve can come from the ventral nerve cord along the body wall both on the right and on the left side (Figs. 2a–2c).

Terebellides cf. stroemii

General Organization of the Nervous System. The ventral nerve cord contains 1–2 segmental nerves per segment; it is split to form circumpharyngeal connectives near the peristomium but does not form ventral and dorsal roots, then surrounds the esophagus and comes to the brain (Figs. 6a–6e; Fig. 7a). The nerves come from the anterior–lateral parts of the brain to the upper part of the mouth and buccal tentacles; paired stomatogastric nerves start to the ventral side of the mouth, where they form a net of processes; some of the processes are branched and surround the esophagus (Fig. 6a, 6b, 6d, 6e; Fig. 7a).

Innervation of Branchiae. The branchiae are innervated by paired segmental nerves of the first and second chaetigers. Two pairs of nerves start from the nerve cord in each of these segments and come along the body wall. The segmental nerves are connected by longitudinal nerves going on the lateral sides of the body closer to the dorsum. The nerves of the anterior pair are joined with each other and with the posterior pair of nerves; a nerve that comes along the body also starts from the anterior pair of nerves (Figs. 6a–6e, Figs. 7a, 7b). To the dorsal side from these transverse nerves, two processes come from each pair of segmental nerves to the anterior and posterior parts, respectively. All these nerves have transversal connections. The anterior stalk nerves come into the anterior branchial lobes, while the posterior nerves come to the posterior lobes. Smaller nerves come from the lobes to each branchial process (Figs. 7a, 7b; Figs. 8a–8f).

DISCUSSION

Confocal laser scanning microscopy provided a detailed picture of the location of nervous system elements in the area of branchiae and the structure of the nervous system in *Cossura* and *Terebellides*.

Cossura

The family of Cossuridae is a poorly studied group of polychaetes. The internal structure (body cavity, tentacles, and the muscle system) was only studied in one species, *Cossura pygodactylata* (Tzetlin, 1994; Rouse, Tzetlin, 1997; Zhadan et al., 2014, 2015). The nervous system of Cossuridae has not been studied. We determined the structural features of the nervous system that differ between Cossuridae and all other annelids. We did not find any ventral or dorsal roots of the circumpharyngeal connectives. Such a structure of the anterior part of the nervous system without four transversal connections in the brain is not common in

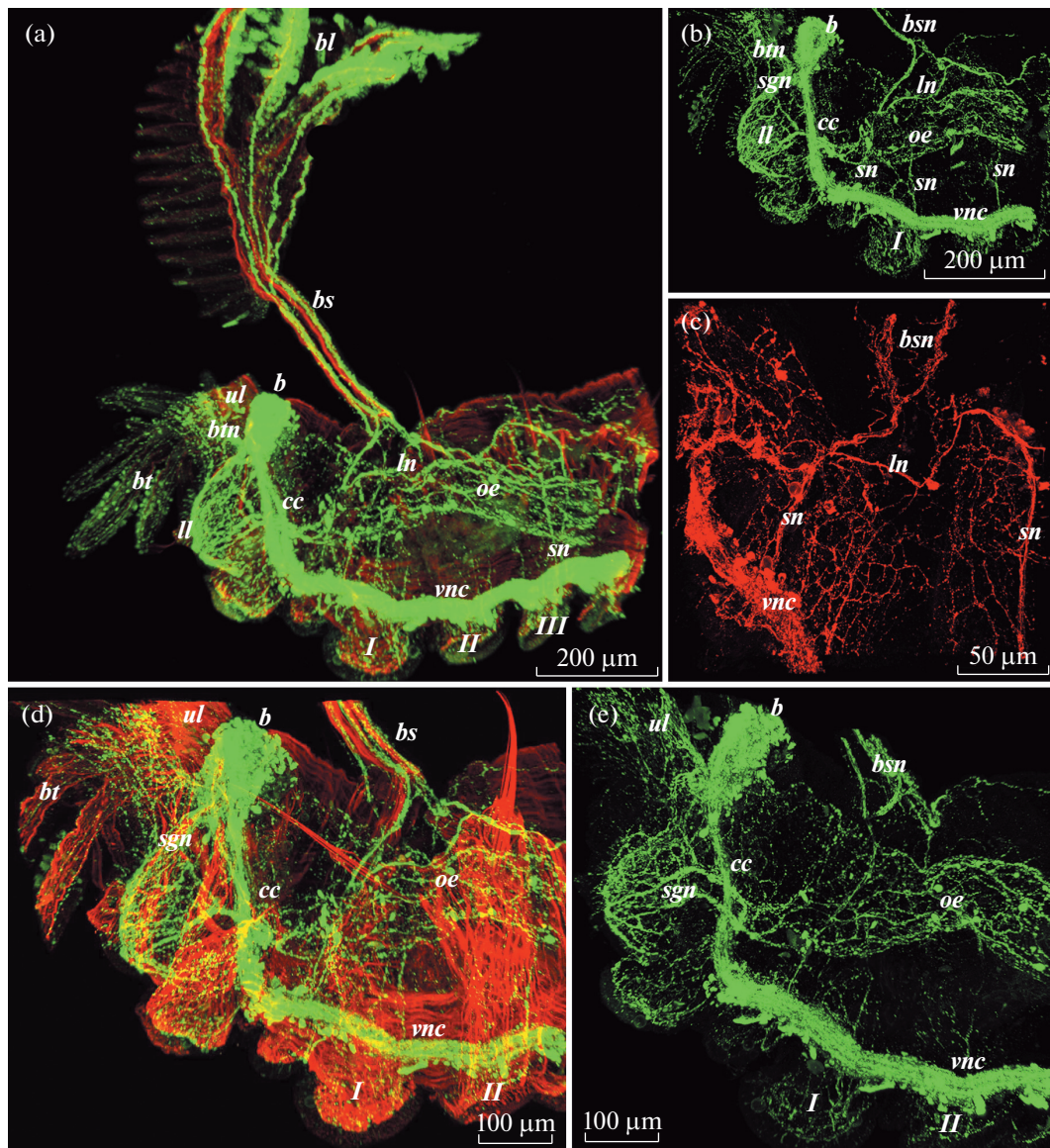


Fig. 6. *Terebellides* cf. *stroemii*, a–e cLSM, lateral views, staining: (a, d) for f-actin (red) and FMRF-amide (green); (c) for tubulin (red); I–III are the chaetigers; b, brain; bl, branchial lobes; bs, branchial stalk; bsn, the nerves of the branchial stalk; bt, buccal tentacles; btn, the nerves of the buccal tentacles; cc, circumpharyngeal connectives; ll, lower labium; ln, longitudinal nerve; oe, esophagus; sn, segmental nerves; sgn, stomatogastric nerves; ul, upper labium; vnc, ventral nerve cord. Scale: (a–b) 200 μ m; (c) 50 μ m; (d, e) 100 μ m.

annelids; it was observed only in Opheliidae, *Protodriloides* (Protodriloidae), Terebelliformia, Oweniidae, and Echiurida (Orrhage, Müller, 2005; Rimskaya-Korsakova et al., 2016). The nerve that starts from the circumpharyngeal connectives and ends up near the nuchal organs has not been found in any other polychaetes; the function of this nerve is unknown. Another characteristic feature is the ganglionization of the ventral nerve cord. Such a feature is also rare in annelids (Orrhage, Müller, 2005).

Innervation of Buccal Tentacles. We found that the buccal tentacles of *Cossura* are innervated by the stomatogastric nerves that start in the posterior part of the brain. This supports the hypothesis of Zhadan et

al. that the buccal tentacles are the processes of the dorsal axial part of the nonmuscular pharynx (Zhadan et al., 2014). The buccal tentacles originate from the dorsal part of the axial pharynx and have been found in some species of Opheliidae in the genera of *Armandia* and *Ophelina*. However, these genera are distant from Cossuridae and Opheliidae in their phylogenetic position and have a different structure of tentacles, which indicates that the buccal tentacles developed independently in these taxa (Tzetlin, Zhadan, 2009; Zhadan et al., 2015).

Innervation of the Branchial Filament. We found that the branchial filament of *Cossura* is innervated by one unpaired segmental nerve that starts from the ven-

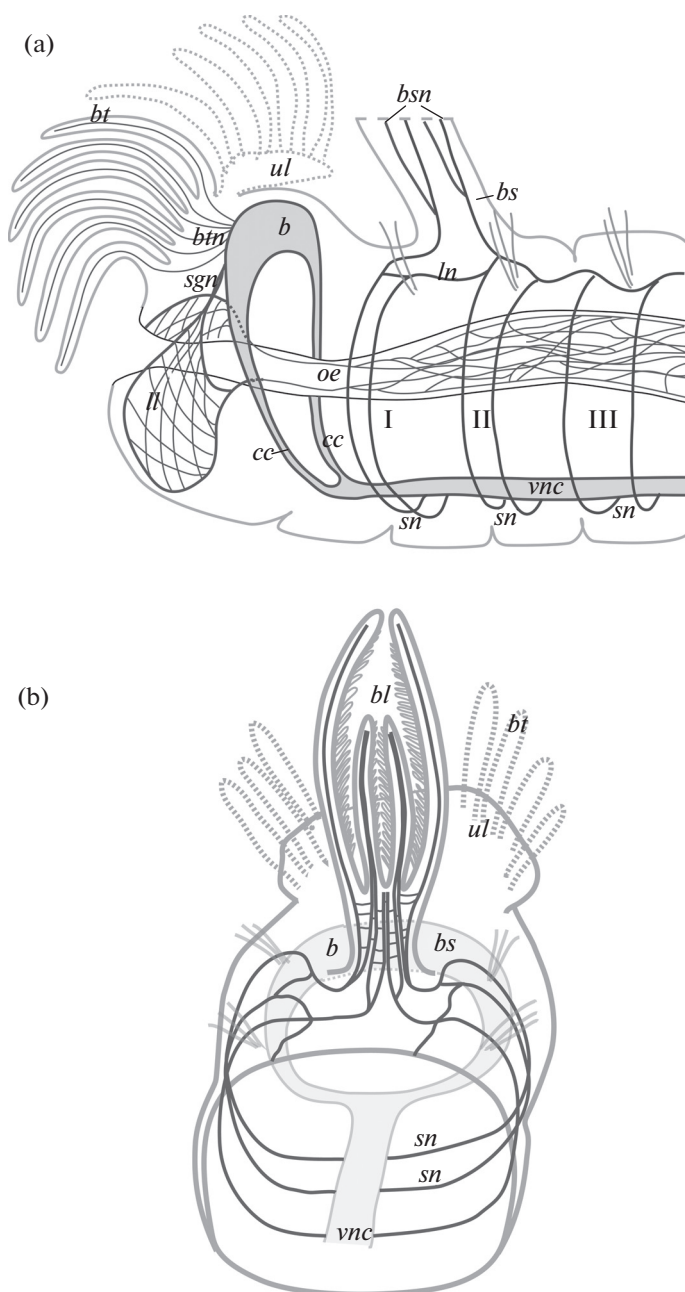


Fig. 7. *Terebellides* cf. *stroemii*, the nervous system structure: (a) lateral view, (b) posterior view; I–III are the chaetigers; b, brain; bl, branchial lobes; bs, branchial stalk; bsn, the nerves of the branchial stalk; bt, buccal tentacles; btn, the nerves of the buccal tentacles; cc, circumpharyngeal connectives; ll, lower labium; ln, longitudinal nerve; oe, esophagus; sn, segmental nerves; sgn, stomatogastric nerves; ul, upper labium; vnc, ventral nerve cord.

tral nerve cord. This nerve lies transversely through the segment and comes to the basis of the branchial filament. Thus, we made the following conclusions: (1) The branchial filament of *Cossura* is an unpaired structure that was not formed by the junction of paired branchiae and that does not originate from the prostomial or peristomial appendages. (2) The branchial filament originates from the shift of one of the paired segmental branchiae of the second chaetiger to the dorsal side with parallel reduction of the second seg-

mental branchia. Interestingly, the branchial filament of most of the 12 studied samples was innervated by the left segmental nerve, or by the right segmental nerve in some samples. The branchial filament of *Cossura* is similar in its innervation type to the paired branchiae of Amphinomida (Purschke et al., 2016).

The innervation of branchial filaments in other species of *Cossura* is of interest; the filaments located on segments 3, 4, or 5 could be innervated by nerves originating from the second segment or another segment.

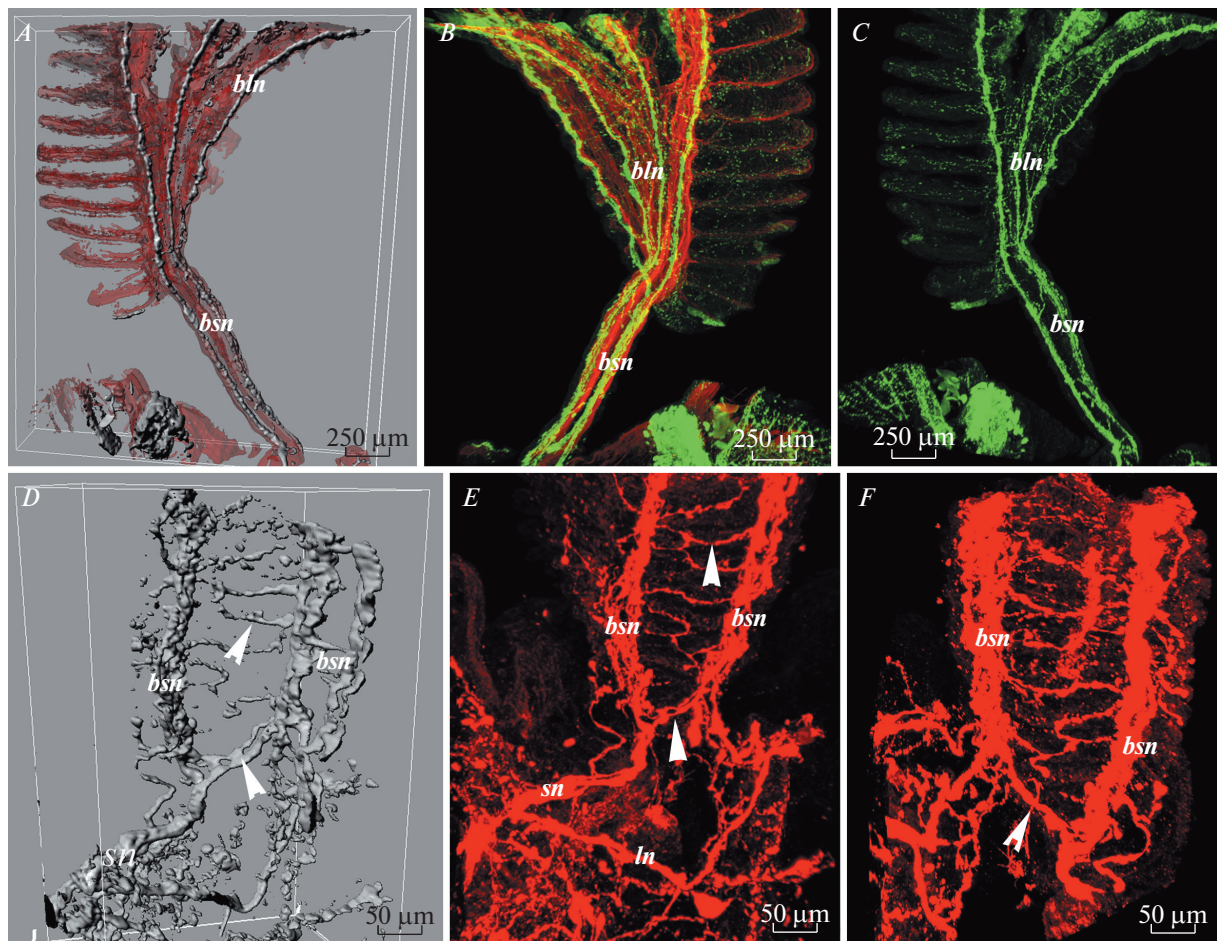


Fig. 8. *Terebellides* cf. *stroemii*, the innervation of the branchial organ, cLSM, staining: (a) for f-actin (red) and FMRF-amide (3D-reconstruction); (b) for f-actin (red) and FMRF-amide (green); (c) for FMRF-amide; (d) for tubulin (3D-reconstruction); (e, f) for FMRF-amide; bln, the nerves of the branchial lobes; bsn, the nerves of the branchial stalk; ln, longitudinal nerve; sn, segmental nerves. The arrows designate the transverse connections between the nerves of the branchial stalk.

Terebellides

Although a large number of studies have been conducted on the morphological properties of *Terebellides* (Steen, 1883; Storch, Alberti, 1978; Michel et al, 1984; Jouin-Toulmond, Hourdez, 2006), the structure of the nervous system in this genus and the whole family has not been described.

Structure of the Circumpharyngeal Connectives.

The general structure of the nervous system in the anterior part of the body in *Terebellides* is similar to that in other Terebelliformia: Terebellidae, Ampharetidae, and Pectinariidae (Orrhage, 2001). The first common feature is the structure of circumpharyngeal connectives. Similarly to other genera of Terebelliformia studied, the circumpharyngeal connectives of *Terebellides* are not split to form the dorsal and ventral roots and enter the brain as one structure.

Innervation of Buccal Tentacles. The buccal tentacles of *Terebellides* are innervated by nerves that start from the anterior lateral parts of the brain; stomatogastric nerves are also very close. Thus, our data con-

firm the conclusion of Orrhage (Orrhage, 2001) that the stomatal tentacles of Terebelliformia are not homologous with either antennae or palps of other annelids.

Innervation of branchiae. Interestingly, the innervation of branchiae in *Terebellides* is significantly more complex than that of the branchial filament of *Cossura* with numerous transverse connections, divisions, and nerve junctions. The branchiae of *Terebellides* are similar in the type of innervation with the paired branchiae of Amphinomida (Purschke et al., 2017). Our study confirmed the paired nature of branchiae in *Terebellides*, i.e., that it originates from the junction of separate branchiae. Basing on the number of innervating segmental nerves, we conclude that the branchial organ of *Terebellides* is formed by the junction of two pairs of branchiae, as was suggested by most authors (Ushakov, 1955; Zhirkov, 2001; Holthe, 1986, 1986a; Hutchings, Peart, 2000; Muir, 2001).

ACKNOWLEDGMENTS

The authors are grateful to N.N. Rimskaya-Korsakova for a helpful review.

This study was supported by the Russian Foundation for Basic Research, project nos. 15-04-05875, 15-29-02447, and 16-04-00343. The part of the study conducted using the confocal laser scanning microscope was supported by the Russian Science Foundation, project no. 14-50-00029.

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Translated by Ya. Lavrenchuk