

Sense organs in polychaetes (Annelida)

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Abstract

Polychaetes possess a wide range of sensory structures. These form sense organs of several kinds, including the appendages of the head region (palps, antennae, tentacular cirri), the appendages of the trunk region and pygidium (parapodial and pygidial cirri), the nuchal organs, the dorsal organs, the lateral organs, the eyes, the photoreceptor-like sense organs, the statocysts, various kinds of pharyngeal papillae as well as structurally peculiar sensory organs of still unknown function and the apical organs of trochophore larvae. Moreover, isolated or clustered sensory cells not obviously associated with other cell types are distributed all over the body. Whereas nuchal organs are typical for polychaetes and are lacking only in a few species, all other kinds of sensory organs are restricted to certain groups of taxa or species. Some have only been described in single species till now. Sensory cells are generally bipolar sensory cells and their cell bodies are either located peripherally within the epidermis or within the central nervous system. These sensory cells are usually ciliated and different types can be distinguished. Structure, function and phylogenetic importance of the sensory structures observed in polychaetes so far are reviewed. For evaluation of the relationships of the higher taxa in Annelida palps, nuchal organs and pigmented ocelli appear to be of special importance.

Introduction

Polychaetes respond to a variety of sensory stimuli and consequently possess a wide range of sensory structures (Mill, 1978; Welsch et al., 1984). These form sense organs of several kinds, including (1) the appendages of the head region, namely palps, antennae, and tentacular cirri, (2) appendages of the trunk region and pygidium, the parapodial cirri and pygidial cirri, (3) the nuchal organs, (4) the dorsal organs, (5) the lateral organs, (6) the eyes, (7) the photoreceptor-like sense organs, (8) the statocysts, (9) various kinds of pharyngeal papillae and (10) the apical organs present in trochophore larvae. Moreover, isolated or clustered sensory cells not obviously associated with other cell types are distributed throughout the body.

Whereas nuchal organs and eyes are present in most polychaete species, all other kinds of sensory structures are restricted to certain higher taxa, to a

certain group of closely related species or have, so far, only been found in single species. In polychaetes sensory structures have been reviewed by Bullock (1965), Mill (1978), Verger-Bocquet (1984, 1992), Eakin & Hermans (1988) and Storch & Schlötzer-Schrehardt (1988), those of Clitellata by Jamieson (1981, 1992), Sawyer (1986) and Fernandez et al. (1992).

A major problem is still to determine the sensory stimuli which the sensory structures mediate (Mill, 1978; Schlawny et al., 1991). Usually, responses after application of various chemical, optical or tactile stimuli have been obtained by electrophysiological recordings from nerves rather than individual receptor cells. Thus, function has mostly been deduced from structural correspondences to sensory cells for which the function has already been determined (e.g., Mill, 1978; Jouin et al., 1985). A promising approach to address these problems might be immunological labelling of specific receptor neurons (Michel et al., 1999).

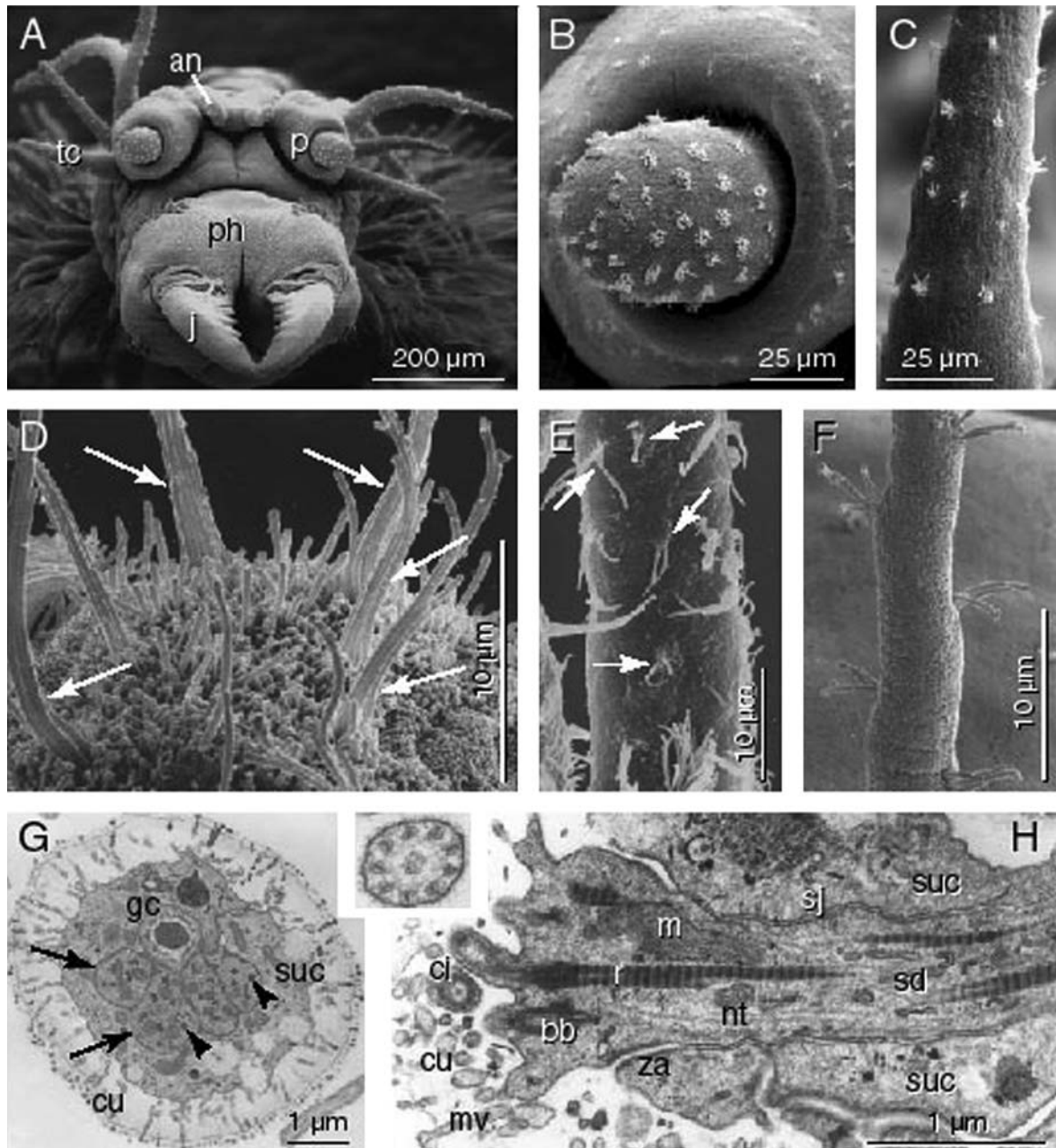


Figure 1. Multiciliate penetrative sensory cells. (A–C) *Nereis* sp. (A) Frontal view of anterior end with antennae (an), palps (p) and tentacular cirri (tc); j jaws, ph pharynx, (B) Tip of biarticulated palp with numerous sensory cilia. (C) Enlargement of first ventral tentacular cirrus. (D) *Protodrilus ciliatus*; tip of prostomium with various groups of different sensory cilia, some of which form cirri (arrows). (E) *Protodriloides symbioticus*; ventral view of palp with various kinds of sensory cells (arrows). (F) *Microphthalmus listensis*; tentacular cirrus with similar groups of sensory cilia. (G, H) *Polydora commensalis*; sensory papilla on palp. (G) Cross section through papilla with four sensory dendrites (arrows) and a gland cell neck (gc) surrounded by a single supporting cell (suc). In the dendrites 3–7 rootlets (arrowheads) are visible. (H) Longitudinal section of sensory dendrite (sd) with basal body (bb) of cilia (ci), rootlets (r), neurotubules (nt), m, mitochondrion; mv, microvilli; sj, septate junction; za, zonula adhaerens. Inset: cross section of cilium with $9 \times 2 + 2$ axoneme lacking dynein arms. D, E modified from Purschke (1993), G, H Purschke & Dauer (unpubl.). Micrographs A–C: S. Raabe.

To date the function of many sensory structures found in polychaetes is still uncertain or completely unknown.

Sensory cells

Sensory cells or receptor cells are generally bipolar primary sensory cells, the cell bodies of which are either located peripherally within the epidermis or lie within the central nervous system (Storch & Schlötzer-Schrehardt, 1988; Verger-Bocquet, 1992). As a result, there are differences in the degree of development of their dendritic processes. The peripheral dendritic processes are normally embedded in the respective epithelium, reach the epithelial surface and thus are connected to the adjoining cells by typical junctional complexes, i.e. a zonulae adhaerens followed by a septate junction (Fig. 1H). Generally the dendritic processes are ciliated and may bear a number of additional microvilli. With the exception of photoreceptor cells, the only known instance of sensory cells with microvilli alone is that reported by Dorsett & Hyde (1969) for the prostomial appendages of *Nereis diversicolor*.

A given type of sensory cell may occur in isolation, clustered, or in sense organs. Clustered sensory cells form small buds or papillae, generally composed of a few receptor cells; however, up to 16 cells have been found in sensory papillae in the caudal body region of *Arenicola marina* and up to 200 cells on the palps of *Lycastis terrestris* (see Storch, 1972; Jouin et al., 1985). Many species possess comparatively high numbers of sensory cells (Storch & Schlötzer-Schrehardt, 1988 for ref.). Since they respond to various sensory stimuli, the sensory cells differ structurally within individuals and between species. Even in the smallest polychaete known, the dwarf male of *Dinophilus gyrociliatus*, with a body length of 50 μm , no less than 40 out of a total of 68 neurons are sensory; these can be assigned morphologically to four different types (Windoffer & Westheide, 1988). This diversity is almost in the same range as has been observed in larger species (e.g., Schlawny et al., 1991; Jamieson, 1992; Purschke 1993, 1999). In spite of fine structural variations, sensory cells may be classified by the number of cilia and whether these cilia penetrate the cuticle or not, or

whether they are intraepithelial (e.g., Welsch et al., 1984; Jamieson, 1992): (1) multiciliate penetrative sensory cells, (2) uniciliate penetrative sensory cells, (3) multiciliate non-penetrative sensory cells, (4) uniciliate non-penetrative sensory cells, (5) basal ciliated sensory cells. Only the first two types are externally visible (Figs 1A–F, 2A). However, care must be taken, as there are other functions of external ciliation besides detection of sensory stimuli and not every cilium, tuft of cilia or ciliary band visible in the light or scanning electron microscope is necessarily sensory or even part of a sense organ (Figs 4D, G–I, 6A, B).

Multiciliate penetrative sensory cells

Multiciliate sensory cells of this type are the most abundant of all annelid sensory cells (Fig. 1A–H). These cells differ greatly in terms of number and length of cilia; these may appear to be linked to each other to form cirri (Fig. 1D), although this could not be confirmed with transmission electron microscopy (e.g., Purschke, 1993). Sometimes different types are situated close together as, for example, on the prostomium or the palps in species of Protodrilida (Fig. 1D, E). In other species such receptor cells appear more uniform (Fig. 1B, C, F). These sensory cells are also extremely variable in other respects: length and number of additional microvilli, presence or absence of ciliary rootlets, structure of these rootlets, additional cytoskeletal elements and other fine-structural features (Fig. 1G, H). The number of cilia per cell ranges from 2 to more than 20 (Bantz & Michel, 1972; Michel, 1972; Storch & Schlötzer-Schrehardt, 1988; Schlawny et al., 1991; Verger-Bocquet, 1992; Purschke, 1993, 1999; Purschke & Jouin-Toulmond, 1994; Böggemann et al., 2000; Hessling & Purschke, 2000; Purschke & Hessling, 2002). Although mostly equipped with an axoneme showing the typical $9 \times 2 + 2$ pattern of microtubules (Fig. 1H inset), often associated with dynein arms, in many cases cilia of these cells appear to be more or less immobile (Jouin et al., 1985; Amieva et al., 1987; Purschke, 1993). It is generally assumed that these structurally different sensory cells have different functions (Toulmond et al., 1984; Jouin et al., 1985; Schlawny et al., 1991).

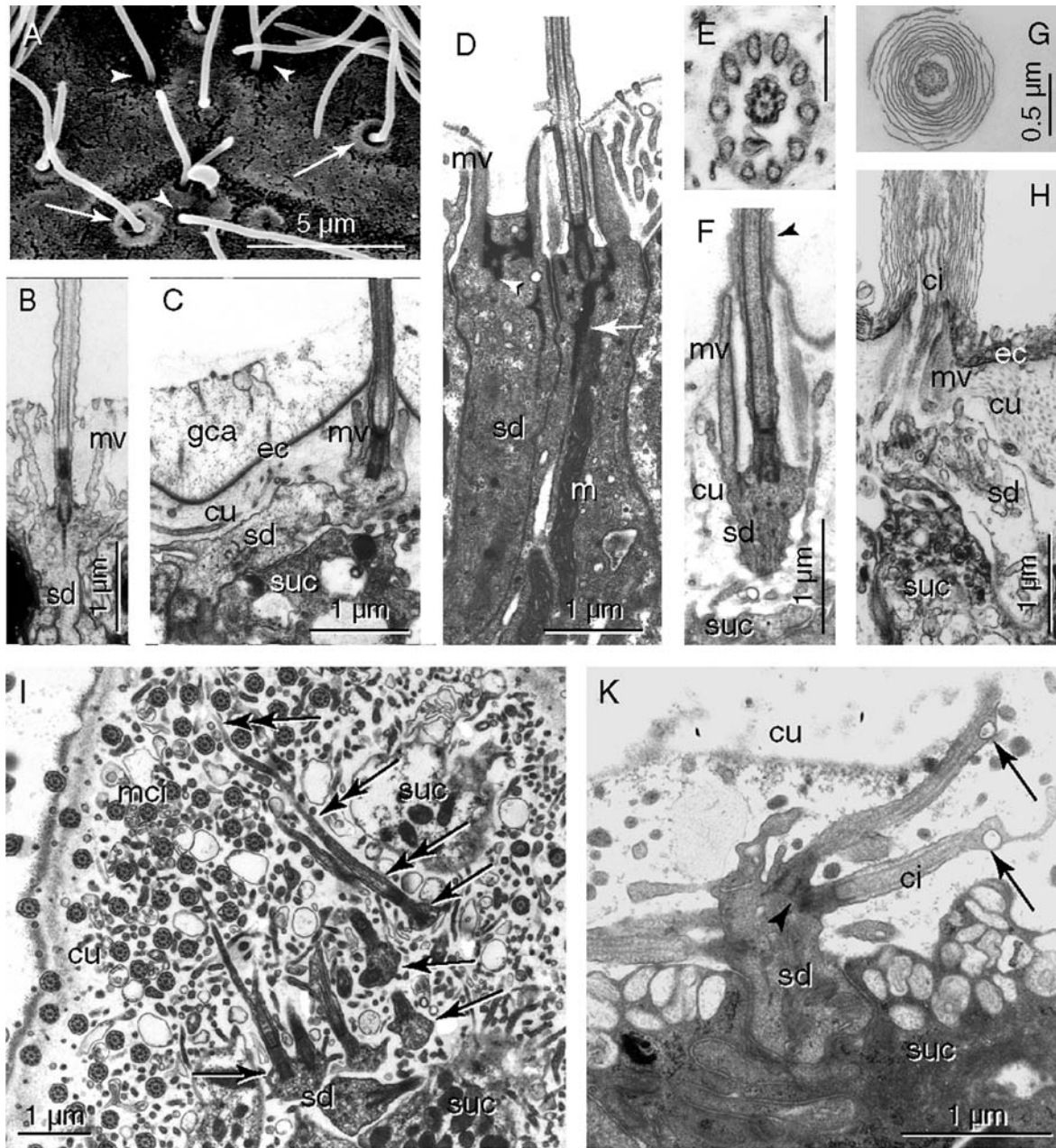


Figure 2. Sensory cells (A–H). Uniciliate penetrative sensory cells. (A) *Paranerilla limicola*; uniciliate sensory cells on the prostomium, some with collar (arrows), others without (arrowheads). SEM micrograph. (B) *Microphthalmus similis*; sensory cilium surrounded by typical microvilli (mv). (C–H) Collar receptors. (C) *Kefersteinia cirrata*; sensory dendrite (sd) projecting above surface of supporting cells (suc). Collar of microvilli not penetrating epicuticle (ec). (D) *Parenterodrilus taenioides*; collar receptors forming pore in the cuticle. Note well-developed cytoskeletal system connecting rootlet and microvilli (arrow, arrowhead). (E–F) *Polygordius appendiculatus*; cilium surrounded by 10 long microvilli, cilium basally ensheathed by epicuticle (arrowhead). Scale bar in E represents 0.5 μm . (G–H) *Glycera tridactyla*; cilium of collar receptor ensheathed by membrane-like epicuticular layers. (I–K) Non-penetrative sensory cells. (I) *Parenterodrilus taenioides*; uni- and biciliate cells (arrows) with long cilia running parallel to epithelial surface (double arrows). (K) *Stygocapitella subterranea*; sensory dendrite giving rise to numerous short cilia (ci), each with a small vacuole (arrows) and a thin process. Note absence of rootlets (arrowhead). – ci, cilium; cu, cuticle; ep, epicuticle; gca, glycocalix; m, mitochondrion; mv, microvillus; sd, sensory dendrite; suc, supporting cell. A modified from Worsaae & Kristensen (2003), D, E modified after Purschke & Jouin-Toulmond (1994), K modified from Purschke (1999).

Uniciliate penetrative sensory cells

Uniciliate sensory cells have only rarely been reported in polychaetes but most likely they are present in most if not every species. Although reviews only mention their occurrence in Nereidiidae (Dorsett & Hyde, 1969; Boilly-Marer, 1972a), they have since been found in Aeolosomatidae, Arabellidae, Dinophilidae, Dorvilleidae, Eunicidae, Glyceridae, Hesionidae, Lumbrinereidae, Lysaretidae, Nerillidae, Onuphidae, Opheliidae, Pisionidae, Polygordiidae, Protodrilidae, Sphaerodoridae, Spionidae, (Windoffer & Westheide, 1988; Schlawny et al., 1991; Purschke 1993; Hayashi & Yamane, 1994; Purschke & Jouin-Toulmond, 1994; Hessling & Purschke, 2000 and unpubl. obs.). In most cases the thin sensory dendrites (diameter about 1 μm) extend above the level of the surrounding epithelial cells (Fig 2C, F, H). Although usually equipped with a

typical $9 \times 2 + 2$ axoneme (Fig 2E, G), the cilia mostly appear more or less immobile and stiff. They rest on basal bodies, and a rootlet system may be absent (Figs 2C, F, H, 6H), ill-defined (Fig. 2B) or extremely well-developed (Figs 2D, 6I). In the last case the cytoskeleton of the surrounding microvilli is often associated with the rootlet (Figs 2D, 6I). Two types of such sensory cells may be distinguished, discernable even by scanning electron microscopy (Fig. 2A): In the first type the cilia may be surrounded by typical microvilli, not reaching the cuticular surface (Fig. 2B), or microvilli are lacking (Fig. 6G, H). In the second type the cilia are surrounded by a circle of mostly 10 microvilli (Figs 2C–H, 6G, I). These microvilli are parallel to the cilium, comparatively thick and may create a pore in the cuticle open (Figs 2D, 6I). In these cases a small cuticular bulge surrounding the cilium is visible in SEM (Fig. 2A). The sensory cilia may be ensheathed

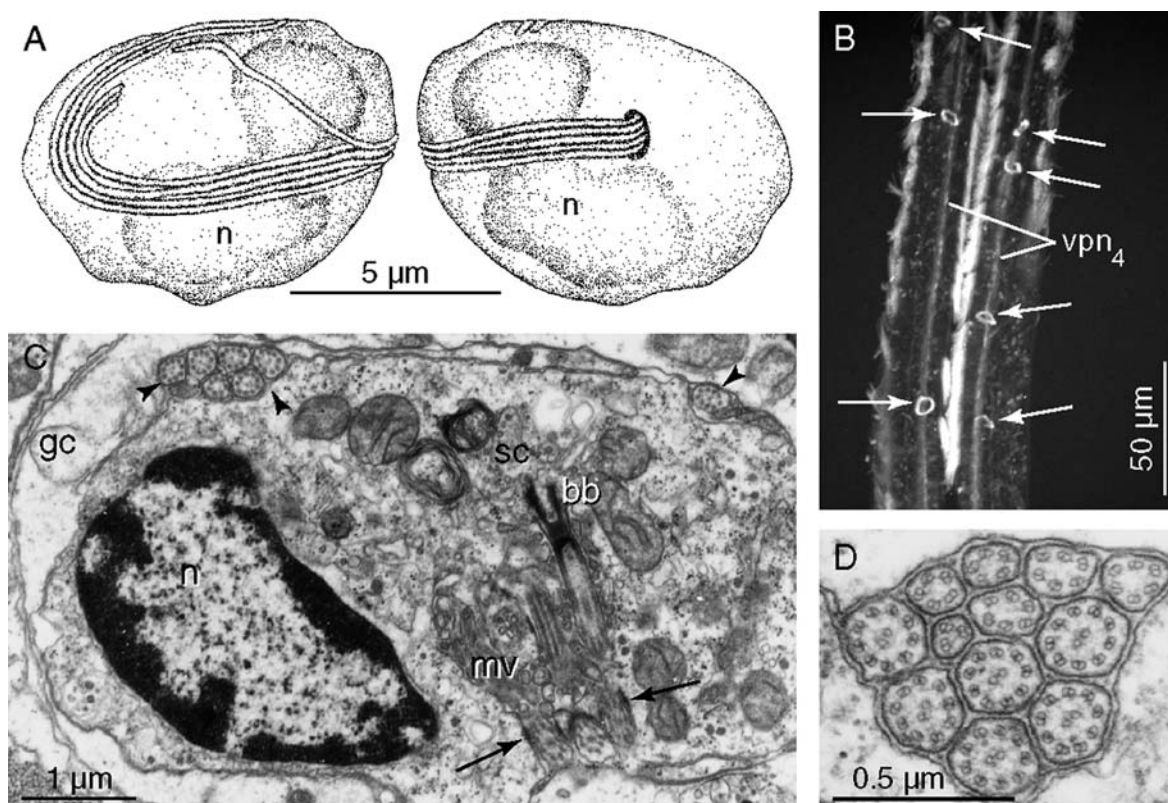


Figure 3. Basal ciliated cell. *Protodriloides chaetifer*. (A) Reconstruction showing both sides of the cell and bundle of cilia surrounding cell body. (B) Palps with asymmetrically arranged basal ciliated cells (arrows), anti-tubulin staining of ciliary loop, confocal laser-scanning microscopic image. (C) Cell body with cilia emerging in depression, the latter with microvilli; note electron-dense material at opening of depression (arrows); arrowheads point to cross sections of cilia. (D) Cross-section of sensory cilia close to apices, note absence of dynein arms. – bb, basal body; gc, glial cell; sc, sensory cell; mv, microvilli; n, nucleus. A–B from Purschke & Müller (1996).

in part or completely by the epicuticle (e.g., Polyordiidae (Fig. 2F), Nereidiidae (see Storch, 1972; Storch & Schlötzer-Schrehardt, 1988), Pisionidae). In Glyceridae they are wrapped in membrane-like epicuticular layers (Fig. 2G, H). This second type of receptor is generally called collar receptor (Schlawny et al., 1991; Purschke, 1993). It is widespread in invertebrates and thus most likely represents a plesiomorphy for Annelida (e.g., Ax, 1995). The function of these uniciliate cells is generally regarded to be mechanoreceptive.

Non-penetrative sensory cells

Non-penetrative sensory cells may either be uniciliate or multiciliate (Fig. 2I, K). They have been reported for many species (Windoffer & Westheide, 1988; Verger-Bocquet, 1992; Purschke & Jouin-Toulmond, 1994). As a rule the dendritic processes project above the level of the adjacent epidermal cells and form more or less distinct bulbs. In uni- or biciliate cells the cilia are comparatively long and run parallel to the body surface in the basal layer of the cuticle (Fig. 2I). Basal bodies are mostly without rootlets and the axonemes show various patterns of reduction. As a rule at least the two central tubules are lacking. In these cells the axonemal microtubules may successively be lost, finally resulting in microvillus-like structures without microtubules (Fig. 2I). Such microvillus-like microtubule-less cilia can still be recognized as such because a basal body is still present. In multiciliate receptors the cilia are often shorter and project in various directions (Fig. 2K). In *Stygocapitella subterranea*, for instance, the axonemal microtubules are 1–1.5 μm long and of equal length. Where the microtubules end, a small vesicle is present and the cilia give rise to a thin process devoid of microtubules (Fig. 2K). The function of these cells is controversial; the possibilities under discussion range from chemoreception to mechanoreception (see Windoffer & Westheide, 1988).

Basal ciliated cells

Basal ciliated sensory cells were first described for oligochaetes (Myhrberg, 1979) and to date only one polychaete taxon, Protodriloidae, is known to possess such cells (Purschke & Müller, 1996).

These cells are not associated with supporting cells; they are embedded between epidermal cells and do not reach the epithelial surface. A bundle of 3–15 cilia emerges from a small depression of the cell body. From this depression the cilia extend to the surface and twist once around the cell (Fig. 3A–D). This bundle of cilia can be detected with confocal LSM after labelling with anti- α -tubulin (Figs. 3B, 10B). These cells have been found in the anterior part of the brain and in the palps. The cilia have a typical $9 \times 2 + 2$ axoneme but without dynein arms (Fig. 3D). Nothing is known about the function of these sensory cells.

Sense organs

The sensory cells described above are present on the trunk and on the appendages, such as palps, antennae, tentacular cirri and the pygidial cirri. They likewise occur in the pharyngeal epithelium and pharyngeal papillae (see e.g., Bantz & Michel, 1972; Michel, 1972; Böggemann et al., 2000; Tzetlin & Purschke, 2005). The same applies to the most important sense organ of the polychaete larvae, the apical organ, which usually comprises a few multiciliate penetrative sensory cells and various supporting cells (Heimler, 1983, 1988; Lacalli, 1981; Marsden, 1982; Storch & Schlötzer-Schrehardt, 1988; Verger-Bocquet, 1992). The epithelia and cuticle of the appendages are similar to those of the trunk and will, therefore, not be described here. In the palps of the taxa united as Canalipalpata by Rouse & Fauchald (1997) coelomic cavities are present (Orrhage, 1964). A fine-structural study has been done in Protodrilida (Purschke, 1993; Purschke & Jouin-Toulmond, 1994): In *Protodrilus* spp. and *Saccocirrus* spp. the palps are supplied with coelomic canals filled with coelenchyme cells. These canals are not connected to other coelomic cavities. Fluid is added through podocytes present at a junctional zone with blood vessels in the prostomium. These palps are also equipped with blood vessels and their musculature is well developed. In species of Phyllodocida, such as in Hesionidae, the antennae and palps are usually thin and thread-like. Coelomic cavities, musculature and blood vessels are absent. However, motility is achieved by epithe-

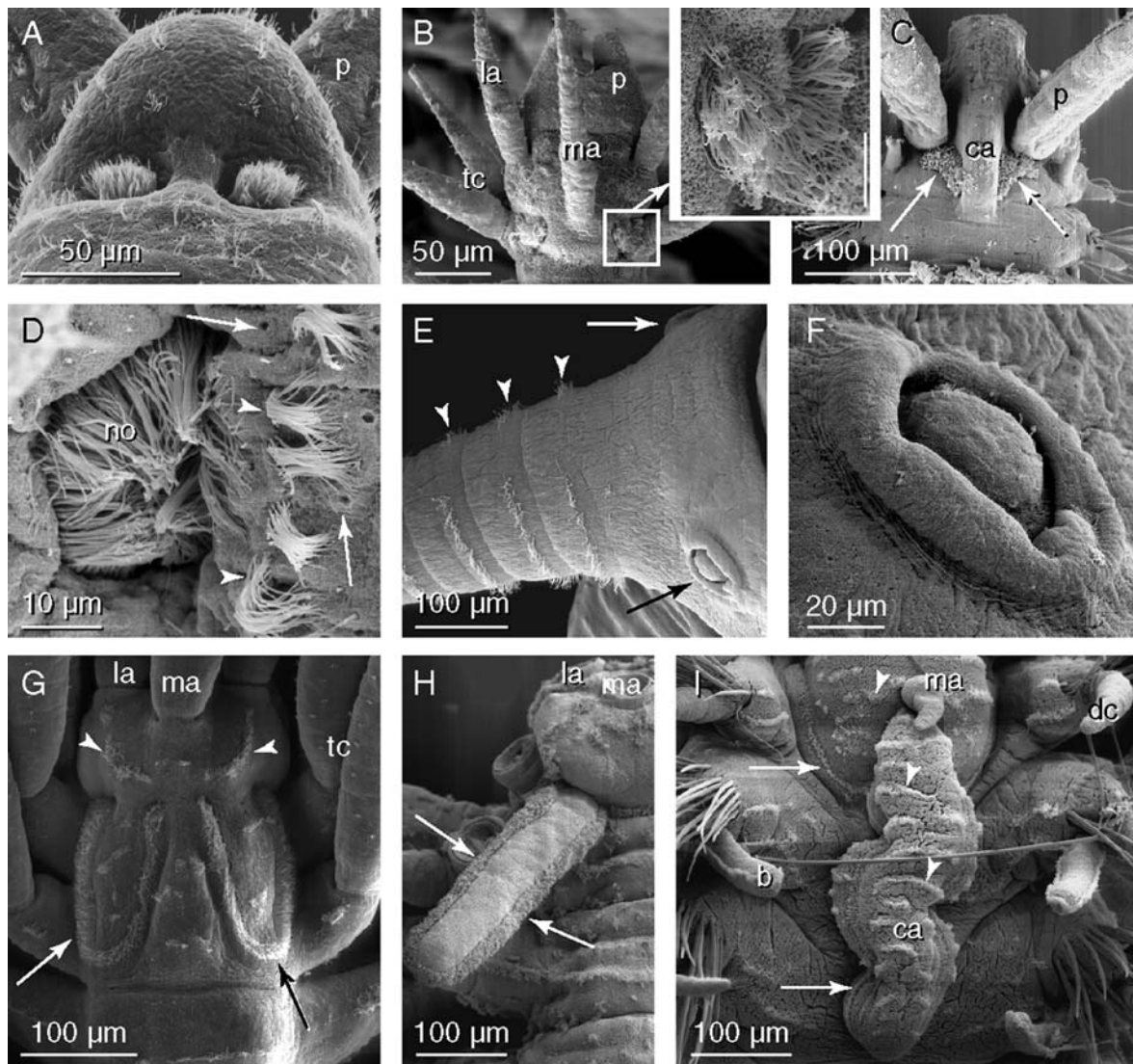


Figure 4. Nuchal organs SEM micrographs. (A–H) Typical appearance of nuchal organs as ciliated grooves or pits. (A) *Saccocirrus papilloceus*. (B) *Brania subterranea*; inset: enlargement of right nuchal organ. (C) *Polydora cornuta*; nuchal organs (arrows) situated on both sides of the caruncle (ca) behind the palps (p). (D) *Protodorvillea kefersteini*; nuchal organ (no) anterior to peristomial cilia (arrowheads); arrows point to gland cell openings. (E–F) *Glycera tridactyla* (E) Base of prostomium with nuchal organs (arrows) and rings of sensory cilia (arrowheads). (F) Detail of withdrawn nuchal organ. (G–I) Examples of hypertrophied nuchal organs. (G) *Autolytus pictus*; nuchal epaulettes (arrows) fused with peristomium; bands of cilia on prostomium (arrowheads). (H) *Amblyosyllis formosa*; appendage-like nuchal epaulettes (arrows) with ciliary band on the edges. (I) *Eurythoe complanata*; caruncle (ca) and prostomium with longitudinal ciliary bands representing nuchal organs (arrows) and transverse rows of cilia (arrowheads). – b, branchia; ca, caruncle; dc, dorsal cirrus; la, lateral antenna; ma, median antenna; no, nuchal organ; p, palp; tc, tentacular cirrus; – A modified from Purschke (1997), B, F modified from Purschke (2002a), micrographs C–E, G–I: S. Raabe.

liomuscular cells and stiffness by rootlet-like skeletal elements (Boilly-Marer, 1972b; unpubl. obs.). The innervation of the appendages is described in Orrhage & Müller (2005).

Nuchal organs

Nuchal organs are generally regarded as chemo-sensory (Storch & Schlötzer-Schrehardt, 1988;

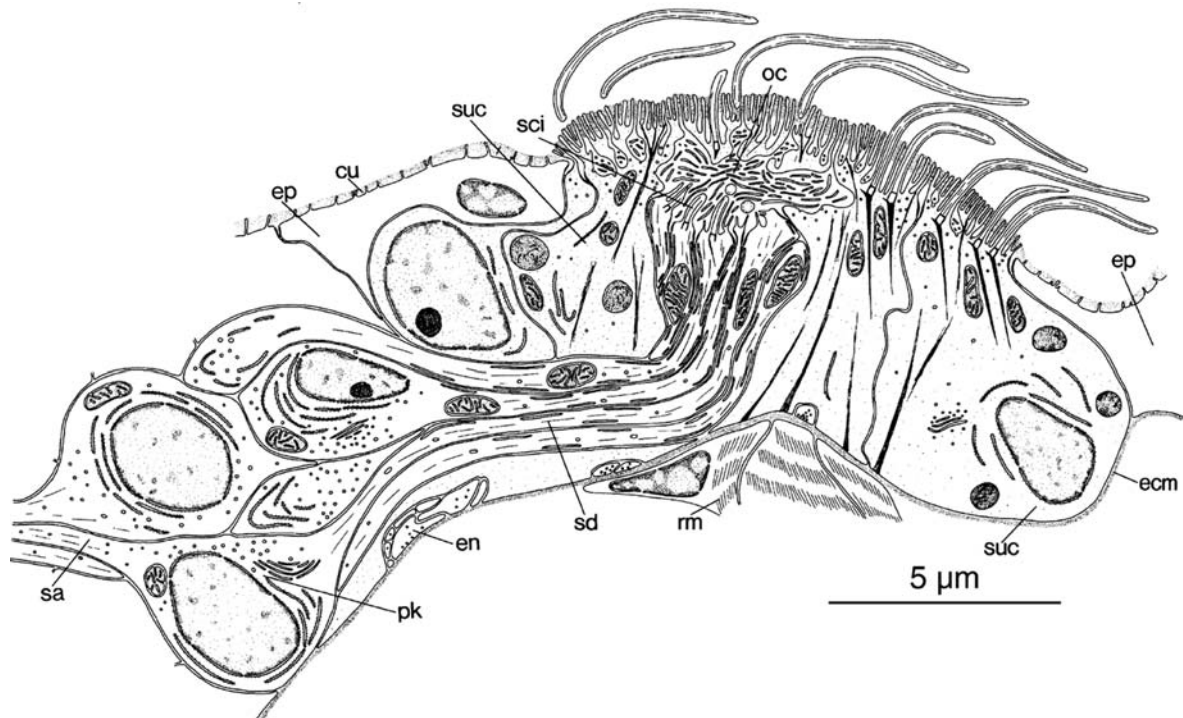


Figure 5. *Nerillidium troglochaetoides*. Reconstruction of nuchal organ exemplifying general organisation of nuchal organs: Ciliated supporting cells (suc) with modified cuticle and microvilli covering olfactory chamber (oc), monociliary sensory dendrites (sd), the perikarya (pk) of which form the nuchal ganglion that gives rise to axons (sa) running towards the brain; basiepithelial efferent nerve (en) innervating retractor muscle fibres (rm) and supporting cells. – cu, cuticle; ep, epidermal cell; ecm, extracellular matrix; sci, sensory cell cilium. From Purschke (1997).

Verger-Bocquet, 1992; Purschke, 1997). They have become the most important sensory structure of Annelida in terms of their phylogenetic value. The reason is that they are basically present in every species of polychaetes but absent in Clitellata without exception. There are sharply differing opinions as to whether this absence in Clitellata is primary or secondary, i.e., a loss (Fauchald & Rouse, 1997; Purschke, 1997, 1999, 2002; Rouse & Fauchald, 1997; Purschke et al., 2000; Rouse & Pleijel, 2001). In contrast to Clitellata, in the few cases of polychaetes lacking nuchal organs, such as Psammodrilidae, Pisionidae, Siboglinidae, and *Parergodrilus heideri* (see Purschke, 1997, 2000), this absence is always interpreted as a loss. Nuchal organs have been found in many polychaete species for which absence of the organs was assumed or at least considered likely (see Purschke, 1997). The light microscopical histology of these organs is well-known since Rullier's (1951, 1954) investi-

gations; their ultrastructure has recently been reviewed (Purschke, 1997).

Nuchal organs are mostly visible as a pair of ciliated areas or spots located dorsally or dorso-laterally at the posterior edge of the prostomium (Fig. 4A–D). The cilia here are kinocilia and may be located in grooves or pits (Fig. 4A–D). These organs may be considerably larger and extend posteriorly on one or several segments (Fig. 4G–I). One of the best known examples are Amphinomidae, in many species of which a caruncle is formed as a bulging sensory area arising from the prostomium and supplied with longitudinal and transverse ciliary bands (Fig. 4I). Most likely, only the longitudinal ciliary bands represent the nuchal organ proper (unpubl. obs.). This might be the reason for different interpretations of the function of this structure (e.g., Storch & Welsch, 1969; Ameyaw-Akumfi, 1976; Storch & Schlötzer-Schrehardt, 1988). A caruncle may also be present

in Spionidae, Trochochaetidae, Poecilochaetidae and Chrysopetalidae. In Spionidae the caruncle is straight with a smooth surface and the nuchal organs lie beside the caruncle, as either one pair (e.g., *Polydora cornuta*: Fig. 4C) or two pairs of ciliary bands (e.g., *Malacoceros fuliginosa*: Fig. 6A) (see Schlötzer-Schrehardt, 1986, 1987; Purschke, 1997; Jelsing, 2002a,b). These ciliary bands show considerable variation and may extend over several segments (Jelsing, 2002a,b).

Other examples of hypertrophied nuchal organs are the so-called nuchal epaulettes present in certain Syllidae (Fig. 4G, H) or Phyllodocidae (see Eibye-Jacobsen, 1991; Pleijel, 1991; Rouse & Pleijel, 2001). Whereas in *Autolytus* spp. (Syllidae), the epaulettes are completely fused with the trunk (Fig. 4G), they are appendage-like in *Amblyosyllis formosa*. A continuous ciliary band is present on the edges of all nuchal epaulettes, whereas the center is unciliated (Fig. 4G, H). These structures have not been investigated by transmission electron microscopy so far. The biological significance of these large organs is not clear since other species, often closely related to these taxa, possess nuchal organs which are not hypertrophied (Lewbart & Riser, 1996; Rhode, 1990a; Purschke, 1997).

An enlargement of these sensory organs may also be achieved by duplication: two pairs of nuchal organs are present in most (all?) Dorvilleidae and many Opheliidae (Rhode, 1989; Purschke, 1997). The size of nuchal organs may vary considerably even between closely related species.

On the other hand, especially in burrowing forms or those with a highly modified anterior end, the nuchal organs can be completely withdrawn (Fig. 4E, F) or are situated more or less internally and are invisible from the exterior; e.g., Sabellidae, *Stygocapitella subterranea*, *Hrabeiella periglandulata*, *Potamodrilus fluviatilis* (see Orrhage, 1980; Purschke, 1986, 1997, 2000; Purschke & Hessling, 2002). In Sabellidae the nuchal organs have a rather uncommon position and form a pair of pouches arising from the dorsal epithelium of the mouth cavity. This aberrant position is very likely due to the development of the branchial crown (Orrhage, 1980; Purschke, 1997). In the other species cited above, the nuchal organs are situated in deep pits and communicate with the exterior *via* small pores hardly visible even in scanning electron microscopy.

Regardless of their different external structure these organs show an overall fine-structural similarity (Fig. 5), and there is no doubt about their homology in Annelida (Rouse & Fauchald, 1997; Purschke, 1997, 2002; Rouse & Pleijel, 2001). The organs have a number of characters in common, as follows. The visible cilia are mobile and are located on the supportive cells. They are responsible for a rapid exchange of sensory stimuli by generating water currents. The sensory cells are bipolar primary sensory cells, the perikarya of which form the nuchal ganglia and their processes the nuchal nerve (Fig. 5). The nuchal nerve emanates directly from the brain as is the case for the efferent innervation, which is always separate. Usually these nerves are part of the dorsal pair of longitudinal nerves (Orrhage & Müller, 2005).

As a rule the dendrites are monociliate. Cilia, ciliary branches and true microvilli fill a subcuticular space called the olfactory chamber, which is protected by specialized cuticular or microvillar layers formed by the supporting cells. Differences between taxa include the number of ciliated supporting and sensory cells as well as the specific structure of the protective layer. These differences may be autapomorphies for certain taxa, such as the paving-stone-like microvillar cover present in Spionida and Protodrilida (Schlötzer-Schrehardt, 1986; Purschke, 1997; Jelsing, 2002b). The number of sensory cells varies from two in *Potamodrilus fluviatilis* to several hundred in *Polyophtalmus pictus* and *Armandia polyophtalma* (see Purschke, 1997; Purschke & Hessling, 2002). For many large species studied so far, e.g., *Nereis diversicolor*, *Glycera rouxi*, *Nephtys caeca* (see Whittle & Zahid, 1974), the number of sensory cells has not been determined.

Whether the absence of nuchal organs in Clitellata is primary or secondary is crucial for the systematization of Annelida (McHugh, 1997, 2000; Purschke, 1997, 2002a; Rouse & Fauchald, 1997; Westheide, 1997; Westheide et al., 1999; Purschke et al., 2000). Evidence for a primary absence would support a sister-group relationship of Polychaeta and Clitellata, the nuchal organs being the sole autapomorphy of Polychaeta, whereas evidence of a loss would support the placement of Clitellata as an ingroup of the paraphyletic 'Polychaeta'. Evidence for a loss of nuchal organs in Clitellata comes from the reduc-

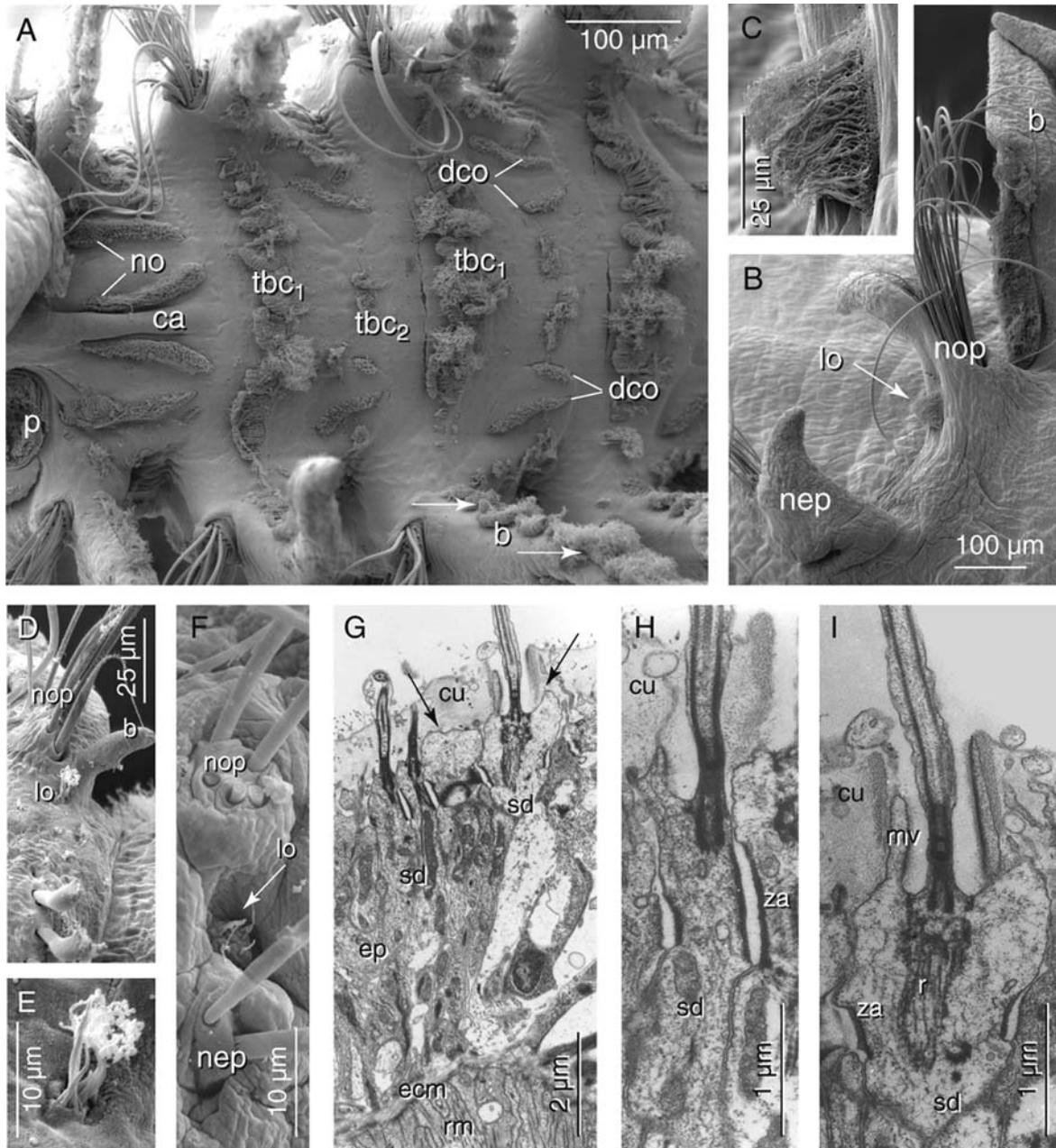


Figure 6. Dorsal and lateral ciliated organs. (A) *Malacoceros fuliginosus*; dorsal view of anterior end with nuchal organs (no) and dorsal ciliated organs (dco). Two transverse bands of cilia per segment (tbc_1 , tbc_2), arrows point to ciliary band on branchia (b). (B–I) Lateral ciliated organs. (B, C) *Scoloplos armiger*; lateral organ (lo) at base of notopodium (nop). (D–E) *Polydora cornuta*; lateral organ below notopodium. (F–I) Opheliidae. (F) *Ophelia rathkei*; small lateral organ between noto- and neuropodium. (G–I) *Polyophthalmus pictus*. (G) Section through entire organ with retractor muscle (rm) and two types of monociliary sensory dendrites (sd); arrows point to collar receptors. (H) Tip of dendrite with asymmetrically situated cilium adjacent to collar receptor. (I) Collar receptor with net-like rootlet system (r). – b, branchia; ca, caruncle; cu, cuticle; do, dorsal organ; ecm, extracellular matrix; ep, epidermis; lo, lateral ciliated organ; mv, microvillus; nep, neuropodium; no, nuchal organ; nop, notopodium; p, palp; rm, retractor muscle; sd, sensory dendrite; za, zonula adhaerens. Micrographs A–F: S. Raabe, S. Göbel, B. Rohling and W. Mangerich.

tion or absence of these organs in terrestrial polychaetes, the lack of epidermal cilia in Clitellata, the backward displacement of the brain and the reduction of the prostomium (Hessling & Westheide, 1999; Purschke, 1999, 2000; Hessling et al., 1999; Purschke et al., 2000). In certain polychaetes a similar arrangement can be observed. For instance, in species of *Pisione* the anterior end is extremely modified, with a reduction of the prostomium and displacement of the brain. The large brain is situated in the first three segments, nuchal organs are obviously absent and have been lost (Siewing, 1953; Purschke, 1997; Rouse & Fauchald, 1997).

Developing nuchal organs are visible in metatrochophores (Rullier, 1951; Åkesson, 1962, 1967; Bhup & Marsden, 1982). They develop from episphere cells while the trochoblasts of the prototroch become disintegrated and are prostomial in origin (Åkesson, 1962, 1967). Ultrastructural studies on the development have not been carried out to date. There are no significant structural differences between nuchal organs of juveniles and adults in Opheliidae and Spionidae (West, 1978; Schlötzer-Schrehardt, 1986, 1987, 1991). Changes observed mainly concern the overall size and number of cells and sometimes a shift in position.

Apart from the Annelida, structures named nuchal organs are present in Sipuncula. They are situated on the introvert either between or below the tentacles (Rice, 1993). So far, ultrastructural studies have only been carried out for one species, *Onchnesoma squamatum* (see Purschke et al., 1997). This study did not favour a homology hypothesis, but additional studies in Sipuncula appear to be necessary before a final conclusion can be drawn. These findings are in contrast to the view of Åkesson (1958) derived from comprehensive light microscopic investigations. Thus, according to our present knowledge, the nuchal organ of Annelida either represents an autapomorphy of Annelida, or in case of a sister-group relationship between Polychaeta and Clitellata, an autapomorphy of the former (see Purschke, 2002a).

Dorsal organs

Dorsal ciliated organs may be of different kinds and not all of them are sensory. For instance, these

structures may serve in spermatophore formation and transfer or simply generate water currents. This seemed to be true for Spionidae as well: Schlötzer-Schrehardt (1987, 1991) showed that in *Pygospio elegans* these organs are neither sensory nor have a common origin with nuchal organs but probably play a role in sperm transfer. Thus, these investigations were used to disprove earlier views (Söderström, 1927; Rullier, 1951; Orrhage, 1964). Recently, Jelsing (2002a, b) reinvestigated these organs in a comprehensive study, including several species of Spionidae. It was shown that there are various kinds of dorsal ciliation, including transverse and longitudinal bands (Fig. 6A). The longitudinal bands proved to be structurally identical to nuchal organs, so that these structures are chemosensory as well and serially homologous to nuchal organs. These structures are in fact absent in *P. elegans*. These investigations clearly demonstrate that generalisations have to be done with care and far-reaching conclusions drawn from a single species may lead to false and premature statements. However, whether the dorsal organs are innervated by the elongated nuchal nerve, as suggested by Söderström (1927) and others, remains to be proven. The dorsal organs described for Orbiniidae may also represent homonomous nuchal organs (Eisig, 1914), but this has yet to be confirmed by ultrastructural studies.

Lateral organs

Lateral ciliated organs are ciliated pits or papillae present between noto- and neuropodia in Amphinomidae, Syllidae, Eunicida, Spionidae, Opheliidae, Orbiniidae, Paraonidae, Scalibregmatidae and Pectinariidae (Fig. 6B–I; see Rouse & Pleijel, 2001; Purschke, unpubl. obs.). In the Opheliidae *Ophelia rathkei* and *Polyophthalmus pictus* these organs consist of a group of uniciliate penetrative sensory cells (Fig. 6G–I). Some of these cells are collar receptors, others are without a collar of strong microvilli. In the latter the cilium is situated eccentrically on the dendrite and is closer to the collar receptor (Fig. 6G, H). In the collar receptor a rootlet system is well-developed and connected to small hemidesmosome-like structures present between cilium and surrounding microvilli. This structure is the same as described for the dorsal cirrus organ present at the lower side of the not-

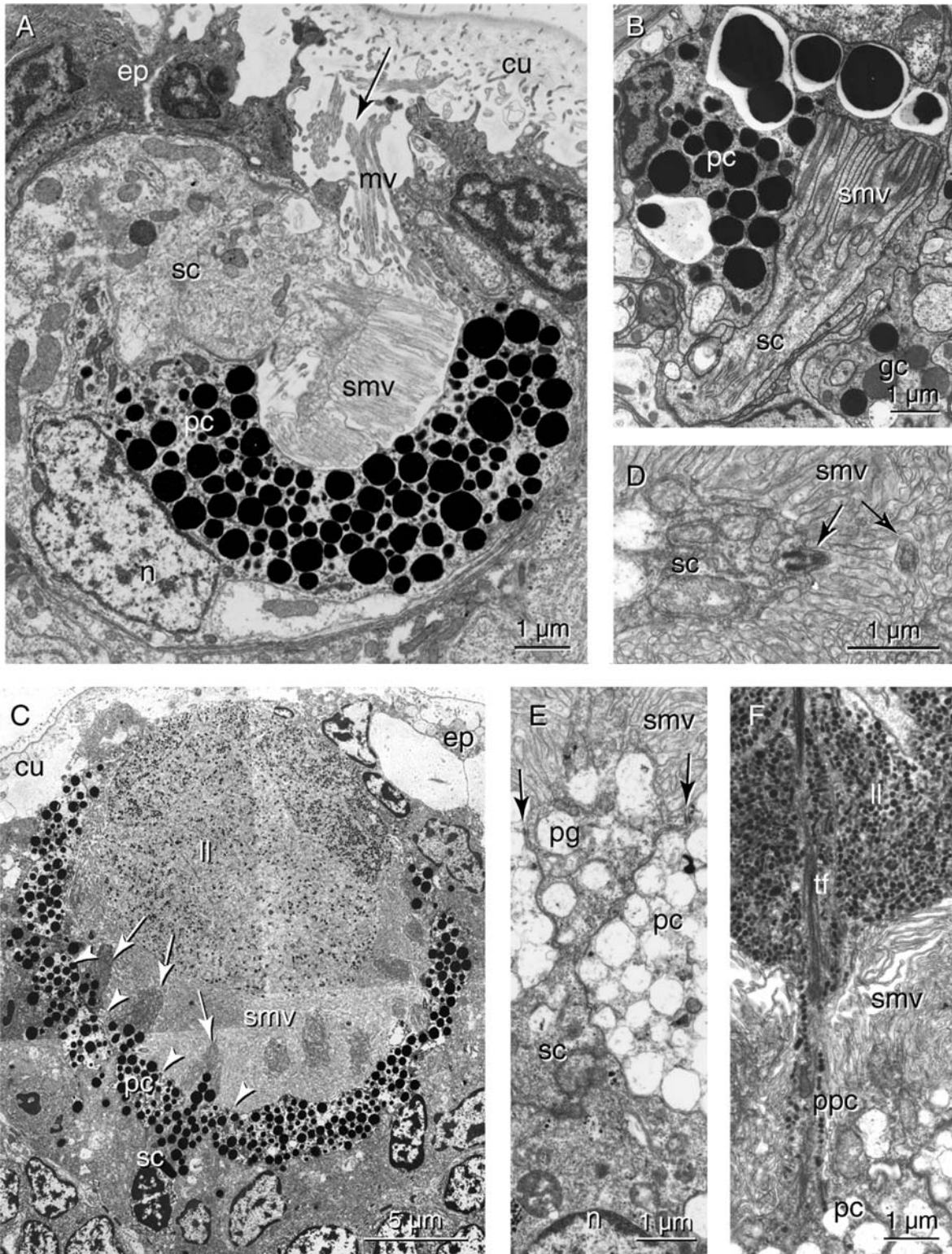


Figure 7. Cerebral eyes. (A) *Saccocirrus papilloceus*. Bicellular ocellus; pigment cell (pc) and rhabdomic photoreceptor cell (sc), part of epidermal cell layer; eye cup open to exterior (arrow). (B) *Microphthalmus similis*. Ocellus situated deeper in prostomial tissue. (C–F) Multicellular ocelli. (C) *Gyptis propinqua*. Eye cup consisting of alternating pigment (arrowheads) and sensory cells (arrows). (D–F) *Kefersteinia cirrata*. (D) Microvilli-bearing process of sensory cell (sc) with vestigial cilium (arrows). (E) Sensory cell (sc) with pigment granules (pg) between pigmented supporting cell, arrows point to junctional complexes. (F) Process of pigment cell (ppc) extending above sensory microvilli (smv) and forming lens-like structure (ll). – cu, cuticle; ep, epidermis; gc, glial cell; ll, lens-like structure; mv, microvillus; n, nucleus; pc, pigment cell; pg, pigment granules; ppc, process of pigment cell; sc, sensory cell; smv, sensory cell microvillus; tf, tonofilaments. A modified from Purschke (1992).

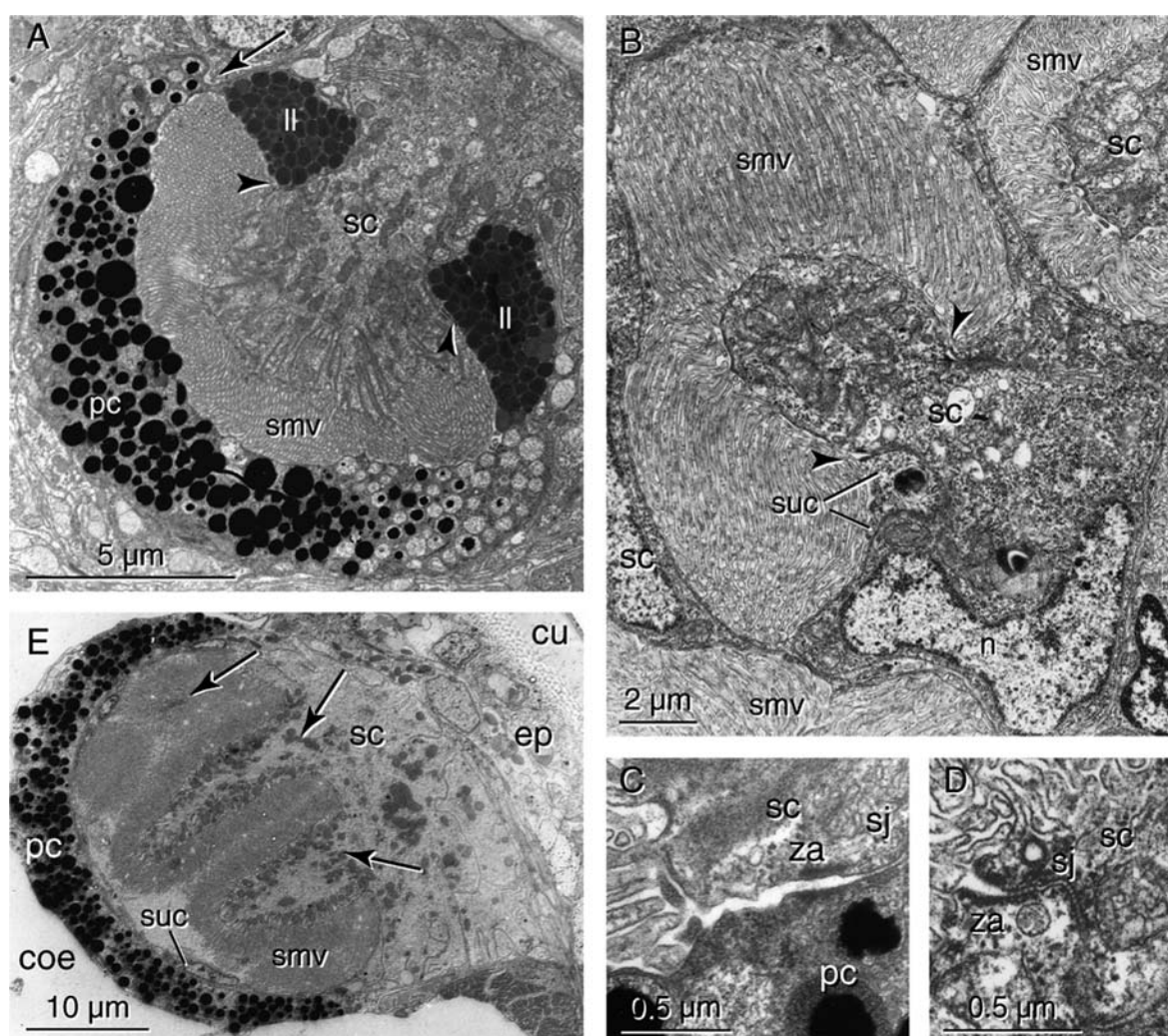


Figure 8. Eyes. (A–D) *Polyophthalmus pictus*. (A) Cerebral pigmented ocellus; note lens-like process (ll) connected to cell body of pigment cell (arrow); arrowheads point to junctional complexes enlarged in C. (B) Cerebral unpigmented rhabdomic ocellus embedded in area made up of numerous such ocelli; arrowheads point to cell junctions shown in D. (C–D) Enlargement of junctional complexes of ocelli shown in A, B: (C) Pigmented ocellus. (D) Unpigmented ocellus. (E) *Armandia polyophthalma*: Segmental ocellus made up of large sensory cell (sc) with several rhabdomic processes (arrows), unpigmented supporting cells (suc) and layer of mesodermal pigment cells (pc). – cu, cuticle; coe, coelom; ep, epidermis; n, nucleus; pc, pigment cell; sc, sensory cell; sj, septate junction; smv, sensory microvilli; suc, supporting cell; za, zonula adhaerens. A, B, D modified from Purschke (2003). E modified from Purschke et al. (1995).

opodia, or for the dorsal cirri, in various species of Eunicida (Hayashi & Yamane, 1994, 1997). This indicates that these organs are most likely homologous and do not represent a new type of sense organ. As argued by Rouse & Pleijel (2001), these organs should be given the same name and their phylogenetic value as an autapomorphy of Eunicida appears to be questionable. Whether this also applies to the lateral organs of Orbiniidae has still to be proven; from their appearance in SEM they seem to be different, in that they are made up of a brush of densely arranged cilia as is characteristic of multiciliate cells (Fig. 6B, C). This likewise applies to the bands of cilia present between dorsal cirrus and neuropodium in Amphinomidae as well as in *Syllides longocirrata* and other Syllidae (unpubl. obs.). An ultrastructural comprehensive investigation of these lateral organs across various taxa is needed to address the question of homology.

In contrast to these organs, the corresponding structures of Protodrilidae are clearly related to the reproductive system in being the organs of spermatophore formation (Nordheim, 1991). The lateral organs of *Myzostoma* have been regarded as chemoreceptive and structurally similar to nuchal organs by Eeckhaut & Jangoux (1993). However, similarities to nuchal organs have been considered superficial, and homonymy with nuchal organs has been excluded by Purschke (1997). Instead, the number of sensory cells appears to be rather low, so that other functions are conceivable as well.

Eyes

Pigmented ocelli

Most polychaetes have some type of eyes or ocelli, a diminutive eye. Zoologists have always been fascinated by the structure and function of eyes and photoreceptors, and there is an abundant literature on those of Annelida. Recent reviews have been published by Verger-Bocquet (1984, 1992) and Eakin & Hermans (1988). Theories on the evolution of eyes have been put forward by, e.g., Eakin (1963, 1982), Vanfleteren & Coomans (1976), Salvini-Plawen & Mayr (1977), Salvini-Plawen (1982), Vanfleteren (1982) and more recently using genetic and developmental data by Gehring & Ikeno (1999), Gehring (2001) and Arendt & Wittbrodt (2001).

Most eyes of polychaetes are within or adjacent to the brain and are commonly termed cerebral eyes. Others are situated on the tentacular crown in certain Sabellidae and Serpulidae, on the trunk segments, for instance in Opheliidae, Eunicidae and Sabellidae, and, finally, on the pygidium in certain Sabellidae. These eyes are called branchial ocelli, segmental ocelli or pygidial ocelli, respectively. These latter eyes are structurally much more diverse and completely different in structure compared with cerebral eyes. In addition, there is a high diversity of unpigmented ocelli and photoreceptor-like structures, often associated with or adjacent to the brain.

In size and complexity such organs range from a small ocellus composed of only two cells, one pigmented supportive and one sensory cell, which overall is only 6 μm or less in diameter, as in *Microphthalmus similis* (Fig. 7B), to large eyes of about 1 mm in diameter, made up of thousands of cells forming complex retinæ, lenses and other accessory structures in Alciopidae and other planktonic polychaetes (Eakin & Hermans, 1988; Verger-Bocquet, 1992). In Alciopidae the large eyes protude laterally from the anterior end and leave a small space between them for the brain (Hermans & Eakin, 1974).

The term photoreceptor is used here to designate the photoreceptive structure of the sensory cell (Eakin & Hermans, 1988). A great expanse of the membranes bearing the light-absorbing photopigment, often in a highly ordered and regular pattern, is characteristic of photoreceptors. These membranes take the form of an array of microvilli or lamellae in rhabdomeric receptors, whereas in ciliary receptors they are outfoldings or infoldings of a ciliary membrane or, rarely, groups of cilia. A phaosome is a seemingly intracellular vacuole into which the microvillar or ciliary photoreceptors project. The phaosome arises by invagination of the apical cell membrane, the only area capable of developing microvilli or cilia (Purschke, 2002b). All three types of photoreceptors have been found in polychaetes. In addition, supportive cells are associated in some way with the photoreceptor cells. The former contain granules of shading pigment, presumably different kinds of melanins (Eakin & Hermans, 1988). These cells are also involved in the formation of lens-like structures and vitreous bodies.

In bicellular ocelli the pigment cell and the sensory cell form an extracellular cavity into which the photoreceptor projects (Figs. 7A, B, 8A). The cells are connected to one another by typical junctional complexes: a zonula adhaerens followed by a septate junction (Fig. 8C). As the photoreceptors are housed in the concavity of the pigment cell, ocelli of this type must become inverse. In many of these small bicellular ocelli, the microvilli extend as a dense brush border from the flat surface of the receptor cell (e.g., *Protodrilus* spp., *Saccocirrus* spp., *Microphthalmus listensis*, *Microphthalmus similis*, see Eakin et al., 1977; Pietsch & Westheide, 1985; Purschke, 1992; Fig. 7A, B). An increase in the number of receptive structures is achieved by evagination of the apical cell membrane, so that the sensory cell forms a mushroom-like process bearing densely arranged microvilli (e.g., Spionidae, Opheliidae, Polygordiidae; see Hermans & Cloney, 1966; Brandenburger & Eakin, 1981; Rhode, 1991; Bartolomaeus, 1993; Purschke, 2003; Fig. 8A).

In larger cerebral eyes, the number of cells may increase considerably, but the general structure remains similar. That is, the two cell types form a continuous epithelium around an extracellular cavity into which the sensory processes project (Fig. 7C–E; Purschke, 2003). In this epithelium pigmented supportive cells and sensory cells alternate. The cell bodies of the sensory cells are situated below the pigment layer (Fig. 7C). Usually the orientation of the sensory processes becomes everse. That is, inverse or everse design apparently reflects functional constraints and is clearly correlated with the number of cells involved in cerebral eyes of polychaetes (Purschke, 2002b). Exceptions to this rule have been described in Flabelligeridae, where the two cell types are not intermingled but separated from one another as in certain Platyhelminthes (Spies, 1975). In these eyes the photoreceptors have an inverse design. These functional constraints in orientation of photoreceptors have not been recognized in previous reviews (Eakin & Hermans, 1988; Verger-Bocquet, 1992; Arendt & Wittbrodt, 2001).

As a rule the single sensory process is cone-shaped or columnar and bears microvilli on all sides (Eakin & Hermans, 1988). These microvilli are straight and highly ordered. At the tip of the sensory process a rudimentary cilium may be

present, as is the case in many bicellular ocelli (Fig. 7D). The sensory processes often contain pigment granules as well (Fig. 7C, E). In all eyes the microvilli forming the rhabdomeres are comparatively uniform in size and measure 0.07–0.1 μm in diameter and about 1–1.5 μm in length.

In addition, a lens-like structure is present in most ocelli of this type. These lenses are either formed by the supportive cells as vesicle-containing processes (Fig. 7C, F) or a secretion given off by these cells, or are formed by one or a few specialized lenticular cells (Eakin & Hermans, 1988; Verger-Bocquet, 1992). Such multicellular eyes are present in species of the Phyllococida and have been found so far in Syllidae, Hesionidae, Nereidiidae, Phyllococidae, Alciopidae, Polynoidae, Aphroditidae (Fischer & Böckelmann, 1965; Hermans & Eakin, 1974; Zahid & Golding, 1974; Singla, 1975; Bocquet, 1976, 1977; Verger-Bocquet, 1983a; Eakin & Brandenburger, 1985; Rhode, 1991). Very likely this type of eye is also present in Amphinomidae (unpubl. obs.). The eyes described in *Capitella* sp. I by Rhode (1993) may also belong to this type and thus may represent the only exception. Although the author regards these eyes as unique for Annelida, the adult eyes develop in the same way as other multicellular eyes but show signs of disintegration of the pigment cells after development.

This distribution indicates that this type of multicellular eye could be an antapomorphy for a taxon Aciculata sensu Rouse & Fauchald (1997). However, it is noteworthy that a similar everse type of eye is present in Sipuncula and Mollusca, indicating homology (Hermans & Eakin, 1969; Rosen et al., 1979; Land, 1984; Bartolomaeus, 1992a; Blumer, 1995; Sturrock & Baxter, 1995; Arendt & Wittbrodt, 2001).

In *Ophryotrocha puerilis* and other *Ophryotrocha* spp. a pair of ocelli is present at the posterior margin of the brain. Although situated in the peristomium, they have been regarded as cerebral by Rhode (1990b). These eyes are exceptional not only in their position in the anterior end but also in their structure (Zavarzina, 1987; Rhode, 1990b): the sensory cell bears several rhabdomeric sensory processes which are enveloped by a thin supportive cell almost devoid of pigment granules. The eye cup is formed by a layer of flat additional cells separated from the

ocellus proper by an extracellular matrix. These cells contain layers of refractive crystalline platelets. The presence of an ECM indicates that two different germ layers are involved. But according to the assumption of Rhode (1990b) that the ocelli develop from the brain, the platelet-bearing cells should be mesodermal in origin instead of epidermal. Moreover, another dorvilleid, *Protodorvillea kefersteini*, possesses ocelli as described above (Purschke, unpubl. obs.). This is indicative of the presence of a secondary, newly evolved eye in *Ophryotrocha* spp. The same may apply to the eye in *Nerilla antennata*, which has an unusual structure and is composed of platelet (supportive) cells, corneal (supportive) cells and two sensory cells facing each other with their rhabdomeres (see Eakin et al., 1977; Eakin & Hermans, 1988).

In trochophore larvae of polychaetes the same type of small ocelli has been described (Eakin & Westfall, 1964; Holborow & Laverack, 1972; Brandenburger & Eakin, 1981; Verger-Bocquet, 1983a; Marsden & Hsieh, 1987; Bartolomaeus, 1987, 1992b; Rhode, 1992, 1993). Usually there is one pair of bicellular ocelli, but the number of cells as well as the number of eyes may be higher (Bartolomaeus, 1992b, 1993). These latter situations have been regarded as secondarily evolved by Bartolomaeus (1992b). These eyes may persist in the adults or may be replaced by the eyes of the adults during later development (Rhode, 1992, 1993; Bartolomaeus, 1993). During ontogenesis it is evident that the larval eyes are formed within the epithelial layer of the prostomial epidermis. After development has been completed, a pore in the eye cup may persist (Marsden & Hsieh, 1987; Bartolomaeus, 1992b; Rhode, 1992). In other species the cavity of the eye is completely closed and the ocelli are more deeply recessed into the prostomial tissues (Brandenburger & Eakin, 1981; Marsden & Hsieh, 1987; Bartolomaeus, 1992b). Such a pore may still be present in species in which the eyes of the trochophores are transferred to the adults. For instance, in *Saccocirrus* spp. (see Eakin et al., 1977; Purschke, 1992) the supportive and sensory cells are still part of the epithelium and are connected to the adjacent epidermal cells by typical apical junctional complexes (Purschke, 1992). The eye cup communicates with the subcuticular space *via* a small pore

lined by an array of microvilli formed by the pigment cell, a feature unknown for other ocelli. The adult eyes develop likewise in the prostomium and in these eyes, too, a pore and a connection to the subcuticular space may still be present after differentiation has been completed (Verger-Bocquet, 1992; Rhode, 1993).

Homology of cerebral eyes is generally assumed in Bilateria (e.g., Pietsch & Westheide, 1985; Bartolomaeus, 1992b; Arendt & Wittbrodt, 2001). However, a special problem appears to arise from the fact that the ocelli present in annelid larvae either degenerate and are replaced by the eyes of the adults in certain taxa or are retained in the adults in other polychaete taxa. In Mollusca the adult eyes always develop from larval eyes but are absent in basal groups (Salvini-Plawen, 1982). In spite of this difference homology of the adult eyes is conceivable since these eyes are structurally similar. Moreover, in polychaete larvae the number of cells involved and the number of eyes developed is variable between taxa investigated (see Bartolomaeus, 1992b). In these larval eyes the supportive cells have the ability to develop lens-like structures: e.g., in Syllidae, Opheliidae, or *Arenicola marina* (Verger-Bocquet, 1983b; Bartolomaeus, 1992b, 1993; Purschke, unpubl. obs.). Recent genetic work also argues for a monophyletic origin of the different types of cerebral ocelli found in extant Bilateria, all of which may have evolved from a prototypic eye by adaptive radiation (Gehring & Ikeo, 1999; Gehring, 2001). This support comes from the observation that the same master control gene *Pax6* is involved in eye development in all taxa studied so far. In addition, these cerebral eyes are formed in the *Otx*-territory (Arendt & Wittbrodt, 2001). This idea of homology of cerebral eyes throughout all Bilateria has been challenged by Arendt & Wittbrodt (2001) because in rhabdomic invertebrate and ciliary chordate photoreceptors non-homologous cascades of phototransduction have been observed. These authors conclude that the primary rhabdomic photoreceptor cells were lost in the stem lineage of Vertebrata and these cells were replaced by ciliary receptors.

Unpigmented ocelli

In addition to the pigmented ocelli, various kinds of ocelli without shading pigment have been

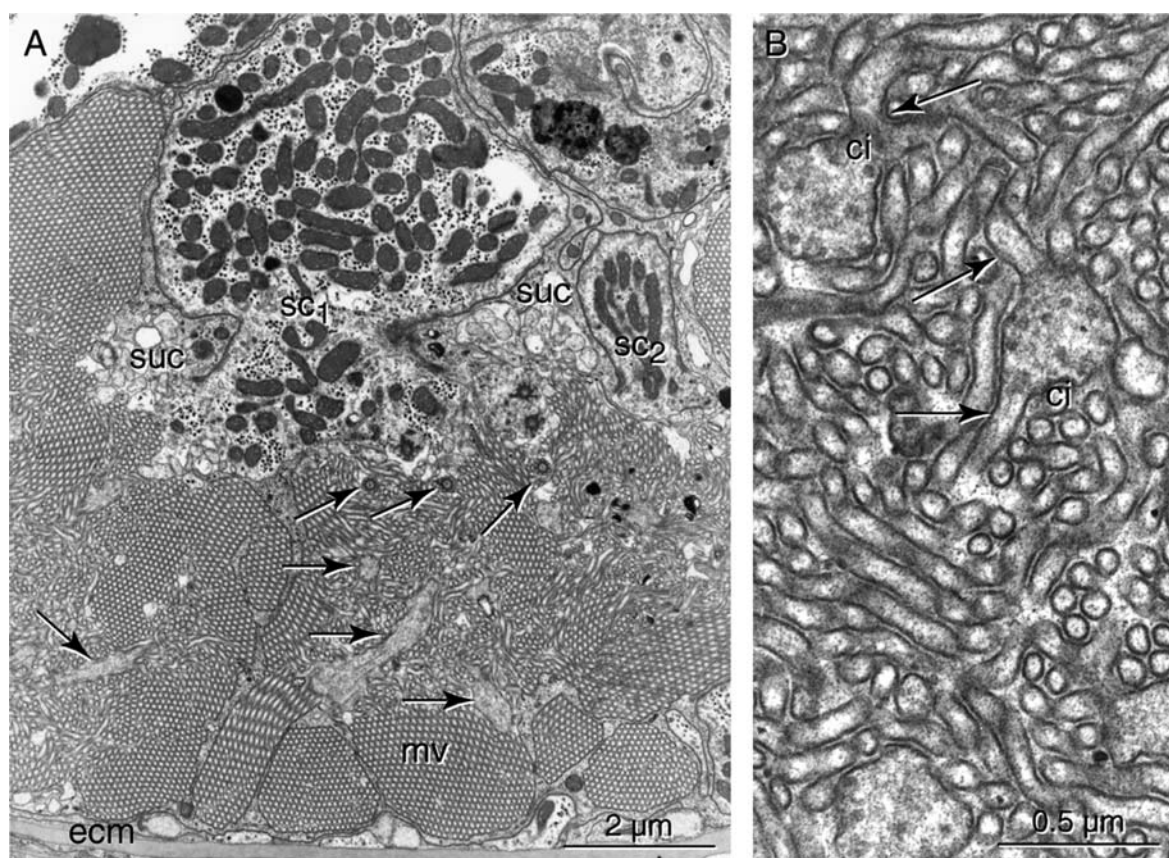


Figure 9. Ciliary photoreceptor-like sense organ. *Microphthalmus similis*. (A) Ocellus made up of 2 sensory cells (sc_1 , sc_2) and 1 supporting cell (suc) surrounding microvillus-like sensory processes (mv); arrows point to cilia. (B) Basal part of cavity with cilia (ci) giving of microvillus-like branches (arrows), note aberrant pattern of axonemal microtubules. – ci, cilium; ecm, extracellular matrix; mv, microvillus; sc_1 , sc_2 , sensory cell 1 + 2; suc, supporting cell.

found. These sensory structures have rhabdomeric, ciliary or phaosomous receptors. The last two types will be referred to as photoreceptor-like sense organs below. Sense organs of the first type are structurally similar to pigmented ocelli, usually consisting of two cells – one supportive and one rhabdomeric sensory cell – forming an extracellular cavity (Fig. 8B, D) which houses the photoreceptive microvilli. An accessory centriole or a more or less reduced cilium may be present in the sensory cell. As a rule, the microvilli of the receptor cells are considerably longer than in pigmented ocelli and may reach up to 6 μm in length. Such ocelli have been observed in the brain or prostomium of *Ophelia rathkei*, *Armandia brevis*, *Armandia polyophthalma*, *Polyophthalmus pictus*, *Saccocirrus krusadensis*, *Heteromastus filiformis*,

Pygospio elegans, *Scolecopsis squamata*, *Eteone longa*, *Phyllodoce mucosa*, *Nephtys caeca*, *Eulalia viridis*, and *Microphthalmus* spp. (see Hermans & Cloney, 1966; Zahid & Golding, 1974; Whittle & Golding, 1974; Pietsch & Westheide, 1985; Schlötzer-Schrehardt, 1987; Rhode, 1991; Purschke, 1992, 2003; Bartolomaeus, 1993). There may only be a pair or a few ocelli of this type in individuals of a given species, but in *P. pictus* and in *A. polyophthalma* there are about 70 or 50, respectively. The main difference from pigmented ocelli is just the absence of pigment in the supportive cell, which usually becomes rather thin and may be only 40–80 nm in diameter (Purschke, 1992). These structural similarities may give some evidence for an evolution from pigmented ocelli by loss of the shading pigment, a view supported by

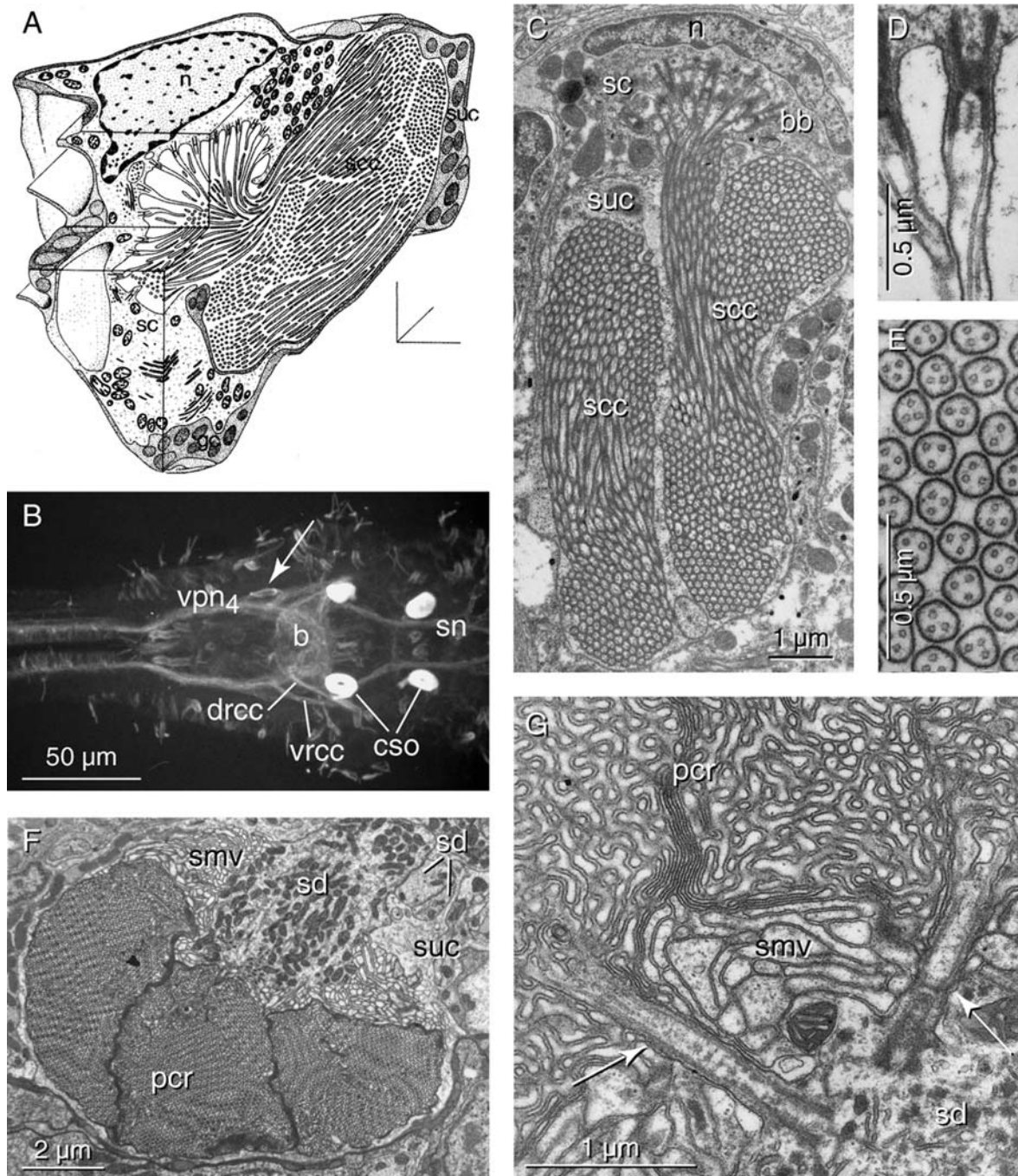


Figure 10. Ciliary photoreceptor-like sense organs. (A–E) *Protodriloides* spp. (A) *P. chaetifer*. Reconstruction of ciliary sense organ composed of sensory cell (sc) and glial supporting cell (suc). (B) *P. symbioticus*. Position of ciliary prostomial sense organs (cso) behind the neuropile of the brain (b), arrow points to basal ciliated cell; confocal laser scanning microscopic image, anti- α -acetylated-tubulin immunoreactivity. (C) *P. symbioticus*. Sensory cell (sc) with emerging sensory cilia (scc); cilia form coiled bundle. (D–E) *P. chaetifer*. Ultrastructure of cilia. (D) Base of cilia with basal body and basal region of axoneme. (E) Cross section of cilia with 3×1 axoneme. (F, G) *Protodrilus ciliatus*. So-called statocyst. (F) Low-power micrograph showing 3 paracrystals (pcr), sensory microvilli (smv), the three sensory dendrites (sd) and thin supporting cell (suc). (G) Cilia (arrows) without rootlets emerging from dendrite of large sensory cell splitting off and forming paracrystals. – b, brain; bb, basal body; cso, ciliary sense organ; drcc, dorsal root of circumoesophageal connective; n, nucleus; pcr, paracrystal; sc, sensory cell; scc, sensory cell cilium; sd, sensory dendrite; smv, sensory microvillus; sn, stomatogastric nerve; suc, supporting cell; vph₄, ventral palp nerve₄; vrcc, ventral root of circumoesophageal connective. A–E modified from Purschke & Müller (1996), G modified from Purschke (1990b).

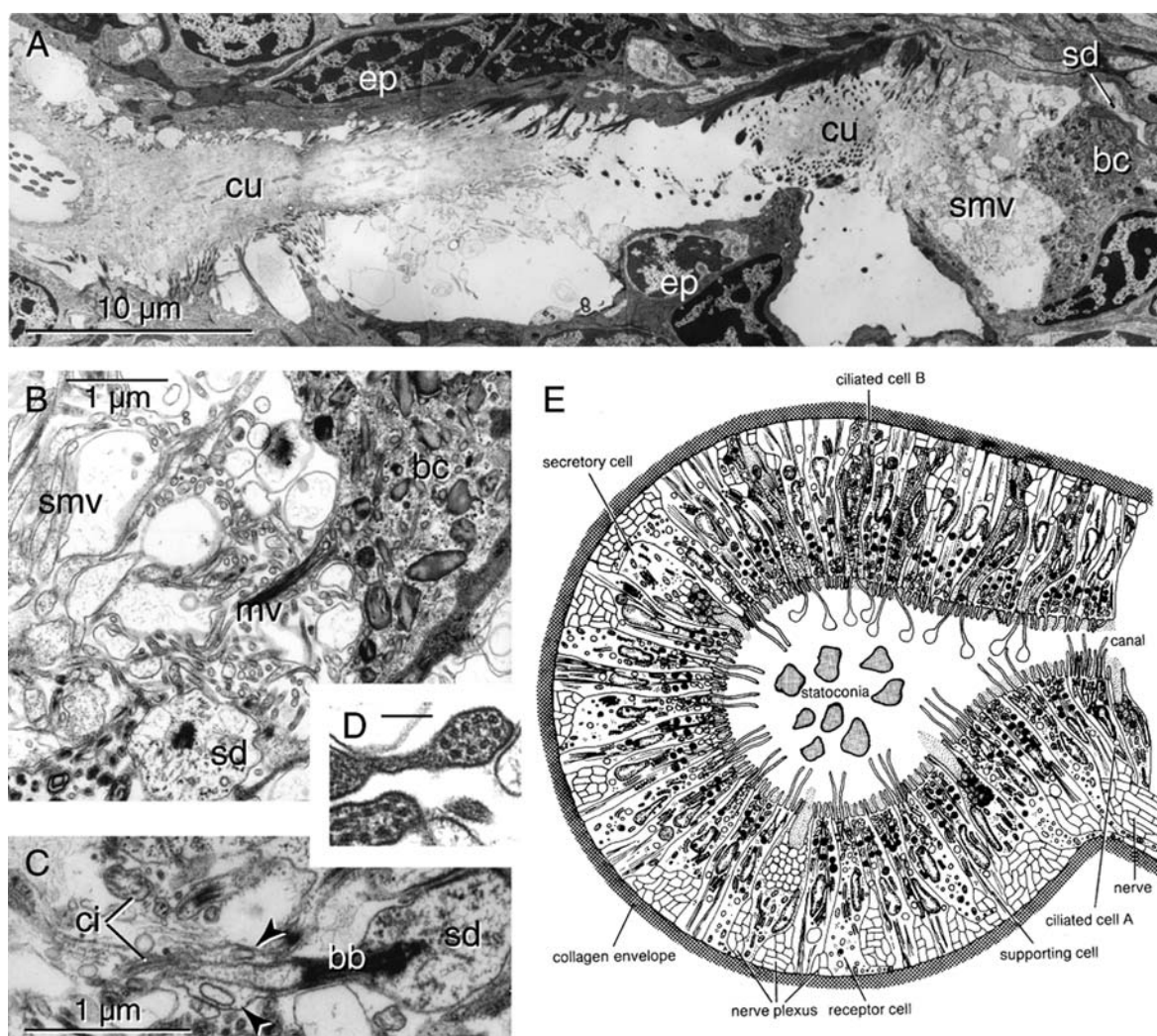


Figure 11. Other types of sense organs. (A–D) *Fauveliopsis adriatica*. Tube-like sense organ of unknown function. (A) Sense organ in longitudinal section, tube lined by epidermal invagination (ep) and filled with cuticular material (cu), at the base filled with microvillus-like sensory processes (smv). (B) Base of sense organ with sensory microvilli (smv), sensory dendrite (sd) and basal cell (bc) containing numerous vesicles. (C) Sensory dendrite with cilium, arrowheads: vesicles present in cilium. (D) Cross section of cilium with branches; scale represents 0.2 µm. (E) *Arenicola marina*. Statocyst with statoconia, epithelium made up of secretory, supporting ciliated and ciliated sensory cells. – bb, basal body; bc, basal cell; ci, cilium; cu, cuticle; ep, epidermis; mv, microvilli; sd, sensory dendrite; smv, sensory microvillus. A–D Langhage et al., unpubl., E from Storch & Schötzer-Schrehardt (1988) after Nowak (1978).

similar events observed in several platyhelminth species (Sopott-Ehlers, 1984, 1988, 1991). The functional significance of such ocelli is unknown and some hypotheses have been suggested by Bartolomaeus (1993).

Probably the so-called type-2 ocelli present in *Saccocirrus papillocercus* also belong to this type

(Purschke, 1992). These are multicellular organs composed of several supportive cells and rhabdomic sensory cells, forming a spherical structure into which the photoreceptors project. The rhabdomeres are formed by flattened cell processes already discernable in the light microscope with interference contrast.

Segmental ocelli

Segmental ocelli as well as tentacular and pygidial ocelli are structurally different from cerebral eyes and thus most likely represent independently evolved structures. When experimentally induced, expression of *Pax6* triggers development of cerebral eyes in any body region in the animals tested so far (Gehring, 2001). Thus, development of differently structured ocelli in the trunk of polychaetes thus favours the hypothesis of convergent evolution.

Segmental ocelli are present in certain Opheliidae, Eunicidae, Syllidae and Sabellidae, all of which represent different structural plans (Kernéis, 1968; Hermans, 1969; Dragesco-Kernéis, 1980; Verger-Bocquet, 1981; Purschke et al., 1995). In the opheliid taxa *Armandia* and *Polyopthalmus* the segmental ocelli are positioned somewhat in front of the parapodia. They are situated below the cuticle and epidermal cells and consist of a large rhabdomeric receptor cell, a layer of thin supportive cells and a layer of pigment cells (Fig. 8E). The sensory and supportive cells form an extracellular cavity housing the photoreceptors, while the pigment cells are mesodermal and separated from the overlain cells by an extracellular matrix which is continuous with that below the epidermis. The sensory cell is inverse and possesses several sensory processes bearing microvilli; the number of processes is species-specific and is between 10 and 25 (Hermans, 1969; Purschke et al., 1995).

In *Syllis spongicola* each chaetigerous segment of the stolon develops a pair of eyes situated below the dorsal parapodial cirri. Each compound eye consists of several units made up of supportive cells and sensory cells, being separated from one another by mucous cells. The sensory cells are characterized by an invagination of the apical photoreceptor-bearing surface and are thus phaosomous. The rhabdomeric photoreceptor has an additional vestigial cilium (Verger-Bocquet, 1981).

In the sabellid *Dasychone bombyx* these ocelli have a corresponding position between noto- and neuropodia. The ocelli are composed of several pigment and few sensory cells forming a follicle-like epidermal invagination (Kernéis, 1968; Dragesco-Kernéis, 1980). The follicle is filled with

a cuticular lens. The photoreceptors are rhabdomeric. The eyes present in the eunicid *Eunice viridis* apparently represent a fourth type of such secondarily evolved eyes (Eaking & Hermans, 1988).

Branchial ocelli

Branchial ocelli, present in Sabellidae and Serpulidae, are compound eyes consisting of numerous repetitive units (reviewed by Verger-Bocquet, 1992). In various Sabellidae each unit contains a photoreceptor cell characterized by stacks of parallel and modified cilia called lamellar sacs. The cilia have a $9 \times 2 + 0$ axoneme without rootlets. A lens-like structure formed by other supportive cells than the pigment cells is also present. Apart from this common feature, there is a great diversity between species. In Serpulidae the sensory cells possess highly ordered microvilli and a stack of ciliary membranes.

Pygidial ocelli

Pygidial ocelli are present in certain Sabellidae not permanently living in tubes. These animals crawl with the pygidium in front and the tentacular crown folded up. The ultrastructure of such ocelli has been studied in *Chone ecaudata* by Ermak & Eakin (1976). They consist of a group of three types of epidermal cells: secretory cells, pigment cells and photoreceptor cells. The sensory cells are rhabdomeric, bearing numerous microvilli and two cilia lying in a depression of the cell underneath the cuticle.

Photoreceptor-like sense organs

There are various kinds of other photoreceptor-like sensory structures in polychaetes. Usually the sensory cells are ciliary, producing a great expanse of ciliary membranes as is the case in typical photoreceptors. These structures are housed in an extracellular cavity formed by sensory and supportive cells but shading pigment is normally absent in these sensory structures. Although they are structurally similar to photoreceptor structures, clear experimental evidence for light perception is lacking. Thus, other modalities are conceivable as well (see Eakin & Hermans, 1988; Rhode, 1992). Recently, presence of opsin was proven in ciliary photoreceptors of *Platynereis dumerilii*,

indicating possible photoreceptive function of these ciliary receptors among polychaetes and Bilateria and thus their overall homology (Arendt et al., 2004).

Many polychaete species investigated possess at least one type of such organs, often in addition to typical pigmented eyes (e.g., Pietsch & Westheide, 1985; Rhode, 1991; Purschke, 1992; Bartolomaeus, 1993; Purschke & Jouin-Toulmond, 1994). These organs show a great diversity in number, position and structure between taxa and our knowledge about their diversity and occurrence is still rather incomplete. Thus, their importance as characters for high-level phylogenetic inference is slight, but these structures may be very useful at lower levels: species-specific differences between closely related species have repeatedly been reported (e.g., Pietsch & Westheide, 1985; Purschke, 1990a, b, 1992; Purschke & Jouin-Toulmond, 1993, 1994).

Formerly these organs were mostly called phaosomes, following the terminology of clitellate photoreceptors. However, phaosomes as defined above are extremely rare in polychaetes (Purschke, 2002b): Mostly, these structures are associated with supporting cells and the sensory cells form an extracellular cavity with them. This fact has either been overlooked because the supportive cells are relatively inconspicuous, or it has simply been neglected (e.g., Sensenbaugh & Franzén, 1987; Rhode, 1991). True phaosomes are, for instance, present in the palps of Protodrilidae (Purschke, 1993, 2003; Purschke & Jouin-Toulmond, 1993) or in Siboglinidae (Nørrevang, 1974).

The range of diversity can be demonstrated by the following examples. Species of *Microphthalmus* possess an unpaired ocellus-like structure at the posterior end of the brain (Fig. 9A, B; Pietsch & Westheide, 1985). It is characterized by a huge cavity, 10–20 μm in diameter, housing numerous microvillus-like structures. There are one or two sensory cells, each giving rise to 8–20 cilia with basal branches indistinguishable from regular microvilli (Fig. 9B). More peripherally these structures are highly ordered and resemble a rhabdome (Fig. 9A). In addition, different paired ciliary sense organs have been found anteriorly in the prostomium of *Microphthalmus*. These anterior organs are somewhat similar to those described from the brain of *Nereis pelagica*, *Eulalia viridis*,

Anaitides mucosa, *Eteone longa*, *Lepidonotus helotyplus* and *Saccocirrus* spp (type-1 ocelli). There are usually a few cilia and ciliary branches often contain a single microtubule (Dhainaut-Courtois, 1965; Whittle & Golding, 1974; Gotow, 1976; Rhode, 1991; Purschke, 1992).

A completely different type of photoreceptor-like sense organ has been found in *Protodriloides* spp. (Fig. 10A–E; Purschke & Müller, 1996). Situated in the anterior end close to the brain, the organs can be labelled with antibodies against tubulin (Fig. 10B). Their most characteristic feature is a sensory cell giving rise to a bundle of approximately 200 unbranched cilia (Fig. 10A, C). These are strictly parallel and rolled up several times in an extracellular cavity bordered by a supportive cell. The cilia are 50–100 μm long, lack rootlets and have an extremely modified axoneme: just above the basal body the $9 \times 2 + 0$ pattern is transformed into a 3×1 pattern. Such organs have not been found in any other polychaete species.

The ‘statocysts’ present in most *Protodrilus* species also belong to this type (Fig. 10F, G; Purschke, 1990a,b). Regardless their size, these organs consist of a cup-shaped supportive cell and three ciliary sensory cells. The most striking feature is that the cilia of the largest sensory cell form paracrystalline structures (Fig. 10F). These paracrystals are made up of highly folded and regularly arranged ciliary membranes (Fig. 10G). The cilia of the remaining sensory cells form microvillus-like branches. There are species-specific differences in terms of size, number of cilia and structure of ciliary membranes. In view of this structure a function as statocyst appears to be questionable. Recently, rather similar organs were found in juveniles of various species of Spionida (Hausen, 2001). These structures are regarded as homologous with the ‘statocysts’ of Protodrilidae, giving additional support for a closer relationship of these taxa as suggested previously (see Purschke, 1993). Interestingly these organs are only present in larvae and juveniles in Spionida. They are reduced and disappear in adults. Given that there is a close relationship to the Protodrilidae, occurrence of these sense organs in the latter would speak in favour of a progenetic origin of these interstitial polychaetes.

Other types of sensory organs

A completely new type of sense organ has recently been found in *Fauveliopsis* cf. *adriatica* (Fig. 11A–D; Langhage et al., unpubl. obs.). Situated at the anterior end of the retractile prostomium of this species, these organs can be characterized as epidermal follicles extending deeply into the brain. Each is multicellular and about 40 μm deep; the lumen is filled with cuticular material except for the most posterior part (Fig. 11A). The posterior part is somewhat widened and filled with microvillus-like processes of a few sensory cells (Fig. 11B). What appears to be microvilli are mostly branches of cilia which intermingle with regular microvilli also originating from these cells. A conspicuous non-sensory cell with numerous dense vesicles forms the terminal end of the tube (Fig. 11A, B). The function of these tube-like sense organs is completely unknown. The organs appear to have some similarities with the ocellar tubes of Sipuncula (Hermans & Eakin, 1969; Rice, 1993). Further observations must show whether similar organs are present in other polychaete taxa and, for example, whether the so-called saccular apparatus in *Glycera dibranchiata* described from light microscopic observations by Simpson (1959) is a similar structure.

Statocysts

True statocysts are present in a small number of polychaete taxa such as Arenicolidae, Orbiniidae, Terebellidae and Sabellidae (Verger-Bocquet, 1992; Rouse & Pleijel, 2001). Ultrastructural studies have been carried out in only two species: *Arenicola marina* and the aulophora larva of *Lanice conchilega* (Fig. 11E; Heimler, 1983; Storch & Schlötzer-Schrehardt, 1988). Since then, no other data have been presented. The statocysts may be closed or open epidermal vesicles. The statocysts proper consist of supportive cells, gland cells and one to three types of sensory cells lining a cavity which mostly contains several statoliths. For details see Storch & Schlötzer-Schrehardt (1988) and Verger-Bocquet (1992). The scattered occurrence and variable position suggests that these organs are convergently evolved in the respective taxa, in spite of an overall similarity which might be due to functional constraints.

Conclusions

There exists a great diversity of sensory structures and sense organs in polychaetes. Whereas the structure of the sensory cells seems to be more or less completely known, this does not apply to the sense organs as a whole. Of great phylogenetic importance are palps, nuchal organs and pigmented ocelli. A remarkable aspect is the broad range of unpigmented ocelli and photo-receptor-like structures; sometimes three or four different presumed light-sensitive organs are present in one species. As demonstrated by some examples, the extent of sense organ diversity has not yet been explored and many mysteries are still waiting discovery and functional interpretation.

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References

- Åkesson, G., 1958. A study of the nervous system of the Sipunculoidea with some remarks on the development of the two species *Phascolion strombi* Montagu and *Golfingia minuta* Keferstein. Undersökningar över Öresund 38: 1–249.
- Åkesson, G., 1962. The embryology of *Tomopteris helgolandicus* (Polychaeta). Acta Zoologica (Stockholm) 43: 135–199.
- Åkesson, G., 1967. The embryology of the polychaete *Eunice kobienensis*. Acta Zoologica (Stockholm) 48: 141–192.
- Ameyaw-Akumfi, C., 1976. The function of the caruncle of an amphinomid *Eurythoe* sp. – a histological investigation. Zoologischer Anzeiger 196: 318–322.
- Amieva, M. R., C. G. Reed & J. R. Pawlik, 1987. Ultrastructure and behavior of the larva of *Phragmatopoma californica* (Polychaeta: Sabellariidae): identification of sensory organs potentially involved in substrate selection. Marine Biology 95: 259–266.
- Arendt, D. & J. Wittbrodt, 2001. Reconstructing the eyes of Urbilateria. Philosophical Transactions of the Royal Society of London B356: 1545–1563.

- Arendt, D., K. Tessmar-Raible, H. Snyman, A. W. Dorrestein & J. Wittbrodt, 2004. Ciliary photoreceptors with a vertebrate-type opsin in an invertebrate brain. *Science* 306: 869–871.
- Ax, P., 1995. *Das System der Metazoa I*. Fischer, Stuttgart, 1–226.
- Bantz, M. & C. Michel, 1972. Les cellules sensorielles des papilles de la trompe chez *Glycera convoluta* Keferstein (Annélide Polychète). *Zeitschrift für Zellforschung* 134: 351–366.
- Bartolomaeus, T., 1987. Ultrastruktur des Photorezeptors der Trophophora von *Anaitides mucosa* Oersted (Phyllodocidae, Annelida). *Mikrofauna Marina* 3: 411–418.
- Bartolomaeus, T., 1992a. Ultrastructure of the photoreceptor in the larvae of *Lepidochiton cinereus* (Mollusca, Polyplacophora) and *Lacuna divaricata* (Mollusca, Gastropoda). *Microfauna Marina* 7: 215–236.
- Bartolomaeus, T., 1992b. Ultrastructure of the photoreceptors in certain larvae of the Annelida. *Microfauna Marina* 7: 191–214.
- Bartolomaeus, T., 1993. Different photoreceptors in juvenile *Ophelia rathkei* (Annelida, Opheliida). *Microfauna Marina* 8: 99–114.
- Bhup, R. & J. R. Marsden, 1982. The development of the central nervous system in *Capitella capitata* (Polychaeta, Annelida). *Canadian Journal of Zoology* 60: 2284–2295.
- Blumer, M., 1995. The ciliary photoreceptor in the teleplanic veliger larvae of *Smaragdia* sp. and *Strombus* sp. (Mollusca, Gastropoda). *Zoomorphology* 115: 73–81.
- Bocquet, M., 1976. Ultrastructure de l'organe photorécepteur d'*Autolytus pictus* (Annélide Polychète). Étude chez la souche, le stolon parvenu à maturité sexuelle et la tête régénérée. *Journal de Microscopie et de Biologie Cellulaire* 25: 61–66.
- Bocquet, M., 1977. Étude ultrastructurale de l'organe photorécepteur d'*Odontosyllis ctenostoma* S/F: Eusyllinae (Annélide Polychète). *Journal of Ultrastructure Research* 58: 210–217.
- Böggemann, M., D. Fiege & G. Purschke, 2000. Ultrastructure of the proboscoidal papillae in some *Glycera* species (Annelida: Polychaeta: Glyceridae). *Cahiers de Biologie Marine* 41: 143–153.
- Boilly-Marer, Y., 1972a. Étude ultrastructurale des cirres parapodiaux de Nereidiens atokes (Annélides Polychètes). *Zeitschrift für Zellforschung* 131: 309–327.
- Boilly-Marer, Y., 1972b. Présence de cellules de type myoépithélial chez les Nereidae (Annélides Polychètes). *Journal de Microscopie* 15: 253–256.
- Brandenburger, J. L. & R. M. Eakin, 1981. Fine structure of ocelli in larvae of an archiannelid *Polygordius cf. appendiculatus*. *Zoomorphology* 99: 23–36.
- Bullock, T. H., 1965. Annelida. In T. H. Bullock & G. A. Horridge (eds), *Structure and Function in the Nervous System of Invertebrates*. Vol. I. Freeman and Company, San Francisco, U.S.A., 661–789.
- Dhainaut-Courtois, N., 1965. Sur la présence d'un organe photorécepteur dans le cerveau de *Nereis pelagica* L. (Annélide Polychète). *Comptes Rendus Hebdomadaires des Seances de l'Académie des Sciences Ser. D* 261: 1085–1088.
- Dorsett, D. A. & R. Hyde, 1969. The fine structure of the compound sense organs in the cirri of *Nereis diversicolor*. *Zeitschrift für Zellforschung* 85: 243–255.
- Dragesco-Kernéis, A., 1980. Taches oculaires segmentaires chez *Dasychone* (Annélides Polychètes). Etude ultrastructurale. *Cahiers de Biologie Marine* 21: 287–302.
- Eakin, R. M., 1963. Lines of evolution in photoreceptors. In D. Mazia & A. Tyler (eds), *General Physiology of Cell Specialization*. McGraw-Hill, New York, 393–425.
- Eakin, R. M., 1982. Continuity and diversity in photoreceptors. In J. A. Westfall (ed.), *Visual Cells in Evolution*. Raven, New York, 91–105.
- Eakin, R. M. & J. L. Brandenburger, 1985. Effects of light and dark on photoreceptors in the polychaete annelid *Nereis limnicola*. *Cell and Tissue Research* 242: 613–622.
- Eakin, R. M. & C. O. Hermans, 1988. Eyes. In W. Westheide & C. O. Hermans (eds), *The Ultrastructure of Polychaeta*. *Microfauna Marina* 4: 135–156.
- Eakin, R. M. & J. A. Westfall, 1964. Further observations on the fine structure of some invertebrates eyes. *Zeitschrift für Zellforschung* 62: 310–322.
- Eakin, R. M., G. G. Martin & C. T. Reed, 1977. Evolutionary significance of fine structure of archiannelid eyes. *Zoomorphologie* 88: 1–18.
- Eeckhaut, I. & M. Jangoux, 1993. Integument and epidermal sensory structures of *Myzostoma cirriferum* (Myzostomida). *Zoomorphology* 113: 33–45.
- Eibye-Jacobsen, D., 1991. A revision of *Eumida* Malmgren, 1865 (Polychaeta: Phyllodocidae). *Steenstrupia* 17: 81–140.
- Eisig, H., 1914. Zur Systematik, Anatomie und Morphologie der Ariciiden nebst Beiträgen zur generellen Systematik. *Mitteilungen aus der Zoologischen Station zu Neapel* 21: 153–593.
- Ermak, T. H. & R. M. Eakin, 1976. Fine structure of the cerebral and pygidial ocelli in *Chone ecaudata* (Polychaeta: Sabellidae). *Journal of Ultrastructure Research* 54: 243–260.
- Fauchald, K. & G. W. Rouse, 1997. Polychaete systematics: past and present. *Zoologica Scripta* 26: 71–138.
- Fernandez, J., V. Téllez & N. Olea, 1992. Hirudina. In F. W. Harrison (ed.), *Microscopic Anatomy of Invertebrates*. Vol. 7 Annelida. Wiley-Liss., New York, 323–394.
- Fischer, A. & J. Böckelmann, 1965. Morphology and structural changes of the eye of *Platynereis dumerilii* (Polychaeta). In Rohen, J. W. (ed.), *The Structure of the Eye II*. Symposium Stuttgart: F.K. Schattauer, 171–174.
- Gehring, W. J., 2001. The genetic control of eye development and its implications for the evolution of the various eye-types. *Zoology* 104: 171–183.
- Gehring, W. J. & K. Ieko, 1999. *Pax 6* mastering eye morphogenesis and eye evolution. *Trends in Genetics* 15: 371–377.
- Gotow, T., 1976. Photoreceptor-like cells in the prostomium of a scaleworm, *Lepidonotus helotypus*. *Zoological Magazine (Tokyo)* 85: 265–269.
- Hausen, H., 2001. Untersuchungen zur Phylogenie "spiomorpher" Polychaeten (Annelida). *Logos*, Berlin, 1–142.
- Hayashi, I. & S. Yamane, 1994. On a probable sense organ newly found in some eunicid polychaetes. *Journal of the*

- Marine Biological Association of the United Kingdom 74: 765–770.
- Hayashi, I. & S. Yamane, 1997. Further observations of a recently found sense organ in some euniciforms, with special reference to *Lumbrineris longifolia* (Polychaeta, Lumbrineridae). *Bulletin of Marine Science* 60: 564–574.
- Heimler, W., 1983. Untersuchungen zur Larvalentwicklung von *Lanice conchilega* (Pallas) 1766 (Polychaeta, Terebellomorpha). Teil III: Bau und Struktur der Aulophora-Larve. *Zoologische Jahrbücher der Anatomie* 111: 411–478.
- Heimler, W., 1988. Larvae. In W. Westheide and C.O. Hermans (eds), *The Ultrastructure of Polychaeta*. Gustav Fischer Verlag, New York, pp. 353–371.
- Hermans, C. O., 1969. Fine structure of the segmental ocelli of *Armandia brevis* (Polychaeta: Opheliidae). *Zeitschrift für Zellforschung* 96: 361–371.
- Hermans, C. O. & R. A. Cloney, 1966. Fine structure of the prostomial eyes of *Armandia brevis* (Polychaeta: Opheliidae). *Zeitschrift für Zellforschung* 72: 583–596.
- Hermans, C. O. & R. M. Eakin, 1969. Fine structure of cerebral ocelli of a sipunculid, *Phascolosoma agassizii*. *Zeitschrift für Zellforschung* 100: 325–339.
- Hermans, C. O. & R. M. Eakin, 1974. Fine structure of the eyes of an alciopid polychaete, *Vanadis tagensis*. *Zeitschrift für Morphologie der Tiere* 79: 245–267.
- Hessling, R. & W. Westheide, 1999. CLSM analysis of development and structure of the central nervous system in *Enchytraeus crypticus* (“Oligochaeta”, Enchytraeidae). *Zoomorphology* 119: 37–47.
- Hessling, R., Müller, M. C. & W. Westheide, 1999. CLSM analysis of serotonin-immunoreactive neurons in the central nervous system of *Nais variabilis*, *Slavina appendiculata* and *Stylaria lacustris* (Oligochaeta: Naididae). *Hydrobiologia* 406: 223–233.
- Hessling, R. & G. Purschke, 2000. Immunohistochemical (cLSM) and ultrastructural analysis of the central nervous system and sense organs in *Aeolosoma hemprichi* (Annelida, Aeolosomatidae). *Zoomorphology* 120: 65–78.
- Holborow, P. L. & M. S. Laverack, 1972. Presumptive photoreceptor structures of the trophophore *Harmothoe imbricata* (Polychaeta). *Marine Behaviour and Physiology* 1: 139–156.
- Jamieson, B. G. M., 1981. *The Ultrastructure of the Oligochaeta*. Academic, London, New York, 1–462.
- Jamieson, B. G. M., 1992. Oligochaeta. In F.W. Harrison (ed.), *Microscopic Anatomy of Invertebrates*. Vol. 7 Annelida. Wiley-Liss., New York, 217–322.
- Jelsing, J., 2002a. Ultrastructural studies of dorsal ciliated organs in Spionidae (Annelida: Polychaeta). *Hydrobiologia* (in press).
- Jelsing, J., 2002b. Ultrastructural investigations on the cephalic and metameric nuchal organs of *Spio* cf. *filicornis* (Polychaeta: Spionidae). *Zoomorphology* 121: 213–220.
- Jouin, C., C. Tchernigovtzeff, M. F. Baucher & A. Toulmond, 1985. Fine structure of probably mechano- and chemoreceptors in the caudal epidermis of the lugworm *Arenicola marina* (Annelida, Polychaeta). *Zoomorphology* 105: 75–82.
- Kernéis, A., 1968. Ultrastructure de photorécepteurs de *Dasychone* (Annélides Polychètes Sabellidae). *Journal de Microscopie* (Paris) 7:40a (Abstract).
- Lacalli, T., 1981. Structure and development of the apical organ in trochophores of *Spirobranchus polycerus*, *Phyllodoce maculata* and *Phyllodoce mucosa* (Polychaeta). *Proceedings of the Royal Society of London B212*: 381–402.
- Land, M. F., 1984. Molluscs. In Ali, M.A. (ed.), *Photoreception and Vision in Invertebrates*. Vol. 74. Plenum and NATO Sci. Aff. Div., New York, London, 699–725.
- Lewbart, G. A. & N. W. Riser, 1996. Nuchal organs of the polychaete *Parapionosyllis manca* (Syllidae). *Invertebrate Biology* 115: 286–298.
- Marsden, J. R., 1982. Morphological evidence for neural activity in prototrochal and neurotrochal cells of the trochophore larva of the serpulid polychaete, *Galeolaria caespitosa*. *International Journal of Invertebrates Reproduction* 5: 289–297.
- Marsden, J. R. & J. Hsieh, 1987. Ultrastructure of the eyespot in three polychaete trochophore larvae (Annelida). *Zoomorphology* 106: 361–368.
- McHugh, D., 1997. Molecular evidence that echiurans and pogonophorans are derived annelids. *Proceedings of the National Academy of Sciences of the United States of America* 94: 8006–8009.
- McHugh, D., 2000. Molecular phylogeny of the Annelida. *Canadian Journal of Zoology* 78: 1873–1884.
- Michel, C., 1972. Etude ultrastructurale et histochimique des papilles de la gaine de la trompe de *Notomastus latericeus* Sars (Annélide Polychète Sédentaire). *Zeitschrift für Zellforschung* 128: 482–503.
- Michel, W. C., P. Steullet, H. S. Cate, C. J. Burns, A. B. Zhainazarov & C. D. Derby, 1999. High resolution functional labelling of vertebrate and invertebrate olfactory receptor neurons using agmatine, a channel-permeant cation. *Journal of Neuroscience Methods* 90: 143–156.
- Mill, P. J., 1978. Sense organs and sensory pathways. In P. J. Mill (ed.), *Physiology of Annelids*. Academic, New York, London, 63–114.
- Myhrberg, H. E., 1979. Fine structural analysis of the basal epidermal receptor cells in the earthworm (*Lumbricus terrestris*). *Cell and Tissue Research* 203: 257–266.
- Nordheim, H. v., 1991. Ultrastructure and functional morphology of male genital organs and spermatophore formation in *Protodrilus* (Polychaeta, Annelida). *Zoomorphology* 111: 81–94.
- Nørrevang, A., 1974. Photoreceptors of the phaosome (Hirudinean) type in a pogonophore. *Zoologischer Anzeiger* 193: 297–304.
- Orrhage, L., 1964. Anatomische und morphologische Studien über die Polychaetenfamilien Spionidae, Disomidae and Poecilochaetidae. *Zoologisk Bidrag Uppsala* 36: 335–405.
- Orrhage, L., 1980. On the structure and homologues of the anterior end of the polychaete families Sabellidae and Serpulidae. *Zoomorphology* 96: 113–168.
- Orrhage, L. & M. C. M. Müller, 2005. Morphology of the nervous system of Polychaeta (Annelida). *Hydrobiologia* 535/536 (Dev. Hydrobiol. 179): 79–111.
- Pietsch, A. & W. Westheide, 1985. Ultrastructural investigations of presumed photoreceptors as a means of discrimination and identification of closely related species of the

- genus *Microphthalmus* (Polychaeta, Hesionidae). *Zoomorphologie* 105: 256–276.
- Pleijel, F., 1991. Phylogeny and classification of the Phyllozoa (Polychaeta). *Zoologica Scripta* 20: 225–261.
- Purschke, G., 1986. Ultrastructure of the nuchal organ in the interstitial polychaete *Stygocapitella subterranea* (Parergodrilidae). *Zoologica Scripta* 16: 13–20.
- Purschke, G., 1990a. Fine structure of the so-called statocysts in *Protodrilus adhaerens* (Protodrilidae, Polychaeta). *Zoologischer Anzeiger* 224: 286–296.
- Purschke, G., 1990b. Ultrastructure of the “statocysts” in *Protodrilus* species (Polychaeta): reconstruction of the cellular organisation with morphometric data from receptor cells. *Zoomorphologie* 110: 91–104.
- Purschke, G., 1992. Ultrastructural investigations of presumed photoreceptive organs in two *Saccocirrus* species (Polychaeta, Saccocirridae). *Journal of Morphology* 211, 7–21.
- Purschke, G., 1993. Structure of the prostomial appendages and the central nervous system in the Protodrilida (Polychaeta). *Zoomorphologie* 113: 1–20.
- Purschke, G., 1997. Ultrastructure of nuchal organs in polychaetes (Annelida) – new results and review. *Acta Zoologica (Stockholm)* 78: 123–143.
- Purschke, G., 1999. Terrestrial polychaetes – models for the evolution of the Clitellata (Annelida)? *Hydrobiologia* 406: 87–99.
- Purschke, G., 2000. Sense organs and central nervous system in an enigmatic terrestrial polychaete, *Hrabeiella periglandulata* (Annelida). *Invertebrate Biology* 119: 329–341.
- Purschke, G., 2002. On the ground pattern of Annelida. *Organisms Diversity and Evolution* 2: 181–196.
- Purschke, G., 2003. Ultrastructure of phasosomous photoreceptors in *Stylaria lacustris* (Naididae, “Oligochaeta”, Clitellata) and their importance for the position of the Clitellata in the phylogenetic system of the Annelida. *Journal of Zoological Systematics and Evolutionary Research* 41: 100–108.
- Purschke, G. & C. Jouin-Toulmond, 1993. Ultrastructure of presumed ocelli in *Parenterodrilus taenioides* (Polychaeta, Protodrilidae) and their phylogenetic significance. *Acta Zoologica (Stockholm)* 74: 247–256.
- Purschke, G. & C. Jouin-Toulmond, 1994. Ultrastructure of sense organs and the central nervous system in *Parenterodrilus taenioides* and their phylogenetic significance in the taxon Protodrilida (Annelida, Polychaeta). In J.-C. Dauvin, L. Laubier & D. J. Reish (eds), *Actes de la 4ème Conférence internationale des Polychètes. Mémoires du Muséum National d’histoire Naturelle* 162: 119–128.
- Purschke, G., Z. Ding & M. C. Müller, 1995. Ultrastructural differences as a taxonomic marker: the segmental ocelli of *Polyophthalmus pictus* and *Polyophthalmus qingdaoensis* sp.n. (Polychaeta, Opheliidae). *Zoomorphologie* 115: 229–241.
- Purschke, G. & M. C. Müller, 1996. Structure of prostomial photoreceptor-like sense organs in *Protodriloides* species (Polychaeta, Protodrilida). *Cahiers de Biologie Marine* 37: 205–219.
- Purschke, G., F. Wolfrath & W. Westheide, 1997. Ultrastructure of the nuchal organ and cerebral organ in *Onchmesoma squamatum* (Sipuncula, Phascolionidae). *Zoomorphologie* 117: 23–31.
- Purschke, G., R. Hessling & W. Westheide, 2000. The phylogenetic position of the Clitellata and the Echiura – on the problematic assessment of absent characters. *Journal of Zoological Systematics and Evolutionary Research* 38: 165–173.
- Purschke, G. & R. Hessling, 2002. Analysis of the central nervous system and sense organs in *Potamodrilus fluviatilis* (Annelida: Potamodrilidae). *Zoologischer Anzeiger* 241: 19–35.
- Rhode, B., 1989. Ultrastructural investigations on the nuchal organ of the protandric polychaete, *Ophryotrocha puerilis* (Polychaeta, Dorvilleidae). *Zoomorphologie* 108: 315–322.
- Rhode, B., 1990a. Ultrastructure of nuchal organs in some marine polychaetes. *Journal of Morphology* 206: 95–107.
- Rhode, B., 1990b. Eye structure of *Ophryotrocha puerilis* (Polychaeta: Dorvilleidae). *Journal of Morphology* 205: 147–154.
- Rhode, B., 1991. Ultrastructure of prostomial receptors in four marine polychaete species (Annelida). *Journal of Morphology* 209: 177–188.
- Rhode, B., 1992. Development and differentiation on the eye in *Platynereis dumerilii* (Annelida, Polychaeta). *Journal of Morphology* 212: 71–85.
- Rhode, B., 1993. Larval and adult eyes in *Capitella* spec. I (Annelida, Polychaeta). *Journal of Morphology* 217: 327–335.
- Rice, M. E., 1993. Sipuncula. In F.W. Harrison & M.E. Rice (eds), *Microscopic Anatomy of Invertebrates*. Vol. 12 Onychophora, Chilopoda and lesser Protostomata. Wiley-Liss, New York, 237–325.
- Rosen, M. D., C. R. Stasek & C. O. Hermans, 1979. The ultrastructure and evolutionary significance of the ocelli in the larva of *Katharina tunicata* (Mollusca: Polyplacophora). *Veliger* 22: 173–178.
- Rouse, G. W. & K. Fauchald, 1997. Cladistics and polychaetes. *Zoologica Scripta* 26: 139–204.
- Rouse, G. W. & F. Pleijel, 2001. *Polychaetes*. Oxford University, New York, 354 pp.
- Rullier, F., 1951. Étude morphologique, histologique et physiologique de l’organe nuchal chez les annélides polychètes sédentaires. *Annales de l’Institut Océanographique de Monaco* 25: 207–341.
- Rullier, F., 1954. L’organe nuchal de *Sthenelais boa* (Johnston). *Comptes Rendus Hebdomadaires des Séances de l’Académie des Sciences Series D* 238: 1351–1353.
- Salvini-Plawen, L. von, 1982. On the polyphyletic origin of photoreceptors. In Westfall, J. A., (ed.), *Visual Cells in Evolution*. Raven, New York, 137–154.
- Salvini-Plawen, L. von & E. Mayr, 1977. On the evolution of eyes and photoreceptors. In Hecht, M. K., W. C. Sterne & B. Wallace (eds), *Evolutionary Biology*, Vol. 10. Plenum, New York, 207–263.
- Sawyer, R. T., 1986. *Leech Biology and Behaviour*, Vol. 1. Clarendon, Oxford, 418 pp.
- Schlawny, A., C. Grünig & H.-D. Pfannenstiel, 1991. Sensory and secretory cells of *Ophryotrocha puerilis* (Polychaeta). *Zoomorphologie* 110: 209–215.
- Schlötzer-Schrehardt, U., 1986. Ultrastructural investigation of the nuchal organs of *Pygospio elegans* (Polychaeta). I. Larval nuchal organs. *Helgoländer Meeresuntersuchungen* 40: 397–417.

- Schlötzer-Schrehardt, U., 1987. Ultrastructural investigation of the nuchal organs of *Pygospio elegans* (Polychaeta). II. Adult nuchal and dorsal organs. *Zoomorphology* 107: 169–179.
- Schlötzer-Schrehardt, U., 1991. Ultrastructural differentiation of nuchal and dorsal organs during postembryonic and sexual development of *Pygospio elegans* Claparède (Polychaeta: Spionidae). *Ophelia Supplement* 5: 633–640.
- Sensenbaugh, T. & A. Franzén, 1987. Fine structural observations of the apical organ in the larva of *Polygordius* (Annelida: Polychaeta). *Scanning Microscopy* 1: 181–189.
- Siewing, R., 1953. Morphologische Untersuchungen am “Kopf” der Pisionidae (*Pisione puzae* nov. spec. Annelida, Polychaeta). *Zoologischer Anzeiger* 150: 298–313.
- Simpson, M., 1959. The sacular apparatus in the brain of *Glycera dibranchiata*. *Journal of Morphology* 104: 561–590.
- Singla, C. L., 1975. Ultrastructure of the eyes of *Arctonoe vittata* Grube (Polychaeta, Polynoidae). *Journal of Ultrastructure Research* 52: 333–339.
- Söderström, A., 1927. Über segmental wiederholte “Nuchalorgane” bei Polychäten. *Zoologisk Bidrag Uppsala* 12: 1–18.
- Sopott-Ehlers, B., 1984. Feinstruktur pigmentierter und unpigmentierter Photoreceptoren bei Proseriata (Plathelminthes). *Zoologica Scripta* 13: 9–18.
- Sopott-Ehlers, B., 1988. Fine structure of photoreceptors in two species of the Prolethophora. *Fortschritte der Zoologie* 36: 221–227.
- Sopott-Ehlers, B., 1991. Comparative morphology of photoreceptors in free-living plathelminths – a survey. *Hydrobiologia* 227: 231–239.
- Spies, R. B., 1975. Structure and function of the head in flabelligerid polychaetes. *Journal of Morphology* 147: 187–208.
- Storch, V., 1972. Elektronenmikroskopische Untersuchungen an Rezeptoren von Anneliden (Polychaeta, Oligochaeta). *Zeitschrift für Mikroskopisch-Anatomische Forschung* 85: 55–84.
- Storch, V. & U. Welsch, 1969. Zur Feinstruktur des Nuchalorgans von *Eurythoe complatana* (Pallas) (Amphinomidae, Polychaeta). – *Zeitschrift für Zellforschung* 100: 411–420.
- Storch, V. & U. Schlötzer-Schrehardt, 1988. Sensory structures. In W. Westheide & C.O. Hermans (eds), *The Ultrastructure of Polychaeta*. *Microfauna Marina* 4: 121–133.
- Sturrock, M. G. & J. M. Baxter, 1995. The fine structure of the pigment body complex in the intrapigmented aesthetes of *Callochiton achatinus* (Mollusca: Polyplacophora). *Journal of Zoology London* 235: 127–141.
- Toulmond, A., C. Tchernigovtzeff, P. Greber & C. Jouin, 1984. Epidermal sensitivity to hypoxia in the lugworm. *Experientia* 40: 541–542.
- Tzetlin, A. & G. Purschke, 2005. Pharynx and intestine. *Hydrobiologia* 535/536 (Dev. Hydrobiol. 179): 197–223.
- Vanfleteren, J. R., 1982. A monophyletic line of evolution? Ciliary induced photoreceptor membranes. In J. A. Westfall (ed.), *Visual Cells in Evolution*. Raven, New York, 107–136.
- Vanfleteren, J. R. & A. Coomans, 1976. Photoreceptor evolution and phylogeny. *Zeitschrift für zoologische Systematik und Evolutionsforschung* 14: 157–169.
- Verger-Bocquet, M., 1981. Etude comparative, au niveau infrastructural, entre l’œil de souche et les taches oculaires du stolon chez *Syllis spongicola* Grube (Annelide Polychète). *Archives de Zoologie Expérimentale et Générale* 122: 253–258.
- Verger-Bocquet, M., 1983a. Les organes photoréceteurs des Syllidiens (Annelides Polychètes). *Année Biologie* 22: 169–185.
- Verger-Bocquet, M., 1983b. Étude infrastructurale des organes photoréceteurs chez les larves de deux Syllidiens (Annelides, Polychètes). *Journal of Ultrastructure Research* 84: 67–72.
- Verger-Bocquet, M., 1984. Photoreception et vision chez les Annelides. In Ali, M. A., (ed.), *Photoreception and Vision in Invertebrates*. Plenum, New York, London, 289–334.
- Verger-Bocquet, M., 1992. Polychaeta: sensory structures. In F. W. Harrison (ed.), *Microscopic Anatomy of Invertebrates*. Vol. 7 Annelida. Wiley-Liss., New York, 181–196.
- Welsch, U., V. Storch & K. S. Richards, 1984. Epidermal cells. In J. Bereiter-Hahn, A. G. Matoltsy & K. S. Richards (eds), *Biology of the Integument. I. Invertebrates*. Springer, Heidelberg, New York: 269–296.
- West, D. L., 1978. Comparative ultrastructure of juvenile and adult nuchal organs of an annelid (Polychaeta, Opheliidae). *Tissue and Cell* 10: 243–257.
- Westheide, W., 1997. The direction of evolution within Polychaeta. *Journal of Natural History* 31: 1–15.
- Westheide, W., D. McHugh, G. Purschke & G. W. Rouse, 1999. Systematization of the Annelida: different approaches. *Hydrobiologia* 402: 291–307.
- Whittle, A. C. & D. W. Golding, 1974. The fine structure of prostomial photoreceptors in *Eulalia viridis* (Polychaeta: Annelida). *Cell and Tissue Research* 165: 379–398.
- Whittle, A. C. & Z. R. Zahid, 1974. Fine structure of nuchal organs in some errant polychaetous annelids. *Journal of Morphology* 144: 167–184.
- Windoffer, R. & W. Westheide, 1988. The nervous system of *Dinophilus gyrotilatus* (Annelida: Polychaeta). I. Number, types and distribution pattern of sensory cells. *Acta Zoologica* 69: 55–64.
- Worsaae, K. & R. M. Kristensen, 2003. A new species of *Paranerilla* (Polychaeta: Nerillidae) from northeast Greenland waters, arctic ocean. *Cahiers de Biologie Marine* 44: 23–39.
- Zahid, Z. R. & D. W. Golding, 1974. Structure and ultrastructure of the central nervous system of the polychaete *Nephtys*, with special reference to photoreceptor elements. *Cell and Tissue Research* 149: 567–576.
- Zavazina, E. G., 1987. New data on photoreceptor structure in *Ophryotrocha dimorphica* (Polychaeta, Eunicida). *Doklady Akademii NAUK SSSR* 294: 224–227 (in Russian).