

# Muscular system of euconodont animals and their systematic position (Euconodontophylea)

A.P. Kasatkina & G.I. Buryi

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The muscular system of euconodont animals was studied in detail on the basis of the photographs of imprints from the Lower Carboniferous Shrimp Bed of Granton (Scotland), Upper Ordovician Soom Shale (South Africa), and Silurian Waukesha biota (North America). Superficial body structures are for the first time recognized for euconodont animals: external rings (annulation) (*Panderodus* imprint) and their traces (specimens 2 and 3 from Granton). This makes them looking like many invertebrates, such as annelids, priapulids, or pentastomids, and different from primitive chordates. In all other imprints of euconodont animals, a deep frontal break reaching their central part uncovers the inner transversal structures of the body, muscular fibers. As in invertebrates, they have different orientation. The medial apices of the fibers can be directed obliquely towards either the head (specimens 1, 2, 4, 5, 7 from Granton, and *Promissum pulchrum* Kovacs-Endrxdy imprints) or the tail (specimens 2 and 6 from Granton) or to be perpendicular to the body axis (specimens 3-5 from Granton). Discontinuity of the transversal structures (specimens 1 and 6) appears to occur in the euconodont animals. This suggests that the transversal obliquely-oriented structures visible on the euconodont imprints, are not myomers typical of chordate animals. Differently directed position of medial apices of the obliquely-oriented muscular fibers depends, probably, on physical state (direction of movement) of the animal. The longitudinal median structure, in our opinion, cannot be considered a chord, but is rather a gut extending from pharynx to anus. Apparently, in spite of visual similarity, the euconodont animals under study cannot be classified as chordates, or chaetognaths, or pentastomids. Their muscular system differs from that of all known groups of animals and shows its own unique structure: its inner transversal structures are muscular fibers, which externally look like rings (annulation). This supports our earlier conclusion (Kasatkina & Buryi, 1997) that euconodonts constitute a separate phylum, Euconodontophylea Kasatkina & Buryi, 1997.

A.P. Kasatkina, Pacific Oceanological Institute, Far Eastern Branch, Russian Academy of Sciences, Vladivostok 690041, Russia.

G.I. Buryi, Far East Geological Institute, Far Eastern Branch, Russian Academy of Sciences, Vladivostok 690022, Russia.

## INTRODUCTION

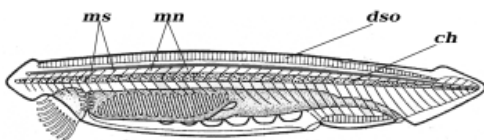
Anatomy of soft tissues of euconodont animals is visible on the photos of the imprints from the Lower Carboniferous deposits of Granton, Scotland (Aldridge et al., 1993) and the Upper Ordovician Soom Shale, South Africa (Aldridge & Theron, 1993). It is represented by serially recurrent transversal structures that sometimes crosscut two longitudinal median lines (probably, the intestine walls). Researchers of the specimen 1 from Granton have found in the body posterior the traces of about 33 such transversal structures arranged on one side from the distinct axial line. In their opinion, a fine obliquely-oriented striation typical of these structures may be an evidence of their V-like form (with their apices directed toward the head) and thus be similar to myotomes in amphioxus and fishes (Briggs

et al., 1983). They also report that the Granton specimen 2 of euconodont animal "...preserves clear evidence that the somites are V-shaped... The apices are directed anteriorly, except at the anterior of the trunk where they appear to be directed posteriorly" (Aldridge et al., 1986, p. 282). As more and more imprints are studied, the initial ideas of the form and direction of the transversal structures in euconodont animals undergo some changes. It has become apparent that on some intervals of specimens 3 and 4 from Granton the transversal structures are almost perpendicular to the body axis (in dorsal or ventral view) rather than obliquely-oriented. In some cases (specimens 2 and 6), they have V-like form with the apices directed not forward (to the head) but backwards (to the tail) (Kasatkina & Buryi, 1999). Besides, in the frontal parts of specimens 2 and 3 from Granton, where the plane of the break,

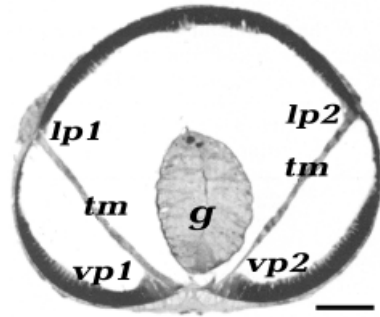
probably, goes along the outer side of the body, there are external transversal structures in the form of segmentation or annulation. The imprint of the euconodont animal from the Silurian Waukesha biota in North America turned to be broken also along the outer side of the body that made its external segmentation accessible for observation (Mikulic et al., 1985).

Information on the structure of the euconodont muscle system is very important for establishing their relation with other groups of animals. The internal obliquely-oriented structures are rather significantly developed in vertebrates. So, it is not surprising that, when similar structures were found in the imprints from Granton, those animals were classified as chordates. However, the V-like structures of the latter differ greatly from the transversal structures of euconodonts. The muscular system of the very primitive chordates (*Amphioxus*) consists of two muscle ribbons arranged symmetrically on the body sides, and each of them is divided by connective-tissue septa (myosepta) into 50 to 60 muscle myomers. The myomers are composed of the ordered muscle tissue – myonema (*mn*) and dividing it myoseptum (*ms*) and have the form of a horizontally-lying letter V with its apex directed always towards the head (Fig. 1; Fig. 1 in Briggs & Kear, 1994; and Fig. 2-2 in Carroll, 1988). This angle is developed because the myosepta, to which myonemas are attached, are rigidly fixed. Points of attachment of myosepta are the dorsal storage organs (*dso*) above and the chord (*ch*), which is always more dorsal than the gut (*g*), on the side. The collagen material of the myosepta gives no way to myonemas to shift and form angles of different configuration and direction. Such way of attachment allows vertebrates to have a rigid connection of the transversal structures, or myomers, to the animal skeleton. In primitive chordates, the apices of these structures are always oriented toward the head.

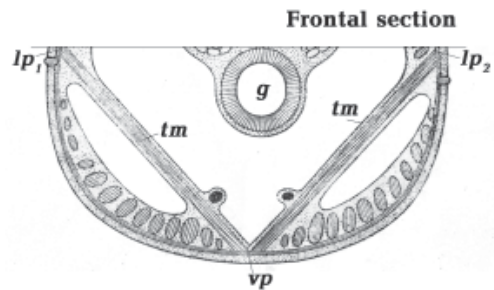
Invertebrates, for example chaetognaths (Bone & Duvert, 1991; Casanova & Duvert, 2002) and pentastomids (Zenkevich, 1951), show another pattern of arrangement of the internal transversal muscular system. As distinct from the primi-



**Fig. 1.** Scheme of morphology of lancelet, *Branchiostoma lanceolata*, side view (after Briggs & Kear, 1994): *mn*, myonema; *ms*, myosepta; *dso*, dorsal storage organ; *ch*, chord.



**Fig. 2.** Transversal section of a chaetognath (*Eukrohnia fowleri*) showing the position of transversal muscles (*tm*), lateral (*lp*<sub>1</sub> and *lp*<sub>2</sub>) and ventral (*vp*<sub>1</sub> and *vp*<sub>2</sub>) points of their attachment to body, and gut (*g*) (after Casanova & Duvert, 2002). Scale: 100  $\mu$ m.



**Fig. 3.** Schematic transversal section of a pentastomid showing transversal muscles (*tm*), lateral (*lp*<sub>1</sub> and *lp*<sub>2</sub>) and ventral (*vp*) points of their attachment to body, and gut (*g*).

tive chordates, in the center of the chaetognath body (Fig. 2) there is a gut (*g*). Symmetrical fibers of the transversal muscular system (*tm*) are on the ventral side, and the points of their attachment are on the sides (*lp*<sub>1</sub> and *lp*<sub>2</sub>) and below the gut (*vp*<sub>1</sub> and *vp*<sub>2</sub>). The pattern of arrangement of the transversal muscle system in invertebrates (for example in pentastomids, Fig. 3) depends on the point, from which a researcher views an object. In the dorsal view, the ventral point of attachment of the transversal muscles or fibers (*vp*) is not visible because of the gut; in the ventral view, a maximum length of fibers and the point of their convergence are observed; in the lateral view, only one muscle fiber of this symmetrical transversal structure is seen. In addition, the internal transversal structures of invertebrates in a quiescent state look like parallel muscle fibers perpendicular (in ventral or dorsal view) to the body axis, and in active movement they take the form of the obliquely-oriented V-shaped structures superficially similar to those of chordates. However, as distinct from chordates, the medial apex of each muscle or muscle fiber in

pentastomids is simultaneously its ventral point of attachment or the point of convergence (*vp*). This medial apex can be of different orientation, towards the head or towards the tail, depending of the direction the animal moves. In some invertebrates (for example, chaetognaths and pentastomids), the internal transversal muscle system is discontinuous (it is observed not along the whole length of the body), whereas in branchiostomes (lancelet), cyclostomes (lamprey, hagfish), and fishes, the myomers are situated continuously over the whole length of the body from head to terminal. Unlike the chordates, there are external transversal structures, as segmentation or annulation, on the body of many invertebrates (Schram, 1973).

The authors consider in detail the features of structure of the muscle system in euconodont animals, so that to discuss a possibility of their classification as either chordate animals or a separate phylum, Euconodontophylea Kasatkina & Buryi, 1997.

Photographs and descriptions of seven imprints of euconodont animals from the Lower Carboniferous Shrimp Bed of Granton, Scotland (Briggs et al., 1983; Aldridge et al., 1986, 1993), imprint of *Promissum pulchrum* Kovacs-Endrxdy from the Upper Ordovician Soom Shale, South Africa (Aldridge & Theron, 1993), and imprint of *Panderodus* from the Silurian Waukesha biota, North America (Mikulic et al., 1985) were used for this article.

The authors realize the complexity of the problem posed, which is primarily connected with limited morphological investigations of paleontological material using isolated photos, so all observations and conclusions of this paper are proposed as one of the possible interpretations.

## DESCRIPTION OF TRANSVERSAL STRUCTURES IN IMPRINTS OF EUCONODONT ANIMALS

The preservation degree of the study imprints of euconodont animals is different. In specimen 5 and especially specimen 6 from Granton, one can observe excellent preservation virtually of the whole animal: head, body, and tail parts. Kasatkina & Buryi (1999) described the smallest details of the structure of specimen 6. Specimen 1 has been preserved rather well, but specimens 2-4 are more fragmented. Specimen 7 from Granton and imprint of *Promissum pulchrum* Kovacs-Endrxdy from South Africa, which, probably, underwent decay through its burial in the sediment (Briggs & Kear, 1994), are in the worst state. Preservation of the material was undoubtedly affected by numerous pressings of imprints by shrimps and fractures crosscutting them.

**Specimen 1 (IGSE 13821, 13822).** In our opinion, in its frontal part, at a distance of 11 mm from the beginning of the body, discontinuity of the transversal muscle system takes place. Farther backwards there appear the obliquely-oriented parts of the transversal structures (muscle fibers), which occur on the left from the longitudinal median structure (probably, gut). We think that the angle of inclination of these muscle fibers relative to the longitudinal median structure gradually increases towards the tail. In this part of the imprint, there are 16 fibers with medial apices oriented towards the head before the contraction by a foreign body and about four such fibers after the contraction (see the Table).

**Specimen 2 (RSM GY 1986.17.1).** In the first third of the imprint where the plane of the break, probably, goes along the external side of the body or slightly deeper from its surface, the ribbed lateral contours of 4 to 5 muscle rings are observed (Aldridge et al., 1986, Fig. 1B). After the outer pressing there is, apparently, a shallow cutting of the body that stops short of reaching its central part (the median longitudinal structure, supposedly gut, is not visible). Sixteen rather wide obliquely-oriented muscle fibers are exposed with medial apices oriented mainly towards the apical end (Aldridge et al., 1986, Fig. 1A). However, two last muscle fibers, probably, have apices directed backwards.

**Specimen 3 (HU Y221).** In our opinion, the transversal muscular system is represented mainly by external annulation. At a distance of 20 mm from the beginning of the body to the first slight pressing of the imprint by the foreign body, the relief lateral parts of 16 to 17 outer rings are observed to be arranged at right angles to the body axis. Farther backwards up to the big second pressing, a median longitudinal structure appears looking like two parallel lines (probably, a gut). The transversal muscular system in this part of the body is represented by poorly visible obliquely-oriented symmetrical muscle fibers with medial apices inclined slightly towards the head. The point of their convergence appears to be below the gut. This suggests that the imprint is disposed with its dorsal side to a researcher. Most part of this side is concealed by the break, i.e. the imprint is lying on its ventral side. Farther after the big second pressing, one can descry six to eight parallel muscle fibers perpendicular to the body axis.

**Specimen 4 (BM X1065).** In the first third of the imprint, poorly-exhibited obliquely-oriented transversal structures are observed with their medial apices supposedly directed forward (1 to 2 muscle fibers are visible). Farther towards the terminal there are 6-8 muscle fibers perpendicular to the body axis followed, probably, by disconti-

**Table.** Muscular system of euconodont animals.

Specimen	Discontinuity in arrangement of transversal structures	External rings (annulation)	Muscular fibers			Source
			perpendicular to median line	oriented towards head	oriented towards tail	
Specimen 1 (IGSE 13821, 13822)	+			20		Briggs et al., 1983, Fig. 1, A, B
Specimen 2 (RSM GY 1986.17.1)		4-5		16	2	Aldridge et al., 1986, Fig. 1, A, B
Specimen 3 (HU Y221)		16-17	6-8			Aldridge et al., 1986, Fig. 4A
Specimen 4 (BM X1065)			6-8	1-2+8		Aldridge et al., 1986, Fig. 5A
Specimen 5 (RMS GY 1992.41.1)			15	28		Aldridge et al., 1993, Figs 3, 5
Specimen 6 (RMS GY 1992.41.2)	+				37	Aldridge et al., 1993, Fig. 8
Specimen 7 (RMS GY 1992.41.3)				17		Aldridge et al., 1993, Figs 10-12
Giant euconodont from South Africa (GSSA C721)				33		Gabbot et al., 1995, Fig. 1
<i>Panderodus</i> euconodont (UW 4001/7a)		19				Mikulic et al., 1985, Fig. 2, g

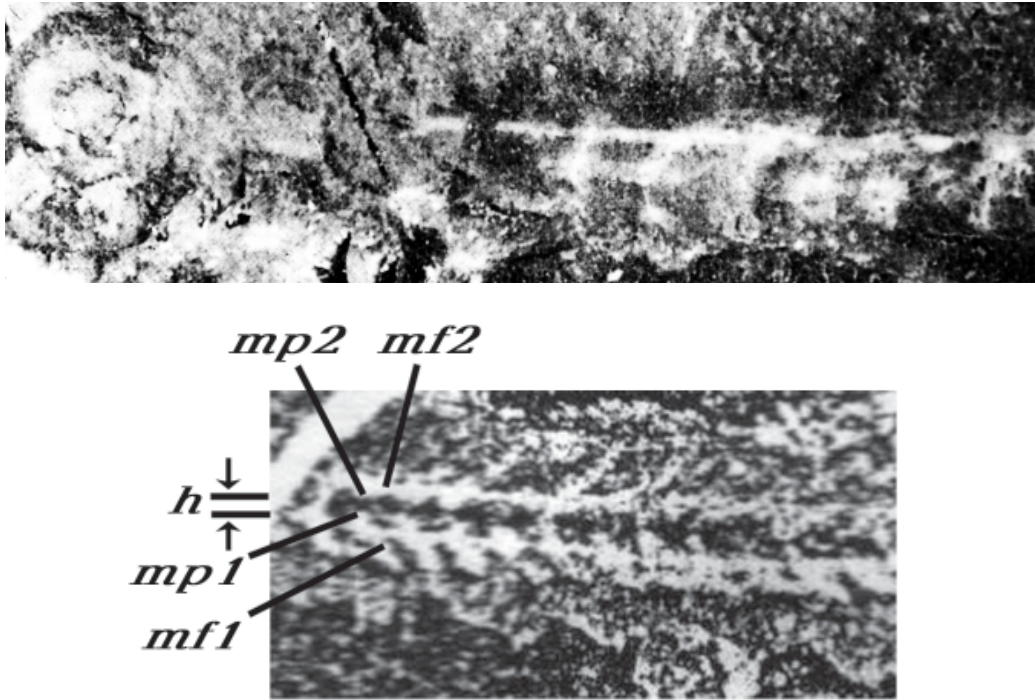
nuity in the transversal muscular system. In the back third of the imprint there are, in our opinion, eight obliquely-oriented muscle fibers with their medial apices directed towards the head.

**Specimen 5 (RMS GY 1991.41/1).** Over the whole length of the body, the transversal structures at first sight are V-shaped with their medial apices directed towards the head (about 43 fibers are observed). But the muscle fibers in the anterior half differ from those in the back part. The muscle fibers first appear at a distance of 1.7 mm from the back end of the paired rounded structures – H elements (Buryi & Kasatkina, 2004). They are wider than fibers in the back part of the imprint and are arranged nearly perpendicularly to the median line, especially in the very frontal part, and about 15 in number (Fig. 4a). Following the rupture in the rock crosscutting the imprint, the muscle fibers (about 28 in number) become narrow and obliquely oriented with their medial apices towards the head and are 0.3 mm apart. In the spaces between them, two longitudinal median parallel lines (supposedly, walls of the gut) are clearly seen. In this part of the body, the symmetrical, directed to each other at an acute angle members of the muscle fibers do not converge to a common point. A dark space 0.14 to 0.28 mm long is between them (Fig. 4b). It seems also that the symmetrical parts of each muscle

fiber alternate with each other. In the very back part of the tail division, one can observe not the transversal structures, but the external rays of lateral fins.

**Specimen 6 (RMS GY 1992.41.2)** (Fig. 5). We think that the body division starts at a distance of 2 mm from a narrow slit-like transversal mouth that occurs in this imprint at the left, and not at the right as it is stated in the caption to Fig. 8 by Aldridge et al., (1993). Two longitudinal median parallel lines spaced at an interval of 0.5 mm originate here and extend to the anus on the tail end. From the beginning of the body division, discontinuity of the transversal muscular system, probably, takes place for about 8 mm, when only two parallel lines are clearly seen, and there are no transversal structures cutting them. Then, against the background of the same light parallel lines, there appear similar light obliquely-oriented transversal structures – about 37 muscle fibers with their medial apices directed to the terminal. At a distance of 7 mm to the tail end, V-shaped transversal structures are no longer observed.

**Specimen 7 (RMS GY 1992.41.3).** It is a poorly preserved body part. About 17 muscle fibers have been preserved. They appear to be inclined towards the head and are arranged to the left of the supposed gut. Only five fibers are observed on the opposite side.



**Fig. 4.** Muscular fibers of specimen 5 of the euconodont animal from Granton (after Aldridge et al., 1993): *a*, wide ring-like fibers surrounding the gut in the frontal part of the body; *b*, narrow obliquely-oriented fibers, sometimes having no common point of attachment in back part of the body; *h*, distance between the points of attachment (*mp1* and *mp2*) of muscular fibers to the left (*mf1*) and to the right (*mf2*) of the sagittal axis.

**Imprint of *Promissum pulchrum* Kovacs-Endrödy (specimen C 721 GSSA).** At a distance of 24 mm from H elements, to the right and to the left of the supposed median longitudinal structure (gut?), there are in pairs 33 poorly preserved muscle fibers directed with their medial apices to the head and extending for 73 mm.

**Imprint of *Panderodus* (specimen UW4001/7a).** “The specimen is incomplete but traces of about 19 segments are evident” (Mikulic et al., 1985, p.716). In our opinion, these segments are the outer rings (annulation).

**SPECIFIC FEATURES OF THE MUSCULAR SYSTEM OF EUCONODONT ANIMALS**

Detailed study of the body morphology in nine imprints of euconodont animals allows recognition of the following specific features. At our sight, the internal structures of the body are not visible in some imprints, because the plane of opening appears to go along the outer side (imprint of *Panderodus*) or just below the body sur-

face (frontal parts of specimens 2 and 3 from Granton). In this case, superficial body structures (annulation) are observed that is supported by presence of 19 external muscle rings in the imprint of *Panderodus* and 4 to 5 and 16 to 17, respectively, ribbed lateral contours (supposedly, traces of such rings) in the specimens 2 and 3. We think that in other imprints of euconodont animals, a deep frontal break, extending to their central part, uncovers the internal transversal structures of the body. These transversal structures look like isolated muscle fibers of different form and orientation. Obliquely-oriented and perpendicular muscle fibers are distinguished. The obliquely-oriented muscle fibers can be arranged only on one side from the longitudinal median structure, supposedly gut (specimen 1), or on both sides symmetrically with it (all other imprints). Their inclination angle to this longitudinal median structure seems variable. In specimen 1, it appears to increase towards the tail part. The obliquely-oriented symmetrical muscle fibers of specimens 5 and 6 seem to be V-shaped. However, detailed consideration of such struc-

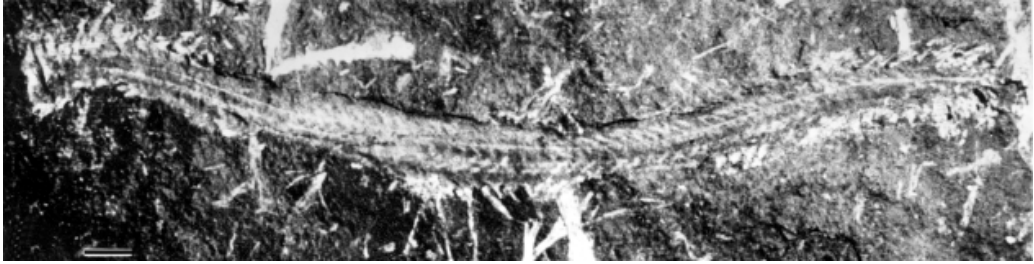


Fig. 5. Specimen 6 (RMS GY 1992.41.2) of euconodont animal from Granton (after Aldridge et al., 1993). Scale: 2 mm.

tures somewhere in the frontal and back parts of the body suggests that it is not the case. The muscle fibers of the body anterior part in specimen 5 are not “V-shaped”, but more likely perpendicular to the body axis, ring-shaped, surrounding the gut (Fig. 4a). The muscle fibers of the back part of the body in this imprint are also not “V-shaped”, as they do not have a common point of attachment or convergence with each other, i.e. their medial apices do not form a V-shaped structure. Between the medial points of attachment (*mp*) of the muscle fibers (*mf*), there is a hiatus (*h*) of 0.14 to 0.28 mm in size (Fig. 4b). It appears that the medial apices of the obliquely-oriented symmetrical muscle fibers of euconodont animals can be directed both towards the head (specimens 1, 2, 4, 5, 7 from Granton and *Promissum pulchrum* imprint) and oppositely, to the tail (specimens 2 and 6). Arrangement of muscle fibers perpendicular to the body axis is observed in specimens 3, 4 and 5. Discontinuity of the transversal structures also may be found in euconodont animals (specimens 1 and 6). In our opinion, different directions of the obliquely-oriented muscular system depends on the direction of the animal movement. In primitive chordates and fishes, myomers, rigidly fixed with myosepta, do not change their direction. Only organs (for example, tail, fins, and body itself) change direction.

#### ASSUMPTION OF RELATION OF EUCONODONT ANIMALS

Specific features revealed in the body morphology of euconodont animals significantly supplement the notion of both their external appearance and internal structure. Owing to the fact that in some cases the plane of break uncovers the imprint surface, it has become apparent that the narrow, elongate, worm-like body of euconodont animals exhibits also the external rings (annulation). This makes them look like many invertebrates, such as annelids, priapulids, pentastomids, and different from primitive chordates. The in-

ternal transversal structures of euconodont animals have their own morphological features. In specimen 1 from Granton, for example, muscle fibers are visible only on one side from the longitudinal median structure. This suggests that the pattern of attachment of muscles in euconodont animals is similar to that of chaetognaths and pentastomids, in which only lateral part of the transversal muscles is visible in side view (Figs 2, 3). Most important is the fact that, just as in invertebrates, the transversal structures in euconodont animals are of different orientation (their medial apices can be directed towards either the head or the tail). This allows us to suggest that the transversal obliquely-oriented structures visible on the euconodont imprints are not myomers typical of chordates. To make sure of this, it is sufficient to compare the transversal structures in Fig. 1 and Fig. 5 in this paper. Fig. 1 shows the myomers of primitive chordates with their angle directed towards the head. In Fig. 5, the transversal structures of euconodont animal have their angles directed toward the tail. Examination of all imprints allows conclusion that the muscular system of euconodont animals exhibits differently directed position of this angle that, probably, depends on physical state (direction of movement) of the animal. This is in contrast to fishes and primitive chordates, in which myomers are always rigidly fixed and do not change their direction.

The longitudinal median structure, in our opinion, cannot be considered a chord, as some researchers think (Morris, 1989; Aldridge et al., 1993; Donoghue et al., 2000), but rather a gut extending from pharynx on the frontal part to anus on the back end, as Aldridge et al. (1986), the first researchers, reported. In spite of visual similarity, the euconodont animals studied can be attributed neither to chordates nor chaetognaths nor pentastomids. They differ from all groups of animals. Thus, the muscular system of euconodont animals is characterized by its own specific unique structure. Most likely, the internal transversal structures characteristic of them are the

muscle fibers that are visible outside as rings (annulation). The foregoing assumption supports our earlier conclusion (Kasatkina & Buryi, 1997) that euconodonts represent a separate phylum, Euconodontophylea Kasatkina & Buryi, 1997.

#### Acknowledgements

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