

Muscular system in polychaetes (Annelida)

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Abstract

The structure of the polychaete muscular system is reviewed. The muscular system comprises the muscles of the body wall, the musculature of the parapodial complex and the muscle system of the dissepiments and mesenteries. Various types of organisation of the longitudinal and circular components of the muscular body wall are distinguished. In Opheliidae, Polygordiidae, Protodrilidae, Spionidae, Oweniidae, Aphroditidae, Acoetidae (= Polyodontidae), Polynoidae, Sigalonidae, Phyllodocidae, Nephtyidae, Pisionidae, and Nerillidae circular muscles are lacking. It is hypothesised that the absence of circular muscles represents the plesiomorphic state in Annelida. This view contradicts the widely accepted idea of an earthworm-like musculature of the body wall comprising an outer layer of circular and an inner layer of longitudinal fibres. A classification of the various types of parapodial muscle construction has been developed. Massive and less manoeuvrable parapodia composed of many components like those of *Aphrodita* are regarded to represent the plesiomorphic state in recent polychaetes. An analysis of the diversity of the muscular structure supports the hypothesis that the primary mode of life in polychaetes was epibenthic and the parapodial chaetae had a protective function.

Introduction

Polychaetes and the entire taxon Annelida are soft-bodied animals. Their mobility and the maintenance of the body shape are affected by their muscular system. The polychaete muscular system consists of several components such as circular and longitudinal fibres of the body wall, parapodial, chaetal, oblique, diagonal, dorsoventral fibres, as well as muscular structures elements of septa and mesenteries. Therefore, the knowledge of the construction of the muscle system of polychaetes is important for our understanding of the life styles observed and evolutionary trends in this group.

The ultrastructure of the muscle tissues of polychaetes was studied in detail and is well described (e.g., Mattisson, 1969; Eguileor & Valvassori, 1977; Lanzavecchia et al., 1988; Gardiner, 1992). Usually polychaete muscle fibres are dou-

ble obliquely striated with the non-contractile parts located on the narrow side. But several other types of fibres including hirudinean-like fibres and cross-striated muscle cells have been described as well. These fibres mainly occur in specialised organs. Since the ultrastructure has repeatedly been reviewed (e.g., Lanzavecchia et al., 1988; Gardiner, 1992) we will only deal with available data on the anatomical structure of those muscular systems which have not been reviewed recently and which have not been considered for phylogenetic implications since the comprehensive studies of Storch (1968) and Mettam (1971).

Since the 19th century annelids and polychaetes, in particular, have been considered to possess a muscular body wall consisting of an outer layer of circular and an inner layer of longitudinal

muscle fibres (e.g., Meyer, 1887, 1888). In addition diagonal fibres may also be present in the body wall. Circular muscle fibres are transversely oriented and form a cylinder, which is not even interrupted near the ventral nerve cord (Fig. 1). This pattern of organisation of the musculature has been widely accepted and has almost unchanged been adopted as characteristic for annelids in recent publications and textbooks of invertebrate zoology (Fig. 1a–c) (e.g., Storch & Welsch, 1986; Brusca & Brusca, 1990; Westheide & Rieger, 1996). However, already in the end of the 19th and the beginning of the 20th century it was noted that the so-called Archannelida had poorly developed or even lacking circular musculature (Salensky, 1907). Absence of circular muscle fibres not only in archannelids but also in several other polychaete species was mentioned in a number of publications (e.g., McIntosh, 1917; Hartmann-Schröder, 1958). Hartmann-Schröder (1958) and Orrhage (1962) were the first who reported lack of circular muscle fibres not only in aberrant or interstitial polychaete species but in larger species belonging to Opheliidae and Spionidae as well. These findings stimulated additional

investigations which revealed that absence of circular muscle fibres occurs more often in polychaetes than generally assumed. Until today the lack of circular muscles has been recorded in macrobenthic, meiobenthic, parapodia-bearing as well as sedentary species of the following taxa: Opheliidae, Polygordiidae, Protodrilidae, Spionidae, Oweniidae, Aphroditidae, Polyodontidae, Polynoidae, Sigalonidae, Phyllodocidae, Chrysopetalidae, Nephtyidae, Pisionidae and Nerillidae (McIntosh, 1917; Hartmann-Schröder, 1958; Orrhage, 1964; Jouin & Swedmark, 1965; Mettam, 1967, 1971; Storch, 1968; Hermans, 1969; Gardiner & Rieger, 1980; Tzetlin, 1987; Ivanov & Tzetlin, 1997; Tzetlin et al., 2002a). This apparent widespread lack of circular muscle fibres raised the question whether this feature is due to convergence or represents a homologous but plesiomorphic character (Tzetlin et al., 2002a, b). The answer has far reaching consequences for our understanding of evolutionary pathways in annelids. For instance, since circular muscles are most likely important for burrowing forms but are unnecessary for animals which proceed by movements with their parapodia or cilia, this question is re-

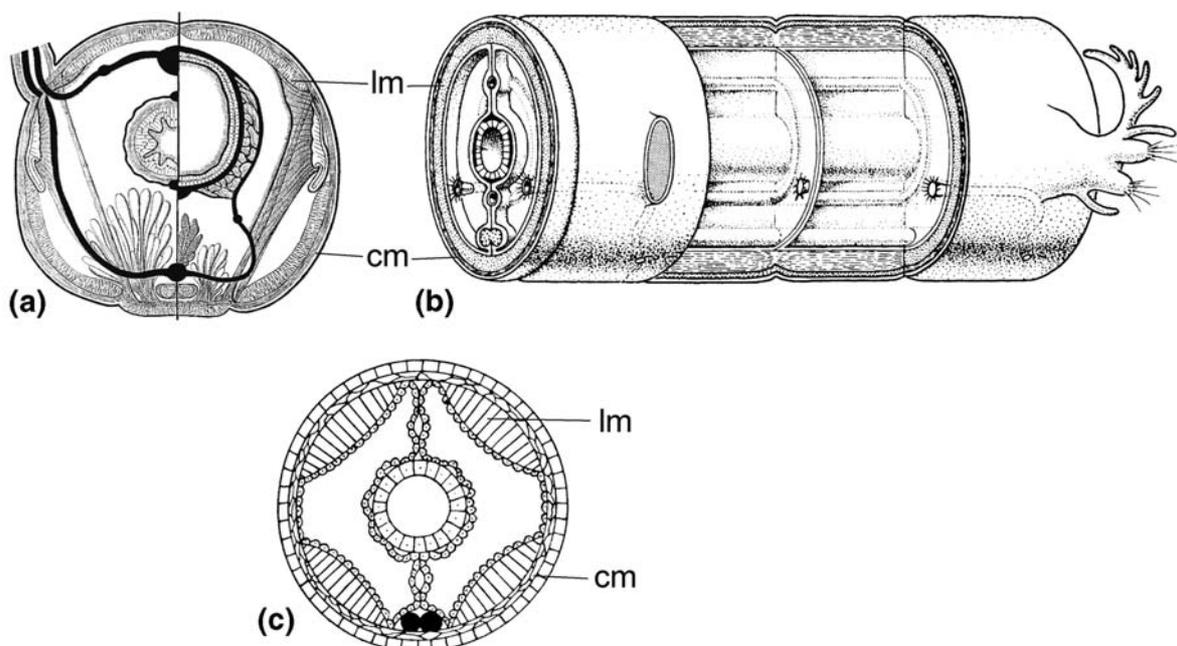


Figure 1. General arrangement of body wall musculature. (a) *Amphitrite rubra*, diagram of transversal section through midbody region. (b) Schematic organisation of segments in Annelida. (c) Annelid body plan. cm – circular muscles, lm – longitudinal muscles. (a) After Meyer (1887), (b) after Westheide & Rieger (1996), (c) after Storch & Welsch (1986).

lated to whether the polychaete stem species was epi- or endobenthic.

Until now the diversity of polychaete muscle system has usually been studied by means of routine histology, transmission as well as scanning electron microscopy (Mettam, 1967; Storch, 1968; Tzetlin et al., 2002a). At least some of these data are based on results without complete reconstruction of the muscular system of the body wall. In

such cases the authors could have overlooked poorly developed muscular elements. Therefore, labelling of F-actin and subsequent confocal laser scanning microscopy is a comparatively new, excellent and accurate method for investigation of muscle fibre arrangements (Tzetlin et al., 2002b). Each muscle cell is labelled individually and, provided that the specimens do not exceed an appropriate size, can be followed along its entire

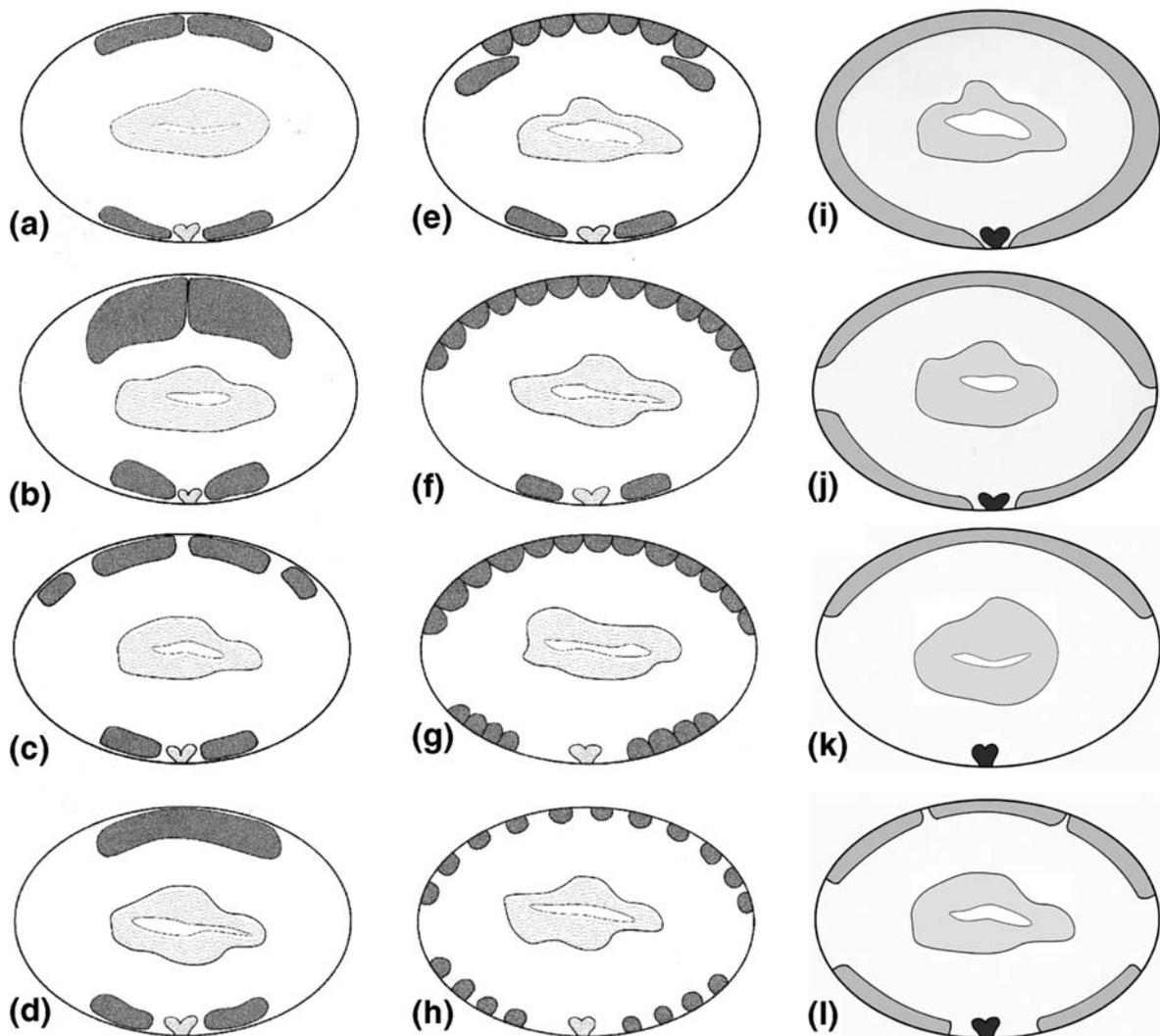


Figure 2. Position of muscles in the body wall of polychaetes. Schematic representations. (a–h) Longitudinal muscles. (a) Phyllodocidae, Glyceridae, Nerillidae, Ampharetidae etc., (b) Polynoidae, Aphroditidae, (c) Amphinomidae, (d) Terebellidae, (e) Eunicidae, Sabellidae, (f) Syllidae, (g) Nephtyidae, (h) Scalibregmidae, (i–l) Circular muscles, (i) Maldanidae, (j) Amphinomidae, (k) Nereidae, (l) Phyllodocidae.

length. Thus, this method allows investigating absence or presence of a certain type of muscle cell with a greater degree of certainty, especially if these muscles are poorly developed and hardly visible in histological sections. This method has been successfully applied in various taxa of small invertebrates as well (e.g., Rieger et al., 1994; Wanninger et al., 1999; Hochberg & Litvaitis, 2001; Müller & Schmidt-Rhaesa, 2003). To date such studies have only been carried out for a limited number of polychaete species and do not encompass the whole diversity of polychaete muscular systems. These studies will be reviewed below but these facts necessitate the need for reinvestigations of annelid musculature in a broader range of taxa.

Circular muscles

Circular and other transverse fibres usually underlay the extracellular matrix of the integument and are poorly developed compared to the longitudinal underlying the layer of circular muscles if present at all (Meyer, 1887; Westheide & Rieger, 1996). Circular muscle fibres are found in various taxa such as Amphinomidae, Nereididae, Hesionidae, Glyceridae, and other Phyllodocida, Nerillidae, Capitellidae, Maldanidae, Arenicolidae, and Terbellidae. However, the structure and arrangement of these fibres vary greatly and various types may be distinguished.

In species of Glyceridae, Capitellidae, Maldanidae and Arenicolidae circular fibres are arranged

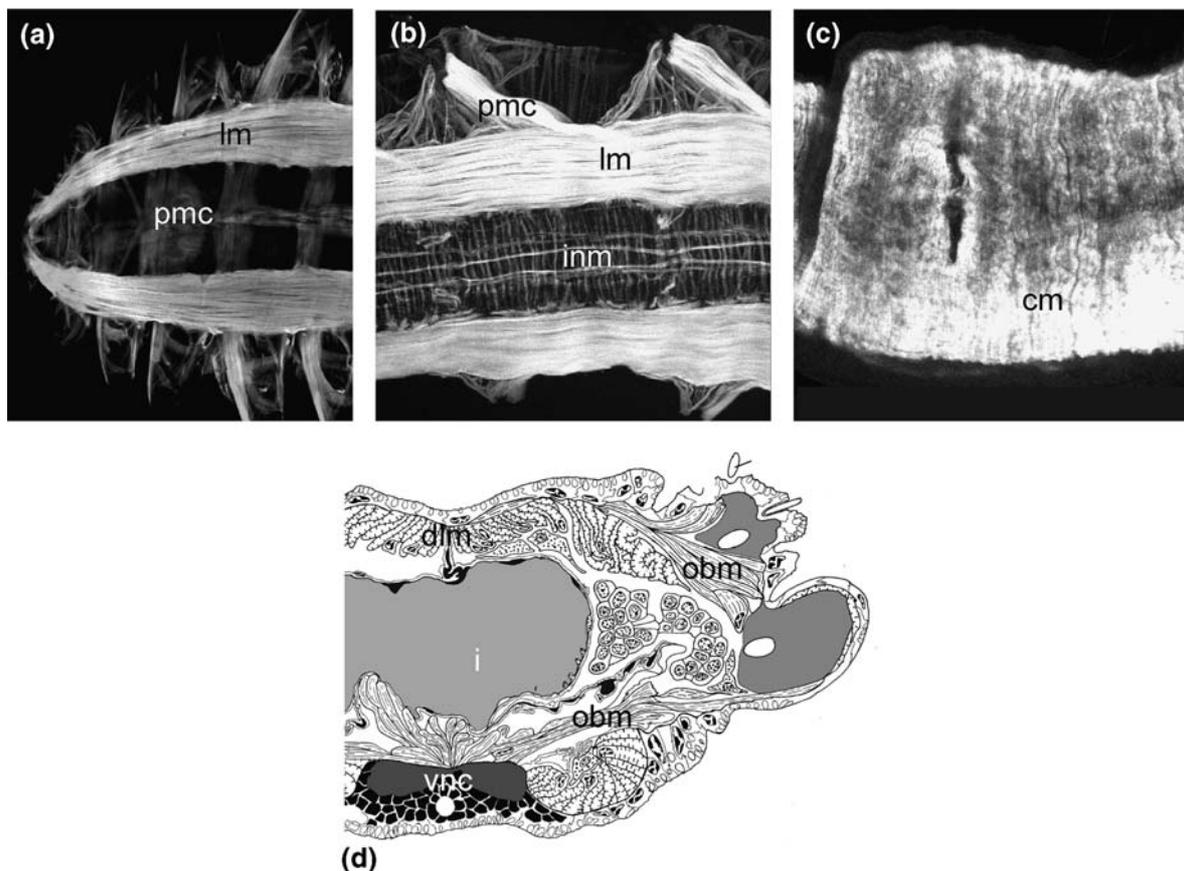


Figure 3. Arrangement of body wall muscle system. (a) *Dysponetus pygmaeus*, anterior end, ventral view. (b) *Prionospio cirrifera*, two midbody segments in dorsal view. (c) *Paraxiella praetermissa*, midbody, lateral view. (d) *D. pygmaeus*. Drawing of cross-section through midbody segment with different muscle systems. dlm – dorsal longitudinal muscle, i – intestine, lm – longitudinal muscle, obm – oblique muscle, pmc – parapodial muscle complex, vnc – ventral nerve cord. (a–c) cLSM micrographs after phalloidin-labelling, (d) after TEM observations. (a) After Tzetlin et al., 2002b, (b) After Tzetlin et al. (2002a).

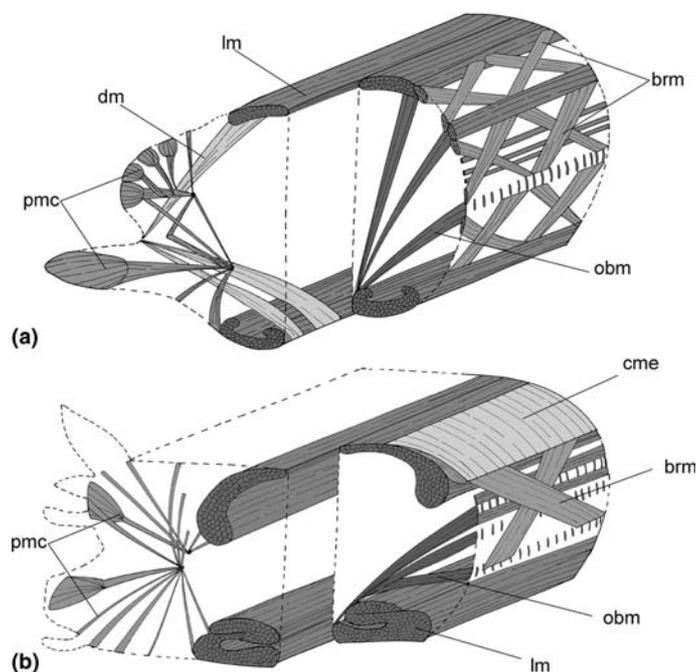


Figure 4. Schematic reconstructions of muscle systems. (a) *Aphrodite* sp., (b) *Nereis* sp. brm – bracing muscle, cme – circular muscle element, dm – diagonal muscle, lm – longitudinal muscle, obm – oblique muscle, pmc – parapodial muscle complex. After various authors.

following a pattern which corresponds to the traditional view of muscle arrangement in polychaetes (Wells, 1944, 1950; Clark, 1964). Transversal muscle fibres form almost closed circles, only interrupted at the intraepithelial nerve cord (Figs 2i and 3c). It is noticeable that even in these species the circular fibres are less developed than the longitudinal muscle fibres. The fibres form an almost complete cylinder without gaps even at the parapodia (Fig. 3c). There are, however, no circular fibres at the border of the segments. This pattern is interpreted as an adaptation to an enhanced mobility and better conjunction of the segments.

In Amphinomidae, Nerillidae and Terebellidae the circular muscles are interrupted near the parapodia (Fig. 2j and l; Storch, 1968; Marsden & Lacalli, 1978). Transverse fibres are only present in certain parts of the body and, thus, can hardly be called circular muscle cells. They are either restricted to the dorsal side (Figs 2k and 6b; e.g., Hesionidae, Nereididae) or on the ventral side as in Phyllodicidae (Storch, 1968).

In several taxa circular or transverse fibres are completely lacking. This has been observed in

Aphroditidae, Chrysopetalidae, Pisionidae, Spionidae and Opheliidae (Figs 3a, b, d, 4a, b, 5a and b; see Brown, 1938; Mettam, 1971; Tzetlin, 1987; Tzetlin et al., 2002a, b, unpubl. obs.). These findings indicate that absence of circular muscle fibres is not an unusual case but a fairly common phenomenon instead (Tzetlin et al., 2002b).

In order to maintain the shape of the body it has to be expected that weak transversal muscles or entirely lacking circular muscle fibres are compensated by another system. In some taxa this requirement is achieved by so-called bracing muscles of some taxa (Fig. 4a and b). These muscles are located diagonally among the longitudinal fibres, cross each other and form a lattice. The maximal number of these groups is three: they are located ventrally, dorsally and laterally in *Aphrodita aculeata* (Fig. 4a; see Mettam, 1971). In cross-sections these muscles look like circular fibres and, most likely, were erroneously taken for them by other authors. In addition to regulating the body wall constrictions, the bracing muscles reach the parapodial muscles, so that they may be attributed to the parapodial muscle complex.

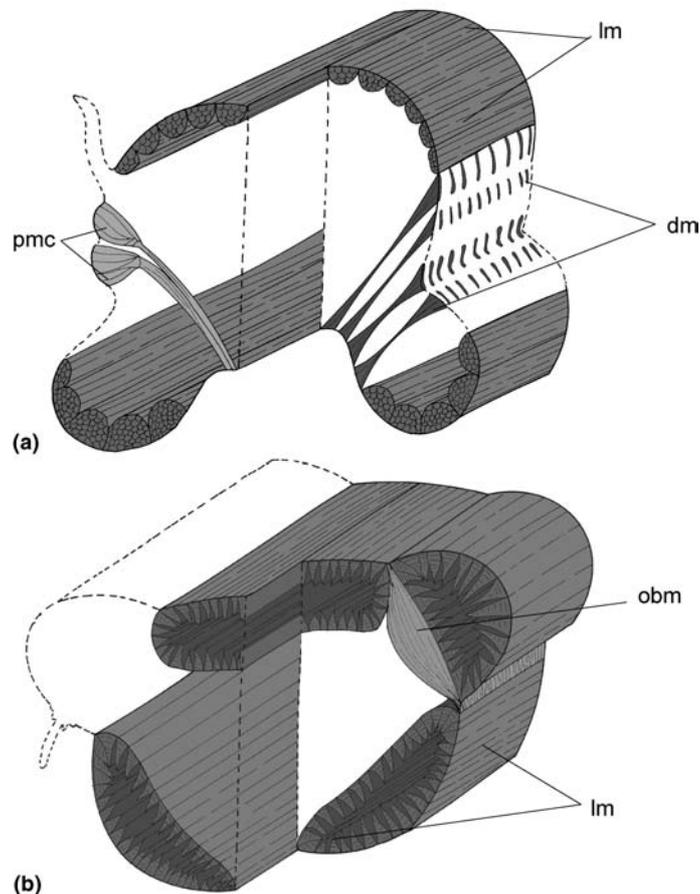


Figure 5. Schematic reconstructions of muscle systems. (a) *Ophelia* sp., (b) *Pisionidens tchesunovi*. dm – diagonal muscle, lm – longitudinal muscle, obm – oblique muscle. (a) After various authors, (b) After Tzetlin (1987).

Longitudinal muscles

Longitudinal muscles run along the whole body length and usually form discrete bands. The fibres making up the bands are arranged in different patterns (Fig. 6). A band may be formed by large flattened cells lying in a single row and not being covered by the coelothelium. The nuclei of these cells are usually located on the distal part facing the coelomic cavity (Fig. 6a for Sphaerodoridae, Phyllodocidae; Tzetlin, 1987). A similar pattern is observed in Chrysopetalidae (Tzetlin et al., 2002a). However, at least a part of the bundles are covered by coelothelial cells. Sometimes the nuclei are located in the distal parts between the myofilaments or in epithelium-like processes forming a cover above the myofilaments-containing parts of the

fibres (Fig. 7a and b; Phyllodocidae, see Ivanov, in press). Such processes may be misinterpreted as a coelothelium on histological sections. Each muscle cell of a longitudinal muscle band contacts the subepidermal extracellular matrix along its entire length.

In Pisionidae bands of longitudinal fibres are also formed by similar cells with their nuclei located on the distal parts devoid of myofilaments. However, the band of cells is rolled up forming a closed ellipse with a central cavity on cross-sections. The nuclei are situated in the inner part of the cavity (Fig. 6b). Such bands are covered by a coelothelium (Tzetlin, 1987).

In other taxa with well-developed longitudinal muscles these bands are rolled up differently producing a multilayered pattern of fibres. Here the

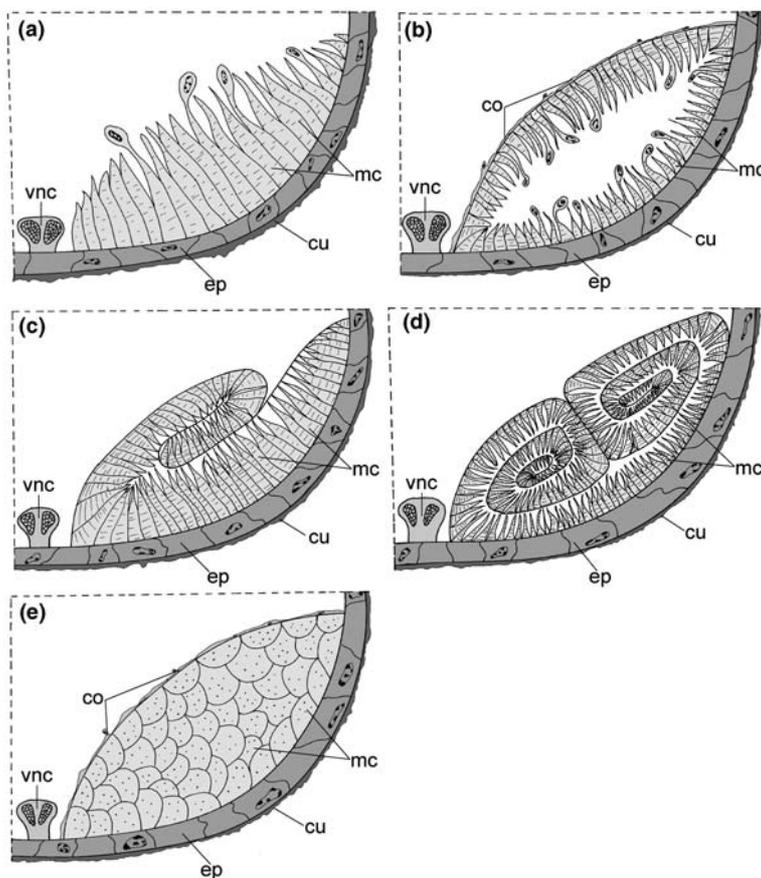


Figure 6. Patterns of arrangement of muscle fibres within longitudinal bands in polychaetes. (a) Phyllodocidae, (b) Pisionidae, (c, d) Sabellidae, Nereididae, (e) Aphroditidae. co – coelothelium, cu – cuticle, ep – epidermis, vnc – ventral nerve cord.

fibres do not form a closed cylinder but form helices with each coil tightly adjoining the previous one. The number of convolutions varies. Such bands may be s-shaped (Nereididae) or may consist of two reverse helices (Sabellidae) (Fig. 6c and d; Johansson, 1927).

Finally, a band may be formed by rounded muscle cells tightly adjoining each other. The nuclei are located centrally and are surrounded by myofilaments (hirudinean-type of muscle fibre). Each bundle is covered by a coelomic epithelium. Such bands may be rounded or flat with folded edges in cross-sections (Fig. 6e; Aphroditidae, see Storch, 1968).

In addition to these different constructions of muscle bands their number and position varies as well (Storch, 1968): (1) Four longitudinal muscle bands, two running ventrally and two running

dorsally either show the same diameter as in Phyllodocidae, Glyceridae, Ampharetidae, Nerillidae, Chrysopetalidae and many other taxa (Fig. 2a; Clark, 1964; Tzetlin et al., 2002a) or the dorsal bands are more massive than the ventral ones (Fig. 2b; Eunicidae, Sabellidae). (2) Six longitudinal bands with two ventral, two dorsolateral and two dorsal bands are found in Polynoidae, Aphroditidae, Chrysopetalidae; (Fig. 2c; e.g. Tzetlin et al., 2002a). (3) In Nephtyidae and Hesionidae three longitudinal muscle bands are present, two of them running ventrally and one being located dorsally (Fig. 2e). The single dorsal band most likely corresponds to two merged dorsal bands. (4) The dorsal bands consist of up to 10 or even more smaller bundles being assembled closely to each other (Fig. 2e–g). Along with these muscles there are two dorsolateral bands and two

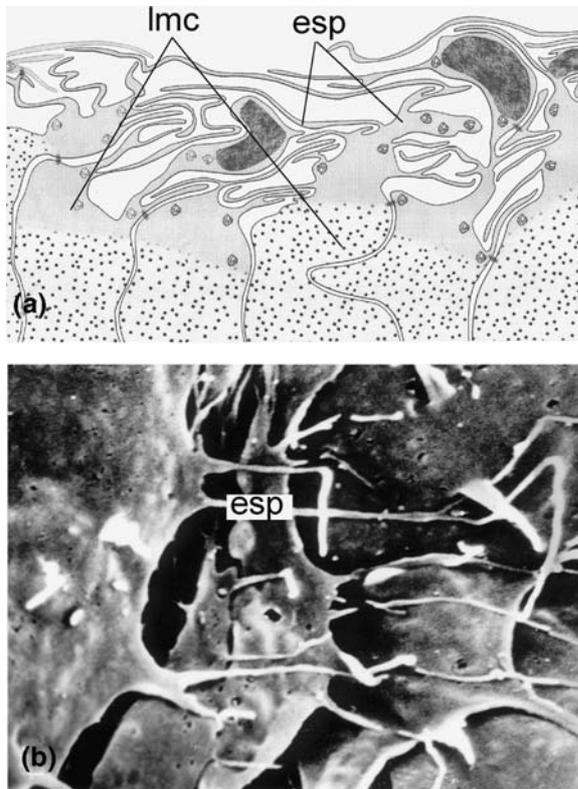


Figure 7. *Phyllodoce groenlandica*. Longitudinal muscle cells (lmc). A Drawing of distal parts of muscles cells with epithelium-like processes (esp). A SEM micrograph. After Ivanov (2002).

ventral bands in Amphinomidae (Fig. 2e). In Syllidae the dorsal musculature extends laterally and there are only two ventral bands (Fig. 2f). In Terebellidae there are ventral bundles apparently comprising the ventral band being broken into bundles (Fig. 2f). (5) The longitudinal musculature is formed by small bundles which are not contacting each other and are evenly distributed (Fig. 2h).

On the ventral nerve cord a ventral median muscle may be present which may be interpreted to belong to the mesenterial musculature or rep-

resent an additional type of longitudinal muscle such as has been described for Chrysopetalidae (Tzetlin et al., 2002b).

Parapodial muscle complex

Unfortunately, data on the muscle arrangement in parapodia are scarce. Mettam (1967, 1971) described the parapodial muscle complex in species belonging to three different families of the errant type while only fragmentary data on the structure of parapodia of sedentary polychaetes are available (Brown, 1938; Dorsett, 1961; Storch, 1968). Data on spioform parapodia are lacking.

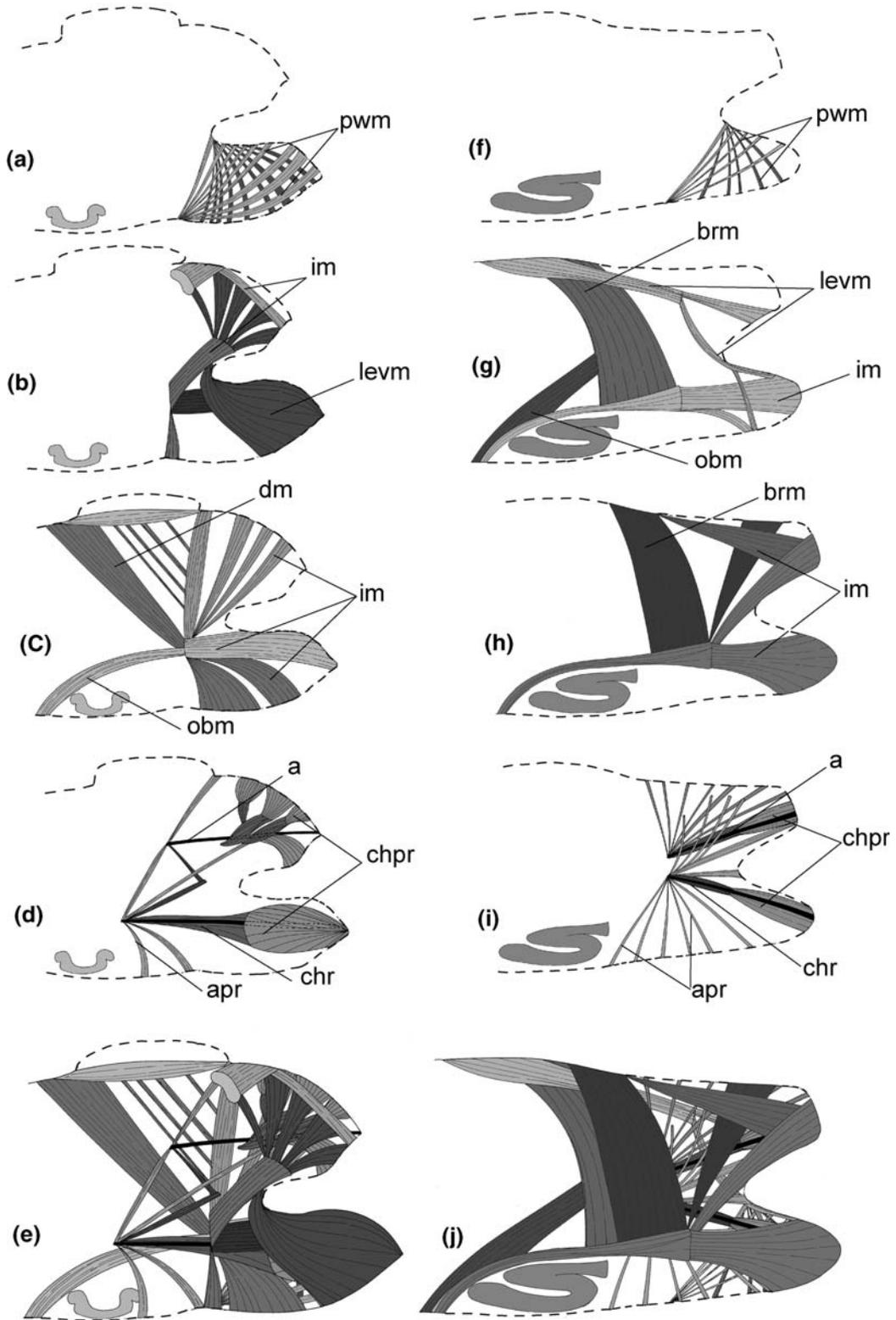
Musculature of errant parapodia

The musculature of the parapodial complex in errant polychaetes (Aciculata) consists of numerous muscles and individual muscle fibres. They will be divided in a number of functional groups according to Mettam (1967, 1971).

The muscles associated with the parapodial wall are usually only found in neuropodia (Fig. 8a and f). They start from the bases of neuropodia with two bundles, then radiate diagonally towards the upper edge of the neuropodia forming a dense lattice.

There are numerous muscles running inside the parapodium described in detail by Mettam (1967, 1971) (Fig. 8b, c, g and h). He discriminates many groups of muscles and numbers the muscles within each group. It appears more feasible only to name the main groups of muscles but not paraphrase these studies. Inside each parapodium the muscles run from the base to the tip, noto- and neuropodial intrinsic muscles are passing each other. It is noteworthy that they are neither attached to the bases of the aciculae nor connected with each other. These muscles con-

Figure 8. Schematical representation of parapodial muscle complex. (a–e) *Aphrodite* sp. (a) Parapodium wall muscles. (b, c) Different groups of intrinsic parapodial muscles. (d) Muscles associated with chaetae. (e) Complete parapodial musculature. (f–j) *Nereis* sp. (f) parapodium wall muscles. (g, h) Different groups of intrinsic parapodial muscles. (i) Muscles associated with chaetae. (j) Complete parapodial musculature. a – acicula, apr – protractor of acicula, brm – bracing muscle, chpr – chaetal protractor, chr – chaetal retractor, dm – diagonal muscle, im – intrinsic muscle, inm – intestinal muscle, levM – levator muscle, obm – oblique muscle, pwm – parapodium wall muscle. After Mettam (1971).



siderably vary in number and size between species (Fig. 8b, c, g and h). In *Aphrodite aculeata* the notopodial intrinsic muscles are connected with the depressor muscles of the notopodial chaetae. Each notopodium possesses a lot of diagonal and transversal (circular) muscles. The levator muscle passes inside the neuropodium. The bracing muscles mentioned above reach the bundles of these intrinsic muscles.

The muscles associated with the chaetae include muscles connected to the aciculae as well as those attached to the regular chaetae (Fig. 8d and f). Retractor muscles approach each acicula. The muscles of the acicula and the neuropodium may be connected. Each bundle of chaetae is supplied with retractors and protractors. The retractors of the chaetae are attached to the bases of the aciculae. The pattern of muscle arrangement is similar for neuro- and notopodia.

If the figures showing the different muscle complexes (Fig. 2a–d and f–i) are combined, it is evident that the number of muscles in *Aphrodite aculeata* is two times larger than in *Nereis* sp. (39 vs. 20); surprisingly the mobility of the parapodia in *A. aculeata* is limited. Moreover, despite the muscles decline in number and size in *Nereis* sp., the animal is much more mobile (Fig. 8e and j). Generally a few types of muscles associated with the chaetae are distinguished, like acicula retractors as well as retractors and protractors of the bundles of chaetae (e.g., Nephtyidae; Fig. 9a) and muscles connecting the bases of the aciculae may be added in e.g., Aphroditidae and Scalibregmatidae (Fig. 9b; Storch 1968; Mettam 1971). Similar oblique muscles may be present in the neuropodia such as in Amphinomidae (Fig. 9d).

Musculature of sedentary parapodia

According to the data available parapodia of sedentary polychaetes are all alike in structure. Retractors and protractors of the chaetal bundles are present (Brown, 1938; Storch, 1968). Oblique muscles starting from the notopodial bases and running towards the ventral nerve cord are added to the complex in Terebellidae (Fig. 9b; Storch, 1968). The lack of information does not allow discussing the structure of the intrinsic muscles in these polychaetes.

Muscles of septa and mesenteria

The septa or dissepiments consist of the extracellular matrix situated between the adjoining coelomic epithelia or muscle cells (Fig. 10i). In addition blood vessels are formed by gaps within this extracellular matrix. The orientation of the muscles can be dorsoventral, oblique, or transverse, or they radiate from the intestine to the body wall (Fig. 10e–h). The septa may be complete as well as reduced to various extend. Accordingly the muscle cells differ in shape and size. This depends on the life style of the species, which may either dig in the sediment, crawl with their parapodia or moves by ciliary gliding (Clark, 1964). In Terebellida, the septa of the anterior part of the body are modified into the gular membrane (Fig. 10a–d; Zhadan & Tzetlin, in press), which creates additional hydrostatic pressure necessary for the protrusion of the mouth appendages. Gular membranes differ in shape between species and may have additional protrusions or blind-ending sacs. The pressure created by the gular membrane is high enough to promote expansion ('inflating') of the mouth tentacles. If, however, the animals burrow in the sludge using their large proboscis, such as *Artacama* spp., constrictions of the body wall rather than the gular membrane promotes extension of the anterior part of the body (Fig. 10k). In Arenicolidae anterior septa are modified to form a gular membrane and are highly muscularised as well (Wells, 1952, 1954). In this taxon the septa serve in creating high hydrostatic pressure used for protrusion of the proboscis and burrowing movements.

Types of body shape

In cross-sections the body of polychaetes mostly appears to be oval-shaped or rounded. If the species possess parapodia, these structures markedly protrude laterally, especially in errant forms, e.g., Nereididae; Fig. 4b). The oblique muscles in such animals pass from the middle of the ventral side to the bases of the parapodia (Mettam, 1967; Storch, 1968). The bands of longitudinal muscles form protrusions on the body surface. Such a pattern is especially visible in Opheliidae (Fig. 5a) Here oblique muscles start from the midventral line resulting in a more or less pronounced ventral ridge

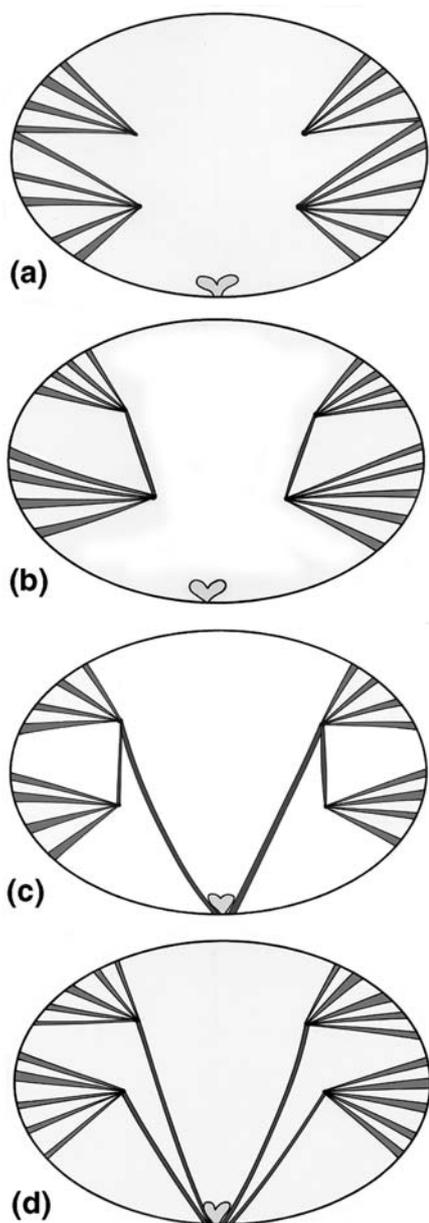


Figure 9. Different patterns of muscles associated with the chaetae. (a) Nephtyidae, (b) Aphroditidae, Scalibregmidae, (c) Terebellidae, (d) Amphinomidae.

(Brown, 1938; Hartmann-Schröder, 1958). An opposite pattern of oblique muscle arrangement resulting in corresponding grooves can be observed in certain Pisionidae as e.g. in *Pisionidens tchesunovi* (Fig. 5b; Tzetlin, 1987). Here, the oblique muscles start beneath the single dorsal band and reach the body surface below the dorsolateral bands.

Conclusions and outlook

Despite the comparatively small number of species studied in detail, it is evident that the muscular system of polychaetes is much more complex and diverse than it is described in popular zoological textbooks and manuals. The parapodia are the most vivid and typical organs in polychaetes although they may lack in certain taxa (Westheide, 1997; Purschke, 2002). However, many items remain to be studied. The discussion which type of parapodium could be regarded as the most primitive type for polychaetes, for instance, is more than 100 years old (see Ushakov, 1972). Moreover, presence or absence of parapodia in the annelid stem species is still a matter of discussion and depends on the rooting of the phylogenetic trees or in other words on the reading direction of evolutionary changes (e.g., McHugh, 1997; Rouse & Fauchald, 1997; Westheide, 1997; Westheide et al., 1999). We will not consider this discussion in detail, but would like to focus on a remarkable observation. The parapodia of Aphroditidae are used for simple movements only, although the muscular apparatus of these parapodia is very complex and massive. As is evident from Mettam's (1967, 1971) data, parapodia of Nereididae are formed by a much smaller number of muscles but possess a greater mobility including a greater diversity of movements. Although not studied in detail Tzetlin et al. (2002a) stated that the musculature of Chrysopetalidae is similar to that of Aphroditidae. The parapodia of sedentary polychaetes also consist of a small number of muscles according to the few data available. These data most likely favour the hypothesis of Westheide & Watson Russel (1992) according to which those parapodia are the most primitive ones that are noticeably located at the dorsal side. If the parapodia are divided into neuro- and notopodia the dorsal chaetae play a protection role such as in Chrysopetalidae and Aphroditidae.

As is evident from the presented data, many polychaete taxa are characterised by the absence of circular muscles in the body wall. It has been observed in Opheliidae, Polygordiidae, Protodrilidae, Spionidae, Oweniidae, Aphroditidae, Acoetidae, Polynoidae, Sigalonidae, Phyllodocidae, Chrysopetalidae, Nephtyidae, Pisionidae and Nerillidae (Salensky, 1907; McIntosh, 1917; Hartmann-

Schröder, 1958; Orrhage, 1964; Jouin & Swedmark, 1965; Mettam, 1967, 1971; Storch, 1968; Hermans, 1969; Gardiner & Rieger, 1980; Tzetlin, 1987; Ivanov & Tzetlin, 1997; Tzetlin et al., 2002a, b). Absence of these fibres has also been reported in *Jennaria pulchra* an enigmatic taxon with strong affinities to Annelida (Rieger, 1991). This suggests that the lack of circular fibres may not be rare exception but a common situation in many polychaetes.

The view that a complete muscular lining comprising outer circular and inner longitudinal fibres belongs to the ground pattern in Annelida can be traced back to the ideas of Clark (1964, 1981) regarding an oligochaete-like burrowing animal as stem species of the entire group. How-

ever, since the body cavity often lacks segmental compartments formed by complete septa, the propulsive movements caused by the antagonistic actions of circular and longitudinal fibres characteristic for larger oligochaetes are only rarely found in polychaetes (Lanzavecchia et al., 1988). In these polychaetes antagonists of the longitudinal fibres are either dorsoventral, transverse, parapodial or the remaining longitudinal fibres themselves. The ideas of Clark (1964, 1981) have recently been supported by the cladistic analyses of Rouse & Fauchald (1995, 1997), but challenged by McHugh (1997) and Westheide (1997), who, among others, consider an epibenthic parapodia-bearing and not an earthworm-like organism to be the stem species in Annelida.

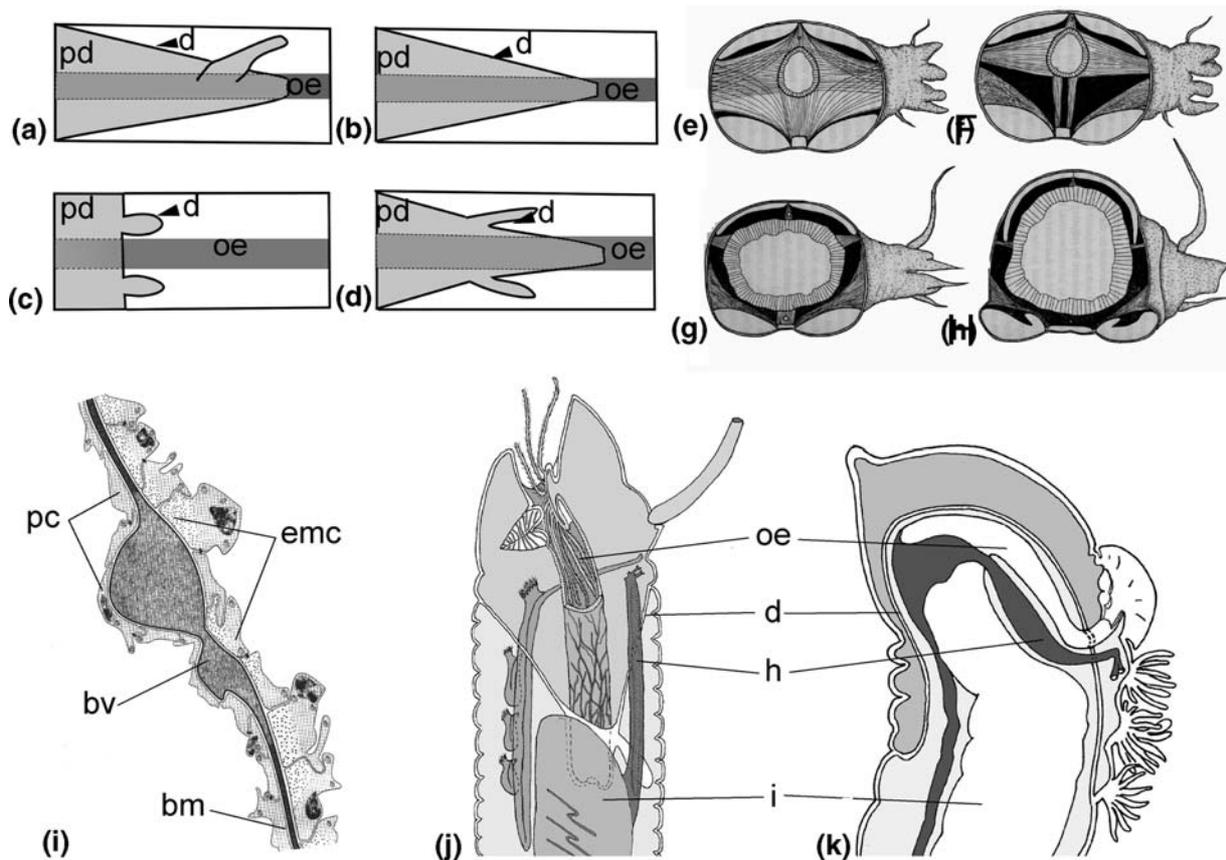


Figure 10. Structure of gular membrane (diaphragm). (a–d) Anterior part of body cavity of Terebellidae. (e–h) Supposed successive reduction of septa to form gular suspensory muscle. (i) Ultrastructure of dissepiment in Phyllodocidae. (j) Alvinellidae, sagittal section of anterior part. (k) *Artacama* sp. (Terebellidae), sagittal section of anterior end. bm – basal membrane, bv – blood vessel, cm – circular muscle, d – diaphragm, emc – epithelial muscle cell, h – heart, I – intestine, lm – longitudinal muscle, oe – oesophagus, pc – peritoneal cell, pd – prediaphragmal cavity. (a–d, j, k) After Zhadan & Tzetlin (in press), (e–h) After Clark (1964), (i) After Ivanov (2002).

Since circular muscles are especially important for burrowing forms and are not necessary for animals which proceed by movements of their parapodial appendages and chaetae (Mettam, 1971, 1985), the absence of such muscles in extant epibenthic polychaetes is related to the question, whether these muscles were present in the ancestral annelid or not. In case this stem species was in fact epibenthic and equipped with parapodia, these circular muscles do not appear to be a prerequisite for the complex movements shown by errant polychaetes. This scenario is in accordance with Mettam's (1985) hypothesis that the ancestral annelid had only longitudinal muscles used for rapid contractions of the body. Here the question arises which pattern of longitudinal muscle fibre arrangement might be the primitive. If we follow the hypothesis of Rouse & Fauchald (1997) an arrangement of longitudinal muscles in bands should be regarded as the most primitive pattern. However, which of the various patterns observed appears to be difficult to answer on our present knowledge. If parapodia-bearing taxa with protective chaetae will – with respect of their muscular system – prove to be comparatively close to the annelid stem species, a pattern of four or six bands should be the most primitive one.

In any case lack of circular fibres should now very seriously be considered in the discussion of the ground pattern of Annelida. However, further studies are required until a more definite conclusion can be drawn and how the different transverse fibres fit into this pattern, i.e. whether they represent reduced circular fibres or stages towards the development of circular muscles.

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