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Zoomorphology

On the Structure and Homologues of the Anterior End of the Polychaete Families Sabellidae and Serpulidae

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Summary. The nature and homologues of the appendages of the anterior end of the polychaete families Sabellidae and Serpulidae have long been discussed. The main purpose of the present investigation, in which seven sabellid and eight serpulid species are studied, is to contribute towards the solution of these problems. At the same time, however, the present study, within its limited range, aims to enlarge our knowledge of the anatomy of the polychaetes in general. Such a knowledge, it is argued, is a prerequisite for further consideration of the phylogeny of the Polychaeta.

As shown in many earlier papers, the architecture of the cephalic nervous system and the innervation of the organs and appendages of the anterior end of polychaetes constitute reliable instruments for elucidating the morphological significance of these structures. In the present paper, consequently, extra consideration is given to descriptions of the central nervous system of the sabellids and serpulids studied.

The integumental depression found in front of and below the brain of all the sabellids and serpulids here studied is described by the term "dorsal pit". It is concluded that the dorsal pit within each family in all probability represents a homologous structure, but it is in no way proven that the dorsal pit of the sabellids is equivalent to that of the serpulids.

Some earlier literature maintains that paired antennae [*antennes de première paire* in Binard and Jeenerś (1928) terminology] are found in some sabellids and serpulids. In the present paper it is maintained that these structures must instead be interpreted as nuchal organs. Such organs are found in all the sabellid and serpulid species here studied.

The Pruvot-Meyer theory which claims that the joint pore of the thoracic nephridia of the "serpulimorphic" families is equivalent to the nuchal organ of other polychaetes is shown to be without foundation, and it is consequently rejected.

The histology, vascularization, and innervation of the branchial crown and the appendages of the dorsal lip of the mouth of the species investigated are described. It is concluded that the branchial crown and some (but not

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all) appendages of the dorsal lip are equivalent to the palps (when present) of the "spiomorphic", the "drilomorphic", and the "errant" polychaetes.

The appendages of the dorsal lip of the mouth, in most faunistic literature called palps, are found to represent structures of three different kinds and origins: (a) branchial radioli which have become separated from the crown and have fused with the lip, (b) branchial pinnulae which have undergone a similar process of dislocation, and (c) new formations from the walls of the mouth cavity. It is proposed that in comparative-anatomical works these appendages should be called (a) lip-associated radioli, (b) lip-associated pinnulae, and (c) outgrowths of the dorsal lip respectively. As a joint and anatomically neutral term to be used in faunas and descriptions of the outer morphology, the expression "appendages of the dorsal lip" or, more briefly, "(dorsal) lip processes" is proposed.

The interrelationships of the Sabellariidae, the Sabellidae, and the Serpulidae are discussed, as is the taxonomic subdivision of the last two families. In agreement with some earlier authors although contrary to others it is thereby maintained that:

1) the suborder Serpulimorpha Hatschek (1893) (inclucing sabellariids, sabellids, and serpulids) does not constitute a natural systematic unit;

2) the sabellids and serpulids, although markedly different in many respects (thoracic membrane, operculum, branchial skeleton), are probably closely related to each other. Earlier arguments supporting this view are corroborated by data on the dorsal lip processes and the architecture of the brain of the two families;

3) Rioja's (1923) division (based on setal structures) of the Sabellidae into the three subfamilies Sabellinae, Fabriciinae, and Myxicolinae is supported by the anatomical data emphasized in the present paper; and

4) within the Serpulidae the genera *Apomatus* and *Protula* should be referred to the subfamily Filograninae [as proposed by Rioja (1923), followed, among others, by Fauvel (1927), and Hartmann-Schröder (1971)] and not to the Serpulinae, [as maintained by Hartman (1959) and Fauchald (1977)]. Again, the view presented by the present author is founded on anatomical data (the morphological value of the dorsal lip processes of the genera in question).

1. Introduction

1.1. Terminology

Figure 1 shows the anterior end of one representative of each of the families Sabellariidae, Spionidae, Serpulidae, and Sabellidae. Most terms referring to the outer morphology which are used in this paper are presented in this figure. Others will be discussed later.

The terminology referring to basic structures in the polychaete cephalic nervous system is the same as used in my sabellariid paper (Orrhage 1978, Table 1). Special terminological questions concerning the sabellids and serpulids are treated under the respective headings in the text.

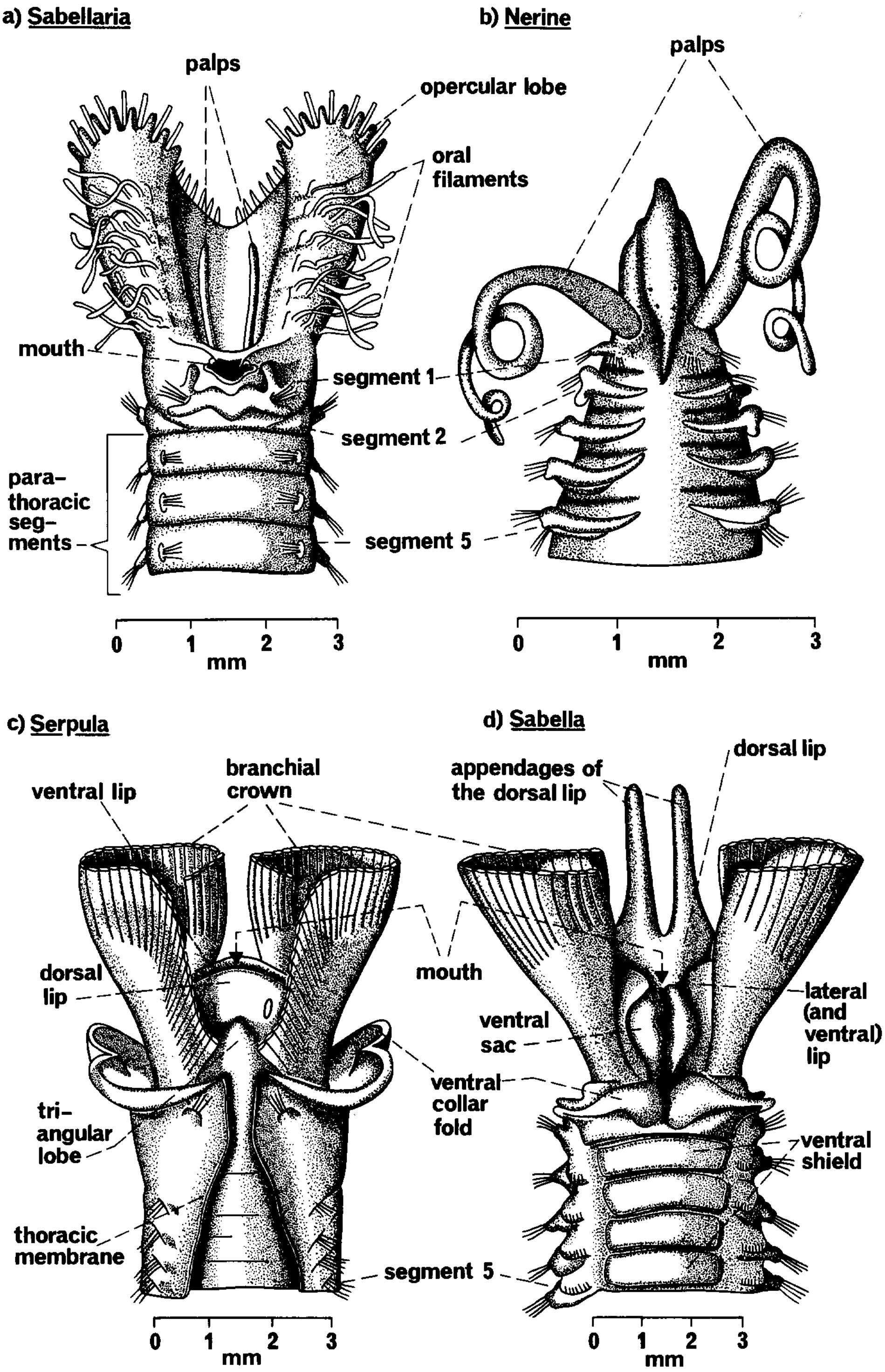


Fig. 1. The anterior end of (a) *Sabellaria alveolata* (Fam. Sabellariidae), ventral view, after Orrhage (1978); (b) *Nerine cirratulus* (Fam. Spionidae), dorsal view; (c) *Serpula vermicularis* (Fam. Serpulidae), dorsal view; (d) *Sabella penicillus* (Fam. Sabellidae), ventral view. In the *Serpula* and *Sabella* figures the distal parts of the branchial crown are cut off

Table 1. Terminology and homologies of anterior end appendages of the Sabellariidae, the Sabellidae, the Serpulidae and the Spionidae according to some earlier authors

Present designations	Sabellariidae		Sabellidae and/or Serpulidae			Spionidae	
	palps	oral filaments	paired antennae	appendages of the dorsal lip	branchial crown	palps	mouth region
Pruvot (1885)			vraies antennes, appendices coniques				
				pretendues antennes – + – (palpes)	cirrhes branchiaux		
Meyer (1888)	Stirntentakel, Stirnfühler, hämale Kopftentakel		Zapfen, Stirnfühler, hämale Kopftentakel				
				fühlerartige (-förmige) Lippenfortsätze, Lippenzipfel, Lippenzapfen			
		Mundtentakel, Tentakelfäden, neurale Kopftentakel			Kopfkiemen neurale Kopftentakel	Tentakel	
Johansson (1927)	Palpen			Mundanhänge – + – (Palpen)	Siebapparat		
		Mundfäden				Fanganhänge	stark ausgezogene laterale Partien der Oberlippe?
Binard and Jeener (1928)	appendices pairs, antennes de première paire		appendices de la dépression frontale, antennes de première paire				
		tentacules du capuchon operculaire, antennes de deuxième paire		appendices (languettes) de la lèvre dorsale, + antennes de deuxième paire (palpes)	branchies cephaliques,	palpes, antennes de deuxième paire	

On the basis of asymmetry, coiled tube, operculum development (not from the most dorsal but from the second radiolus of the branchial crown), hermaphroditism, embryonal development, and the number of thoracic segments, Pillai (1970) elevated the subfamily Spirorbinae Chamberlin to the rank of a separate family. He has had many followers, e.g., Knight-Jones et al. (1975a and b), Bailey-Brock and Knight-Jones (1977), Fauchald (1977), Knight-Jones (1978), and Knight-Jones and Fordy (1979). Pillai's proposal is accepted also by the present author. For this reason and since no material of the Ficopomatinae Pillai (1960) was available, the term Serpulidae as used in this paper comprises the subfamilies Serpulinae and Filograninae as defined by Rioja (1923).

Such terms as "errant", "sedentary", "spiomorphic", and "drilomorphic" polychaetes will sometimes be found in the present paper. Although in all probability such concepts do not delimit any natural systematic units, they are used here as well-known and practical collective terms. Thus, for instance, "spiomorphic" polychaetes here include the families Spionidae Sars, Trochochaetidae Pettibone (Disomidae Mesnil sensu Hannerz), Poecilochaetidae Hannerz, Apistobranchidae Mesnil and Caullery, Magelonidae Cunningham and Ramage, Orbiniidae Hartman (Ariciidae Audouin and Milne-Edwards), Paraonidae Cerruti, Flabelligeridae Saint-Joseph (Chlorhaemidae Malmgren), and Chaetopteridae Audouin and Milne-Edwards.

1.2. Purpose of the Present Investigation

In earlier papers the author has reported on his studies of the architecture of the central nervous system of most "spiomorphic" and of some "drilomorphic" polychaete families (Orrhage 1964a and b, 1966, 1974). In these papers the structure of the appendages of the anterior end of spionids, trochochaetids, poecilochaetids, apistobranchids, chaetopterids, flabelligerids, magelonids, and cirratulids was accounted for and the nature and homologues of these appendages were discussed mainly on the basis of their innervation, with reference of course to earlier literature on this subject (e.g., Binard and Jeener 1928; Gustafson 1930; Hanström 1928, 1930; Holmgren 1916; Johansson 1927; Söderström 1920).

During my studies on the structure and evolution of the anterior end of the Sabellariidae (Orrhage 1978) the problems long discussed concerning the nature and the homologues of the anterior appendages of the sabellids and serpulids were actualized. Table 1 reflects some of these problems and also shows the terms used by Pruvot (1885), Meyer (1888), Johansson (1927), and Binard and Jeener (1928) to refer to appendages of the anterior end of the polychaete families included in the table. A study of table raises the following questions (among others):

1. Are paired antennae to be found in the sabellids and/or the serpulids? According to Pruvot, Meyer, and Binard and Jeener, paired antennae are found in the Sabellidae (especially well developed in *Sabella*) and Meyer, and Binard and Jeener considered them homologous to the palps of the sabellariids. Johansson, on the other hand, could not find any such appendages. Neither Evenkamp

(1931) nor Nicol (1931) mention paired antennae in the sabellid species they studied (*Laonome kroyeri, Euchone papillosa* and *Sabella pavonina*, respectively).

2. Is the presence of appendages of the dorsal lip typical of the entire family of Sabellidae?

3. Are there any serpulids bearing such appendages?

4. Do the appendages of the dorsal lip (when present) constitute parts of the sabellid/serpulid branchial crown (Pruvot, Johansson, Binard and Jeener) or are they, as Meyer maintained, *von der Mundhöhlenwandung hervorgesprosste Neubildungen* (new structures springing out from the wall of the mouth cavity)?

a) If the appendages of the dorsal lip do not form parts of the branchial crown, which parts (if any) of the sabellariid, spionid, etc., body are then equivalent to i) the appendages of the dorsal lip and ii) the branchial crown of the sabellids and serpulids?

b) If, on the other hand, the appendages of the dorsal lip (when present) do constitute parts of the branchial crown, are then these two types of appendages taken together

i) homologous to the palps of the spionids (Binard and Jeener) and, consequently, also to the palps of the other "spiomorphic" polychaetes and of the cirratulids (cf. Orrhage 1964a–1974) or are they not (Johansson 1927)?

ii) homologous to the palps of the sabellariids (Johansson 1927) or not (Binard and Jeener 1928)?

iii) homologous to the oral filaments of the sabellariids (Binard and Jeener 1928) or not (Johansson 1927)?

In spite of many earlier investigations (e.g., Pruvot 1885; Meyer 1888; Johansson 1927; Evenkamp 1931; Rullier 1951), some of which are quite detailed, the question of the existence of nuchal organs in the sabellids and serpulids seems to be far from settled. This necessitates a renewed discussion of Pruvot's (1885) and Meyer's (1888) idea of the homology between the nephridial pore of the serpulids and the nuchal organs of other polychaetes.

The purpose of the present investigation, however, is not only to contribute towards a solution of the above-mentioned homology problems. Within its limited range, it also aims at enlarging our knowledge of the anatomy of the polychaetes in general. Since our information on the structure of this animal group is unfortunately quite fragmentary, more information is a prerequisite of future studies of the interrelationships of the polychaete families, and of discussions on the phylogenetic connections between Polychaeta and other invertebrate groups.

1.3. Disposition of Matters

In the different chapters below, the families and species investigated are not always treated in the same order. This is not by chance, but the result of pedagogical considerations. The structure, for instance, of the appendages of the anterior end of *Serpula, Apomatus,* and *Protula* is much easier to depict after the appendages of the sabellids have been described, while the central nervous system of this family, on the other hand, is much more easily understood in the light of observations regarding the architecture of the serpulid brain. These inversions of the order of treatment of the subjects are, it is hoped, compensated for by the insertion of numerous subheadings.

2. Material and Methods

Among sabellids and serpulids the following species, here assigned to the subfamilies proposed by Rioja (1923), were investigated:

Sabellidae Malmgren
  Sabellinae Rioja: *Sabella penicillus* Linné, *Potamilla reniformis* (O.F. Müller).
  Fabriciinae Rioja: *Euchone papillosa* (Sars), *E. rubrocincta* (Sars), *E. analis* (Kröyer), *Chone infundibuliformis* Kröyer.
  Myxicolinae Rioja: *Myxicola infundibulum* (Renier).

Serpulidae Johnston
  Serpulinae Rioja: *Serpula vermicularis* Linné, *Pomatoceros triqueter* (Linné), *Ditrupa arietina* (O.F. Müller), *Hydroides norvegica* Gunnerus, *Placostegus tridentatus* (Fabricius).
  Filograninae Rioja: *Apomatus similis* Marion and Bobretzky, *Protula tubularia* (Montagu), *Filograna implexa* Berkeley.

Most of this material was collected during stays at the Kristineberg Marine Biological Station in Fiskebäckskil (west coast of Sweden), at the Tjärnö Marine Biological Station near Strömstad (west coast of Sweden), and at the Katla Field Centre, Vikurbakki, Eyjafjördur (north coast of Iceland). After narcotization in MS 222, menthol, or chloretone this material was treated with Bouin, Bouin-Hollande, Bouin-Duboscq-Brasil, Heidenhain's "Susa", Zenker, Helly, or formalin-alcohol solutions.

A minor part of the material belonged to the collections of the Swedish Museum of Natural History in Stockholm and to the Museum of the Zoological Institute in Uppsala (Sweden). This material was fixed in formalin-alcohol (Stockholm) or placed at my disposal in the form of section series dating from the 1920's (Uppsala).

For the purpose of comparison I have re-studied the "spiomorphic", the "drilomorphic", and the sabellariid species enumerated in my 1964a to 1978 papers. For the collection and the fixation of these forms, the reader is referred to the papers in question.

After the paraffin embedding and serial sectioning of all the above material except that borrowed from Uppsala, the slides were stained with iron haematoxylin, Ehrlich's haematoxylin, Azan, or the van Gieson method. The thickness of the sections was mostly 4 or 5 µm; in some cases, however, it was 7 or 8 µm.

3. Observations

3.1. *The Dorsal Pit*

The structures that will be briefly described below have, with varying degree of accuracy, been treated under the names of *Stirneinsenkung* (Meyer 1888), *Integumenteinsenkung* (Johansson 1927), *depression frontale* (Binard and Jeener 1928), and "dorsal pit" (Nicol 1931).

3.1.1. Sabellidae

Nicol (1931) described the dorsal pit in *Sabella pavonina* in the following way (cf. the present Fig. 2g–l): "Between the dorsal lip and the dorsal body wall

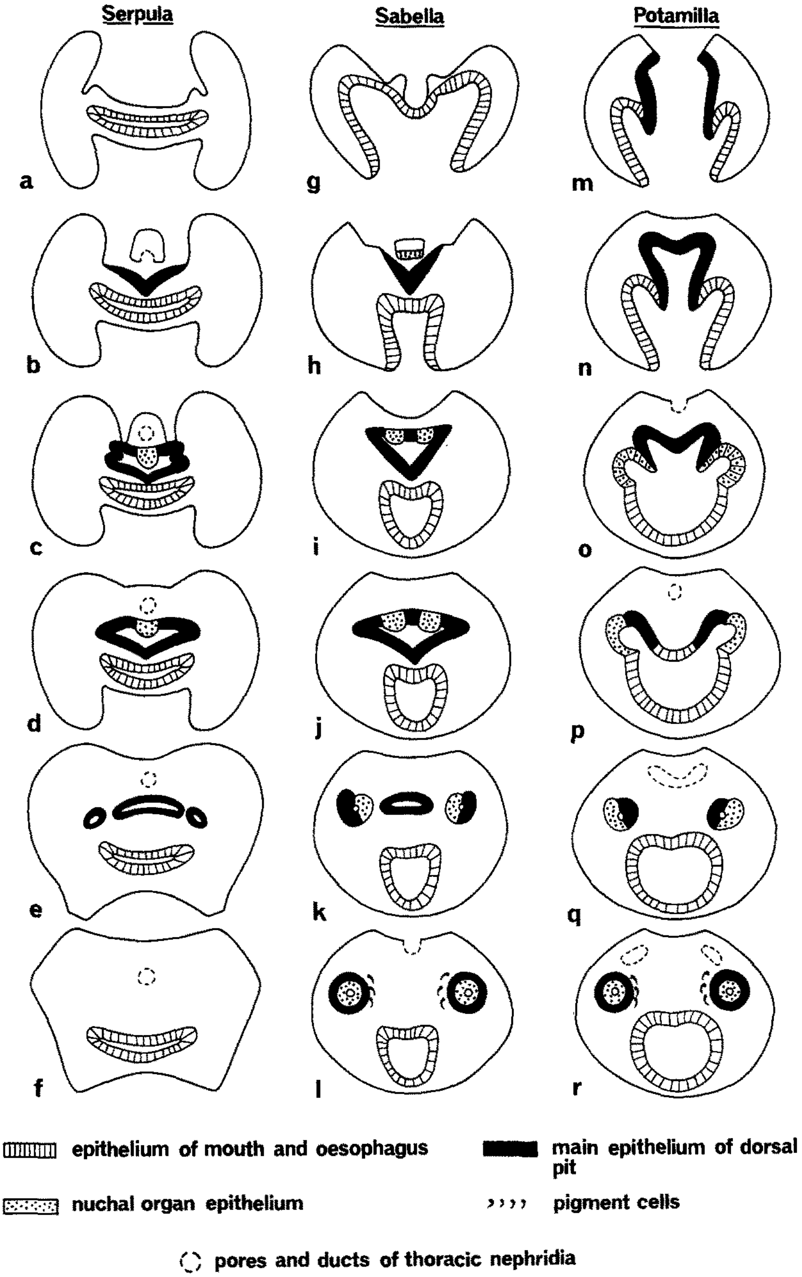


Fig. 2. Six schematical transverse sections through the anterior end of (**a–f**) *Serpula vermicularis*, (**g–l**) *Sabella penicillus*, and (**m–r**) *Potamilla reniformis*. For further explanation, see text

is a deep pit formed by an inpushing of the surface epithelium. The shape of the pit in transverse section is roughly triangular, the base lying along the dorsal body wall and the apex filling the triangular fold in the dorsal lip. The epithelium lining the pit is similar to that of the dorsal body wall. ... The pit runs back until it reaches the anterior margin of the cerebral ganglia. ... "(Here it)" divides into three finger-like processes lying in the same plane, but of unequal lengths. The central one runs back for a short distance ... The lateral processes pass backwards in the angle between the cerebral ganglia and the lateral connectives, and end on a level with the most posterior portion of the internal supporting skeleton. At the same level as the end of the central process the lumen of the lateral processes becomes very narrow, and the lining cuticle fuses together to form a central hyaline rod; pigment appears in the cells towards the middle line, and the ganglion cells become associated with the epithelium on that side also."

My section series of *Sabella penicillus* confirm most of the above observations. However, the hyaline material in the narrowest parts of the lateral processes does not fill the whole lumen of these canals and the epithelium lining this very narrow lumen seems to consist of two histologically different components (see 3.2.2.1).

In *Potamilla reniformis* (Fig. 2m–r) the dorsal epithelium of the dorsal lip is made up of columnar and sparsely ciliated cells, and it contains few mucous cells. This epithelium is in open connection with the mouth and further backwards it constitutes the roof of the oesophagus (Fig. 2n–o). On a level with the anterior margin of the brain, this special epithelium together with parts of the dorsolateral and heavily ciliated oesophagus epithelium, which here form two shallow pouches, are separated from the rest of the tissues lining the oesophagus lumen (Fig. 2o–p), thus forming two lateral canals; these, as in *Sabella*, end blindly in the vicinity of the circum-oesophageal connectives. Here, precisely as in *Sabella*, the median parts of the canals are surrounded by pigment (Fig. 2r).

In the *Chone* and the *Euchone* species I have studied, structures almost identical to those just described in *Potamilla reniformis* are found. The same is true of *Myxicola infundibulum*, although here the long horizontal rows of pigmented cells lie outside the lateral canals.

As can be seen from the above descriptions, striking structural and histological similarities exist between the dorsal pit of *Sabella* and the mouth-oesophagus canal systems of the other sabellids here studied. In spite of the fact that in *Sabella* the dorsal pit is entirely separated from the alimentary canal, and notwithstanding the intimate contact between the oesophagus and the anterior parts of the canal systems of the other sabellids, it can hardly be doubted that the principal parts of these organs are homologous in *Sabella, Potamilla, Euchone, Chone,* and *Myxicola*. Accordingly, these organs should be given the common name of a 'dorsal pit'.

3.1.2. Serpulidae

In the serpulids, too, a depression of the surface epithelium is found between the dorsal lip and the dorsal body wall. In *Serpula vermicularis* (cf. Fig. 2a–f) the entrance of this depression is situated immediately under the tip of the triangular lobe (cf. Fig. 1c). The invagination, which in transverse section has the shape of a horizontal slit, extends backwards below the brain where it ends on a level with the commissures of the ventral roots of the circum-oesophageal connectives (see 3.4.2.1). No canal systems like those found in the sabellids were observed, but the depression is faintly trilobed in its hindmost part (Fig. 2e). The ventral, lateral, and dorsolateral margins of the depression are lined with columnar cells devoid of cilia but strongly cuticularized. In the mid-dorsal area of the depression the epithelium is quite different (see 3.2.2.2).

In all the other serpulid species studied here a frontal depression, structurally and histologically quite similar to that just described in *Serpula*, is found. There thus seems to be no doubt that these epithelial depressions in the serpulids are equivalent.

3.1.3. Terminological Note

It must perhaps be questioned whether the frontal depression of the serpulids is homologous to the dorsal pit of the sabellids. It is true that the general position of the two structures is similar. On the other hand, the canal system of the sabellid dorsal pit has no equivalents in the serpulids. Whatever the final answer to this question may be, both the epithelial depressions of the serpulids and the frontal invaginations described above in sabellids will, for practical reasons, here be called dorsal pits.

3.2. Paired Antennae and Nuchal Organs

3.2.1. Earlier Literature

In the dorsal pit of *Sabella pavonina* Pruvot (1885) found *"deux appendices coniques, très courts"* (two very short conical appendages), which he called *vraies antennes*. According to Pruvot these appendages were innervated from the median and dorsal parts of the brain (*les ganglions cérébroides internes* in his terminology). In the dorsal pit of *Spirographis spallanzanii* Meyer (1888) found *zwei Paar parallele, bewimperte Leisten, welche vorn mit einem Paar kurzer, kegelförmiger Zapfen enden* (two pairs of parallel, ciliated ridges, ending anteriorly in a pair of short, conical structures). In Meyer's opinion these *Stirnfühler*, or *hämale Kopftentakel*, were equivalent to the conical appendages observed by Pruvot in *Sabella* (see Table 1). According to Meyer, rudiments of such *Stirnfühler* were also to be found in *Eupomatus* (=*Hydroides*) and *Psygmobranchus* (=*Protula*). In Binard and Jeener's (1928) interpretation of the morphology of the anterior end of sabellids and serpulids, the presence of what they called *appendices de la dépression frontale* (*antennes de première paire*) in the dorsal pit of *Sabella* and *Spirographis* plays decisive role.

In his comprehensive work on the nuchal organ of the "sedentary" polychaetes, Rullier (1951) dealt also with the families Sabellidae and Serpulidae. One reason for his occasionally somewhat puzzling results (see 4.3) could be that, while emphasizing the difficulties in discerning a *"cerveau antérieur"* (forebrain), a *"cerveau moyen"* (midbrain), and a *"cerveau postérieur"* (hindbrain) in the "sedentary" polychaetes, he sometimes seems to adhere to Racovitza's (1896) idea of a tripartition of the polychaete brain. However helpful this idea might have seemed when it was put forward, it has, in my opinion, as our knowledge of the architecture of the polychaete brain has expanded instead become in recent decades an obstacle to unbiased observation and thought (cf. Orrhage 1978). The main reason, however, for the difficulties which Rullier encountered seem to lie in the fact that neither through earlier publications nor through his own observations has he had reliable information concerning the architecture of the cephalic nervous system of the taxa he discusses.

3.2.2. Present Observations

3.2.2.1. Sabellidae. In *Sabella penicillus* I have rediscovered the *appendices* briefly described by Pruvot (1885) and Binard and Jeener (1928). In my section series, however, these structures do not appear as 'taps' or 'tentacles'. They should be discribed, rather, as follows (cf. Fig. 2h–l): in the 'roof' of the anterior and median part of the dorsal pit, a tissue is found which consists of ciliated cells, mucous cells, and some sensory neurons. Further back, this tissue is subdivided into two longitudinal fillets or keels running on each side of the median line. In transverse sections these structures are more or less triangular and extend nearly to the hindmost part of the central process of the dorsal pit. Here they diverge and part of their ciliated epithelium associates with the lateral parts of the 'normal' epithelium of the dorsal pit, thus forming the median parts of the epithelium of the lateral processes of the dorsal pit. The epithelium of the posterior parts of these lateral pit processes, which are medially surrounded by pigment, seems to consist of both types of epithelial cells mixed together.

On account of their histology, their position, and their innervation (see 3.4.2.7), the heavily ciliated dorsal keels just described in *Sabella* are interpreted in the present paper as nuchal organs.

In spite of configurational differences between, on the one hand, *Sabella* and, on the other, *Potamilla, Chone, Euchone* and *Myxicola,* the dorsal pit of all these genera has above been considered homologous (see 3.1.1). Consequently, in the four last-mentioned genera, the dorsolateral and heavily ciliated epithelium of the mouth cavity (which in the form of a shallow pouch separates itself from the rest of the tissues lining the oesophagus and, further back, together with dorsal tissue elements, forms the lateral pit processes) might, in spite of its somewhat aberrant position, be interpreted as a nuchal organ. Actually, in *Potamilla, Chone* and *Euchone,* such a supposition is strongly supported by the innervation of these epidermal pouches (see 3.4.2.5–7).

3.2.2.2. Serpulidae. As already stated (see 3.1.2), the epithelium of the mid-dorsal part of the dorsal pit of *Serpula vermicularis* differs markedly from the epithelium of the rest of the pit (Fig. 2c–d): In contrast to the strongly cuticularized epithelium lining the ventral, lateral and dorsolateral parts of the pit, most of the cells of the mid-dorsal pit epithelium are heavily ciliated, while others contain mucous substances or represent sensory neurons. On account of its innervation (see 3.4.2.1), this sensory epithelium is here interpreted as a nuchal organ.

As already emphasized (see 3.1.2), a frontal depression, structurally and histologically quite similar to that of *Serpula*, is found in all the serpulid species here studied. As far as the quality of the present material permits, it has further been established that the sensory epithelium in the dorsal part of the pit of all serpulids studied is innervated in a similar way as in *Serpula* (see 3.4.2.2–4).

3.3. The Branchial Crown and the Appendages of the Dorsal Lip

3.3.1. Earlier Literature

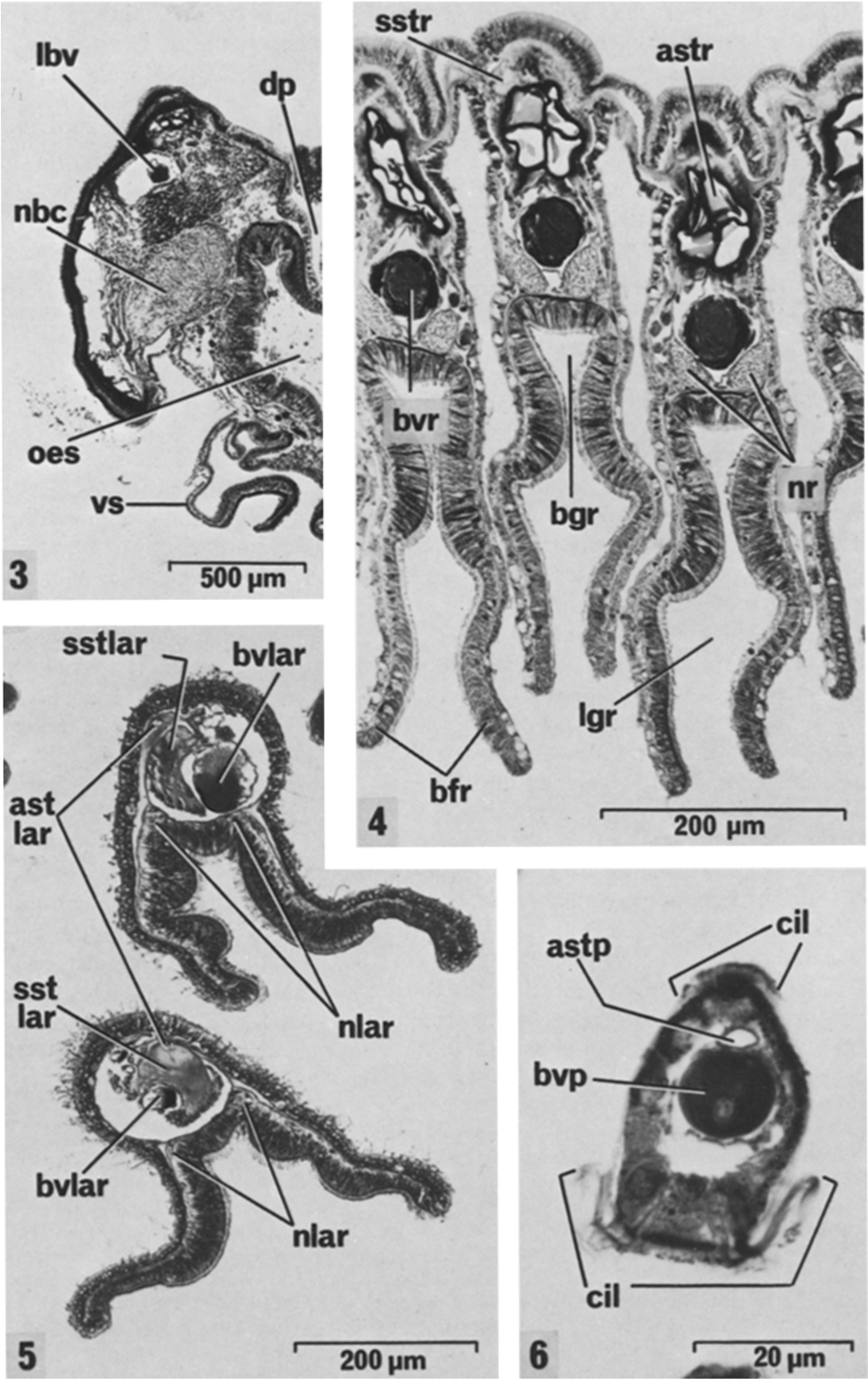
The anatomy and histology of the branchial crown and of the appendages of the dorsal lip of sabellids and serpulids have earlier been subjected to investigations of varying thoroughness. Thus, for instance, Viallanes (1886) and Brunotti (1888) studied the genera *Sabella* and *Branchiomma* respectively, and as an introduction to his studies on the feeding mechanism and other physiological functions of *Sabella pavonina* Nicol (1931) gave an admirable account of the food collecting apparatus of this species.

3.3.2. Present Observations

3.3.2.1. Sabella penicillus. As regards *Sabella penicillus* I have been able not only to verify many of the observations made by Nicol (1931), but also to make certain additional observations of importance for the present investigation. The most significant data (Figs. 3–6) about the organs in question can be summarized as follows.

The branchial crown consists of two lobes of semicircularly arranged radioli, with 10–40 radioli in each lobe. In each radiolus is an offshoot of the supporting tissues of the anterior end of the animal. Further back in the body, this skeleton is composed of two different parts: a central axis consisting of large cells (Fig. 4: *astr*), and a surrounding sheath (Fig. 4: *sstr*) consisting of a material opague in the preparations. Directly from the large branchial blood vessel (Fig. 3: *lbv*), which further back communicates with the dorsal vessel, a smaller vessel

Figs. 3–6. *Sabella penicillus.* **Fig. 3.** Transverse section through the oesophagus region, left side. Bouin-Duboscq-Brasil. Iron haematoxylin-eosin. Thickness of section 5 µm. ×40. **Fig. 4.** Transverse section through the base of part of the branchial crown. Bouin. Iron haematoxylin-eosin. Thickness of section 5 µm. ×70. **Fig. 5.** Transverse section through the appendages of the dorsal lip. Formol-alcohol. Iron haematoxylin-eosin. Thickness of section 5 µm. ×130. **Fig. 6.** Transverse section through a pinnula. Zenker. Iron haematoxylin. Thickness of section 5 µm. ×1,150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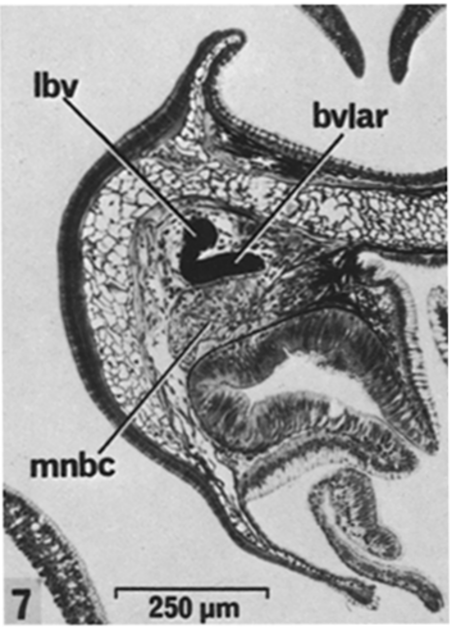
is branched off to each radiolus (Fig. 4: *bvr*). Two nerves (*nr*) are found running along the basal groove (*bgr*) of the radiolus. These nerves are in direct contact with the nerve of the branchial crown (cf. Fig. 3: *nbc* and 3.4.2.7). The epithelium of the radioli is accurately described by Nicol (1931).

Each radiolus bears a double row of pinnulae. In each pinnula (Fig. 6), an offshoot of the central axis of the supporting skeleton of the radiolus is present (*astp*), but no rudiments of the surrounding sheath are found in the pinnula. The centrally situated blood vessel (*bvp*) is a branch of the longitudinal blood vessel of the radiolus (Fig. 4: *bvr*). The pinnula is innervated from the nearest longitudinal nerve of the radiolus (Fig. 4: *nr*). The epithelium of a pinnula is a direct continuation of the epithelium of its radiolus. It is composed of ciliated, non-ciliated, and mucous-secreting cells all described in detail by Nicol (1931).

The front edge of the dorsal lip of the móuth seems to be drawn out into two tapering structures (Fig. 1d: *appendages of the dorsal lip*), called by earlier authors 'palps' (Pruvot 1885; Fauvel 1927; Nicol 1931), *'appendices'*, *'languettes'* (Binard and Jeener 1928) etc., (Table 1). In the centre of these appendages both types of skeletal structures are found: a central axis consisting of a single column of cells (Fig. 5: *astlar*) enveloped in a thick surrounding sheath (*sstlar*). Like the supporting tissues of the radioli, the skeleton of these appendages of the dorsal lip is a direct offshoot of the supporting capsule of the anterior end of the animal. Just as in the radioli, the appendages receive their blood (*bvlar*) directly from the large branchial blood vessels (Fig. 3: *lbv*). In each appendage, two longitudinal nerves (Fig. 5: *nlar*) are found. Their position in relation to other parts of the appendage is similar to that found in the radioli and, like the nerves running along the basal groove of the radioli, they are in direct contact with the nerve of the branchial crown (cf. Fig. 3: *nbc* and 3.4.2.7). The epithelium of the dorsal face of the appendages of the dorsal lip resembles that of the dorsal body wall. Their ventral epithelium is continuous with and indistinguishable from that of the basal folds of the most dorsal radiolus. Detailed information concerning the histology of the epithelia of the appendages of the dorsal lip of *Sabella* is given by Nicol (1931).

All the data regarding the structure of the radioli, of the pinnulae and of the appendages of the dorsal lip in *Sabella* summarized above suggest that the appendages of the dorsal lip are radioli which have wandered down to and fused with the dorsal lip of the mouth.

Figs. 7–11. *Potamilla reniformis*. **Fig. 7.** Transverse section through the anterior end on a level with the branching off of the blood vessel of the mediad appendages of the dorsal lip; left side. Bouin. Iron haematoxylin-eosin. Thickness of section 5 µm. × 80. **Fig. 8.** Transverse section through the anterior end cut a little more anteriorly than Fig. 7; left side. Bouin. Iron haematoxylin-eosin. Thickness of section 5 µm. × 80. **Fig. 9.** Transverse section through the dorsal part of the left lobe of the branchial crown. Part of the dorsal lip and its left median appendage (the left lip-associated radiolus) are also seen. Bouin. Iron haematoxylin-eosin. Thickness of section 5 µm. × 140. **Fig. 10.** Transverse section through the dorsal part of the left lobe of the branchial crown cut a little more anteriorly than Fig. 9. Bouin. Iron haematoxylin-eosin. Thickness of section 5 µm. × 140. **Fig. 11.** Transverse section through radioli, pinnulae, and lip-associated structures. Bouin. Iron haematoxylin-eosin. Thickness of section 5 µm. × 140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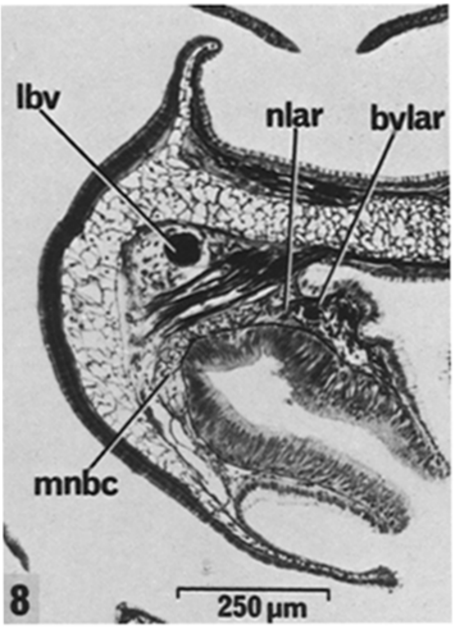
7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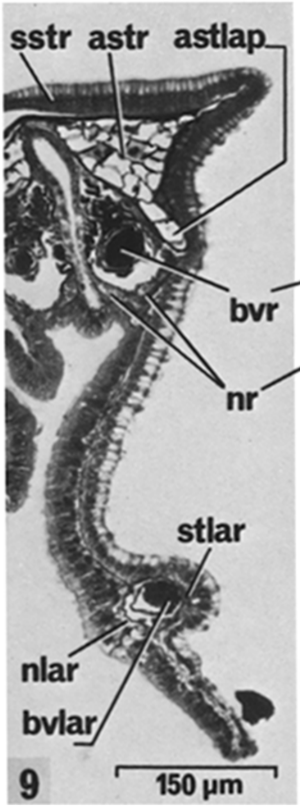
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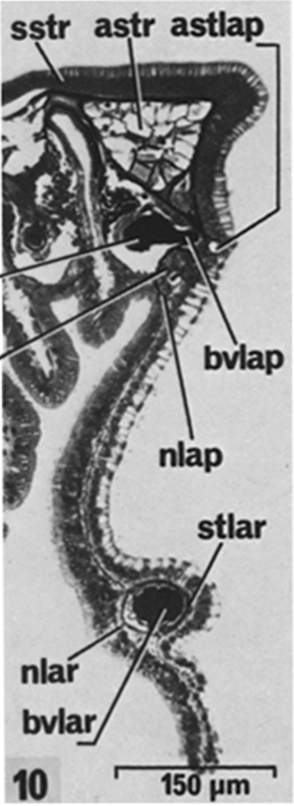
9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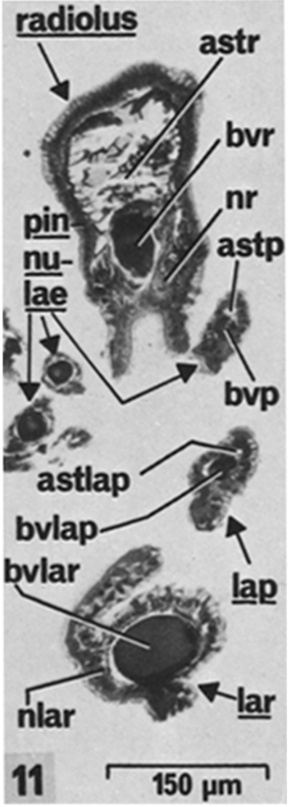
10


radiolus
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astp
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bvlap
lap
bvlar
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150 µm

11

3.3.2.2. Potamilla reniformis. The radioli of the branchial crown of *Potamilla* are built like those in *Sabella* just described: they are supported by the two types of skeletal tissue, the central axis and the surrounding sheath (Figs. 9 and 10: *astr* and *sstr*, respectively), and contain a blood vessel (*bvr*) emanating directly from the large branchial vessel (Figs. 7 and 8: *lbv*) and two longitudinal nerves (*nr*) which branch from the median nerve of the branchial crown (*mnbc*).

The pinnulae of *Potamilla* (Fig. 11) resemble those of *Sabella*, a fact emphasized by Nicol (1931).

The front edge of the dorsal lip of *Potamilla* does not have two appendages as in *Sabella*, but four; two mediad and two more lateral ones. There are many similarities between the mediad lip appendages in *Potamilla* and those found in *Sabella:* they occupy similar positions; they are supported mainly by offshoot: from the surrounding sheath of the skeleton capsule; they contain a blood vessel (Figs. 9–11: *bvlar*) which branches directly from the large branchial blood vessel (*lbv;* Figs. 7–11); their longitudinal nerves (Figs. 8–11: *nlar*) derive directly from the median nerve of the branchial crown (*mnbc;* Fig. 8); and their dorsal epithelium is continuous with and indistinguishable from the epithelium of the dorsal body wall, which holds true also of their ventral epithelium and the epithelium of the basal folds of the most dorsal radiolus of the branchial crown (Fig. 9). Thus, as in *Sabella*, the mediad appendages of the dorsal lip of *Potamilla* must, on the basis of these anatomical and histological data, be interpreted as radioli which have become separated from the rest of the branchial crown and have fused with the dorsal lip of the mouth.

The lateral appendages of the dorsal lip, on the other hand, show great similarities with a pinnula: they are supported only by an offshoot of the central axis of the supporting skeleton of the most dorsal radiolus (Figs. 9–11: *astlap*); their blood vessel (Figs. 10–11: *bvlap*) derives from the blood vessel of the most dorsal radiolus (Figs. 9–10: *bvr*); their nerve (Fig. 10: *nlap*) branches from one of the longitudinal nerves of the most dorsal radiolus (Fig. 10: *nr*); and their epithelium is histologically indistinguishable from the epithelium of a pinnula (Fig. 11). From the similarities between the pinnulae and the lateral appendages of the dorsal lip of *Potamilla*, it may be concluded that the lateral appendages represent pinnulae which have become separated from the most dorsal radiolus of the branchial crown and have fused with the dorsal lip of the mouth.

3.3.2.3. Euchone papillosa, E. analis and *Chone infundibuliformis.* In the *Euchone* and *Chone* species I have studied, the anatomy and histology of the branchial crown and appendages of the dorsal lip are in principle similar to that just described in *Potamilla reniformis.* Here, too, the front edge of the dorsal lip of the mouth shows four tapering structures, the two most median of which are equivalent to a pair of radioli while the two most lateral represent slightly modified pinnulae of the most dorsal radiolus of each half of the branchial crown. The ten or so most proximal dorsal pinnulae of this radiolus are thick. This is especially the case in *Euchone analis*, which probably led Pruvot (1885) and Meyer (1888) to refer to a very great number (12 pairs) of *antennes* and *Lippenzipfel* in this species. Fauvel (1927) and Hartmann-Schröder (1971), on the contrary, mention only two 'palps'.

3.3.2.4. Myxicola infundibulum. Myxicola infundibulum is equipped with two appendages on the dorsal lip. The quality of my preparations of this species does not permit any certain interpretation of the nature of these appendages.

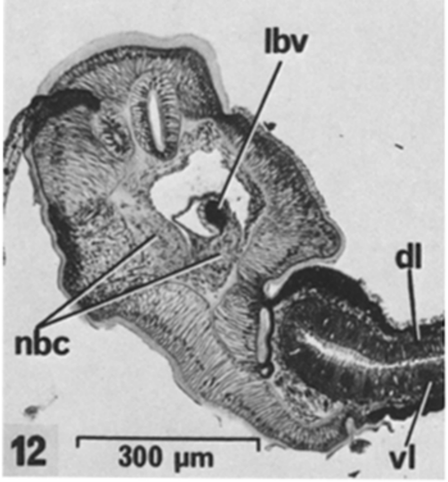
3.3.2.5. Pomatoceros triqueter. The branchial crown of the serpulids is in most respects similar to that of the sabellids. It is, for instance, divided into two lateral lobes, each bearing a great number of radioli bordered with two rows of pinnulae. In the serpulids, however, there is no real equivalent to the well-developed branchial skeleton of the sabellids; the presence of the opercula and the opercular stalks (modified radioli) causes an asymmetry in the serpulid branchial crown; and, as emphasized by Nicol (1931), the ciliation of the pinnulae differs somewhat in the two families.

In the lateral parts of the front edge of the dorsal lip of *Pomatoceros triqueter* are found two small triangular appendages, called *'palpes'* by Fauvel (1927) and others. They are innervated from the longitudinal nerve of the most dorsal ipsilateral radiolus (Fig. 14: *nmdr* and *nlap*) and their blood vessel (Figs. 13–15: *bvlap*) stems not from the large branchial vessel (Fig. 12: *lbv*) but from the vessel of the most dorsal radiolus of the branchial crown (Figs. 13–15: *bvmdr*). Thus, in two essential points they resemble ordinary pinnulae. From these similarities and in view of their position, which corresponds to that of the lateral appendages of the dorsal lip in *Potamilla, Euchone,* and *Chone,* it may be concluded that these appendages in *Pomatoceros* represent modified pinnulae of the most dorsal radiolus of the branchial crown.

3.3.2.6. Ditrupa arietina, Hydroides norvegicus, and *Placostegus tridentatus.* In all three of these species the branchial crown, the operculum, and the appendages of the dorsal lip resemble structurally those described in *Pomatoceros.* Consequently, the appendages of the dorsal lip of these species, called by Meyer (1888) *'Lippenzipfel'* (in *Eupomatus = Hydroides*), must be regarded as homologous to a pinnula of the most dorsal radiolus of the branchial crown.

3.3.2.7. Serpula vermicularis. According to Fauvel (1927), among others, Serpula is devoid of 'palpes'. This is true inasmuch as no appendages protrude from the anterior edge of the dorsal lip. However, my section series show that on each side of the triangular lobe (Fig. 1c) part of the dorsal lip is formed like a keel or torus. This structure contains a blood vessel which is a ramification of the blood vessel of the next most dorsal radiolus of the branchial crown. Furthermore, this torus is innervated from the longitudinal nerve of this radiolus. Thus, like the lateral appendages of the dorsal lip of *Potamilla reniformis, Euchone papillosa, E. analis,* and *Chone infundibuliformis* and like the appendages of the dorsal lip of *Pomatoceros triqueter, Ditrupa arietina, Hydroides norvegicus,* and *Placostegus tridentatus,* these tori on the lateral parts of the dorsal lip of *Serpula* are in all probability equivalent to pinnulae of a radiolus, although here they are very rudimentary.

3.3.2.8. Apomatus similis and Protula tubularia. In my material of *Apomatus similis* and *Protula tubularia* I have seen what Fauvel (1927) called palps in these species. My observations may be summarized as follows (Figs. 16–18).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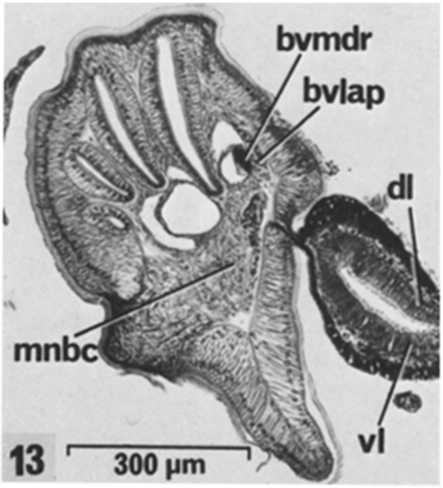
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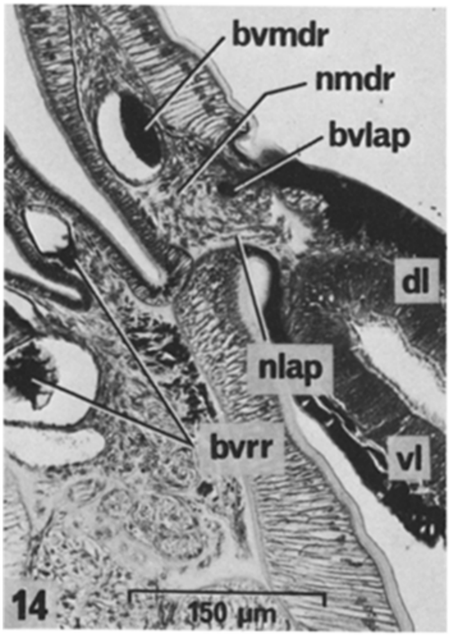
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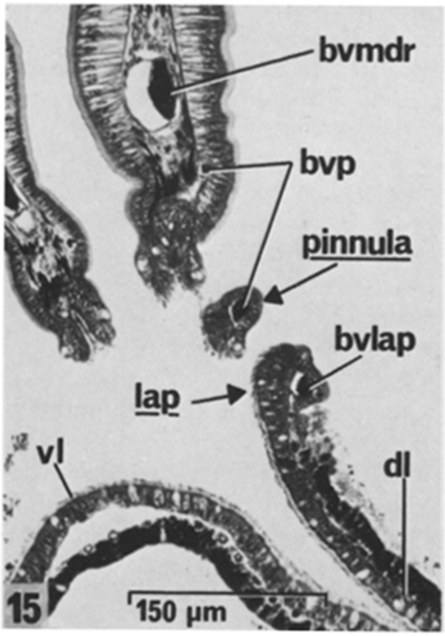
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15
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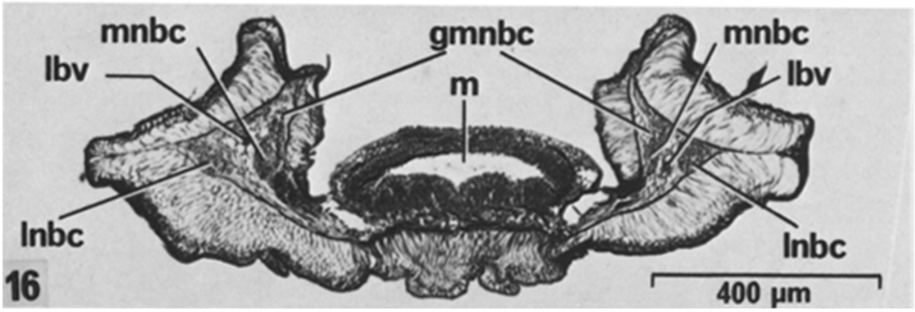
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16
400 µm

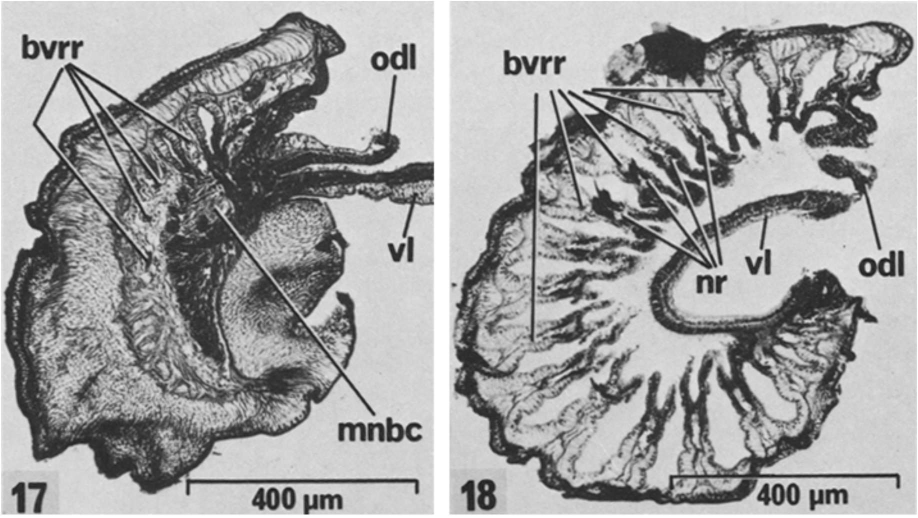


Fig. 17 and 18. *Apomatus similis.* **Fig. 17.** Transverse section through the base of the left branchial lobe. Formol-alcohol. Iron haematoxylin. Thickness of section 5 µm. × 75. **Fig. 18.** Transverse section through the left branchial lobe cut a little more anteriorly than Fig. 17. Formol-alcohol. Iron haematoxylin. Thickness of section 5 µm. × 75

As in *Serpula* (Fig. 1c), the ventral lip is more protrusive than the dorsal lip. The dorsal lip is 'emarginated', which means that only its lateral parts are seen in transverse sections cut near the anterior most end of the body (Fig. 17). These lateral parts are turned up in the dorsal direction and, still more anteriorly, are transformed into rather long, forwardly directed outgrowths (Fig. 18: *odl*). These outgrowths are vascularized neither from the large branchial vessel (Fig. 16: *lbv*) nor from any of the longitudinal vessels of the radioli (Figs. 17–18: *bvrr*), but in the same diffuse way as the rest of the mouth region. Furthermore, these outgrowths are innervated neither from the median nerve of the branchial crown (Figs. 16–17: *mnbc*) nor from any of the longitudinal nerves of the radioli (Fig. 18: *nr*), but through a branch of the common trunk of the nerves of the alimentary canal and the mouth region (see 3.4). Thus, their vascularization and innervation do not suggest that these outgrowths of

Figs. 12–15. *Pomatoceros triqueter.* **Fig. 12.** Transverse section through the base of the left branchial lobe. Heidenhain's 'Susa'. Iron haematoxylin-eosin. Thickness of section 5 µm. × 80. **Fig. 13.** Transverse section through the left branchial lobe cut a little more anteriorly than Fig. 12. Heidenhain's 'Susa'. Iron haematoxylin-eosin. Thickness of section 5 µm. × 80. **Fig. 14.** Transverse section through the dorsal part of the left lobe of the branchial crown cut a little more anteriorly than Fig. 13. Heidenhain's 'Susa'. Iron haematoxylin-eosin. Thickness of section 5 µm. × 170. **Fig. 15.** Transverse section through radioli, pinnula, mouth lips, and lip-associated pinnula. Heidenhain's 'Susa'. Iron haematoxylin-eosin. Thickness of section 5 µm. × 170. **Fig. 16.** *Apomatus similis.* Transverse section through the mouth region. Formol-alcohol. Iron haematoxylin. Thickness of section 5 µm. × 75 the dorsal lip of *Apomatus* and *Protula* could be equivalent to the lip-associated radioli or pinnulae found in the species treated earlier in this paper. Instead, these two criteria suggest hat the "palps" of *Apomatus* and *Protula* should be interpreted as outgrowths from the dorsal wall of the mouth cavity.

3.3.2.9. Filograna implexa. The small body size of *Filograna implexa* renders it almost impossible to make any absolutely reliable observations about the vascularization and innervation of the appendages of the dorsal lip of this species. My section series, however, indicate that the *palpes* (Fauvel's term) of *Filograna* emanate from the dorsal lip in a way very similar to that of *Apomatus* and *Protula.*

3.4. The Architecture of the Cephalic Nervous System

3.4.1. Earlier Literature

Among older comprehensive works dealing, at least in part, with the anatomy of the central nervous system of Sabellidae and Serpulidae, those written by de Quatrefages (1850) and Claparède (1873) should be mentioned. In the present context, however, it must be said that these investigations are to a large extent of purely historical interest.

Pruvot (1885) successfully studied *Sabella pavonina, Myxicola infundibulum,* and *Serpula philippi* (=*S. vermicularis*), and Meyer (1887–1888) made a quite admirable investigation of the central nervous system of *Eupomatus* (=*Hydroides*) *lunuliferus* and *Psygmobranchus protensus* (=*Protula tubularia*); he also studied representatives of the genera *Sabella, Spirographis,* and *Myxicola.*

As the first analysis of the commissures of a serpulid brain, Johansson's (1927) investigation of the cephalic nervous system of *Serpula vermicularis* marked a great step forward. Johansson's terminology, however, sometimes falters, some of his figures seem rather obscure and some are inconsistent with his text. Johansson's description of the central nervous system of *Euchone papillosa* is extremely difficult to interpret; this is due partly to confusion in his terminology and partly to the lack of any schematic drawing. Not until I had studied my own section series did Johansson's description of the cephalic nervous system of *Euchone papillosa* become intelligible to me, at least in its essentials. Johansson encountered great difficulties in analyzing the commissures of the brain of *Sabella penicillus,* which is in no way surprising (see 3.4.2.7).

Thus, when studying my own and older section series of different serpulid species, it has been fairly easy to understand the descriptions of *Hydroides* and *Serpula* given by Meyer and Johansson, respectively. To my regret I must admit that this is not the case with Binard and Jeener's (1928) description of the brain of *Pomatoceros triqueter.* This part of Binard and Jeener's famous work I have earlier (1966) characterized as highly schematic. Unfortunately I must still adhere to this opinion.

Close and comprehensive as the works of Meyer and Johansson may be in many respects, they are insufficiently accurate for the purpose of the present investigation. I therefore, submit the following descriptions of the cephalic nervous system of some sabellid and serpulid species.

3.4.2. Present Observations

3.4.2.1. Serpula vermicularis. The following account is illustrated by Figs. 19–23. Figure 19 is a general picture and Figs. 20–22 show different details. In all these figures the various components occupy a somewhat unnatural position; the commissures of the anterior part of the brain are thus drawn too far forward and the posterior commissures are located too far back. This presentation is to make the figures easier to survey. The natural positions of the commissures in relation to each other are shown in Fig. 23.

The ventral nerve cord communicates with the brain through the circum-oesophageal connectives (*cc*). In its anterior part each *cc* divides into the dorsal root (*drcc*) and the ventral root (*vrcc*). The *vrcc* is much stronger than the *drcc*. Each *drcc* has a double connection with the *cc:* the anterior (*acdrcc*) and the posterior coil (*pcdrcc*) of the *drcc*. In the space between these coils is located part of the ventro-lateral longitudinal body muscles.

The brain is traversed by seven commissures: in its anterior part are the dorsal (*dcdr*) and the ventral (*vcdr*) commissures of the *drcc;* the dorsal (*dcvr*) and the ventral (*vcvr*) commissures of the *vrcc* are in the hind part of the brain. These four commissures correspond to what Johansson in his analysis called, respectively, commissures 7, 6, 3, and 1. – In the foremost part of the brain, a moderately strong commissure is found (Figs. 19 and 21: *aac*) which connects the nerve of the branchial crown (*nbc*) of one side of the animal with the corresponding nerve of the other side; through two longitudinal tracts (Fig. 21: *llat* and *rlat*), some of the fibres of the *aac* run to the *vcvr*. It is noteworthy that the fibres running in the *llat* connect the right half of the *aac* and the *vcvr;* correspondingly, the fibres of the *rlat* extend into the left half of the *aac* and *vcvr*. – Just behind the *vcdr* is found a large commissure, the ventral association commissure (Figs. 19, 21, and 23: *vac*); through a posterior tract (Fig. 21: *ptvac*) the *vac* communicates with the *vrcc*, and through an anterior tract (Fig. 21: *atvac*) it is associated with the *nbc;* laterally, a great part of its densely packed fibres run to a pair of ganglia (Fig. 21: *lgvac*). Of the ventral association complex thus described, Johansson observed its *vac* (*Kommissur 4*) and its ganglia (*vordere Lateralganglien*). – Immediately behind the *dcdr* lies the seventh commissure of the brain, the dorsal association commissure (Figs. 19, 21, and 23: *dac*) which, through an anterior and a posterior tract (Fig. 21: *atdac* and *ptdac*), communicates with the more proximal parts of the *nbc* and with the *vrcc*, respectively. Johansson observed the *dac* (*Kommissur 5*) and, according to him, this commissure should connect a pair of lateral ganglia (*hintere Lateralganglien*) which, however, I could not find.

From the hindmost part of the brain a large nerve runs to the dorsal blood vessel (Figs. 19 and 22: *ndbv* = Meyer's *unpaarer Gefässnerv* and Johansson's *dorsaler Gefässnerv*). This nerve includes fibres from the *dcvr* (Fig. 22: *mprndbv* and *lprndbv*), but most of its fibres come from two lateral ganglia (Fig. 22:

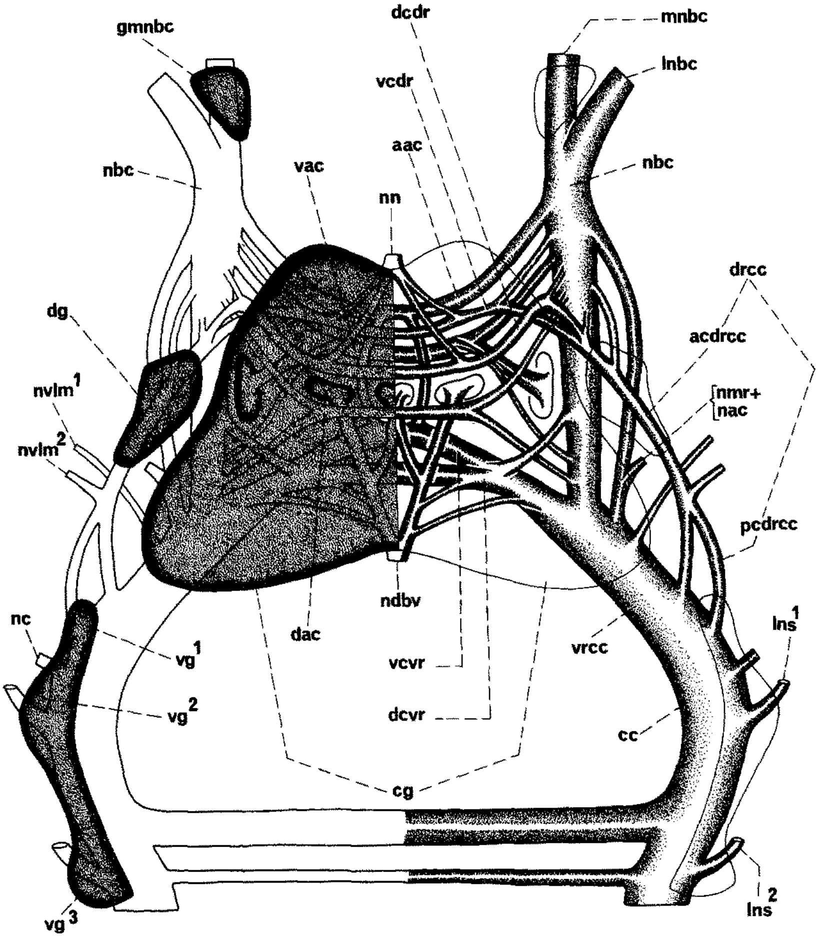


Fig. 19. *Serpula vermicularis.* The cephalic nervous system. Semischematic, dorsal view

lgndbv) and a double median ganglion (Fig. 22: *mgndbv*), all situated in the anterior ventral part of the brain. The tracts (Fig. 22: *stndbv* and *ctndbv*) running from these ganglia backwards to the *ndbv* divide the brain into two parts: an antero-dorsal part including the *vcdr, dcdr, aac, vac,* and *dac* and a postero-ventral part including the *vcvr* and *dcvr*. With the exception of the *mgndbv*, which he did not observe, Johansson clearly understood the architecture of this part of the *Serpula* brain.

The strong nerve trunks running to the branchial crown (including the appendages of the dorsal lip; see 3.3.2.7), the *nbc*, are rooted in the central nervous system in the following way [Fig. 20; the seemingly strange numbering of the roots and the term 'palp nerve roots' (*pnr*) are explained in 4.3]: From the *vrcc* emanate two very voluminous roots: *pnr*$^{1-3}$ [=Meyer's *innerer Nerv der Kopfkiemen* and Johansson's *hinterer (unterer) Nerv des Siebapparates*] and

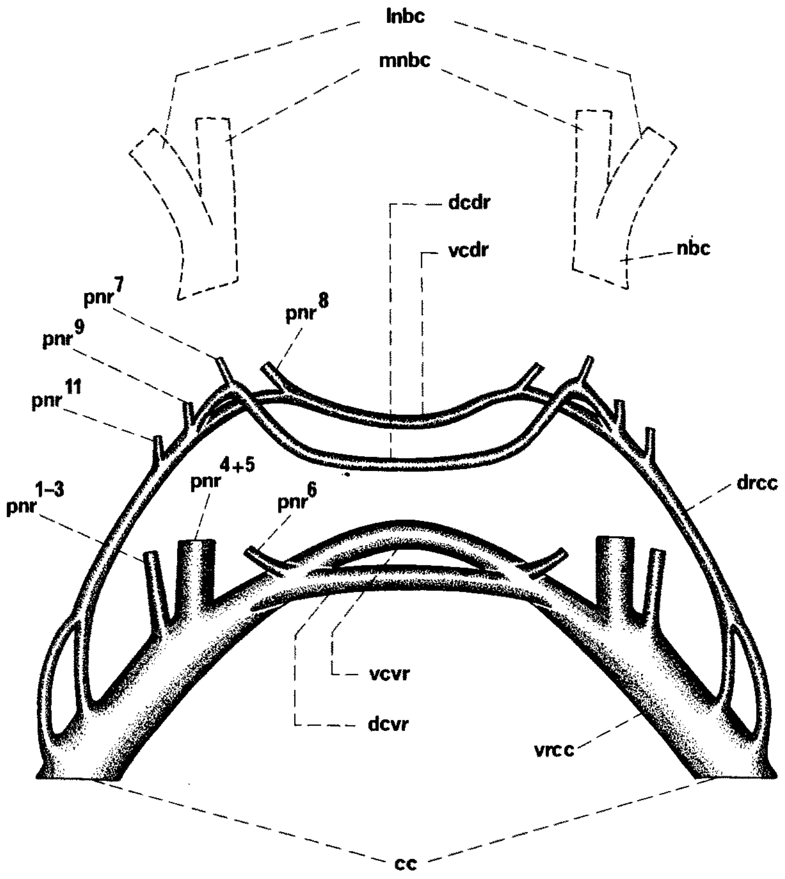


Fig. 20. *Serpula vermicularis*. The dorsal and ventral roots of the circum-oesophageal connectives, their brain commissures, and the palp nerve roots (the nerve roots of the branchial crown). Semischematic, dorsal view

pnr^{4+5} (observed, it appears, neither by Meyer nor by Johansson); from the *dcvr* and the *vcvr* comes a bundle of fibres (*pnr*^{6}), and the *dcdr* and the *vcdr* each gives off a nerve to the *nbc* (*pnr*^{7} and *pnr*^{8}, respectively); finally two nerves (*pnr*^{9} and *pnr*^{11}) leave the undivided *drcc* and join the other branchial nerve roots mentioned above. It appears that Johansson saw some indication of the four last-mentioned roots leading to the branchial crown.

From the foremost part of the brain, medially, a nerve [Fig. 19: *nn* = Meyer's *mittleres Stirnnervenpaar* and Johansson's *vorderes medianes Nervenpaar*] runs forward to the ciliated area situated in the roof of the dorsal pit (see 3.1.2., 3.2.2.2., and Fig. 2c–d). As surmised by Johansson, this nerve is rooted in the *dcdr* and the *vcdr* (Fig. 19). From the histology of the area mentioned and the way in which its nerve is attached to the central nervous system, this area here is interpreted as a nuchal organ (see further 4.3.5).

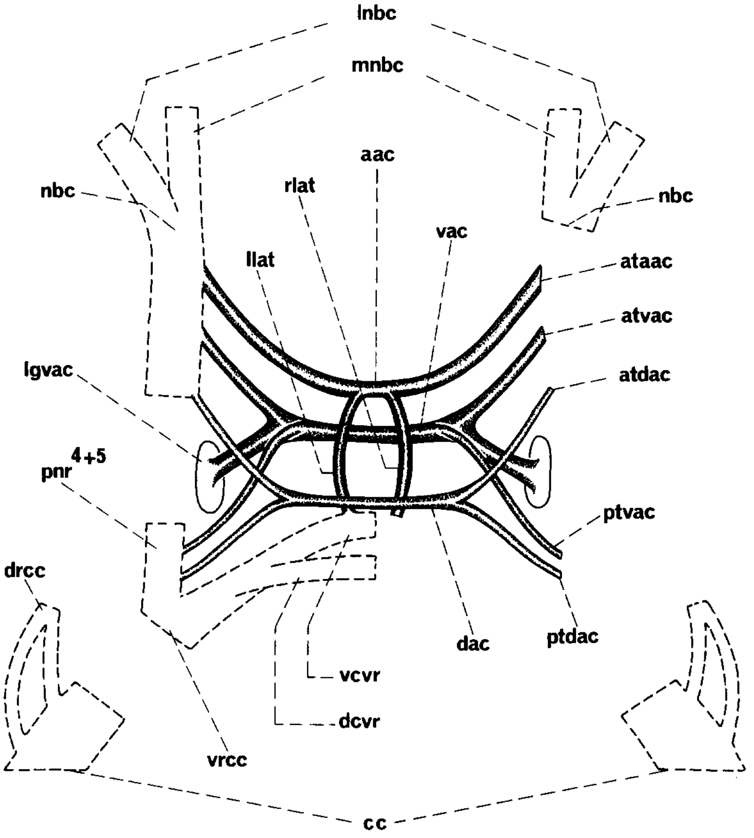


Fig. 21. *Serpula vermicularis*. The association systems of the brain. Semischematic, dorsal view

Joining the *pnr*$^{1-3}$ proximally, a bundle of fibres (Fig. 19: *nmr*+*nac*) runs from the *vrcc* to the mouth region and the oesophagus (Meyer's and Johansson's *Mundnerv* and *Oesophagealnerv*).

The foremost part of the ventral bundles of the longitudinal muscles is innervated by two pairs of nerves, one (Fig. 19: *nvlm*^{1} = Meyer's *seitlich-hinteres Nervenpaar*) emanating from the *vrcc*, and one (Fig. 19: *nvlm*^{2} = Meyer's *seitlich-oberes Nervenpaar*) from the *drcc*.

The nerves running to the collar (*nc*) and the two first segments (*lsn*^{1} and *lsn*^{2}) leave the *cc* and the ventral nerve cord in the way schematically outlined in Fig. 19.

According to Johansson a commissure (his *Visceralkommissur* or *Kommissur 2*) could be found in the most ventral part of the brain. This commissure should connect fibres of the branchial crown and mouth-nerves of one side of the animal with corresponding elements of the other side. Neither in my own section series nor in some series studied by Johansson has it been possible for me to detect this commissure.

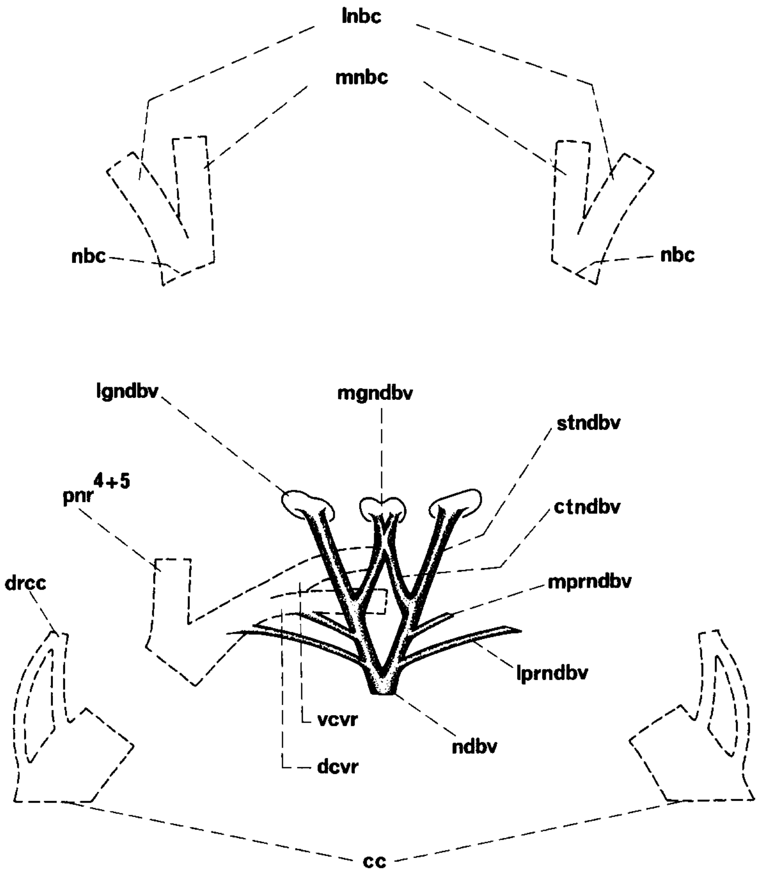


Fig. 22. *Serpula vermicularis.* The roots and the ganglia of the nerve to the dorsal blood vessel. Semischematic, dorsal view

In *Eupomatus* (=*Hydroides*) *lunuliferus* Meyer observed a pair of nerves (*das obere, hintere Nervenpaar*) which, emanating from the dorsal and median part of the brain, should run along the ectal parts of the thoracic nephridia. Neither Johansson nor I have succeeded in finding these nerves in *Serpula vermicularis*.

The brain is surrounded by ganglia cells (Fig. 19: *cg*), the configuration of which has been described in detail by earlier authors. Along each *drcc* is found a ganglion, the dorsal ganglion (Fig. 19: *dg*). Since it is distinctly separated from the *cg*, Meyer called it *paracerebrales Ganglion*. The *lgvac, lgndbv,* and *mgndbv* have been mentioned above. Laterally and ventrally the *cc* and the ventral nerve cord are covered with ganglia cells. These are especially numerous where the *drcc* and the *vrcc* of each side fuse (the first ventral ganglion; Fig. 19: vg^1) and where the lns^1 and the lns^2 issue (the second and third ventral ganglion; Fig. 19: vg^2 and vg^3, respectively).

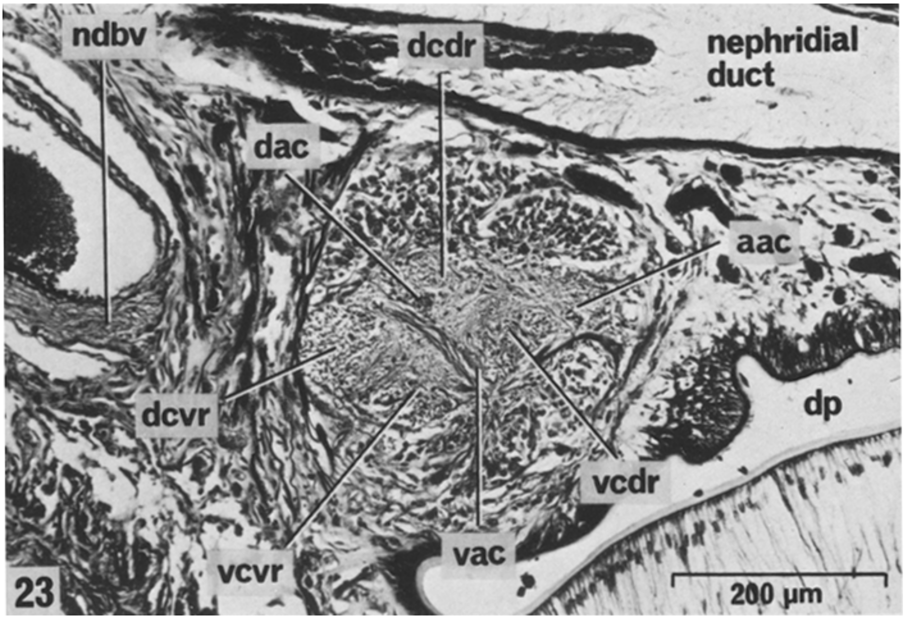


Fig. 23. *Serpula vermicularis.* Median sagittal section through the brain. Anterior end to the right. Formol-alcohol. Iron haematoxylin. Thickness of section 7 µm. × 125

3.4.2.2. Pomatoceros triqueter. According to Binard and Jeener (1928), the dorsal and ventral parts of the neuropile of the brain of *Pomatoceros triqueter* are not distinctly separated from each other. The fact that these authors did not analyze the commissures led them to believe that the branchial crown is almost exclusively innervated from the fibril mass of the dorsal roots of the circum-oesophageal connectives. On the basis of the information given by these authors, it would seem impossible to make any fruitful comparisons with other polychaete families.

Pomatoceros triqueter is much smaller than *Serpula vermicularis* and, consequently, more difficult to analyze. A study of my section series, however, has provided a basis for the following statements (Fig. 24).

As in *Serpula,* the circum-oesophageal connective on each side of the animal is divided into an anterior dorsal (*drcc*) and a posterior ventral (*vrcc*) root. In *Pomatoceros,* however, the *drcc* is proportionally much stronger than in *Serpula*. In the brain each root is subdivided into a ventral and a dorsal commissure (*vcdr, dcdr, vcvr,* and *dcvr*).

The anterior association commissure (*aac*) and its longitudinal tracts (*llat* and *rlat*) are easily observed. The ventral association complex with its commissure (*vac*) and its ganglia (*lgvac*) are also formed like those in *Serpula;* it has not, however, been possible to find any posterior tracts of the *vac* (cf. Fig. 21: *ptvac*). The dorsal association commissure (*dac*) is also quite distinct, but in contrast to *Serpula* no posterior tracts (cf. Fig. 21: *ptdac*) could be observed in *Pomatoceros.*

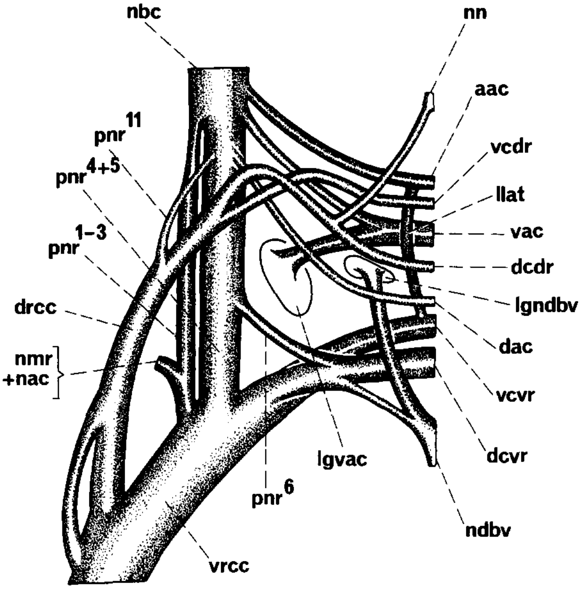


Fig. 24. *Pomatoceros triqueter.* The neuropile of the cephalic nervous system and two lateral ganglia. Semischematic, dorsal view; left side

Nor was it possible to see any curved tracts of the nerve of the dorsal blood vessel (*ndbv*), and on each side of the median line the *ndbv* is associated to the *dcvr* with only one bundle of fibres. It is impossible to say whether this bundle corresponds to the *mprndbv* or to the *lprndbv* in *Serpula*, or, perhaps, to both.

The roots *pnr*$^{1-3}$ and *pnr*$^{4+5}$ of the nerve to the branchial crown (*nbc*) lie very close to each other and the *pnr*^{6} and *pnr*^{11} are quite distinct.

The presence of the very strong opercular stalk causes a pronounced asymmetry in the cephalic nervous system.

The nuchal nerves (*nn*) which Binard and Jeener, on grounds to which we will return in 4.3.6 alternately called 'nerfs nucals' and 'nerfs néphridiens', emanate from the *dcdr*. As in *Serpula* they innervate a ciliated area in the 'roof' of the dorsal pit (see 3.1.2 and 3.2.2.2) but some of its fibres are in contact with the external pore of the thoracic nephridia.

From the brief account given above and a further comparison between Figs. 19 and 24, it can be seen that the cephalic nervous systems of *Pomatoceros* and *Serpula* are almost identically constructed. In all probability the differences mentioned above could be explained by the considerably smaller dimensions of *Pomatoceros;* under such circumstances it is difficult to observe with certainty such tiny structures as, for instance, *pnr*^{7} or a possible connection of the *nn* with the *vcdr*.

3.4.2.3. Ditrupa arietina, Hydroides norvegica, and Placostegus tridentatus. My section series of *Ditrupa, Hydroides,* and *Placostegus* show that the cephalic nervous system of these three genera is like that of *Serpula* and *Pomatoceros.*

The proportions of the components of the systems may differ slightly, but the relations of the elements to each other and to the various parts of the body are entirely similar.

3.4.2.4. Apomatus similis and Protula tubularia. Apomatus similis is much smaller than *Serpula vermicularis.* This is very much the case also with my specimens of *Protula tubularia.* In spite of this it has been possible to observe an almost complete resemblance between the architecture of the cephalic nervous system of *Apomatus* and *Protula* and *Serpula.* As in *Pomatoceros,* however, it has been impossible to certify the presence of the curved tracts and median ganglion of the nerve of the dorsal blood vessel (cf. Fig. 22: *ctndbv* and *mgndbv,* respectively). Furthermore, the dorsal association commissure is slightly less distinct in *Apomatus* and *Protula* than in *Serpula* (cf. Fig. 21: *dac*).

There were two reasons for a check on the cephalic nervous system of *Apomatus* and *Protula:* first, these genera are often referred to another subfamily than *Serpula, Pomatoceros, Ditrupa, Hydroides* and *Placostegus* as treated above (Rioja 1923; Fauvel 1927; Hartmann-Schröder 1971) and, consequently, some marked discrepancies in the central nervous system might be expected to exist between the representatives of the two subfamilies; second, and in the present context still more important, it has been emphasized by Fauvel (1927), Hartmann-Schröder (1971) and others that the filogranin genera are equipped with unusually large "palps" (for serpulids). – From the above account it is clear that no pronounced differences seem to exist between the subfamilies Serpulinae and Filograninae (sensu Rioja) in the architecture of their cephalic nervous systems. It has already been emphasized (see 3.3.2.8) that from their innervation and blood supply the "palps" of *Apomatus* and *Protula* must be interpreted as being simple outgrowths from the dorsal wall of the mouth cavity.

3.4.2.5. Euchone papillosa. My observations on the cephalic nervous system of *Euchone papillosa* are summarized in Figs. 25–27. These figures were designed like Figs. 19–22 (*Serpula*) and for the same reasons. This manner of illustration facilitates the comparison between representatives of each of the families Serpulidae and Sabellidae.

The brain is connected to the ventral nerve cord through the circum-oesophageal connectives (*cc*). Each connective is in its anterior part split into a slender dorsal (*drcc*) and a thick ventral (*vrcc*) root. Each *drcc* has two points of attachment in the *cc*. The anterior coil of the *drcc* (*acdrcc*) encircles the dorsolateral bundle of the longitudinal body muscles; the posterior coil (*pcdrcc*) encircles the ventro-lateral bundle of these muscles. This confirms Johansson's observations.

The seven transverse brain commissures observed in the serpulids are present also in *Euchone,* although they are slightly differently situated. The three association commissures are all found in the anterior part of the *Euchone* brain; the foremost one, the anterior association commissure (Figs. 25 and 27: *aac*), connects the bases of the two lateral nerves to the branchial crown (*lnbc*) with each other, while some of its fibres form two longitudinal tracts (Fig. 27: *llat* and *rlat*) to the *vcvr* of the *cc*. Each of these longitudinal tracts connects fibres

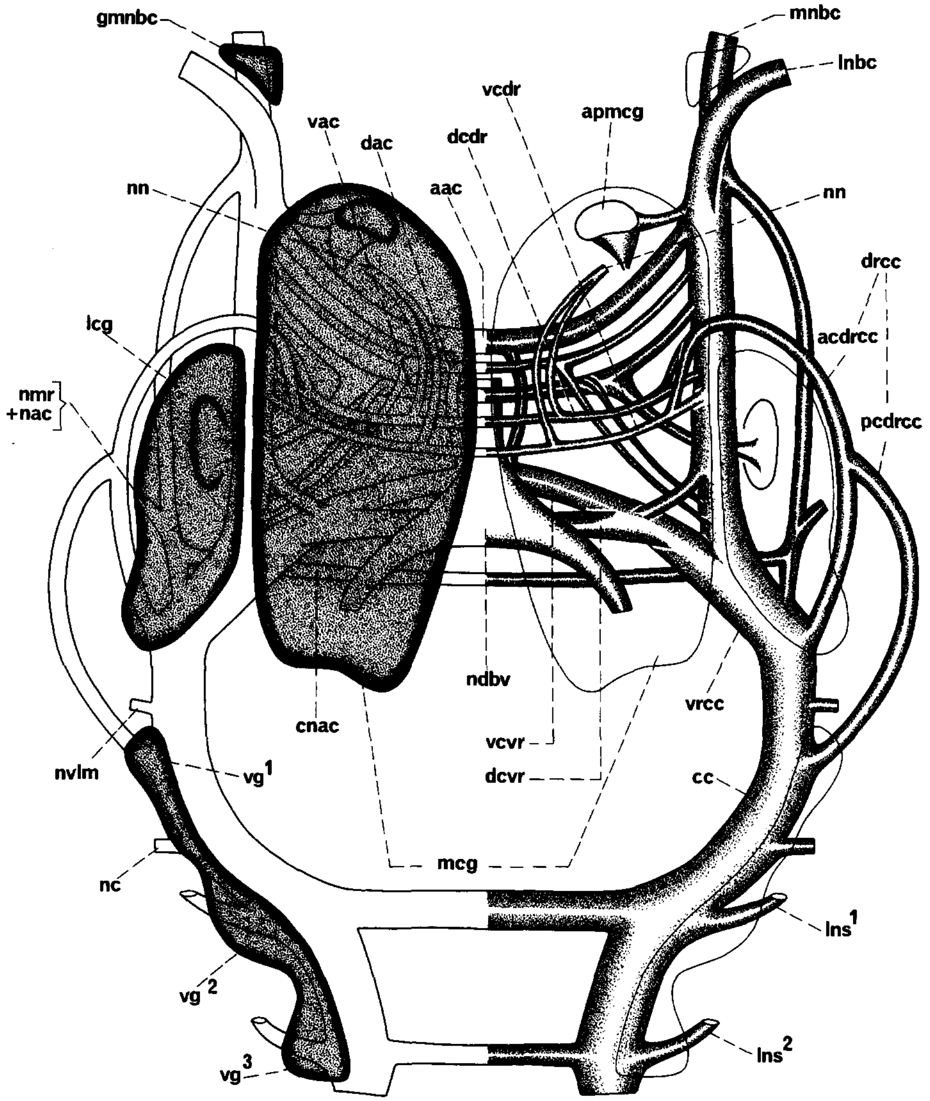


Fig. 25. *Euchone papillosa.* The cephalic nervous system. Semischematic, dorsal view

coming from the contralateral *aac* and *vcvr* of the *cc*. – The next foremost commissure is the dorsal association commisure (*dac*), with its anterior (*atdac*) and posterior (*ptdac*) tracts running to the fused palp nerve roots 4, 5, and 6 (see below) and the *vrcc*. Through its anterior (*atvac*) and posterior (*ptvac*) tracts, the *vac* connects fibres from its lateral ganglia (*lgvac*) with the fused palp nerve roots 4–6 (see below) and the *vrcc*, respectively.

Each of the two roots of a *cc* (the *vrcc* and the *drcc*) communicates with the corresponding contralateral root through two commissures, thus forming

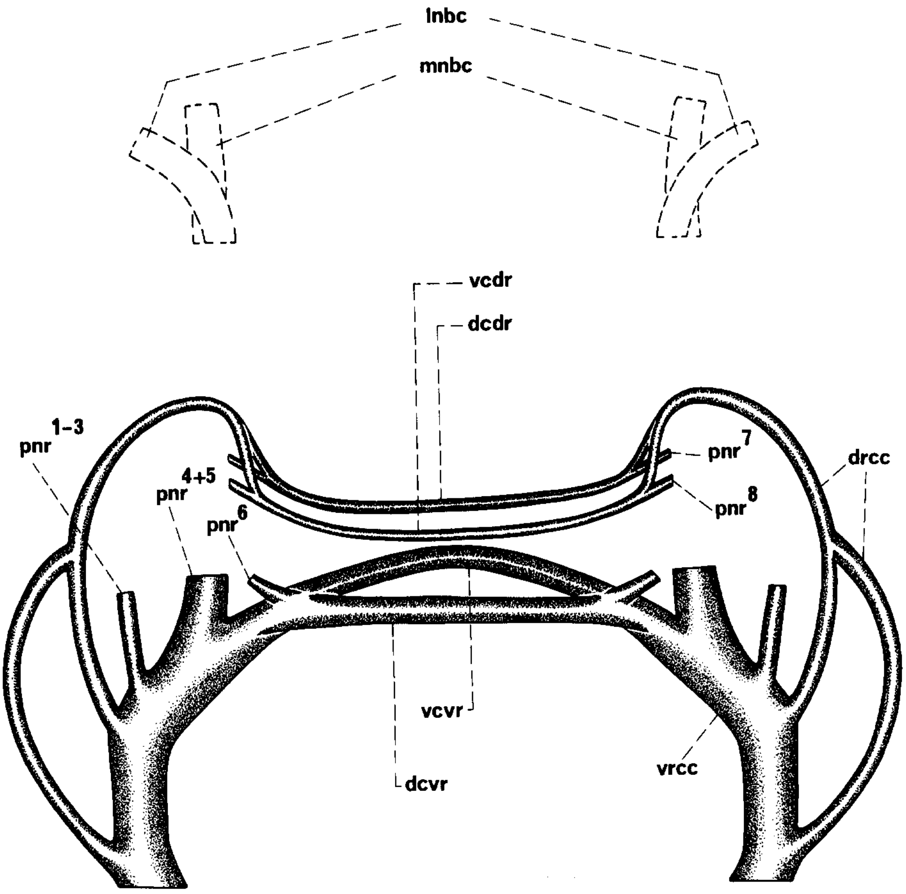


Fig. 26. *Euchone papillosa.* The dorsal and ventral roots of the circum-oesophageal connectives, their brain commissures, and the palp nerve roots (the nerve roots of the branchial crown). Semischematic, dorsal view

four transverse commissures in the brain: the ventral (*vcdr*) and the dorsal (*dcdr*) commissures of the *drcc* and the ventral (*vcvr*) and the dorsal (*dcvr*) commissures of the *vrcc*. All these commissures of the *cc* are situated in the hinder part of the brain (Figs. 25 and 28).

In all probability Johansson (1927) observed or at least surmised the presence of the seven commissures in the *Euchone* brain since, in his own words, he here found *im Großen Ganzen dieselben Kommissuren wie im Serpula-Gehirn.* Presumably he also saw the commisure of pnr^{1-3} and of the nerves to the alimentary canal and the mouth region (Fig. 25: *cnac;* note that this commissure is placed in an exaggerated posterior position in Fig. 25. Its natural position in relation to the other commissures of the brain is shown in Fig. 28. As previously emphasized, I have not, contrary to Johansson, found any equivalent to this commissure in the serpulid material studied.

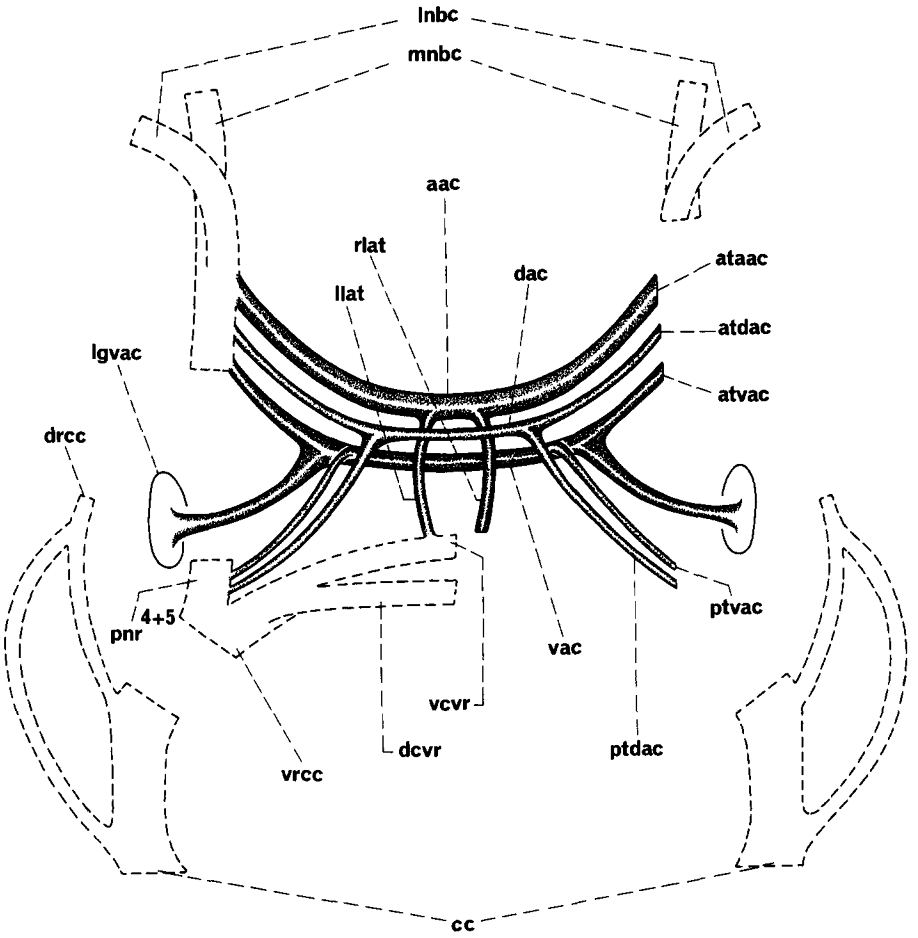


Fig. 27. *Euchone papillosa.* The association systems of the brain. Semischematic, dorsal view

The three association commissures and the commissures of the *drcc* are separated from those of the *vrcc* by a neuropile lamina (Figs. 25 and 28: *ndbv*) running to the dorsal blood vessel. This structure thus occupies a position similar to that of the tracts of the nerve to the dorsal blood vessel of the serpulids. On the other hand, no equivalents have been found in *Euchone* to the ganglia of these tracts observed, for instance, in *Serpula* (cf. Fig. 22: *mgndbv* and *lgndbv*).

Each half of the branchial crown (including the appendages of the dorsal lip; see 3.3.2.3) is innervated by two strong nerve trunks, a median (*mnbc*) and a lateral (*lnbc*). Besides the anterior tracts of the three association commissures mentioned above, these nerve trunks contain also the following elements (Fig. 26; regarding the term 'palp nerve roots' and the seemingly strange numbering of these elements, the reader is referred to 4.3.3 and 4.3.4): from the

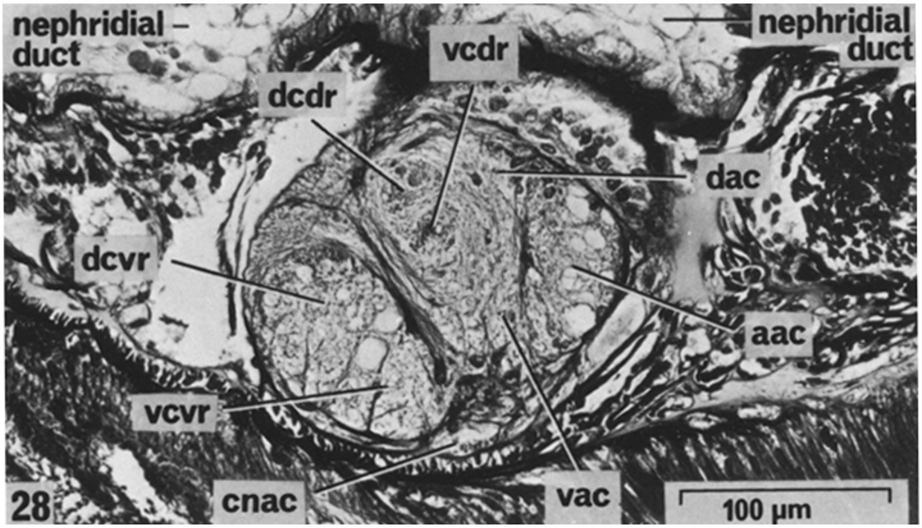


Fig. 28. *Euchone papillosa.* Median sagittal section through the brain. Anterior end to the right. Formol-alcohol. Iron haematoxylin. Thickness of section 5 µm. × 280

vrcc come two roots, namely the strong *pnr*$^{1-3}$ (Johansson's *unterer Siebapparatennerv*) and the still more voluminous *pnr*$^{4+5}$ (observed, it appears, neither by Meyer nor by Johansson); from the *dcvr* and the *vcvr* emanates the *pnr*^{6}, and the *dcdr* and the *vcdr* each give off a nerve (*pnr*^{7} and *pnr*^{8}, respectively) to the nerve trunks of the branchial crown.

On each side of the animal two nerve roots, emanating from the *dcdr* and the *vcdr* respectively, run forward in the ventrolateral direction. They soon fuse and form a nerve (Fig. 25: *nn*) leading to the heavily ciliated pouch which, as already described (see 3.1.1 and 3.2.2.1) is made up of parts of the tissues lining the mouth cavity and the lateral pit process. On the basis of anatomical and histological data, and in spite of its somewhat aberrant position, this pouch was assumed to be a nuchal organ (see 3.2.2.1). This supposition, as will be shown by comparisons with other "sedentary" polycheates (see 4.3.4 and 4.3.5), is strongly supported by its innervation.

United to the *pnr*$^{1-3}$ in their proximal parts, the nerves to the mouth region and the oesophagus (Fig. 25: *nmr*+*nac*; Johansson's *Mund- und Oesophagusnerv*) emanate from the lateral part of the *vrcc*.

The foremost part of the ventral bundles of the longitudinal muscles is innervated from those parts of the *cc* which lie between the two points of attachment of the *drcc* (Fig. 25: *nvlm*).

The way in which the nerves to the collar (*nc*) and to the two first segments (*lns*^{1} and *lns*^{2}) leave the *cc* and the ventral nerve cord is shown schematically in Fig. 25.

The configuration of the ganglia cells surrounding the neuropile of the brain has been described in detail by earlier authors. It will thus be sufficient for our present purposes, with reference to Fig. 25, to call attention to the following facts. The median cerebral ganglion (*mcg; Johansson's dorso-medianes Ganglion*) is divided into two halves; in the foremost part of each half a region is found where the cells are small and especially rich in chromatin (*apmcg;* Johansson's *vorderes Dorsalganglion*); most of the axons of these cells run to the nuchal organ, others are in contact with the *lnbc*. – In all probability the lateral cerebral ganglia (*lcg;* Johansson's *laterale Ganglien*) constitute only a part of the median cerebral ganglia separated from them by the well-developed dorsal longitudinal muscles of the body. The idea that the lateral cerebral ganglia of *Euchone* are equivalent to the dorsal ganglia of *Serpula* is inconsistent with their position and their connections with other parts of the cephalic nervous system. – The ganglia of the ventral association system (Fig. 27: *lgvac*) have been mentioned above. – The lateral and ventral sides of the *cc* and the ventral nerve cord are faced with ganglia cells. These are specially numerous where the roots of the circum-oesophageal connective of each side fuse (=the first ventral ganglion; Fig. 25: vg^1) and around the points of attachment of the first and the second lateral nerves (=the second and the third ventral ganglion; vg^2 and vg^3, respectively).

3.4.2.6. Euchone rubrocincta, E. analis, and Chone infundibuliformis. According to my section series of these species, their cephalic nervous system is built like that of *Euchone papillosa.*

3.4.2.7. Sabella penicillus and Potamilla reniformis. My observations on *Sabella* are summarized in Fig. 29. I have (like Johansson 1927) encountered great difficulty in analyzing the brain of *Sabella* (see 3.4.1). Despite having studied some thirty section series of material fixed in the different solutions used in this investigation I, too, have been unable to discern any distinct commissures here. Furthermore, in my material of *Sabella,* I have seen no indications of the dorsal roots of the circum-oesophageal connectives being incorporated into the brain or into the nerves of the branchial crown as was maintained by Meyer (1888) and Binard and Jeener (1928), respectively, concerning *Spirographis spallanzanii.* Instead, as in *Euchone,* the dorsal root of *Sabella* encircles the longitudinal body musculature. Thus, the dorsal root of *Sabella,* like that of all the sabellids (and serpulids) studied so far, has two points of attachment to the circum-oesophageal connective. In contrast to the ventral roots, the dorsal roots of *Sabella* are extremely thin and in some section series rather difficult to observe.

Two strong nerve roots emanate from the ventral root of the circum-oesophageal connective: the ventral (Fig. 29: *vrnbc*) and the dorsal (*drnbc*) root of the nerve of the branchial crown. They occupy a position similar to that of pnr^{1-3} and pnr^{4+5}, respectively, in the *Euchone* and *Chone* species studied here. The dorsal root is in contact also with the anterior parts of the brain. The details of this contact are unclear but it is noteworthy that this region of contact occupies a position similar to that of the anterior tracts of the three association commissures in the *Euchone* and *Chone* species here studied.

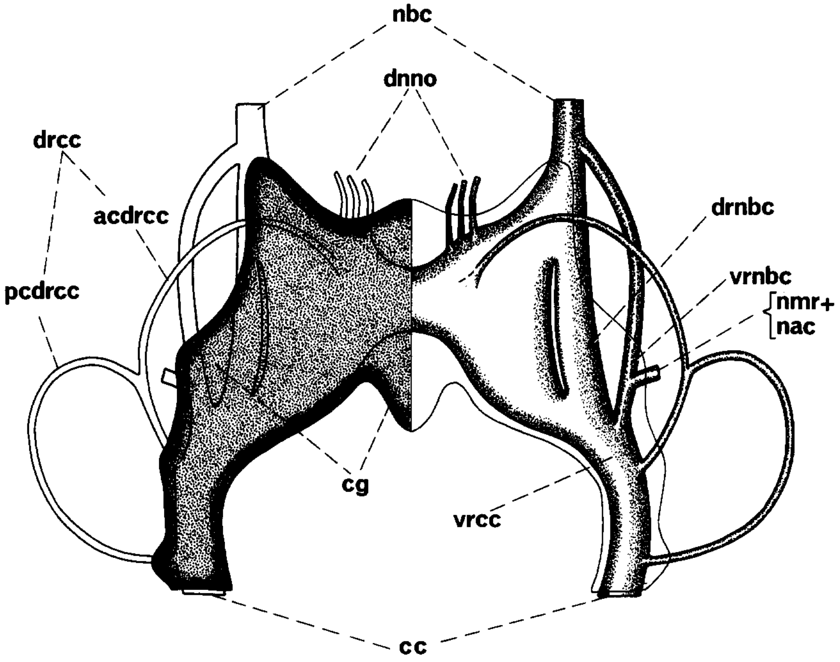


Fig. 29. *Sabella penicillus.* The cephalic nervous system. Semischematic, dorsal view

In front of the brain the dorsal and the ventral roots fuse, thus forming the nerve of the branchial crown (*nbc*).

Joining the *vrnbc* proximally, a bundle of fibres (*nmr*+*nac*) runs from the circum-oesophageal connective to the mouth region and the oesophagus.

From the front end of the brain two diffuse nervous lamina (*dnno*) run to what on other grounds (position and histology) were supposed to be nuchal organs (see 3.2.2.1). It is noteworthy that these nervous laminae occupy positions similar to those of the nuchal nerves in the *Euchone* and *Chone* species studied. This strengthens the supposition that the two 'keels', which consist of ciliated, mucous, and sensory cells and run on each side of the median line of the 'roof' of the dorsal pit, extending into its lateral processes, should be interpreted as nuchal organs.

The commissures of the cephalic nervous system of the other representative of the subfamily Sabellinae studied, *Potamilla reniformis,* are as difficult to analyze as those of *Sabella*. What has been said concerning the circum-oesophageal connectives, the roots of the nerves to the branchial crown, and the innervation of the alimentary canal and the supposed nuchal organs in *Sabella* applies equally to *Potamilla.*

3.4.2.8. Myxicola infundibulum. The cephalic nervous system of *Myxicola infundibulum* could be analyzed in considerable detail. Of the commissures found in the brain of *Chone* and *Euchone* I have discovered all in *Myxicola* except those of the dorsal root of the circum-oesophageal connectives. Here I have seen only one commissure; it is impossible to say if this commissure is equivalent to the dorsal or the ventral commissure (or both) of the dorsal root of the circum-oesophageal connective in *Chone* and *Euchone*.

In my preparations of *Myxicola* it was impossible to see any posterior tracts of the anterior and ventral association commissures.

Among the roots of the nerve to the branchial crown I have found the same ones in *Myxicola* as in *Chone* and *Euchone*. Only one nerve root, however, emanates from the single commissure of the dorsal root of the circum-oesophageal connective. It is impossible to determine whether this nerve root is equivalent to pnr^7 or pnr^8 (or both) in *Euchone* and *Chone*.

In my section series no nerves are seen running from the dorsal root of the circum-oesophageal connective or from its commissure to the nuchal organs, but these organs are otherwise innervated like those in *Euchone papillosa* and *Chone infundibuliformis*.

4. Discussion

4.1. Present Designations of Nerve Elements

In the discussion below, some of my earlier papers dealing with problems similar to those of the present study are cited. My 1964a to 1974 papers on these subjects were written, however, in German. This is the main reason why some terminological differences exist between these papers and the present one as regards *inter alia*, certain common and basic structures in the polychaete cephalic nervous system. However, in my 1978 paper, which was written in English, I included a table (Table 1, p. 346) which forms a bridge between these 1964 to 1974 terms and the corresponding terms used in later papers. The reader is referred to that table, should it be necessary.

When, in papers prior to 1978, I have discussed the innervation and the homologies of the appendages of the anterior end of different polychaete families, I have written about palp *nerves*. In the present paper, however, as in that of 1978, I have instead laid stress on their *roots*. This allows much greater accuracy of analysis and discussion. On the other hand, this change of approach may also cause certain difficulties when comparing the present results and those of 1978 with the observations reported in my earlier papers. In this respect, too, my 1978 paper might be of assistance; in Table 2 (p. 376) of that paper, the new numbers of the palp nerve roots are plotted against my earlier designations of the palp nerves of the families Sabellariidae, Apistobranchidae, Trochochaetidae, Spionidae, Poecilochaetidae, and Magelonidae. In the present paper the new numbering of these nerve elements is used.

4.2. Earlier Investigations of "Sedentary" Polychaetes

4.2.1. *"Spiomorphic"* and *"Drilomorphic"* Families

According to my earlier observations (1964a) the palps of the spionids are innervated by a great number of palp nerve roots. In *Nerine foliosa*, for instance, no less than eight such roots are found [Fig. 30f: palp nerve roots (*pnr*) 4, 5, 6, 7, 9, 10, 11, and 12]. With the exception of number 10, all these roots are found also in *Nerine cirratulus, N. bonnieri, Nerinides tridentata, Spio filicornis, Scolelepis fuliginosa, Pygospio elegans, Polydora ligni* and *Laonice cirrata*. In *Spiophanes kröyeri* and *Prionospio steenstrupi* neither palp nerve root 10 nor 12 could be found. In *Nerinides tridentata* palp nerve roots 4 and 5 have in all probability fused, thus forming a single root from the median part of the ventral root of the circum-oesophageal connective. – In all the spionid species discussed so far the point of attachment of pnr^{11} to the dorsal root of the circum-oesophageal connective is surrounded by a distinct ganglion, the dorsal ganglion (Fig. 30f: *dg*).

With the palp nerve roots of the spionids and their variation within the family as a basis, I made comparisons between the spionids and the Poecilochaetidae and the Trochochaetidae (1964a; see the present Fig. 30d and e, respectively), the Apistobranchidae, the Chaetopteridae, the Flabelligeridae, the Magelonidae and other "spiomorphic" and some "drilomorphic" families (1966, 1974). Primarily on the basis of their innervation, but also by studying their cavities, musculature, and vascularization, I was able to homologize the paired anterior appendages (the palps) found in some of these families. In my 1966 paper I furthermore made comparisons between my observations of the above-mentioned families and certain information from earlier literature concerning, among other families, the serpulids and the sabellariids. The homologies mentioned above were in some instances in accordance with, in other cases contrary to the interpretations put forward by earlier authors. For a detailed discussion of this part of the problem complex the reader is referred to the publications mentioned above.

4.2.2. The *Sabellariidae*

Primarily through my analysis of the cephalic nervous system and the innervation of the oral filaments (Fig. 1a) of the Sabellariidae (1978; cf. the present Fig. 30a) it was possible to refute Johansson's (1927) and Binard and Jeener's (1928) view of these appendages as being homologous to the palps (*die Fanganhänge* in Johansson's terminology) of the spionids. On the other hand, I was able to verify Johansson's tentative idea that the oral filaments of the sabellariids were simply the extended lateral parts of the upper lip of the mouth.

According to studies of their innervation, cavities, musculature, and vascularization the paired appendages which insert in front of and dorsal to the mouth of the sabellariids (the 'palps' of Fig. 1a) are equivalent to the palps (when present) of, among others, the "spiomorphic" polychaetes, the nereids, and the aphroditids. This interpretation agrees with Johansson's assumption that the *Fühler* of the flabelligerids are homologous to the palps of the sabellariids, but disagrees with Binard and Jeener's view of these appendages as being *antennes de première paire.*

4.3. Present and Earlier Investigations of Sabellidae and Serpulidae. Comparisons with Other Families

4.3.1. The Circum-oesophageal Connectives and Their Brain Commissures.

In the "spiomophic" and "drilomorphic" polychaete families previously studied by the present author (1964a, 1966, 1974), the ventral roots of the circum-oesophageal connectives lie in front of the dorsal roots (Fig. 30d–f). In the Sabellariidae this is not exactly the case; here all the four roots (and commissures) of the connectives are situated in approximately the same transversal plane (cf. Orrhage 1978, Fig. 8). As emphasized above, in the sabellids and serpulids the ventral roots are situated behind the dorsal (Figs. 19 and 25). The conditions thus found in the three last-mentioned families could be explained by a more or less pronounced cephalization of the dorsal parts of the anterior segments, a process which may have caused the brain to 'turnover' in the course of evolution. Regarding the cephalization of the anterior segments and supposed evolutionary changes in the cephalic nervous system of the sabellariids, the reader is referred to Orrhage (1978, pp. 364–365).

When drawing Fig. 17a of my 1978 paper I slightly altered the course of the dorsal root of the circum-oesophageal connective of *Sabellaria alveolata.* This was to facilitate comparison between the sabellariids and some "spiomorphic" families. For the same reasons, the positions of the roots of the connective and the brain commissures in *Sabellaria, Euchone,* and *Serpula* are altered in the present Figs. 30a–c in a corresponding way. The purpose of the present Fig. 31 is to show that there are no differences in principle between the way in which, for instance, these nerve elements are illustrated in Fig. 20 (≈Fig. 31a) and in Fig. 30c (=Fig. 31d): in all these figures the relations of the different elements to each other are exactly the same, and in Fig. 31b and c we find conceivable stages of transition from 31a (≈Fig. 20) to 31d (=Fig. 30c). It should perhaps be emphasized at this point that among Remane's (1956) major criteria for identifying homologies [criterion of position, criterion of the special quality of structures, and criterion of connections through intermediary forms (continuity criterion)] the criterion of position is not based on topographical or geometrical similarities, but on similarities in the interrelations of the structural elements present (*Lageähnlichkeit im Gefüge*). Hanson's (1977) reformulation of this Remanian criterion in no way alters its usefulness in the present context.

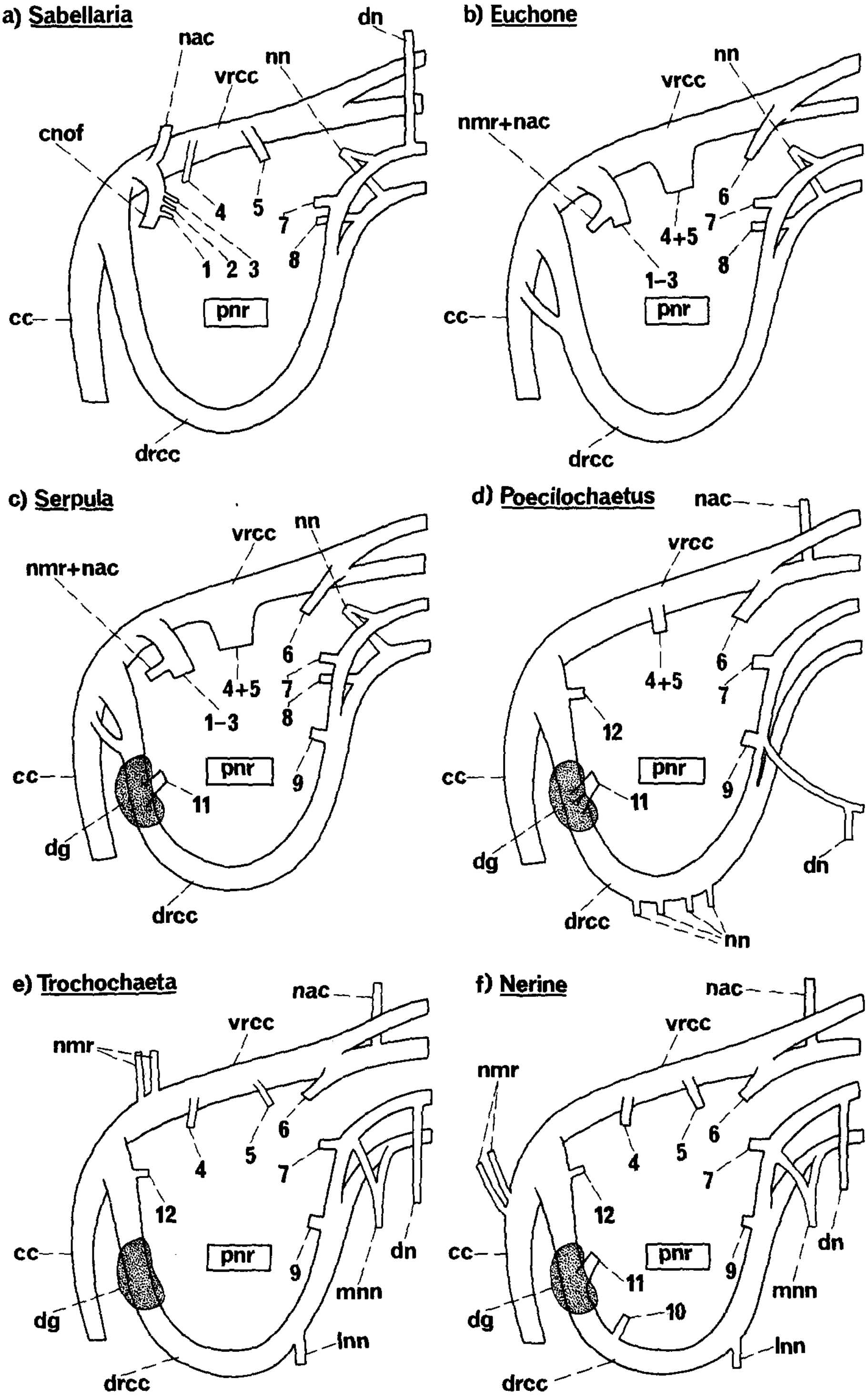
The diagrams shown in Fig. 31 can also be used in an entirely different manner. We can assume that the configuration of the roots of the circum-oesophageal connective and their commissures in the brain as illustrated in Fig. 31d represents a primitive organization of the "sedentary" polychaete brain, on the grounds that this organization is present in the "Spiomorpha" as well as the "Drilomorpha", which, for other reasons, can be interpreted as primitive among the "sedentary" polychaetes. If we read the diagrams backwards in the order d–a, we obtain an illustration of how these parts of the central nervous system of the serpulids may have become inverted during the cephalisation of the segments of the anterior end. A corresponding series of figures could easily be drawn for the sabellids. Such a series, like the series d–a in Fig. 31 must, of course, be taken for what it is: an hypothesis.

As shown in Fig. 30 there is in principle a total accordance between the families there represented as regards the roots of the circum-oesophageal connectives and the four brain commissures of these roots. The only discrepancy is that in the sabellids and the serpulids the dorsal root has two points of attachment in the circum-oesophageal connective instead of one. The same resemblances are found also in the Apistobranchidae, the Flabelligeridae, the Magelonidae, the Paraonidae, the Orbiniidae, the Cirratulidae, the Scalibregmidae, the Opheliidae (Orrhage 1966, 1974) and in the "errant" families (Gustafson 1930).

4.3.2. The Innervation of the Mouth region and the Alimentary Canal

In the sabellids and the serpulids (Fig. 30b and c) the nerves to the mouth region and the alimentary canal (*nmr*+*nac*) emanate from the lateral part of the ventral root of the circum-oesophageal connective. The common nerve of the oral filaments (*cnof*) and the nerve to the alimentary canal (*nac*) of the sabellariids (Fig. 30a) are rooted in the central nervous system in an entirely similar manner. This holds true also for the nerves to the mouth region (*nmr*) of the trochochaetids (Fig. 30e) but, judging from the other diagrams in Fig. 30, it is the case neither with the nerves to the mouth region (*nmr*) of the spionids (Fig. 30f) nor with the nerve of the alimentary canal (*nac*) of the poecilochaetids (Fig. 30d), the trochochaetids (Fig. 30e) and the spionids (Fig. 30f). These differences, however, in the innervation of the mouth region and the alimentary canal between, on the one hand, the sabellariids, the sabellids and the serpulids and, on the other, the poecilochaetids, the trochochaetids, and the spionids is only ostensible; this is evident from the following facts: 1) the nerves of the mouth region emanate from the lateral part of the ventral root of the

Fig. 30. The dorsal and ventral roots of the circum-oesophageal connective and their brain commissures; the roots of the palp nerves and of the nerves of the branchial crown (*pnr* 1–12); the roots of the nuchal nerves, of the dorsal nerves, and of the nerves to the mouth and the alimentary canal; the dorsal ganglion. (**a**) *Sabellaria alveolata*, (**b**) *Euchone papillosa*, (**c**) *Serpula vermicularis*, (**d**) *Poecilochaetus serpens*, (**e**) *Trochochaeta multisetosa*, and (**f**) *Nerine foliosa*. Dorsal view; left side; schematic. Diagram (**a**) after Orrhage (1978); diagrams (**d–f**) after Orrhage (1964 and 1978). To facilitate the comparison between the sabellariids, the sabellids, and the serpulids on the one hand and the other families represented here on the other, the course of the dorsal root of the circum-oesophageal connective in *Sabellaria*, *Euchone*, and *Serpula* is altered compared with the original drawings (see Orrhage 1978, Fig. 8, and Figs. 19 and 25 of the present paper, respectively). See also Fig. 31


a) Sabellaria
dn
nac
nn
vrcc
cnof
4
5
7
8
1 2 3
pnr
cc
drcc
b) Euchone
nn
vrcc
nmr+nac
6
7
4+5
8
1-3
pnr
cc
drcc
c) Serpula
vrcc
nn
nmr+nac
6
4+5
7
8
1-3
pnr
9
11
cc
dg
drcc
d) Poecilochaetus
nac
vrcc
6
4+5
7
12
pnr
11
9
cc
dg
dn
drcc
nn
e) Trochochaeta
nac
vrcc
nmr
6
4
5
7
12
pnr
dn
9
mnn
cc
dg
lnn
drcc
f) Nerine
nac
vrcc
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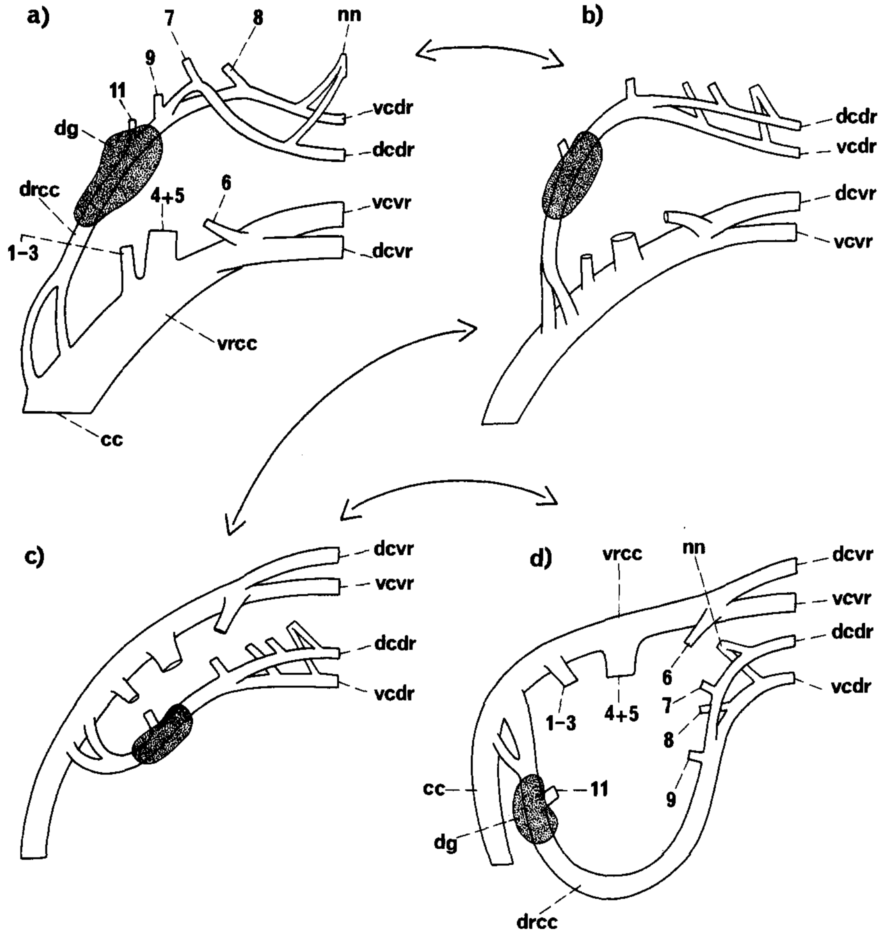

Fig. 31. *Serpula vermicularis.* The dorsal and ventral roots of the circum-oesophageal connective and their brain commissures; the roots of the nerves to the branchial crown and of the nuchal nerve; the dorsal ganglion. Dorsal view, left side. (**a**) the schematized natural position of the elements (cf. Figs. 19 and 20); (**d**) the position of the same elements as they are drawn in Fig. 30c; (**b**) and (**c**) hypothetical stages of transition from (**a**) to (**d**) or *vice versa*

circum-oesophageal connective also in many spionids (e.g., *Spio filicornis, Laonice cirrata, Spiophanes kröyeri,* and *Prionospio steenstrupi* (Orrhage 1964a, Text-fig. 5); 2) in the sabellariids, most of the fibres of the common nerve of the oral filaments (*cnof*) come from behind the point of junction of the dorsal and ventral roots of the circum-oesophageal connective (Orrhage 1978, Fig. 9); this holds true also for the nerves to the mouth region (*nmr*) of the sabellids, the serpulids, the trochochaetids, and the spionids; 3) in the four last-mentioned families and in the poecilochaetids the nerve of the alimentary canal (*nac*) is allied only to the ventral root of the circum-oesophageal connective (or to the ventral commissure of this root) and, as I emphasized in 1978, this is the case also with the nerve of the alimentary canal of the sabellariids; in this context it is of interest to note that the oesophageal nerve of the flabelligerids and the apistobranchids also emanates from the ventral root of the circum-oesophageal connective and that, in the apistobranchids, this nerve is connected to its corresponding contralateral nerve through a commissure (*die praeorale Kommissur* in my 1966 and 1974 papers; cf. the commissure *cnac* in the sabellids).

Thus, Fig. 30 could give the impression that there are great differences between these families as regards the innervation of the mouth and the alimentary canal; however, no such differences actually exist.

4.3.3. Homologues of the Nerve Roots of the Branchial Crown

The reader is referred below, unless otherwise stated, to Fig. 30 and Table 2. Since the central nervous system of the Sabellinae could not be analyzed (see 3.4.2.7), this subfamily is excluded from the following discussion.

The present observations have shown that the branchial crown of the Serpulidae is innervated through seven roots, and that of the sabellids through five roots emanating from different parts of the cephalic nervous system. The nerve root which in these families has been designed as pnr^{1-3} occupies a position corresponding to palp nerve roots 1, 2, and 3 of the sabellariids: they emanate from the ventral root of the circum-oesophageal connective and in close conjunction with the nerves of the mouth region and alimentary canal.

The nerve roots pnr^{4+5} of the sabellids and the serpulids occupy a position somewhere between those occupied by palp nerve roots 4 and 5 in the sabellariids, the trochochaetids, and most spionids and a position entirely similar to that occupied by palp nerve root 4+5 in the poecilochaetids, the magelonids (Orrhage 1966, Fig. 5: *unterer Palpennerv* and 1978, Fig. 17f: "pnr^{4+5}"), the flabelligerids (Orrhage 1966, Fig. 4: "PN^{c}") and some spionids (Orrhage 1964a, Textfig. 15b: "$PN^{6}+PN^{7}$").

On account of its emergence from the most median part of the ventral root of the circum-oesophageal connective, nerve root 6 of the branchial crown of the sabellids and the serpulids could be homologized with palp nerve root 6 of the poecilochaetids, the trochochaetids, the spionids, the apistobranchids (Orrhage 1978, Fig. 17b), and the corresponding element in the flabelligerids (Orrhage 1966, Fig. 4).

The position of nerve root 7 of the branchial crown of the sabellids and the serpulids makes it in all probability equivalent to palp nerve root 7 of the sabellariids, the poecilochaetids, the trochochaetids, the spionids, and the apistobranchids (Orrhage 1978, Fig. 17b).

The connection of nerve root 8 of the branchial crown of the sabellids and the serpulids to the ventral commissure of the dorsal root of the circum-oesophageal connective (lateral to the ventral root of the nuchal nerve, *nn*) supports the idea that this root is equivalent to palp nerve root 8 of the sabellariids, the apistobranchids (Orrhage 1978, Fig. 17b), and the corresponding element of the flabelligerids (Orrhage 1966, Fig. 4).

Nerve root 9 of the branchial crown of the serpulids occupies a position

Table 2. The palp nerve roots (Sabellariidae, Poecilochaetidae, Trochochaetidae, Spionidae) and the nerve roots of the branchial crown (Sabellidae, Serpulidae) homologized in the present paper. Cf. Fig. 30

<table>
<tr><th></th><th colspan="12">Nerve root number</th></tr>
<tr><th></th><th>1</th><th>2</th><th>3</th><th>4</th><th>5</th><th>6</th><th>7</th><th>8</th><th>9</th><th>10</th><th>11</th><th>12</th></tr>
<tr><td>Sabellariidae</td><td>☐</td><td>☐</td><td>☐</td><td>☐</td><td>☐</td><td></td><td>☐</td><td>☐</td><td></td><td></td><td></td><td></td></tr>
<tr><td>Sabellidae</td><td colspan="3">☐</td><td colspan="2">☐</td><td>☐</td><td>☐</td><td>☐</td><td></td><td></td><td></td><td></td></tr>
<tr><td>Serpulidae</td><td colspan="3">☐</td><td colspan="2">☐</td><td>☐</td><td>☐</td><td>☐</td><td>☐</td><td></td><td>☐</td><td></td></tr>
<tr><td>Poecilochaetidae</td><td></td><td></td><td></td><td colspan="2">☐</td><td>☐</td><td>☐</td><td></td><td>☐</td><td></td><td>☐</td><td>☐</td></tr>
<tr><td>Trochochaetidae</td><td></td><td></td><td></td><td>☐</td><td>☐</td><td>☐</td><td>☐</td><td></td><td>☐</td><td></td><td></td><td>☐</td></tr>
<tr><td>Spionidae</td><td></td><td></td><td></td><td>☐</td><td>☐</td><td>☐</td><td>☐</td><td></td><td>☐</td><td>[☐]</td><td>☐</td><td>☐</td></tr>
</table>

corresponding to that of palp nerve root 9 of the poecilochaetids, the trochochaetids, the spionids, and the apistobranchids (Orrhage 1978, Fig. 17b).

From its position, and the fact that its base is surrounded by a separate ganglion (*dg*), nerve root 11 of the branchial crown of the serpulids can be homologized to palp nerve root 11 of the poecilochaetids, the spionids, and the magelonids (Orrhage 1978, Fig. 17f) and, further, to the corresponding elements of the chaetopterids (Orrhage 1966, Fig. 3: "$PN^{ä}$") and the flabelligerids (Orrhage 1966, Fig. 4: "PN^{b}").

No equivalents to palp nerve roots 10 (only present in some spionids) and 12 (present in many, but not all, spionids, in trochochaetids, and in poecilochaetids) were found in the other families discussed here.

The homologies of the nerve roots treated above are summarized in Table 2.

4.3.4. Interpretation of the Appendages of the Anterior End

4.3.4.1. The Branchial Crown. Mainly from of the great similarities in innervation, I have earlier (1966) stated that the paired appendages (*die Palpen*) inserted in the anterior end of most "spiomorphic" families and of the cirratulids must be interpreted as homologous. From the literature (e.g. Retzius 1895; Hamaker 1898; Hempelmann 1911; Holmgren 1916; Bernert 1926; Binard and Jeener 1928; Gustafson 1930; Korn 1958; Åkesson 1963) I further found that these appendages are probably equivalent to the palps of the nereids and the aphroditids (Orrhage 1966), an opinion in part maintained by Binard and Jeener (1928), among others. In my 1974 paper I reported data supporting the idea put forward by some earlier authors that the *'antennae'* of the protodrilids were homologous to the above-mentioned palps. In my 1978 paper, finally, I came to the same result concerning the large, paired appendages of the sabellariids (see the present Fig. 1a: '*palps*').

In the light of the experiences just summarized, and on the basis of the comparative analysis of the innervation of the branchial crown of the sabellids and the serpulids (see 4.3.3, Fig. 30, and Table 2), it seems quite clear that this organ constitutes the main part of a homologue to the palps of all the families just discussed. Table 1 shows that this agrees with both Meyer's (1888) and Binard and Jeener's (1928) opinions of the spionids, but not the sabellariids; it further agrees with Johansson's (1927) idea concerning the sabellariids, but not the spionids.

4.3.4.2. The Appendages of the Dorsal Lip of the Mouth. It was shown in 3.3 that the sabellids and the serpulids may be equipped with one or two of the following three types of appendages on the dorsal lip of the mouth: (1) branchial radioli which have become separated from the crown and have fused with the lip (*Sabella penicillus, Potamilla reniformis, Euchone papillosa, E. analis,* and *Chone infundibuliformis*), (2) branchial pinnulae which have become separated from the most dorsal radiolus of the crown and have fused with the lip (*Potamilla reniformis, Euchone papillosa, E. analis, Chone infundibuliformis, Pomatoceros triqueter, Ditrupa arietina, Hydroides norvegica, Placostegus tridentatus,* and, although here very inconspicuous, *Serpula vermicularis*), (3) new formations from the walls of the mouth cavity (*Apomatus similis, Protula tubularia,* and probably *Filograna implexa*).

It will be clear from the above remarks that questions 2, 3, and 4 as put forward in section 1.2 can be answered as follows:

(2) The presence of appendages of the dorsal lip seems to be typical of the sabellids.

(3) Many serpulids show distinct appendages on the dorsal lip.

(4) Some of the appendages of the dorsal lip of the sabellids and the serpulids (the lip-associated radioli and the lip-associated pinnulae) constitute parts of the branchial crown, while others are structures *sui generis* (new formations from the wall of the mouth cavity). Consequently, Pruvot (1885), Johansson (1927), and Binard and Jeener (1928) were all correct *in part* concerning the nature of the appendages in question. Their generalizations, however, were too broad considering the material investigated. Thus, Meyer was wrong when talking about the *Lippenfortsätze* (*Lippenzipfel, Lippenzapfen*) as *von der Mundhöhlenwandung hervorgesprosste Neubildungen* (see 1.2), and Johansson, and Binard and Jeener went too far when they stated that all *Mundanhänge* or *appendices (languettes) de la lèvre dorsale* were parts of the branchial crown.

4.3.4.3. Terminological proposals. It has been shown that the branchial crown and some (but not all) of the appendages of the dorsal lip of the sabellids and the serpulids are equivalent to the palps of the "spiomorphic" polychaetes, the nereids, and the aphroditids. In analogy with earlier proposals by the present author (Orrhage 1978) and from the purely comparative anatomical point of view it might then, of course, be maintained that these parts of the sabellid and the serpulid body should also be called palps. However, the term branchial crown, while not reflecting the main function of the organ, is a well-known and easily understood term, as are the corresponding terms in German and French (*Kiemenkrone* and *panache branchial,* respectively). Furthermore, from the above discussion, the application of the term palp in this context would be extremely impractical, because in some cases (e.g., *Apomatus* and *Protula*) it would include the branchial crown only, in others (e.g., *Pomatoceros* and *Sabella*) it would include the branchial crown and two appendages of the dorsal lip of the mouth, and in still other cases (e.g., *Potamilla* and *Euchone*) it would include the branchial crown, plus four or more such appendages. On these grounds it is proposed here that the filtering part of the palp should retain the name of branchial crown, or alternatively gill crown. This proposal is, so far, totally in line with that of Nicol (1931).

However, the appendages of the dorsal lip of the sabellids and the serpulids are, at least in faunistic literature, often called palps (Fauvel 1927; Hartmann-Schröder 1971; cf. also Nicol 1931). For three reasons the term palp in this context is quite inappropriate: (1) it includes structures of three different kinds and origins, (2) two of these structures are equivalent to a minor part only of the concept palp as this term is used in modern literature on the comparative anatomy and phylogeny of the Polychaeta, (3) the third structure called a palp has nothing to do with this concept in its modern sense.

On these grounds it its proposed here that in comparative anatomical works the three kinds of appendages found on the dorsal lip of the mouth in the Sabellidae and the Serpulidae should be called lip-associated radioli (e.g. in *Sabella*), lip-associated pinnulae (e.g. in *Pomatoceros*), and outgrowths of the dorsal lip (e.g., in *Apomatus*).

As a joint and anatomically neutral term to be used in faunas and in descriptions of the outer morphology, the expression appendages of the dorsal lip or, more briefly (dorsal) lip processes is suggested to encompass all three kinds of appendages.

4.3.5. Nuchal Organs or Paired Antennae

4.3.5.1. Sabellidae. Johansson (1927) denies the existence of nuchal organs in *Sabella.* In the present paper, however, structures have been noted in the 'roof' of the dorsal pit of *Sabella,* the histology of which suggests a sense organ (see 3.2.2.1). Similar observations were made by Rullier (1951) who characterized these organs as nuchal organs because, according to him, they were innervated from *la masse postérieure du cerveau.* As shown (see 3.4.2.7), however, these organs in *Sabella* are not innervated from the hind but from the front end of the brain. This observation agrees with that made by Binard and Jeener (1928) in *Spirographis spallanzanii.* As already discussed, however, (see 4.3.1) in all sabellids (and serpulids) in which the brain could be analyzed, the dorsal roots of the circum-oesophageal connectives (and their commissures) lie in front of the ventral roots (and their commissures). Contrary to this, in all "spiomorphic" and "drilomorphic" forms earlier studied by the present author the dorsal roots lie behind the ventral roots. This means that when the nerve lamina running to the ciliated 'roof' of the dorsal pit of *Sabella* leaves the anterior front of the brain, it emanates in all probability from that part of the *Sabella* brain which is equivalent to the hindmost part of the brain of the "spiomorphic" and "drilomorphic" polychaetes. It seems probable that Rullier, unaware as he was of the architecture of the sabellid brain, when maintaining that the nuchal organ in *Sabella* was innervated from *la masse postérieure du cerveau,* was influenced by his interest in the Racovitzan idea of a tripartition of the polychaete brain, according to which the nuchal organ should be innervated from a *cerveau postérieur*. The structures of *Sabella* discussed here, which are interpreted by the present author and Rullier as nuchal organs, correspond to what Pruvot (1885), Meyer (1888), and Binard and Jeener (1928) considered to be paired antennae.

In the vicinity of the mouth of *Euchone papillosa* Johansson (1927) observed a pouch which he characterized as a *Sinnesorgan.* Evenkamp (1931) denied the existence of this structure but designated another part of the animal, situated *weiter oben im Kopfsegment* (further above in the head segment) as a *Flimmergrube* (ciliated pit). Judging from his Fig. 10 Evenkamp might have experienced difficulties in distinguishing between the dorsal and the ventral side of *Euchone;* in my preparations of that species I have found Evenkamp's *'Flimmergrube'* and been able to establish that this structure is nothing but a slightly separated part of the ciliated epithelium of the ventral side of the worm.

In *Chone infundibuliformis* Rullier (1951) found the ciliated pocket observed by Johansson (1927) in *Euchone papillosa,* and as emphasized (see 3.2.2.1) I have established the existence of this organ in *Chone, Euchone, Potamilla,* and *Myxicola* species. The extension of this organ, however, is much greater than was observed by Johansson and Rullier (see 3.1 and 3.2). According to my comparative studies on these species Rullier's observations on *Jasminiera elegans* can hardly be correct.

The structures are innervated by a nerve, the two roots of which emerge from the dorsal and ventral commissures of the dorsal root of the circumoesophageal connective (see 3.4.2.5 and Figs. 25 and 30b: *nn*). This is the way in which the nuchal organs are innervated in the sabellariids (Orrhage 1978; see the present Fig. 30a), and the median nuchal nerves of the trochochaetids, the spionids (Fig. 30e and f: *mnn*), and the flabelligerids (Orrhage 1966, Fig. 4: *iNlN*) are rooted in the same manner.

From their histology (see 3.2.2.1) and the way in which they are innervated, the structures in question are interpreted as nuchal organs. No evidence has been published for any paired antennae in *Potamilla, Euchone, Chone,* or *Myxicola.*

4.3.5.2. Serpulidae. According to Johansson (1927) and Rullier (1951) the serpulids are devoid of nuchal organs. In all serpulid species studied by the present author, however, structures have been found which, on account of their histology and position (see 3.2.2.2), could be conceived as nuchal organs. As these structures are innervated in the same way as the nuchal organs of the sabellariids and the sabellids (Figs. 30a–c) and as their nerves are rooted in the brain in precisely the same way as the median nuchal nerves of the trochochaetids, the spionids (Fig. 30e and f: *mnn*), and the flabelligerids (Orrhage 1966, Fig. 4: *iNlN*) there seems to be no doubt about their morphological value.

No one has been able to verify Meyer's (1888) statement concerning the presence of rudiments of paired antennae in *Hydroides* and *Protula*. Neither in these genera nor in any other serpulid genus studied here have I found structures deserving the name of paired antennae.

4.3.5.3. Summarizing Remarks. In none of the sabellid and serpulid species investigated have I found any structures which can be interpreted as *vraies antennes* (Pruvot), *Stirnfühler* (=*hämale Kopftentakel*) (Meyer), or *antennes de première paire* (Binard and Jeener). In those body regions where, according to these earlier authors, such appendages were to be found, I have instead noted the presence of sensory epithelium structures which for several reasons (see above) must be interpreted as nuchal organs.

4.3.6. Nuchal Organs or Nephridial Pores? (On the Pruvot-Meyer Theory)

From his observations on *Serpula Philippi* Mörch (=*Serpula vermicularis*) Pruvot (1885) derived a theory according to which the joint pore of the thoracic nephridia of this species could be homologous to a nuchal organ. Meyer (1888) adopted this view and extended it to all serpulids as well as to the sabellids and the sabellariids. Söderström (1920) cautiously demurred to this idea, and Johansson (1927) totally rejected it. Binard and Jeener (1928) on the other hand, accepted it without objection.

Rullier (1951) discussed Meyer's arguments and found most of them untenable. Among other things he pointed out that, in the Sabellidae, nuchal organs and the common nephridial pore are present together; consequently these two structures cannot be homologous to each other. The present author has verified these observations by Rullier as regards the Sabellidae and the Sabellariidae (Orrhage 1978). It has further been shown that nuchal organs are found even in the Serpulidae. For this reason alone the thoracic nephridial pore of this family cannot be homologous to the nuchal organs.

From the present observations of the serpulids, however, it is understandable that the Pruvot-Meyer theory was proposed. In *Serpula*, for instance, the nephridial pore and the nuchal organ lie quite close to each other (although, as emphasized above, they have nothing in common as regards their innervation); in *Pomatoceros* the contact between the two structures is actually so intimate that some of the fibres of the nuchal nerve have become connected to the nephridial pore. To judge from the state of matters in other serpulids and in the sabellids, this condition in *Pomatoceros* must be interpreted as a secondary phenomenon,

From these facts it should be evident that, although in some cases very closely situated, the thoracic nephridial pore and the nuchal organ in sabellids and serpulids are separate structures. The Pruvot-Meyer theory is without foundation.

4.3.7. Systematic Considerations

4.3.7.1. Serpulimorpha Hatschek 1893 as a systematic unit. In all probability following Meyer (1888), Hatschek (1893) united the Hermellidae (Sabellariidae) and the Serpulidae s. lat. into the suborder Serpulimorpha. Benham (1896) followed the same lines: his *branche Cryptocephala* included the two suborders Sabelliformia (the families Sabellidae, Eriographidae, Amphicorinidae and Serpulidae) and Hermelliformia (the family Hermellidae). Hatschek's concept of Serpulimorpha frequently recurs in the literature (e.g., Hempelmann 1931; Friedrich 1938; Hartmann-Schröder 1971).

The two main reasons given by Meyer for a close relationship between the Sabellariidae, the Sabellidae, and the Serpulidae were the presence of a common pore of the thoracic nephridia and the pretended homology between the food sampling organs of the three families. However, Johansson pointed out (1) that the nephridial pores in Sabellariidae are paired (cf. also Dehorne 1908, 1935, 1952), (2) that the thoracic nephridia of this family are in his opinion situated in the fifth segment while those of the Sabellidae and Serpulidae are to be found in the second, and (3) that, accordingly, the thoracic nephridia of the sabellids and serpulids cannot be homologous to those of the sabellariids. In my sabellariid paper (1978), however, I have shown that what Johansson discerned as the fifth segment in this family must be interpreted as the second segment; consequently the thoracic nephridia of the three families are in all probability equivalent to each other. On the other hand, in agreement with Dehorne and Johansson, I have been able to establish that in the sabellariids, as distinct from the sabellids and serpulids, the pores of these nephridia are paired.

Meyer's second main reason for a closer phylogenetic connection between the sabellariids and the sabellids and serpulids, the homology between their food sampling devices, is dismissed as untrue by Johansson. My studies of the sabellariids (1978) and the sabellids and serpulids (present paper) verify his opinion.

It is thus evident that the main arguments put forward in favour of a close relationship between, on the one hand, the sabellariids and, on the other, the sabellids and the serpulids are not sound. [The systematic position of the Sabellariidae is still obscure, as is clearly shown by a comparative study of the opinions put forward by, for instance, Ushakov (1955), Dales (1962), Clark (1969), and Fauchald (1977).]

4.3.7.2. Spirorbidae Pillai 1970 as a Systematic Unit. I agree entirely with the reasons given by Pillai (1970) for the separation of the spirorbids into a separate family. As emphasized already (see 1.1) Pillai has had many followers.

4.3.7.3. The Interrelationship of the Sabellidae and the Serpulidae. It seems to be unanimously agreed that the sabellids and the serpulids are closely related to each other (see the literature quoted in 4.3.7.1). One of the main arguments put forward is the great similarity in the morphology and the structure of the branchial crown of the two families. The present work corroborates this by the discovery in both families of pinnulae detached from the crown and associated with the dorsal lip of the mouth. Furthermore, this investigation has emphasized great resemblances between the sabellids and the serpulids in the architecture of the brain. In this context the presence of the four commissures of the roots of the circum-oesophageal connectives is uninteresting, because this is a feature found in almost all the polychaetes investigated by the present author (see 4.4.1). The anterior, dorsal, and ventral association commissures, however, are here of the utmost interest: these commissures, like their tracts of various kinds, are found in both families but do not exist in any other "sedentary" polychaete so far studied.

4.3.7.4. Characters Distinguishing the Sabellidae from the Serpulidae. Among characters distinguishing the sabellids from the serpulids, Meyer (1888) mentioned *die Complication des Mundes durch eine stärkere Entwicklung der Lippenfortsätze* (complication of the mouth through stronger development of the appendages of the dorsal lip) and *die Einverleibung der paracerebralen Stränge in das Gehirn* (incorporation of the paracerebral nerves into the brain). In the species studied in the present investigation, lip-associated radioli are found only among the sabellids. Lip-associated pinnulae, on the other hand, have been shown to be present in both families. As regards the alleged incorporation of the dorsal root of the circum-oesophageal connective into the brain [or into the nerve of the branchial crown (Binard and Jeener 1928)], it has been shown (see 3.4.2.5–8) that in all the sabellid species studied this root, although in some instances very thin, is clearly visible in a position entirely comparable to that of the dorsal root of the circum-oesophageal connective of the serpulids.

Although, consequently, some of the characters stated by Meyer have been shown in the present investigation to be less valid than formerly thought, the sabellids and the serpulids are clearly distinguished from each other by many marked differences, e.g., the presence of the thoracic membrane in the serpulids (with some exceptions) but not in the sabellids, the presence of opercula in the serpulids (also with some exceptions) but not in the sabellids, and the different structure of the branchial skeleton and of the tubes of the two families.

4.3.7.5. Subfamilies Within the Sabellidae. Mainly on the basis of setal structures and configuration, Rioja (1923) divided the Sabellidae into the three subfamilies Sabellinae, Fabriciinae, and Myxicolinae. These subfamilies are congruent with the denominations Sabellidae, Amphicorinidae, and Eriographididae as used by Meyer (1888).

The proposal by Rioja was largely followed by later authors (Fauvel 1927; Hartman 1959; Hartmann-Schröder 1971; Fauchald 1977). Mainly on the basis of his anatomical and histological studies Johansson (1927), however, combined the Fabriciinae Rioja and the Myxicolinae Rioja into one subfamily which he, somewhat inappropriately, called 'Fabriciinae mihi'. According to Johansson the members of this new subfamily were characterized and distinguished from the Sabellinae Rioja by the following qualities:

i) their longitudinal muscle cells were not 'cylindrical' (as in Sabellinae) but more or less of the 'nematoid type',

ii) their branchial crowns were innervated not by one (as in Sabellinae) but by two nerves on each side of the animal, one nerve (*der innere Nerv*) rooted in the anterior corner of the brain and in the vicinity of the visceral nerve, the other (*der äussere Nerv*) rooted in the anterior corner of the brain,

iii) they were provided with a pair of special sense organs (*Flimmerorgane*) which were not present in the Sabellinae,

iv) in their thorax no acicular uncini (as in the Sabellinae) were found, but only uncini with long shafts.

A closer examination of these arguments raises the following objections [points (i)–(iv) below refer to the correspondingly lettered characters above]:

i) muscle cells of the 'nematoid type' are present not only in some sabellids and in the nematods, but also in the Nematomorpha (Bock 1913), the "Archiannelida" (Salensky 1907), the Oligochaeta (Rohde 1885), and in the Polychaeta among the Spionidae, the Trochochaetidae, the Poecilochaetidae (Attems 1902; Söderström 1920; Orrhage 1962, 1964a, 1964b), the Magelonidae (Romieu 1923; Orrhage 1962), the Paraonidae (Strelzov 1979), the Opheliidae (Prenant 1929), the Ampharetidae (Orrhage 1962), the Serpulidae (Johansson 1927), and the Nereidae (Defretin 1949). It may be said, then, that this character is widely spread within the Annelida, and indeed within the Protostomia as a whole. These facts may be interpreted in two different ways: the character has developed in parallel in the different taxa quoted above, or it constitutes a primitive trait still remaining in these taxa. In either case the feature is of negligible value as a phylogenetic systematic character (Orrhage 1964b),

ii) through the analysis given in the present paper it was shown that no major differences in the rooting of the nerves of the branchial crown exist between the Sabellinae, on the one hand, and the Fabriciinae and the Myxicolinae on the other. But in the two sabellin species here investigated, it was impossible to analyze the commissures of the brain. Since this phenomenon could not be explained by faulty preparation methods, it seems that, in this respect, there is a marked difference between the Sabellinae and the Fabriciinae-Myxicolinae. However, just as we cannot group into one subfamily all polychaetes, the brains of which it is possible to analyze with the methods here used, neither is this a character which *per se* links the two subfamilies Fabriciinae and Myxicolinae together,

iii) in the present work the special sense organs, described by Johansson as typical of "his" subfamily Fabriciinae, were shown to be present also in *Potamilla reniformis* which (even by Johansson) is referred on other grounds to the Sabellinae. Furthermore, because of their histology and innervation these organs have above been interpreted as nuchal organs and in the present paper nuchal organs have been shown to exist in all the families and subfamilies studied,

iv) contrary to the Sabellinae, it is true, only uncini with long shafts are present in the thorax of the Fabriciinae and the Myxicolinae. However, against the claim that these two subfamilies may be unified into one using this character, one must inter alia consider that:

– the abdominal uncini of the Fabriciinae are present in short, discrete tori, while the corresponding structures in the Myxicolinae form almost complete cinctures around the body,

– in the Myxicolinae an extremely high basal web is present, reaching almost to the tip of each radiolus of the branchial crown, and
– the tube of the Myxicolinae is hyaline and mucoid while that of the Fabriciinae is membraneous and more or less encrusted with extraneous particles.

Summarizing the above, it may be said that Rioja's division of the Sabellids into the three subfamilies of his still seems to reflect a phylogenetic reality and that the reasons given by Johansson for unifying the Fabriciinae and the Myxicolinae into one subfamily are not valid.

4.3.7.6. Subfamilies Within the Serpulidae. Being without appropriate material of the Ficopomatinae Pillai (1960) and having adopted Pillai's (1970) idea of the Spirorbidae as a separate family, the present author must here restrict the discussion to the following short note concerning the two subfamilies Serpulinae and Filograninae proposed by Rioja (1923).

Hartman (1959) and Fauchald (1977), among others, refer the genera *Apomatus* and *Protula* to the Serpulinae while according to Rioja, Fauvel (1927), and Hartmann-Schröder (1971) these genera belong to the Fabriciinae. It was emphasized that, among the serpulid genera studied by the present author, *Apomatus, Protula* and, in all probability, *Filograna* are the only ones without lip-associated pinnulae and the only ones to be equipped instead with outgrowths of the dorsal lip (3.3.2.8 and 9, 3.4.2.4 and 4.3.4.2). These observations may strengthen Rioja's original idea of the systematic position of *Apomatus* and *Protula*. On the other hand: for a thorough discussion of serpulid subfamily systematics and phylogeny, the reader is referred to the comprehensive work by Uchida (1978).

4.4. The Architecture of the Polychaete Brain as a Phylogenetic Instrument

For the elucidation of problems like those studied here, the structure of the central nervous system is often employed, and for excellent reasons. This suggests the following summarizing and concluding remarks concerning the possibilities of using the architecture of the polychaete brain as a phylogenetic systematic character.

4.4.1. Information Provided by General Features

Gustafson (1930) stated that in the brain of the "errant" polychaetes the circumoesophageal connective of one side of the animal is divided into a ventral and a dorsal root, each root communicating with that of the other side through a dorsal and a ventral commissure. In earlier papers (1964a, 1966, 1974, 1978) I have shown that similar conditions are found in the brain of the "spiomorphic" and "drilomorphic" polychaetes, as well as in the sabellariids. In the present paper it was shown that four, directly connective-associated brain commissures are found also in the sabellids and the serpulids. These commissures, on account of their position and relations to the other parts of the brain are in all probability homologous to each other and they are widely spread within the polychaete system. Accordingly they should be interpreted as primitive and general features characteristic of the polychaetes. This conclusion, of course, precludes every possibility of using these commissures, if in their 'normal' configuration, as an instrument for elucidating the interrelationships of the different polychaete families. Future work will show to what extent they can be used to elucidate the interrelationship between the Polychaeta and the other annelid groups or between annelids and arthropods.

When, on the other hand, in the earlier literature as in the present paper, the morphological value (the homologies) of the appendages of the anterior end of polychaetes are inferred (inter alia) from their innervation, these conclusions are based on the discovery of similarities or general features.

4.4.2. Information Provided by Special Characters

The general organization of the polychaete brain thus being useless for studies of the phylogeny within the Polychaeta, deviations from this general formation may be helpful in this respect. The following five examples are given:

a) From general similarities in the architecture of the cephalic nervous system, the Spionidae, the Trochochaetidae, and the Poecilochaetidae must be interpreted as closely related to each other; on the other hand, these families are clearly distinguished from each other by specialities in the innervation of their palps and nuchal organs (Orrhage 1964a).

b) To judge from special traits in the innervation of the palps, the Apistobranchidae are closely related to the spionids, the poecilochaetids, and, above all, the trochochaetids, while the presence of a prepharyngeal commissure is a special character which the Apistobranchidae share only with the Magelonidae and the Paraonidae among the "spiomorphic" and the "drilomorphic" polychaetes (Orrhage 1974).

c) Strelzov (1979) has favoured me by using some of the data given in my 1966 paper in elucidating the systematic position of the Paraonidae. According to Strelzov some special characters in the cephalic nervous system of the paraonids, the apistobranchids, and the magelonids suggest that these families "originated from one root"; the data emphasized by Strelzov are inter alia, the presence of a prepharyngeal commissure, the position of the nuchal ganglia, and the way in which the nerves of the nuchal organs issue from the circumoesophageal connectives (cf. Orrhage 1966, Figs. 2, 5, and 6; Strelzov 1979, Fig. 8).

d) From the data just mentioned and noting inter alia, specialities in the innervation of the palps, and the particular rooting of the oesophageal nerves, I have revived Hatschek's (1893) idea of a closer relationship between the Protodrilidae and the Spionidae (Orrhage 1974).

e) Finally, I have in this paper interpreted the presence of the unique association commissures with their tracts of various kinds in the sabellids and the serpulids as special characters indicating a close phylogenetic relationship between these two families.

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Abbreviations

aac	anterior association commissure
acdrcc	anterior coil of *drcc*
apmcg	anterior part of *mcg*
astlap	axis of supporting tissue of *lap*
astlar	axis of supporting tissue of *lar*
astp	axis of supporting tissue of pinnula
astr	axis of supporting tissue of radiolus
ataac	anterior tract of *aac*
atdac	anterior tract of *dac*
atvac	anterior tract of *vac*
bfr	basal fold of radiolus
bgr	basal groove of radiolus
bvlap	blood vessel of *lap*
bvlar	blood vessel of *lar*
bvmdr	blood vessel of the most dorsal radiolus
bvp	blood vessel of pinnula
bvr	blood vessel of radiolus
bvrr	blood vessels of radioli
cc	circum-oesophageal connective(s)
cg	cerebral ganglion
cil	cilia
cnac	commissure of *nac* and *nmr*
cnof	common nerve of oral filaments
ctndbv	curved tract of *ndbv*
dac	dorsal association commissure
dcdr	dorsal commissure of *drcc*
dcvr	dorsal commissure of *vrcc*
dg	dorsal ganglion
dl	dorsal lip
dn	dorsal nerve from *dcdr*
dnno	diffuse nervous lamina of nuchal organ
dp	dorsal pit
drcc	dorsal root of *cc*
drnbc	dorsal root of *nbc*
gmnbc	ganglion of *mnbc*
lap	lip-associated pinnula
lar	lip-associated radiolus
lbv	large branchial blood vessel
lcg	lateral cerebral ganglion
lgndbv	lateral ganglion of *ndbv*
lgr	lateral groove of radiolus
lgvac	lateral ganglion of *vac*
llat	left longitudinal association tract
lnbc	lateral nerve of branchial crown
lnn	lateral nuchal nerve
lns^1	lateral nerve of segment 1
lns^2	lateral nerve of segment 2
lprndbv	lateral posterior root of *ndbv*
m	mouth
mcg	median cerebral ganglion
mgndbv	median ganglion of *ndbv*
mnbc	median nerve of branchial crown
mnn	median nuchal nerve
mprndbv	median posterior root of *ndbv*
nac	nerve(s) of the alimentary canal
nbc	nerve of the branchial crown
nc	nerve of collar
ndbv	nerve of the dorsal blood vessel
nlar	nerve of *lar*
nmdr	nerve of the most dorsal radiolus
nmr	nerve(s) of the mouth region
nn	nuchal nerve
nlap	nerve of lip-associated pinnula
nr	nerve(s) of radiolus (-i)
nvlm^1 *nvlm*^{2}	nerves to ventral longitudinal muscles
odl	outgrowths of the dorsal lip
oes	oesophagus
pcdrcc	posterior coil of *drcc*
pnr^1 *pnr*^{2} etc.	first, second, etc., palp nerve root
ptdac	posterior tract of *dac*
ptvac	posterior tract of *vac*
rlat	right longitudinal association tract
sstlar	surrounding sheath of supporting tissue of *lar*
sstr	surrounding sheath of supporting tissues of radiolus
stlar	supporting tissue of *lar*
stndbv	sagittal tract of *ndbv*
vac	ventral association commissure

vcdr	ventral commissure of *drcc*	*vl*	ventral lip
vcvr	ventral commissure of *vrcc*	*vrcc*	ventral root of *cc*
vg^1	first ventral ganglion	*vrnbc*	ventral root of *nbc*
vg^2	second ventral ganglion	*vs*	ventral sac
vg^3	third ventral ganglion		

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