

Metameric structures in the subepidermal nervous system of the nemerteans with review of the metamerism in Nemertea

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ABSTRACT: The subepidermal nervous system of five nemertean species (*Tubulanus* sp., *Hubrechtella juliae*, *Cephalothrix simula*, *Quasitetrastemma stimpsoni*, and *Ototyphlonemertes martynovi*) was studied using antibodies against serotonin (5-HT) and catecholamines (for *H. juliae* only) together with confocal laser scanning microscopy. *Tubulanus* sp. and *H. juliae* have closely situated transverse (semicircular) nerves connecting the dorsal nerve and/or the lateral nerve cords. Two kinds of metameric structures are found in the subepidermal nervous system of *C. simula*: closely situated transverse nerves and well-developed ring nerves spaced 380–750 µm apart. Closely situated transverse subepidermal nerves connect two subdorsal and two subventral longitudinal nerves in *Q. stimpsoni* and *O. martynovi*. Juvenile specimens of *Q. stimpsoni* (four days after hatching) lack both transverse and longitudinal subepidermal nerves. The examples of metamerism in nemertean morphology are discussed. The metameric ring nerves and rhynchocoel septa of cephalotrichid nemerteans are of chief interest, but further investigations of both structures are necessary for correct evolutionary interpretations.

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KEY WORDS: *Cephalothrix*, metamerism, nemerteans, ring nerves, rhynchocoel septa, subepidermal nervous system.

Элементы метамерии в субэпителиальной нервной системе немертин с обзором метамерных структур Nemertea

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РЕЗЮМЕ: Приведены данные о субэпителиальной нервной системе у 5 видов немертин (*Tubulanus* sp., *Hubrechtella juliae*, *Cephalothrix simula*, *Quasitetrastemma stimpsoni* и *Ototyphlonemertes martynovi*), полученные методами конфокальной ска-

нирующей лазерной микроскопии с использованием антител против серотонина (для *H. juliae* – против катехоламинов). У *Tubulanus* sp. и *H. juliae* выявлены близкорасположенные поперечные (полукольцевые) нервы, соединяющие дорсальный нерв и (или) боковые нервные стволы. У *C. simula*, помимо этих нервов, выявлены хорошо развитые кольцевые нервы, расположенные на расстоянии 380–750 мкм друг от друга. У *Q. stimpsoni* и *O. martynovi* близкорасположенные поперечные нервы соединят субдорсальные и субвентральные продольные нервы. У ювенильных *Q. stimpsoni* (возраст 4 суток) субэпителиальная нервная система развита слабо, не имеет явных продольных и поперечных элементов. Обсуждаются проявления метамерии у немертин. Наибольший интерес представляет наличие у Cephalotrichidae метамерных кольцевых нервов и ринхоцельных септ, однако для эволюционных интерпретаций необходим дальнейшее исследование этих структур.

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КЛЮЧЕВЫЕ СЛОВА: кольцевые нервы, метамерия, немертины, ринхоцельные септы, субэпителиальная нервная система, *Cephalothrix*.

Introduction

The presence of metameric structures in the so-called parenchymatous worms has aroused much interest among zoologists, since this allows the interpretation of these facts either in the context of their origin from annelids (or other metameric forms) or as the predecessor of present metamerism (McIntosh, 1873–1874; Hubrecht, 1887; Sedgwick, 1898, etc.). Although the search of the vestiges of metamerism in the nemerteans has been pursued for more than 130 years, there is no convincing evidence supporting the presence of segmentation in their ancestors (and, equally, the lack of segmentation). In the present paper, we briefly outline new data on the metamerism of the subepidermal nervous system of the nemerteans with analysis of the metameric structures in representatives of this phylum.

Many authors consider metamerism to be segmental repetition of homologous body parts (see Maggenti, 2005). Willmer (1990) applies ‘metamerism’ only to cestodes; in other cases he uses either ‘segmentation’ (for arthropods, annelids, and vertebrates) or ‘serial repetition’ (for other groups). Couso (2009) applies the following definitions: a) in a serial pattern, a

single organ or structure is repeated along the animal body without further functional or developmental consequences; b) metamerism indicates the existence of at least two sets of such coordinated, serially repeated organs along the main axis of the body, and assumes the existence of related patterning mechanisms; c) segmentation is the most extreme example of metameric organisation and entails the metameric repetition of most organs of the body, such as in some cases the adult body itself seems formed by repeated physical units, the segments. It is important to note that Couso (2009) regards Nemertea as a ‘metameric phylum’. Russian zoologists generally adopt a broader interpretation of the term ‘metamerism’, including in it both serial pattern and segmentation (see Beklemishev, 1969). In the present paper, we adhere to this approach.

The interest to the study of the metamerism of the subepidermal nervous plexus is caused by that the main part of the nemertean nervous system (primarily the brain and lateral nerves) is in an ancestral form was subepidermal, and this is the case with most palaeonemerteans and hubrechtids (Hubrecht, 1887; Bürger, 1895, 1897–1907).

In the course of evolution of various nemertean groups the brain and (or) lateral nerve

cords have shifted into the body wall musculature or, as in hoplonemerteans, beneath the body wall musculature. Nevertheless, the subepidermal nervous plexus is retained in the archi- and hoplonemerteans and its study began recently (Zaitseva et al., 2007). Similar to palaeoneemerteans, in heteronemerteans the brain, lateral nerve cords, and the commissural plexus connected with them are located outside the outer circular musculature of the body wall. However, because of the presence of the outer longitudinal musculature, most of the nervous system in Heteronemertea is not directly subepidermal, but embedded in the extracellular matrix separating the outer longitudinal muscle layer and the outer circular muscle layer. In heteronemerteans, the subepidermal nervous plexus *per se* may originate after the outer longitudinal musculature has formed in a pilidiophoran ancestor.

As early as the 19th century, it was known that the “commissural plexus” of the heteronemerteans and the subepidermal nervous plexus of the palaeoneemerteans might have metameric structure (Hubrecht, 1887; Bürger, 1895, 1897–1907; Punnett, 1901, etc.); nevertheless, this phenomenon has hardly been studied in the second half of the 20th century.

Materials and methods

All species examined in this research were collected in Peter the Great Bay of the Sea of Japan: *Tubulanus* sp. (undescribed species from family Tubulanidae, order Tubulaniformes) — 2 specimens; *Hubrechtella juliae* Chernyshev, 2002 (family Hubrechtellidae, order Hubrechtiformes) — 3 specimens; *Cephalothrix simula* (Iwata, 1952) (family Cephalotrachidae, order Archinemertea) — 3 specimens; *Quasitetrastemma simpsoni* (Chernyshev, 1992) (family Tetrastemmatidae, order Monostilifera) — 2 adult specimens and 4 juveniles (4 days after hatching) (a more complete information on the cultivation techniques of the larvae and juveniles of this species is given in a work of Chernyshev, 2008); *Ototyphlonemertes martynovi* Chernyshev, 1993 (family Ototyphlonemertidae, order Monostilifera) — 1 specimen.

For confocal laser-scanning microscope (CLSM) investigations live nemerteans were fixed for 1 hour in 4% formaldehyde in PBS (with prior relaxation in $MgCl_2$), rinsed in PBS and permeabilized for one hour in 1% triton X-100 in PBS. Then specimens were washed with PBS, incubated for 1 hour in a blocking solution consisting of 1% bovine serum albumin (BSA) and 10% normal serum of goat in PBS. For detecting the serotonergic nervous system the proboscis pieces were transferred to a solution of anti-serotonin (5-HT, polyclonal, rabbit, diluted 1:2000, Immunostar) primary antibody in PBS with 1% BSA. For observation of the catecholaminergic nervous system the proboscis fragments were placed in anti-tyrosinehydroxylase (polyclonal, rabbit, diluted 1:1000, Immunostar) primary antibody in PBS with 1% BSA. In all cases the material was kept for 24 hours at +4°C in the primary antibody, then rinsed in phosphate buffer and incubated for 2 hours at room temperature in goat-anti-mouse Alexa 488 (Invitrogen) immunoglobulin G, diluted 1:800 in PBS. Pieces of the bodies were washed in PBS and immersed in Mowiol 4-88 (Aldrich) and mounted on glass slides. The specimens were examined with an LSM-510 Meta confocal microscope (Carl Zeiss, Germany). The obtained images series were analyzed with CLSM-510 Meta software. Images were further processed with Photoshop CS2 to adjust contrast and brightness and to create digital line drawings.

Results

Tubulanus sp. (Figs. 1A, B). The subepidermal nervous system showed intense immunoreactivity to serotonin. In the area of the stomach and anterior intestine, the dorsal nerve is connected with the lateral nerve cords by a subepidermal network of nerve processes, of which few are transverse. On the ventral side of the body, the ventral nerve was not observed, the lateral nerve cords are connected with each other by subepidermal transverse (or more exactly semicircular) nerves spaced 30–50 μm apart.

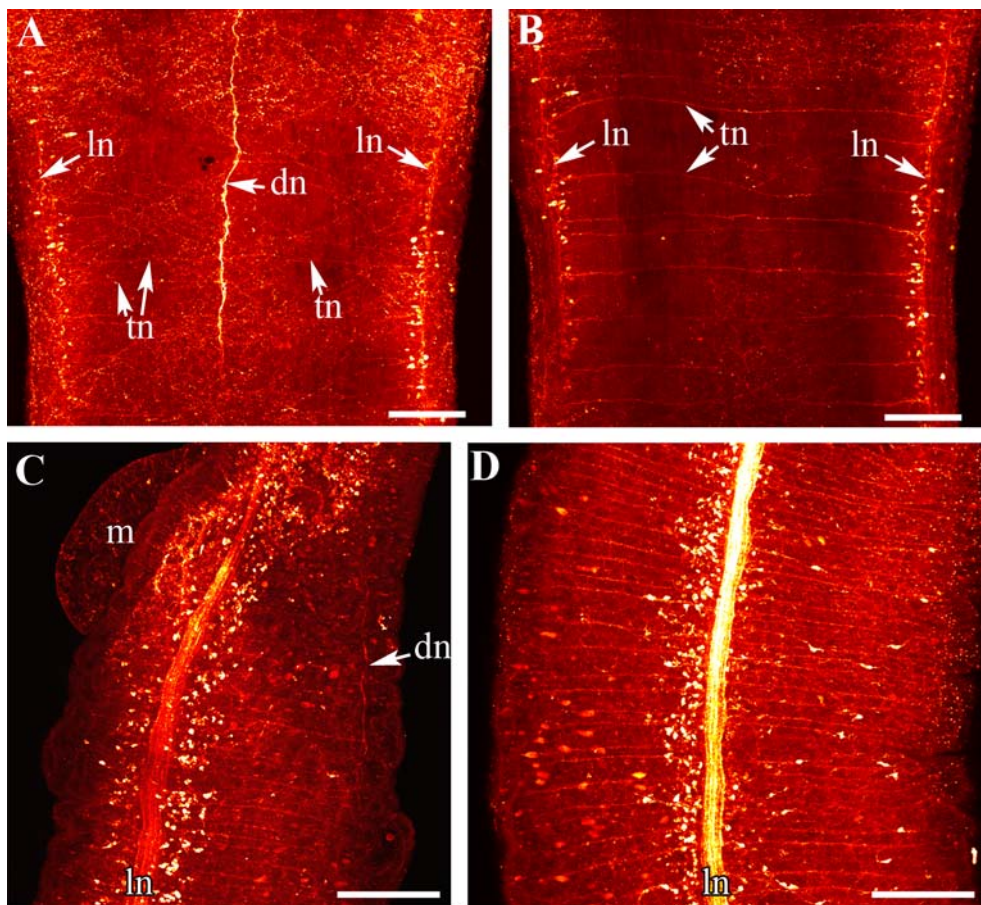


Fig. 1. Distribution of the serotonin (A, B) and catecholamine (C, D) immunoreactivity of the nemertean nervous system, Z-projections of the longitudinal confocal sections.

A, B — *Tubulanus* sp., foregut region (A — dorsal view; B — ventral view); C, D — *Hubrechtella juliae*, lateral view (C — foregut region; D — intestine region). Abbreviations: dn — dorsal nerve; ln — lateral nerve cord; m — mouth; tn — transversal (semicircular) nerve. Scale bar 100 μ m.

Рис. 1. Распределения серотониновой (A, B) и катехоламиновой (C, D) иммунореактивности в нервной системе немертин, Z-проекция продольных оптических срезов в CLSM.

A, B — *Tubulanus* sp., область передней кишки (A — вид дорсально, B — вид вентрально); C, D — *Hubrechtella juliae*, вид сбоку (C — область передней кишки; D — область средней кишки). Обозначения: dn — дорсальный нерв; ln — латеральный нерв; m — рот; tn — поперечный (полукольцевой) нерв. Масштаб 100 мкм.

Hubrechtella juliae. (Fig. 1C, D). The sub-epidermal nervous system showed intense immunoreactivity to catecholamine (the staining with antibodies against serotonin was poor). The dorsal nerve is short and terminates in the stomach area; the ventral nerve was not revealed. The dorsal nerve and the lateral nervous cords are connected by a strongly developed subepidermal nerve plexus, which contains transverse (semicircular) nerves spaced 20–30 μ m

apart. The lateral nerve cords behind the dorsal nerve are also connected by transverse nerves (dorsally or ventrally).

Cephalothrix simula (Figs. 2A–C). The sub-epidermal nervous system showed intense immunoreactivity to serotonin. The dorsal nerve is distinct in the anterior body region, it gives rise to thin transverse (semiring) nerves spaced 30–50 μ m apart from each other. Well-developed large subepidermal ring nerves are 380–750 μ m

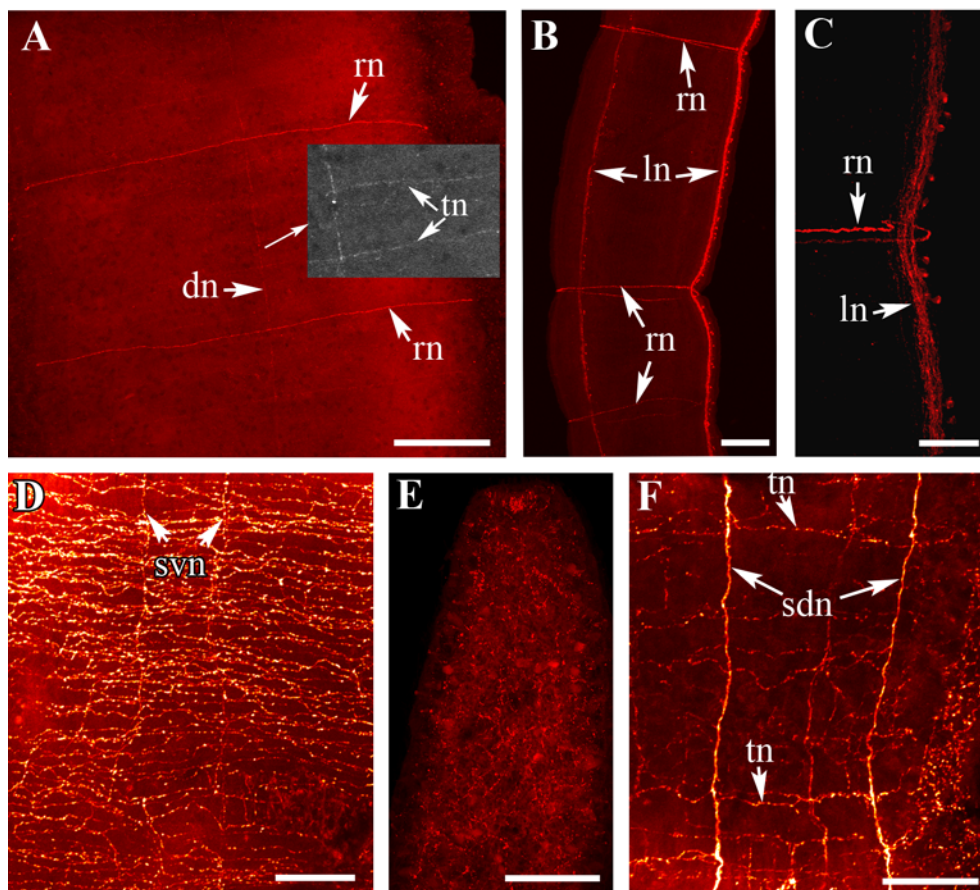


Fig. 2. Distribution of the serotonin immunoreactivity of the nemertean nervous system, Z-projections of the longitudinal confocal sections.

A–C — *Cephalothrix simula* (A — foregut region, dorsal view; B, C — posterior body region, dorso-lateral view); D, E — *Quasitetrastemma stipsoni* (D — intestine region of the adult specimen, ventral view; E — anterior half of the juvenile specimen, 4 days after hatching, dorsal view); F — *Ototyphlonemertes martynovi*, intestine region, dorsal view. Abbreviations: dn — dorsal nerve; ln — lateral nerve cord; rn — ring nerve; sdn — subdorsal nerve; svn — subventral nerve; tn — transversal (semicircular) nerve. Scale bar: A, B — 200 μ m, C — 100 μ m, D–F — 50 μ m.

Рис. 2. Распределения серотониновой иммунореактивности в нервной системе немертин, Z-проекция продольных оптических срезов в CLSM.

A–C — *Cephalothrix simula* (A — область передней кишки, вид дорсально; B, C — область задней части тела, вид дорсо-латерально); D, E — *Quasitetrastemma stipsoni* (D — область средней кишки половозрелой особи, вид вентрально; E — передняя половина тела ювенильной особи возрастом 4 дня, вид дорсально); F — *Ototyphlonemertes martynovi*, область средней кишки, вид дорсально. Обозначения: dn — дорсальный нерв; ln — латеральный нерв; rn — кольцевой нерв; sdn — субдорсальный нерв; svn — субвентральный нерв; tn — поперечный (полукольцевой) нерв. Масштаб: A, B — 200 мкм, C — 100 мкм, D–F — 50 мкм.

apart from each other. The anterior-most ring nerves are located at the very beginning of the intestinal region, the posterior-most are not far from the posterior end of the body. These ring nerves run in close proximity to the neuropil of the lateral nerve cords but do not appear to be

connected with the serotonergic nerve fibers of the latter (Fig. 2C).

Quasitetrastemma stipsoni (Figs. 2D, E) showed significant immunoreactivity to serotonin. Thin transverse nerves spaced 5–15 μ m apart are predominant in the subepidermal nerve

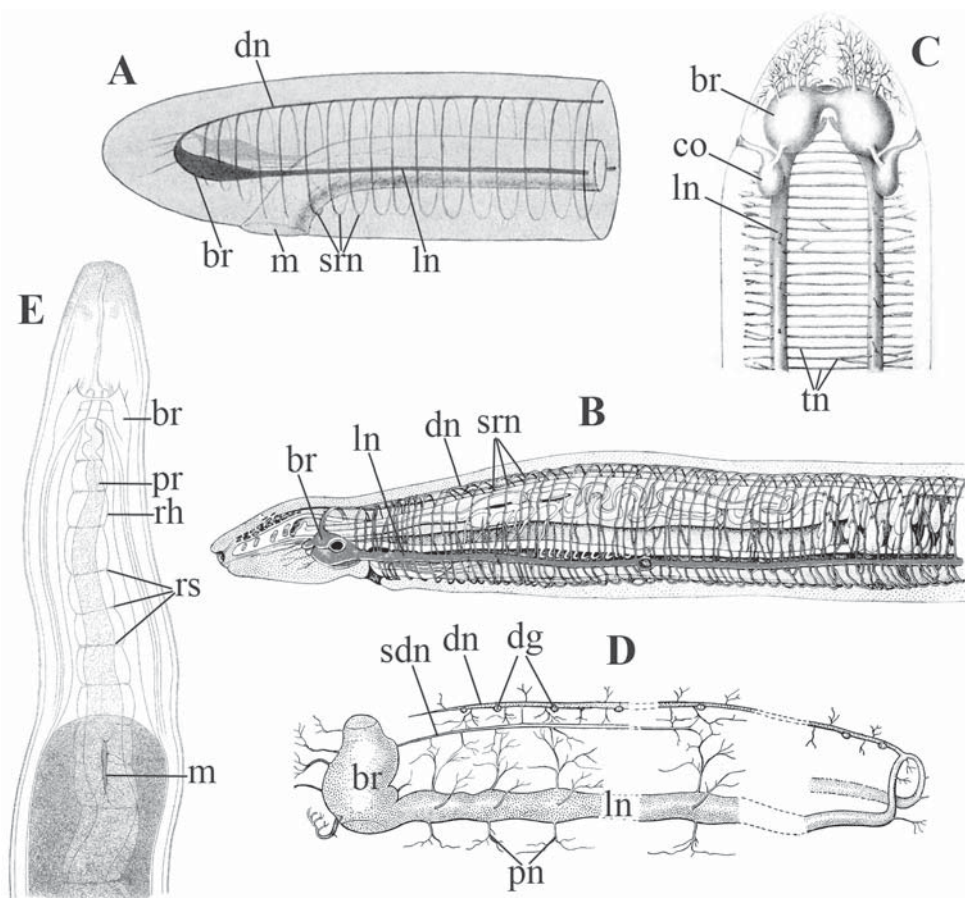


Fig. 3. Schematic representations of nemertean morphology.

A — nervous system of an anoplan nemertean (from Hubrecht, 1887); B — nervous system of *Tubulanus* (after Bürger, 1897–1907, reproduced from Goncharoff, 1961); C — nervous system of *Hubrechtionemertes lankesteri* (from Hubrecht, 1887); D — nervous system of *Neuronemertes aurantiaca* (from Coe, 1933); E — head region of *Cephalothrix linearis* (from McIntosh, 1873–1874). Abbreviation: br — brain; co — cerebral organ; dg — dorsal “ganglia”; dn — dorsal nerve; ln — lateral nerve cord; m — mouth; pn — peripheral nerves; pr — proboscis; rh — rhynchocoel; rs — rhynchocoel septa; srn — semicircular nerves; sdn — subdorsal nerve; tn — transversal nerves.

Рис. 3. Схемы строения немертин.

A — схема строения нервной системы невооруженной немертины (из: Hubrecht, 1887); B — схема строения нервной системы *Tubulanus* (по: Bürger, 1897–1907, из: Goncharoff, 1961); C — схема строения нервной системы *Hubrechtionemertes lankesteri* (из: Hubrecht, 1887); D — схема строения нервной системы *Neuronemertes aurantiaca* (по: Сое, 1933); E — строение головной части *Cephalothrix linearis* (по: McIntosh, 1873–1874). Обозначения: br — мозг; co — церебральный орган; dg — дорсальные «ганглии»; dn — дорсальный нерв; ln — латеральный нерв; m — рот; pn — периферические нервы; pr — хобот; rh — ринхоцель; rs — ринхоцельные септы; srn — полукольцевой нерв; sdn — субдорсальный нерв; tn — поперечный нерв.

plexus. The subepidermal nerve plexus is connected with a pair of subdorsal and a pair of subventral nerves but is not connected with the lateral nerve cords. In juvenile *Q. stimpsoni* 4 days of age, the subepidermal nerve plexus is

poorly developed; no transverse elements were revealed (the subdorsal and subventral nerves were not found either).

Ototyphlonemertes martynovi (Fig. 2F) has a subepidermal nervous system similar to that of

Q. stimpsoni with two subdorsal and two subventral nerves; however, irregular transverse nerves are spaced wider apart from each other (30–50 μm).

Discussion

The Dutch zoologist Ambrosius Hubrecht was the first to pay attention to the metamerism of the nemertean nervous system. Using reconstructions of the nervous system based on serial histological sections, he described metameric arrangement of the transverse (semicircular) nerves in several heteronemerteans (Hubrecht, 1887). In all of Hubrecht's diagrams, these nerves are shown to be connected with the dorsal and lateral nerves, which in heteronemerteans are located between the outer longitudinal and the outer (middle) circular musculature of the body wall, forming the commissural nerve plexus. Hubrecht depicted the semicircular nerves as regularly arranged, which is particularly evident in his diagram of organization of the nemertean nervous system (Fig. 3A). This regular pattern may have been influenced by the fact that Hubrecht considered Nemertea to be the ancestor group to chordates and therefore searched in the nemerteans for any manifestations of "future" metamerism of the lower Chordata (*Amphioxus*). Bürger (1895, 1897–1907) confirmed the presence of metamERICALLY arranged nerves in the heteronemertean genus *Cerebratulus*; however, a thorough reconstruction of the nervous system of *Tubulanus* revealed that the subepidermal ring nerves are not arranged as regularly (Fig. 3B) as in Hubrecht's diagrams.

Of much more interest is the reconstruction (Hubrecht, 1887) of the nervous system in the polystiliferous hoplonemertean *Hubrechtone-mertes lankesteri* (Hubrecht, 1887), which shows the metamERICALLY arranged commissures connecting the lateral nerve cords that, in turn, give rise to metameric peripheral nerves (Fig. 3C). *H. lankesteri* belongs to the suborder Reptantia (order Polystilifera), whose representatives exhibit metamerism of the lateral rhynchocoel diverticula and the blood system (metameric

transverse vessels), in addition to metamerism of the intestinal diverticula and gonads, which is typical of the hoplonemerteans. Such orthogonal nervous system has not been described in other Reptantia; however, it should be borne in mind that almost all reconstructions of the nervous system in the 20th century were mainly concerned with the brain and surrounding nerves. For example, Thompson (1908) described 13 metameric ventral commissures between the lateral nerves that are located immediately behind the main ventral commissure of the brain in *Cerebratulus lacteus* (Leidy, 1851).

A special case of metamerism has been described in the pelagic nemertean *Neuronemertes aurantiaca* Coe, 1926. The metameric peripheral nerves of this worm connect the lateral nerve cords with the subdorsal and dorsal nerves lying under the epidermis; the latter bears metamERICALLY arranged ganglia (Fig. 3D) (Coe, 1933).

Brinkmann (1917) pursued a search for metameric structures in Pelagica, because he considered pelagic nemerteans to be the descendants of Reptantia. Nevertheless, no traces of metamerism in the structure of the nervous system have been found.

The methods of indirect immunocytochemistry and CLSM have opened new possibilities in the study of the nemertean nervous system; however, there are very few studies in this area. The most important data are those on the structure of the nervous system of nemertean larvae, in which no vestiges of metamerism have been revealed thus far (Chernyshev, Magarlamov, 2010; Maslakova, 2010; von Döhren, 2011). Beckers and coauthors (2011) studied the nervous system of the heteronemertean *Lineus* (= *Poseidon*) *viridis* (Müller, 1774), in which the nerve cell processes of only the commissural nerve plexus are oriented in a circular pattern, demonstrating weak metamerism. We found this structural pattern in all five species studied and, in our opinion, it reflects the arrangement of muscle fibers in the outer circular musculature, which is abutted by the subepidermal (commissural in the heteronemerteans) nerve plexus. This pattern is partially manifested during the

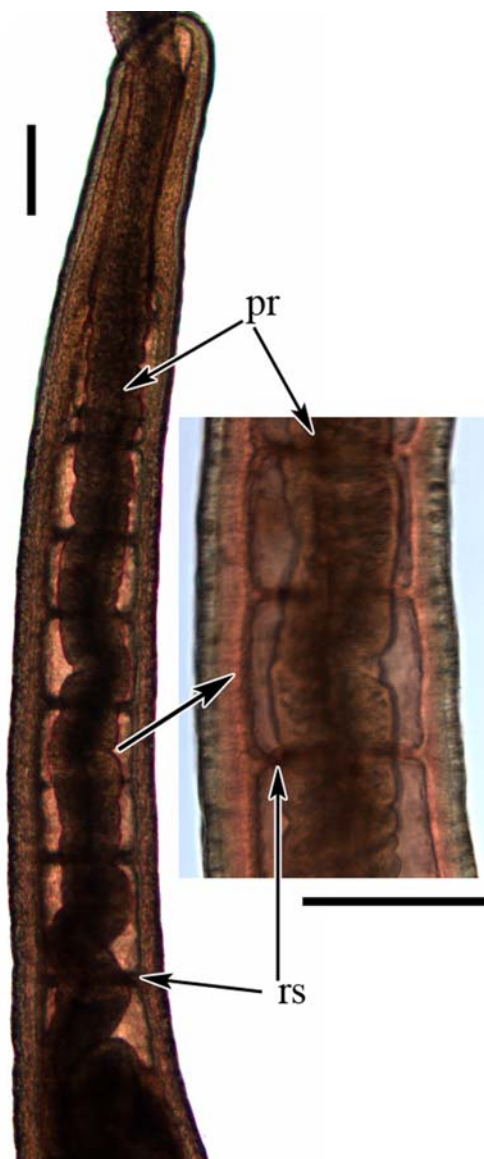


Fig. 4. Anterior portion of *Cephalothrix cf. spiralis* (Sea of Japan).

Abbreviation: pr — proboscis; rs — rhynchocoel septa. Scale bar 0.2 mm.

Рис. 4. Передняя часть *Cephalothrix cf. spiralis* (Японское море).

Обозначения: пр — хобот; rs — ринхоцельная септа. Масштаб 0,2 мм.

contraction of the body when the integuments of many nemerteans are thrown into small epidermal folds — “pseudosegmentation” (after Korochevich, 1977). Judging by the absence of

regular transverse elements in the subepidermal nervous system of the early juvenile stages of *Q. simpsoni*, serial pattern appears in the hoploneurteans later in the development.

The ring nerves of *C. simula* should be regarded in a different way: they are well developed, spaced widely apart, and cannot be associated with any peculiarities of the body contraction. Taking into account the total body length in this species (up to 20–30 cm), the total number of these nerves is to be significant. There are some mentions in the literature of the ring nerves in the nemertean genus *Cephalothrix* (Chernyshev, 2011; Beckers, Bartolomaeus, 2011¹) but this is a first thorough description of them. The presence of such metameric nerves encourages the search for other metameric structures in the cephalotrichid morphology. The Cephalotrichidae (erroneous spellings ‘Cephalotrichidae’ or ‘Cephalotricidae’) lack either intestinal diverticula or transverse blood vessels, or any matemeric patterns of arrangement of the gonads and nephridia. Nevertheless, McIntosh (1873–1874) described a series of septa in the rhynchocoel of living *Cephalothrix linearis* (Rathke, 1799), which are distinctly visible during the contraction of the worms (Fig. 3E). Gerner (1969) revealed similar septa in the rhynchocoel of *Cephalothrix mediterranea* Gerner, 1969. We observed the formation of temporary septa during the contraction of the rhynchocoel wall in *Cephalothrix cf. spiralis* Coe, 1930 from Peter the Great Bay (Sea of Japan) (Fig. 4). Other members of the Cephalotrichidae may also have similar septa they could be distinguished in histological sections (pers. observation). Outside Cephalotrichidae, a rhynchocoelic septae were described in the heteronemerteans *Gorgonorhynchus repens* Dakin et Fordham, 1931 and *Dendrorhynchus zhanjiangensis* Yin et Zeng, 1984 that contracted in the process of fixation, thus imparting a monil-

¹ After the present paper had been approved for publication, a new work on the nervous system of the arch- and palaeonemerteans appeared (Beckers et al., 2013). The ring nerves were found only in *Cephalothrix filiformis* (Johnston, 1828). In three species, the neurites of the intraepidermal plexus form a weak metameric pattern (the authors named it “ladder-like meshwork”).

iform morphology to the rhynchocoel (Sun, 2006); it should however be considered that these nemerteans have a branched proboscis with complicated structure.

Since the rhynchocoel is viewed as a modified coelomic cavity (Turbeville, Ruppert, 1985), its metameric structure in nephalotrichids is very interesting. The rhynchocoelic metamerism has only been discussed in one group—the suborder Reptantia, whose representatives have paired lateral diverticula. These structures are considered to be apomorphic, because they are not found in other representatives (including basal members) of the phylum. The metamerism of the rhynchocoel in the Cephalotrichidae (which, along with Tubulanidae s.l. and Carinonidae, represent the most basally branching clades within the phylum (Andrade et al., 2012)) deserves thorough attention. This group possesses a complex of unique synapomorphies (nephridia with terminal mushroom units, the brain enclosed by longitudinal musculature, subepidermal diagonal musculature, cephalic rhynchocoel vessel—see Chernyshev, 2013), which allow considering it as a relatively specialized family among the palaeonemerteans. In this context, an evolutionary evaluation of any metameric structure found only within a family or even a genus (as is the case with *Neuroneimertes*) in terms of ancestral metamerism can hardly be valid.

In addition, there is thus far no ground to associate the metamerism of the nervous system and that of the rhynchocoel in the Cephalotrichidae, because the ring nerves are located behind the mouth and the rhynchocoel septa are located both behind and in front of the mouth.

In a previous study (Chernyshev, 2011), we noted that metameric structures characterize evolutionarily advanced taxa of nemerteans and, as a rule, are synapomorphies of these groups. Thus, the metamericly arranged diverticula of the rhynchocoel are interpreted as a synapomorphy of the suborder Reptantia, while the metameric transverse vessels - as a synapomorphy of the clade Tetraophthalmida in the suborder Reptantia.

The best known example of metamerism in nemerteans is that of the genus *Annulonemertes*, which includes one described and two undescribed species of “segmented” nemerteans (Berg, 1985; Chernyshev, Minichev, 2004). Molecular-phylogenetic analysis (Sundberg, Strand, 2007) revealed that the metamerism of *Annulonemertes* is an apomorphic state that involves only the epidermis and musculature and, in the opinion of the authors, cannot be referred to as true segmentation. The metamerism of *Annulonemertes* is considered by them as a possible adaptation for life in the interstitial environment.

Some species of *Cephalothrix* (namely, *C. mediterranea*) also live in the interstitial zone; however, it is not clear what advantages they may gain from metamerism. *C. simula* is a relatively long nemertean living under the stones, among the calcereous algae, within the rhizoids of laminarians and the roots of seagrasses; hence, the metamerism of its nervous system cannot be explained by the unusual habitat. We can suggest three interpretations of the presence of the ring nerves in *Cephalothrix*: (1) synapomorphy of the Cephalotrichidae or of the entire order Archinemertea (Cephalotrichidae + Cephalotrichellidae); (2) an adaptive feature of nemerteans having a very long body; and (3) plesiomorphic state descended from the ancestral group. In the second and third cases, the findings of these metameric nerves could also be expected in other groups of nemerteans. Evidently, the nervous system of the palaeonemerteans needs further investigations using the immunocytochemical methods and confocal laser scanning microscopy, because the metameric structures in these long worms are difficult to reveal with the traditional methods (serial histological sections).

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