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Systematics, evolution and phylogeny of Annelida – a morphological perspective

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Abstract Purschke, G., Bleidorn, C. and Struck, T. 2014. Systematics, evolution and phylogeny of Annelida – a morphological perspective . *Memoirs of Museum Victoria* 71: 247–269.

Annelida, traditionally divided into Polychaeta and Clitellata, is an evolutionary ancient and ecologically important group today usually considered to be monophyletic. However, there is a long debate regarding the in-group relationships as well as the direction of evolutionary changes within the group. This debate is correlated to the extraordinary evolutionary diversity of this group. Although annelids may generally be characterised as organisms with multiple repetitions of identically organised segments and usually bearing certain other characters such as a collagenous cuticle, chitinous chaetae or nuchal organs, none of these are present in every subgroup. This is even true for the annelid key character, segmentation. The first morphology-based cladistic analyses of polychaetes showed Polychaeta and Clitellata as sister groups. The former were divided into Scolecida and Palpata comprising Aciculata and Canalipalpata. This systematisation definitely replaced the old concept of dividing polychaetes into Errantia and Sedentaria, whereas the group Archiannelida had already been abandoned. The main critics came from a contradicting hypothesis relying on scenario based on plausibility considerations regarding Clitellata as highly derived annelids nesting within polychaetes and rendering the latter paraphyletic. In this hypothesis the absences of typical polychaete characters were regarded as losses rather than as primary absences. However, to date attempts to unambiguously identify the sister group of Clitellata on the basis of morphological characters have failed. Thus, two hypotheses on the last common annelid ancestor have been put forward either being an oligochaete-like burrowing animal or a parapodia-bearing epibenthic worm. These attempts to understand the major transitions in annelid evolution are reviewed and discussed in the light of new morphological evidence such as photoreceptor cell and eye evolution as well as the evolution of the nervous system and musculature. We also discuss the plausibility of these scenarios with regard to recent advances in molecular phylogenetic analyses.

Keywords polychaetes, oligochaetes, Clitellata, Sedentaria, Errantia, ground pattern, morphology

Introduction

Annelida, traditionally divided into Polychaeta and Clitellata (Rouse and Fauchald, 1995, 1998; Bartolomaeus et al., 2005), is an evolutionary ancient and ecologically important group comprising approximately 16,500 species occurring in marine, limnetic and terrestrial habitats (Struck, 2011; Struck et al., 2011). Their biological importance relies not only on the comparatively high number of species but also on their often high abundance. Although some species can be found in the plankton throughout their entire life span, annelids usually constitute a significant part of the endo- and epibenthos where they occupy almost every existing ecological niche in the marine environment. They occur from the deep sea to the supralittoral zones of sandy beaches. However, the vast majority of the limnetic and terrestrial species belong to only one clade, called Clitellata, the members of which show specific adaptations to terrestrial life (e.g. Purschke, 1999, 2002). Obviously due to subsequent adaptive radiations, this broad ecological range occupied by annelids resulted in a high morphological diversity (fig. 1A-L).

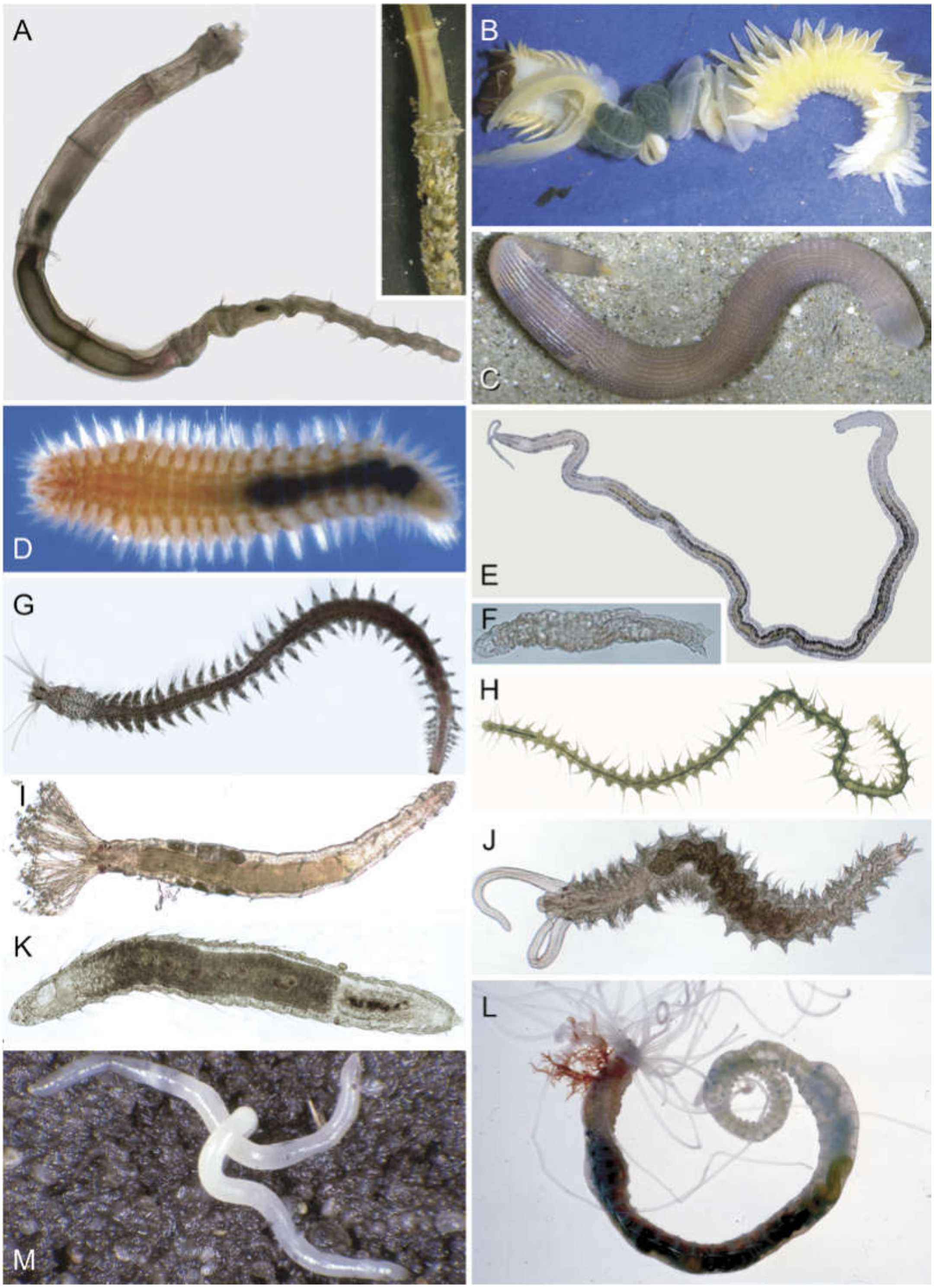

Figure 1. Examples of annelid diversity. A-D. Members of the basal radiation; A. *Owenia fusiformis*, Oweniidae, length about 100 mm, Inset: part of the tube. B. *Chaetopterus variopedatus,* Chaetopteridae, length about 250 mm. C. *Sipunculus nudus,* Sipuncula, length about 350 mm. D. *Eurythoe complanata,* Amphinomidae, length about 140 mm. E-F. Former Archiannelida; E: *Protodriloides chaetifer,* Protodrilida, length about 13 mm*;* F. *Diurodrilus subterraneus*, length about 440 *µ*m. G-H. Errantia; G. *Platynereis dumerilii,* Nereididae, length about 100 mm. H. *Microphthalmus similis*, incertae sedis, length about 18 mm. I-M. Sedentaria. I. *Fabricia stellaris,* Sabellidae, length about 4 mm. J. *Pygospio elegans,* Spionidae, length about 25 mm. K. *Ophelia rathkei,* Opheliidae, length about 8 mm. L. *Lanice conchilega*, Terebellidae, juvenile, length up to 300 mm. M. *Enchytraeus* sp. Clitellata, length about 15 mm. Originals B, C, D: W. Westheide, Osnabrück.

This diversity is the main reason why the phylogenetic relationships among Annelida are still one of the largest unsolved problems in metazoan phylogeny (Rouse and Fauchald, 1995, 1997; Eibye-Jacobsen and Nielsen, 1996; Westheide, 1997; Westheide et al., 1999; Rouse and Pleijel, 2001, 2003; Purschke, 2002; Bartolomaeus et al., 2005; Struck, 2012). The main problems concern the monophyly of Annelida, the organisation or character composition of the annelid stem species, monophyly versus paraphyly of Polychaeta, the inter-relationships between the various annelid subtaxa as well as the taxon composition of the group (Bartolomaeus et al., 2005; Struck et al., 2011; Struck, 2012). Morphological and molecular evidence increases that taxa which were formerly recognised as separate "phyla" are now regarded as part of the annelid radiation, namely Pogonophora (now Siboglinidae), Echiura, Myzostomida, and Sipuncula (reviewed by Halanych et al., 2002; Struck, 2012; but see Eibye-Jacobsen and Vinther, 2012).

The taxon composition of this presumed monophyletic group Annelida including these former "phyla" is crucial for reconstructing the characters of the annelid stem species or its last common ancestor (Purschke, 2002). As a result of the controversial hypotheses on the taxon composition and phylogeny of Annelida, two hypotheses regarding the last common ancestor have been put forward: either an oligochaete-like burrowing animal, or a parapodia-bearing epibenthic worm. Consequently polychaetes may be monophyletic or paraphyletic (see Bartolomaeus et al., 2005; Struck, 2011). Irrespective of the taxa included, the state of almost every character considered varies greatly among annelids making ground pattern reconstruction a difficult task. Although there is general agreement that Annelida are organisms with a multiple repetition of identically organised segments (Bartolomaeus et al., 2005; Struck, 2011; Hannibal and Patel, 2013), there are certain taxa in which even this so-called key-character is virtually absent: e.g., Echiura, Sipuncula, *Diurodrilus* (Purschke et al., 2000; Wanninger et al., 2005; Worsaae and Rouse, 2008; Nielsen, 2012; Golombek et al., 2013). The number of segments varies between species and may comprise between only 6 or fewer (e. g. *Parapodrilus psammophilus* Westheide, 1965) to more than 1,000 segments (e. g. *Eunice aphroditois* (Pallas, 1788)) resulting in body lengths varying from less than 600 μm to about 6 m (see Paxton, 2000). Presence of segmentally arranged chitinous chaetae is another key-character of annelids (Hausen, 2005a). However, the pleisomorphic condition regarding shape and structure of these chaetae and whether these chaetae were primarily situated in lobe-like appendages, the parapodia, is also a matter of discussion (Rouse and Fauchald, 1997; Bartolomaeus et al., 2005; Struck, 2011). Also, some taxa lack chaetae in all stages of their life cycle (e.g., Polygordiidae; see Ramey et al., 2012).

The aims of the present paper are (1) to briefly review the systematics of annelids, (2) to discuss morphological characters presumably important for the reconstruction of the ground pattern, (3) to elucidate the question of paraphyly of polychaetes, and (4) to identify directions of future research in annelid morphology and phylogeny. Finally, all these are discussed in the light of current molecular phylogenetic analyses of Annelida.

Annelid Systematics

Since the first phylogenetic analyses of molecular and morphological datasets, approximately 20 years ago (Rouse and Fauchald, 1997; McHugh, 1997), systematics of Annelida has been undergoing major reassessments after a period of relative stability. Although a detailed historical review of traditional annelid systematisation can be found in Struck (2012), some highlights are briefly summarised. Annelida as a separate group was first recognised by Lamarck (1802) and included polychaetes, earthworms and echiurans. Audouin & Milne Edwards (1834) divided Annelida into annélides errantes, annélides tubicoles (ou sédentaires), annélides terricoles (= Capitellida + oligochaetes), and annélides soucieuses (= Hirudinea). Errantia included the more vagile forms and Sedentaria the more or less sessile, often microphagous annelid groups. In this concept Annelida obviously was not divided into Polychaeta and Clitellata (or Oligochaeta). The division of Annelida into Polychaeta and Oligochaeta goes back to Grube (1850), retaining the division of polychaetes into two major groups which he called Rapacia and Limivora. This classificatory concept of subdividing polychaetes into Errantia and Sedentaria has been widely accepted and was in use with some modifications for more than 100 years (e. g., Hartmann-Schröder, 1971). A third major annelid group, called Archiannelida, comprising several groups of seemingly simply organised, small annelids was introduced later by Hatschek (1878, 1893). This grouping mirrors the view that "simple equals primitive" (e. g. Jamieson, 1992; but see Hughes et al., 2013).

Archiannelids show an apparently simple organisation and may retain characters otherwise typical for annelid larvae such as ciliary bands used for locomotion (Figs 1E, F, 6C). Their segmentation is often hardly recognisable and many species possess neither chaetae nor parapodia. Most archiannelid species are members of the meiofauna of marine sediments (interstitial annelids). Errantia may be morphologically characterised by well-developed parapodia often equipped with dorsal and ventral cirri, prostomial antennae and palps, usually with a high number of homonymous segments, one or several pairs of tentacular (peristomial) cirri, a pair of pygidial cirri, and adult individuals usually with one or two pairs of pigmented, multicellular eyes (fig. 1G, H). Often three subgroups are distinguished: Amphinomida, Eunicida, and Phyllodocida. By contrast, Sedentaria are much more diverse (fig. 1I-L) and may be characterised by more or less simple or even lacking parapodia, usually without dorsal and ventral cirri, typically with hooked chaetae (uncini); palps and pygidial cirri are either absent or present whereas antennae and peristomial appendages are always lacking. Pigmented adult eyes are usually of the larval type in this group; i.e. bicellular only, comprising one photoreceptor and one pigment cell. These polychaetes often have fewer segments than errant polychaetes and the body may be divided into different regions (Hartmann-Schröder, 1971; Fauchald, 1977; Bartolomaeus et al., 2005; Purschke et al., 2006; Suschenko and Purschke, 2009). With respect to the characters mentioned above Clitellata show simple chaetae and lack parapodia as well as any appendage on the prostomium, peristomium and pygidium (fig. 1M). On the other hand, clitellates show an exclusive combination of numerous characters such as the clitellum, hermaphroditism, a specific type of spermatozoon, a dorsal pharynx, a specific type of photoreceptor cell (= phaosome), and a posteriorly dislocated brain, supporting their monophyly (Purschke, 2002; Bartolomaeus et al., 2005).

Dales (1962, 1963) was among the first to question this traditional concept (Dales, 1963, p. 64): "The polychaetes are, indeed, most usually divided into two subclasses, the Errantia and the Sedentaria. This division is not a natural one, however, and does not reflect the way in which these worms, have evolved ...". He proposed a classification based on analysing the distribution of characters such as buccal organs and nephridia. A similar approach has been adopted by Storch (1968) using muscular systems as the most important characters. Although neither classification gained general acceptance, polychaete subtaxa usually were placed at equal rank in the following years, retaining Polychaeta and Clitellata as highest ranked taxa. Fauchald (1977), obviously inspired by Clark's (e.g. 1964) ideas of an earthworm-like annelid ancestor, placed the oligochaete-like forms at the base of the polychaetes. Although listed without any interrelationships specified, Fauchald (1977, p. 7) stated: "the sequence of families indicates an increasing morphological distance from the ancestral polychaete" implying that the groups listed first were presumably closer to the annelid stem species than the following ones. In parallel, Archiannelida was recognised as an artificial, presumably polyphyletic assemblage of interstitial annelids primarily adapted to life in the mesopsammon (e. g., Hermans, 1969; Fauchald, 1974; Westheide, 1985, 1987).

Westheide (1997) questioned the sister group relationship of Polychaeta and Clitellata and considered Polychaeta paraphyletic and Clitellata being sister to an unknown polychaete taxon. However, in the same year the first hypothesis based on cladistic analyses was published (fig. 2A; Rouse and Fauchald, 1997). This phylogenetic hypothesis was widely accepted in a comparatively short period of time, introduced to many textbooks and is still in use – of course with some modifications (see e. g. Rouse and Pleijel, 2001, 2003). These first morphological-based cladistic analyses of polychaetes showed Polychaeta and Clitellata as sister groups contradicting the hypothesis of a paraphyletic Polychaeta (Westheide, 1997). In the hypothesis of Rouse and Fauchald (1997) Polychaeta were divided into Scolecida and Palpata. Scolecida comprised the more or less oligochaete-like appendage-less polychaetes, whereas Palpata contained all palp-bearing polychaetes. Palpata were subdivided into Aciculata and Canalipalpata. Irrespective of the fact that Aciculata and Errantia comprise the same subtaxa, this systematisation replaced the old concept dividing polychaetes into Errantia and Sedentaria. Interestingly, as already suggested by Bartolomaeus (1995, 1998) and by the hypothesis of Rouse & Fauchald (1997), Pogonophora forms a polychaete in-group (which was subsequently called Siboglinidae), but Echiura and Sipuncula were still excluded from Annelida based mainly on the lack of annelid key characters such as segmentation and chaetae.

The main criticism on the hypothesis of Rouse & Fauchald (1997) came from a contradicting hypothesis which regarded Clitellata as highly derived annelids forming a polychaete in-group and rendering the latter paraphyletic (Purschke, 1997, 1999, 2000, 2002, 2003; Westheide, 1997; Westheide et al., 1999; Bartolomaeus et al., 2005). Although to date all attempts have failed to unambiguously identify the sister group of Clitellata, in this hypothesis the absence of typical polychaete characters in Clitellata and Echiura is regarded as losses rather than as primary absences (Purschke, 1997, 1999; Purschke et al., 2000).

It is suggested that cladistic analyses using morphological data may fail to recognise absent characters as losses rather than as primary absences (Purschke et al., 2000; Bleidorn, 2007; see Fitzhugh, 2008). Thus, the sister-group relationship Polychaeta-Clitellata as found in Rouse and Fauchald (1997) may have been biased by the misinterpretation of a number of convergently lost characters. Likewise the highly derived nature of several characters of Clitellata related to their adaptations to terrestrial life was not recognised. In contrast, according to Rouse & Fauchald (1997) Clitellata should more or less resemble the annelid stem species. For the same reasons exclusion of Echiura and Sipuncula from Annelida might represent an analytical artifact. Careful analyses of the development of the latter taxa provided evidence for a reduced rather than absent segmentation (Hessling, 2002; Hessling and Westheide, 2002; Tzetlin and Purschke, 2006; Kristof et al., 2008).

This morphology based cladistic hypothesis was never supported by molecular phylogenetic analyses, but if included Clitellata usually appeared as a polychaete in-group (e.g., McHugh, 1997; Bleidorn et al., 2003; Rousset et al., 2007; Zrzavy et al., 2009; Struck et al., 2007, 2008, 2011; Weigert et al., 2014). In addition, monophyly of the basal group Scolecida was never recovered by molecular analyses. Whereas the first molecular analyses suffered from low or lack of support for deep nodes in the annelid tree, current analyses now relying on phylogenomic datasets based on hundreds of genes show high support for even deep nodes in the annelid tree (Struck et al., 2011; Weigert et al., 2014; but see Kvist and Siddall, 2013). These analyses recover a basal grade comprising several enigmatic taxa such as Chaetopteridae, Oweniidae, Magelonidae as well as Sipuncula and Amphinomidae (Weigert et al., 2014). The vast majority of annelid taxa form a monophyletic group named Pleistoannelida (Struck, 2011), with Errantia and Sedentaria being the highest ranked sister groups, the latter including Clitellata (fig. 2B). However, it should be noted here that the taxon composition and definition of both Errantia and Sedentaria is slightly different from the traditional concepts (Struck et al., 2011; Struck, 2012; Weigert et al., 2014). Interestingly, a comparison of trees obtained from phylogenomic analyses to those obtained using morphological data show that the major difference is the placement of the root of the annelid tree either within the former Palpata or close to Clitellata, respectively (Struck, 2012).

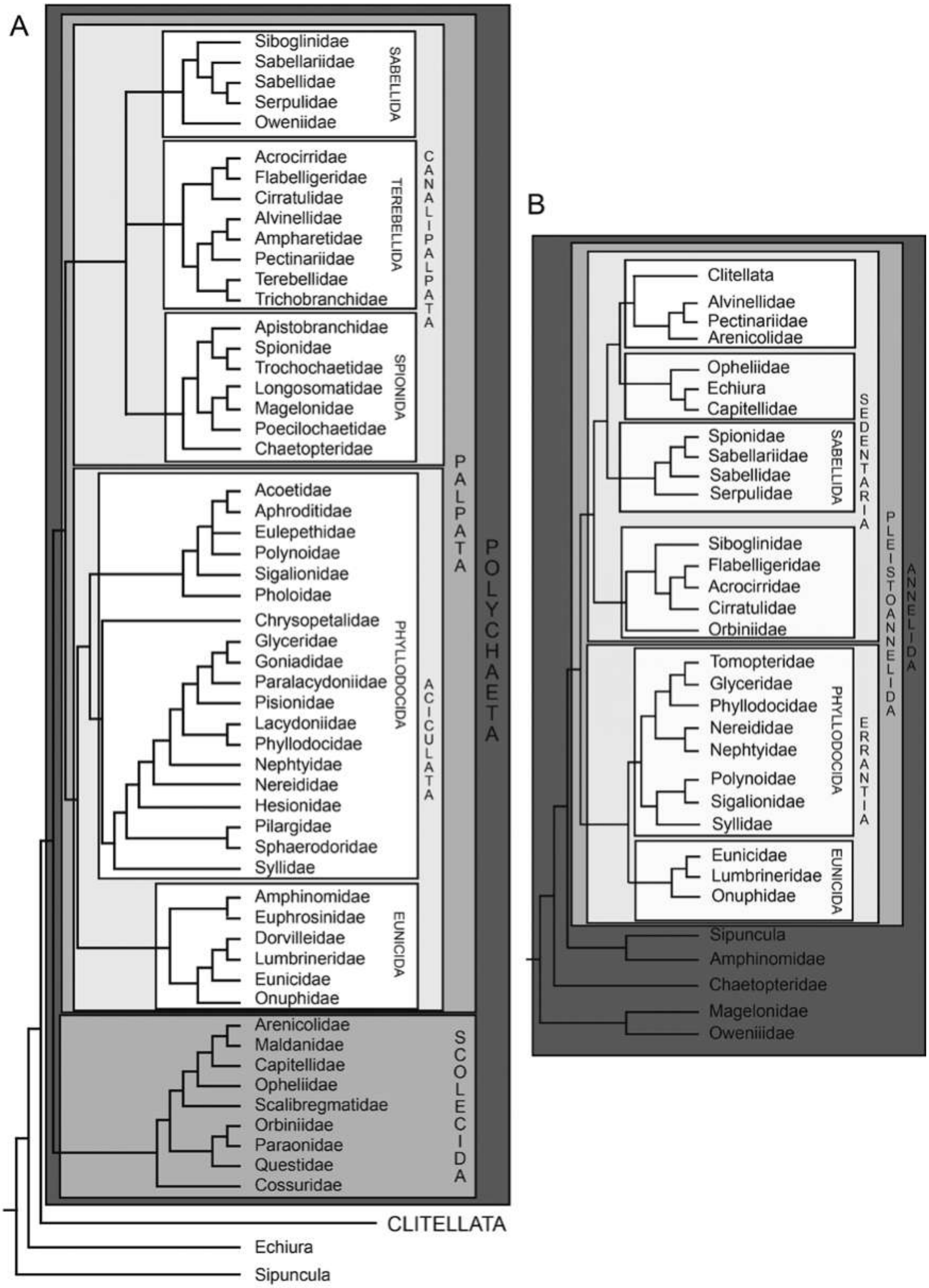

Figure 2. Phylogenetic hypotheses of annelid relationships. A. Cladistic analysis based on morphological data (modified from Rouse and Fauchald 1997). B. Phylogenetic tree based on phylogenomic data (modified after Struck et al. 2011; Weigert et al. 2014).

Morphological characters of Annelida

This conflict on the systematisation of Annelida may lead to differences in the reconstruction of the annelid ground pattern. Despite existence of certain outstanding studies on annelid anatomy, earlier polychaete systematics was largely based on external morphology (reviewed e.g. by Fauchald and Rouse, 1997) and even though some of these studies were extremely comprehensive, additional morphological characters are needed to develop well-founded homology hypotheses (Fauchald and Rouse, 1997; Müller, 2006). Recently, fine structural investigations (cLSM, TEM, SEM) as well as developmental ones have provided such data and may provide better evidence for homology considerations (e.g., Orrhage and Müller, 2005; Müller, 2006; Hunnekuhl et al., 2009; Suschenko and Purschke, 2009; Wilkens and Purschke, 2009a, b; Filippova et al., 2010; Döring et al., 2013; Lehmacher et al., 2014; see also Fauchald, 1977; Fauchald and Rouse, 1997). These studies have mainly focussed on the muscular system, nervous system and sensory organs. Another source of data is the determination of the so-called molecular fingerprint (gene expression patterns) of cell types for homology assessments (e. g. Arendt, 2008; Arendt et al., 2009; Döring et al., 2013).

Given the two main opposing morphology-based phylogenetic hypotheses discussed above it is surprising that the differences in the ground pattern of the annelid stem species are smaller than might be expected. According to Fauchald (1974) the ancestral annelid resembled a polychaete and was characterised by complete septation, distinct segments, chaetae and low parapodial folds, anterior end without appendages and a burrowing lifestyle. The stem species was a marine, gonochoristic, broadcast spawner with a planktotrophic larva. This hypothesis was only slightly changed after Rouse and Fauchald's (1997) cladistic analysis: according to this hypothesis the last common ancestor of Annelida was homonomously segmented, the longitudinal musculature not forming a continuous layer but consisted of 4-5 longitudinal bands, the gut as a straight tube with dorsolateral folds in the foregut, chaetae all simple capillaries, the prostomium distinctly set off but with no appendages, nuchal organs, and internal supporting chaetae and parapodia absent. The annelid stem species after Weigert et al. (2014) was homonomously segmented, with longitudinal muscle bands, the gut forming a straight tube with dorsolateral folds in the foregut (microphagous deposit feeder), simple chaetae emerging from parapodia, prostomium and peristomium present with palps, and bicellular eyes present. Thus the main differences are the structure of the prostomium, presence or absence of anterior appendages, the presence of nuchal organs, the nature of the eyes and structure of parapodia. Therefore, these structures and others which have largely been neglected, such as the cuticle and the nervous system, will now be discussed in more detail. Other character complexes will only be mentioned briefly as they have been discussed previously or they will not be discussed as they lack any phylogenetic signal with respect to this question (e.g., Purschke, 2002; Bartolomaeus et al., 2005). These include the mesoderm, the coelom and the nephridia (Rieger and Purschke, 2005; Bartolomaeus and Quast, 2005), pharynx and intestine (Tzetlin and Purschke 2005) as well as the biphasic life cycle (Rieger, 1994; Rieger and Purschke, 2005; Nielsen, 2012).

Segmentation

The annelid body generally consists of a small presegmental region, the prostomium, a segmented trunk, and a small postsegmental region, the pygidium (fig. 3A-C; see Fauchald and Rouse, 1997; Hutchings and Fauchald, 2000; Rouse and Pleijel, 2001; Purschke, 2002; Bartolomaeus et al., 2005). The prostomium contains the brain (cerebral ganglia) as well as the most important sensory structures. The pygidium bears a terminally or dorsally positioned anus. The mouth is situated ventrally in the first segment, usually called the peristomium. New segments are formed in the posterior growth zone in front of the pygidium. Each segment generally comprises a pair of ganglia in the ventral nerve cord, a pair of coelomic cavities, a pair of metanephridia, and paired ventral and dorsal groups of chaetae (see Purschke, 2002; Bartolomaeus et al,. 2005). The leeches show obvious signs of reduced but still recognisable segmentation: for instance, the ventral nerve cord clearly allows the number of segments comprising the body to be determined (Purschke et al., 1993).

Most annelid groups regarded as lacking segmentation such as Siboglinidae, Echiura, Sipuncula and *Diurodrilus* generally show signs of suppression or reduction of segmentation (fig. 1C, F). Among these Siboglinidae are the most obviously segmented, when the often-missing posterior part of the body was found (Webb, 1964; Southward, 1988; Southward et al., 2005). Only subtle traces of segmentation have been found in developmental stages of echiuroids and sipunculans whereas in adults all signs of segmentation are absent (Hessling and Westheide, 2002; Hessling, 2003; Wanninger et al., 2005; Kristof et al., 2008). Species of *Diurodrilus*, a group of small interstitial animals, do not exhibit any signs of segmentation even in the nervous system (Worsaae and Rouse, 2008): However, molecular phylogenetic data and other morphological characters clearly support the inclusion of this taxon within Annelida (see Golombek et al., 2013).

Whereas formerly segmentation in arthropods and annelids has generally been assumed to be a synapomorphic character, the early molecular phylogenetic analyses raised doubts regarding a single evolutionary origin of segmentation in these taxa (for summary see Dordel et al., 2010). Increasing molecular developmental data demonstrates evidence for a convergent origin of segmentation (see Shankland and Seaver, 2000; Seaver, 2003; De Rosa et al., 2005; Seaver et al., 2012). However, others have proposed that the last common ancestor of Bilateria was already segmented (de Robertis et al., 2008; Couso, 2009; Chesebro et al., 2013).

Cuticle

Without exception a collagenous cuticle completely covers the annelid epidermis (Storch, 1988; Gardiner, 1992; Hausen, 2005b). The cuticle is composed of an amorphous or filamentous matrix that usually houses layers of parallel collagen fibres which are oriented perpendicularly between the layers (fig. 4A-E). Presumably the matrix is composed of different

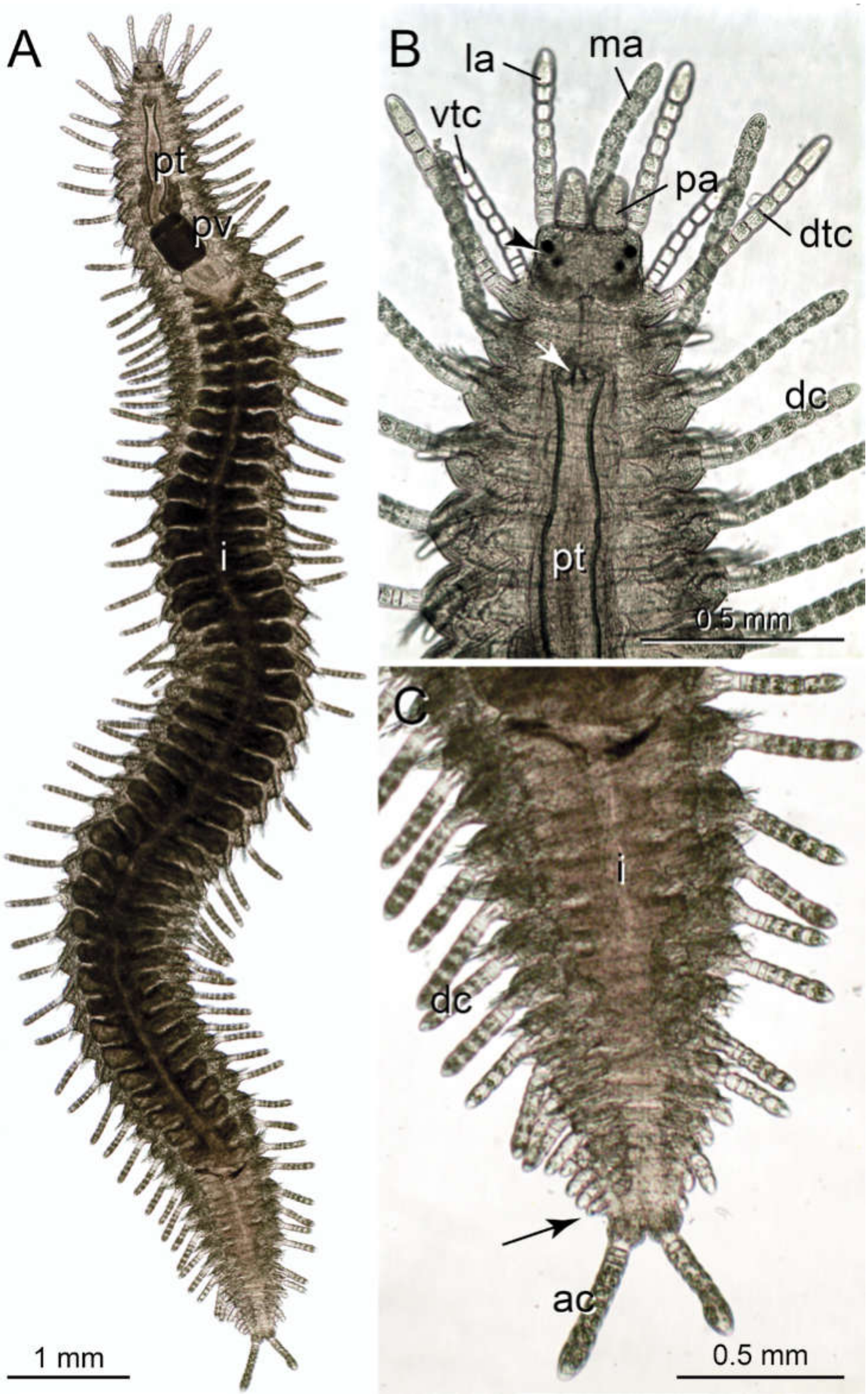

Figure 3. General organization of an annelid exemplified with *Trypanosyllis coeliaca* (Errantia, Syllidae). A. Entire animal. B. Enlargement of head region; arrowhead: pigmented eyes; arrow: pharynx tooth. C. Posterior end with growth zone (arrow). - ac = anal cirrus, dc = dorsal cirrus, dtc = dorsal tentacle cirrus, i = intestine, la = lateral antenna, ma = median antenna, pa = palp, pt = pharyngeal tube, pv = proventricle. Micrographs of living specimen.

mucopolysaccharides and hyaluronic acid (Hausen, 2005b). The uppermost part is usually devoid of collagen fibres and is called an epicuticle. The cuticle is traversed by microvilli extending above the surface and either forms isolated epicuticular projections or multiple tips. This uppermost part is covered by a glycocalix. A cuticle exhibiting these characteristics is found in all major annelid clades including Sipuncula, although considerable variation occurs (fig. 4A-E). The cuticle may vary in thickness, number of microvilli, or development of collagen fibres. Especially in larvae and adults of small or interstitial species the collagen fibres appear to be less developed, sometimes more irregularly arranged or even absent. In these cases the cuticle more or less resembles the egg envelope from which it originates (Eckelbarger, 1978). However, there are other examples of polychaetes with less well-developed layers of collagen fibres among polychaetes such as found in chaetopterids, oweniids, magelonids, apistobranchids and psammodrilids (fig. 4 D, E; Kristensen and Nørrevang, 1982, Hausen, 2001, 2005b, 2007). Absence of collagen fibres in the cuticle is thus observed in most groups belonging to the basal radiation according to Weigert et al. (2014) indicating that the presence of grids of collagen fibres probably is an autapomorphy of the clade comprising Amphinomida , Sipuncula and Pleistoannelida. Thus, the relevance of the cuticle as a phylogenetic important character and as a possible autapomorphy of the entire group has so far been underestimated (Purschke, 2002).

Chaetae and Parapodia

Chaetae are generally regarded as the most characteristic and important taxonomic feature of Annelida. They constitute the most thoroughly studied annelid structures (for references see Rouse and Fauchald, 1995, 1997; Westheide, 1997; Rouse and Pleijel, 2001; Hausen, 2005a). Chaetae have various functions and may aid in locomotion on the substrate, anchoring the body inside the tubes, protecting and defending the body, supporting parapodia, etc. Accordingly they show an extraordinary structural diversity and often exhibit species-specific characters (Hausen, 2005a). On the basis of light microscope investigations several types of chaetae are distinguished (Rouse, 2000; Rouse and Pleijel, 2001). The most common type represented by thin tapering cylinders is the simple or capillary chaetae, which may be smooth or have various additional substructures and ornamentations (fig. 5A, F). Capillaries are often regarded as representing the plesiomorphic type (Rouse and Fauchald, 1997; Rouse and Pleijel, 2001; Struck et al., 2011).

Irrespective of their external diversity, the formation and ultrastructure of chaetae appears very uniform: Each chaeta is made up of many longitudinal tubules consisting of chitin cross-linked by proteins situated in epidermal follicles. Chaetae are formed by a single cell called a chaetoblast and its dynamic microvilli are responsible for the variations in form and diameter of tubules as well as the external structure of the

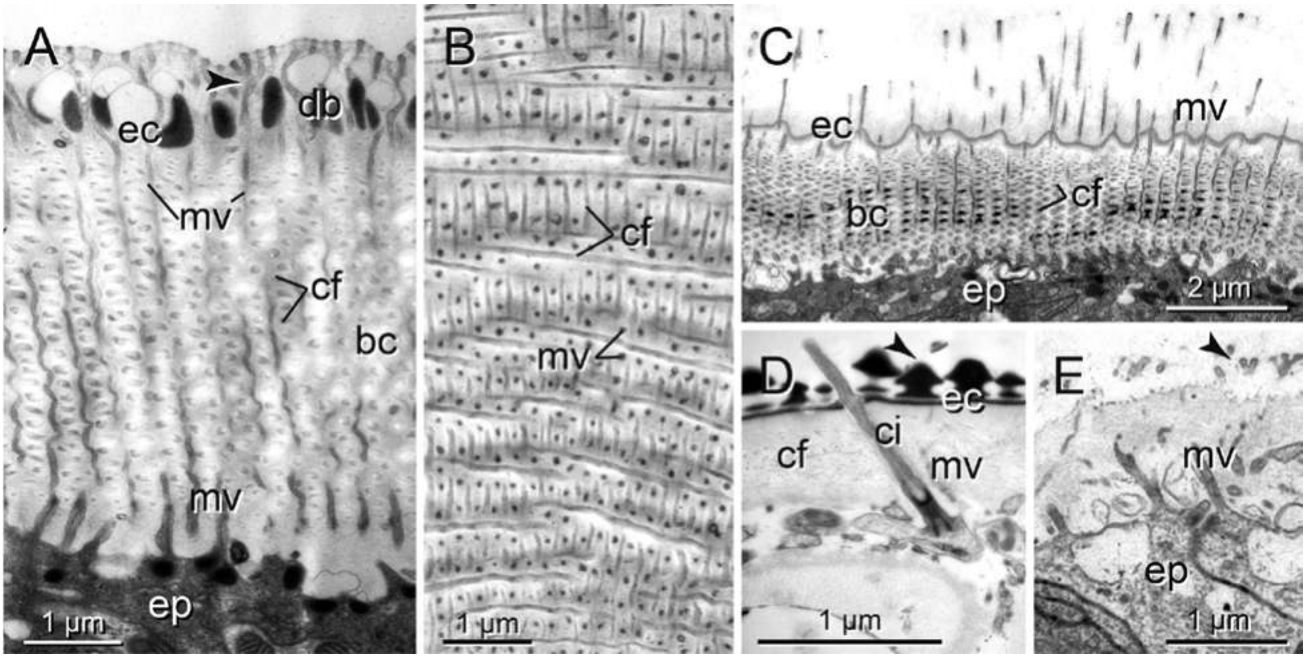

Figure 4. Cuticle ultrastructure of annelids. A-B. *Eurythoe complanata* (Amphinomidae). A. Cross section of cuticle on the trunk. Cuticle made up of layers of parallel collagen fibres (cf) traversed by microvilli (mv), which branch apically above the epicuticle (ec, arrowhead), epicuticle (ec) with dense bodies (db). B. Tangential section showing arrangement of collagen fibres and microvilli. C. *Polygordius appendiculatus* (Polygordiidae). Microvilli extend far above epicuticle (ec). D. *Sphaerodoropsis minuta* (Sphaerodoridae). Cuticle with irregularly arranged hardly visible collagen fibres (cf), covered by dark disk-like structures (arrowhead); cuticle traversed by cilium (ci) of receptor cell. E. *Ophiodromus pallidus* (Hesionidae). Cuticle without collagen fibres, microvilli branch above cuticle (arrowhead). – bc = basal cuticle, cf = collagen fibre, ci = cilium, db = dense body, ec = epicuticle, mv = micovillus. TEM micrographs.

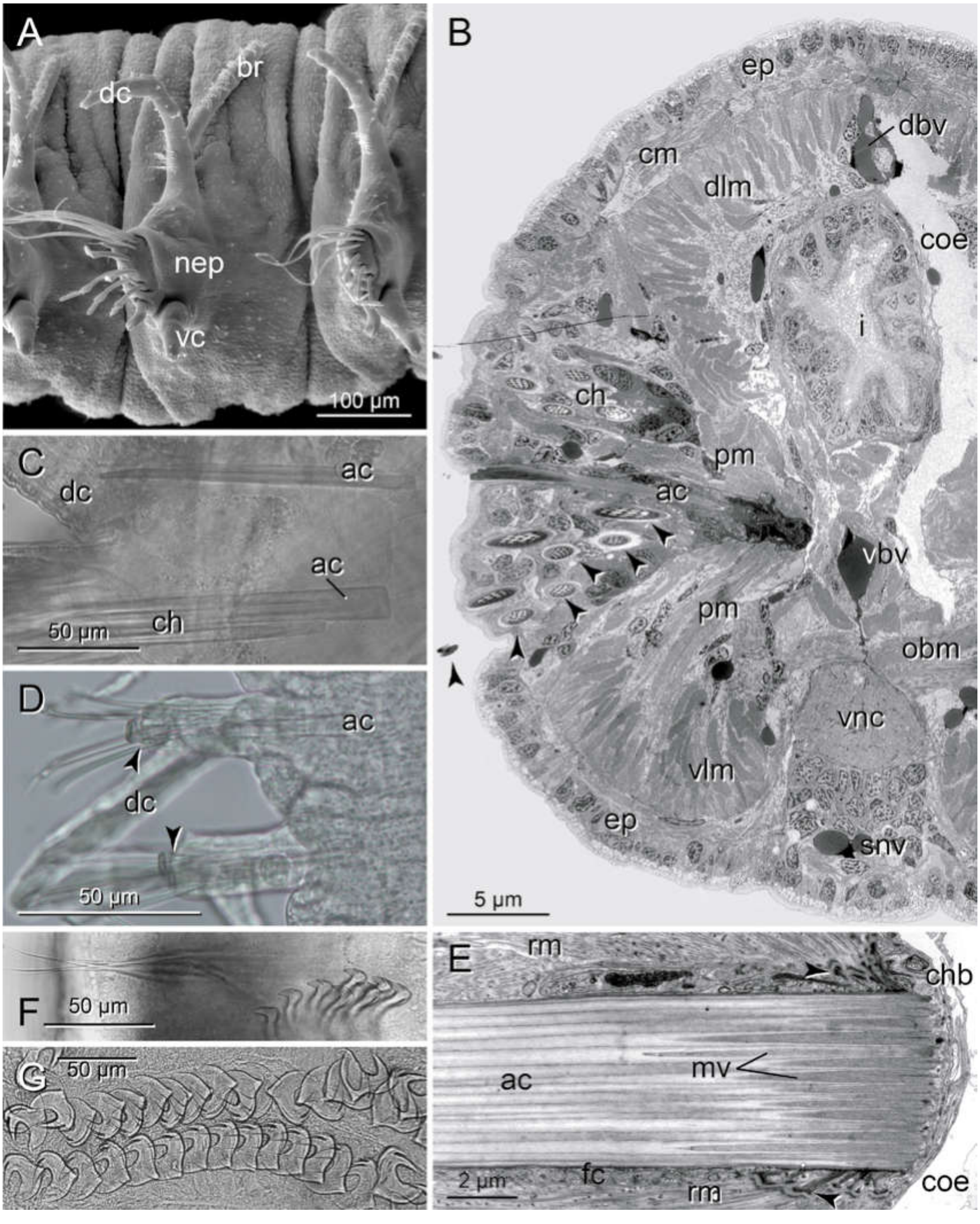

Figure 5. Parapodia and chaetae. A. *Eunice pennata* (Eunicidae); parapodium comprised of dorsal cirrus (dc), neuropodium (nep), ventral cirrus (vc) and branchia (br); acicula invisible. SEM micrograph. B. *Scoloplos armiger* (Orbiniidae). Cross section showing parapodium with supportive chaetae and chaetal sac; arrowheads point to sectioned chaetae. TEM micrograph. C. *Syllidia armata* (Hesionidae); notopodium restricted to dorsal cirrus and acicula (ac). D. *Streptosyllis websteri* (Syllidae). Aciculae (ac) extending outside parapodial lobe (arraowheads). E. *Sphaerodopsis minuta* (Sphaerodoridae). Acicula with chaetoblast (chb); arrowheads point to junctional complexes. F. *Fabricia stellaris* (Sabellidae). Parapodium of thorax with capillaries and uncini. G. *Lanice conchilega* (Terebellidae). Uncini. - ac = acicula, br = branchia, ch = chaeta, cm = circular muscle, coe = coelom, dc = dorsal cirrus, dlm = dorsal longitudinal muscle, ep = epidermis, dbv = dorsal blood vessel, fc = follicle cell, i = intestine, mv = microvillus, nep = neuropodium, obm = oblique muscle, pm = protractor muscle, rm = retractror muscle, snv = subneural blood vessel, vbv = ventral blood vessel, vc = ventral cirrus, vlm = ventral longitudinal muscle, vnc = ventral nerve cord. C, D, F, G: micrographs from living specimens, slightly squeezed.

chaetae (fig. 5B, E; Purschke, 2002; Hausen, 2005a). As a rule these tubules show diminishing diameters from the centre to the periphery. The chaetoblast forms the base of an epidermal follicle lined by follicle and typical epidermal supportive cells; the follicle cells lacking a cuticle (fig. 5E). Follicle cells and the chaetoblast also function in mechanical coupling of the chaeta due to prominent myoepithelial junctions, extensive intermediate filaments and apical hemidesmosomes (fig. 5E; Specht, 1988; Hausen, 2005a). Depending on the arrangement and function chaetae may be individually moveable or form functional groups situated in a common chaetal sac.

Among the various types of chaetae, a few have been used to define higher-level in-group relationships including aciculae (fig. 5B-D, E), uncini, hooks (fig. 5F, G) and paleae (Bartolomaeus et al., 2005; Hausen, 2005a). The former are supportive chaetae in parapodia, deeply anchored in the tissues and normally not exposed to the exterior although in certain taxa they can protrude slightly (fig. 5B-D; Fauchald and Rouse, 1997; Rouse and Pleijel, 2001; Hausen, 2005a). Aciculae are not formed in the same chaetal sacs as the other chaetae in the same fascicle (fig. 5B). These chaetae function as skeleton for the entire parapodial lobes. Aciculae have been regarded as being homologous in Amphinomida, Eunicida and Phyllodocida and represent the most important synapomorphic character uniting these groups as Aciculata (Rouse and Fauchald, 1997). However, supporting chaetae are also present in other polychaete groups such as Chaetopteridae, Orbiniidae, Apistobranchidae, Psammodrilidae and Myzostomida (Hausen, 2005a). Nevertheless, there is a still ongoing debate as to whether these supportive chaetae are homologous or convergent structures (Fauchald and Rouse, 1997; Rouse and Pleijel, 2001; Hausen, 2005a; Hoffmann and Hausen, 2007; Struck, 2011; Struck et al., 2011; Eibye-Jacobsen and Vinther, 2012). As stated by, e.g. Rouse and Pleijel (2001, p.23): "aciculae are formed exactly in the same manner as the projecting chaetae", this question can hardly be solved by morphological studies alone.

Other types of chaetae, which have received much attention, are the hooks and uncini. Such chaetae are usually present in tube-building polychaetes (fig. 5F, G). Due to a high degree of similarity in structure and in their process of formation they have been regarded to be homologous across polychaetes, potentially supporting a clade uniting those taxa bearing this character (Bartolomaeus et al., 2005; Hausen, 2005a). An opposite view was taken by Rouse and Fauchald (1997) who, based on their cladistic analyses, regarded uncini as being evolved independently in several lineages. Recent phylogenomic studies (Struck et al., 2011; Weigert et al., 2014) have not helped resolving this question, since taxa such as Oweniidae and Chaetopteridae, either possessing hooks or uncini, are part of the basal annelid radiation. Struck et al. (2011) indicated these chaetae as a possible apomorphy for Sedentaria and thus they also hypothesised convergent evolution of this type of chaetae. However, it has not been ruled out, whether these highly specific chaetae were also present in the annelid stem species and have been lost repeatedly. Parsimony-based ancestral character state reconstructions point to that direction.

Appendages of the prostomium - antennae and palps

Head appendages include antennae, palps, peristomial cirri and in more cephalised polychaetes also cirri of anterior segments (Rouse and Pleijel, 2001) (Figs 3A, B, 6A-E, 10G, I). Among these, only antennae and palps appear phylogenetically informative for the deep nodes since peristomial cirri are restricted to a few taxa within Eunicida and Phyllodocida.

Antennae are prostomial sensory appendages usually present in representatives of Amphinomida, Eunicida and Phyllodocida (Rouse and Pleijel, 2001; Purschke, 2002). There may be a pair of lateral antennae and an unpaired median antenna resulting in between 0 and 3 appendages. Generally they are more or less digitiform (Figs 6A, B, 7A, B) ranging from smooth to articulated and are divided into a basal ceratophore and a ceratostyle. Due to their corresponding innervation pattern they have been regarded as homologous throughout annelids (fig. 11F; Orrhage and Müller, 2005). Antennae are innervated from the dorsal commissure of the dorsal root of the circumoesophageal connectives. Each lateral antenna receives one nerve whereas in the median antenna there are two nerves separated by a muscle band attaching to its base. Whether this also applies for the unpaired median appendages (antennae or occipital tentacles) present in certain Spionidae and Paraonidae is a matter of discussion (see Orrhage, 1966; Fauchald and Rouse, 1997; Rouse and Pleijel, 2001; Orrhage and Müller, 2005). However, their innervation pattern is the same as in the median antenna of the errant forms and their homology would imply that they represent the plesiomorphic condition and that repeated losses have occurred in sedentary polychaetes. Again antennae may then be an autapomorphy of a clade comprising Pleistoannelida, Amphinomida and Sipuncula.

A pair of palps is present in many but not all annelids (Rouse and Pleijel, 2001; Purschke, 2002) (Figs 6A-E, 10G, I). In contrast to antennae, palps exhibit a considerably greater structural diversity. Often two types of palps are distinguished: prostomial (also called sensory or solid) and peristomial (also termed grooved, feeding or hollow) palps (Fauchald and Rouse, 1997; Rouse and Pleijel, 2001; Struck et al., 2011). However, irrespective of these classifications, it must be kept in mind that palps of any kind are sensory but only the so-called sensory palps are solely sensory (Amieva and Reed, 1987; Purschke, 2002, 2005).

Moreover, the terms solid or hollow palps are somewhat misleading, since all palps usually comprise mesodermal tissues at least in the form of musculature and often coelomic cavities as well (Orrhage, 1964, 1974; Gardiner, 1978; Amieva and Reed, 1987; Purschke, 1993). This is also the case for the palpophores of *Nereis* sp. which possesses sensory palps (fig. 6D, E). Irrespective of the presence of coelomic cavities, these mesodermal tissues are separated by a distinct extracellular matrix from the epidermis and nerves (Purschke, 1993). Coelomic cavities forming hollow palps are for example present in Protodrilidae and Saccocirridae (fig. 6C; see Purschke, 1993, Purschke and Jouin-Toulmond, 1994), taxa which have been assigned by Rouse and Fauchald (1997) to belong to Canalipalpata and which lack feeding palps.

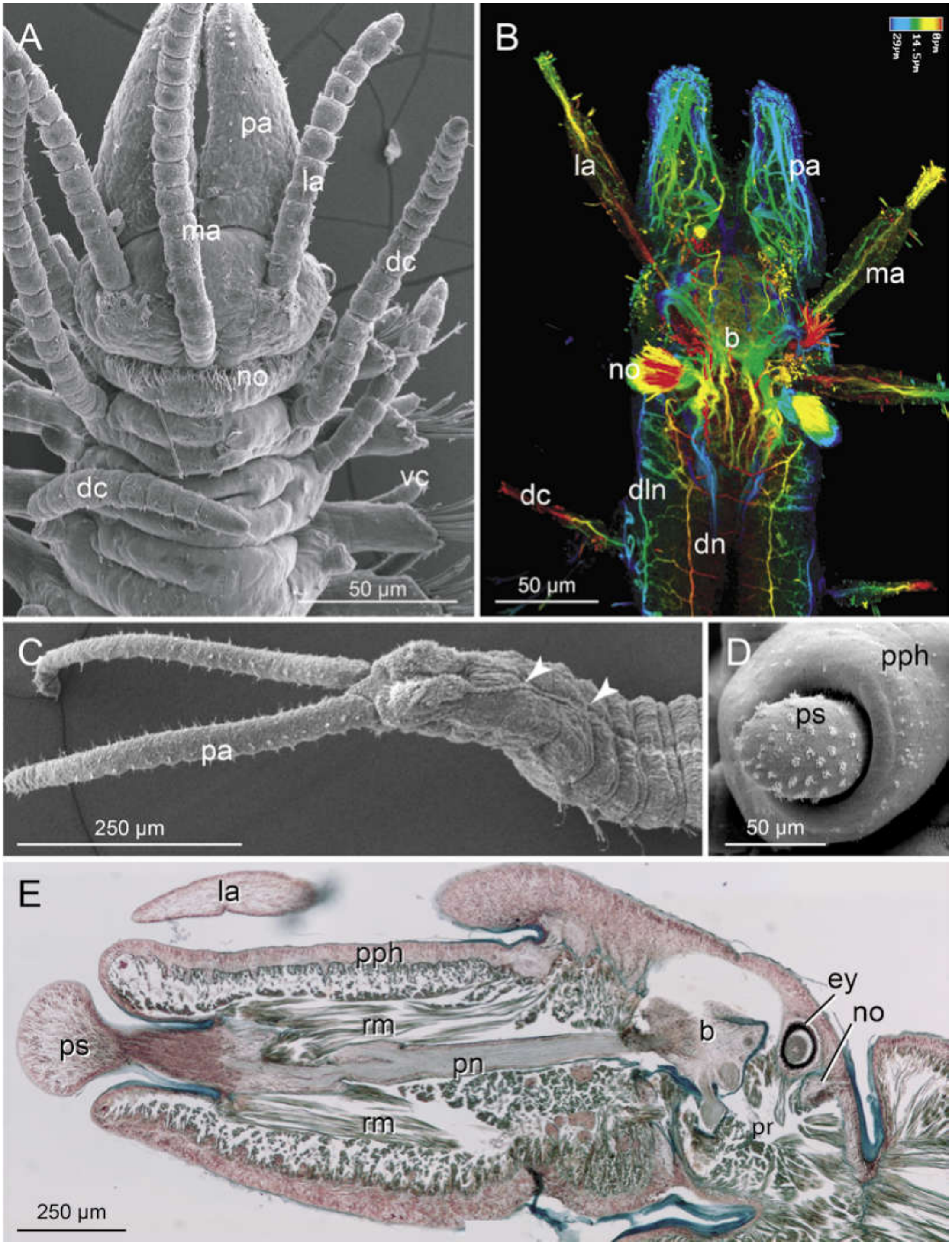

Figure 6. Head appendages and innervation. A. *Syllis* sp. (Syllidae). Anterior end with palps (pa), median (ma) and lateral antennae (la), nuchal organs (no), tentacular cirri on the right broken off. B. *Parapionosyllis labronica* (Syllidae). Dorsal view, nervous system labelled with antibody against acetylated □-tubulin, appendages supplied with prominent nerves, depth coding. C. *Saccocirrus* sp. (Saccocirridae). Ventral view, note ventral ciliated band (arrowheads), palps (pa) supplied with numerous ciliated sensory cells. D, E. *Nereis* sp. (Nereididae). Palp. D. Palp composed of palpophore (pph) and palpostyle (ps) the latter with numerous sensory cilia. E. Longitudinal section showing musculature and coelomic cavity inside palpophore (pph) and connection of palp nerve (pn) with the brain (b). - b = brain, dc = dorsal cirrus, dln = dorsolateral nerve, dn = dorsal nerve, ey = eye, la = lateral antenna, ma = median antenna, no = nuchal organ, pa = palp, pn = palp nerve, pph = palpophore, pr = prostomium, ps = palpostyle, rm = retractor muscle, vc = ventral cirrus. A, C, D: SEM micrographs, Originals S. Raabe & W. Mangerich, Osnabrück; B: cLSM micrograph, original M. Kuper, Osnabrück; E: Azan staining.

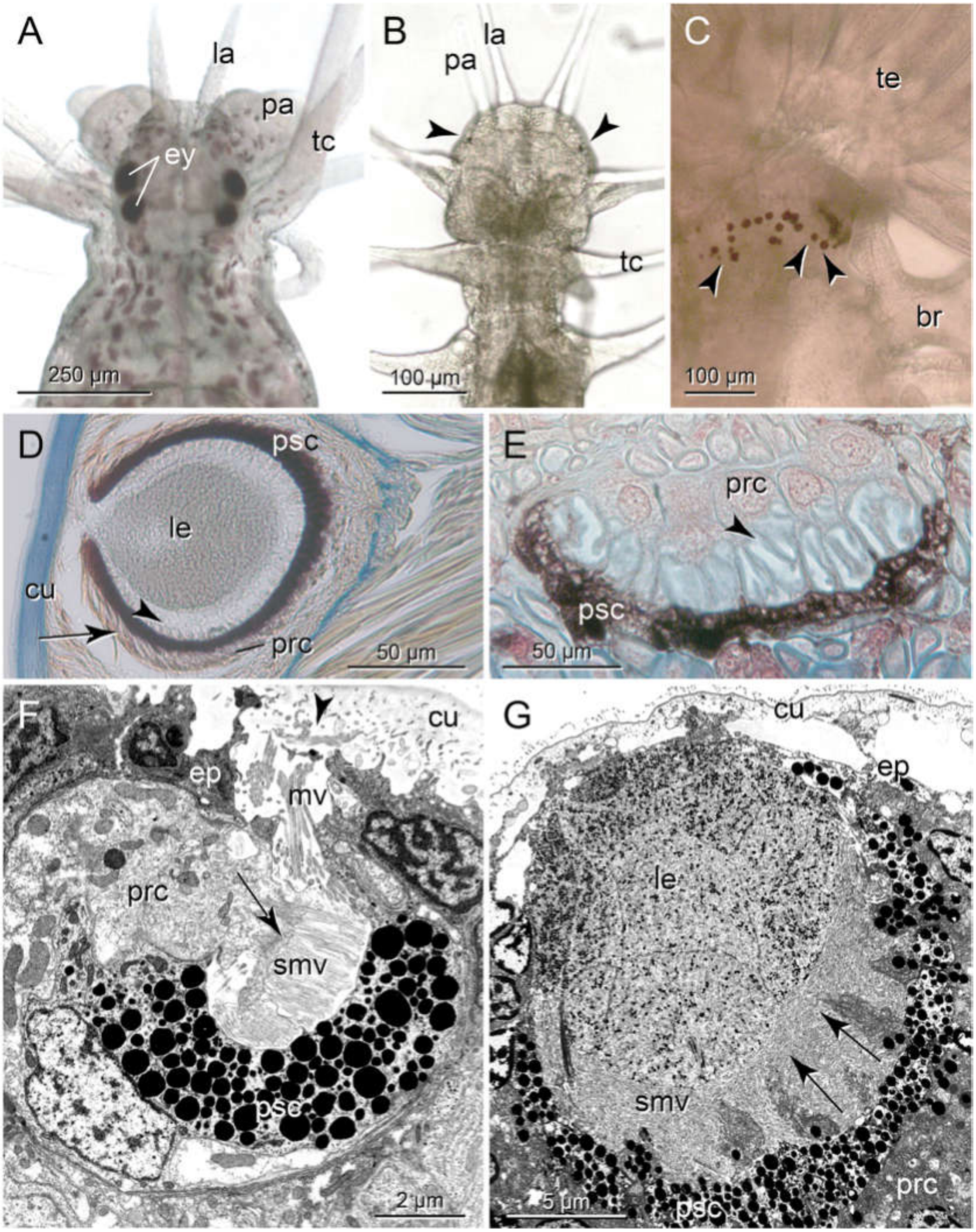

Figure 7. Pigmented eyes. A. *Platynereis dumerilii* (Nereididae). Two pairs of adult eyes (ey) situated on the prostomium. B. *Microphthalmus similis* (Errantia, incertae sedis). Arrowheads point to small prostomial eyes. C. *Nicolea zostericola* (Terebellidae). Numerous small pigmented eyes below tentacular crown (arrowheads). D. *Nereis* sp. (Nereididae). Section showing pigmented eye with lens (le); arrowhead points to zone with rhabdomeres, arrow: marks layer of cell bodies of photoreceptor cells below pigment cell layer (psc). E. *Piscicola geometra* (Clitellata). Pigmented eye with phaosomous photoreceptor cells (prc), arrowhead points to phaosomes. F. *Saccocirrus papillocercus* (Saccocirridae). Small pigmented eye, structurally indistinguishable from larval eye; arrow indicates inverse orientation of photoreceptive structures, eye cup communicates with exterior via small pore (arrowhead). G. *Gyptis propinqua* (Hesionidae). Multicellular-pigmented eye with lens, arrows indicate converse orientation of photoreceptive processes. - br = branchia, cu = cuticle, ep = epidermis, ey = eye, la = lateral antenna, le = lens, pa = palp, prc = photoreceptor cell, psc = pigmented supportive cell, smv = sensory microvilli, tc = tentacular cirri, te = tentacle. A-C: micrographs from living animals; D, E: histological sections, Azan staining; F, G: TEM micrographs.

However, this placement has not been supported by recent molecular phylogenetic investigations and so their systematic position remains unresolved (e. g. Struck et al., 2008; Zrzavý et al., 2009; Golombek et al., 2013). Also *Protodriloides* (Fig 1E), which is regarded as closely related to these taxa, possesses palps without coelomic cavities but with musculature and blood vessels (Purschke, 1993). Moreover, in molecular analyses by Struck et al. (2008) and Zrzavý et al. (2009) Polygordiidae usually fall in the same clade comprising Protodrilidae and Saccocirridae although Polygordiidae may be one of only a few examples for polychaetes with true "solid" palps since their stiff palps lack both musculature and coelomic cavities (Wilkens and Purschke, 2009a). The same applies to the appendages of Sphaerodoridae which are devoid of musculature and are stiff as well (Filippova et al., 2010). Previously it has been assumed that palps of all errant taxa lack musculature, coelomic cavities and blood vessels (Purschke, 2005). But analyses of Syllidae and Dorvilleidae as well as of Nerillidae revealed the presence of well-developed musculature in the palps of errant polychaetes (Filippova et al., 2006, 2010; Müller and Worsaae, 2006). A highly developed muscular system is also present in, e.g., the palps of adults in Magelonidae (see Filippova et al., 2005), which are placed in the basal part of the annelid tree in a recent phylogenomic analysis (Weigert et al., 2014).

Irrespective of whether adult palps are prostomial or peristomial, they are regarded as homologous due to their corresponding innervation from the dorsal and ventral roots of the circumoesophageal connectives (Fauchald and Rouse, 1997; Rouse and Pleijel, 2001; Orrhage and Müller, 2005). There are up to 12 palp nerve roots, which can be homologised due to their positions and relations to other nervous elements (Figs 6E, 11F; Orrhage and Müller, 2005). However, no annelid taxon studied to date exhibits all these roots and so far a ground pattern has not been reconstructed. Usually there are two main palp nerve roots (comparatively thick nerves

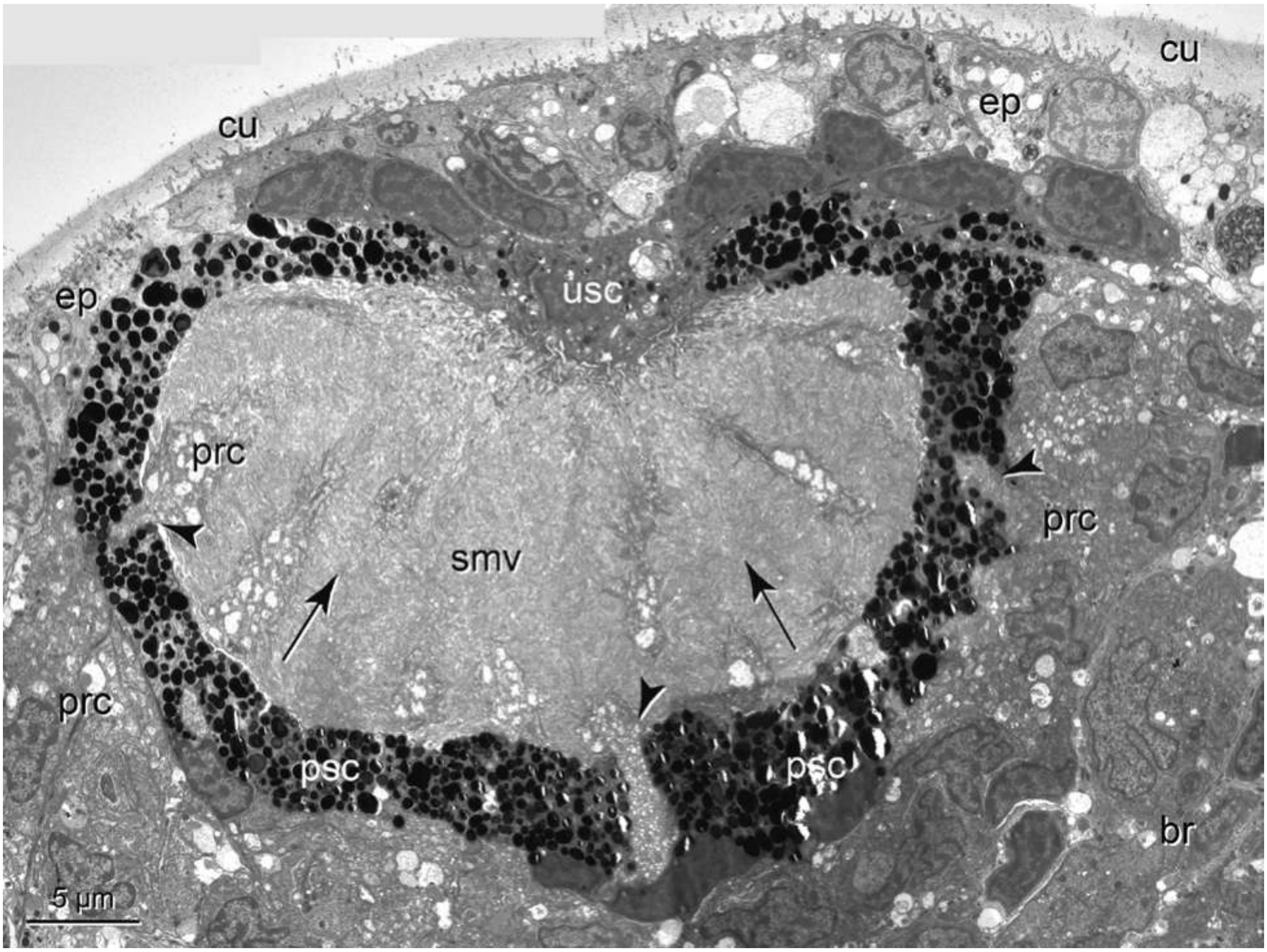

Figure 8. *Macrochaeta clavicornis* (Acrocirridae). 2nd pair of pigmented eye, typical multicellular adult eye with converse oriented photoreceptive processes (arrows), lens absent. Pigment cup formed by a layer pigmented supportive cells (psc) penetrated by processes of rhabdomeric photoreceptor cells (prc), pupil formed by unpigmented supportive cells (usc). Cu = cuticle, ep = epidermis, prc = photoreceptor cell, psc = pigmented supportive cell, smv = sensory microvilli, usc = unpigmented supportive cells. Original: I. Dykstra, Osnabrück.

comprising numerous neurites) which are situated on both circumoesophageal roots (fig. 11F). Some roots appear to be restricted to a smaller group of taxa such as roots Nos. 1, 2 and 3 which have only been found in Sabellariidae, Serpulidae and Sabellidae. On the other hand, roots No. 6 on the ventral and root No. 9 on the dorsal root of the circumoesophageal connective have been reported in most taxa investigated and may be promising candidates for having been present in the

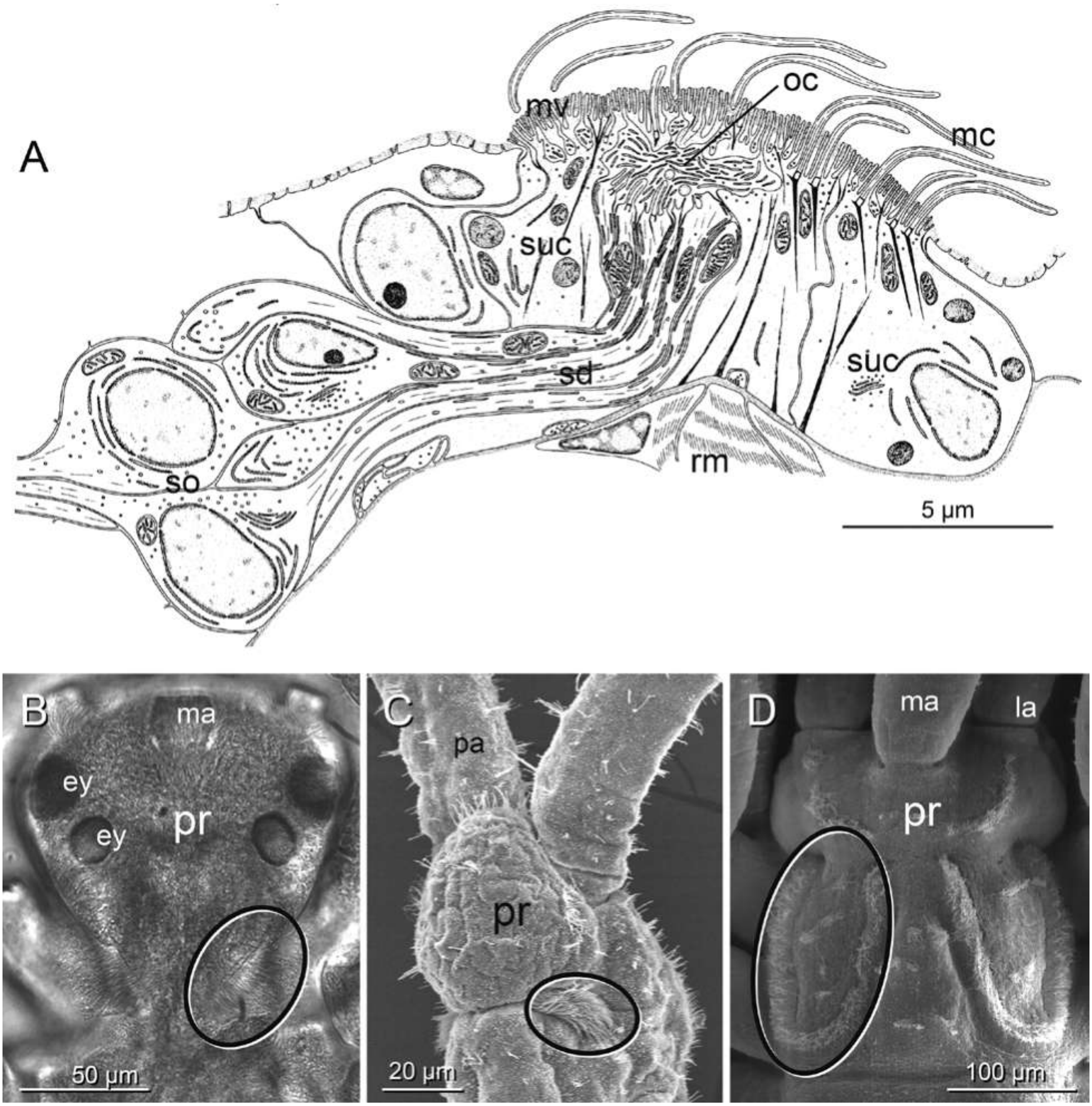

Figure 9. Nuchal organs. A. Schematic representation of nuchal organ in *Nerillidium troglochaetoides* (Nerillidae). After TEM observations, modified from Purschke (1997). B. *Eusyllis* (?) sp. (Syllidae). Nuchal organs (encircled) visible as ciliary patches in the posterior region of the prostomium, micrograph from living animal. C. *Saccocirrus* sp. (Saccocirridae). Nuchal organs form oval patches (encircled). D. *Myrianida prolifera* (Syllidae). Nuchal epaulettes form u-shaped ciliary band extending posteriorly on peristomium and 1st chaetiger. - ey = eye, la = lateral antenna, ma = median antenna, mc = motile cilium, mv = microvillus, oc = olfactory chamber, pa = palp, pr = prostomium, rm = retractor muscle, sd = sensory dendrite, so = soma of receptor cell, suc = supportive cell. C, D: SEM micrographs, W. Mangerich, S. Raabe, Osnabrück.

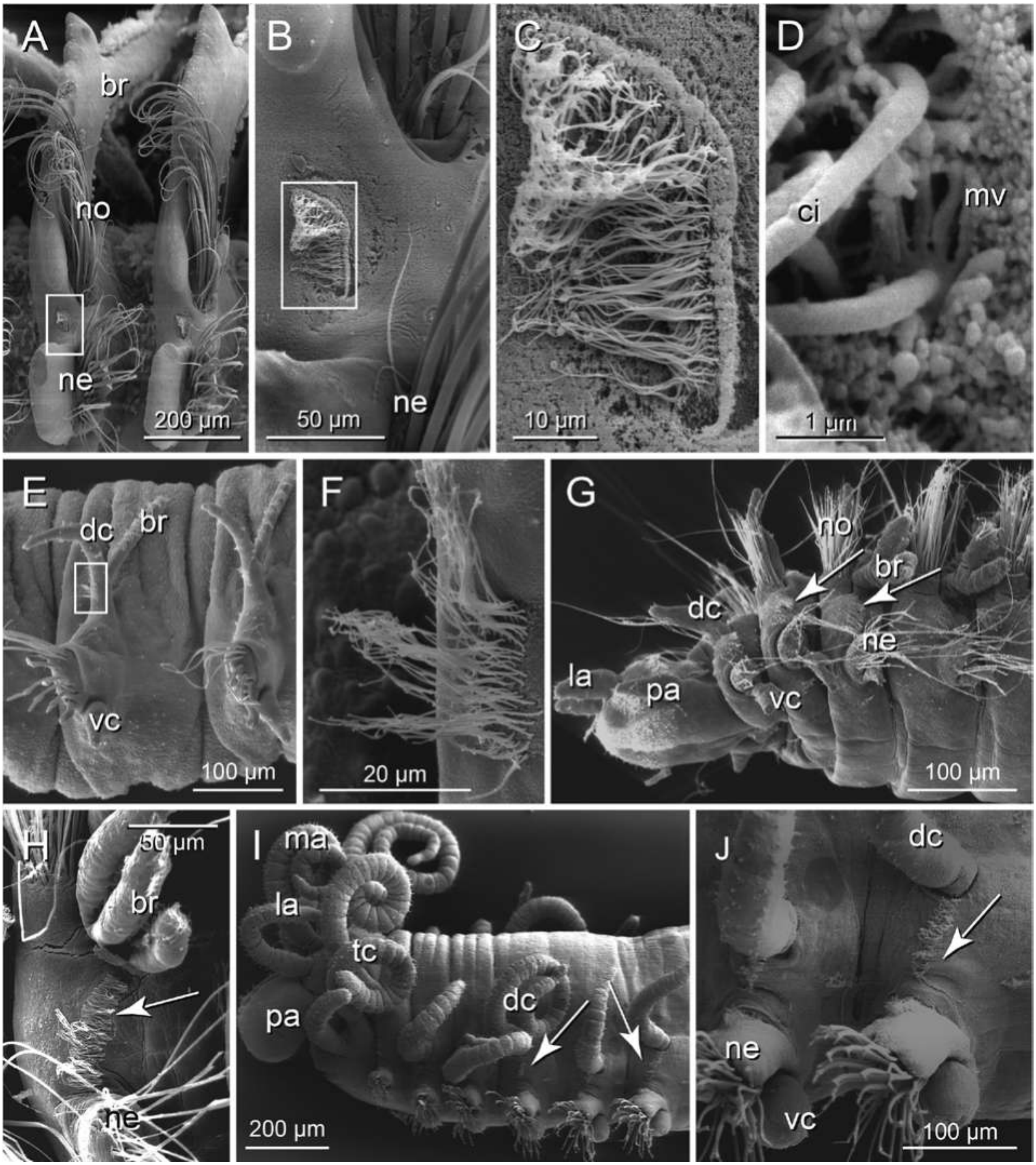

Figure 10. Lateral organs. A-D. *Malacoceros fuliginosus,* (Spionidae). A. 2 parapodia with lateral organ (boxed) between noto- (no) and neuropodium (ne). B. Enlargement of left parapodium, lateral organ visible as ciliary brush. C. Enlargement of B, note cilia arranged in distinct rows. D. Base of 2 collar receptors with single sensory cilium (ci) and circle of microvilli (mv). E-F. *Eunice pennata* (Eunicidae). Lateral organ (dorsal cirrus organ). E. 2 parapodia showing position of lateral organ (boxed). F. Enlargement of boxed area from E. G-J. Lateral organ like ciliary bands of unknown function between noto- and neuropodia in polychaetes. G-H. *Eurythoe complanata* (Amphinomidae). G. Anterior end, lateral view; arrows point to ciliary bands between noto- and neuropodia. H. enlargement of parapodium. I-J. *Syllis* sp. (Syllidae). I. Anterior end lateral view, parapodia with ciliary bands (arrows). J. Enlargement of parapodia with ciliary bands (arrow). - br = branchia, no = notopodium, ne = neuropodium, ci = cilium, mv = microvillus, dc = dorsal cirrus, vc = ventral cirrus, la = lateral antenna, pa = palp, ma = median antenna, tc = tentacular cirrus. SEM Micrographs; originals E, F M: Nesnidal, Osnabrück, G-J S; Raabe, Osnabrück

annelid ground pattern (Wilkens and Purschke, 2009b). Taxa regarded as belonging to the basal radiation (see Weigert et al., 2014) do not show a unique pattern but at least nerve root No. 6 is usually present. In developing and regenerating spionids the palps buds appear at the posterior edge of the prostomium and their peristomial position is achieved later on (e.g. Blake and Arnofsky, 1999; Lindsay et al., 2008). This feature may suggest a prostomial origin in general. Also in Apistobranchidae the palps are inserted in front of the nuchal organs and should therefore be prostomial. However, a prostomial origin may not be supported by observations in cirratulids (Petersen, 1999) where the palps originate more posteriorly.

Most of the palp-less taxa have been placed in Scolecida by Rouse and Fauchald (1997). They regard the absence of palps as the plesiomorphic character state in their "Scolecida-Palpata" hypothesis whereas in the "Errantia-Sedentaria" hypothesis absence is interpreted as a loss which must have happened more than once (Bartolomaeus et al., 2005, Struck, 2011; Struck et al., 2011; Weigert et al., 2014).

The entire prostomium is a highly sensory area innervated by a complicated network of nerves originating from the brain independent of the palp nerve roots (see Orrhage and Müller, 2005). Interestingly, such palp nerve roots have also been reported from taxa which do not possess palps (Scalibregmatidae, Paronidae and Orbiniidae; see Orrhage and Müller, 2005; Wilkens and Purschke, 2009b). This has been taken as an indication of reduction of palps in those taxa, rather than their primary absence. While representatives of several scolecidan taxa have not been investigated, preliminary investigations in Opheliidae (Purschke, unpubl. obs.) indicate occurrence of palp nerve roots in this family which contradicts previous studies (Orrhage, 1966). In certain species of Scalibregmatidae a secondary gain of palps from prostomial horns has been hypothesised based on a cladistics analysis (Martínez et al., 2013).

On the other hand, the tentacles present in the terebellomorph polychaetes Alvinellidae, Ampharetidae, Pectinariiidae, and Terebellidae have been regarded as representing multiple grooved palps (Rouse and Pleijel, 2001), even though from the structure of the anterior nervous system there is no evidence for the existence of palps and antennae in the latter three families (Orrhage, 2001). Instead it has been concluded that the tentacles of these belong to the alimentary canal and should be termed buccal tentacles (Orrhage, 2001). Moreover, their central nervous system appears to be highly derived and structurally simple (Orrhage, 2001; Heuer et al., 2010). However, this has been questioned by Zhadan and Tzetlin (2002). Likewise, a proof that the appendages in Siboglinidae are really palps is still lacking although normally assumed (see Rouse and Pleijel, 2001).

Eyes

Most annelids possess some kind of photoreceptor cells or light sensitive organ (Rouse and Pleijel, 2001; Purschke, 2005; Purschke et al., 2006). Due to their extreme structural diversity they have been regarded as difficult to evaluate in phylogenetic analyses (Fauchald and Rouse, 1997). There may be up to three different types of photoreceptor cells (PRCs): rhabdomeric PRCs, ciliary PRCs and phaosomous PRCs (Figs 7E-G, 8). The former two types, rPRCs and cPRC, occur with supportive cells either with shading pigment (PSC) or without pigment (USC). Only eyes (or ocelli) with PSC allow discrimination of the direction of light source (for reviews see Purschke, 2005; Purschke et al., 2006). These eyes may be divided into different types: larval and adult eyes (characterised by their molecular fingerprint and usually by their different structure) as well as cerebral and so-called ectopic eyes occurring elsewhere on the body (Purschke et al., 2006; Arendt et al., 2009). Depending on the taxa considered there may be 0, 1, 2 or 3 pairs of cerebral eyes (fig. 7A-C); and certain species may possess more eyes and sometimes in odd numbers (e. g. Terebellidae).

Larval type of eye. The so-called larval type of eye usually consists of only two cells: a PSC and an rPRC forming an inverse ocellus with the sensory processes projecting away from the incoming light (fig. 7F; Purschke, 2005; Purschke et al., 2006). In certain cases these eyes are still part of the epidermal epithelium and connected to the outside via a small pore (e. g. *Saccocirrus* spp. fig. 7F; see Arendt et al., 2009). Such ocelli are generally present in trochophores and may be formed and functional within 24 h after fertilisation (Dorresteijn, 2005). Such simple eyes are perfectly adapted sensory structures for positive or negative phototaxis (Jékely et al., 2008). Such eyes may occur in adults of certain species as well and, based on structural data, it is impossible to determine if they represent persisting larval eyes or diminutive adult eyes. With few exceptions of specialised eye types such larval type eyes have been regarded as being restricted to adults of sedentarian taxa (Purschke et al., 2006; Purschke and Nowak, 2013). The fate of the larval eyes in ontogeny is not completely known as it is, hard to follow especially in large species. Moreover, whereas formerly a replacement by the adult eyes has generally been assumed to occur besides rare cases of persistence (Purschke et al., 2006; Purschke and Nowak, 2013), recent investigations indicate probable persistence even in species for which a replacement by the adult eyes has been assumed (Backfisch et al., 2013). A unique example of larval eyes being transformed into adult eyes occurs in *Capitella teleta* (Yamaguchi and Seaver, 2013). So in this species the adult eyes are a mixture of both larval and adult eye structures and further studies are needed to determine how often this phenomenon occurs in other species.

Adult type of eye. Typical adult eyes in annelids are multicellular comprising rPRCs with shading pigment, PSCs and USCs. These cells form a continuous epithelium in which rPRCs and PSCs intermingle resulting in a converse (everse) eye with the sensory processes projecting towards the light (Figs 7D, F, G, 8; Purschke et al., 2006; Suschenko and Purschke, 2009). As these eyes develop from epidermal anlagen, they may still be connected with the exterior by a more or less prominent duct (Purschke and Nowak, 2013). Adult eyes of this kind are known to occur in Phyllodocida, Eunicida and Amphinomida, whereas lenses, which are typically formed by the PSCs, have only been found among Phyllodocida (Purschke et al., 2006; Suschenko and Purschke, 2009). Very likely, two pairs of adult eyes belong to the ground pattern of Phyllodocida, Eunicida and Amphinomida. Given the phylogenetic hypothesis of Weigert et al. (2014) this means this is a plesiomorphic feature that has been lost secondarily in Sedentaria. On each side the eyes develop from a common anlage and split into two eyes each after initial formation (Dorresteijn, 2005; Backfisch et al., 2013). However, in these taxa several representatives exist which usually possess rather small eyes of unknown affiliation to either larval or adult eyes. This is especially the case for the so-called eyespots which are present in many representatives of Syllidae, but also occurs in several other members of these groups. So far only a few species have been investigated. Several examples of miniaturisation of adult eyes are reported in errant polychaetes (Purschke and Nowak 2013; Purschke unpubl. obs.).

In sedentarian polychaetes miniaturised adult eyes are present as well, for example in *Fauveliopsis* cf. *adriatica* and with respect to their proposed phylogenetic position more importantly in the orbiniid *Scoloplos armiger* (Wilkens and Purschke, 2009b; Purschke, 2011). The pigmented eyes of Sipunculida are also structurally similar to the adult eyes of polychaetes (Purschke, 2011), which are especially important in the "new annelid phylogeny" where Sipuncula are part of the annelid radiation (Dordel at al., 2010; Weigert et al., 2014). Among Sedentaria, Flabelligeridae and Accrocirridae are known to possess rather large eyes and should be examined to determine if they represent typical adult annelid eyes. Whereas Flabelligeridae have been described to possess an unusual platyhelminth type of pigmented eye of inverse design (see Purschke et al., 2006), preliminary observations in *Macrochaeta clavicornis* (Sars, 1835) (Accrocirridae), which possess three pairs of eyes, an anterior minute pair and two larger pairs situated more posteriorly, showed that the minute eye probably is a reduced adult eye. The second pair is an adult eye without doubt (fig. 8) and the most posterior pair is of the platyhelminth type. This implies that the inverse eye most likely represents a new acquisition in a taxon at least comprising these two families within Cirratuliformia. However, these studies have to be extended to more species of Cirratuliformia to test this hypothesis. Further investigations must show whether the small eyes present in other sedentarian annelids also represent miniaturised adult eyes. For *Capitella teleta* Blake et al., 2009 it may be that the eye is unique as it is a mixture of the larval and adult eye (Yamaguchi and Seaver, 2013). Also the findings in the leech *Helobdella robusta* (Shankland et al., 1991), fit into this general picture (Döring et al., 2013). It could be shown that the PRCs probably have been derived from those of the adult annelid eye, whereas the eyes as such evolved *de novo* in the stem lineage of leeches (e.g. fig. 7E).

In summary, gene expression studies support that the larval eye in annelids is homologous to the pigmented eyes of other bilaterians (e. g. under control of *pax6*; Arendt et al., 2002; Dorresteijn, 2005; Backfisch et al., 2013; Döring et al., 2013). At some point in the annelid lineage adult eyes must have evolved, no later than in the last common ancestor of Amphinomidae, Sipuncula and Pleistoannelida. Whether they might already belong to an earlier emerging lineage has yet to be determined and needs to be investigated in Oweniidae, Magelonidae, Apistobranchidae and Chaetopteridae which are regarded as belonging to the first, basal radiation in annelids (Struck, 2011; Weigert et al,. 2014). However, histological investigations of *Chaetopterus variopedatus* indicate that adult eyes are present (Martin and Anctil, 1984). Probably there are parallel events of miniaturisations and progressive reductions or losses of adult (and larval) eyes, one of which is characteristic for the lineage comprising most sedentary groups including Clitellata (Döring et al., 2013). Besides the pigmented eyes there are other photoreceptive structures, which may have a similar phylogenetic importance but further investigations are necessary (see Hausen, 2007; Wilkens and Purschke, 2009a).

Nuchal organs

Nuchal organs are situated at the posterior edge of the prostomium and are visible as densely ciliated structures, which can be withdrawn in many forms (fig. 9A-D) (Purschke, 1997, 2002, 2005). Especially in many burrowing, tube-building sessile or terrestrial forms they may be completely internalised. Despite their external diversity (fig. 9B-D) they show an overall structural similarity and are composed of a few identical cell types throughout (fig. 9A). Thus, their homology is generally accepted (Rouse and Fauchald, 1997; Rouse and Pleijel, 2001; Purschke, 2005).

Whereas their absences in polychaetes usually were regarded as losses, the absence of nuchal organs in Clitellata was mostly seen as primary resulting in recognition of nuchal organs as the most important autapomorphy for the taxon Polychaeta (Rouse and Fauchald, 1997). On the other hand, there is evidence that there is a high probability that Clitellata have also lost nuchal organs (e. g. Purschke, 1997, 1999, 2000, 2002). Interestingly, all molecular phylogenetic studies conducted so far revealed Clitellata in a highly derived position among the polychaetes supporting the latter view (Weigert et al., 2014). By contrast, some taxa such as Oweniidae need to be re-examined to determine if nuchal organs are present as vestiges, or if they are really absent. Thorough investigations by Hausen (2001) confirmed the absence of nuchal organs in two species of *Magelona* and presence in Apistobranchidae. At present it remains unresolved whether these structures were present in the last common ancestor of Annelida or have evolved later within the annelids.

Lateral organs

Ciliated bands, papillae or pits which occur between noto- and neuropodia in many sedentary polychaetes represent sensory organs consisting of two types of uniciliated receptor cells and supportive cells (Purschke and Hausen, 2007). These organs are commonly termed lateral organs (fig. 10A-D). Besides sedentary polychaetes, such organs have been shown to be present in Eunicida as well, here called dorsal cirrus organ due to the lack of a typical notopodium in these taxa (fig. 10E, F; Hayashi and Yamane, 1997; Purschke, 2002). However, in Eunicida only one receptor cell type is present (Hayashi and Yamane, 1997; Purschke, unpubl. obs.). Similar ciliary bands have also been observed in representatives of Amphinomidae and Syllidae, but histological investigations are still needed (fig. 10G-J).

For a robust phylogenetic assessment of the evolution of lateral organs data of some important taxa is missing and especially their occurrence in representatives of the basal annelid radiation should be (re)investigated. According to the literature lateral organs are present in Magelonidae and Apistobranchidae but absent in Chaetopteridae and Oweniidae (Fauchald and Rouse, 1997). However, their fine structure is unknown. Given a questionable presence in amphinomids the resulting picture currently is puzzling allowing several equally parsimonious explanations, either as ground pattern character or as convergently evolved structures occurring in several lineages.

Central nervous system

The central nervous system in Annelida is generally described as a rope-ladder nervous system consisting of a prostomial brain connected with the ventral nerve cord via double circumoesophageal connectives (Bullock and Horridge, 1965; Orrhage and Müller, 2005; Müller, 2006; Lehmacher et al., 2014). The ventral nerve cord was generally seen as rope-ladder-like chain of paired segmental ganglia connected by connectives and commissures. However, as already stated by Bullock and Horridge (1965) a considerable degree of variation in polychaetes exists making it difficult to deduce phylogenetic hypotheses (fig. 11A-H).

Müller (2006) considered a nervous system with the following characters as the ground pattern in annelids: (1) paired circumoesophageal connectives consisting of dorsal and ventral roots interconnected via two intracerebral commissures each; (2) a ventral nerve cord comprising primarily five connectives; (3) numerous commissures per segment; (4) numerous segmental nerves per segment and (5) peripheral nervous system with several longitudinal pairs of nerves and one median unpaired nerve. The highest numbers reported so far are 17 longitudinal nerves in *Saccocirrus papillocercus* (see Orrhage and Müller, 2005) and up to 18 segmental nerves in *Polygordius appendiculatus* (see Lehmacher et al., 2014). Thus the entire nervous system has an orthogonal appearance and a typical rope-ladder-like nervous system is a rare exception or does not exist at all (fig. 11A-E). From this pattern all nervous system structures observed may have derived. For instance, the most common polychaete nervous system shows partly fused circumoesophageal connectives, whereas in clitellates they are completely fused forming simple connectives throughout (fig. 11C, D). Interestingly, during ontogenesis and regeneration experiments this fusion can be observed and each annelid nervous system starts with double circumoesophageal roots (e.g. Hessling and Westheide, 1999; Müller, 2004, 2006; Müller and Henning, 2004). The same applies for the structure of the ventral cord.

The question of whether the nervous system has a basiepithelial or subepidermal position in the ground pattern is still a matter for discussion. However, as already discussed (Bullock and Horridge, 1965; Martin and Anctil, 1984; Purschke, 2002; Orrhage and Müller, 2005) a basiepidermal position is more common than formerly thought. Interestingly, species with a subepidermal position of the nervous system in adults may have a basiepidermal position in juveniles (e.g., *Scoloplos armiger;* Purschke, unpubl. obs.). In this case ontogeny may reflect the direction of evolution for this character. In many species the ventral nerve cord usually lies between the ventral longitudinal muscle bands bulging into the body cavity but is still part of the epidermis as documented by a continuous ECM with the epidermis (Figs 5B, 11E). As a consequence circular muscle fibres are generally interrupted in this area (Lehmacher et al., 2014). Alternatively, the nerve cord may be subepithelial for a short distance allowing the circular fibres to pass below it.

Whether the nerve cord was actually a medullary cord (fig. 11B) and not subdivided into connectives and ganglia (fig. 11C, D) in the ground pattern is another point of discussion. However, this seems to be a comparatively rare case in Annelida occurring in highly derived annelids such as oligochaetous Clitellata and a few polychaetes such as *Polygordius* spp. (see Lehmacher et al., 2014). Although ganglia and connectives are reported to occur in *Chaetopterus variopedatus* (see Martin and Anctil, 1984), annelid species regarded to be part of the basal radiation should be reinvestigated for this character.

Within the polychaete brain several ganglia (neuropils encased by associated neuronal somata) may be distinguished (fig. 11F-G; Orrhage and Müller, 2005). There are more than 25 pairs in errant forms whereas especially in many sedentary species there are no distinguishable ganglia at all (Heuer et al., 2010). Thus, with a few exceptions the former authors discouraged any efforts of homologising ganglia in annelids. However, recently, the so-called mushroom bodies, which were first identified by Holmgren (1916) in polychaetes, came back into the phylogenetic discussion (fig. 11G, H; Heuer et al., 2010). Heuer et al. (2010) regarded mushroom bodies as an ancient structure already present in the annelid stem species and their absence in many annelids as reductions. Since typical mushroom bodies have only been shown to exist in Nereididae and Aphroditiformia and to a lesser degree in a few other errant taxa, as an alternative it has been proposed that mushroom bodies evolved within Errantia or even in one or some of their subtaxa as well as independently in arthropods (Struck, 2012; Struck et al., 2014). This view is held because so far these structures are unknown in any taxon regarded to be basal in the annelid radiation irrespective of which of the conflicting hypotheses is considered (fig. 2A, B).

Musculature

A body wall musculature consisting of an outer layer of circular and an inner layer of longitudinal fibres was generally considered to represent the annelid ground pattern (Dales, 1963; Pilato, 1981; Purschke and Müller, 2006). These muscles may be accompanied by other muscle systems such as oblique, diagonal, bracing and dorso-ventral fibres as well as muscles belonging to the parapodia. The existence of these different muscles indicates that the entire muscular system in annelids is highly diverse and complex. In the meantime, it is generally accepted that the longitudinal fibres do not form a complete cylinder rather they are arranged in discrete bands with four bands representing the ground pattern (fig. 5B; Rouse and Fauchald, 1995, 1997; Tzetlin and Filippova, 2005, Lehmacher et al., 2014). Usually the musculature is ventrally interrupted

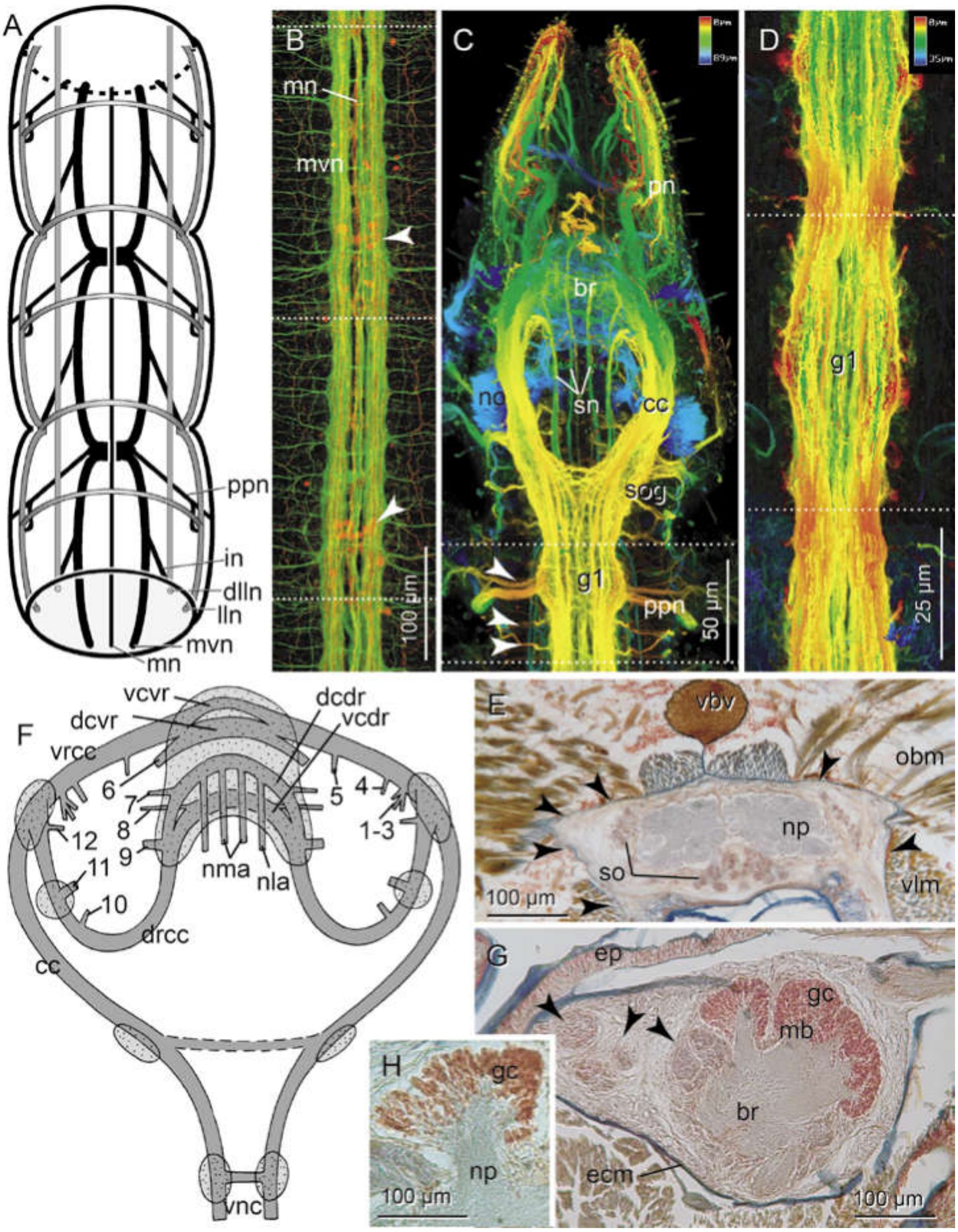

Figure 11. Nervous system and brain. A. Nervous system of the trunk with longitudinal and segmental circular nerves exemplified by *Parapodrilus psammophilus* (Dorvilleidae). Ventral cord consists of unpaired median (mn) and main paired nerves (mvn). B-D. Anti α-tubulin immunoreactivity; dotted lines indicate segment borders. B. *Polygordius appendiculatus* (Polygordiidae), ventral nerve cord (green) comprising three closely apposed neurite bundles, serotonergic perikarya (red) in a repetitive pattern although distinct ganglia are absent (medullary cord). Note high number of segmental nerves. C-D. *Brania clavata* (Syllidae); depth coding images. C. Brain (b) and ventral nerve cord in ventral view, ventral cord consists of several closely apposed nerves forming 3 bundles behind 1st ganglion (g1), 4 segmental nerves (arrowheads, ppn) in each segment; brain gives rise to several stomatogastric nerves (sn). D. Ventral cord in the trunk region. F. General diagram of the cephalic nervous system in polychaetes, numerals refer to palp nerve roots, somata stippled. E-H. *Nereis* sp. (Nereididae). E Ventral nerve cord in basiepithelial position (arrowheads refer to epidermal extracellular matrix). F. Parasagittal section with mushroom bodies (mb), note subepithelial position of brain; arrowheads point to cerebral ganglia. H Enlargement of anterior part of mushroom body with stalks of globuli cells (gc). – br = brain, cc = circumoesophageal connective, dcdr = dorsal commissure of drcc, dcvr = dorsal commissure of vrcc, dlln = dorsolateral longitudinal nerve, drcc = dorsal root of cc, ecm = extracellular matrix, ep = epidermis, g1 = 1st ganglion, gc = globuli cell, in = intestine, lln = lateral longitudinal nerve, mb = mushroom body, mn = median nerve of ventral cord, mvn = main nerve of ventral cord, nla = nerve of lateral antenna, nma = nerve of median antenna, no = nuchal organ, np = neuropil, obm = oblique muscle, pn = palp nerve, ppn = parapodial nerve, sn = stomatogastric nerve, so = somata of neurites, sog = suboesophageal ganglion, vbv = ventral blood vessel, vcdr = ventral commissure of drcc, vcvr = ventral commissure of vrcc, vlm = ventral longitudinal muscle, vrcc = ventral root of cc. A, F: modified from Müller and Orrhage (2005). Micrographs; B C: Lehmacher, C, D: M. Kuper, Osnabrück.

and separated by the ventral nerve cord and this may also apply to the circular fibres. These latter fibres are always less developed than the longitudinal ones and are likely to be absent in a number of taxa. Whether these absences are plesiomorphic or apomorphic is still being discussed and requires more data from a variety of polychaete taxa (see Tzetlin and Filippova, 2005; Purschke and Müller, 2006). Since these fibres are sometimes very delicate, investigations with modern methods such as cLSM are highly desirable (see Lehmacher et al., 2014). Recently, the oblique fibres running from the lateral sides to the ventral midline received closer attention and apparently their importance has been underestimated probably because the situation as present in earthworms had been regarded as representing the annelid ground pattern (see Purschke and Müller, 2006 for discussion).

Conclusions

In conclusion the question as to which characters belong to the last common ancestor of annelids has not been resolved although there has been considerable progress in recent years. Probably, the last common ancestor of annelids had a biphasic life cycle with a planktonic acoelomate larva and a benthic coelomate adult (including blood vascular system and metanephridia), a collagenous cuticle without being arranged in layers of parallel fibres, an epidermis with at least a few ciliated cells (responsible for generating water currents or movements of the animals), a homonomous segmentation, longitudinal muscle bands, ill-defined or lacking circular muscle fibres, oblique muscles running to the ventral midline, a nervous system comprising a prostomial brain and a ventral nerve cord comprising five connectives linked to the brain via double circumoesophageal connectives and additional longitudinal nerves that give the entire nervous system an orthogonal appearance, a foregut with dorsolateral ciliated folds (microphagous deposit feeder), a gut forming a straight tube, simple chaetae and parapodia and a head consisting of a prostomium and a peristomium with feeding palps, larval bicellular eyes and adult multicellular eyes.

Such adult eyes are not restricted to the errant forms and among the putative basal branching groups multicellular adult eyes are present at least in Chaetopteridae, Sipuncula and Amphinomida. A duplication event of the adult eyes possibly occurred in the stem lineage of Amphinomida and Pleistoannelida. There is a high degree of probability of parallel events of miniaturisations and progressive reductions or even losses of adult (and larval) eyes, one of which is characteristic for the lineage comprising most sedentary groups including Clitellata. The latter possess unique photoreceptor cells (phaosomes) derived from typical annelid rhabdomeric photoreceptor cells and occasionally secondarily developed pigmented eyes (fig. 7E; Döring et al., 2013).

Whether nuchal organs belong to the annelid ground pattern (Rouse and Fauchald, 1995, 1997) currently remains unresolved since their absence in Oweniidae, Chaetopteridae, Magelonidae and Sipuncula has yet to be confirmed. A similar scenario is conceivable for the lateral organs as well as for other characters such as the basiepithelial position of the ventral nerve cord and whether it is divided into ganglia and connectives or represents a medullary cord. In view of the new molecular phylogeny (Struck et al., 2011; Weigert et al., 2014) several members of the basal branching groups should be re-investigated to elucidate the characters of the annelid stem species.

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