

# Evolution of body wall musculature

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**Synopsis** A body wall musculature comprising an outer layer of circular fibers and an inner layer of longitudinal fibers is generally seen as the basic plan in Annelida. Additional muscles may be present such as oblique, parapodial, chaetal, and dorsoventral muscles. The longitudinal muscle fibers do not form a continuous layer but are arranged in distinct bands in polychaetes. Mostly there are four to six bands, usually including prominent ventral and dorsal bands. However, other patterns of muscle band arrangement also exist. The ventral nerve cord lies between the two ventral bands in certain polychaetes, and is covered by an additional longitudinal muscle band of comparatively small size. In many polychaetes with reduced parapodia and in Clitellata a more or less continuous layer of longitudinal fibers is formed. Clitellata is the only group with a complete layer of longitudinal musculature. Circular fibers are usually less developed than the longitudinal muscles. However, recent investigations employing phalloidin staining in combination with confocal laser scanning microscopy revealed that absence of circular muscles is much more widely distributed within the polychaetes than was previously known. This necessitates thorough reinvestigations of polychaete muscle systems, and this feature has to be taken into account in further discussions of the phylogeny and evolution of Annelida.

## Introduction

On the basis of morphological characters the Annelida, traditionally subdivided into Polychaeta and Clitellata, are usually considered to form a monophyletic group (Rouse and Fauchald 1997; Westheide and others 1999; Purschke 2002). However, so far molecular analyses have failed to prove their monophyly: usually they fall into a cluster that also includes mollusks, sipunculans, and other taxa now usually called Lophotrochozoa (for example, Rota and others 2001; Ruiz-Trillo and others 2002; Struck and others 2002; Bleidorn and others 2003; Halanych 2004; Jördens and others 2004). The proposed ground plan of Annelida, their monophyly, and the systematization of the higher taxa constituting Annelida are still under discussion (for example, Purschke 2002). From the morphological point of view this discussion is a prominent example of different phylogenetic assessments leading to conflicting hypotheses about phylogenetic relationships and the direction of evolutionary changes (Westheide and others 1999). The main open questions regarding evolution and phylogeny of Annelida concern the monophyly of Annelida, their sister group, the higher taxa that must be included, the relationships among the annelidan subtaxa, the group at the base of the annelid tree, and, thus, the reading direction of evolutionary changes. The problem whether Clitellata is an in-group or the

sister of polychaetes appears to be more or less solved now, since there is increasing evidence from both morphological and molecular data that the traditional view, in which Clitellata is positioned as sister of monophyletic Polychaeta (Rouse and Fauchald 1997; Ax 1999), has to be rejected in favor of the hypothesis that regards Clitellata as an in-group of the paraphyletic polychaetes (for example, McHugh 1997; Purschke 1997, 2002; Westheide 1997; Martin 2001; Struck and others 2002). However, so far these investigations have failed to predict the sister taxon of Clitellata within the polychaetes. Moreover, as suggested by morphological data, molecular analyses likewise confirm that Siboglinidae (Pogonophora) and Echiura are not only closely related to Annelida but also form in-group taxa as well (McHugh 1997; Kojima 1998; Halanych and others 2001; Bleidorn and others 2003).

The structure of the muscular system may contribute toward answering all of these questions, and at least may help to understand the evolution of these animals. A body wall musculature comprising an outer layer of circular fibers and an inner layer of longitudinal fibers is generally seen as the basic plan in Annelida (Dales 1963; Lanzavecchia and others 1988; Gardiner 1992; but see Tzetlin, Zhadan, and others 2002; Tzetlin and Filippova 2005). This hypothesis goes back to the ideas of Clark (1981), who proposed that

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the coelom arose as an adaptation for burrowing and thus the body of burrowing oligochaetous Clitellata with well-developed circular and longitudinal fibers was thought to be closest to the annelid stem species. Although it is well known that circular fibers are less developed than the longitudinal ones and sometimes “tend towards reduction in errant polychaetes”, absence was regarded as a rare exception (Lanzavecchia and others 1988; Gardiner 1992; Jamieson 1992). The longitudinal fibers are considered not to form a continuous layer but to be arranged in discrete and distinctly separated bands (Avel 1959; Stolte 1969; Rouse and Fauchald 1995, 1997). This feature proved to be an autapomorphy of Articulata in the analyses of Rouse and Fauchald (1997). In addition, more muscle systems may be present: oblique, dorsoventral, parapodial, chaetal, septal, mesenteric muscles as well as muscles associated with the gut. In the present review we will especially consider the musculature of the body wall. Since polychaetes are highly diverse in size and form, this also applies to their muscular system, the architecture of which is extremely variable among the various taxa. This indicates the importance of this structural complex for the discussion and understanding of annelid phylogeny.

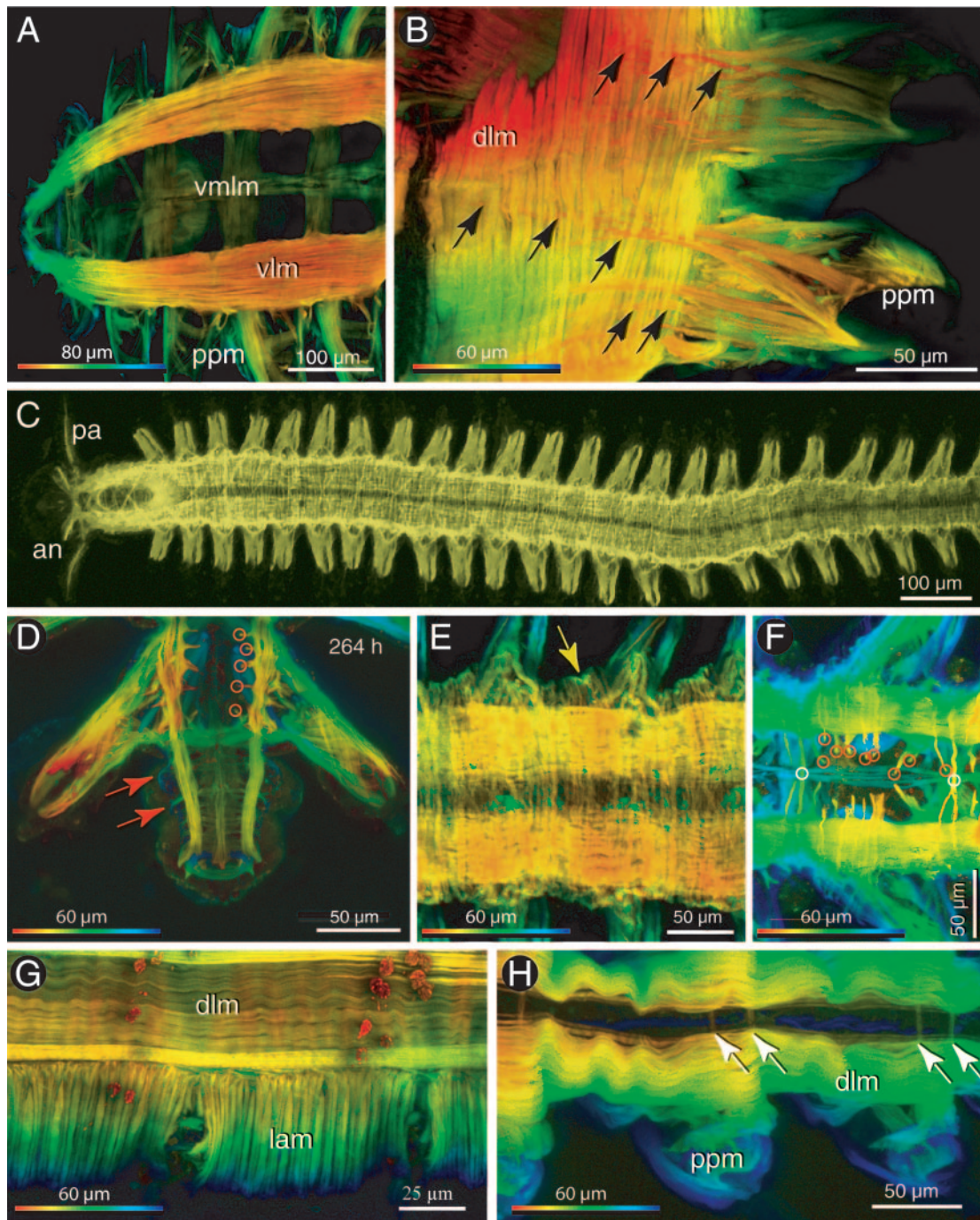
Discussing the evolution of Annelida, one has to keep in mind that most likely the annelid stem species exhibited a biphasic life cycle with a planktonic larva and a benthic adult (for example, Nielsen 2001). These two stages differ in their organization, as is evident in the organization of the mesoderm and probably the muscular system as well. The larva is small and acoelomate, whereas the adult is larger and usually coelomate. In addition, repeated events of progenesis are postulated to have occurred in several lineages and as a result the adults may also be acoelomate (Rieger and Purschke 2005).

Detailed descriptions of the polychaete muscular systems are rare (Mettam 1967, 1971; Storch 1968; Pilato 1981; Tzetlin and Filippova 2005). Formerly, these data have been obtained by means of dissections, histological investigations, and transmission electron microscopy. Recently, confocal laser scanning microscopy (cLSM) came into use, allowing visualization of the entire musculature by labeling the F-actin subset with fluorochrome-conjugated phalloidin (for example, Tyler and Rieger 1999; Möllers and Müller 2001; Tzetlin, Zhadan, and others 2002; Müller and Schmidt-Rhaesa 2003; Müller and Sterrer 2004; Müller and others 2004; Telke and others 2005). If specimens are comparatively small, this method has the advantage that whole mounts can be examined (Fig. 1C), enabling reconstructions from 3D image stacks.

## Circular muscles

Circular and other transverse muscle fibers usually underlie the extracellular matrix (ECM) of the epidermis. They are less well developed than the longitudinal ones and are not easy to follow in histological sections. Thus, misinterpretations may have happened; for instance, transverse fibers are only present dorsally, laterally, or ventrally and can hardly be called circular (Figs 1G, H and 5). Moreover, such muscles may actually belong to the parapodial muscle complex (Fig. 1B; see Mettam 1967, 1971; Tzetlin, Zhadan, and others 2002). In cross sections these muscle fibers often simulate true circular fibers.

As is the case for all Clitellata (Fig. 4B), circular fibers are present in various taxa of polychaetes (Tzetlin and Filippova 2005). In species of Glyceridae, Capitellidae, Maldanidae, and Arenicolidae they are arranged in a pattern corresponding to the traditional view of muscle arrangement, in that these muscles form an almost complete cylinder only interrupted at the ventral nerve cord (Tzetlin and Filippova 2005). In other taxa such as Amphinomidae, Nereididae, Hesionidae, and other Phyllodocida, Eunicida, and Terebellidae these fibers are less developed. In Dorvilleidae these transverse fibers run from their dorsal origin laterally and diverge to surround the parapodia anteriorly and posteriorly (Fig. 1E; Filippova and others 2006; Müller and Hinken, unpublished data). These fibers elongate and turn ventrally. Only those lying in the intersegmental furrow connect to corresponding fibers on the other side to form a true circular muscle (Fig. 1F, white circles). The other fibers are united into six to nine symmetrically arranged pairs terminating paramedially in *Dorvillea kastjani* (Fig. 1F, red circles), whereas in *Dorvillea bermudensis* all fibers terminate paramedially with a distinct gap between them occupied by the ventral nerve cord (Müller and Hinken, unpublished data). In the anterior part transverse fibers are completely absent; they start in the first or second chaetiger. Interestingly, in regenerating fragments initially complete rings of transverse fibers are formed, but these are subsequently disrupted as development proceeds (Fig. 1D, M. C. M. Müller and T. Hinken, unpublished data). Very likely this pattern is correlated with the formation of the ventral nerve cord, which usually has a basiepithelial position in polychaetes even in comparatively large species (Fig. 3B and C). Further investigations must show whether this can also be observed during regular development. However, the presence of complete circular fibers in clearly progenetic species, *Dinophiltus gyrotiliatus* and *Parapodrilus psammophilus* (M. C. M. Müller, unpublished data), indicates that this very likely is in fact a juvenile character.



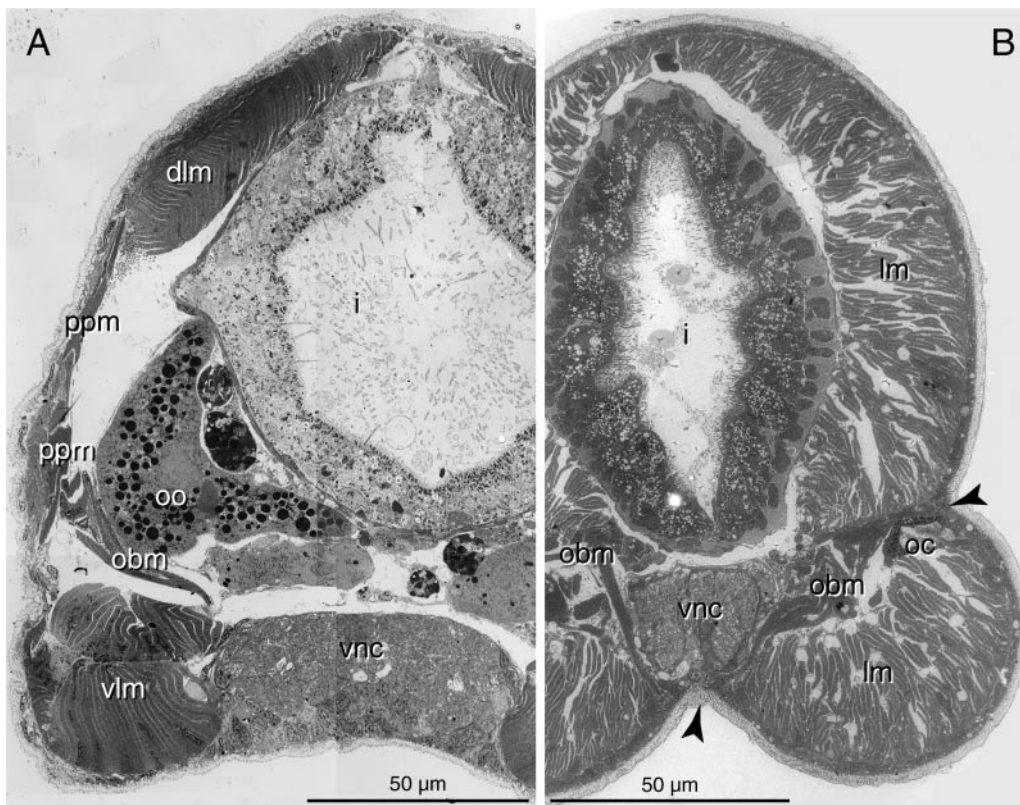
**Fig. 1** F-actin muscular subset of adult specimen, cLSM micrographs. Anterior oriented to the left, only in B and D to the top. Depth coded images: red indicates distal, blue central structures; the depth of the image-stack is indicated above the spectral bar. (A and B) *Dysponetus pygmaeus*. (A) Ventral view with widely separated longitudinal muscles; transverse elements absent. (B) Dorsal view. The parapodial muscles lie above and are intermingled (black arrows) with the longitudinal strands. (C and D) *Dorvillea bermudensis*. (C) Dorsal view of head with palps (pa) and antennae (an), peristomium and anterior 23 segments. (D) Ventral view of posteriorly regenerating animal. Within the regenerate true circular fibers (red arrows) are present. (E and F) *Dorvillea kastjani*. (E) Dorsal view with numerous transverse fibers running ventrally along the lateral sides (yellow arrow). (F) On the ventral side the transverse fibers terminate before the midline (red circles); only those within the segmental furrow are interconnected (white circle). (G) *Magelona* sp. Dorsolateral view. The transverse lateral muscles (lam) lie beneath the longitudinal strands. (H) *Nerilla antennata*. Dorsal view with two transverse fibers (white arrows) per segment. Dorsal (dlm), ventromedial (vmlm), and ventral (vlm) longitudinal muscles; parapodial muscles (ppm). A and B modified from Tzetlin, Zhadan, and others (2002); C and D M. C. M. Müller and T. Hinken, unpublished data; E and F modified from Filippova and others (2006); G modified from Filippova and others (2005); and H modified from Müller and Worsaae (2006).

Within Nerillidae transverse muscle elements are present only in *Nerilla antennata*, in the form of two small and inconspicuous fibers in each segment (Fig. 1H). In *N. antennata* these fibers form small arcs that are restricted to the dorsal region and thus can hardly be regarded as circular muscles (Müller and Worsaae 2006). Although transverse fibers are well developed in Spionida, true circular fibers are lacking (Figs 1G and 5B). In *Magelona* sp. and *Prionospio cirrifera* the transverse fibers are densely arranged and connect the dorsal and the ventral bundle of longitudinal fibers (Figs 1G and 5B). In the area of overlap the transverse fibers run underneath the longitudinal ones, resulting in a reverse arrangement in this area.

Circular fibers are completely absent in Chrysopetalidae, which is evident in a ventral view of *Dysponetus pygmaeus* showing only longitudinal muscles and those of the parapodial complex (Fig. 1A). Although on the dorsal side transverse fibers are visible between the longitudinal fibers, the former run into the parapodia (Fig. 1B, see also Tzetlin, Dahlgren, and Purschke 2002). This applies not only

to this small meiofaunal species but to the larger species of *Chrysopetalum* as well (Tzetlin, Dahlgren, and Purschke 2002; M. C. M. Müller, unpublished data). This may also be the case in several other taxa previously reported to possess circular fibers. Absence of circular muscles has so far been demonstrated in species of Aphroditidae, Chrysopetalidae, Magelonidae, Nephtyidae, Nerillidae, Opheliidae (Fig. 2B), Oweniidae, Phyllodocidae, Pisionidae, Polygordiidae, Polynoidae, Protodrilidae, Sigalionidae, and Spionidae (see Tzetlin, Zhadan, and others 2002; Tzetlin and Filippova 2005 for references). For the reasons mentioned above, this list may be far from complete. Absence of circular fibers has also been reported for *Jennaria pulchra*, an aberrant worm-like species with annelid affinities (Rieger 1991). These examples show that the lack of circular muscle fibers may not be a rare departure but a common situation in many polychaetes.

Lack of or weakly developed circular fibers is compensated by so-called bracing (diagonal) fibers (Tzetlin and Filippova 2005), which can be found on the dorsal side where they cross in the dorsal midline, forming a



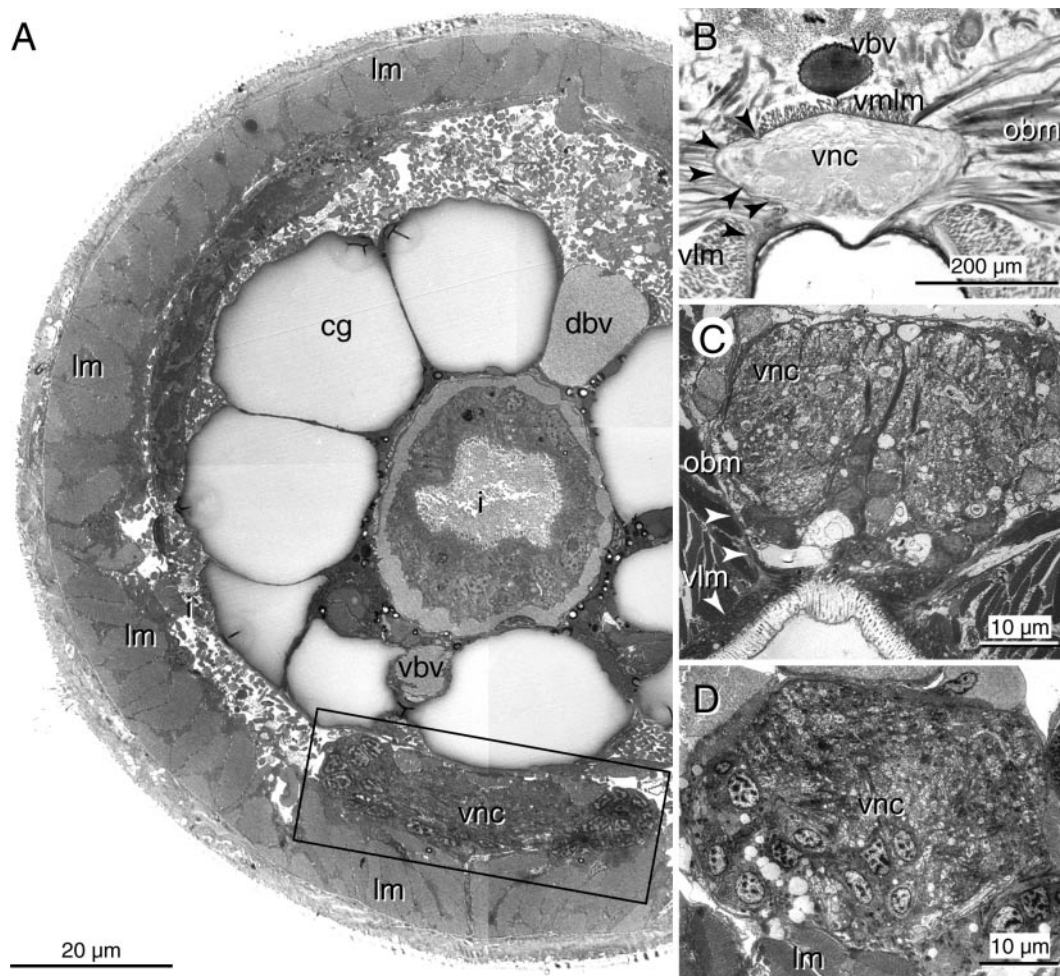
**Fig. 2** Range of arrangement of body wall musculature in polychaetes. Cross sections between parapodia, TEM. (A) *Sinohesionie genitaliphora* (Hesionidae, Phyllodocida). Longitudinal musculature in two pairs of prominent bundles, dorsal and ventral (dlm, vlm), oblique muscles (obm), and parapodial muscles (ppm). No obvious circular fibers. i, intestine; oo, oocyte; vnc, ventral nerve cord. (B) *Polyophthalmus qingdaoensis* (Opheliidae). Longitudinal musculature forms continuous layer interrupted only where the oblique muscle (obm) and ventral nerve cord (vnc) attach to the epidermis (arrowheads). Note absence of circular fibers. i, intestine; oc, segmental ocellus; A modified from Purschke (2002).

lattice-like arrangement (Figs 1C, E and 5A). Such fibers may be present dorsally, laterally, or ventrally (Mettam 1971). In cross sections these fibers look like transverse muscles and, most likely, were erroneously taken for circular fibers by other authors.

### Longitudinal muscles

Longitudinal muscles run along the whole body length and usually form discrete bands (Fig. 2A). Number and position of bands varies considerably among the different polychaete taxa (Storch 1968; Tzetlin and Filippova 2005). Ventrally these bands are normally separated from each other by the ventral nerve cord,

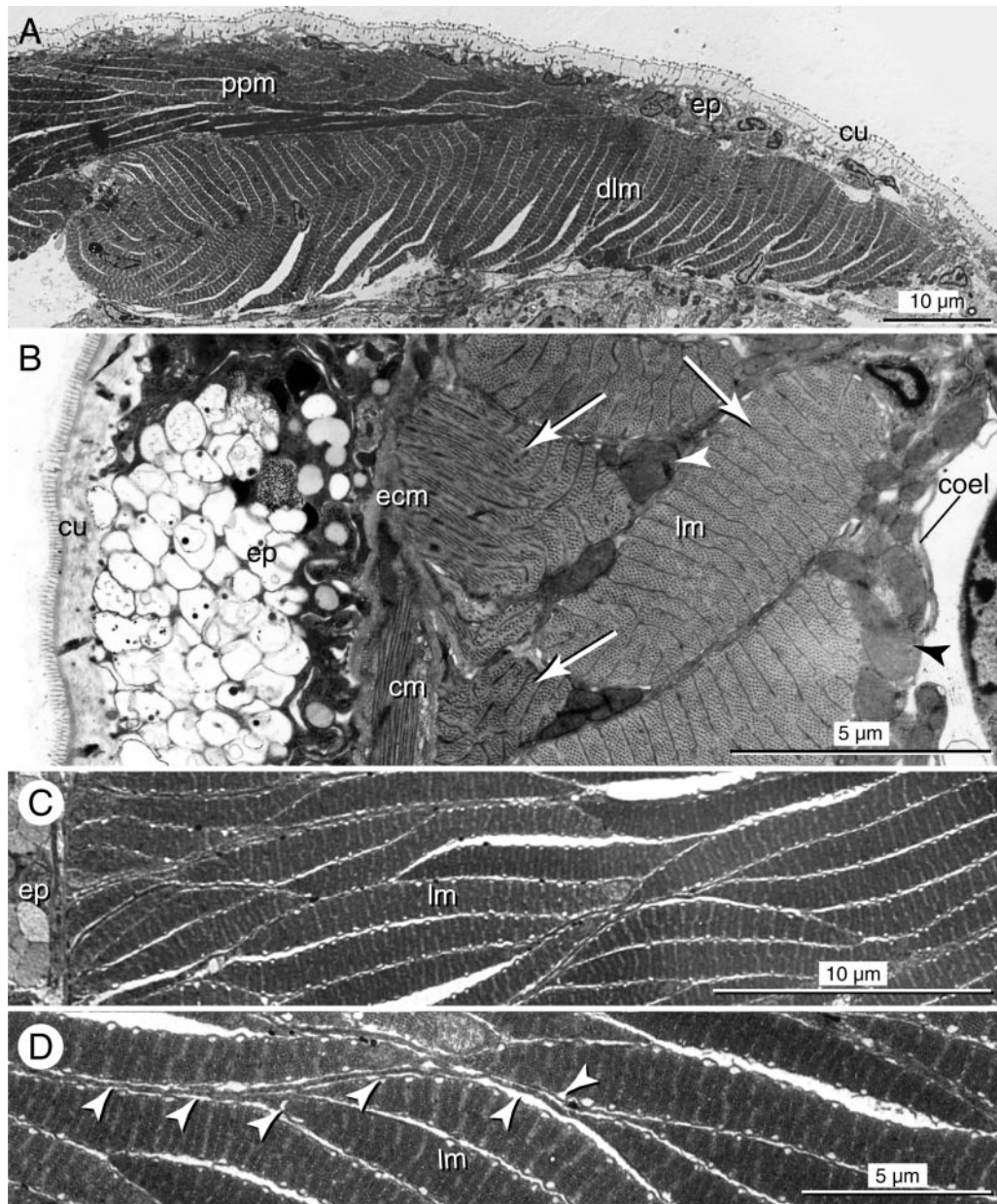
which, although usually basiepithelial, bulges into the body cavity (Figs 2A, B and 3B, C). Presence of four bands, two ventral and two dorsal, appears to be the most common pattern (Fig. 2A). These bands may be more or less equally developed ventrally or dorsally (for example, Phyllodocidae, Glyceridae) or the ventral bands are more prominent (for example, Eunicidae, Sabellidae). In addition to these bands an unpaired band of fibers may be present above the ventral nerve cord in certain taxa, such as Chrysopetalidae (Fig. 1A; see Tzetlin, Zhadan, and others 2002), Nereididae (Fig. 2B), Hesionidae (see Westheide 1967), Nerillidae (see Müller and Worsaae 2006), Dorvilleidae (Figs 1F and 5A, see



**Fig. 3** (A) Arrangement of body wall musculature in Clitellata [*Marionina preclitellochaeta* (Enchytraeidae)]. Longitudinal fibers (lm) form continuous layer. Circular fibers weakly developed, not visible on photo. Note subepithelial position of ventral nerve cord (boxed, vnc). cg, chloragogen tissue; dbv, dorsal blood vessel; i, intestine; vbv, ventral blood vessel. (B–D) Position of ventral nerve cord and musculature. (B) *Nereis virens* (Nereididae, Phyllodocida). Basiepithelial nerve cord (vnc), arrowheads point to continuous epidermal ECM. Note median longitudinal muscle just above the nerve cord. obm, oblique muscle; vbv, ventral blood vessel; vlm, ventral longitudinal muscle. (C) *Polyophthalmus pictus* (Opheliidae). Basiepithelial nerve cord between ventral longitudinal muscle (vlm) and oblique muscle (obm); arrowheads point to epidermal ECM. (D) *Enchytraeus crypticus* (Enchytraeidae, Clitellata). Subepithelial nerve cord (vnc) below musculature in coelomic cavity. A, C and D, TEM micrographs; B, micrograph of histological section A, modified from Purschke (2002), B courtesy of Prof. W. Westheide, Osnabrück.

Filippova and others 2006), and Capitellidae (M. C. M. Müller, unpublished data). This muscle is sometimes considered to belong to the mesenterial musculature but most likely it represents an additional type of longitudinal muscle. Since this muscle has been overlooked in, for example, *Nereis* sp. so far (Mettam 1967; Storch 1968), nothing can be said about its pattern of occurrence among the polychaetes.

As a departure from this minimal arrangement of four to six distinct bands all patterns can be found, until an almost complete coat of longitudinal fibers is formed. For example, this latter feature is present in Scalibregmatidae, Arenicolidae, and Opheliidae, where this coat is interrupted only where the oblique muscle fibers attach to the body wall and at the ventral nerve cord (Fig. 2B). Diversity of longitudinal muscle band



**Fig. 4** Structure of longitudinal musculature. (A) *Sinohesione genitaliphora* (Hesionidae, Phyllodocida) Dorsal longitudinal muscle fibers form single layer of ribbon-shaped fibers with some shorter fibers in between. cu, cuticle; ep, epidermis; ppm, parapodial muscle fibers. (B) *Lumbricillus bülowi* (Enchytraeidae, Clitellata). Longitudinal fibers two-layered with inner ribbon-shaped fibers and outer triangular fibers (arrows); arrowheads point to position of mitochondria on the narrow side outside contractile part of the fiber. cm, circular muscle fiber; coel, coelothelium; cu, cuticle; ecm, extracellular matrix; ep, epidermis. (C and D) *Polyophthalmus pictus* (Opheliidae), pseudostratified layer of longitudinal fibers, each fiber connected to ECM by means of a thin process (arrowheads). ep, epidermis; lm, longitudinal muscle fiber.

arrangement is described in detail by Tzetlin and Filippova (2005).

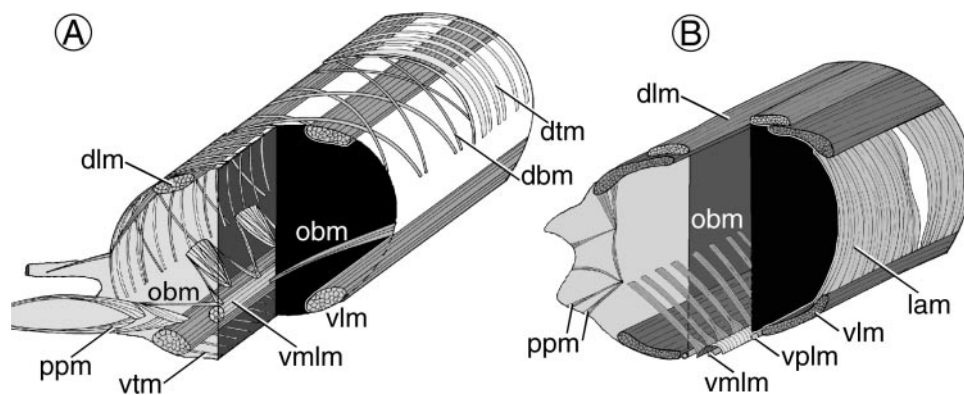
In Clitellata longitudinal muscles are not arranged in bands but form a continuous layer (Fig. 3A). This arrangement of fibers is only possible because the ventral nerve cord has a subepithelial position in Clitellata without exception and regardless the size of the species (Fig. 3A and D). Hence, the brain and the ventral nerve cord lie within the coelomic cavity, enclosed by an ECM or connective tissue and a coelothelium (Stolte 1969; Purschke and others 2000; Purschke 2002, 2003). The interpretation of the longitudinal musculature in Clitellata as being arranged in bands is due to the fact that normally sections through the chaetal region of oligochaetes are shown in textbooks and original articles (for example, Fig. 196 in Avel 1959; Purschke 2002). In these regions the longitudinal fibers are pushed apart to allow the chaetal follicles and muscles to pass between them. Within Hirudinomorpha, only Branchiobdellidae show this pattern, whereas in Hirudinea the fibers are aggregated in groups or fascicles, up to 80 in number (Sawyer 1986). It follows that the character state “longitudinal musculature arranged in bands” found as a synapomorphy of Annelida and Arthropoda in Rouse and Fauchald (1995, 1997) is only present in polychaetes. Regardless of which hypothesis on the position of Clitellata is applied, the feature of a continuous layer has to be interpreted as a derived character state (see Purschke 2002).

Number and arrangement of muscle fibers within the longitudinal bands may differ among annelids. Sometimes the patterns vary even within so-called families. This ranges from a single layer of fibers to true stratified layers (Fig. 4A–D). These layers either form a myoepithelium not covered by coelothelial cells

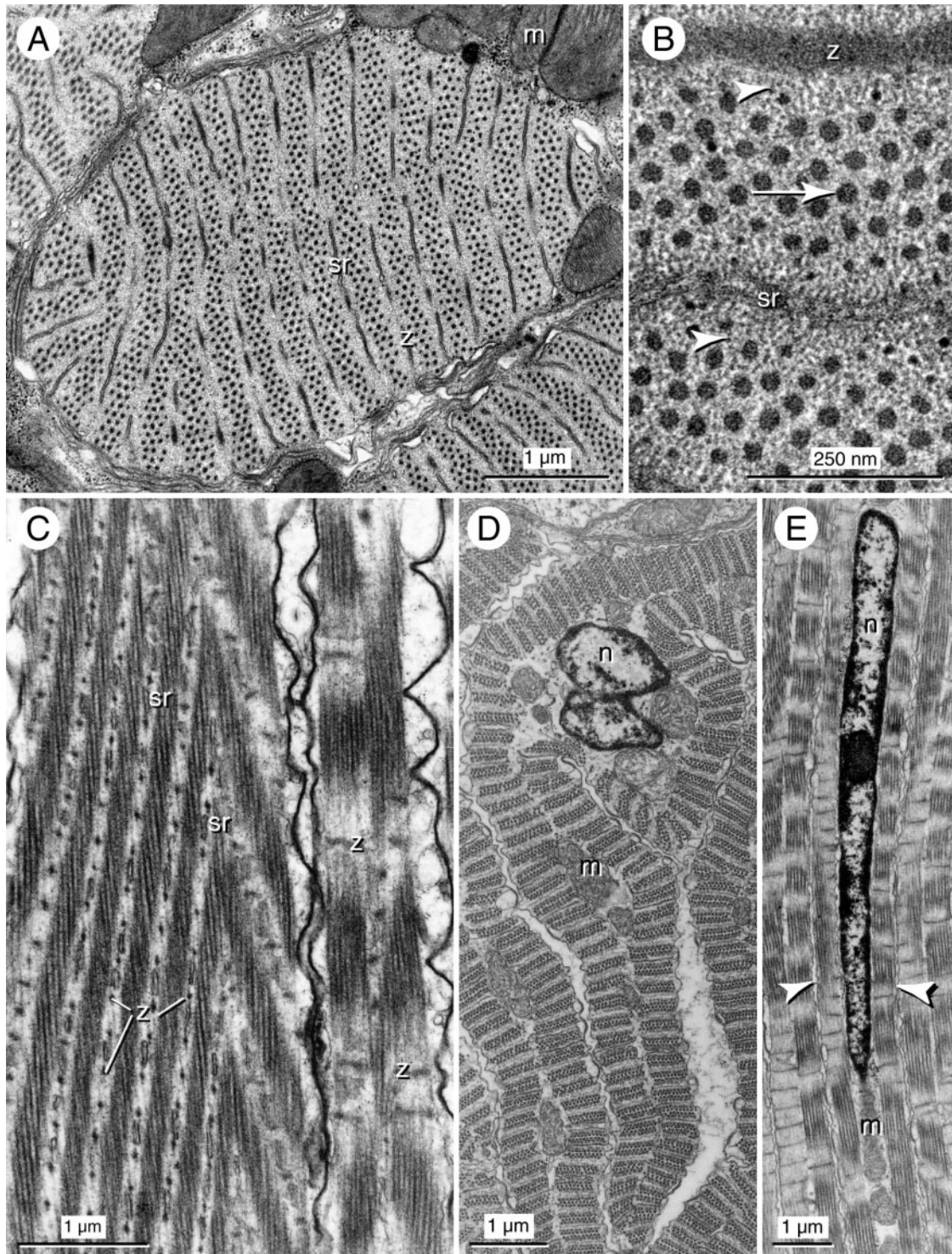
or are covered by a true coelothelium (Bartolomaeus 1994; Rieger and Purschke 2005). In a single layer usually ribbon-shaped muscle cells lie in a single row with their narrow part attached to the ECM and the nuclei on the opposite side (Fig. 4A). Thicker musculature may be formed by such bands when they are convoluted in different patterns (Tzetlin and Filippova 2005): they may be rolled up once, forming a closed ellipse with or without a central cavity as in the ventral muscle band of *Sinohesione genitaliphora* (Fig. 2A), they may be rolled up more times, or they may form an s-shaped structure, producing a multi-layered appearance. In *Polyopthalmus pictus* and other Opheliidae a pseudostratified layer is formed, in which each fiber is in contact with the ECM via a small and indistinct process (Fig. 4C and D). In oligochaetous Clitellata there is a true stratified muscle layer covered by a coelothelium (Fig. 4B). The shape of the individual muscle cells may vary according to the position in the longitudinal musculature. In Enchytraeidae the fibers closest to the circular muscles are triangular in cross section, whereas those facing the coelomic cavity are ribbon-shaped (Fig. 4B). In bands with only ribbon-shaped fibers these may be of different heights (Fig. 4A).

### Other types of muscles

The oblique muscles usually run from the midventral line to the bases of parapodia or in species with more or less reduced parapodia attach to the body wall between the notopodial and neuropodial chaetae (Figs 2A, B and 5A, B). Ventrally they attach to the epidermis on either side of the ventral nerve cord (Fig. 3B and C). The attachment zones may be visible in more or less pronounced furrows, which are well known in Opheliidae (Fig. 2B). Data on the parapodial musculature



**Fig. 5** Schematic drawings of the F-actin muscular architecture of midbody region. (A) *Dorvillea kastjani*. (B) *Magelona* sp. Dorsal (dlm), ventral (vlm), ventral paramedial (vplm), and ventromedial (vmlm) longitudinal muscles; dorsal (dtm), lateral (lam), and ventral (vtm) transverse muscles; dorsal bracing muscles (dbm); oblique muscles (obm); parapodial muscles (ppm). A redrawn from Filippova and others (2006), B redrawn from Filippova and others (2005).



**Fig. 6** Ultrastructure of obliquely striated annelid muscle fibers. (A) *Lumbricillus bülowi* (Enchytraeidae, Clitellata). Cross section of ribbon-shaped longitudinal fiber showing typical arrangement of sarcoplasmic reticulum (sr), z-rods (z), and myofilaments. (B) *Stygocapitella subterranea* (Parergodrilidae). Enlargement showing thick (arrows) and thin (arrowheads) myofilaments between sarcoplasmic reticulum (sr) and z-rods (z). (C) *Microphthalmus carolinensis* (Hesionidae, Phyllococida). Longitudinal section of two fibers: on the left typical double oblique striation pattern ( $x$ - $y$  plane), on the right seemingly cross-striation pattern ( $x$ - $z$  plane). sr, sarcoplasmic reticulum; z, z-rod. (D and E) *Nerilla antennata* (Nerillidae, Phyllococida). Hirudinean type of muscle fibers with central sarcoplasm containing nucleus (n) and mitochondria (m). Longitudinal fibers of body wall. (D) Cross section. (E) Longitudinal section ( $x$ - $z$  plane); arrowheads mark plasma membrane of single fiber. C courtesy of Prof. W. Westheide, Osnabrück.



are rare and mainly refer to errant polychaetes. Extensive descriptions have been made by Mettam (1967, 1971) and Storch (1968). Only a few species have been studied by cLSM (Filippova and others 2006; Müller and Worsaae 2006). According to Mettam (1967, 1971) the parapodial muscles are divided into a number of functional groups, including pro- and retractors of the aciculae and chaetae as well as the intrinsic muscles of the parapodia (reviewed by Tzetlin and Filippova 2005). To date our knowledge is too scanty to decide whether these muscles might be of some phylogenetic significance on a higher systematic level. Septa and mesenteries consist of adjacent coelothelia with an ECM in between. These coelothelia may be made up of myoepithelial cells. The extent of muscle development depends on the life style of the species. Strong muscular septa are present in the anterior part of Terebellidae, Capitellidae, and Arenicolidae, where these septa are involved in producing the pressure necessary for protrusion of the mouth appendages or pharynx (see Tzetlin and Filippova 2005).

## Ultrastructure

Ultrastructure of annelid muscle fibers is comparatively well known and has been reviewed by Lanzavecchia and others (1988) and Gardiner (1992), so only a brief summary will be given here. As a rule annelid muscle fibers are of the double obliquely striated type (Fig. 6A–E). These fibers can be viewed as cross-striated fibers having an extremely regular structure. The striation angle depends on the degree of contraction and usually is between 2° and 15° (Fig. 6C; Lanzavecchia and others 1988). Each fiber has only one nucleus. The obliquity occurs because filaments at corresponding positions in the fibers are longitudinally staggered by a fraction of their length. This pattern is only visible in longitudinal sections following the longer axis of the fiber, commonly called the  $x$ - $z$  plane. If a section is slightly tilted with respect to this axis the double oblique striation pattern becomes obvious (Fig. 6C). This pattern is due to a helical arrangement of the functional units, the so-called sarcomeres, which extend only to about half of the width of a fiber. In cross sections (so-called  $x$ - $y$  plane) each fiber appears to be divided into radial fields consisting of groups of myofilaments separated by  $z$ -rods and sarcoplasmic reticulum (Fig. 6A and B). Each field consists of an area with only actin filaments, followed by a zone containing actin and myosin filaments and a central area with only myosin filaments (Fig. 6B). Depending on contraction of the fiber, the width of each zone varies. Due to the helical arrangement of the contractile elements, there is one plane in

longitudinal sections in which the fibers appear as cross-striated fibers (Fig. 6C and E). This plane, called the  $y$ - $z$  plane, usually represents the narrow axis of a muscle cell. Mostly the muscle fibers are of this so-called flattened or ribbon-shaped type. It is further characterized by separation of the contractile and non-contractile part in that the sarcoplasm containing nucleus, mitochondria, and glycogen is found on the narrow side of fiber, in longitudinal fibers often facing toward the coelomic cavity (Figs 4A, B and 6A). In the median the two halves with myofilaments are apposed to each other rather than being separated by a myofibril-free zone.

Besides this type of helical or double-striated muscle other fibers may be found. There is a great diversity of muscle fibers among the polychaete taxa regarding shape and type, ranging from various kinds of smooth muscles, single-striated muscles to true cross-striated muscles (Lanzavecchia and others 1988; Gardiner 1992). Among the helical fibers two types can be distinguished: those having no central cytoplasmic axis and those with a central cytoplasmic axis. In the latter, the nucleus and mitochondria are positioned centrally and the whole contractile apparatus is located peripherally (Fig. 6D and E). Such fibers are thought to represent an autapomorphy of Hirudinea but are present in certain taxa of polychaetes as well. For instance, in Nerillidae the musculature of the body wall is also composed of such fibers, which in all probability evolved convergently in this taxon of meiofaunal polychaetes with uncertain affinities. Presence of an unusual muscle fiber type may thus represent another apomorphic feature or may help to find the putative sister group.

## Conclusions

Structure and arrangement of muscle fibers probably have high potential for phylogenetic considerations. Absence of circular fibers occurs more often than previously assumed and may either be primary or secondary. A different arrangement of muscles in developing stages may give some indication about the muscle arrangement in the annelid stem species and may enable clarification of the reading direction of evolutionary changes. However, the database is still not large enough to allow such far-reaching conclusions; clearly, further comparative studies are needed before a more definite answer can be given. In contrast, the diversity of fiber ultrastructure may be useful in providing characters to define certain subordinate taxa such as Hirudinea and Nerillidae, but most likely will be of minor importance for clarifying the interrelationships of annelids on a broader scale.

Absence or weak development of circular and other transverse fibers clearly speaks in favor that these fibers are of minor importance for the complex movements exhibited by many polychaetes. These fibers appear to be important mainly for forms that burrow by means of peristaltic movements in comparatively hard substrates; thus, earthworms represent a plan of organization formerly thought to be close to the annelid stem species. In contrast, many polychaetes are epibenthic or use their parapodia for walking and swimming. The most important muscular system obviously is the longitudinal musculature, which is subdivided into at least four functional groups represented by distinct bands that can be used independently to facilitate the diverse movements observed in extant polychaetes.

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*Conflict of interest:* None declared.

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