

## Morphology of the nervous system of Polychaeta (Annelida)

Lars Orrhage<sup>1</sup> & Monika C.M. Müller<sup>2,\*</sup>

<sup>1</sup>Berzeliigatan 21, S-412 53, Göteborg, Sweden

<sup>2</sup>Spezielle Zoologie, Fachbereich 5, Universität Osnabrück, D-49069 Osnabrück, Germany

(\* Author for correspondence: Tel.: +49-541-969-2858/2859, Fax: +49-541-969-2587,

E-mail: mcmueller@biologie.uni-osnabrueck.de)

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### Abstract

The article summarizes our up to date knowledge about the morphology of the annelid, especially the polychaete, central and peripheral nervous system. Since the cephalic nervous system was in the focus of controversial discussions for decades, the structure of its neuropile, associated ganglia and nerves is reviewed in detail. The enormous variation of the ventral nerve cord and peripheral nerves is presented as well as a theory how this might have evolved. A ground pattern of the polychaete nervous system is suggested, based on developmental and regeneration studies.

### Introduction

In Annelida as well as in other invertebrate taxa the nervous system is considered to be a most conservative organ system (Bullock & Horridge, 1965; Orrhage, 1974; Rouse & Fauchald, 1997; Müller, 1999b). Studies on the structure of the polychaete brain and the metameric nervous system have therefore proved to be of particular value in assessing homologies of various anterior appendages (Gustafson, 1930; Remane, 1963; Orrhage, 1974, 1980; Golding, 1992; Purschke & Jouin-Toulmond, 1994; Hessling & Purschke, 2000, Purschke, 2000) and of other structures. The morphology of the central nervous system (CNS) of Polychaeta was first investigated by dissection, then by light and electron microscopy and nowadays by combination of immunohistochemistry and confocal laserscanning microscopy (cLSM). Understanding the organization of the CNS is useful for (1) elucidating the interrelationships of the polychaete families, (2) resolving the much-debated question of the conceivable segmentation of the polychaete brain and (3) productively discussing the phylogenetic connections between Polychaeta and other invertebrate taxa (Orrhage, 1980–2001).

### The brain

Orrhage (1964–2001) and Orrhage & Eibye-Jacobsen (1998) analyzed the cephalic nervous system of 32 families of Polychaeta; in 28 of them the brain and associated nerves could be analyzed in detail.

#### *The commissures of the circumesophageal connectives*

Judging from his figures, Rohde (1887) discovered that the brain of *Lepidasthenia elegans* ('*Polynoe elegans*') contains four transverse commissures. Two of them (a dorsal and a ventral one, *dc*, *vc*) were in contact with an anterior (ventral, *vr*) circumesophageal root while the other two were connected to a posterior (dorsal, *dr*) root of the connectives. In the present chapter these commissures are designated *dcvr*, *vcvr*, *dcd* and *vcd*, respectively. Having examined Amphinomidæ, some Polynoidæ, Aphroditidæ and Nereididæ, Gustafson (1930) certified that Rohde's observations were applicable to 'all errant polychaetes'. Although at that time this statement could have seemed insufficiently well founded, later

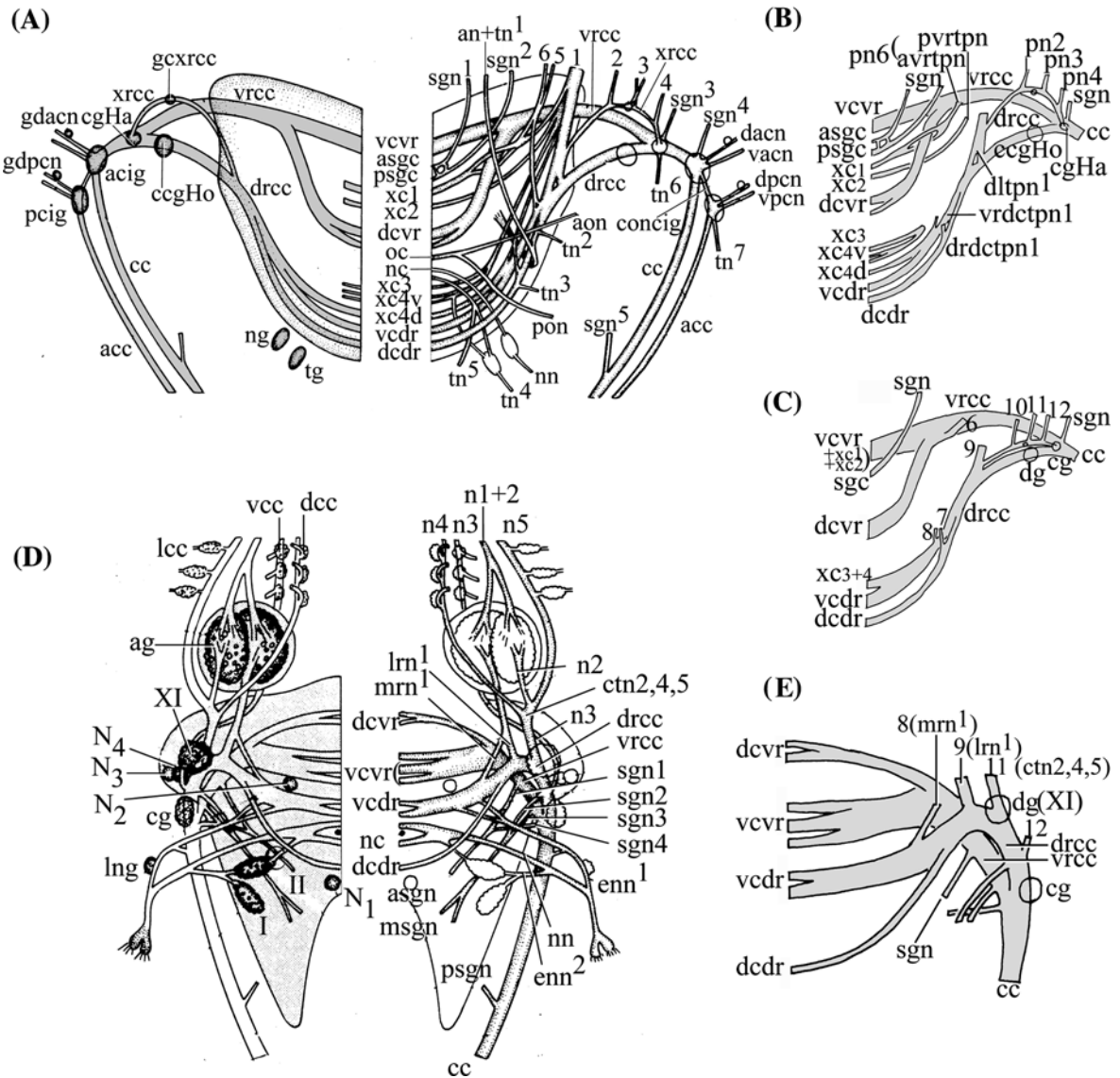
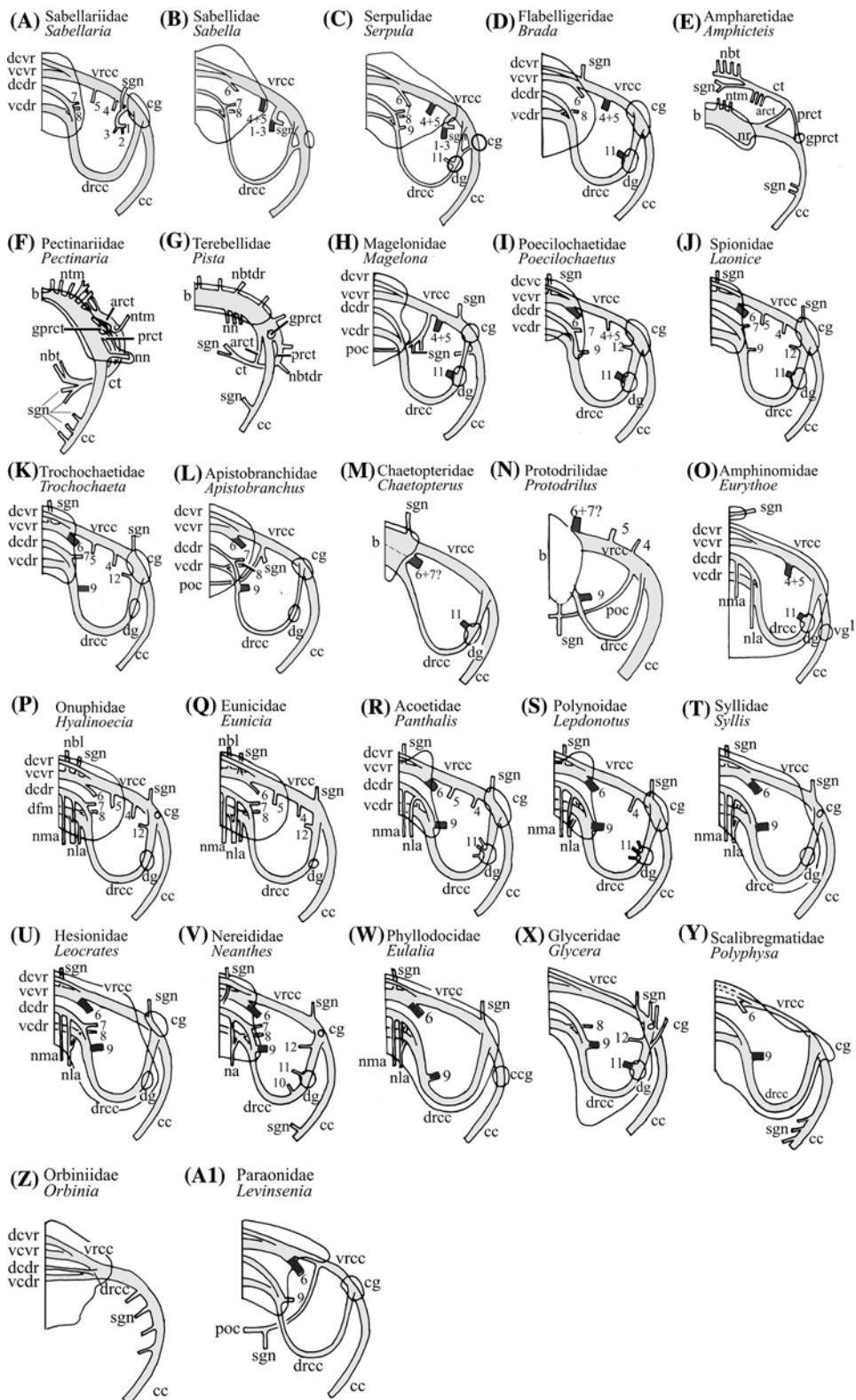


Figure 1. The cephalic nervous system of (A–C) *Neanthes virens*; (D, E) *Glycera rouxii*. Semi-schematic dorsal views. cc – circumesophageal connective; cg – cerebral ganglion; dcd, dcvr – dorsal commissure of the dorsal (drcc) and ventral (vrcc) root of cc; dg – dorsal ganglion; vcdr, vcvr – ventral commissure of the dorsal and ventral root of cc; 1–12 – palp nerve roots. Further abbreviations see abbreviation list. Modified from Orrhage (1993) (A–C); Orrhage (1999) (D, E).

Figure 2. The anterior part of the circumesophageal connective, its dorsal and ventral roots and their brain commissures (when observed). b-brain; nla - nerves of the lateral antenna (when present, O–U, W); nma – nerves of the median antenna (when present, O–U, W); na - nerves of antennae; sgn – stomatogastric nerves; 1–12 – roots of the palp nerves. The main palp nerve roots indicated by blackening. Dorsal view, right side, schematic. For further abbreviations see abbreviation list. Diagrams after or with reference to Orrhage, 1964 (I–K); Orrhage, 1966 (D, H, L, M, Y, Z, A1); Orrhage, 1974 and Purschke, 1993, combined (N); Orrhage, 1978 (A); Orrhage, 1980 (B, C); Orrhage, 1990 (O); Orrhage, 1991 (R, S); Orrhage, 1993 (V); Orrhage, 1995 (P, Q); Orrhage, 1996 (T, U); Orrhage & Eibye-Jacobsen, 1998 (W); Orrhage, 1999 (X); Orrhage, 2001 (E–G).



investigations have been instrumental in strengthening it. Thus, among the ‘errants’ these four transverse commissures are also present in Glyceridae (Figs 1D–E, 2X), Onuphidae and Eunicidae (Fig. 2P–Q), Acoetidae (Fig. 2R), Sigalionidae, Syllidae (Fig. 2T), Hesionidae (Fig. 2U), Phyllocodidae (Fig. 2W) and Goniadidae (Orrhage, 1990–1999; Orrhage & Eiby-Jacobsen, 1998). Many other ‘errant’ families still remain to be examined in greater detail.

Among the ‘sedentaries’, as well, these four transverse commissures have been observed: Sabellariidae (Fig. 2A), Sabellidae (Fig. 2B), Serpulidae (Figs 2C, 3A, B), Flabelligeridae (Figs 2D, 3D,E), Magelonidae (Fig. 2H), Poecilochaetidae (Fig. 2I), Spionidae (Figs 2J, 4A,B), Trochochaetidae (Fig. 2K), Apistobranchidae (Fig. 2L), Scalibregmatidae (Figs. 2Y, 5A,B), Orbiniidae (Figs 2Z, 5C,D), and Paraonidae (Figs 2A<sup>1</sup>, 5E, F) (Orrhage, 1964, 1966, 1978, 1980). Among Opheliidae and Cirratulidae, however, the arrangement is unclear (Orrhage, 1966). In Chaetopteridae (Figs 2M, 4C) it was not possible to analyze the brain in any detail; only an anterior and a posterior part of the neuropile could be discerned. In Protodrilidae (Figs 2N, 4D), Saccocirridae and Nerillidae not even TEM-analyses have revealed anything of the internal structure of the brain (Purschke, 1993, 1997; Purschke & Jouin-Toulmond, 1993, 1994). In the brains of Ampharetidae (Fig. 2E), Pectinariidae (Figs 2F, 3C) and Terebellidae (Figs 2G, 3F), finally, no traces of equivalents to the four commissures of the circumesophageal roots were found (Orrhage, 2001).

#### *Dorsal and ventral roots of the circumesophageal connectives*

In most polychaete families hitherto studied, each circumesophageal connective is proximally divided into a dorsal (*drcc*) and a ventral (*vrcc*) root. Each root on one side of the animal communicates with that on the other side through two commissures, a dorsal and a ventral one (cf. above). In most families the ventral roots lie in front of the dorsal ones. In Sabellariidae, however, all four roots and their commissures are situated in approximately the same transversal plane. In Sabellidae, Serpulidae and Phyllocodidae the *vrcc* is in fact situated behind the *drcc*. More or less laterally the

two roots on each side join, forming a single circumesophageal connective. Thus, von Haffner (1959a, b) maintained that the connectives are simple in the Onuphidae, and according to Ehlers (1864), Gravier (1898), Hanström (1927), Stolte (1932), Manaranche (1966) and Åkesson (1968) this is the case also with the Glyceridae. Even in these families, however, each connective is divided into two roots (e.g., Glyceridae: Müller, 1999b). In all probability the difficulties encountered by earlier authors can be explained by the fact that in these families the circumesophageal roots are rather short, in the Glyceridae almost not at all visible outside the brain proper (see also section on neuronal differentiation).

Division of each connective into a dorsal and a ventral root is also found in *Protodrilus* sp. (Orrhage, 1974; Bubko, 1981; Purschke, 1993), *Saccocirrus papillocerus* and *S. krusadensis* (Purschke, 1992, 1993), *Parenterodrilus taenioides* (Purschke & Jouin-Toulmond, 1993, 1994), *Nerillidium troglochaetoides* (Purschke, 1997), Nerillidae (*Mesonerilla intermedia*, *Nerillidium mediterraneum*, *Nerilla antennata*; Müller, 1999b) and *Aeolosoma hemprichi* (Purschke et al., 2000). In Opheliidae the conditions seem a little less clear (Orrhage, 1966) and in *Protodriloides* (Purschke, 1993) as well as in Ampharetidae, Pectinariidae and Terebellidae the connectives are simple.

*Conclusions about the two roots and their commissures.* The presence of double connectives and their four transverse commissures (the later were found in 26 of the 32 families) is a unique and widespread phenomenon within the Polychaeta. This speaks in favor of these structures being old and distinctive characteristics of the Polychaeta, homologous in the families where they are found. Because nothing comparable is present in the Clitellata (Purschke et al., 2000) or Arthropoda, this pattern might be an apomorphy of the Polychaeta and represent part of the cephalic ground pattern. Absence of the dorsal root and the four commissures in the ‘terebellomorph’ families as well as in the Myzostomidae (Müller & Westheide, 2000), however, reduces confidence in this ground pattern.

#### *The optic commissure and the optic nerves*

Only some of the studied forms have eyes and even a comparative study of the families that are

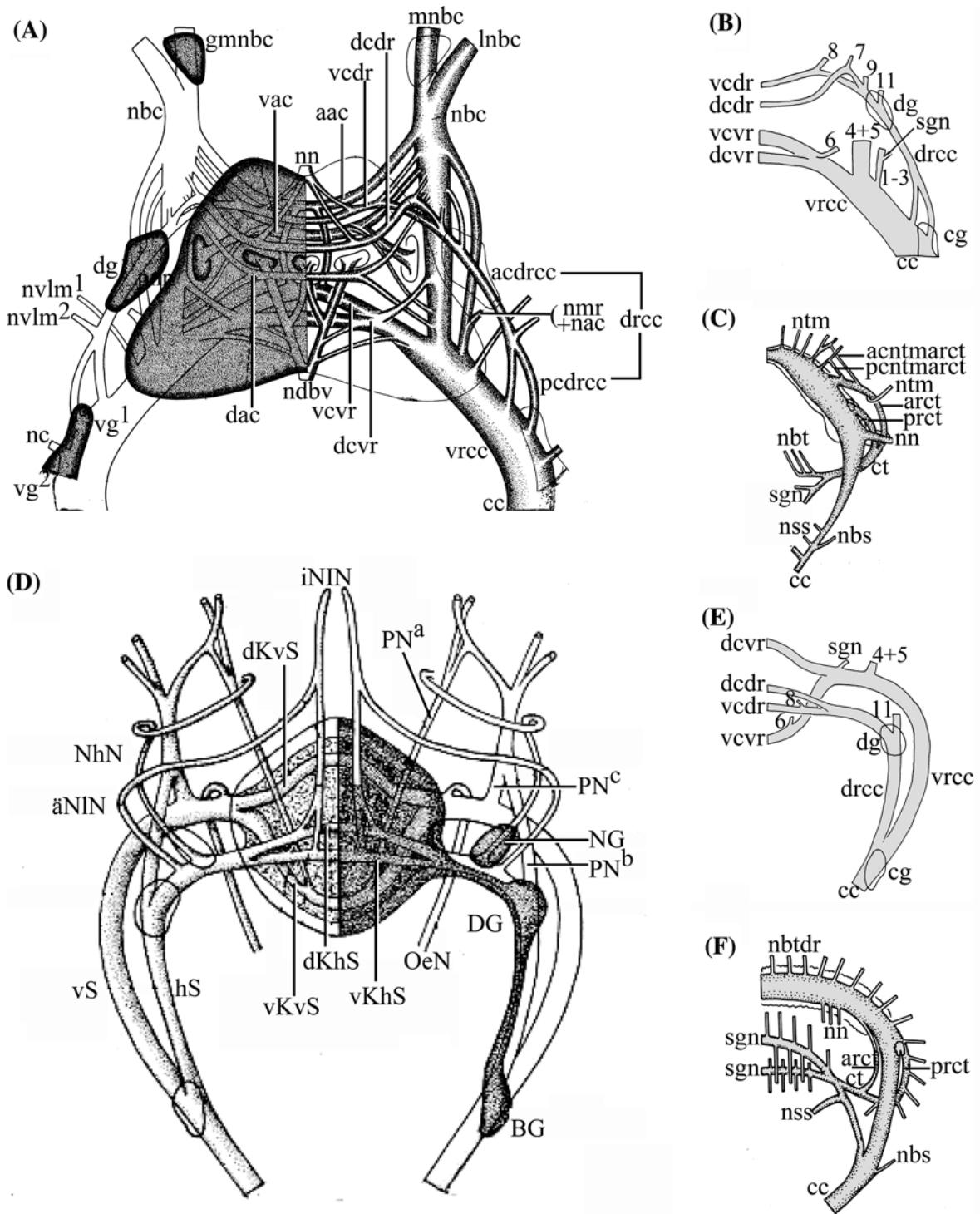


Figure 3. The cephalic nervous system of (A, B) *Serpula vermicularis*; (C) *Pectinaria (Amphictene) auricoma*; (D, E) *Brada vilosa*; (F) *Pista cristata*. Semi-schematic dorsal views. cc – circumesophageal connective; cg – cerebral ganglion; dcd, devr – dorsal commissure of the dorsal (drcc) and ventral (vrcc) root of cc; dg – dorsal ganglion; sgn – stomatogastric nerve; vcd, vcvr – ventral commissure of the dorsal and ventral root of cc; 1–11 – palp nerve roots. Further abbreviations see abbreviation list. Modified from Orrhage, 1980 (A, B); Orrhage, 2001 (C, F); Orrhage, 1966 (D, E).

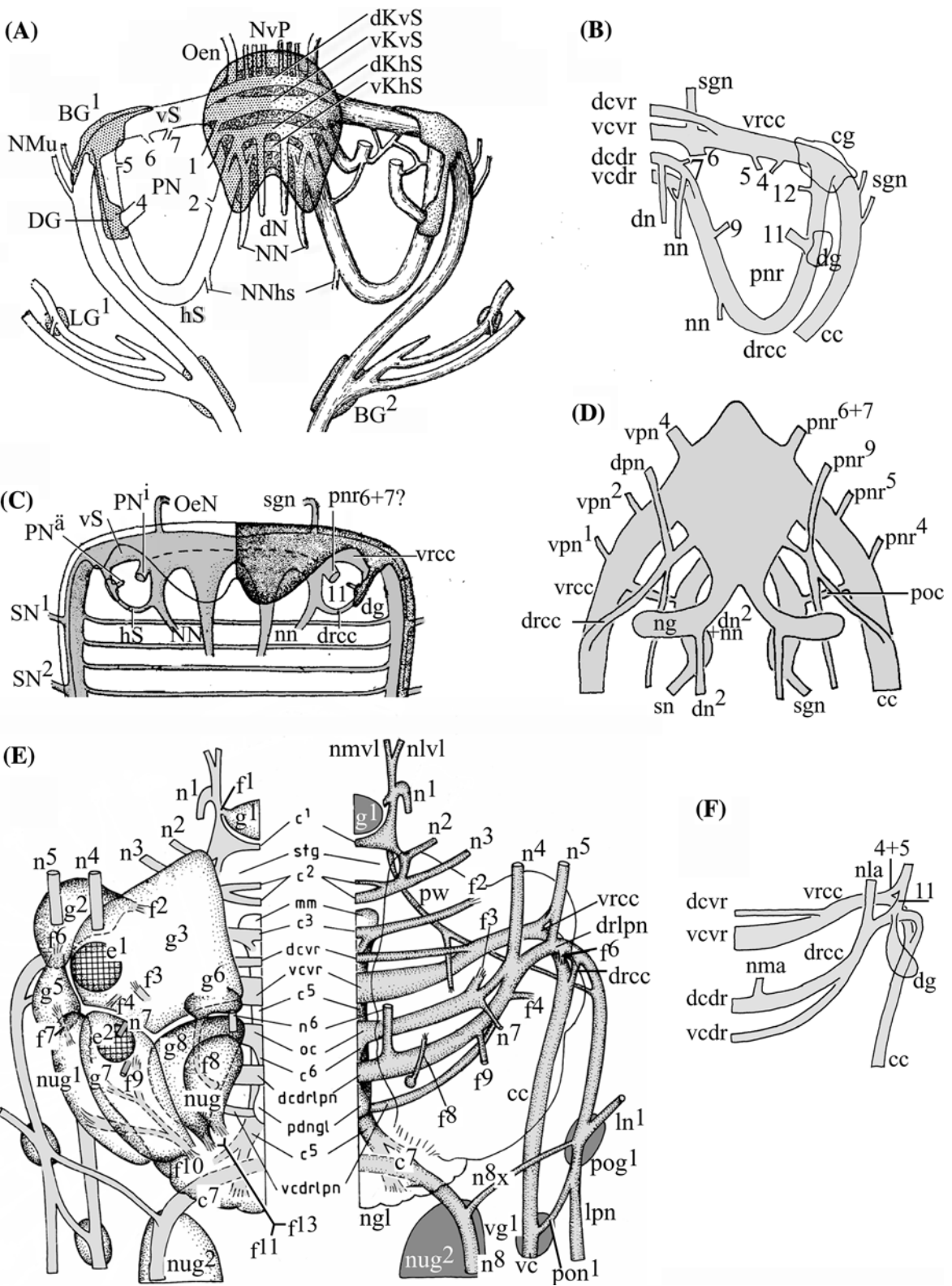


Figure 4. The cephalic nervous system of (A, B) *Scolecipis cirratulus* and *S. bonnieri*; (C) *Spiochaetopterus typicus*; (D) *Protodrilus* spp.; (E, F) *Eurythoe complanata*. Semi-schematic dorsal views. cc – circumesophageal connective; cg – cerebral ganglion; dcd, dcvr – dorsal commissure of the dorsal (drcc) and ventral (vrcc) root of cc; dg – dorsal ganglion; dpn – dorsal palp nerve; nla – nerve of lateral antenna; nma – nerve of median antenna; vcd, vcvr – ventral commissure of the dorsal and ventral root of cc; vpn – ventral palp nerve; 1–12 – palp nerve roots. Further abbreviations see abbreviation list. Modified from Orrhage, 1964 (A); Orrhage, 1966 (C); Orrhage, 1974 and Purschke, 1993, combined (D); Orrhage, 1990 (E, F).

equipped with eyes seems rather unavailing: their optic systems are too differently modelled. Thus, in relation to the other nerve elements in the brain, the position of the optic commissure is very different. It may be found (1) between the dorsal commissure of the ventral root (*dcvr*) and the ventral commissure of the dorsal root (*vcd*) (Nereididae), (2) between the ventral commissure of the ventral root (*vcvr*) and the dorsal commissure of the dorsal root (*dcd*) (Amphinomidae, Polynoidae, Onuphidae, Syllidae), (3) between the ventral commissures of both roots (Hesionidae), or (4) between the dorsal commissures of both roots (Orrhage, 1990–1996, Orrhage & Eibye-Jacobsen, 1998). The families may also differ markedly from one another as concerns the course of the optic nerves: in families with only two eyes, the optic nerve may run ventral to *dcd* (situated in the anteriormost part of the brain; Phyllodocidae) or dorsal to both roots and their commissures (Onuphidae). In families with four eyes the anterior optic nerve (*aon*) may be found (1) ventral to *drcc* (Polynoidae), (2) dorsal to *vrcc* (Syllidae), (3) dorsal to *dcd* and *vcd* (Nereididae), or (4) between *vcd* and the main part of *dcd* (actually penetrating the *dcd*, Hesionidae). The posterior optic nerve (*pon*) of the four-eyed forms may be found between *vcd* and *dcd* (Polynoidae, Syllidae, Hesionidae; in the last of these penetrating the *dcd*) or running dorsal to both *vcd* and *dcd* (Nereididae) (Orrhage, 1991–1996; Orrhage & Eibye-Jacobsen, 1998).

These facts indicate that it is futile to try to give any summarizing general picture of the polychaete optical system at present.

#### *The nuchal commissure and the nuchal nerves*

Among the Canalipalpata and the Scolecida hitherto analyzed, only Orbiniidae is equipped with a separate nuchal commissure (Fig. 5C: *NK*; 5D:

*nc*). It is connected to both commissures of the dorsal root (*vcd*, *dcd*) and to a nuchal center (Fig. 5C, *GZNZ*) which, in turn, is associated with the central neuropile of the brain. From this nuchal commissure emanate the nerves of the nuchal as well as those of the dorsal organs. Among other 'sedentary' families studied, there is a considerable variation of the attachment site of the nuchal nerves to the brain: in Ampharetidae, Pectinariidae and Terebellidae, as well as in Protodrilidae (Fig. 4D,  $dn^2 + mn$ , Purschke, 1993; Purschke & Jouin-Tolmound, 1993), Saccocirridae (Purschke, 1992, 1993) and Nerillidae (Purschke, 1997) the nuchal nerves emerge diffusely from the (latero-) caudal parts of the brain. This is the case in Chaetopteridae, too, but here the *drcc* is also more directly involved. In Flabelligeridae (Fig. 3D: *iNIN*, *NhN*, *äNIN*), Spionidae (Figs. 4A: *NN*, *NNhS*; 4B: *mn*) and Trochochaetidae the nuchal nerves are distinctly associated with *dcd* and *vcd*, while in Sabellariidae, Sabellidae and Serpulidae they emanate only from them. In Scalibregmatidae the nuchal nerves are associated only with *dcd*, whereas in Poecilochaetidae, Apistobranchidae and Paraonidae they arise from *drcc*.

With the exception of Syllidae, Hesionidae and the four aphroditacean families studied, in all aciculate forms so far analyzed, a nuchal commissure is found. Its position in relation to the other nerve elements in the brain, however, is very different (Orrhage, 1990, 1993, 1997; Orrhage & Eibye-Jacobsen, 1998). In the Amphinomidae, Onuphidae and Eunicidae the nuchal commissure is situated in the hind-most part of the brain. In the last two taxa this commissure is split into three parts; furthermore, here an additional nuchal nerve emanates from *drcc*. In Syllidae and Hesionidae the nuchal organs are innervated from two posterior ganglia (*pg*) which are associated with *dcd* and *oc* (sic!). In Nereididae the nuchal commissure is situated in the middle of the brain (between the commissures of *vrcc* and *drcc*) and in

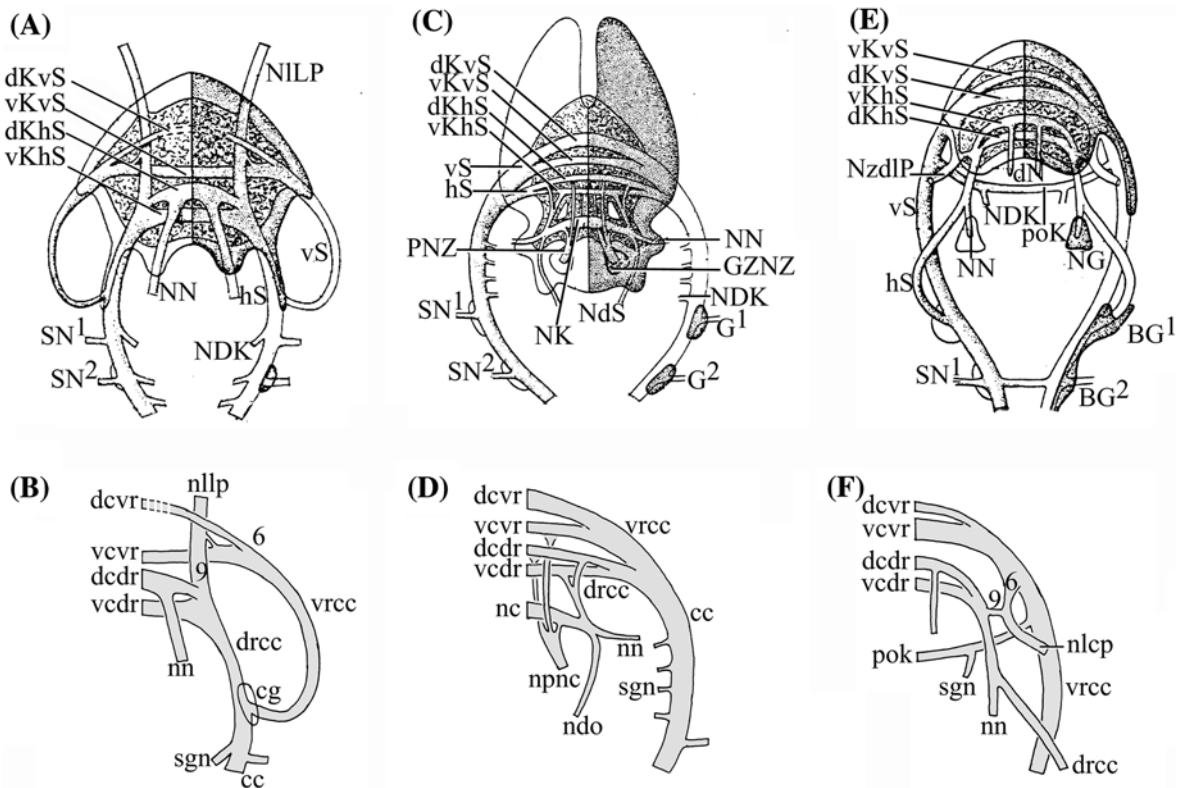


Figure 5. The cephalic nervous system of (A, B) *Polyphysa crassa*; (C, D) *Phylo norvegica* and *Orbinia sertulata*; (E, F) *Levinsenia gracilis* and *Paradoneis lyra*. Semi-schematic dorsal views. cc – circumesophageal connective; cg – cerebral ganglion; dcdv, dcvr – dorsal commissure of the dorsal (*drcv*) and ventral (*vrcc*) root of cc; vcdv, vcvr – ventral commissure of the dorsal and ventral root of cc; 6, 9 – palp nerve roots. Further abbreviations see abbreviation list. Modified from Orrhage, 1966 (A, C, E).

Phyllodocidae it is still more anteriorly located. The nuchal organs of Glyceridae and Goniadidae are innervated from a nuchal commissure and from *vcdv*. These observations indicate that at present a general pattern of the polychaete nuchal system cannot be reconstructed.

#### Central ganglia

Different numbers of paired ganglia are reported within the brain of Polychaeta: 26 in *Hediste diversicolor* ('*Nereis diversicolor*', Holmgren, 1916), 25 in *Nephtys* sp. (Clark, 1958), 26 in *Hermodice carunculata* (Fitzsimmons, 1964) and 17 in *Glycera convoluta* (Manaranche, 1966). Whereas Clark (1958) could homologize the posterior ganglia of *Nephtys* sp. with those of *Hediste diversicolor*, other authors emphasized great difficulties in making meaningful comparisons, e.g., between

*Hediste diversicolor* and *N. irrorata* (Defretin, 1956), *Hermodice carunculata* and *Nephtys* sp. (Fitzsimmons, 1964) and *Glycera convoluta*, *Hediste diversicolor* and *Nephtys* sp. (Manaranche, 1966). Like Fitzsimmons (1964), Marsden & Galloway (1968) are skeptical of the possibility of homologizing ganglia in various polychaete brains. With some exceptions (cf. below), in many polychaete brains it has not been possible to discern any separate ganglia at all, especially not in the central neuropile of the 'sedentaries'. This, in combination with the severe obstacles to homologizing ganglia of one family with those of others, discouraged further endeavors in this field.

#### The commissural ganglion

In 21 of the 32 families studied a commissural ganglion (*cg*) is found at the lateral junction of



*vrcc* and *drcc*. It was called ‘Hamaker’s commissural ganglion’ (*cgHa*) by Binard & Jeener (1926, 1928) and by Orrhage (1966, 1990, 1993, 1995, 1999); it has also been referred to as ‘first ventral ganglion’ (Orrhage, 1964, 1966, 1974: *BG*<sup>1</sup>; 1978, 1990: *vg*<sup>1</sup>). The dimensions of this ganglion are different in the various families. It is quite large in Sabellariidae, Flabelligeridae, Poecilochaetidae, Spionidae, Trochochaetidae, Apistobranchidae, Acoetidae, Aphroditidae, Polynoidae, Sigalionidae and Hesionidae. In 10 other families it is of medium size or very small, especially in the Onuphidae, Nereididae, Glyceridae and Goniadidae (Fig. 2). The inconspicuous dimensions of the commissural ganglion of Nereididae and Onuphidae as well as its total absence in Eunicidae, provide one of the main arguments against Binard & Jeener’s (1928) theory of a segmentation of the polychaete brain. In Cirratulidae, Ampharetidae, Pectinariidae, Terebellidae, Protodrilidae and Orbiniidae no equivalents to the commissural ganglion were found. The first ventral ganglion of Amphinomidae (*vg*<sup>1</sup>) and the ganglion of the circumesophageal connective of Phyllodocidae (*cgc*) are more posteriorly located, which prevents a homologization with the commissural ganglion of other families.

#### *The dorsal ganglion and its role in the innervation of the palps*

In 20 of the 32 families studied there is a ganglion (*dg*; *DG*) on the dorsal or dorso-lateral side of the *drcc* (Fig. 3A, B, D, E). Its cells are remarkably large and plasma-rich. This is the ‘optical ganglion’ of many earlier authors (e.g., Retzius, 1895). Holmgren (1916) called it ‘cerebrales Kommissuralganglion’, a more neutral term. In many papers (e.g., Binard & Jeener, 1926, 1928) it is treated under the name of ‘Holmgren’s cerebral commissural ganglion’. In his comparative discussions Orrhage (1966, 1990, 1991, 1993, 1995, 1996, 1999) used this term (*cgcHo*). It is equivalent to the fifth ganglion (Fig. 4E: *g*<sup>5</sup>; 4F: *dg*) of the Amphinomidae and to the eleventh ganglion (Fig. 1D: *XI*; 1E: *dg*, (*XI*)) of the Glyceridae and Goniadidae. In eight of these 20 families the dorsal ganglion is of great importance for the innervation of the palp (Flabelligeridae, Magelonidae, Poecilochaetidae, Spionidae, Chaetopteri-

dae, Amphinomidae, Glyceridae and Goniadidae; Fig. 2). In Serpulidae, Acoetidae, Aphroditidae, Polynoidae and Sigalionidae the dorsal ganglia play a less prominent role in this respect. This holds true also for the Nereididae where, in fact, *Nereis pelagica* is devoid of real dorsal ganglia (Orrhage, 1993). These facts constitute further arguments against Binard & Jeener’s (1928) theory of the segmentation of the polychaete brain (Orrhage, 1993, 1995). In still other families the dorsal ganglia have nothing to do at all with the innervation of the palps (Trochochaetidae, Apistobranchidae, Onuphidae, Eunicidae, Syllidae, Hesionidae). Here a comparison between the closely related Poecilochaetidae, Spionidae and Trochochaetidae is of special interest. In the two first-mentioned families the dorsal ganglia serve as a base for one of the two main palp nerve roots. In the Trochochaetidae the nerve emanating from the dorsal ganglion is instead in contact with the first lateral ganglion. For a probable explanation of these surprising conditions the reader is referred to Orrhage (1964). In Sabellariidae, Sabellidae, Cirratulidae, Ampharetidae, Pectinariidae, Terebellidae, Protodrilidae, Phyllodocidae, Opheliidae, Scalibregmatidae, Orbiniidae and Paraonidae no dorsal ganglia were observed.

#### **Innervation of anterior appendages – homology conclusions**

##### *Median antenna*

Most of the Amphinomidae, Onuphidae, Eunicidae, Acoetidae, Aphroditidae, Polynoidae, Sigalionidae, Syllidae, Hesionidae and Phyllodocidae species studied by Orrhage (1990–1996) and Orrhage & Eibye-Jacobsen (1998) are equipped with a median antenna or a nuchal papilla. The nerves (*nma*) of each of these appendages are attached to the median part of the *drcc* through two (or four: Onuphidae, Eunicidae) roots. These facts were interpreted as a proof that these appendages are homologous *inter se*. In all probability they are also equivalent to the occipital tentacle found in many Spionidae (Figs 4A,B: *dN*, *dn*) (Orrhage, 1966; Foster, 1971; Fauchald & Rouse, 1997).

### Lateral antennae

The nerves (*nla*) of the lateral antennae emanate from the lateral parts of *dcd*r (Amphinomidae) or from this commissure and the central neuropile of the brain (Acoetidae, Polynoidae, Sigalionidae, Syllidae, Hesionidae, Phyllodocidae). In Nereididae the nerves of the antennae are congruent with the first tegumentary nerve (Figs 1A: *an* + *tn*<sup>1</sup>, 2V: *na*). In Onuphidae and Eunicidae the lateral antennal nerves are also in contact with the dorsal fibril mass (*dfm*), a structure which is in all probability and at least *partim* homologous with the *vcd*r of other families. Apart from these small variations there are fundamental similarities in the innervation of the lateral antennae of the families so far studied. This indicates that these appendages are homologous *inter se*.

### Palps

Out of the 32 families analyzed, 22 were found to be equipped with palps (in the sense of Binard & Jeener, 1928; Orrhage, 1964–2001; Orrhage & Eibye-Jacobsen, 1998). In Scalibregmatidae and Paraonidae palp nerves but no protruding palps were found. In Ampharetidae, Pectinariidae, Terebellidae and Orbiniidae no traces of palps or palp nerves could be found.

According to Orrhage and earlier authors, a polychaete palp is innervated through two or more nerve roots emanating from the *drec* and the *vrec* and their commissures. Their positions and relations to other nerve elements make it possible to homologize the palp nerve roots of one family with those present in other taxa. Until now 12 such palp nerve roots (*pnr*<sup>1–12</sup>) were found. Additional nerve roots or nerves have been observed by Purschke (1993). In most families two of them were interpreted as main roots on account of their dimensions. The results are summarized in Figure 2 and Table 1 [excluded are Cirratulidae (not sufficiently analyzed), Opheliidae (contradictory results) as well as Ampharetidae, Pectinariidae, Terebellidae and Orbiniidae (no palps or homologous structures present)].

*Evaluations.* At first sight these results could give the impression of a great heterogeneity. Thus the number of palp nerve roots common in different taxa varies from eight (in Sabellidae and

Serpulidae) to zero (Apistobranchidae compared with Magelonidae and Amphimomidae). The cleft between Apistobranchidae and Magelonidae/Amphinomidae can, however, be bridged by a gradual comparison from Apistobranchidae upwards (Table 1). Apistobranchidae and Trochochaetidae possess three common roots (*pnr*<sup>6, 7, 9</sup>); *pnr*<sup>6</sup> and *pnr*<sup>9</sup> being the main roots. Trochochaetidae and Spionidae possess six common roots (*pnr*<sup>4, 5, 6, 7, 9, 12</sup>); in both families *pnr*<sup>6</sup> is a main root. Spionidae and Poecilochaetidae possess seven common roots (*pnr*<sup>4, 5, 6, 7, 9, 11, 12</sup>), *pnr*<sup>6</sup> and *pnr*<sup>11</sup> being the main roots. Finally, Poecilochaetidae and Magelonidae possess three common roots (*pnr*<sup>4, 5, 11</sup>); *pnr*<sup>4</sup> and *pnr*<sup>5</sup> are fused and *pnr*<sup>11</sup> is one of the main roots.

Apart from the heterogeneity, similar innervation patterns are also striking. In Trochochaetidae, Apistobranchidae, Acoetidae, Aphroditidae, Polynoidae, Sigalinoidae, Syllidae, Hesionidae, Nereididae and Phyllodocidae *pnr*<sup>6</sup> and *pnr*<sup>9</sup> are the main roots (Table 1). Palp nerve root *pnr*<sup>9</sup> is also the main root in Protodrilidae, Scalibregmatidae, Glyceridae and Goniadidae and thus the innervation of the prostomia of the latter two families resembles the innervation of the palps in the other mentioned taxa. Equivalents to the other main root (*pnr*<sup>11</sup>) in Glyceridae and Goniadidae are found in Flabelligeridae, Magelonidae, Poecilochaetidae, Spionidae, Chaetopteridae and Amphinomidae. The above demonstration of conformity (through intermediate states) in the innervation of palps, branchial crowns, prostomia and special areas of the prostomium of the 26 families lead to the homology conclusion, that are graphically represented in Figure 6 (Goniadidae excluded).

A summarizing picture of the twelve palp nerve roots observed by Orrhage (1964–1999) and Orrhage & Eibye-Jacobsen (1998) and their positions and relations to other cephalic nerve elements is given in Figure 7. As emphasized in earlier papers (Orrhage, 1995, 1999), such a diagram must be looked upon as a preliminary one, mirroring only the present-day knowledge. Thus, in all probability, additional nerves, nerve roots and other significant structures will be observed (cf. *Protodrilus* in Purschke, 1993) and it must be further emphasized that none of the families studied is equipped with all nerve elements.

Table 1. The palp nerve roots of 26 of the 32 families studied by Orrhage (1964–1999) and Orrhage &amp; Eiby-Jacobsen (1998) are shown

	Nerve root number											
	nerve roots attached to the ventral root or its ventral commissure						nerve roots attached to the dorsal root or its commissures					
	1	2	3	4	5	6	7	8	9	10	11	12
Sabellariidae (5, 25, 36)	□	□	□	□	□		□	□				
Sabellidae (5, 25, 31, 37, 46)	■	■	■	■	■	□	□	□				
Serpulidae (5, 14, 25, 31, 37, 46)	■	■	■	■	■	□	□	□	□		□	
Flabelligeridae (5, 25, 34, 53)				■	■	□		□			■	
Magelonidae (34)				■	■						■	
Poecilochaetidae (3, 33)				□	□	■	□		□		■	□
Spionidae (5, 18, 33, 56)				□	□	■	□		□	□	■	□
Trochochaetidae (33, 54)				□	□	■	□		■			□
Apistobranchidae (34)						■	□	□	■			
Chaetopteridae (26, 29, 34, 51)						???					■	
Protodrilidae (6, 30, 35, 47, 49, 50, 52)						???			■			
Amphinomidae (15, 38, 56)				■	■						■	
Onuphidae (5, 15, 17, 20, 41)				□	□	□	□	□				□
Eunicidae (5, 15, 17, 20, 41)				□	□	□	□	□				□
Acoetidae (39)				□	□	■			■		□	
Aphroditidae (4, 5, 15, 17, 39)				□	□	■			■		□	
Polynoidae (1, 5, 15, 17, 39)				□		■			■		□	
Sigalionidae (17, 39)				□		■			■		□	
Syllidae (11, 15, 27, 42)						■			■			
Hesionidae (5, 15, 22, 42)						■	□	□	■			
Nereididae (5, 12, 15, 16, 17, 23, 40)						■	□	□	■	□	□	□
Phyllodocidae (5, 8, 13, 45)						■			■			
Glyceridae (2, 5, 14, 17, 28, 43, 55)								□	■		■	□
Goniadidae (14, 43)								□	■		■	
Scalibregmatidae (10, 17, 34)						□			■			
Paraonidae (7, 19, 34)						■			□			

When discernible, the two main roots of each family are emphasized through dark gray. Relevant literature is given in brackets behind the family name. Not included information: Ampharetidae, Pectinariidae, Terebellidae (5, 9, 21, 24, 32, 44); Saccocirridae (47); Nerillidae (48); Orbiniidae (34).

*Literature:* Åkesson, 1963 (1), 1968 (2); Allen, 1904 (3); Bernert, 1926 (4); Binard & Jeener, 1928 (5); Bubko, 1981 (6); Cerruti, 1909 (7); Eiby-Jacobsen, 1993 (8); Fauvel, 1897 (9), 1927 (10); Gidholm, 1967 (11); Gilpin-Brown, 1958 (12); Gravier, 1896 (13), 1898 (14); Gustafson, 1930 (15); Hamaker, 1898 (16); Hanström, 1927 (17), 1928c (18), 1930 (19); Heider, 1925 (20); Hesse, 1917 (21), 1925 (22); Holmgren, 1916 (23); Holthe, 1986 (24); Johannson, 1927 (25); Joyeux-Laffuie, 1890 (26); Malaquin, 1893 (27); Manaranche, 1966 (28); Martin & Ancil, 1984 (29); Merker & Vaupel von Harnack, 1967 (30); Meyer 1887-1888 (31); Nilsson, 1912 (32); Orrhage, 1964 (33), 1966 (34), 1974 (35), 1978 (36), 1980 (37), 1990 (38), 1991 (39), 1993 (40), 1995 (41), 1996 (42), 1999 (43), 2001 (44); Orrhage & Eiby-Jacobsen, 1998 (45); Pruvot, 1885 (46); Purschke, 1993 (47), 1997 (48); Purschke & Jouin-Toulmond 1993 (49), 1994 (50); Racovitza, 1896 (51); Salensky, 1907 (52); Schlieper, 1927 (53); Söderström, 1920 (54); Stolte, 1932 (55); Storch, 1913 (56).

### Oral filaments

The slender appendages of the lateral parts of the ventral side of the operculum of Sabellariidae were

earlier quite differently interpreted: as palps homologous with those of the Spionidae (Johansson, 1927) or with those of the 'errants' (Binard & Jeener, 1928). On account of their innervation, the

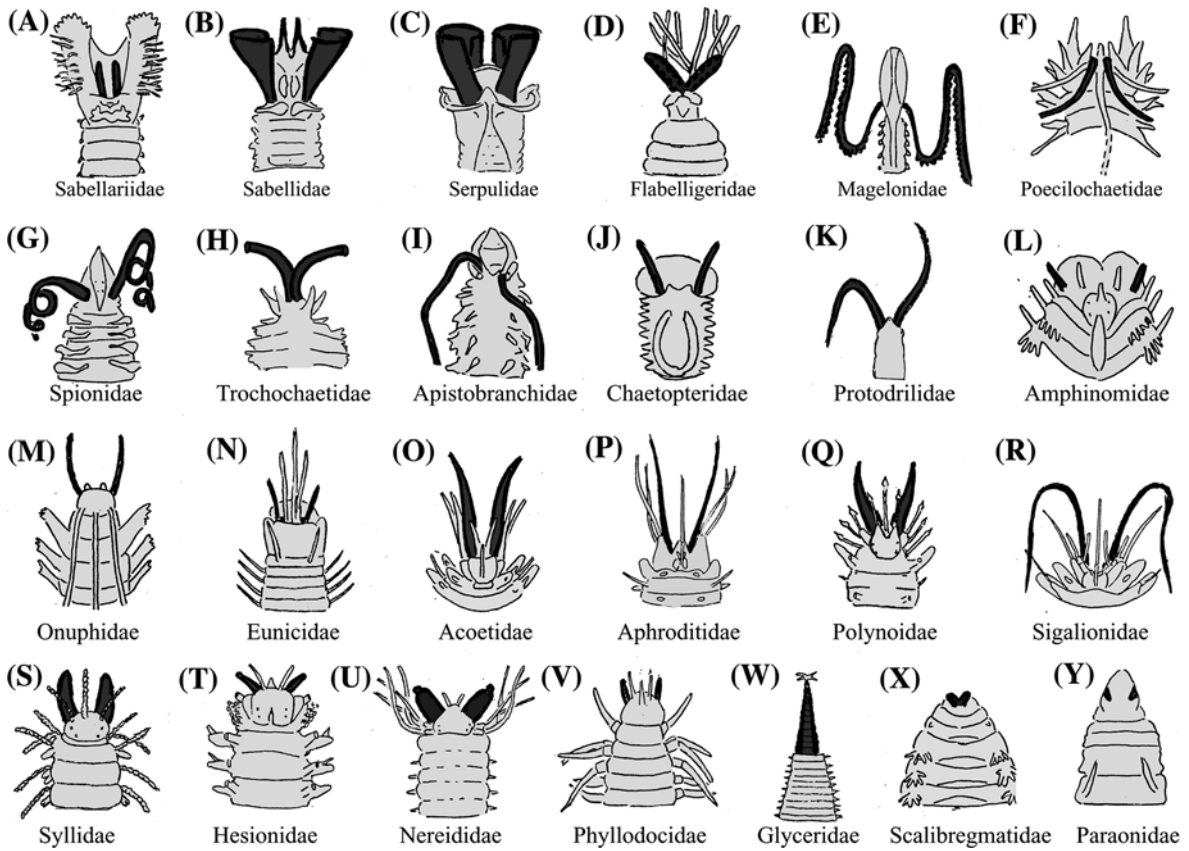


Figure 6. Anterior ends of representatives of 24 of the 32 families studied by Orrhage (1964-1999) and Orrhage & Eibye-Jacobsen, (1998). The palps of the Nereididae and their homologues in the other taxa are blackened.

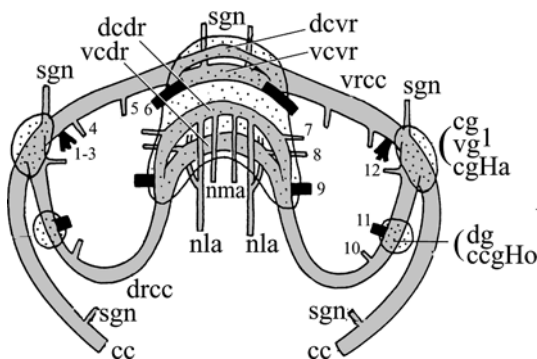


Figure 7. A synopsis of the palp nerve roots (1-12), nerves of median (nma) and lateral (nla) antennae and the stomatogastric nerves (sgn) found in families studied by Orrhage (1964-1999) and Orrhage & Eibye-Jacobsen (1998). None of these families are equipped with all nerve elements shown in the figure. ccgHo - Holmgren's cerebral commissural ganglion; cgHa - Hamaker's commissural ganglion. For further abbreviations see Figure 1 and present text. Modified after Orrhage, (1995, 1999).

two thick appendages situated in front of the mouth constitute palps. The oral filaments are nothing but extended lateral parts of the upper lip of the mouth (Orrhage, 1978).

*Detached branchial radioli and pinnulae; outgrowth of the dorsal wall of the mouth cavity*

The appendages of the dorsal lip of Sabellidae and Serpulidae represent various structures: in the Sabellidae they consist of radioli which have become separated from the branchial crown (*Sabella*) or they are made up of both, radioli and pinnulae (*Potamilla*, *Euchone*, *Chone*). The dorsal lip appendages of Serpulinae consist of separated pinnulae only (*Serpula*, *Pomatoceros*, *Ditrupe*, *Hydroides*, *Placostegus*). When designating these structures as palps, Johansson (1927) and Binard

& Jeener (1928) and others, were correct to some extent: these appendages are, as we know now, detached from the branchial crowns, which in themselves are equivalent to the palps. In maintaining that also the dorsal lip appendages of Filograninae are homologous with palps, however, these authors went too far: at least in *Apomatus*, *Protula* and probably *Filograna* they constitute outgrowths of the dorsal wall of the mouth cavity (cf. Orrhage, 1980).

### *Buccal lips*

In Amphinomidae and Eunicidae, among other families, the anteriormost part of the prostomium may be equipped with outgrowths of different size and form. In the Amphinomidae these appendages were previously interpreted and designated as palps (Racovitza, 1896; Malaquin & Dehorne, 1907; Storch, 1913). On each side of an amphinomid, four nerves run to the buccal lips (Fig. 4E: *nvl*, *nmvl*,  $n^2$ ,  $n^3$ ). These nerves are intimately associated with the stomatogastric ganglion ( $g^1$ ) and the stomatogastric nerve ( $n^1$ ). The eight nerves of the buccal lips and the stomatogastric nerves have the two anteriormost transverse brain commissures ( $c^1$ ,  $c^2$ ) in common. This center constitutes a complex, that is almost totally isolated from the rest of the brain. No polychaete palps are innervated like the buccal lips of the Amphinomidae. The true palps of this family are situated dorsal to the buccal lips and are innervated as described above. The buccal lips of Onuphidae and Eunicidae have also been homologized with the palps of, for instance, the Aphroditacea (Fauvel, 1923; Heider, 1925; Hanström, 1927; von Haffner, 1959a,b, 1962; Åkesson, 1967a). According to Storch (1913), Binard & Jeener (1928) and Gustafson (1930), however, the buccal lips of Eunicea are nothing but an outgrowth of the prostomium itself. The dorsal and ventral buccal lips of *Hyalinoecia* and *Nothria* and the bilobate buccal lips of *Eunice* (Orrhage, 1995, Fig. 4) are innervated through a number of nerves emanating from *vcvr*. They are rooted in the immediate vicinity of the esophageal nerve. No polychaete palps are innervated like this. The true palps of Onuphidae and Eunicidae are situated dorsal to the buccal lips and innervated as described above. The buccal lips of the Amphinomidae and those present in Eunicea are quite

differently innervated. This does not speak in favor of the buccal lips of the Amphinomidae being homologous with those found in Eunicea. It is likely, therefore, that the use of a common term is misleading and inappropriate.

### *Buccal tentacles*

The buccal tentacles are attached to the upper lip of the mouth, ventral to the tentacular membrane in Ampharetidae and Pectinariidae and to the dorsal ridge in Terebellidae (Orrhage, 2001, Fig. 3). They were earlier interpreted as palps by, e.g., Nilsson (1912), Fauvel (1927) and Binard & Jeener (1928). Rouse & Fauchald (1997) accepted this interpretation, although with hesitation for Terebellidae. In the opinion of Holthe (1986), however, these appendages are originally buccal structures. In Ampharetidae (Fig. 2E) the nerves of the buccal tentacles (*nbt*), the stomatogastric nerves (*sgn*) and the nerves running to the lateral part of the tentacular membrane (*ntm*) emanate from one and the same common tract (*ct*). The median part of the tentacular membrane is innervated by nerves coming from the brain (*ntm*). In Pectinariidae (Figs 2F, 3C) the same intimate contact is present between the nerves of the buccal tentacles (*nbt*) and the anterior stomatogastric nerves (*sgn*). Most of the nerves to the tentacular membrane (*ntm*) emanate from the brain itself. As in the Ampharetidae, however, some of the nerves running to this membrane issue from the common tract of the nerves running to the buccal tentacles and the alimentary canal. In Terebellidae (Figs 2G, 3F) the nerves supplying the buccal tentacles also run to the dorsal ridge (which is homologous with the tentacular membrane of the Ampharetidae and Pectinariidae). Most of them (*nbt<sub>dr</sub>*) emanate from the brain but quite a number are rooted in the tract leading to the anterior stomatogastric nerves.

Summing up, the conditions found in Ampharetidae, Pectinariidae and Terebellidae are variations on the same theme: the intimate contact between the nerves of the buccal tentacles and those of the intestine. It was concluded (Orrhage, 2001) that the buccal tentacles constitute parts of the alimentary canal situated outside the mouth.

In these taxa there are no neuro-anatomical indications of the presence of antennae or palps.

#### *Outgrowths from the tip of the prostomium*

As a consequence of the interpretation of the Glyceridae and Goniadidae prostomium as a pair of fused palps (Hanström, 1927; Manaranche, 1966; Orrhage, 1999), the four appendages at the tip can not be understood as either antennae (Gravier, 1898; Hanström, 1927; Binard & Jeener, 1928) or palps (Binard & Jeener, 1928).

*Conclusions.* Most appendages described in the last five paragraphs may be interpreted as structures sui generis. It seems probable that they are homologous *inter se*, but only within closely related taxa. Thus, for instance, no neuro-anatomical data indicate that the oral filaments of the Sabellariidae are homologous with the outgrowth of the dorsal wall of the mouth cavity of some filigranine genera.

#### **The stomatogastric nerves**

In the simplifications (Fig. 2) of most of Orrhage's (1964–2001) drawings, the attachment of the stomatogastric nerves or nerve roots (*sgn*) are shown. It is not possible to discern any general picture of the innervation of the intestinal canal in the families so far studied: the nerves or nerve roots emanate from almost any part of the CNS.

Hanström (1927, 1930) was the first to propose that during evolution, the stomatogastric nerves of the polychaetes had moved from an original position at the subesophageal ganglion (still prevailing in 'Amphictenidae') to the final position localized in the brain ('Eunicidae', 'Aphroditidae', Phyllodocidae) via the anterior part of the circumesophageal connectives and the ventral part of the brain ('Nereidae'). This idea was previously criticized by Gustafson (1930) and Snodgrass (1938), and the data presented here (Fig. 2) likewise fail to support it: the stomatogastric nerves of the Pectinariidae emanate not only from the circumesophageal connectives near the subesophageal ganglion (Fig. 3C, *nss*) but also from the neuropile of the brain (*sgn*); the fifth stomatogastric nerve of the Nereididae emerges from the

posterior part of the connectives (Fig. 1A, *sgn*<sup>5</sup>) and in the Eunicia a stomatogastric nerve (Fig. 2P, Q, *sgn*) arises from the lateral junction of *drc* and *vrcc* as does the posterior root of the stomatogastric nerve of Aphroditacea and one of the stomatogastric nerves of the Phyllodocidae (Fig. 2W, *sgn*).

#### **The composition of the polychaete brain – segmented or not?**

For years students of polychaete brains have spoken in favor of two fundamentally different interpretations of the constitution of this organ. Partly at least, this was due to the investigators being supporters of one or the other of the three major theories of the origin of metamerism in the Metazoa. Most advocates of the cormen theory (cf. Haeckel, 1866) and the pseudomer theory (cf. Hatschek, 1878) interpreted the polychaete brain as non-segmented. This is in line with the fundamental idea of each of these theories. For the supporters of the cyclomer theory (cf. Sedgwick, 1884; van Beneden, 1891, 1897; Lameere, 1916, 1925), however, the polychaete brain is made up of three segments, equivalent to the medio-ventral and the two following pairs of gastral pockets of the anthozoan body organization and homodynamous with the trunk segments of the Polychaeta.

#### *Non-segmented brain*

Malaquin (1893) interpreted the brain as a single entity, homologous with a body segment. Although Racovitza (1896; supporter of the pseudomer theory) clearly emphasized that his tripartition into fore-, mid- and hind-brain is nothing but a topographic–physiological subdivision, this was misunderstood by later authors (e.g., Nilsson, 1912; Heider, 1925; von Haffner, 1959–1962; Raw, 1949; Martin & Anctil, 1984). According to Holmgren (1916) and Söderström (1920), the nuchal center should hold a somewhat different position because it appears a little later in ontogeny and is something later added to the brain, respectively. In spite of postulating a non-segmented brain in Amphinomidae, Gustafson (1930) could imagine that the palps of the 'errants' constitute segmental structures.

### *Segmented brain*

According to Pruvot (1885) the brain consists of four centers that had migrated from the trunk in the anterior direction, along the esophageal connectives. Nilsson (1912) proposed that the brain is composed of three pairs of segmental podial ganglia pushed forwards. Storch (1913) and Hempelmann (1911) interpret ‘the palp nerve’ as the remnant of an earlier lateral nerve. Storch’s ideas were further developed by Binard & Jeener (1928), advocates of the cyclomer theory. Gustafson (1930) and more thoroughly Orrhage (1993, 1995) criticized their theory and it turned out that the cephalic nervous system and especially the innervation of the palps is more complicated than Binard & Jeener (1928) summarized in their ‘*Schéma de la constitution fondamentale du système nerveux du prostomium*’ (compare with Fig. 7). From the configuration and innervation of the eunicean esophagus and pharyngeal sacs Raw (1949) imagined that the mid-brain of *Eunice* sp. and other taxa is composed of three segmental ganglia which have joined, forming an ‘ancient fore-brain’. He also regarded the nuchal organs as being of segmental origin. In his studies of the Eunicea Orrhage (1995) found no support for Raw’s theory. Since the middle of the 20th Century no major theories concerning the segmentation of the polychaete brain seem to have been put forward. Earlier expectations have been frustrated and it may be that the problem is unsolvable.

### **Neuro-anatomical investigations via immunocytochemistry and cLSM**

Although immunocytochemical (ICC) studies were carried out as early as 1982 (Porchet et al., 1985; Dhainaut-Curtois & Golding, 1988), until recently they were rarely applied in investigations of annelid neuroanatomy. In spite of the great variety of neuroactive substances present in annelids (acetylcholine, monoamines, neuropeptides, amino acids; see Dhainaut-Curtois & Golding, 1988; Windoffer, 1992; Salzet & Stefano 2001), only a few of them are frequently analyzed in immunocytochemical experiments. The two most popular antibodies applied in Annelida are directed against the monoamine 5-hydroxytryptamine (5-HT,

serotonin) and the tetrapeptide Phe–Met–Arg–Phe–NH<sub>2</sub> (FMRFamide). Their antigens are widely distributed within the nervous system (according to Miron & Anctil, 1988, 2–3% of all neurons in *Harmothoe imbricata* contain 5-HT) and therefore the immunoreactivity (IR) enables a detailed reconstruction. The FMRFamide antibody may recognize only the RFamide-motif and the staining is therefore often termed ‘FMRFamide-like immunoreactivity (FMRFamide-L IR); in the following the short term ‘RFamide IR’ will be used. Demonstration of the entire neuronal structures can be achieved via antibodies directed against the neuronal cytoskeleton. Good results were obtained using ICC against bovine neurofilament proteins (210 kDa; Sigger & Dorsett, 1986), acetylated  $\alpha$ -tubulin (Müller, 1999a,b; Müller & Westheide, 2000, 2002) and tyrosinated tubulin (Hessling & Westheide, 2002). The latter two can also be used to detect ciliated structures (e.g. Müller, 2002; Müller et al., 2001; Worsaae & Müller, 2003). Combination of immunocytochemistry and confocal laser-scanning microscopy (cLSM, invented by Minsky in 1984), is an extraordinarily efficient way to analyze the 3D nervous system structure in whole mounts of small and transparent animals. Furthermore, this method is also an efficient way to analyze all neuronal structures, so that the complaint of Dhainaut-Curtois & Golding (1988) ‘...recent investigations on the peripheral and stomatogastric nervous system have been rare...’ has already been or will be corrected in the near future.

### **Neuronal differentiation**

The development of the polychaete nervous system (NS) is still discussed controversially (Voronezhskaya et al., 2003). Investigations on neuronal differentiation contribute new arguments not only to this discussion, but also to the interpretation of the adult nervous system.

#### *Neuronal development during ontogeny*

Two contradictory hypotheses concerning the development of the annelid nervous system exist (Fig. 8). The first theory postulates that the ner-

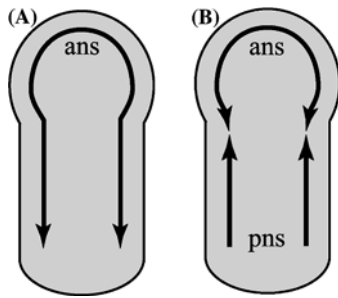


Figure 8. Theories on polychaete neuronal differentiation. (A) The nervous system solely develops from anterior ectoderm. (B) The nervous system develops from two subsystems: the anterior (ans) and the posterior (pns) nervous system.

vous system arises solely from an anterior ectoderm; the connectives grow backwards and form the ventral cord as well (Åkesson, 1968; Lacalli, 1981, 1984; Bhup & Marsden, 1982; Hay-Schmidt, 1995). According to the second theory, a posterior part of the ectoderm gives rise to additional nerves that grow towards the brain; where the anterior and posterior subsystems meet, the nerves arborize and fuse (Bullock & Horridge, 1965; Dorresteijn et al., 1993). According to Hanström (1928b) the presence of two subsystems is plesiomorphic whereas the solely anterior development is derived (as in Turbellaria and Polyplacophora). The presence of two larval types complicates the situation. The adult nervous system appears earlier in development in lecithotrophic than in planctotrophic larvae (Anderson, 1966; Heimler, 1981) and at least in the former the early primordia are retained in the adult system (Anderson, 1973). In lecithotrophic larvae, however, conflicting relations between larval and adult nervous systems are claimed: (1) the two may develop separately (Lacalli, 1984), (2) the

larval system may be incorporated into the adult one (Hay-Schmidt, 1995) or (3) the larval system may form a framework along which the adult system develops (Voronezhskaya et al., 2003). While there is increasing evidence now that the planktotrophic larval nervous system develops from two subsystems (pretrochal and intratrochal (Fig. 9G), Lacalli, 1981, 1984; Voronezhskaya et al., 2003), the question of the development of the adult nervous system remains open.

In lecithotrophic larvae of *Scoloplos armiger* (Fig. 9A–C; Müller 1999b, 2003) and *Parapionosyllis minuta* (Fig. 9, E–G; Berenzen & Müller, unpublished data) the first serotonergic perikarya appear dorsolaterally in the prostomium (Fig. 9A, E). Projecting to the contralateral side, their axons form the first cerebral commissure (Fig. 9C). Next to the growth cones of these posteriorly growing neurites (*agc*) a pair of axons growing towards the anterior can be seen on the ventral side (Fig. 9B, *pgc*). In none of the species could the respective perikarya of the posterior fibers be stained. Thus, in *S. armiger* and *P. minuta* an anterior and a posterior neuronal subsystem are present. But instead of merging, the anterior fibers extend further posteriorly and medially and the posterior fibers anteriorly and laterally (Fig. 9C, E, F). In this way paired circumesophageal connectives are formed, of which the inner nerve pair represents the later ventral and the outer pair the later dorsal root. Immunoreactivity to FMRamide showed an identical developmental pattern in *Scoloplos armiger* (Müller, in press). It is assumed that during neuronal differentiation the paired esophageal connectives fuse to some extent, as is described below.

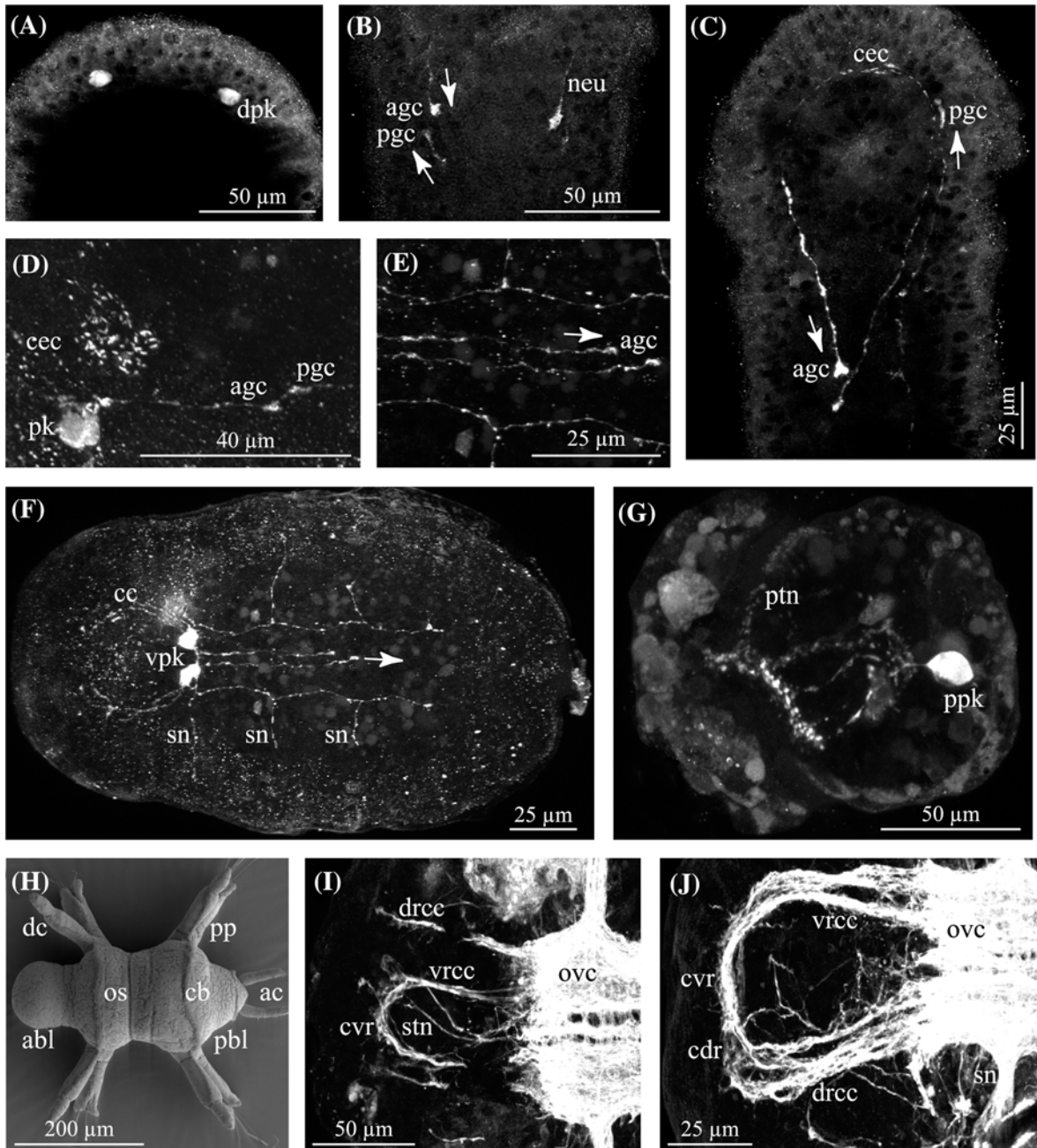
Figure 9. Neuronal differentiation. (A–C) *Scoloplos armiger*. (A) Two spherical serotonergic perikarya (dpk) dorsally in the prostomium. (B) Neurites from anterior neurons grew caudally via anterior growth cones (*agc*); neurites from posterior neurons grew anteriorly via posterior growth cones (*pgc*). Arrows indicate growth direction. (C) In older stages the anterior neurites extend caudally and medially, the posterior ones anteriorly and laterally. *cec* – cerebral commissure. (D–F) *Parapionosyllis minuta*. (D) Two early, laterally located serotonergic perikarya (*pk*) and both growth cones are visible. (E, F) Older stage with mediad and caudad growing anterior neurites (arrow) and more lateral located nerves, formed by the posterior neurites. *cc* – circumesophageal connectives; *sn* – segmental nerve; *vpk* – ventral perikarya. (E) Higher magnification from F. (G) *Phyllodoce mucosa*. In the larva the first serotonergic neurites originate from one large posterior perikaryon (*ppk*). *ptn* – prototroch nerve. (H–J) *Dorvillea bermudensis*. (H) SEM image of a 3-day-old regenerate. Two old segments (*os*) give rise to an anterior (*abl*) and posterior (*pbl*) blastem. *ac* – anal cirrus; *cb* – ciliary band; *dc* – dorsal cirrus; *pp* – parapodium. (I) On both sides two nerves emanate from the old ventral cord (*ovc*). The latter ventral root of the circumesophageal connective (*vrcc*) already formed a commissure (*cvr*); the latter dorsal roots (*drcc*) end blind. *stn* – stomatogastric nerve. (J) In later stages the dorsal roots are also joined via a dorsal commissure (*cdr*). (A–C: Müller, 2003; D, E, F: Berenzen & Müller, unpublished; I, J: Müller & Henning, 2003).



### Neuronal development during regeneration

Regeneration can be regarded as a special case of development. In contrast to embryological development, the new tissue originates from differentiated cells of the amputee (Fig. 9H).

Many investigations of different taxa have demonstrated that the new nervous system of the blastema originates from the old ventral cord of the amputee (e.g., Turbellaria: Reuter et al., 1996; 'Oligochaeta': Yoshida-Noro et al., 2000 Polychaeta: Müller & Berenzen, 2002, Müller



et al., 2003). Following the anterior regeneration in *Dorvillea bermudensis*, Müller & Henning (2003) reported that formation of the new nervous system starts with the outgrowth of two nerves from each side of the old ventral cord (Fig. 9I). The inner pair, the later ventral roots, fuse medially to form the ventral cerebral commissure (Fig. 10F). The outer nerve pair will become the dorsal roots. Both roots split up into two branches (Fig. 10G), of which each later on forms a commissure within the brain (Fig. 10H). The roots are still separated and thus the circumesophageal connectives are paired. The same situation was observed during regeneration in *Eurythoe complanata* and *Marphysa* sp. (Müller & Henning, 2003; Müller, unpublished data) as well as during stolonization in *Autolytus prolifer* (Kreischer & Müller, 2000). In later stages each connective pair merges, proceeding from the ventral cord towards the brain (Fig. 10I). In *D. bermudensis* and *A. prolifer* the fusion stops halfway along the connective (Müller & Henning, 2003), thus producing the typical polychaete anterior nervous system with a single connective that 'splits up' into two roots (Orrhage, 1995; see Fig. 7). In *E. complanata* the fusion is more or less complete and only relatively short roots remain (Orrhage, 1990).

From the data so far collected regarding the development and regeneration of the nervous system it can be concluded that the circumesophageal connectives are paired structures, which are partly fused in annelids possessing dorsal roots including most Polychaeta, and completely fused in 'mono-connective Polychaeta' and Clitellata where, at present dorsal roots are considered to be totally absent (e.g., Bullock & Horridge, 1965; Purschke, 2002). Further studies are needed to demonstrate whether this hypothesis can be corroborated in regenerating anterior ends or by the investigation of stolonizing Clitellata.

### The ventral cord

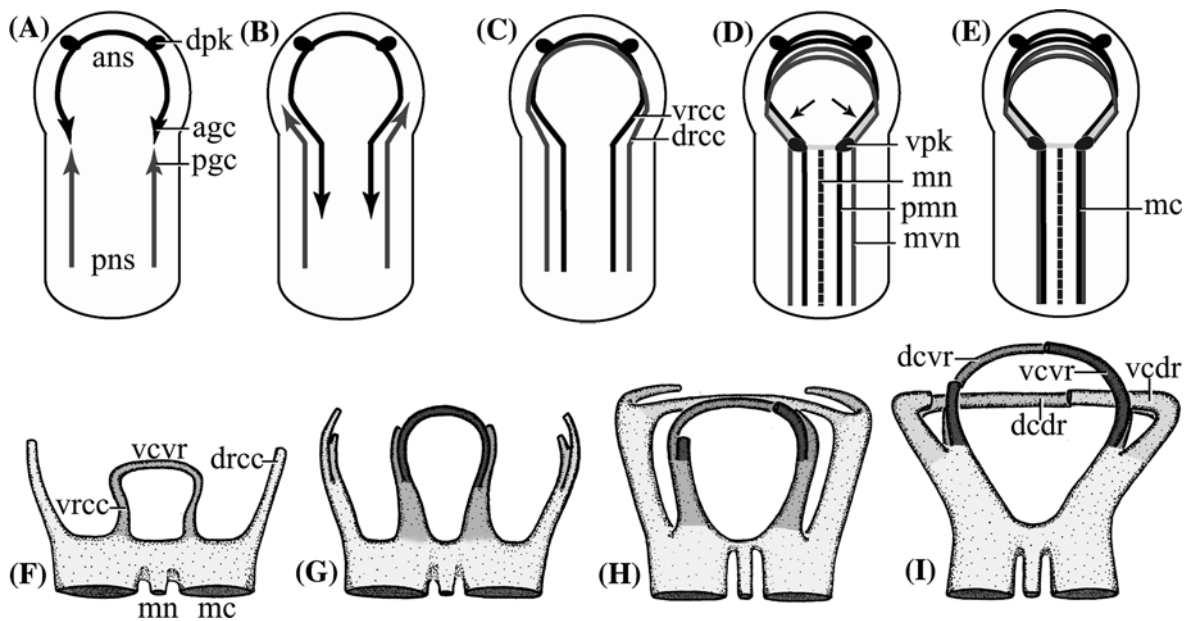
The central nervous system (CNS) is variously embedded within the annelid body tissue. In many polychaetes the CNS retains a basiepithelial (e.g. *Owenia fusiformis*, Coulon & Bessone, 1979) or intraepidermal position, regardless of the body size

(Bullock & Horridge, 1965; Hessling & Purschke, 2000; Tzetlin et al., 2002). Within Bilateria the basiepithelial position is regarded as being the plesiomorphic condition (Bullock & Horridge, 1965). Nevertheless, the polychaete CNS can also be shifted into a subepidermal position, as documented e.g., for *Nephtys* sp. (Clark, 1958), *Nereis diversicolor* (Golding, 1992) and *Myzostoma cirriferum* (Müller, 1999b). In Clitellata, however, the central nervous system is always entirely subepidermal, even in the smallest oligochaete species (Purschke et al., 2000; Purschke, 2002).

The annelid ventral nerve cord is a rope-ladder-like system, consisting of paired segmental ganglia that are connected intersegmentally by connectives and intrasegmentally by commissures. When such a system is illustrated in textbooks, most authors prefer to present an arthropod nervous system (e.g., Westheide & Rieger, 1996). This is due to the fact that 'nervous systems in the Polychaeta exhibit a surprising range of levels in organization' (also Bullock & Horridge, 1965, Golding, 1992;). This variety concerns all elements of the ventral cord (connectives, commissures, ganglia) and the peripheral nervous system (segmental and longitudinal nerves).

### Ventral connectives

Commonly the presence of two separate trunks within the ventral cord is regarded as the plesiomorphic condition. The rare situation of extremely widely separated cords (Dinophilidae, Saccocirridae) as well as their fusion in the mid-ventral line (e.g., Nerillidae) are, according to Bullock & Horridge (1965) an expression of secondary processes. According to the above-mentioned hypothesis concerning the development of the annelid nervous system, four ventral nerves are already present in early stages (Figs. 9C, F; 10C). Furthermore, in many cases a fifth, unpaired median nerve is added. It is assumed that this nerve contains neurites from ventral perikarya that are located at the transition between the esophageal connectives and the ventral cord; however, fibers of the connectives may also contribute to this median nerve (Fig. 10D). The median nerve is documented for many polychaetes (Bullock & Horridge, 1965; Bubko & Minichev, 1972; Ushakova & Yevdonin, 1985, 1987,



**Figure 10.** Neuronal differentiation; schematically demonstrated. (A–E) Development of the serotonergic nervous system during ontogeny (after *Scoloplos armiger*, *Parapionosyllis minuta*), ventral view. (A) The nervous system originates from an anterior (ans) and an posterior (pns) subsystem. The growth cones of the anterior (agc; extending caudally) and the posterior (pgc; extending anteriorly) subsystem are indicated by arrows. dpk – dorsal perikaryon. (B) The anterior system prolongs posteriorly and medially, the posterior one anteriorly and laterally. No fusion occurs. (C) The posterior system forms a second cerebral commissure. The circumesophageal connectives are paired, possessing a dorsal (drcc) and a ventral (vrcc) root. (D) Each root splits up and forms two commissures within the brain. The roots fuse basally (arrows), leaving a dorsal root of different length behind. The first ventral perikarya (vpk) might give rise to the median nerve (mn). pmn – paramedian nerve; mvn – main ventral nerve. (E) The paramedian and the main ventral nerves of each side can fuse and this way form the main cord (mc). (F–I) Development of the cephalic nervous system during regeneration (after *Dorvillea bermudensis*, *Eurythoe complanata*, *Marphysa* sp.), ventral view. (F) From the old nerve cord (mn – median nerve; mc – main cord) two nerve pairs grow anteriorly: the latter ventral (vrcc) and dorsal (drcc) root. The inner nerves form the latter ventral commissure of the ventral root (vcvr). (G) Each root splits up into two nerves. (H) Each nerve forms a commissure. (I) The shape changes and four commissures are present in the brain: ventral (vcvr; vcd) and dorsal (dcvr, dcd) commissures of the ventral and the dorsal root, respectively. (A–E: Müller, 2003; F–I: Müller & Henning, 2003).

1988; Müller & Westheide, 1997, 2002) and only in seven out of 28 investigated species the nerve was absent (*Pisione remota*, *Microphthalmus listensis*, *M. sczelkowi*, *Glycera alba*, *Protodrilus* sp., *Protodriloides chaetifer*, *Saccocirrus papillo-cercus*; Müller, 1999b). In leeches, the median (Faivre's) nerve, which can be totally fused with one connective (Sawyer, 1986), communicates with the stomodaeal system (Bullock & Horridge, 1965). In the simple oligochaete nerve cord such a nerve is hitherto unknown. Presence of the median nerve in nearly all supraordinate polychaete taxa and Hirudinea (Bristol, 1898; Payton, 1981) indicates that it belongs to the basic annelid body plan. Furthermore, presence of the median connective in Arthropoda (Insecta: Hanström, 1928a;

Decapoda: Harzsch et al., 1997; Amphipoda: Gerberding & Scholtz, 1999 suggest that it may be part of the ground pattern of Articulata. Long ago Stummer-Traunfels (1927) considered the median nerve in Myzostomidae (Nansen, 1887) an arthropod character.

Paramedian nerves have been described for Dinophilidae (Donworth, 1986; Beniash et al., 1992; Windoffer, 1992; Müller, 1999b; Müller & Westheide, 1997, 2002), Saccocirridae (Kotikova, 1973; Müller, 1999b), Protodrilidae, Protodriloidae, Ctenodrilidae and Magelonidae (Müller, 1999b). Knowing only about the presence of these nerves in Dinophilidae and Protodrilida, Windoffer (1992) proposed that the paramedian nerves coordinate the ventral cilia used for ciliary

gliding. Staining of a delicate serotonergic plexus between the paramedian nerves, immediately below the ventral band of cilia in Dinophilidae and *Ophryotrocha* larvae (Müller & Westheide, 2002) supports this view. Investigations in Mollusca (Counce et al., 1988; Syed et al., 1988; Stefano et al., 1988) and Plathyhelminthes (Sakharov et al., 1986) demonstrated that 5-HT is involved in commencement of ciliary activity in locomotion and food uptake. This, however, cannot explain the presence of corresponding nerves in Ctenodrilidae and Magelonidae, which show another mode of locomotion.

A penta-neural cord with paired main and paramedian nerves and one unpaired median nerve has thus far been described only for some polychaete larvae (*Ophryotrocha gracilis*, Fig. 11B, C, Müller & Westheide, 2002; *Scoloplos armiger*, Fig. 11A, Müller, 2003; *Myzostoma cirriferum*, Eeckhaut et al., 2003; *Capitella capitata*, *Ophryotrocha* sp., Müller, unpublished data) and adult Dinophilidae (Fig. 11E; Jägersten, 1944; Kotikova, 1973; Windoffer, 1992; Müller, 1999b; Müller & Westheide, 1997, 2002). This unique structure of the nervous system provides evidence for a pro-genetic origin of the dinophilids (see Westheide, 1982, 1984; Westheide & Riser, 1983), due to its common occurrence in larvae, however, it does not justify the conclusion that they are derived from Dorvilleidae or other Eunicida (Müller & Westheide, 2002). Whereas the penta-neural cord persists in Dinophilidae (autapomorphic character), it is only transient in the larvae. All variations found in the ventral polychaete cord can easily be derived from the larval nervous system. Fusion of the two peripheral nerve pairs results in a tri-neural cord (Fig. 10E). This is observable in developmental stages of *Ophryotrocha gracilis* (Fig. 11C) and *Scoloplos armiger* (not shown), and also in the posterior end of adult organisms, where the youngest, posteriormost segment possess five nerves and older, anterior ones only three (Fig. 11D), because the outer ones fuse in an anterior direction. Hypothetical additional primary or secondary absence of the median nerve would result in a di-neural cord (e.g. Glyceridae, Pisionidae). Secondary absence has been described for *Nereis virens*, in which nectochaetae possess a median nerve, whereas it is absent in adults (Ushakova & Yevdonin, 1985, 1988). Finally, midventral

fusion of all nerves would result in a uni neural (simple) cord (some Nerillidae; probably ‘Oligochaeta’). The latter assumption has to be tested by analyzing neuronal differentiation in the respective taxa.

Müller & Westheide (2002) suggested that midventral concentration of the nerves might have a functional explanation in the development of parapodia. In *Parapodrilus psammophilus*, for example, the nerve strands are concentrated in parapodia-bearing segments whereas they are located far apart from each other in the last, parapodia-less segment (Fig. 11G). Combination of parapodia-bearing segments with widely separated nerves can be found in *Saccocirrus*, but rather than using their stump-like parapodia for locomotion, the animals perform ciliary gliding and peristaltic contraction of the body.

#### Ventral ganglia

Medullary nerve cords (perikarya scattered throughout the entire length) are reported only for few polychaetes whereas most taxa possess ganglionated cords (cell-free connectives and concentrated groups of perikarya). The medullary organization might be ancestral, but embryological (Echiura, Priapulida) and phylogenetic (Onychophora) studies speak in favor of a derived character, at least in some cases (Beklemishev, 1960). The ganglia consist of a fibrous core (neuropile, if synaptic connections are present) and a peripheral rind, containing the perikarya (Golding, 1992). Typically the ganglia are located in the midventral center of the respective segment, but caudal shift in anterior body regions and anterior shift in posterior regions is common. Often ganglia span the intersegmental boundary (Smith, 1957); for instance, in *Nereis* they extend from posterior regions of one segment as far as the middle of the following one (Bullock & Horridge, 1965). For all annelid subtaxa fusion of anterior ganglia into a subesophageal ganglionic mass is known. The number of included ganglia differs in Polychaeta: e.g. two in *Ophryotrocha gracilis* (Fig. 11B, C), three in *Microphthalmus*, four in *Pisione remota* and six in *Glycera alba* (Müller, 1999b), whereas it is consistently four in the Naididae (‘Oligochaeta’) and Hirudinea (Hessling et al., 1999; Purschke et al., 1993). Formation of



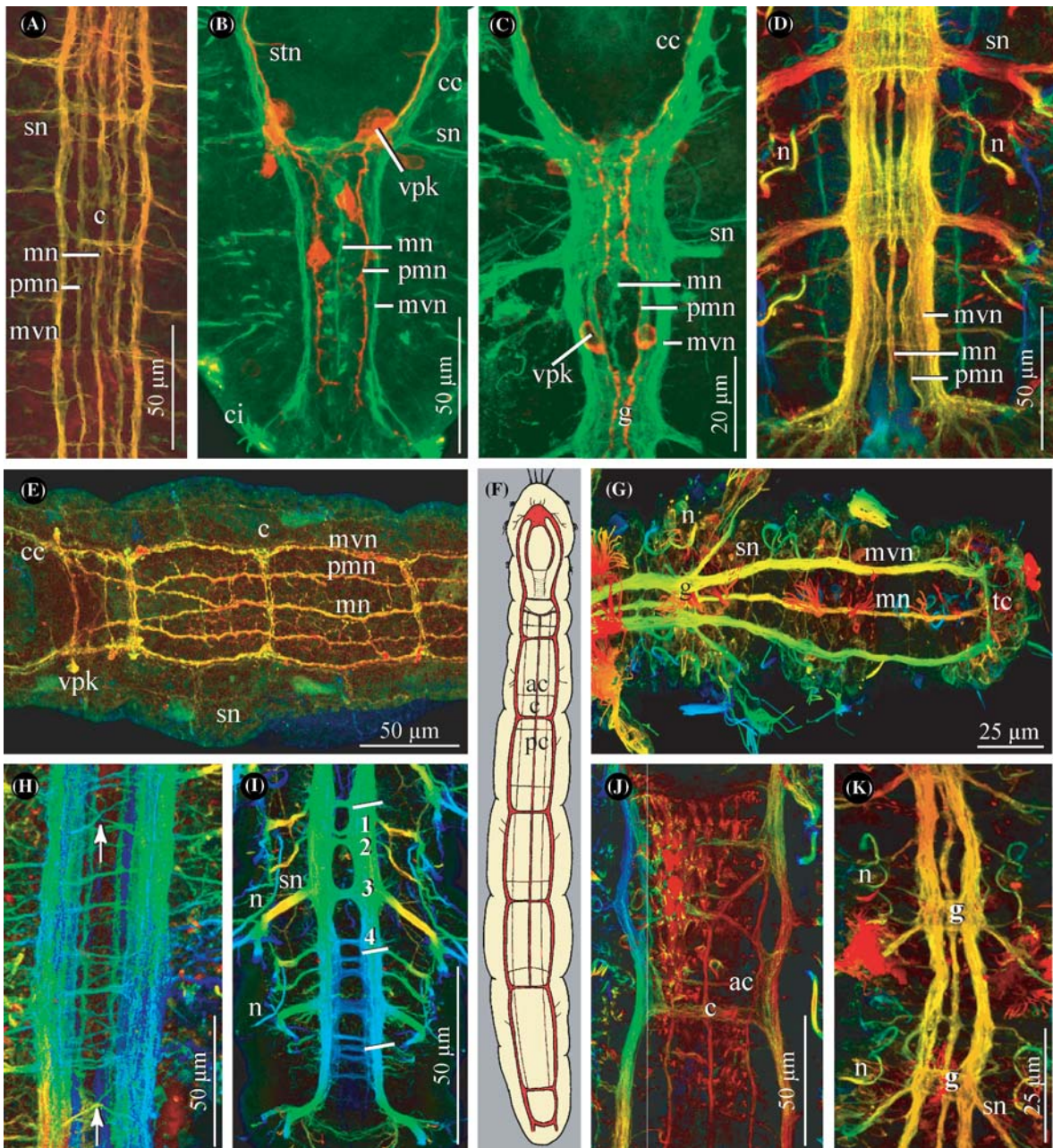


Figure 11. Confocal images (not F), 3D color-coding along the z-axis; red = periphery > blue = center (not B, C). (A) *Scoloplos armiger*, acetylated  $\alpha$ -tubulin-IR (a- $\alpha$ T-IR); ventral cord of a larva with unpaired median (mn), paired paramedian (pmn) and main ventral (mvn) nerves. c – commissure; sn – segmental nerve. (B–D) *Ophryotrocha gracilis*. (B, C) Double staining: red = serotonergic, green = a- $\alpha$ T-IR. (B) Jung larva with five connectives within the ventral cord. cc – circumesophageal connectives; ci – cilia; sn – segmental nerve; stn – stomatogastric nerve; vpk – ventral perikaryon. (C) In older larvae the five connectives persist between the dense neuropile of the ganglia (g). (D) Posterior end of an adult specimen, a- $\alpha$ T-IR. Five connectives are visible in the posteriormost end, further anterior only three connectives persist. n – nephridia. (E) *Trilobodrilus gardineri*; serotonergic IR. Ventral cord with five connectives. (F) *Trilobodrilus axi*. Schematic drawing of the ventral cord. (G) *Parapodrilus psammophilus*, a- $\alpha$ T-IR, posterior end. tc – terminal commissure. (H–K) Ventral cord, tubulinergic IR. (H) *Protodrilus* sp. a- $\alpha$ T-IR. Arrows – repeated chiasmata. (I) *Pisione remota*, a- $\alpha$ T-IR, posterior end. Numbers indicate commissures per segment. (J) *Trilobodrilus hermaphroditus*, a- $\alpha$ T-IR, anterior end. ac – anterior commissure. (K) *Parapodrilus psammophilus*, a- $\alpha$ T-IR. (F: after Müller & Westheide, 2002).

more than one ganglion per segment is claimed for Sabellariidae, Serpulidae, Sabellidae (two/segment) and Pectinarridae (two or three/segment; Beklemishev, 1960). Nothing is known about how this multi-ganglionic pattern differentiates. Subdivision of a primary single ganglia seems to be likely, but this purely speculative hypothesis has to be tested and the presence of this pattern should be reinvestigated.

**Commissures.** The majority of nerve fibers pass to the contralateral side, thus forming well differentiated commissures (Smith, 1957; Golding, 1992). In all investigated nerillid species, *Protodrilus* sp. (Fig. 11H) and *Protodriloides chaetifer*, countless commissures interconnect the ventral cords within which, apart from chiasmata, no distinct pattern could be found. In all other taxa a definite number of commissures per segment is arranged in a segmentally repetitive formation. One (*Platynereis dumerilii*) up to seven (*Chaetopterus variopedatus*, Martin & Anctil, 1984; *Saccocirrus papillocercus*, Müller, 1999b) commissures can be counted, of which one can be termed the 'main' commissure because it is broader than the others (Müller & Westheide, 2000, 2002). In Dinophilidae, e.g., the median, main commissure is accompanied by thin anterior and posterior ones (Fig. 11F, J). Due to fusion of ganglia, the segmental pattern is often modified in the subesophageal ganglionic mass (Fig. 11J). It can vary even within one specimen: in dinophilids the subordinate commissures are differently reduced and in *Pisone remota* the four commissures present in the posteriormost segment fuse anteriorly in the following sequence: (a) median ones, (b) incorporation of the anterior, (c) incorporation of the posterior one, thus 4, 3, 2 and 1 commissures per segment can be found (Müller, 1999b). Complete fusion of the right and left hemiganglion results in so called 'unitary ganglia' (Fig. 11K, *Parapodrilus psammophilus*; also in 'Oligochaeta'). Even within these concentrations transversal 'Faserbrücken' might be identified (three in *Lumbricus terrestris*, Günther, 1971).

A tendency towards increasing neuropile concentration and parallel reduction of commissure number appears likely, but remains to be confirmed by more data.

**Perikarya.** The neuronal cell bodies are located dorsally and laterally in the supraesophageal

(Fig. 12D,E) and ventrally and laterally in the ventral ganglia (Fig. 12A–C). In Polychaeta and 'Oligochaeta', serotonergic and RFamide cells occur in cerebral and ventral ganglia, whereas they are restricted to the latter in Hirudinea (Marsden & Kerkut, 1969; Wallace, 1981). Whereas 5-HT neurons, if present, are more numerous in the ventral than in the cerebral ganglia (White & Marsden, 1978; Spörhase-Eichmann et al., 1987a, b), it is just the opposite for RFamide. In Polychaeta from two (*Mesonerilla intermedia*) to 18 (*Pisone remota*, Müller, 1999b) and in 'Oligochaeta' from two (Naididae, Hessling et al., 1999) to 80–100 (*Lumbricus terrestris*, Spörhase-Eichmann et al., 1987a, b) 5-HT perikarya can be stained. With one exception (*Nerilla antennata* possesses a single, median neuron) they are arranged in bilaterally symmetrical pairs and are concentrated in two central (often a single cell) and two lateral clusters (Müller, 1999b; Müller & Westheide, 2002). At least some of the lateral neurons innervate the lateral antennae (Müller et al., 2003); therefore this cluster might represent the fifth or the eleventh ganglion in Amphinomididae and Glyceridae, respectively (Figs. 4E, 1D, E). In the ventral cord, 5-HT neurons can either have medullary distribution (e.g. *Saccocirrus papillocercus*) or can be concentrated in ganglia (e.g. *Ophryotrocha gracilis*, Fig. 12A); intersegmental clusters are also documented for Nerillidae (Müller, 1999b). Segmental patterns and, moreover, individual single neurons can hardly be identified in some Polychaeta (Fig. 12A; Müller & Westheide, 2000, 2002). In Naididae ('Oligochaeta', *Nais variabilis*, *Slavinia appendiculata*, *Stylaria lacustris*), however, serotonergic neurons are arranged in an alternating pattern in successive ganglia in posterior regions of the ventral cord, which might be an autapomorphic character for the taxon (Hessling et al., 1999). At the moment information about the distribution patterns of 5-HT neurons is too limited to allow phylogenetic comparisons, such as have been undertaken in other taxa.

### The peripheral nervous system

The peripheral system consists of nerves emanating from the ventral cords (segmental or side



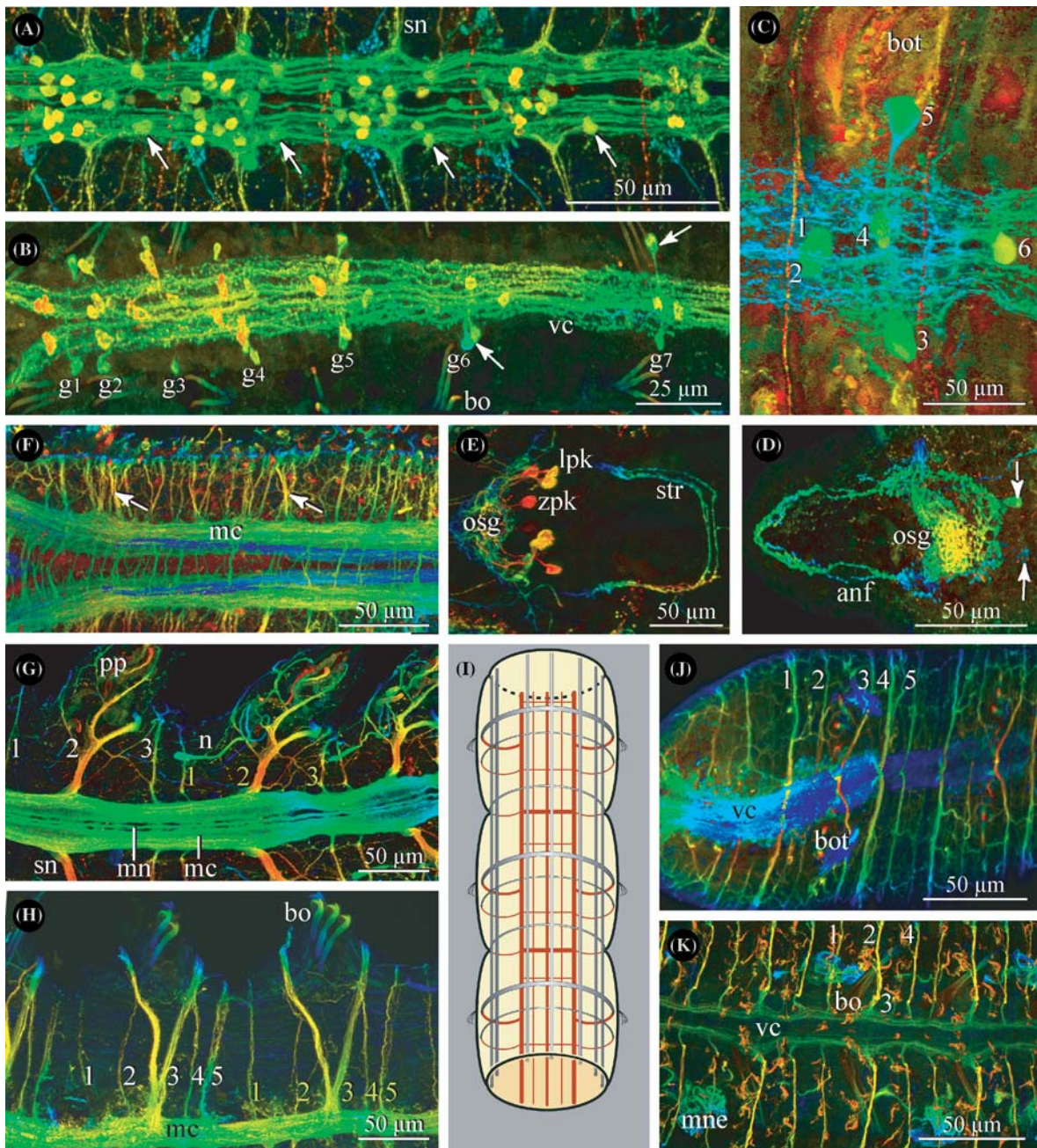


Figure 12. Confocal images (not I), 3D color-coding along the z-axis; red = periphery > blue = center. (A) *Ophryotrocha gracilis*, ventral cord, 5 HT-IR. Arrows indicate repeated perikarya. sn – segmental nerve. (B) *Pristina notopora*, ventral cord, 5 HT-IR. bo – chaetae; g1-g7 – ganglia 1–7; arrows indicate alternating perikarya. (C) *Stylaria lacustris*, single trunk ganglion, 5-HT-IR. bot – chaetal sack; number indicate single perikarya. (D) *Pristina notopora*, 5-HT-IR. Supraoesophageal ganglion (osg) with anteriorly stretching neurites (anf) and dorso-posteriorly located perikarya (arrows). (E) *Trilobodrilus hermaphroditus*, 5-HT-IR. Supraoesophageal ganglion with two central perikarya (zpk) and two groups of lateral perikarya (lpk). – str – stomatogastric ring. (F-K) Lateral nerves, a- $\alpha$ T-IR. (F) *Portodrilus* sp., arrows – repeated thicker nerves (G) *Platynereis dumerilii*. (H) *Polydora cornuta*. (I) *Dinophilus gyrocoliliatus*; schematic drawing. (J) *Enchytraeus albidus*. (K) *Stylaria lacustris*. bot – chaetal sack; mc – main cord; mne – metanephridium; mn – median nerve; n – nephridium; vc – ventral cord; numbers – segmental nerves. (I: after Müller & Westheide, 2002; J: Müller & Hundsdörfer, unpublished).

nerves), additional longitudinal nerves and an intra- or subepidermal plexus.

### Segmental nerves

Bullock & Horridge (1965) regard the presence of three segmental nerves, branching off the ventral cords at the ganglionic level, as the plesiomorphic condition. Whereas Beklemishev (1960) and Hanström (1928b) claimed that all annelids invariably possess three segmental nerves, some authors (e.g. Golding, 1992) reported a fourth pair and even the presence of only two pairs (Bullock & Horridge, 1965). The last condition has been described, e.g., for adult Hirudinea (Livanow, 1904; Nicholls & Van Esen, 1974). Early stages of *Erpobdella octoculata*, however, possess four segmental nerves, which subsequently become fused: first the median ones join one another and then the remaining anterior one is included (Hessling, unpublished data). For oligochaetes four to seven segmental nerves are described (*Stylaria lacustris*: four, Fig. 12K; *Enchytraeus crypticus*: five, Hessling & Westheide, 1999; *E. albidus*: five, Fig. 12J or seven, Bubko & Minichev, 1992). In Polychaeta, the number of nerves per segment ranges from none (*Trilobodrillus hermaphroditus*, Fig. 11F) to numerous (*Protodrillus* sp., Fig. 12F). In parapodia-bearing polychaetes the nerves that innervate the appendages are always thicker than the other ones (Fig. 12G, H). They were called 'segmental nerve 2' by Smith (1957), but the position indicated by this term may be wrong in case the annelid has more than three segmental nerves (Fig. 12H). Because their arborization patterns are variable or not discernible, homologization of the smaller nerves is impossible at present. However, branching of the parapodial nerves follows a fixed pattern: at the base of the parapodium the nerve splits, sending an anterior branch into the ventral cirrus while a posterior branch bends dorsal and innervates the dorsal cirrus (Dorsett, 1976; Müller & Westheide, 2002). Some segmental nerves elongate towards the dorsal side, where they fuse and form circular commissures (Fig. 12I). These nerves innervate ciliary trochs (Fig. 13A), dorsally lo-

cated ciliary patches (Fig. 13D) and possibly dorsal muscle fibers.

### Peripheral longitudinal nerves

The presence of paired lateral nerves in *Harmothoe imbricata* encouraged Storch (1913) to separate Amphinomidae as 'Tetraneura' from all other polychaetes, which he labeled 'Dineura'. Homologizing the respective nerves with lateral nerves of platyhelminthes and pleurovisceral connectives of Amphineura, he regarded the Amphinomidae as ancestral and the dineuralian situation as derived. Afterwards, lateral nerves were described for 'Oligochaeta' (Hanström, 1928b; Beklemishev, 1960; Bubko & Minichev, 1992; Hessling et al., 1999), Hirudinea (Beklemishev, 1960) and a few Polychaeta (Bullock & Horridge, 1965). Recent investigations demonstrated a far more common distribution of lateral nerves in polychaetes: in only three out of 28 species (*Myzostoma cirriferum*, *Parapodrillus psammophilus*, *Potamodrillus fluviatilis*) they were missing (Fig. 13E–J; Müller, 1999b). Moreover, additional longitudinal nerves were found ventrolaterally (Fig. 13A), laterally (13B) and dorsally (Fig. 13C) in larvae as well as in adults (Fig. 13E–J). As many as 17 peripheral longitudinal nerves could be demonstrated in *Saccocirrus papillocercus* (Fig. 13D, F). Together with the circular segmental nerves the longitudinal fibers form a regular grid of perpendicular nerves, which can be called an 'orthogon' (Beklemishev, 1960). From a similar neural arrangement Reisinger (1925, 1972) and Hanström (1928b) developed a theory on the evolution of the central and peripheral spiralian nervous system. This theory suggested, that – in addition to the brain – the longitudinal nerve strands and annular commissures originate from the basiepidermal plexus, become organized so that the commissures and strands are perpendicular to one another and the whole structure is displaced inward as an 'orthogon'. By reduction of the dorsal longitudinal nerve strands and concentration of perikarya into ganglia, this structure then gives rise to the nervous system of the Articulata, with its ventral ganglion chain. By providing evidence that one



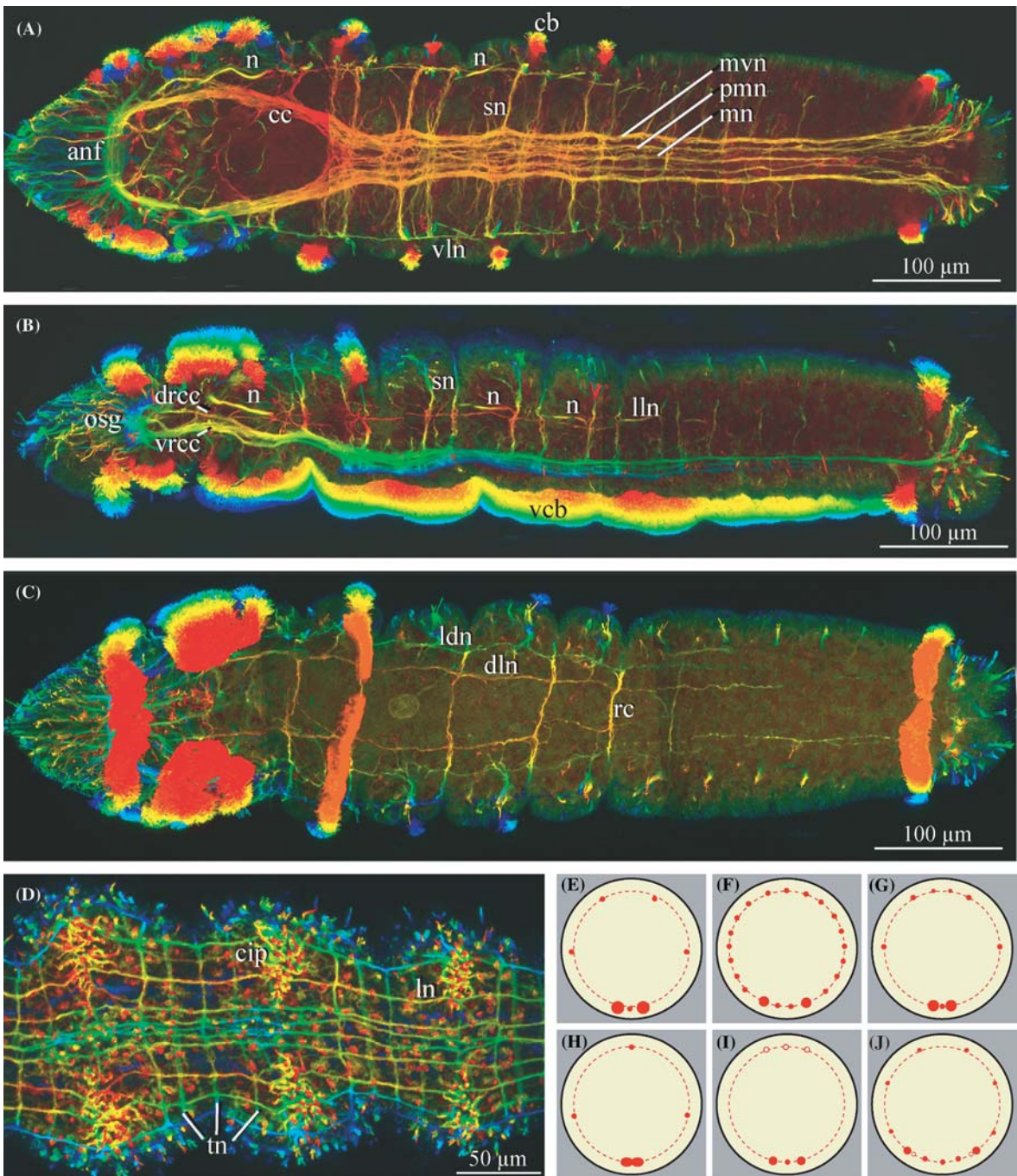


Figure 13. Peripheral nerves. (A–D) Confocal images, 3D color-coding along the z-axis; red = periphery > blue = center. (A–C) *Scoloplos armiger*, a- $\alpha$ T-IR. (A) Ventral view. (B) Lateral view. (C) Dorsal view. (D) *Saccocirrus papillocercus*, a- $\alpha$ T-IR. (E–J) Schematic cross sections with ventral nerve cord and peripheral nerves. The dotted line indicates a possible ring commissure. (E) *Scoloplos armiger*. (F) *Saccocirrus papillocercus*. (G) *Platynereis dumerilii*. (H) *Nerilla antennata*. (I) *Parapodrilus psammophilus*. (J) *Dinophilus gardineri*. anf – anterior neurites; cc – circumesophageal connective; cb – ciliary band; cip – ciliary patch; dorsal (drcc) and ventral (vrcc) root of the circumesophageal connective; dorsolateral (ldn), laterodorsal, lateral (lln) and ventrolateral (vln) longitudinal nerve (ln); median (mn), main (mvn) and paramedian (pmn) nerve of the ventral cord; n – nephridium; rc – ring commissure; sn – segmental nerve; tn – transversal nerve.

of the main arguments for this scenario, an orthogon is absent in the polychaete *Lopadorhynchus*-larva (Hanström, 1928b), Åkesson (1967b) questioned this theory. In fact, homologization of the platyhelminth and annelid 'orthogon' remains difficult, because in many cases the nerves stay in an basiepithelial position in Polychaeta, whereas they are shifted inwards in Platyhelminthes. Because of their different positions and concentrations it is not even possible to homologize the peripheral longitudinal nerves within polychaetes at present. Further investigations have to clarify whether, as has been thought (Westheide & Rieger, 1996), formation or reduction of the neuronal orthogon is in fact correlated with formation and reduction of a muscular orthogon.

### Annelida – Arthropoda

Most authors regard the rope-ladder-like nervous system as an apomorphic character for the Articulata. Whereas the ventral cord is highly variable in Annelida, concerning the position of the connectives, additional longitudinal nerves (unpaired median, paired paramedian) and commissure-number per segment, the Arthropod cord is much more consistent. The Onychophora, however, demonstrate that widely separated cords connected via numerous commissures per segment also occur in Arthropoda. It might be concluded that the nerve cord of the stem species of the Articulata had widely separated connectives, a median nerve and many commissures per segment, and that furthermore, within Annelida and Arthropoda the longitudinal nerves became concentrated in the midline and the number of commissures was reduced by fusion. On the other hand, the recent erection of a taxon Ecdysozoa, comprising Arthropoda and several Nematelminthes taxa, would imply that the segmentation found in annelids and arthropods, and with it the rope-ladder-like nervous system, must be either convergent or an ancestral feature of protostomes or even bilaterians (see Scholtz, 2002 for thorough discussion). Further detailed morphological information e.g. comparison on individual single neuronal level between Annelida and Arthropoda

or Cyloureaalia and Arthropoda is needed to support either the Articulata or the Ecdysozoa.

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## Abbreviations used in Figures 1–7

The figures are taken from papers that are published in German and in English. In the schematic drawings as well as in the list, German and English abbreviations are given in order to enable easy understanding of the original papers.

1 – 12	palp nerve roots
aac	anterior association commissure
acc	accessory connective
acig	anterior cirral ganglion
acntmarct	anterior connection between ntm (nerve of the tentacular membrane) and arct (anterior root of common tract)
ag	annexed ganglion
an + tn	antennal nerve + first tegumentary nerve
äNIN	äußerer Nerv des langgestreckten Nuchalorgans (nuchal nerve)
aon	anterior optic nerve
arct	anterior root of ct (common tract)
asgc	anterior stomatogastric commissure
asgn	anterior stomatogastric nerve
avrtpn	anterior ventro-rostral tract of palp nerve
BG <sup>1, 2</sup>	Bauchganglion 1, 2 (ventral ganglia 1, 2)
c <sup>1–c7</sup>	brain commissures
cc	circum-oesophageal connective
cggHo	Holmgren's cerebral commissural ganglion
cg	commissural ganglion
cgHa	Hamaker's commissural ganglion
com	commissure
conciq	connection between the anterior and posterior cirral ganglia
ct	common tract of sgn ( <i>Pista</i> ), sgn and nbt ( <i>Pectinaria</i> ) sgn, nbt and lntm ( <i>Amphitecis</i> )
ctn	common tract nerve
dac	dorsal association commissure
dacn	dorso-anterior cirral nerve
dcc	dorsal cell cluster
dcdrr	dorsal commissure of dorsal root
dcdrlpn	dorsal commissure of dorsal root and lateral palp nerve
dcdvr	dorsal commissure of ventral root
dg	dorsal ganglion
DG	Dorsalganglion des hinteren Schlundkonnectivs (dorsal ganglion of drcc)
dKhs	dorsale Kommissur des vorderen Schlundkonnectivs = dcdrr
dKvs	dorsale Kommissur des hinteren Schlundkonnectivs = dcdvr
dltpn	dorso-lateral tract of palp nerve
dn, dN	dorsal nerve

dpcn	dorso-posterior cirral nerve	nvl	nerve to the latero-ventral parts of the buccal lips
dpn	dorsal palp nerv	nma	nerve to the median antenna (= n <sup>6</sup> )
drcc	dorsal root of circum-oesophageal connective	nmr	nerve of mouth region
drdctpn	dorsal root of dctpn (dorso-caudal tract of palp nerve)	NMu	Nerven zur Mundöffnung
drlpn	dorsal root and longitudinal podial nerve	nmvl	nerve to the medio-ventral parts of the buccal lips
e <sup>1, 2</sup>	anterior (1) and posterior (2) eye	nn, NN	nuchal nerve
enn	extra nuchal nerve	NNhs	Nuchalnerv des hinteren Schlundkonnectivs (nuchal nerve of drcc)
f <sup>1</sup> – f <sup>1,3</sup>	nerve fibres connecting different parts of the brain	nss	nerve of stomodeal sac
g <sup>1</sup> – g <sup>9</sup>	brain ganglia	ntm	nerve of tentacular membrane
G <sup>1, 2</sup>	ganglia 1, 2	nug <sup>1, 2</sup>	nuchal ganglion 1, 2
gxrcc	ganglion of extra root of cc	nvlm	nerve of the ventral longitudinal muscles
gdacn	ganglion of dorsal anterior cirral nerve	NvP	Nerven zum vordersten Teil des Prostomiums (nerves extending to the anterior part of the prostomium)
gdpcn	ganglion of dorsal posterior cirral nerve	NzdIP	Nerven zum zilierten dorsolateralen Teil des Prostomiums (nerves extending towards the ciliated dorsolateral part of the prostomium)
gmnbc	ganglion of median nerve of branchial crown	oc	optic commissure
GZNZ	im Anschluß an die Nuchalnerven befindliche Ganglionzellen (nuchal ganglia)	Oen, OeN	oesophageal nerve
hS	hinteres Schlundkonnectiv = drcc	pcdrcc	posterior commissure of dorsal root
iNIN	innerer Nerv des langgestreckten Nuchalorgans (nuchal nerve)	pcig	posterior cirral ganglion
lcc	lateral cell cluster	pentmarct	posterior connection between nerve of tentacular membrane and anterior root of cc
LG	Lateralganglion (lateral ganglion)	pdngl	posterior dorsal neuropile with globuli cells
ln	lateral nerve	pn, PN a-c	palp nerve
lnbc	lateral nerve of branchial crown	Pn <sup>a</sup>	äußerer Palpennerv (outer palp nerve)
lng	lateral nuchal ganglion	Pn <sup>i</sup>	innerer Palpennerv (inner palp nerve)
lpn	longitudinal podial nerve	pnr	palp nerve root
lrn <sup>1</sup>	lateral root of first anterior nerve	PNZ	Pilem des Nuchalzentrums
mm	median mass	pog <sup>1</sup>	first podial ganglion
mnbc	median nerve of branchial crown	poK, pok	praeoral commissure
mrn <sup>1</sup>	median root of first anterior nerve	pon <sup>1</sup>	first podial nerve
msgn	median stomatogastric nerve	pon	posterior optic nerve
n <sup>1</sup> – n <sup>8</sup>	brain nerves	prct	posterior root of ct (common tract)
N	giant cell	psgc	posterior stomatogastric commissure
nbc	nerve of branchial crown	psgn	posterior stomatogastric nerve
nbs	nerve of buccal segment	pvrtpn	posterior ventro-rostral tract of palp nerve
nbt	nerves of buccal tentacles	pw	nerve from lateral nerve to brain commissure
nbtldr	nerves of buccal tentacles and dorsal ridge	sgn	stomatogastric nerve
nc, NK	nuchal commissure	SN	side nerve, segmental nerve
ndbv	nerve of the dorsal blood vessel	stg	stomatogastric gap
NDK, sgn	stomatogastric nerve	tg	tegumentary ganglion
ndo, NdS	nerve of dorsal (sensory) organs	tn <sup>1-7</sup>	tegumentary nerve
ng, NG	nuchal ganglion	vac	ventral association commissure
ngl	nuchal glomeruli	vacn	ventral anterior cirral nerve
NhN	Nerv zum hufeisenförmigen Nuchalorgan (nuchal nerve)	vcc	ventral cell cluster
nla	nerve of lateral antenna	vedr	ventral commissure of dorsal root
nlcp	nerve of lateral ciliated pad		
nllp, NILP	nerve of lateral prostomial lobe		



vcdrlpn	ventral commissure of dorsal root and longitudinal podial nerve	vpcn	ventral posterior cirral nerve
vrctpn	ventral root of dorsal-caudal tract of palp nerve	vpn	ventral palp nerve
vcvr	ventral commissure of ventral root	vrcc	ventral root of cc
vg	ventral ganglion	vrctpn	ventral root of dorso-caudal tract of palp nerve
vKhS	ventrale Kommissur des hinteren Schlundkonnektivs = vcdr	vS	vorderes Schlundkonnektiv = vrcc
vKvS	ventrale Kommissur des vorderen Schlundkonnektivs = vcvr	xc	extra commissure
		XI	Manaranche's Nucleus XI (dorsal ganglion)
		xrcc	extra root of cc.