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Structure and development of nephridia in Annelida and related taxa

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Abstract

Two different kinds of filtration nephridia, protonephrida and metanephridia are described in Polychaeta. During ontogenesis protonephridia generally precede metanephrida. While the latter are segmentally arranged protonephridia are characteristic for the larva and are the first nephridial structure formed during ontogenesis. There is strong evidence that both organs depend on the same information and that their specific structure depends on the way in which the coelom is formed and which final expansion it gains. While metanephridia are regarded as homologous throughout the polychaetes, protonephridia seem to have evolved in several

lineages. Some of the protonephridia closely resemble less differentiated stages of metanephridial development, so that protonephridial evolution can be explained by truncation of the metanephridial development. Nevertheless, structural details are large enough to expect information on the polychaete evolution if the data base on polychaete nephridia increases. A comparison of the polychaete metanephridia with those of the Clitellata and Sipuncula reveals some surprising details. In Clitellata the structure of the funnel is quite uniform in microdrilid oligochaetous Clitellata and resembles those of the aeolosomatids. Like the nephridia in the polychaete taxa Sabellida and Terebellida those of the Sipunucla possess podocytes covering the coelomic side of the duct.

Introduction.

Nephridia are basically defined by their function. They eliminate wastes from the amino acid and nucleotide degradation as well as sometimes salt and water from the body. From the variety of such organs filtration nephridia are assumed to belong to the ground pattern of the Bilateria (Bartolomaeus & Ax, 1992, but see Jondelius et al., 2002). In annelids these organs occur as two different structures, protonephridia and metanephridial systems (sensu Ruppert & Smith, 1988). Both organs mediate excretion in two steps: an unspecific filtration of body fluid and subsequent modification of the ultrafiltrate (Fig. 1A, B). This second step is necessary because during filtration not only metabolic wastes but also all substances with a low molecular weight, like certain anions, amino acids and different sugars, pass the filtration barrier. To utilize them again these substances need to be reabsorbed. In both nephridia the ECM acts as filtration barrier, forming a kind of molecular sieve. This matrix needs to be stabilized to withstand the filtration pressure by special perforated cells that mediate filtration, i.e., the terminal cell or podocytes. The ultrafiltrate is modified in a simple duct. This function has been shown and experimentally proven in a number of papers (see Zerbst – Boroffkam & Haupt, 1975; Smith & Ruppert, 1988; Bartolomaeus & Xylander, in prep.; Fig. 1C, D). The structural correlates for these functional demands, however, differ between protonephridia and metanephridial systems. In protonephridia terminal cells span the filtration barrier (Fig. 3D); these cells are directly apposed to the duct and, thus, in a protonephridium both functions are united in a single organ. In metanephridial systems the wall of transcoelomic blood vessels functions as filtration barrier, stabilized by podocytes (Fig. 1E). Modification occurs spatially separated from these cells within the metanephridium. Thus, the term metanephridial

system is only related to the function, because the system is formed up by two structurally independent elements. The term “protonephridium”, however, is related to the function as well as to the structural integrity of this organ (Fig. 2A). The term “metanephridium”, finally, is related to the structural integrity alone, as it only mediates a part of the entire excretory process, i.e. modification of the ultrafiltrate (Fig. 2B). Thus, when using these different terms, we have to keep in mind that they address to completely different affinities of the nephridia.

In annelids both organs, i.e. protonephridia and metanephridia, occur. They are related by the developmental process, because in several taxa protonephridia precede metanephridia while the animals grow (tab. 1). In some annelid taxa protonephridia can be found in all stages of development, while there are metanphridia in all postlarval stages of others. Provided that annelids are monophyletic there should also be some evolutionary connection between both organs.

In this paper we want to summarize the present knowledge on nephridia in annelids and related taxa from a structural, developmental and comparative perspective, which will lead to some evolutionary considerations.

1. Structure

On the structural level organs can be described as a hierarchical system of substructures. The cell types represent the upper level of structural subsets of an organ, followed by cell surface differentiations like cilia, microvilli or structures being offset from the perikaryon. The lowest level is represented by subcellular structures, like organelles or other structures. At least one structural element should be unique to each cell type, should define and characterise it to provide criteria for its identification. In the case of annelid nephridia, however, we will see that these criteria may also be derived from developmental studies or from the structural context into which these cells are embedded. We are convinced that understanding organs as hierarchical system of substructures provides essential coding issues for a cladistic analysis as well as the substrate for primary homology hypotheses. On the level of organs their robustness depends on the number of identical substructures. In this section we therefore want to offer a framework for a proper description of the annelid nephridia as far as possible.

1.1 Protonephridia

On the cellular level protonephridia consist of a subset of at least three different elements, terminal cell, duct cell and nephridiopore cell (Fig. 2A). They surround a compartment that is but a blindly close cellular duct leading from the exterior into the mesodermal tissue. The entire organ is surrounde d by an ECM that is continuous with the subepidermal matrix (Fig. 1A). All cells of the organ adhere to each other by cell junctions. The innermost cell is called terminal cell, flame cell or solenocyte. It mediates filtration by forming the supporting structure of the actual filtration barrier. Generally this filter is a perforated or slashed hollow cylinder that surrounds the cilium and is surrounding microvilli (Figs. 3A, B). As the filter is always connected to the adjacent duct cell by adherens junctions these junctional complexes are an important criterion to discriminate a circle of microvilli from a longitudinally slashed filter. Thus, the terminal cell consists of four substructures, the perikaryon, the filter, a ciliary element and a microvilli element. While the perikaryon must always be present, the remaining three substructures can be modified or lacking. Their presence obviously is independent of each other. Distally, a duct cell is connected to the terminal cell. Like the terminal cell the duct cell is composed of substructures. These are the perikaryon, a ciliary element and a microvilli element. A high number of different vesicles, some of which are coated by clathrin, is characteristic for the cytoplasm of the duct cells and indicates endo-, exo- and transcytotic processes (Figs. 4A, G). The nephridiopore or nephridiopore cell finally connects the duct and the epidermis. The perikaryon of the nephropore cell is below the level of the epidermis. The nephridiopore cell is composed of the same substructures as a duct cell, i.e. a ciliary element and a microvillar element. A high number of different vesicles is characteristic for its cytoplasm and indicates different cytotic processes. In annelids, the nephridiopore cell is not a modified epidermal cell, as already indicated by its position. From the duct cell it can be discriminated by its delayed development; from the epidermal cells by the fact that the nephridiopore cell never sheds a cuticle. On the other hand, the nephridiopore is part of the epidermal layer as it is connected to adjacent epidermal cells by adhaerens junctions (Fig. 4H). Being an intermediate between epidermal cell and duct cell the nephridiopore cell can easily be discriminated from both kinds of cells without knowing its formation in detail.

1.2 Metanephridial system

As mentioned the term metanephridial system is a functional one. This excretory system is composed of two different and spatially separated substructures, the podocytes and the metanephridium. In annelids the podocytes generally rest on the coelomic side of the perivascular ECM (Fig. 2B). Podocytes consist of a perikaryon and a flat peripheral part that is perforated by meandering slits (Fig. 1E). If there are two or more podocytes they will interdigitate and will be connected by adhaerens junctions to each other and to adjacent peritoneal cells or epithelio-muscle cells. The meandering slits are bridged by additional extracellular material which represents the actual site of filtration. Thus, the slashed periphery of the podocytes is the supporting structure of the filtration barrier and is functionally comparable to the filter of the terminal cell. But, in contrast to the latter, it is never connected to duct cells. This is an important criterion to discriminate podocytes from terminal cells.

The metanephridium consists of two substructures, the ciliated funnel and the nephridial duct (Figs. 2A, 6D). The ciliated funnel is composed of non-muscular ciliated cells only. These rest on the septal matrix and are composed of three different substructures, the perikaryon, a microvillar and a ciliary element; a structure offset from the perikaryon is never found. Long and interconnected rootlets anchor the ciliary axoneme to the funnel cell Fig. 6A). Functionally, the funnel cells also serve in releasing the genital products from the coelom during maturity. The nephridial duct consists of non-muscular cells, being composed of three substructures, the perikaryon, a ciliary and a microvillar element. A high number of different vesicles within the duct cells indicate endo-, exo- and transcytosis like it does in protonephridial duct cells Figs. 4C, E). There are a few rare reports describing the nephridiopore cells. These are almost identical to duct cells, but stain more electron-densely (Fig. 9C).

Funnel cells and duct cells can be distinguished by the apical network of interconnected ciliary rootlets, while the duct cells can be identified by their high content of vesicles (Figs. 4C, 6D). Nevertheless, identification of the funnel cells can only be done from the structural context, as a funnel is always connected to a duct. This additional criterion is needed as multiciliated peritoneal cells which are found in some annelids are structurally identical to funnel cells and also possess a strong network of interdigitating ciliary rootlets. A further criterion to distinguish funnel cells from such peritoneal cells is the way they are formed. Funnel cells always differentiate from the same anlage as the duct cells (Figs. 7A-D).

2. Head kidneys in Annelids

In annelids protonephridia generally precede metanephridial systems during ontogenesis and are characteristic for the annelid larva. Nevertheless, in certain species protonephridia prevail in all postlarval stages. The trochophore larva of annelids posseses a pair of nephridia called head kidneys by Hatschek (1878, 1886).

Although Hatschek (1886) used the term for the nephridia of the larva and thus restricted it to those annelids that possess a larva, we will use the term for the first pair of nephridia that is differentiated during development. This organ, however, should be situated anteriorly and closely behind the larval eyes. This term is thus defined by the course of development and the position. Today we know that head kidneys are not restricted to planctotrophic larva, which are usually translucent, so that nephridia could be observed in the living animal under the light microscope. They are also described from lecithotrophic larvae, where they could only be detected on the electron microscopical level. They are, however, completely described in a very few taxa only (tab. 2). Except in the spionids *Pygospio elegans* (Schlötzer-Schrehardt, 1992) and *P. ciliata* (Bartolomaeus, unp.) and the poecilochaetid *Poecilochaetus serpens* (Allen, 1905; Bartolomaeus, unp.) all species studied possess protonephridia that are composed of the above mentioned substructures.

In all species studied thus far, they are found some micrometers caudal to the eyes, generally on the level of the larval mouth. This is in accordance with the definition of the term. These organs are composed of at least three cells, one terminal cell, one duct cell and one nephridiopore cell. As such three-celled organs they are described in *Scoloplos armiger* (Bartolomaeus, 1998), *Spirorbis spirorbis* (Bartolomaeus, 1993b), *Magelona mirabilis* (Bartolomaeus, 1995a) and *Chaetopterus variopedatus* (Bonch-Bruewich & Malakhov, 1986). In certain species the number of terminal cells and duct cells may be increased, like in *Pectinaria auricoma* (Bartolomaeus, 1995a), *Phyllodoce mucosa* (Bartolomaeus, 1989) or *Autolytus prolifer* (Bartolomaeus, 1993a). When compared between the different species, the duct cells and the nephridiopore cell merely differ in their ciliation, in which they may either lack or differ in number of cilia, i.e. being mono- or multiciliated (tab. 2). Compared to this a high structural diversity of terminal cells is found in the different species (Figs. 5A-E).

In the serpulid species studied that far (tab. 2) and in *Scololos armiger* the terminal cell bears a bundle of cilia, sometimes referred to as ciliary flame that extend into the small compartment formed by the cylindrical filter (Fig. 5C). Several short microvilli surround the ciliary flame. In serpulids the filter and the adjacent duct cell interdigitate by small processes (Fig. 3B). This kind of adhesion has sometimes referred to as weir. This structure, composed of rods that alternating protruded from the terminal cell and the duct cell, is characteristic for plathelminthes (Bartolomaeus & Ax, 1992) and is regarded to be a derived condition. The term weir should not be applied for the connection between terminal cell and duct cell in the studied serpulid head kidneys.

In the other annelid head kidneys studied each cilium possess a ring of strong and elongated microvilli surrounding it (Figs. 3A, C). This is characteristic for the protonephridia in *Magelona mirabilis*, in *Pectinaria auricoma*, *Polygordius* sp. as well as in the head kidneys of several phyllodocidan species. *Pectinaria aurocoma* certainly shows the most complex structure as the compartment inside the terminal cell is extremely ramified (Fig. 5F). Each ramus contains a single cilium surrounded by a ring of 10 microvilli. The lateral wall of the compartment is perforated by several slits covered by diaphragms representing the filtration barrier. Each cilium of the multiciliated terminal cell of *Polygordius* sp. is also surrounded by a ring of microvilli (Smith & Ruppert, 1988) (Fig. 5D). In certain species of the Phyllodocidae a filter is lacking, but the circumciliary ring of strong and elongated microvilli is retained and serves as supporting structures for the filtration barrier (Figs.5B, E) . Such terminal cells are called solenocytes, if they are monociliated. If these cells are multiciliated a ring of microvilli surrounds each cilium. A flame of several cilia within a ring of microvilli, but without a filter has never been described..

Only little is known on the formation of these head kidneys. According to older cell lineage studies, the head kidneys are formed by the cells $3c^{22}$ and $3d^{22}$ that sunk into deeper cell layers during early development (Woltereck, 1904, 1905). More recent electron microscopical studies of *P. mucosa* clearly showed that the protonephridum is actually formed underneath the epidermis. When terminal and duct cells are complete the nephropore cell which is formed with some delay, pierces the epidermis and connects the nephridial compartment to the exterior (Figs. 7E ,F). This observation at least corroborates the older information according to which the annelid head kidneys do not develop by ectodermal invagination. However, these

data are extremely isolated and do not allow any definitive statement on the ontogenetic origin of the head kidneys.

Nothing can be said about the evolutionary directions by observing a single structure alone. Thus, any evaluation of the structural variety of the terminal cells is hardly possible without any primary assumption. If one assumes that monociliarity represents a primary condition, different pathways might have caused structural diversity in head kidneys. The one is by reduction of the filter, the other one by gaining a multiciliated condition (see Fig. 5). It can, however, not a priorily be excluded that monociliarity evolved from a multiciliated condition. This has to be assumed for the monociliated epidermal cells in some annelid taxa (see Hausen, this volume) as most parsimonious explanation.

Nevertheless, some concluding remarks can be given for the head kidneys. (1) These organs must be assumed for the annelid ground pattern as those excretory organs which are differentiated at first during ontogenesis, irrespective of whether there was a trochophore or not. (2) Certain head kidneys are organized in that ways which has been hypothesized to represent the primary condition in Bilateria (Bartolomaeus & Ax, 1992). Provided these hypotheses are match the course of evolution, the structure of these head kidneys must represent the primary condition in Annelida. (3) Solenocytes and terminal cells are regarded as homologous. Reduction of the filter and adoption of its function by the microvilli is characteristic for certain Phyllodocida and also characteristic for those phyllodocidan species that possess segmental protonephridia. (4) The head kidneys of the spionid and poecilochaetid species studied thus far are metanephridia (Allen, 1905; Schlötzer Schrehardt, 1992, own unpublished results). This observation deserves detailed analyses in the future.

3 Segmental nephridia

At a certain stage of annelid development a caudal, prepygidial meristematic ring of the larva, the grow zone, increases mitotic activities and gives rise to a large number of identically organized segments. Because of this, annelids can be regarded as animals that have two ontogeneses, one leading from the fertilized egg to the larva or a stage with a quiet terminal grow zone and the second leading to a metamerically organized animal with several identical segments generated by the activity of the grow zone. The nephridia that are generated by this

growth zone will be called segmental nephridia. They can either be protonephridia or metanephridia. In several species these nephridia also release the genital products from the coelom. Such modifications are described in more detail in Bartolomaeus (1999). The nephridial organs that are formed during this process represent segmental repetitions of the same information.

3.1 Protonephridia

In several phyllodocidan species, like those of the Phyllodicidae, Nephtyidae, Glyceridae, Goniadidae, Pisionidae, Sphaerodoridae, Isopilidae Alciopidae, Typhloscolecidae and in several interstitially living taxa, protonephridia can be found in each body segment (see tab. 1). Their terminal cells are always solenocytes (Fig. 3E). In the mentioned phyllodocidan taxa the terminal cells are monociliated. At least in those taxa the species of which have a larger body size, ciliated cells cover the duct and close it completely towards the coelom, so that each cilium of the terminal cells plus its ring of microvilli enter the duct separately (Goodrich, 1945; Smith & Ruppert, 1988; Bartolomaeus, 1989; Smith, 1992) (Fig. 9E). According to its structure these cells must be formed in a late stage of nephridial development (Bartolomaeus, 1989 for *Phyllodoce mucosa*). This assumption was confirmed by studying the nephridial development in glycerids and nephtyids (Bartolomaeus, 1993b). Smith and Ruppert (1988) interpreted this cell as an inverted duct cell, which could not be confirmed by studies into the nephridial formation until today. Nevertheless, it seems unlikely that this cell is a modified coelothelial cell because it is directly connected to duct cells and not separated from them by a matrix, like other cells of the coelomic lining are. Further studies into nephridial formation should provide a clear solution.

There are also records from segmental protonephridia with multiciliated solenocytes. These have been described for *Tomopteris helgolandica* (Tomopteridae) and *Hesionides arenaria* (Hesionidae) (Westheide, 1986; Bartolomaeus, 1997) (Fig. 3F). Here, each protonephridium possess a single terminal cell that bears several cilia, each surrounded by a ring of 10 strong microvilli. In *T. helgolandica* a matrix connects the microvilli thus indicating ultrafiltration of coelomic fluid. Like in the taxa with monociliated solenocytes each cilium plus its ring of microvilli enter the duct separately. After a few micrometer these small compartments join to form a larger ductule wich finally merges with other such ductules to form the nephridial

duct. Both lack such an inverted duct cell like the ones described above. In *T. helgolandica* a large number of cilia emanates from the solenocyte and extends into the coelom.

The multicilated solenocyte of *T. helgolandica* is attached laterally to the funnel of a metanephridium. Although one duct cell provides a short lateral duct which seems to receive the ultrafiltrate of the terminal cell, this duct is not connected to the metanephridial duct but ends blindly. Numerous vesicles inside the duct cell indicate transcytotic processes (Bartolomaeus, 1997).

The duct of all segmental protonephridia consists of multiciliated cells that are connected by apical adhaerens junctions; basally to them septate junction hinder that the duct fluid bypasses the duct cells to get in contact with the interstitial fluid. Microvilli always cover the apical surface of the duct cells. The duct cells contain numerous vesicles, lysosomes and multivesiculated bodies that indicate transcytotic processes. Coated pits and coated vesicles indicate receptor mediated endocytosis of some material from the duct. The duct is always composed of several cells. Generally ciliation, number of microvilli and content of organelles do not differ during the course of the duct. The last few duct cells that form the nephridiopore may stain more electron-densely (Bartolomaeus, 1989) (Figs. 4F, H). All ducts start in one segment and open in the preceding one to the exterior.

In some interstitial annelids, the protonephridia are quite short, being composed of two to found duct cells and one or two terminal cells. These differ tremendously in structure, ranging from multiciliated solenocytes to terminal cells with a lateral tuft of cilia (Brandenburg, 1970; Clausen, 1986; Westheide, 1985). Like a fence a row or double row of strengthened microvilli originating from the latter kind of terminal cell and extending deeply into the duct may separate the ciliary flame from the surrounding interstices or body cavity. These microvilli act as supporting structure for a filtration barrier.

3.2 Metanephridial systems

The majority of annelid nephridia are metanephridia (Goodrich, 1945; tab. 1)). Starting with the funnel in one segment they pierce the septum and open to the exterior in the following segment. The internal opening is enlarged and consists of a wide funnel that rests on the

septum. The cells of the funnel are generally multiciliated and rest on the septal matrix. Adjacent to the funnel epithelio-muscle cells or peritoneal cell are found. These are connected to the funnel cells by adhaerens junctions and also rest on the septal matrix. Generally the cilia of the funnel cell contains two ciliary rootlets, one runs almost parallel to the cell surface, the other, stronger one crosses the cell obliquely while running basally. These rootlets are interconnected by intermediate filaments and form an apical network within the funnel cell (Figs. 6A, D). Beside this there is no difference between funnel cells and adjacent duct cells. During reproduction the density of filaments apparently increases. Because the strong bundles of intermediate filaments stain intensely with certain classical colours the difference between funnels cells and duct cells seems to be greater in histological sections than actually can be confirmed by funnel and duct cell substructures (Bartolomaeus 1999 for discussion). The duct cells are morphologically equivalent to the protonephridial duct cells (Smith & Ruppert 1988; Smith 1992). Like the latter they contain numerous vesicles, lysosomes, multivesculated body and coated vesicles. All there confirm a high endo-, exo- and transcytotic activity of duct cells as predicted by the above mentioned assumption that metanephridia merely modify coelomic fluid (Figs. 4C, E).

Nephridiopore cells have extremely seldom been studied (Bartolomaeus 1989; 1993b; Kuper 2001). There according to studies into the development these cells pierce the epidermis while being formed. There is some evidence that their cytoplasm stains more electron-dense than that of the adjacent duct cell, which could hint a higher protein content and different osmotic affinities. The nucleus is always underneath the level of the epidermis cells, which obviously reflects the way in which the nephropore cell had been formed.

Some information can be obtained from a comparison of the distribution of the metanephridia within a single organism. In all species of the Serpulida, Sabellidae, Sabellariidae and Siboglinidae (formerly Pogonophora) a single pair of nephridia opens into the first segment (Goodrich, 1945; Schulze, 2001). The duct is rather long and extends caudally for a few segments, u-turns frontally and leads to the exterior of the animal on the dorsal side. In certain Terebellida the metanephridia are restricted to a few anterior segments (Smith, 1992). Some of them may share a common duct. In Pectinariidae, Serpulidae and Sabellidae the metanephridium is lined by podocytes that rest on the coelomic side of the perinephridial matrix (Bartolomaeus, 1993b) (Figs. 4B, D). Here, they can not mediate a selective filtration

or bypassing different fluid-filled compartments, because the perinephridial matrix is never housing blood lacunae.

Podocytes surrounding the metanephridial duct are absolutely surprising, as in these taxa podocytes are also found on the perivascular ECM, like in all other species with metanephridia studied until now (Smith & Ruppert, 1988; Bartolomaeus, 1993b). Podocytes normally rest on the perivascular matrix where they span and stabilize the matrix to prevent possible rupture by the filtration pressure (Figs. 1E; 6B, E). They allow a selective fluid transfer between the blood and coelom and are generally believed o adopt the function of the protonephridial terminal insofar as they eliminate metabolic wastes from the blood by ultrafiltration. Functionally the coelomic cavity of Annelida can thus be regarded as large nephridial compartment. Podocytes are polar cells, connected by apical adhaerens junctions to neighbouring cells. They always possess a centriole, sometimes a small vestigial cilium and sometimes myofibrils. The latter has until now merely seen in serpulid and sabellid species (Bartolomaeus, 1993b). Podocytes were found resting on the coelomic side of the main dorsal and ventral vessel as well as on the coelomic sides of the intraseptal vessels (Fig. xx). Podocytes are generally lacking in those species that possess protonephridial excretory organs. *Protodrilus rubropharyngeus* is the only known exception in this respect. This interstitial species has segmental protonephridia; podocytes are found resting on the coelomic side of the septal matrix (von Nordheim & Schrader, 1994).

3.3 Development

Frontal to the anus a meristematic region remains until the animal reaches its final size. This region shows an enormous mitotic activity and gives rise to a certain number of identical segments. Along a caudo-frontal gradient all stages of formation of these segments and their organs can be found. Most of our knowledge of the nephridial development results from ultrastructural studies into the structure of different stages of nephridial formation following a series of section from the caudal meristematic ring to segments containing large coelomic cavities (see Bartolomaeus, 1993b; Bartolomaeus, 1999).

The earliest stage of nephridial formation that can be discriminated from the surrounding tissue consists of three to four cells that surround a small compartment (Fig. 7A). These cells

rest on a very thin and incomplete matrix and show a clear polarity with apical adhaerens junctions and small microvilli extending into the compartment. Earlier stages do not exhibit structures that allow to clearly recognising them as nephridial anlage. However, such a small group of cells marks a starting point of nephridial development that can clearly be identified. While differentiation of the surrounding cells into muscle cells proceeds the cells of the nephridial anlage start to form cilia (Fig. 7B). The number of nephridial cells increases, but the source of these cells is not clear. Although we studied nephridial development in several taxa, there was only clear evidence in regenerating segments that additional nephridial cells result from mitosis of presumptive, but yet weakly differentiated duct cells. The distal duct cells elongate and the distal-most one pierces the epidermis so that the compartment the nephridial cells surrounded during development is now connected to the exterior (Fig. 7C).

Formation of cilia in the cells of the nephridial anlage always starts with a single cilium that forms a short and orimental axoneme (Figs. 8A, B). Its basal structures consist of a basal body with a short lateral basal foot and an accessory centriole lying rectangular to the basal body. In those nephridial cells that will become duct cells, this monociliated stage is passed during formation of several cilia per cell. In some species, however, the proximal nephridial cells remain monociliated. A ring of strong and elongated microvilli is formed and surrounds the cilium. These cells are typical solenocytes (Fig. 8D). This developmental path is characteristic for all species with segmental protonephridia studied thus far (see Bartolomaeus, 1999) as well as for the polynoid species *Harmothoe sarsi* and the pholoid *Pholoe inornata*. In all these species, the proximal and monociliated cells will become solenocytes. In *T. helgolandica* a monociliated intermediate stage has never been observed; here the cilia of the prospective terminal cell are each surrounded by a ring of microvilli.

Our studies into the formation of the nephridia revealed that the developmental pathway the proximal cells take influences the fate of the entire anlage and is responsible for its prospective function as protonephridia or as metanephridium (Bartolomaeus & Ax, 1992; Bartolomaeus, 1993b, 1997, 1999) (see in Fig. 8: D to E versus to F and then C). We, therefore, will take a close look at the developmental of these cells. In each nephridial anlage there is a remarkable asymmetry in the organisation and attachment of the most proximal cells. In protonephridia the terminal cell is directly connected to the adjacent duct cell. There is, however, a remarkable asymmetry in the organisation of the monociliated cells that will influence the entire fate of the anlage. The cilium plus its ring of microvilli are always

laterally to the terminal cell and surrounding muscle cells and cells that will become coelomic lining cells are apposed to both structures (Figs. 7C, 8 B). The same is in species where multicilated proximal cells are found in the nephridial anlage. Except for *T. helgolandica* and presumably some other species with multicilated solenocytes not studied yet regarding their nephridial development, these cells possess a bundle of cilia extending into the duct. This bundle is laterally to the perikaryon and also bears microvilli that may surround the bundle. While the perikaryon is connected to the adjacent cells of the anlage, cilia and microvilli are next to cells of the prospective coelomic lining. Thus, irrespective of the anlage will differentiate into a protonephridium or a metanephridium, cilia and microvilli of the proximal cells are not surrounded by the anlage like those of the adjacent cells of the nephridial anlage are. Instead, these subcellular elements run between cells that will form the coelomic lining later during formation of additional segments. These proximal cells will either form the ciliated funnel or the terminal cells of the nephridium and are not completely surrounded by a matrix. At least the most proximal one are connected to the surrounding muscle cells. Finally fluid accumulation among those cells that surround the nephridial anlage causes formation of a large coelomic cavity by schizocoely. The proximal cells of the nephridial anlage and their cilia and microvilli become exposed to the coelomic fluid and follow the general obliteration of the formerly compact tissue. In the case of a metanephridium the funnel is opened passively (Figs. 7, 8). There is no grafting of ciliated cells onto the duct as proposed by Goodrich (1945).

In case of the protonephridia the proximal cells large retain the position and are not moved apart while the coelomic cavity widens by fluid accumulation. In the small interstitial species this is linked to the smallness of the animals and the small coelomic cavities.In larger species with protonephridia, like nephthyids, phyllodocids, glycerids and others there is at least one cell that covers the proximal duct cells (Goodrich, 1945; Bartolomaeus, 1989) and prevents it from being opened passively. The solenocytes pierce this cell with the cilium and the circumciliary ring of microvilli to enter the duct. At least to species are known that do not possess such a covering cell, i.e. *Harmothoe sarsi* and *Pholoe inornata*. In both species early stages of nephridial development are identical to those in Phyllodocidae, Nephtyidae and Glayceridae, but when the coelom starts to expand by fluid accumulation the solenocytes move aside that the apices of the adjacent duct cells are exposed to the coelomic fluid by forming a funnel. During further development the solenocytes degenerate and a typical metanphridium results from this development (Fig. 9D, F, C).

Presently we assume that protonephridia in polychaetes largely depend on the size of the coelom and the size of the animals. In these animals protonephridia accordingly result from an truncated metanephridial development, so that an early developmental stage is retained. In the stage retained the proximal cells of the anlage bear a lateral bundle of cilia surrounded by a ring of microvilli. Structurally, this resembles a protonephridium without a filter (see for instance Clausen (1986) for *Microphthalmus ephippiophorus* or Brandenburg (1970) for *Dinophilus gyrociliatus*). Comparative studies, however, reveal that it is identical to a developmental stage of a metanephridium. Such an interpretation is fallible, because within a single species such segmental protonephridia resulting from a truncated metanephridial development should clearly differ from the head kidney. Any evolutionary evaluation, however, has to be done in a broad comparison with the general character distribution within the polychaetes. Nevertheless, the above reviewed developmental studies clearly indicate that segmental protonephridia within the polychaetes are not necessarily homologous. Recently, Kuper (2001) showed the enormous variety of terminal sections in syllid segmental organs ranging from small funnels to slit-like terminal openings and lateral ciliary flames that extend into the duct. Several of them clearly resemble stages of metanephridial development so that variety of syllid nephridia can be explained by differently truncated nephridial development. In Phyllodocids, nephtyids and glycerids, however, the protonephridia probably result from covering the proximal section of the duct by a multicilated cell. This could hint at a common ancestry of these taxa.

4 Nephridia in related taxa

4.1 Clitellata

Head kidneys. As a result of a modified ontogenetic process, Clitellata have no larva. There are some secondary larvae in certain hirudinean taxa instead. In some lumbricid, tubificid and hirudinean species the occurrence of head kidneys have been described, which precede the formation of segmental nephridia during development (see Anderson, 1973).
As protonephridia seem to be characteristic for the annelid larva and as they are the first nephridia formed during ontogenesis, one would expect that the first nephridia formed during ontogenesis are also protonephridia in Clitellata, irrespective of whether they show a

secondary larva or not. Recent studies into the ultrastructure of the secondary larva of *Erpobdella octoculata*, however, reveal that its nephridia lack a terminal cell, a characteristic essential to apply the term protonephridia to these organs (Quast & Bartolomaeus, 2001). Nevertheless, the organs are blindly closed toward the body cavity. There is some evidence that these organs are identical to the metanephridia of the adult organisms.

Segmental metanephridia and their formation. Clitellata possess segmental metanephridia which have always been described as resulting from a single anlage (Goodrich, 1945). In all non-hirudinean clitellate annelids these organs drain the coelomic cavity. As in polychaetes the organs consist of a preseptal part and a postseptal duct. Although ultrastructural data on these organs are scarce they exhibit a varity of different shapes and forms have been described that concern the extension of duct, its exterior or interior opening and its possible fusion to form complex organs. The preseptal part consists of a small funnel or nephrostome in microdilous species (Goodrich, 1945; Bunke, 1998, 2000) or of a large and complex nephrostome in megadrilous species. While the latter are reported to possess a central ciliated cell and several marginal cells with cilia, the small nephrostomes always consist of an inner ciliary flame and some marginal cilia. Ultrastructural data of *Dero digitata*, *Nais variabilis* and *Pristina longiseta* (Naididae) show that the funnel consists of a single marginal cell called mantel cell that enwraps a central flame cells (Bunke 2000) (Fig. 6C)). This cell possesses a bundle of cilia that projects into the duct, while the cilia of the mantel cell extend into the coelom. In Aeolosomatidae the metanephridial funnel is identically organized (Bunke 1994) (Fig. 9A, B).

Development of this nephridium has recently been studied by Bunke (2003). The earliest stage of development that can clearly be discriminated from the surrounding mesoderm cells consists of three cells. Their fate appear to be fixed insofar, as the innermost cell that is next and ventral to the septal vessel differentiates into the mantel cell, while the median cell becomes the flame cell. Only the distalmost cell is the stem cell of the canal and generates duct cells by mitotic activities which concern the stem cell itself and its daughter cells. Ciliogenesis has not been described in detail by Bunke(2003), but his figures (Bunke, 2003: Fig. 2C) show numerous centriols within the cytoplasm. The same is seen in developing polychaete nephridia where a monocilated stage is passed and multiplied centriole migrate towards the adluminal cell membrane to induce formation of additional cilia. Bunke (2003) also reports that the ECM separating the duct from the adjacent mesodermal cells is

incomplete during early nephridial development. This is also the case during early nephridial development in polychaetes. Formation of the septa seems here to be parallel to nephridial development. There is no doubt that metanephridia in Clitellata are mesodermal. This has been shown by cell lineage studies (Weisblat et al., 1984; Kitamura & Shimizu, 2000a, b; Shimizu and Nakamoto, 2001; Shimizu et al., 2001). Due to the position of the anlage, this has also to be assumed for polychaetes.

4.2 Echiura

Head kidneys. In trochophore larva of *Echiurus echiurus* possess protonephridia with several monociliated terminal cells (Goodrich, 1945). Such head kidneys are lacking in *Urechis caupo* (Newby, 1940), but can be found in fertile dwarf males of *Bonellia viridis* (Schuchert & Rieger, 1990), where they are multicilated. It has been discussed that these protonephridia evolved secondarily (Schuchert, 1990).

Segmental nephridia and their formation. The larval protonephridia are followed by two different systems which traditionally are assumed to mediate excretion, i.e. paired segmental organs or metanephridia on the level of the ventro-medial large seta and the anal sacs. Ontogenetically the latter originate from a pair of metanephridia situated on either side of the anus. During development these metanephridia acquire additional ciliated funnels and enlarge (Baltzer, 1934). Ultrastructural data of the anal sac funnels show a grid-like arrangement of muscle cells embedded in the ECM between the duct cells and the peritoneum that rests on the coelomic side of the anal sac (Bartolomaeus, unpubl.; Fig. XX). No such muscle cells are found within the matrix between funnel cells and peritoneum. All nephridial cells are multiciliated with two rootlets per cilium. Duct cells differ from funnel cells in the orientation of their rootlets and the larger number of microvilli. The rootlets in funnel cells are partly fused and form a dense intracellular meshwork.

The number of metanephridia differs among Echiura. Some species possess one to three pairs of such organs (Singhal, 1982; Welsch & Storch, 1972) while others like *Ikeda taenioides* is reported to possess up to 300 metanphridia (Baltzer, 1934). The number of organs varies even with a single genus (one pair in *Thalassema diaphanes* (Bock, 1942) and 27 in *T. elegans*

(Baltzer, 1934)). The germ layer origin of metanephidia and anal sacs is unknown; a mesodermal origin seems likely (Baltzer, 1934).

4.3 Sipuncula

Head kidneys have never been described for Sipuncula. The first pair of nephridia that is formed is metanephridial and persists during the entire life time. A single pair of metanephridia seems to represent the plesiomorphic condition in Sipuncula, although their number can be increased up to three pairs (Storch & Welsch, 1972). The excretory function of the metanephridia has been shown by Pinson & Ruppert (1988). In *Golfingia minuta* these organs consist of a ciliated funnel that is directly attached to the body wall (Bartolomaeus, unpubl.). The funnel cells are multiciliated and directly connected to the non-muscular, extremely flat peritoneum that lines the somatic musculature. This lining wraps the U-shaped duct and rests on the perinephridial matrix. Grid-like arranged longitudinal and circular muscles are found all along the course of the nephridium, except the upper one third of the funnel. No muscle cells can be found here. The muscle cells in the region below the funnel are continuous with the body wall muscles. All muscle cells of the nephridium are embedded in the perinephridial matrix and are always true fiber muscle cells (see also Storch & Welsch, 1972 for *Phascolosoma lurco*) (Fig. 6F). The duct in *G. minuta* consists of two different sections, a narrow ciliated descending duct that is continuous with the ciliated funnel and a large, sac-like section that lacks any ciliation. This is the largest and most prominent part of the nephridium. Its diameter is up to 5% of the trunk diameter. The lining cells interdigitate and are connected by adhaerens and septate junctions. The cells contain numerous smaller and larger vesicles of different electron density, lysosomes and endosomes. They all indicate a higher degree of cytotic processes than seen in the ciliated section. There is no matrix between the individual walls of both sections of the duct. The coelomic lining of the sac-like section contains numerous podocytes (Fig. 6E), an observation that has also been reported earlier for other sipunculan species (Serrano & Angulo, 1989). Podocytes bypass different compartments and allow selective fluid transfer between the trunk coelom and the contractile vessel (Pilger & Rice 1987). As the perinephridial matrix never contains any fluid-filled lacunae it remains enigmatic which fluid systems are selectively bypassed by these cells. The nephridioporus is below the level of the funnel. The nephridiopore is formed by several epidermal cells that are directly connected to duct cells. The nephridopore is lined by cuticle

that decreases in diameter towards the duct cells. Strong muscles of the body wall musculature underlie the nephridiopore and nerve cell processes are found in this region.

In a young larval stage (according to Akesson, 1958; Gibbs, 1975) of *G. minuta* revealed some first insights into nephridial development. The nephridial anlage bulged into the coelomic cavity and was covered by flat protrusions of muscle cells and peritoneal cells. The ciliated descending part was neither connected to the coelomic cavity nor to the sac-like section of the duct. This latter was preformed by a double layer of cells. The nephridiopore could already be recognized as an cuticle lined epidermal invagination. Although the epidermal cells directly contacted the cells of the nephridial anlage, no luminal connection was established. Those ciliated duct cells that were next to the coelomic cavity were not covered by any peritoneal or muscular cells not by their protrusion; they were directly exposed to the coelomic fluid. Although it can not definitively be excluded that modified peritoneal cells form the funnel, the present finding indicates that the funnel is formed by duct cells and that the anlage may be opened passively while the coelomic cavity expands.

5. Conclusion

It seems very likely that protonephridial head kidney belong to the ground pattern of the Annelida (Salvini-Plawen, 1980; Bartolomaeus & Ax, 1992; Bartolomaeus, 1998). Provided that a single cilium per cell always represents a primary condition (Rieger, 1976, but see Bartolomaeus, 1995b), monociliated protonephridia consisting of three cells could represent the primary condition. In this respect the head kidneys in *Echiurus echiurus* (Echiura) which's monociliarity is inferred from older literature (Goodrich 1945: Fig. 64B) needs urgently to be studied. However, more data are needed to elucidate the direction of evolution of the head kidneys. Although we assume that segmental nephridia and head kidneys primarily result from repetition of the information to generate a nephridium, the evolved in different directions within the Annelida. Head kidneys are characteristic for the larva, and all constrains that influences their evolution should clearly differ from those that influenced the evolution of segmental nephridia. Thus, the structure of the head kidneys and the structure of the segmental nephridia did not necessarily evolve in parallel.

Despite earlier assumptions (Bartolomaeus, 1989, Bartolomaeus & Ax, 1992) these segmental nephridia are primarily not protonephridia, instead it is more parsimonious to assume that all nephridia formed subsequently to the head kidneys primarily were metanephridia. This is also in accordance with recent cladistic analyses of polychaete phylogeny (Rouse & Fauchald, 1997; Rouse, 1999). Some of these organs, especially those in smaller annelids closely resemble certain stages of metanephridial development. Studies into metanephridial development show that the funnel is formed when the coelomic cavity expands during coelomogenesis. Structural similarity of certain protonephridia and certain stages of the metanephridial development can be explained by a truncated formation of metanephridia due to the restricted size of the coelomic cavities. Such protonephridia should therefore primarily be found small polychaetes with large body sized relatives. The special structure of the solenocytes in the protonephridia of certain phyllodocidans is assumed to reflect common ancestry. This is substantiated by the fact that the apical portion of the duct is coved by a multiciliated cell the cilia and microvilli of the terminal have to pierce to enter the nephridial duct. If this cell prohibits passive opening of the proximal section of the duct to form a typical metanephridial funnel, a different way of forming a funnel at least during maturity should be expected, because the funnel also acts as inner genital opening. In Phyllodocidae and Pisionidae this is acturally the case (Stecher, 1968; Bartolomaeus, 1989); in Nephtyids and Glycerids the genital products are not discharged by the nephridium (see Bartolomaeus, 1999). The protonephridia in these taxa, however, may also results from a trunctated metanephridial development. At least in a pholoid and a polynoid the metanephridia pass a protonephridial a stage with solenocytes during development. Although it has initially (Bartolomaeus & Ax, 1992) been interpreted as recapitulation of the ancestral protonephridium, it may also represent a stage which has been preserved in those taxa with solenocytes by truncation of the development. An alternative way has been proposed by Westheide (1986), who assumed that segmental protonephridia evolved from metanephridia by reduction of the size of the funnel and its final closure by terminal cells. Kuper’s (2001) comparative studies of the nephridia in Syllidae, also support this assumption. A final conclusion on the direction of the nephridial evolution, however, will certainly be inferred from a sound phylogeny of the Phyllodocida. Presently both assumptions are not in accordance with the cladogram presented by Rouse & Fauchald (1997), which on the other hand has some severe weaknesses (see Bartolomaeus et al., this volume).

Further studies into the development of the nephridia and ultrastructural data on the head kidneys are needed for the remaining polychaete taxa. We are convinced that both structures show enough complexity and enough substructural details that their analysis could substantially increase the data base to unravel polychaete evolution. The remarkable correspondence of podocyte lining the nephridia in certain Sipuncula, Sabellida and Terebellida need further attention. It is unique and hardly explainable from a functional point of view. Further comparative studies could help to elucidate the position of the Sipuncula. There are finally corresponding elements in the structure of the metanephridia of Aeolosomatidae and Clitellata. Corresponding nephridial development could revive the discussion on the relationship between both groups and should urgently be studied.

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Figure subheadings

Fig. 1: Function of filtration nephridia. A. Protonephridium. $P_2 > P_1$. Pressure inside the nephridial compartment (P_1)is lower than in the surrounding interstices or body cavity(P_2). B. Metanephridial system. $P_1 > P_2$. Pressure inside the Blood vessel higher than in the coelomic cavity. C, D. *Eulalia viridis* (Phyllodocidae). C.Experimentally applied albumen-gold does not pass the filtration basrrier. D. Experimentally applied iron dextrane passes the filtration barrier and is reabsorbed in the duct (inset). E. *Fabricia sabella* (Serpulidae). Podocyte lining the dorsal vessel in S2.

Fig. 2: A. Protonephridium and B. metanephridial system and their substructures. The sites of ultrafiltration differ in both nephridial systems. Metanephridia may additional serve in releasing genital products (indicated by two egg cells).

Fig. 3: Filtration structures in protonephridia. A.- D. Head kidneys, E. - F. Segmental protonephridia. A. *Magelona mirabilis*, larva. Terminal cell (TC), cross section. A filter surrounds central cilium plus its circumciliary microvilli. B. *Spirorbis spirorbis* (Serpulidae), larva. Terminal cell, cross section. Central ciliary flame is surrounded by microvilli and the filter. (Small arrows mark ECM) C. *Autolytus prolifer* (Syllidae), larva. Terminal cell, cross section. A filter is lacking. D. *Spirorbis spirorbis* (Serpulidae), larva. Filtration barrier (arrows). E. *Glycera alba* (Glyceridae). Solenocytes, cross section. F. *Tomopteris helgolandica* (Tomopteridae). Multicilated solenocyte, longitudinal section (inset: cross section). *blc* blastocoel, *coel* coelom, *ECM* extracellular matrix, *mv* microvilli.

Fig. 4: Modifying structures: duct and nephridiopore. A. *Eulalia viridis* (Phyllodocidae). Ciliated duct cell. B. *Pectinaria koreni* (Pectinariidae). Duct with podocytes resting on its coelomic face (arrows mark filtration barrier). C., D. *Fabricia sabella* (Sabellidae). Aciliated duct and ciliated funnel cells. D. Podocytes resting on the coelomic face of the duct. E. *Nereis diversicolor* (Nereididae). Cross-sectioned convoluted duct (Arrows mark cilia of the duct) F., H. *Glycera alba* (Glyceridae). Duct cells apposed to darker nephridiopore cell and H. nephridiopore. G. *Spirorbis spirorbis* (Serpulidae), larva, duct cell of the duct kidney.

Fig. 5: Terminal cells in head kidneys and segmental nephrida and their possible evolutionary relationships, if monociliarity is assumed to represent a primary condition. A.

Monociliated terminal cell as found in *Magelona mirabilis* (Bartolomaeus, 1995), *Harmothoe imbricata* (Holborow, 1971), *Sabellaria cementarium* (Ruppert & Smith, 1988). B. Solenocytes as found in *Phyllodoce mucosa* head kidneys (Bartolomaeus, 1989) and segmental nephridia of further Phyllodicida (tab. 1). C. Multicilated flame cell as known from different serpulid larva (tab 2). D. Multiciliated terminal cell with a ring of microvilli surrounding each cilium and a common filter as found in Polygordius sp. and *Pectinaria koreni* (F) head kidney (Smith & Ruppert, 1988; Bartolomaeus, 1995) and *Myzostoma cirriferum* segmental protonephridia (Pietsch & Westheide, 1987). E. Multiciliated solenocyte like in *Autolytus prolifer* head kidney (Bartolomaeus, 1993), *Hesionides arenaria* and *Tomopteris helgolandica* segmental protonephridia (Westheide 1986; Bartolomaeus, 1997).

Fig. 6: Metanephridial systems. A. *Pectinaria koreni* (Pectinariidae). Upper lip of nephridial funnel (arrowheads mark adhaerens junctions. B. *Aeolosoma hemprichi* (Aeolosomatidae). Podocytes lining the perintestinal vessel (arrows mark filtration slits). C. *Pristina longiseta* (Naididae). Neprhdial funnel composed of mantel cell (*MC* and flame cell. D. *Fabrica sabella* (Sabellidae). Ciliated funnel (*cf*), adjacent duct and blood vessel (*bv*) of the ciliated funnel. E., F. *Golfingia minuta* (Sipuncula). Podocytes rest on the perinephridial ECM (Arrows mark filtration barrier). F. Ciliated descending branch. Muscle cells (*MyC*) of the nephridial duct are separated by an *ECM*. *coel* coelom, *cr* ciliary rootlets, *DC* duct cell, *ECM* extracellular matrix, mv microvilli, *PtC* peritoneocyte

Fig. 7: Nephridial development. A.–C. Metanephridia in *Ophelia rathkei* (Opheliidae), A. Earliest recognizable anlage of the metanephridium. B. Ciliogenesis and enlargement of the Anlage, penetration of the subepidermal ECM (extracellular matrix). C. Addition of cells, Stronger ciliation in the proximal cells of the anlage, onset of fluid accumulation in the prospective coelomic cavity. D. Movement of the surrounding cells caused by fluid accumulation. Proximal duct cell cilia face the coelom and form the funnel. E.-F. Head kidneys in *Phyllodoce mucosa* (Phyllodocidae). Nephridium is formed in deeper cell layers. Nephridopore cell forms at last (E) and finally pierces the epidermis (F).

Fig. 9: *Aeolosoma hemprichi* (Aeolosomatidae). Nephridial funnel (small arrow) is composed of mantle cell (*MC*) and flame cell (*FC*). The duct (*D*) is highly convoluted; individual sections differ in the number of microvilli. B. Mantel cell with cilium emanating from its surface into the coelom (*coel*). C. Nephridopore does not pierce the cuticle (*Cu*). *Bb* basal body, *EC* epidermis cell

Fig. 8: General scheme of developmental pathways that lead to different nephridial organs. A. Earliest recognizable anlage. B. Ciliogenesis starts in the proximal cells of the anlage. These cilia are laterally to the perikarya and are not completely surrounded by the cells of the anlage. These cells either become the ciliated funnels of the metanephridium during coelomogenesis (C) or they differentiate into solenocytes (D). These either move aside when the proximal section of the duct is passively opened (F) or a further cell covers the proximal section of the duct so that a protonephridium with solenocytes is formed (E). If the temporarily formed solenocytes (D) move aside (F) they degenerate during formation of the funnel. Truncation and modification cause nephridial diversity in polychaetes.

Table 1

Filtration nephridia in Annelida

Taxon	Head kidney, segmental nephridia	Filtration structure	Author
Aberranta	?, ?		
Acoetidae	?, metanephridia	?	Goodrich (1945)
Acrocirridae			
Aeolosomatidae	?, metanephridia	podocytes	Bunke (1994),
Alciopidae	?, protonephridia	solenocytes	Smith & Ruppert (1988)
Alvinellidae	?, metanephridia	?	Zal et al. (1994), Zhadan et al. (2000)
Ampharetidae	?, metanephridia	?	Hessle (1917)
Amphinomidae	?, metanephridia	?	Goodrich (1900)
Aphroditidae	?, metanephridia	?	Fordham (1926); Goodrich (1945)
Apistobranchidae	?, metanephridia	?	Orrhage (1974)
Arenicolidae	?, metanephridia	podocytes	Ashworth (1912), Goodrich (1945); Wells (1959), Bartolomaeus (unpubl.)
Capitellidae	protonephridia, metanephridia	?	Eisig (1879, 1887, 1899), Goodrich (1945)
Chaetopteridae	protonephridia, metanephridia	terminal cell multic.	Bonch-Bruevich & Malakhov (1986), Joyeux-Laffuie (1890), Goodrich (1945)
Chrysopetalidae	?, metanephridia	?	Ehlers (1846), Goodrich (1945), Tzetlin et al. (2001)
Cirratulidae	?, metanephridia	?	Meyer (1887), Goodrich (1945); Olive (1970)
Cossuridae	?, ?		
Ctenodrilidae	?, metanephridia	?	Mesnil (1899), Banse (1969)
Dorvilleidae	?, metanephridia or protonephridia	podocytes or terminal cell multic., terminal cell monoc. in *Diurodrilus*	Smith & Ruppert (1988), Bandenburg (1970), Westheide (1985, 1990), Worsaae & Kristensen (this volume)
Eulepethidae	?, metanephridia	?	Goodrich (1945)
Eunicidae	?, metanephridia	?	Goodrich (1945)
Euphrosinidae	?, metanephridia	?	Gustafson (1930)
Fauveliopsidae	?, ?		
Flabelligerida	?, metanephridia	?	Goodrich (1945)
Glyceridae	?, protonephridia	solenocytes	Brandenburg (1966, 1975), Brandenburg & Kümmel (1961), Goodrich 1899; 1945), Smith & Ruppert 1988)
Goniadidae	?, protonephridia	solenocytes	Goodrich (1899, 1945), Ruppert & Smith (1988)
Hartmaniellidae	?, ?		
Hesionidae	?, protonephridia or metanephridia	solenocytes multic. or terminal cells multic.	Goodrich (1898, 1945), Westheide (1986); Clausen (1986)
Heterospio	?, ?		
Histriobdellidae	?, protonephridia	terminal cell multic.	Shearer (1910), Scharnofske (1984)
Isopilidae	?, protonephridia	solenocytes	Kuper & Purschke (2001: tab.1)

Lacydonia	?, ?		
Lumbrinereidae	?, metanephridia	?	Goodrich (1945)
Magelona	protonephridia, ?	terminal cell monoc.	Bartolomaeus (1995°)
Maldanidae	?, metanephridia	podocytes	Pilgrim (1978), Bartolomaeus (unpubl.)
Nautineliidae		-	
Nephtyidae	?, protonephridia	solenocytes	Brandenburg (1966), Clark (1956), Goodrich (1945)
Nereididae	?, metanephridia	podocytes	Goodrich (1945), Nakao (1974), Smith (1984)
Nerillidae	?, metanephridia or protonephridia		Jouin (1967a), Saphonov & Tzetlin (1994)
Oenonidae	?, ?		
Onuphidae	?, metanephridia	?	Goodrich (1945)
Opheliidae	?, protonephridia, metanephridia	?	Hartmann-Schröder (1958), Brown (1938), McConnaughey & Fox (1949), Bartolomaeus (1993b)
Orbiniidae	protonephridia, metanephridia	terminal cell multic.	Bartolomaeus (1998), Eisig (1914), Goodrich (1945)
Oweniidae	protonephridia, metanephridia	terminal cell monoc. and podocyte-like	Smith et al. (1987); Gardiner (1979)
Paralacydonia	?, ?	-	
Paraonidae	?, protonephridia, metanephridia	?	Strelzov (1979)
Pectinaridae	protonephridia, metanephridia	terminal cell multic.	Bartolomaeus (1995a), Hessle (1917)
Pholoidae	?, metanephridia	-	Bartolomaeus (1999)
Phyllodocidae	protonephridia, protonephridia	solenocytes, solenocytes	Bartolomaeus (1989), Bartolomaeus (1999), Goodrich (1945), Smith & Ruppert (1988)
Pilargidae	?, ?	-	
Pisionidae	?, protonephridia	solenocytes	Messenger et al. (1985), Smith & Ruppert (1988), Stecher (1968)
Poecilochaetus	metanephridia, metanephridia	podocytes	Bartolomaeus (unpubl.); Allen (1905)
Poeobius	?, metanephridia	-	Robbins (1965)
Polygordiidae	protonephridia, metanephridia	terminal cell multic.	Smith & Ruppert (1988); Goodrich (1900, 1945)
Polynoidae	protonephridia, metanephridia	terminal cell monoc., -	Holborow (1971) Goodrich (1945), Bartolomaeus (1999)
Protodrilidae	?, protonephridia	terminal cell multic., podocytes	Nordheim & Schrader (1994)
Psammodrilidae	?, ?		
Questa	?, nephridia		Giere & Erseus (1998)
Sabellariidae	protonephridia, metanephrdia	terminal cell monoc., podocytes	Smith & Ruppert (1988); Meyer (1887), Dehorne (1952), Smith (1986)
Sabellidae	?, metanephridia	podocytes	Goodrich (1945), Orrhage (1980); Bartolomaeus (1993b), Koechlin (1966), Smith & Ruppert (1988)

Scalibregmatidae	?, metanephridia	?	Dehorne & Dehorne (1913), Goodrich (1945)
Serpulidae	protonephridia. metanephridia	terminal cell multic., podocytes	Pemerl (1965), Wessing & Polenz (1974); Goodrich (1945), Bartolomaeus (1993b)
Siboglinidae (Pogonophora)	?, protonephridia or metanephridia	terminal cell monoc., ?	Southward (1993), Gardiner & Jones (1993), Schulze 2001, Southward et al. (this volume)
Sigalionidae	?, metanephridia	?	Goodrich (1945)
Sphaerodoridae	?, protonephridia	solenocytes	Kuper & Purschke (2001)
Sphinter	?, ?		
Spionida	metanephridia, metanephridia	podocytes	Bartolomaeus (unpubl.); Goodrich (1945), Orrhage 1964), Bartolomaeus (1993b), Rice (1980)
Sternaspis	?, metanephridia	-	Vejdovsky (1882); Goodrich (1945)
Syllidae	protonephridia, protonephridia or metanephridia	solenocytes multic., solenocytes multic.	Bartolomaeus (1993a); Goodrich (1945), Smith (1992), Bührmann et al. (1996), Kuper & Westheide (1997), Kuper & Bührmann (1999), Kuper (2001),
Terebellidae	protonephridia, metanephridia	terminal cell multic., podocytes	Heimler (1981, 1983, 1988); Hessle (1917), Goodrich (1945), Smith (1992, Bartolomaeus (1993b)
Tomopteridae	?, metanephridia plus	solenocytes multic.	Smith & Ruppert (1988), Bartolomaeus (1997),
Trochochaeta	?, metanephridia	?	Orrhage (1964)
Typhloscolecidae	?, protonephridia	?	Smith & Ruppert (1988)
Uncispionidae	?, ?	-	

Table 2: Cellular and subcellular elements in ultrastructurally studied head kidneys in Polychaeta (Annelida)

Taxon	Terminal cell				Duct cell			Nephridiopore cell			Author
	Perikarya	Ciliary element	Microvillar element	Filter	perikarya	Ciliary element	Microvillar element	Perikarya	Ciliary element	Microvillar element	
Oweniidae											
Owenia fusiformis	?	One	Several	podocyte -like	several	1	several	?	?	?	Smith et al. 1987
Pectinariidae											
Pectinaria auricoma	2	Several	10 per cilium	+	2	Several	Several	1	-	Several	Bartolomaeus 1995a
Phyllodocidae											
Phyllodoce mucosa	2-3	One	15 per cilium	-	1	several	several	1	several	several	Bartolomaeus 1989
Polygordiidae											
Polygordius sp.	?	several	several	+, per 1-2 cilia	?	?	?	?	?	?	Smith & Ruppert 1988
Polynoidae											
Harmothoe imbricata	1	One	15 per cilium	+	?	several	several	?	?	?	Holborow 1971
Sabellariidae											
Sabellaria cementarium	1-2	1	several	+	1-4	?	?	?	?	?	Smith & Ruppert 1988
Serpulidae											
Serpula vermicularis	1	several	several	+	?	Several	?	?	?	?	Pemerl 1965
Pomatoceros triqueter	1	Several	Several	+	1	Several	Several	-	-	-	Wessing & Polenz 1974
Spirorbis spirorbis	1	Several	Several	+	1	Several	Several	1 several	Several	Several	Bartolomaeus (unpubl.)
Syllidae											
Autolytus prolifer	1	several	10 per cilium	-	2	Several	Several	1	Several	few	Bartolomaeus 1993a
Terebellidae											
Lanice conchilega	2	Several	Several	?	2	Several	Several	1	?	?	Heimler 1981, 1983, 1988

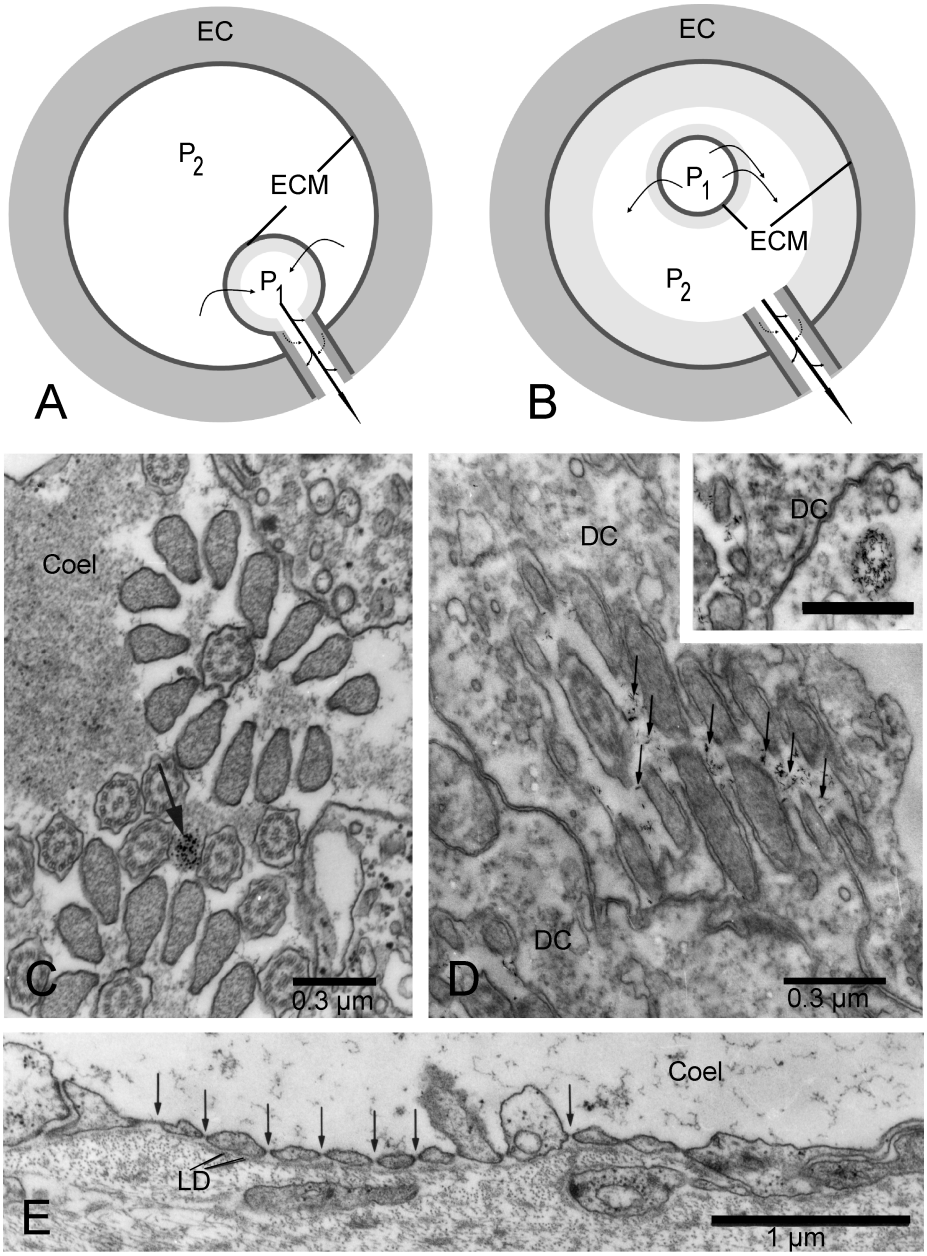

Fig. 1: Function of filtration nephridia. A. Protonephridium. $P_2 > P_1$. Pressure inside the nephridial compartment (P_1)is lower than in the surrounding interstices or body cavity(P_2). B. Metanephridial system. $P_1 > P_2$. Pressure inside the Blood vessel higher than in the coelomic cavity. C, D. *Eulalia viridis* (Phyllodocidae). C.Experimentally applied albumen-gold does not pass the filtration basrrier. D. Experimentally applied iron dextrane passes the filtration barrier and is reabsorbed in the duct (inset). E. *Fabricia sabella* (Serpulidae). Podocyte lining the dorsal vessel in S2.

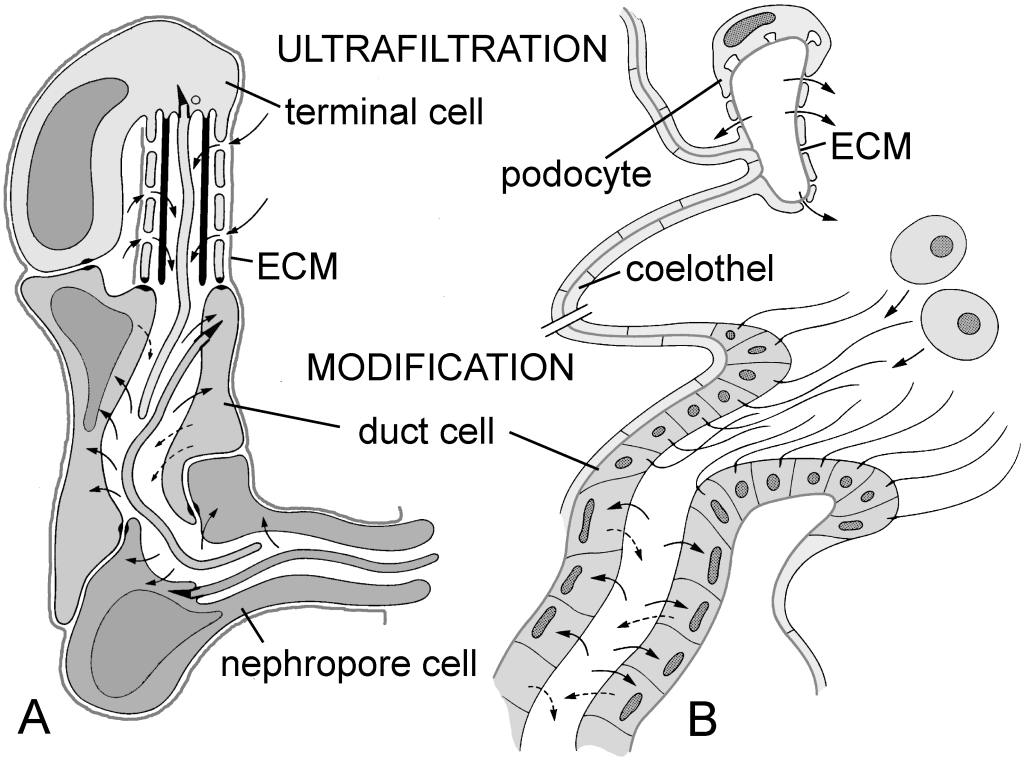

Fig. 2: A. Protonephridium and B. metanephridial system and their substructures. The sites of ultrafiltration differ in both nephridial systems. Metanephridia may additional serve in releasing genital products (indicated by two egg cells).

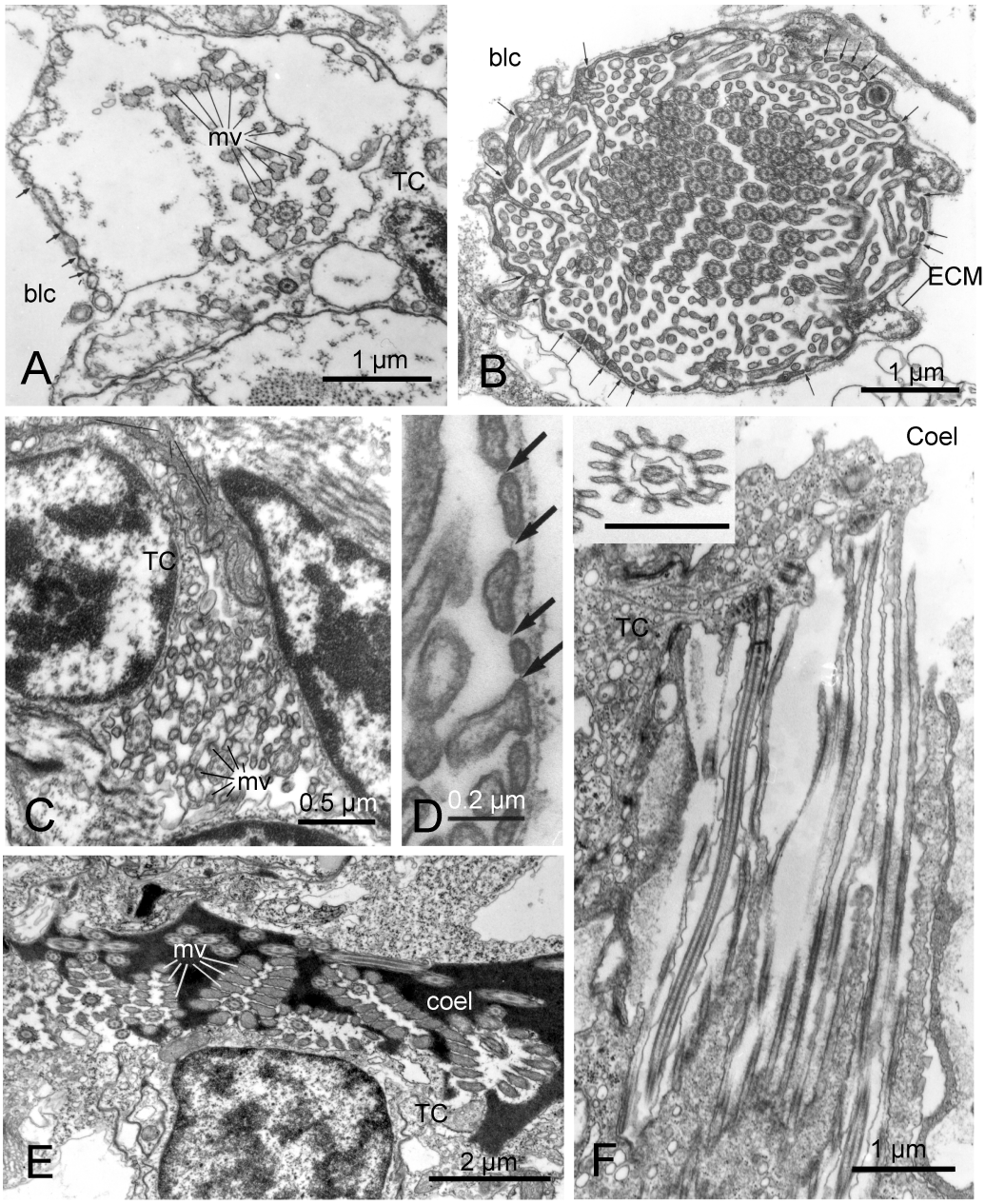

Fig. 3: Filtration structures in protonephridia. A.- D. Head kidneys, E. - F. Segmental protonephridia. A. *Magelona mirabilis*, larva. Terminal cell (TC), cross section. A filter surrounds central cilium plus its circumciliary microvilli. B. *Spirorbis spirorbis* (Serpulidae), larva. Terminal cell, cross section. Central ciliary flame is surrounded by microvilli and the filter. (Small arrows mark ECM) C. *Autolytus prolifer* (Syllidae), larva. Terminal cell, cross section. A filter is lacking. D. *Spirorbis spirorbis* (Serpulidae), larva. Filtration barrier (arrows). E. *Glycera alba* (Glyceridae). Solenocytes, cross section. F. *Tomopteris helgolandica* (Tomopteridae). Multicilated solenocyte, longitudinal section (inset: cross section). *blc* blastocoel, *coel* coelom, *ECM* extracellular matrix, *mv* microvilli.

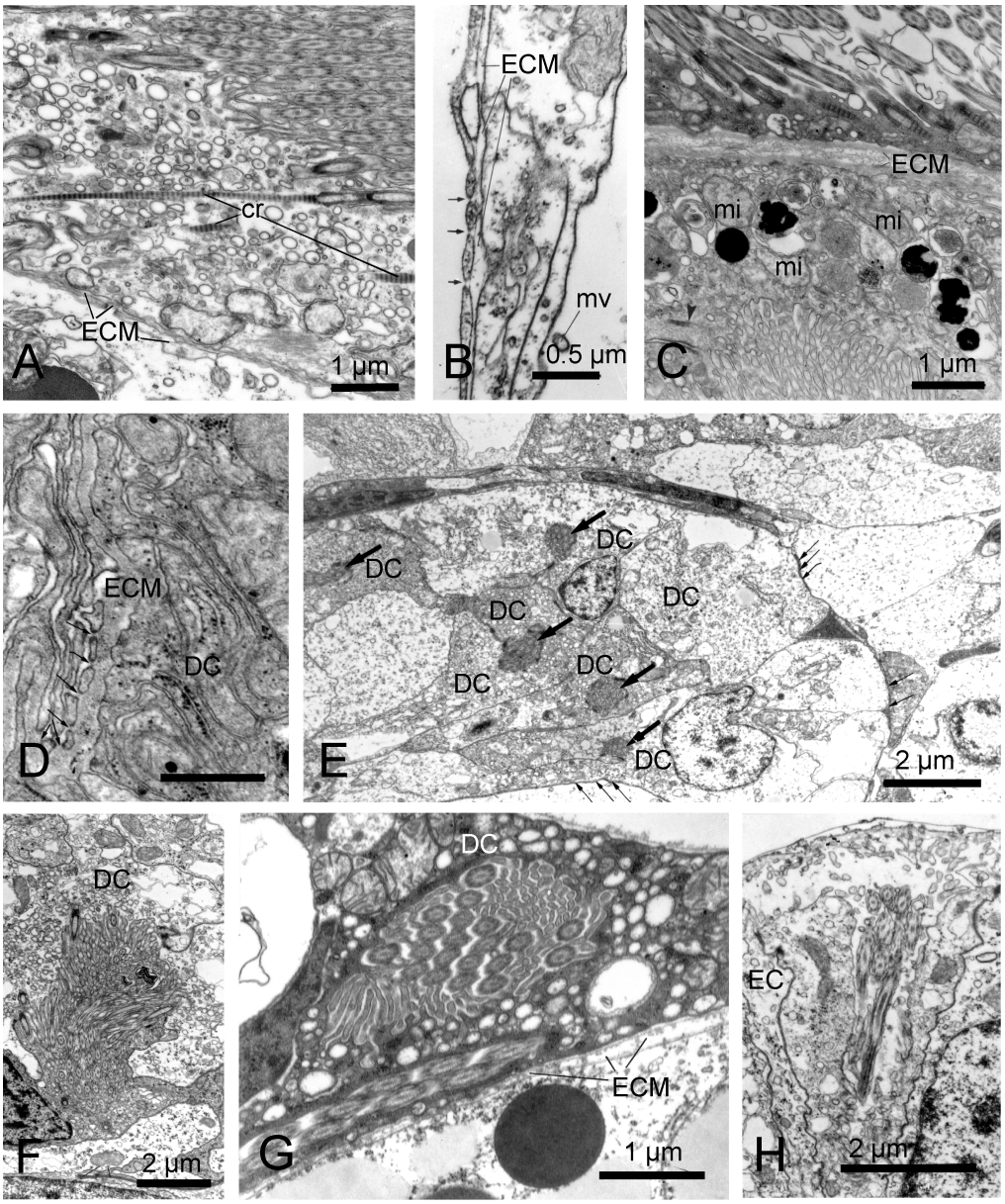

Fig. 4: Modifying structures: duct and nephridiopore. A. *Eulalia viridis* (Phyllodocidae). Ciliated duct cell. B. *Pectinaria koreni* (Pectinariidae). Duct with podocytes resting on its coelomic face (arrows mark filtration barrier). C., D. *Fabricia sabella* (Sabellidae). Aciliated duct and ciliated funnel cells. D. Podocytes resting on the coelomic face of the duct. E. *Nereis diversicolor* (Nereididae). Cross-sectioned convoluted duct (Arrows mark cilia of the duct) F., H. *Glycera alba* (Glyceridae). Duct cells apposed to darker nephridiopore cell and H. nephridiopore. G. *Spirorbis spirorbis* (Serpulidae), larva, duct cell of the duct kidney.

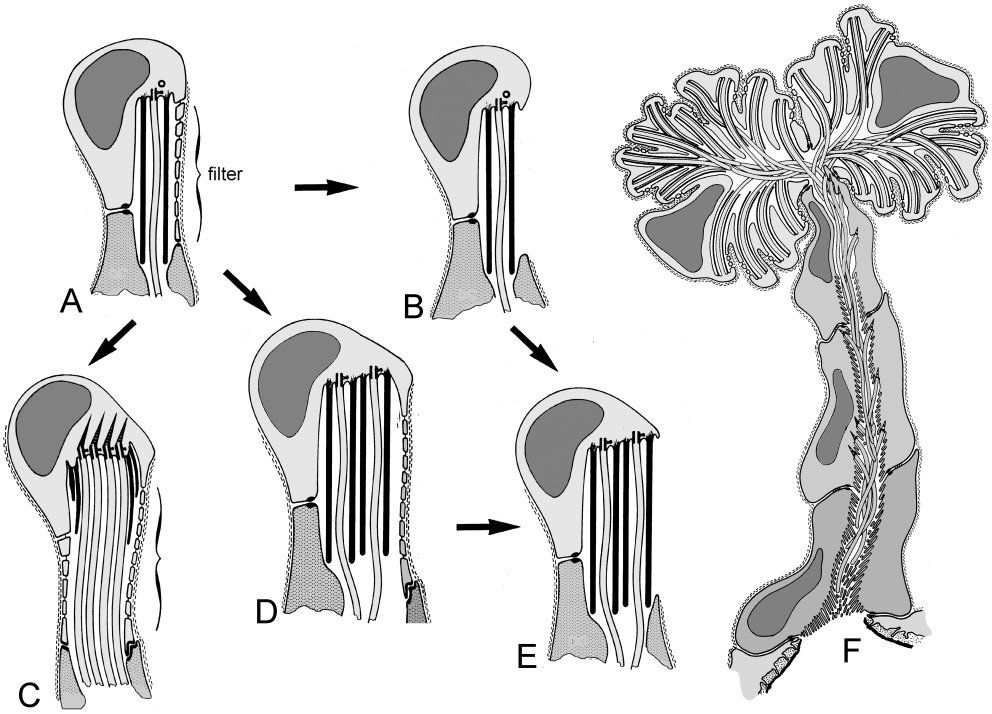

Fig. 5: Terminal cells in head kidneys and segmental nephrida and their possible evolutionary relationships, if monociliarity is assumed to represent a primary condition. A. Monociliated terminal cell as found in *Magelona mirabilis* (Bartolomaeus, 1995), *Harmothoe imbricata* (Holborow, 1971), *Sabellaria cementarium* (Ruppert & Smith, 1988). B. Solenocytes as found in *Phyllodoce mucosa* head kidneys (Bartolomaeus, 1989) and segmental nephridia of further Phyllodicida (tab. 1). C. Multicilated flame cell as known from different serpulid larva (tab 2). D. Multiciliated terminal cell with a ring of microvilli surrounding each cilium and a common filter as found in Polygordius sp. and *Pectinaria koreni* (F) head kidney (Smith & Ruppert, 1988; Bartolomaeus, 1995) and *Myzostoma cirriferum* segmental protonephridia (Pietsch & Westheide, 1987). E. Multiciliated solenocyte like in *Autolytus prolifer* head kidney (Bartolomaeus, 1993), *Hesionides arenaria* and *Tomopteris helgolandica* segmental protonephridia (Westheide 1986; Bartolomaeus, 1997).

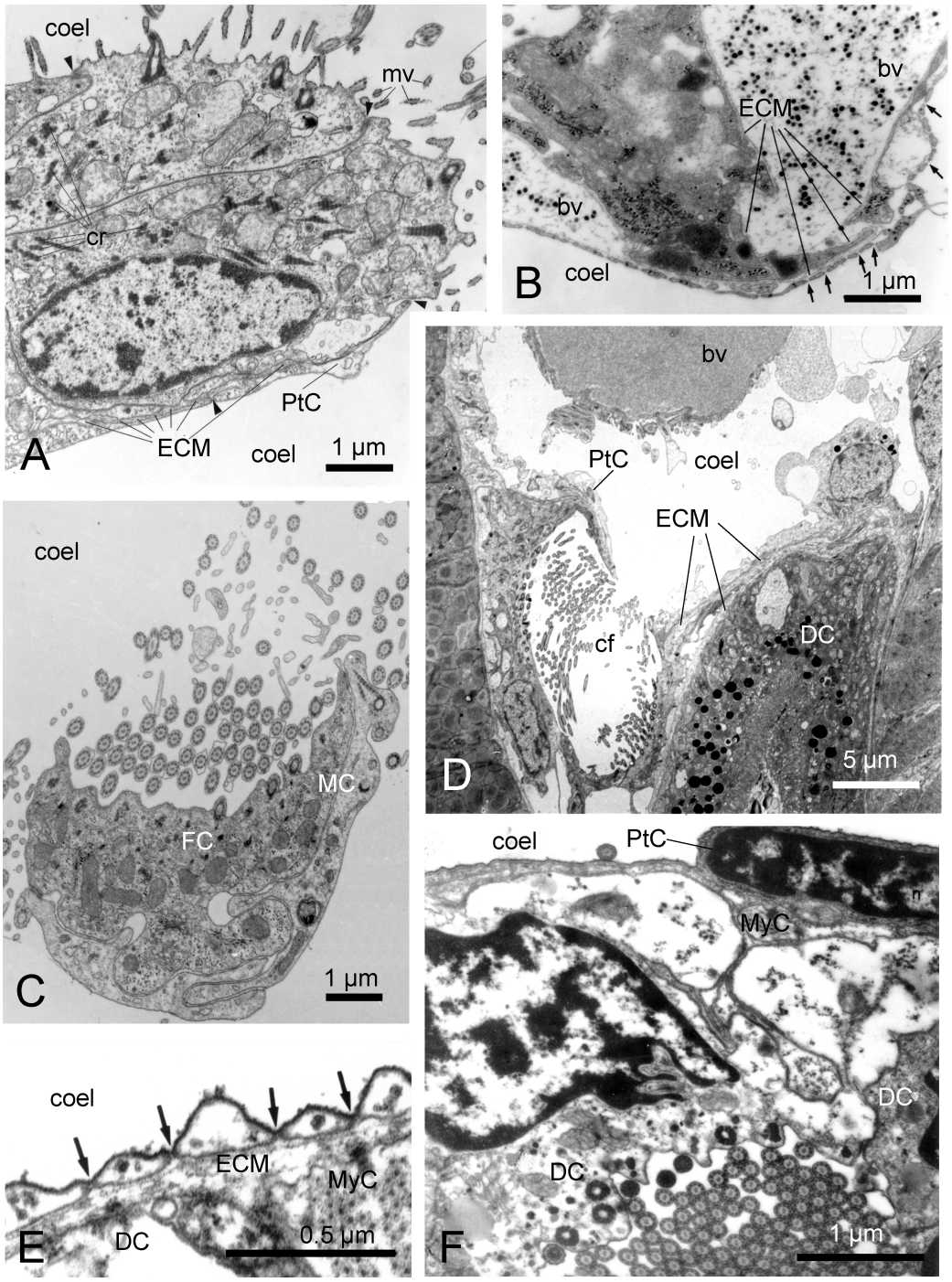

Fig. 6: Metanephridial systems. A. *Pectinaria koreni* (Pectinariidae). Upper lip of nephridial funnel (arrowheads mark adhaerens junctions. B. *Aeolosoma hemprichi* (Aeolosomatidae). Podocytes lining the perintestinal vessel (arrows mark filtration slits). C. *Pristina longiseta* (Naididae). Neprhdial funnel composed of mantel cell (*MC* and flame cell. D. *Fabrica sabella* (Sabellidae). Ciliated funnel (*cf*), adjacent duct and blood vessel (*bv*) of the ciliated funnel. E., F. *Golfingia minuta* (Sipuncula). Podocytes rest on the perinephridial ECM (Arrows mark filtration barrier). F. Ciliated descending branch. Muscle cells (*MyC*) of the nephridial duct are separated by an *ECM*. *coel*

coelom, *cr* ciliary rootlets, *DC* duct cell, *ECM* extracellular matrix, mv microvilli, *PtC* peritoneocyte

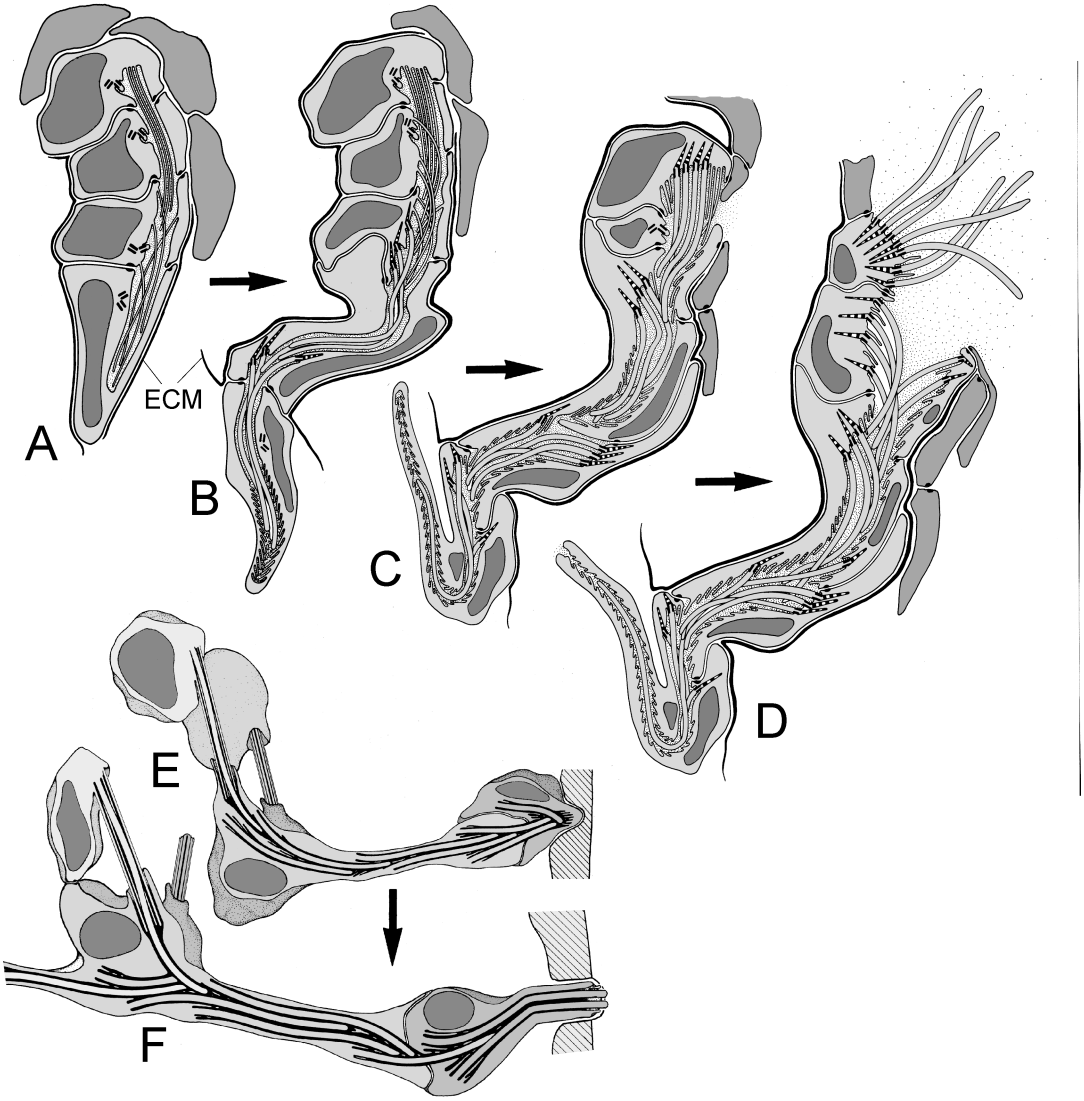

Fig. 7: Nephridial development. A.–C. Metanephridia in *Ophelia rathkei* (Opheliidae), A. Earliest recognizable anlage of the metanephridium. B. Ciliogenesis and enlargement of the Anlage, penetration of the subepidermal ECM (extracellular matrix). C. Addition of cells, Stronger ciliation in the proximal cells of the anlage, onset of fluid accumulation in the prospective coelomic cavity. D. Movement of the surrounding cells caused by fluid accumulation. Proximal duct cell cilia face the coelom and form the funnel. E.-F. Head kidneys in *Phyllodoce mucosa* (Phyllodocidae). Nephridium is formed in deeper cell layers. Nephridopore cell forms at last (E) and finally pierces the epidermis (F).

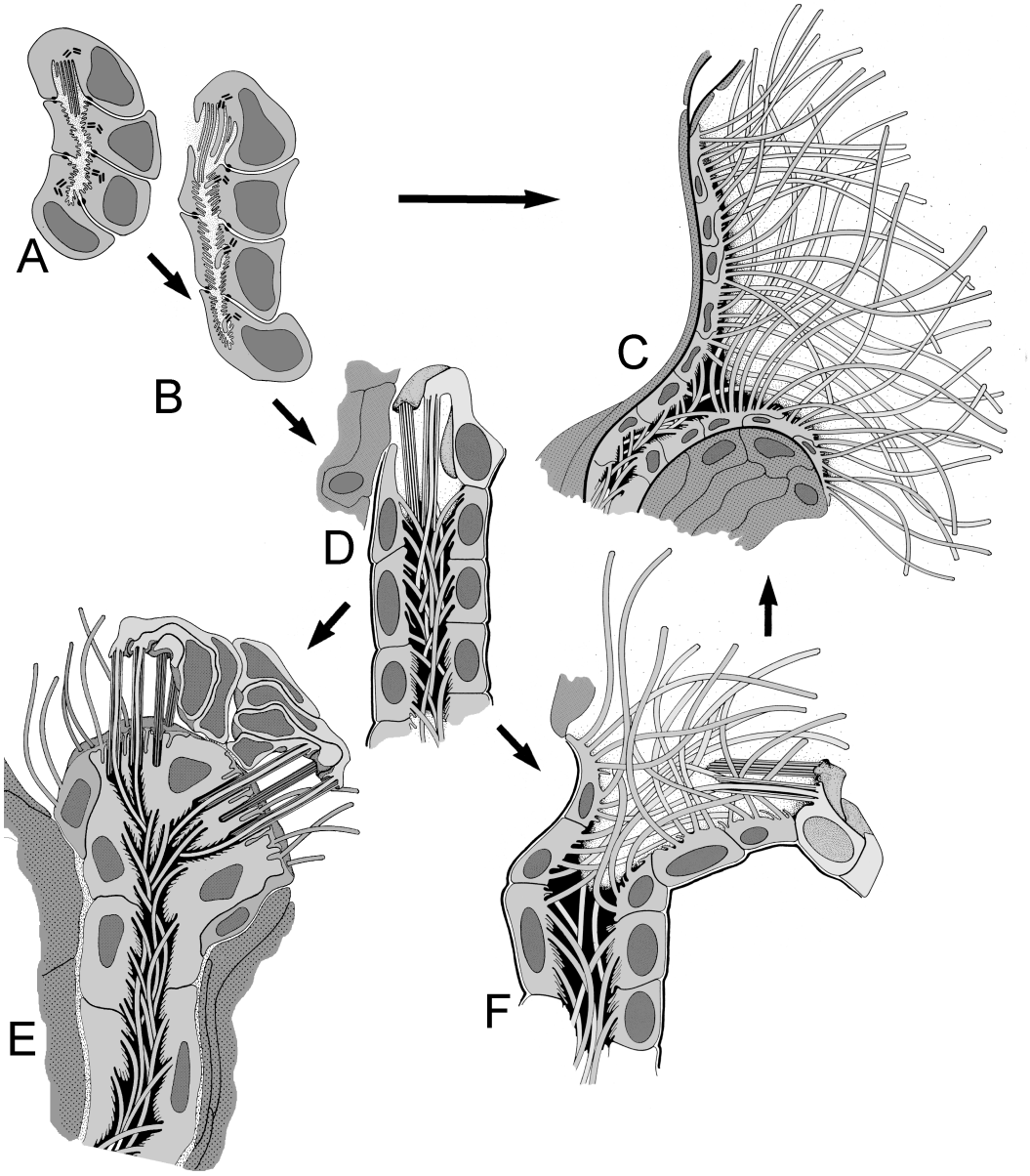

Fig. 8: General scheme of developmental pathways that lead to different nephridial organs. A. Earliest recognizable anlage. B. Ciliogenesis starts in the proximal cells of the anlage. These cilia are laterally to the perikarya and are not completely surrounded by the cells of the anlage. These cells either become the ciliated funnels of the metanephridium during coelomogenesis (C) or they differentiate into solenocytes (D). These either move aside when the proximal section of the duct is passively opened (F) or a further cell covers the proximal section of the duct so that a protonephridium with solenocytes is formed (E). If the temporarily formed solenocytes (D) move aside (F) they degenerate during formation of the funnel. Truncation and modification cause nephridial diversity in polychaetes.

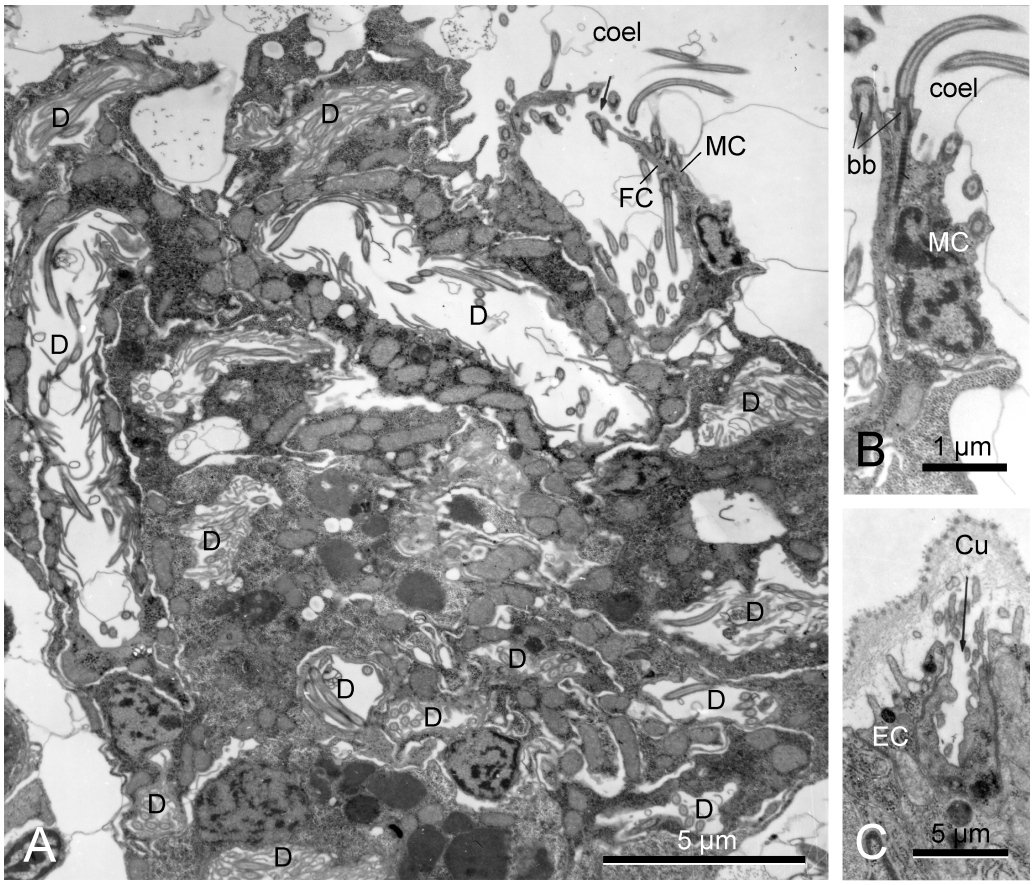

Fig. 9: *Aeolosoma hemprichi* (Aeolosomatidae). Nephridial funnel (small arrow) is composed of mantle cell (*MC*) and flame cell (*FC*). The duct (*D*) is highly convoluted; individual sections differ in the number of microvilli. B. Mantel cell with cilium emanating from its surface into the coelom (*coel*). C. Nephridopore does not pierce the cuticle (*Cu*). *Bb* basal body, *EC* epidermis cell