

Comparative structure of the epidermis in polychaetes (Annelida)

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Abstract

The polychaete epidermis generally consists of a single layer of supportive cells, gland cells and sensory cells. Except for the latter, this paper reviews the recent literature on the annelid epidermis, focussing on the mentioned cell types and the cuticle. The annelid epidermis is compared to that of Sipuncula, Echiura and Myzostomida. Supportive cells predominate in the polychaete epidermis. They show a high structural diversity even within single specimens. Ciliated cells are usually multiciliary and only two cases of monociliary epidermis cells are known. Unambiguous epithilio-muscle cells are only described in feeding palps of a *Magelona* species. Secretory cells release a large number of gland products and some of them are essential for tube secretion. Rather peculiarities of the cells and its arrangement within glands than the ultrastructure of the secretions is useful for phylogenetic considerations. One of the main components of the cuticle is collagen. Recent studies indicate that annelid cuticular collagen differs in several aspects from collagen of the connective tissue and might be of interest for systematics.

Introduction

The epidermis in polychaetes is composed of a cellular monolayer that is covered by a cuticle like in many other invertebrates. The main structural characteristics are well known and were reviewed repeatedly [see Gardiner (1992b); Richards (1978); Richards (1984); Southward (1984); Southward (1993); Storch (1988); Welsch et al. (1984)]. The epidermis inhabits secretory cells, sensory cells and as its main component supportive cells. The latter term is used for all cells, which are not neuronal cells or cells specialized in secretion. Adjacent epidermis cells always are apically connected by zonulae adherentes and septate junctions and rest on an underlying basal matrix. Nevertheless the epidermal monolayer may have a pseudostratified appearance and especially the basal parts of secretory cells may be deeply sunken in into the underlying tissue. Cells that do not extend towards the body surface are mainly basally situated neurons, which can be

abundant in species with an intraepidermal nervous system. Other basal cells only occasionally have been reported and its origin and function is not completely understood [see for discussion Gardiner (1992a); Rieger (1981)].

Sensory cells are widespread in the epidermis of polychaetes. They occur scattered between other epidermis cells or in groups or are parts of more complex sense organs. They are mainly bipolar primary receptor cells and reviewed elsewhere within this issue (see Purschke, 2005).

Supportive cells

Supportive cells show different cell morphologies even within single specimens. This presumably reflects different physiological specializations. Supportive cells may be thin and flattened, or thick and of columnar, cuboidal or of squamous shape and may be differently equipped with cell organelles. They can show pigment vesicles, vacuoles of

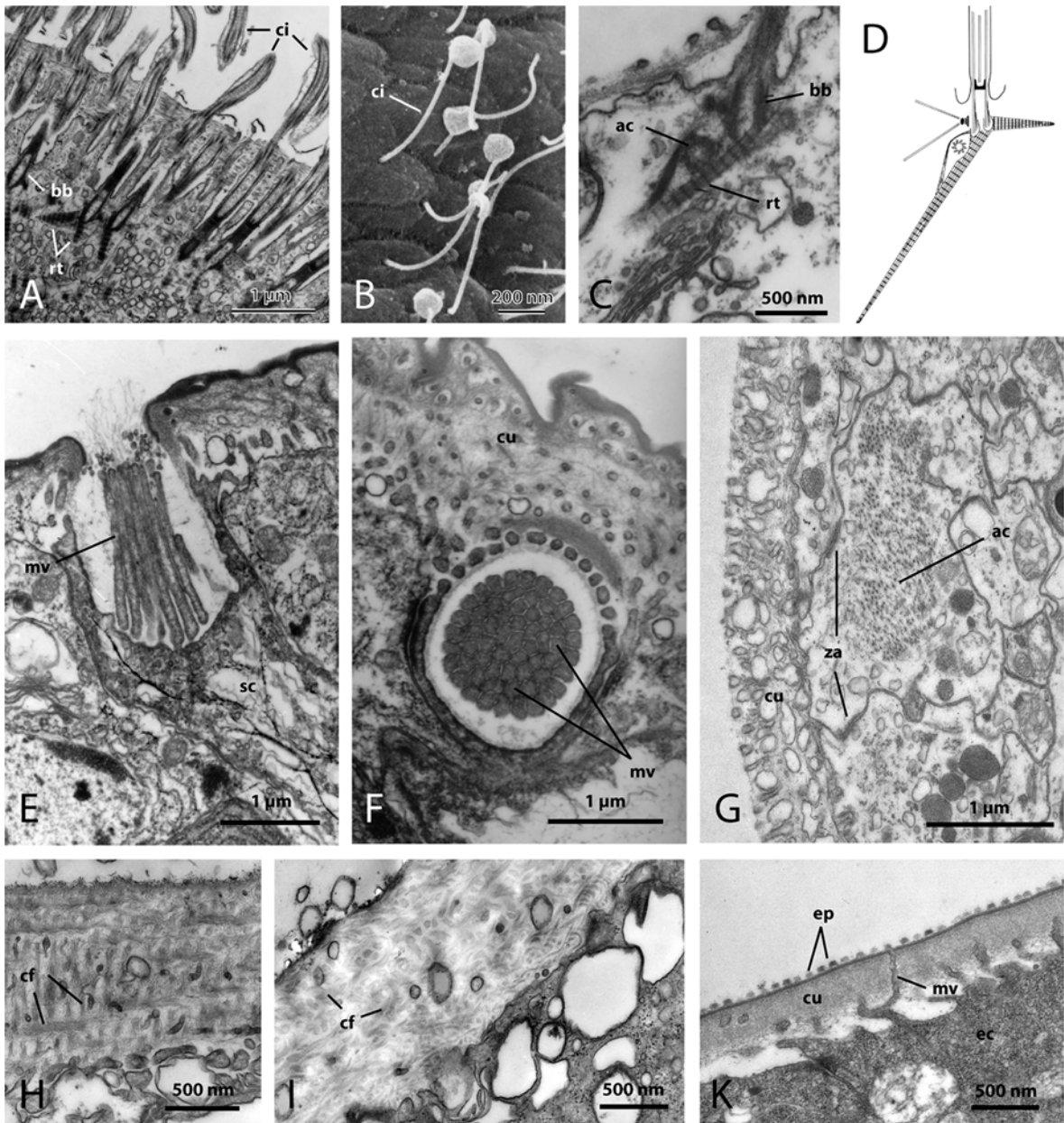


Figure 1. A: *Glycera alba*. Multiciliary epidermal cell. The cilia show a basal body (bb), two rootlets (rt) but no accessory centriol. B–D: *Magelona mirabilis*. Monociliary epidermis cells on larval feeding tentacles. B: SEM micrograph. C: basal ciliary structures with basal body (bb), two rootlets (rt) and one accessory centriol (ac). D: schematic representation. E–F: *Pectinaria auricoma*. Circular arranged microvilli (mv) form a cone around the apical opening of a secretory cell. E: longitudinal section. F: cross section through tip of the microvillar cone. G: *Magelona mirabilis*. Epithelio-muscle cell in papilla of palps of adults with large embedded actomyosin complex (ac) H: *Eulalia viridis*. Collagenous orthogonal grid within the cuticle. I: *Ophiodromus flexuosus*. Collagenous orthogonal grid within the cuticle. K: *Poecilochaetus serpens*, larva. Cuticle devoid of collagen fibres. cf: collagen fibre; cu: cuticle; ec: epidermis cell; ep: epicuticular projection; za: zonula adhaerens.

different size, endocytotic and exocytotic vesicles, and quite different amounts of certain organelles like mitochondria, lysosomes and multivesicular bodies. Supportive cells usually bear microvilli that extend into the cuticle and – according to the above definition – all non-sensory epidermal cells with cilia are supportive cells as well. Most supportive cells contain tonofilament bundles to withstand mechanical stress. These filaments are basally connected to the underlying matrix by hemidesmosomes and often run to the apex of the cells, where they attach to hemidesmosomes at the bases of apical microvilli or project into the microvilli.

If supportive cells bear cilia like in ciliary bands, the cilia almost always occur in higher numbers per cell (Fig. 1A). The cilia lack accessory centrioles, but two striated rootlets are common and usually one rootlet projects deeply into the cell while the other one runs parallel to the apical cell membrane. Only few cases of monociliary epidermal cells are known. Those on the tentacles of *Owenia fusiformis* are interspersed between unciliated and biciliated cells (Gardiner, 1978). Each cilium of the mono- and biciliated cells has one horizontal and one vertical rootlet and is accompanied by an accessory centriole. Further monociliated cells are known from *Magelona mirabilis* (Bartolomaeus, 1995). They occur on the larval feeding tentacles and show one horizontal and one vertical rootlet and an accessory centriole (Fig. 1B–D). Whereas Gardiner (1978) argues for the primary condition of monociliarity in *Owenia*, Bartolomaeus (1995) favours the hypothesis that monociliarity in both species may be caused by a truncated ciliogenesis. This process suppresses formation of further cilia in cells that formerly were multiciliated, because multiciliarity is assumed for the annelidan stem species. According to Gupta & Little (1970) a pair of centrioles is frequently found close to the apical cell surface of unspecialized epidermal cells of several pogonophoran species. One of the centrioles gives rise to a cilium with complete $9 \times 2 + 2$ axonem that protrudes into a canal within the cuticle.

Epithelio-muscle cells are reported of tentacles, cirri and antennae of the syllid *Typosyllis variegata* (Storch, 1988) and in tentacles and parapodial cirri in Nereididae (Boilly-Marer, 1972). A reinvestigation of syllidan cirri, however, showed certain

dissimilarities to all kinds of invertebrate muscle cells. The remarkable fibrillar structures within the epidermis cells are restricted to the apical most cell region and always are directly connected to the zonulae adhaerentes (Bartolomaeus, personal communication) instead of having a more basal position and being in contact to the plasma membrane *via* dense bodies and dense plaques. Thus, the term epithelio-muscle cells should be avoided for these cells. Nevertheless, true epithelio-muscle cells occur in the epidermis of the papilla of the palps in adult *Magelona mirabilis*. The cells contain large acto-myosin complexes, have contact to the cuticle and are interconnected to surrounding epidermis cells by zonula adhaerentes, which show no affinity to the acto-myosin (Fig. 1G).

Secretory cells

Secretory cells are abundant in the polychaete epidermis and are situated separately between the supportive cells or may be grouped within glandular fields or form complex multicellular glands. Mucous secretions assist in maintaining a mucoid film on the body surface or in feeding by forming mucus traps like in *Chaetopterus* species (Flood & Fiala-Médioni, 1982) or *Praxillura maculata* (McDaniel & Banse, 1979) or they enable the transport of food particles to the mouth. They also facilitate reproduction in producing brood chambers or egg cases in many groups. Duo-gland systems, which produce an adhesive and a releasing secretion, are used by many meiofaunal species to hold on the substrate (Martin, 1978; Gelder & Tyler, 1986). Secretions are responsible for the inner lining of burrows or are involved in the tube building process. For this purpose usually different substances produced in different cells are released (Defretin, 1971; Moermans, 1974; Vovelle et al., 1994). Least secretions also can be used to etch burrows in mineralized structures like in *Polydora* (Zottoli & Carriker, 1974).

Secretory cells release their contents *via* pores in the cuticle. The apical cell membrane may form a circle of microvilli surrounding the pore-like opening (Fig. 1E, F) and a lot of microtubules may occur in the cell apex of secretory cells. Both structures are discussed to assist in controlling the

secretion process (Storch & Welsch, 1972; Richards, 1978; Hausmann, 1982; Storch, 1988). In certain secretory cells of *Spiochaetopterus typicus* the opening is surrounded by kinocilia (Storch, 1988). Singular mucous cells in several species of Pogonophora can send a short cilium into an apical lumen underneath the cuticular opening (Gupta & Little, 1970).

Several ultrastructural descriptions of secretory cells reflect the high structural diversity of the secretions from compact material to fine filamentous or granular material packed in vesicles of various sizes or in sometimes highly ordered arrangements, which seemingly may lack a surrounding membrane (Dorsett & Hyde, 1970a, b; Kryvi, 1972; Storch & Welsch, 1972; Hausmann, 1982; Welsch et al., 1984; Hilbig, 1986b; Storch, 1988; Gardiner, 1992b). Histochemical investigations revealed that epidermal cells can secrete many different substances including glycosaminoglycans like hyaluronic acid, different mucopolysaccharids, mucoproteins, proteins, enzymes, phenols, and varying inorganic components (Dorsett & Hyde, 1970a, b; Defretin, 1971; Kryvi, 1971; Moermans, 1974; Bielakoff et al., 1975; Vovelle, 1979; Vovelle & Gaill, 1986; Vovelle et al., 1994). Lectin histochemical investigations indicate the simultaneous production of different carbohydrates within different gland cells in several species (Welsch & Storch, 1986). Only few studies, however, link the histochemical knowledge to the diversity of the electron optical appearance of the secretions. Though the structure of the secretory granules or vesicles presumably largely depends on the chemical nature of its content no correlation between the structure and the chemistry of the secretions has been shown until today. Moreover, the abundance of certain organelles like free ribosomes, rough or smooth endoplasmic reticulum, and golgi stacks corresponds to the histochemical observations. Thus, ultrastructural data of the granules or vesicles of secretory cells are of minor importance for phylogenetic considerations. Other structural peculiarities of individual cells or special arrangements of secretory cells in glandular fields or multicellular glands like in the spiral glands of *Nereis* (Dorsett & Hyde, 1970b) or the pyriform glands of Pogonophora (Southward, 1993) may provide more useful characters. Furthermore standard

histochemical characterization of secretions can presently not determine characters of high phylogenetic relevance. Such characters would have to include protein sequence data and exact biochemistry of the carbohydrates. Higher complexity in carbohydrate structure, however, might decrease its usefulness for systematics, because complexity of carbohydrates in secretions results from enzymatic processing within the Golgi complex so that carbohydrate structure is not as directly connected to the genes as in the case of proteins.

Ultrastructural and biochemical examination of tube building glands in Pogonophora exhibited unique differentiations within the secretory cells and clearly characterized the secreted substances. Pogonophora are the only polychaete group where chitin has been detected within the tubes (Blackwell et al., 1965; Gaill & Hunt, 1986). In *Tevnia jerichonana* and *Riftia pachyptila* many microfibrils or crystallites of β -chitin are parallel embedded in a protein matrix and form together flat ribbon like structures (Gaill et al., 1992a,b). Several crisscrossing layers of these ribbons build up the tube wall. The huge crystallites are composed of up to 6000 β -chitin chains and are secreted by specialized multicellular so called pyriform glands. In *Riftia pachyptila* the secreting cells of these glands bear a lot of cup shaped microvilli like structures, which presumably are the sites of a highly regulated microfibril formation (Southward, 1984; Shillito et al., 1993). Two proteins from the tube of *Riftia pachyptila*, which are thought to tighten the different parts of the tube by protein-protein and specific β -chitin-protein interactions, were sequenced and characterized (Chamoy et al., 2000, 2001). Its mRNA is detectable in special epidermal cells, but never within the chitin secreting pyriform glands.

Cuticle

The cuticle of adult polychaetes is composed of an amorphous or fine filamentous matrix that usually inhabits collagen fibrils. Different mucopolysaccharids and presumably also hyaluronic acid are present within the matrix (Kryvi, 1971; Manavalaramanujam & Sundara Rajulu, 1974; Moermans, 1974; Richards, 1984). Several lectins show a positive reaction to the cuticle and reveal a two

layered distribution pattern of certain carbohydrates (Welsch & Storch, 1986). Cuticular proteins are thought to have a hardening effect that differs from quinone tanning (Manavalaramanujam & Sundara Rajulu, 1974). The collagen fibrils are restricted to the basal zone of the cuticle. The upper collagen free zone is termed epicuticle. This usually shows layers of different electron densities and is covered by a mostly thin surface coat varying from fine filamentous, fuzzy to electron dense granular material (Richards, 1984; Storch, 1988; Gardiner, 1992b). The collagen fibrils in the basal zone very often form a regular multilayered arrangement (Fig. 1H, I). All fibrils of one layer are parallel to each other and to the cell surface, but fibrils of adjacent layers are perpendicularly arranged. The fibrils are oriented 40° – 55° to the body long axis. Such orthogonal grids are widespread within polychaetes (Gupta & Little, 1970; Storch & Welsch, 1970; Richards, 1984; Hilbig, 1986a; Gaill & Bouligand, 1987; Lepescheux, 1988; Storch, 1988; Pilato et al., 1989; Heffernan, 1990; Pilato & la Rosa, 1990; Pilato et al., 1990; Bartolomaeus, 1992; Gardiner, 1992b; Pilato & la Rosa, 1992; Tzetlin et al., 2002) and only few exceptions are known. The fibrils of several adjacent layers can be parallel to each other followed by a perpendicularly directed series of layers like in Glyceridae and Questidae (Storch, 1988) or hexagonal arrangements consisting of fibrils oriented in three different directions exist like in *Typosyllis variegata* (Storch, 1988) or in the gills of *Eunice norvegica* (Hilbig, 1986a) and other arrangements can occur [see Storch (1988)]. Gaill & Bouligand (1987) and Lepescheux (1988) showed that the collagen fibrils of the orthogonal grid in *Alvinella pompejana* and *Paralvinella grasslei* are coiled on several different levels. The collagen fibrils consist of coiled microfibrils, which are composed of triple helices containing the coiled protein chains. The undulating appearance of the fibrils in sections is due to a coiled structure of each fibril. Lepescheux (1988) could not observe endings of individual fibrils and thus assumes the fibrils to be coiled on a larger scale in running around the cylindrical body surface.

In young larvae collagen fibrils may lack completely (Fig. 1K) or are very thin and irregularly arranged (Holborow & Laverack, 1969; Eckelbarger, 1978; Heimler, 1981; Heimler, 1983; Schlötzer-

Schrehardt, 1992). Thicker fibrils being organized in regular orthogonal grids are formed later during ontogenesis. In adults of very small polychaetes like in representatives of the interstitial fauna, however, collagen fibrils may lack or be irregularly arranged as has been shown for *Protodrilus*, *Polygordius*, *Trilobodrilus*, and *Diurodrilus* (Rieger & Rieger, 1976), *Dinophilus* species (Brandenburg, 1970), for certain hesionids (Westheide & Rieger, 1978), *Apodotrocha prognerans* (Westheide & Riser, 1983), *Ophryotrocha diadema* (Hilbig, 1986a), and *Dysponetus* spp. (Tzetlin et al., 2002). These findings can be interpreted as functional adaptations to the small body size or as the result of a progenetic or neotenic evolution. Nevertheless, the lack of a collagenous orthogonal grid is not exclusively restricted to interstitial forms. No fibers are present in the cuticle of *Sabellaria vulgaris* (Storch, 1988) and *Cossura longocirrata* (Rouse & Tzetlin, 1997). The epidermis cells in *Owenia* sp. are only covered by a loose fibrillar matrix and *Spiochaetopterus typicus* also lacks a true cuticle (Storch, 1988). The tube of *Chaetopterus variopedatus*, which shows crisscrossing layers of fibrils, is discussed to be a cuticle that has lost contact to the body wall (Brown & McGee-Russell, 1971).

Supportive cells often send microvilli into the cuticle. If an orthogonal grid is present adjacent microvilli are usually separated by one collagen fibril. The microvilli may terminate within the cuticle or cross it. In the latter case the tips of the microvilli may be somewhat inflated and lay on the apical surface of the cuticle. Those tips are often surrounded by several isolated membrane bound vesicles, which are called epicuticular projections and appear similar to the tips of the microvilli (Fig. 1K). They presumably are pinched off by the microvilli. Both, tips of the microvilli and epicuticular projections, usually are coated by fine filamentous material that may be a special glycocalyx. Many different shapes and electron densities are reported for epicuticular projections.

Comparative morphology

There is no general feature in which the unspecialized epidermis of the body wall of clitellates differs from that in polychaetes (for reviews on clitellate epidermis see Fernández et al. (1992); Jamieson

(1988); Jamieson (1992)). There are also no principle differences in the cellular components and the cuticle shows no significant deviations. The collagen fibrils usually form a regular orthogonal grid, but some modification may exist. While some members of Tubificidae and Naididae show an orthogonal grid, in a couple of oligochaete species all fibrils are parallel oriented or irregularly arranged or lack at all (Gustavsson & Erséus, 2000; Gustavsson, 2001). Fibril arrangement does not correlate with body size in tubificids and naidids and irregular patterns are described for small and large specimens in contrast to the situation in polychaetes. The different arrangements in tubificids and naidids are thought to be useful for phylogenetic analysis.

Ultrastructural data on the epidermis of sipunculids are rare, but at least the structure of the cuticle shows striking similarities to that of annelids. Except the tentacles the entire body of *Phascolion strombus* is covered by a thick cuticle that contains collagen fibrils forming a clear orthogonal grid (Moritz & Storch, 1970). In the second larvae, the so-called pelagosphaera of *Aspidosiphon* sp. and *Paraspidosiphon* sp. the cuticle shows layers of fibrils perpendicular to one another, whereas the fibrils are irregularly arranged in larvae of *Golfingia* species (Rice, 1976). The epidermis in adult sipunculids is generally composed of cuboidal cells with deep basal infoldings (Storch, 1984). Within the trunk region the microvilli of the supporting cells do not pierce the cuticle. In *Themiste lageniformis*, however, epidermal microvilli are found on the oral surface of the tentacles, which show no collagen fibrils within their cuticle (Pilger, 1979; Pilger, 1982). Additionally the tentacles bear many ciliated cells. They are presumably sensory on the aboral surface whereas multiciliated cells on the oral surface bear kinocilia equipped with a short basal foot and only one rootlet in *Themiste lageniformis*. In contrast to this the cilia of multiciliated epidermal cells in the pelagosphaera larva of *Apionsoma misakianum* represent the presumed plesiomorphic state in having two perpendicular rootlets (Lundin & Schander, 2003). The length of the horizontal rootlet secondarily is strongly reduced in the oral multiciliated cells of the tentacles in adult *Phascolion strombus*.

Echiurans have an annelid-like epidermis. In the trunk and the proboscis of *Maxmuelleria lankesteri*

supportive cells of various shape and two types of secretory cells form a monolayer that partly is pseudostratified (McKenzie & Hughes, 1999). The supportive cells send many microvilli in the cuticle and the apices of the secretory cells, which release their contents *via* ducts through the cuticle, are surrounded by microvilli. Cilia are common on the proboscis though this species shows no obvious ciliated groove like other echiurans. The cilia are anchored in the cells by basal bodies and striated rootlets (McKenzie & Hughes, 1999). Monociliated cells which presumably are sensory were found in the trunk but not in the proboscis. In *Maxmuelleria lankesteri* as well as in *Urechis caupo* a lot of membrane bound epicuticular projections cover the cuticle. They are enwrapped by a glycocalyx and sometimes in contact with microvilli of the supportive cells, (Menon & Arp, 1993; McKenzie & Hughes, 1999). The cuticle consists of an outer amorphous and a basal fibrillar zone. The fibrils form no orthogonal grid but are longitudinally arranged in *Maxmuelleria lankesteri* and loosely packed in *Urechis caupo*. Both species inhabit similar looking bacteria within their cuticle. In *Urechis caupo* the secretion of metachromatic acidic mucus might be used to reduce sulphide entry from the anoxic environment (Menon & Arp, 1993).

The epidermis of myzostomids, whose membership within annelids is discussed controversially [see Eeckhaut et al. (2000); Haszprunar (1996); Mattei & Marchand (1987); Müller & Westheide (2000); Rouse & Tzvetlin (1997); Zrzavý et al. (2001)] and contribution in this issue) shows some similarities to that of polychaetes. In *Myzostoma cirriferum* flattened cells which presumably secrete the cuticular material, multiciliated cells of the same shape, and two different kinds of secretory cells are the main cellular components of the epidermis (Eeckhaut & Jangoux, 1993). Nerve cells of the ventral nerve cord send monociliated dendritic processes into the epidermis. In *Myzostoma alatum* and *Pulvinomyzostomum pulvinar* the thickness of the unciliated and multiciliated cells varies between different body parts (Kronenberger, 1997). The cuticle in all three species possesses an inner layer with a matrix of low or moderate electron density. But only in *Myzostoma cirriferum* fibrillar material within the matrix is described. The basal layer is followed by a thin dense layer and another layer with a lucent matrix in all three species (Eeckhaut

& Jangoux, 1993) and see figures in Kronenberger (1997). The positive reaction of the cuticle to van Gieson staining in *Myzostoma cirriferum* is interpreted as a hint for collagen. Microvilli of the epidermis cells penetrate the cuticle and end on the top of the apical electron lucent layer. The tips of the microvilli are swollen, filled with electron dense granular material and covered by fine granular material. The cilia of the multiciliary cells are equipped with ciliary rootlets in all three species. Only in *Myzostoma cirriferum* myoepithelial cells are described (Eeckhaut & Jangoux, 1993). They lie basally within the epidermis and are directed perpendicular to the body long axis. The position of the nuclei of these cells remained unclear.

The collagenous cuticle of annelids, echiurids, and sipunculids is used as one argument for a common ancestry of these taxa (Ax, 2000).

Collagen ultrastructure and biochemistry

There are many observations that collagen fibrils in the cuticle of polychaetes, clitellates, pogonophorans, sipunculids and echiurans are not striated (Richards, 1984; Jamieson, 1988; Storch, 1988; Gardiner, 1992b; Jamieson, 1992; McKenzie & Hughes, 1999). This is in contrast to the collagen fibrils of the connective tissue and has recently been substantiated in further detail. A couple of biochemical studies favour the existence of at least two distinct types of collagens in annelids – a cuticular and an interstitial one. The fibrils of interstitial collagen are located within the extracellular matrix of the tissue underneath the epidermal cells. They show a cross-striation pattern *in situ* in *Alvinella pompejana* and *Riftia pachyptila* and the striation pattern of reconstituted fibrils *in vitro* is similar to that of vertebrate collagen type I (Gaill et al., 1991). Also the molecular mass in *Alvinella pompejana*, *Alvinella caudata*, *Paralvinella grasslei*, *Arenicola marina*, *Nereis diversicolor* and *Riftia pachyptila* of the individual triple helices and its length of 280–300 nm is comparable to vertebrate fibrillar collagen (Gaill et al., 1991; Gaill et al., 1995). The triple helices are composed of three identical α -chains. Such homotrimeric constitution seems not to be typical for all cuticular collagens. Though the cuticular colla-

gen of *Riftia pachyptila* consists of only one chain type (Mann et al., 1996), in *Nereis virens*, *Nereis japonica* and *Alvinella pompejana* A- and B-chains have been described (Kimura & Tanzer, 1977; Sharma & Tanzer, 1984; Gaill et al. 1991;). The triple helices of cuticular collagen belong to the longest collagen molecules so far known. They reach between 2400 and 2600 nm in *Nereis diversicolor*, *Nereis virens*, *Alvinella pompejana*, *Alvinella caudata*, *Paralvinella grasslei* and *Arenicola marina* (Murray & Tanzer, 1985; Gaill et al., 1991; Gaill et al., 1995). Isolated triple-helices show a terminal globular domain like it is known for some vertebrate collagens like type IV and VI. The globular domains connect two or more chains in some of the preparations and may play a role in supermolecular assembly (Gaill et al., 1991; Gaill et al., 1995). The fibrils formed by this type of collagen neither *in situ* nor after reconstitution of isolated triple helices show a striation pattern.

The different types of collagen have different immunological properties. Antibodies raised against cuticular collagen of *Arenicola marina*, *Riftia pachyptila* and *Alvinella pompejana* show each a high affinity to the cuticular collagen of all three species, but a low affinity to interstitial collagen of any species (Gaill et al., 1994). Antibodies against interstitial collagen on the other hand bind effectively to interstitial collagen of all three species, but not to cuticular collagen of any species. It is possible to detect cuticular collagen fibers in *Harmothoe lunulata* and *Riftia pachyptila* immunocytochemically *in situ* with antibodies against cuticular collagen of *Arenicola marina* after freeze-fixation (Nicolas et al., 1997).

There are hints at an unusual posttranslational modification in cuticular collagen. Short carbohydrates of mainly galactose subunits are linked O-glycosidically to threonine residues in *Lumbricus terrestris*, *Nereis virens* and *Riftia pachyptila* (Muir & Lee, 1970; Spiro & Bhoyroo, 1980; Mann et al. 1996). In *Lumbricus terrestris* and *Nereis virens* also serine can be glycosylated and in the latter species an additional glucuronic acid-mannose disaccharid has been detected (Muir & Lee, 1970). In *Riftia pachyptila* the glycosylated threonine is located at the Y-position of the Gly-X-Y triplets of the amino acid sequence and presumably enhances the thermal

stability of the triple helices as an adaptation to hydrothermal environment of the species (Mann et al., 1996; Bann & Bächinger, 2000; Bann et al., 2000). In interstitial collagen of *Riftia pachyptila* and *Alvinella pompejana*, that also lives at hydrothermal vents, thermal stability is achieved by a high degree of hydroxylation of proline in the Y-position like it is usual for many types of collagen (Mann et al., 1992; Sicot et al., 2000).

Molecular phylogeny of annelid collagen just started. Sicot et al. (1997) and Sicot et al. (2000) got a monophyletic grouping of annelidan interstitial collagens within α -chains of fibrillar collagens of different metazoan taxa after a cladistic analysis of some cDNA sequences. No comparable phylogenetic considerations concerning the cuticular collagen have been undertaken so far. Because of the unique triple helix length, lack of striation in the fibrils, immunological properties, existence of a globular domain and the post-translational glycosylation of threonine and serine cuticular collagen might provide useful phylogenetic characters.

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