Ultrastructure of sense organs and the central nervous system in *Parenterodrilus taenioides* and their phylogenetic significance in the taxon Protodrilida (Annelida, Polychaeta)

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SUMMARY

The following sense organs palps, nuchal organs, and presumed unpigmented ocelli, as well as the central nervous system were investigated by electron microscopy in *Parenterodrilus taenioides*. The palps are mobile sensory structures bearing motile cilia and four types of sensory cells, including presumed phaosomous ocelli. The palp canals are small, filled with cell bodies of muscle cells and a few coelenchyme cells. The canals are covered by a cord of coelenchyme cells. The comparatively large nuchal organs are identical in structure with those of the other Protodrilida. There are two types of presumed ocelli located in posterior ganglionic expansions of the brain. The palps are innervated by three nerves originating from the dorsal and ventral roots of the circumoesophageal connective. The most exceptional features of the brain are four ganglionic expansions extending far posteriorly into the head segment. The lateral ones fuse with the small dorsal root of the circumoesophageal connectives. These findings are compared with the sense organs and the nervous system of the other Protodrilida. They clearly corroborate the supposed relationship of the Protodrilida and additional autapomorphies demonstrate the derived position of *P. taenioides*.

RÉSUMÉ

Ultrastructure des organes sensoriels et du système nerveux central de *Parenterodrilus taenioides* et leur signification phylogénétique chez les Protodrilida (Annélides Polychètes)

Les organes sensoriels tels que palpes, organes nucaux, structures assimilées à des ocelles non pigmentés, ainsi que le système nerveux central ont été étudiés au niveau ultrastructural chez *Parenterodrilus taenioides*. Les palpes sont des appen-

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dices sensoriels ciliés et mobiles qui portent quatre types de cellules sensorielles, dont des ocelles de type phaosome. Les canaux internes des palpes sont minces, remplis par les corps cellulaires des cellules musculaires et par quelques cellules du coelenchyme qui forment aussi un cordon cellulaire à la périphérie de chaque canal. Les palpes reçoivent trois nerfs issus des racines dorsales et ventrales des connectifs périoesophagiens. Les organes nucaux, relativement larges, ont une structure identique à ceux des autres Protodrilida. Deux autres types de structures, assimilées à des ocelles non pigmentés, sont logées dans des expansions ganglionnaires postérieures du cerveau. Les caractéristiques les plus remarquables du cerveau sont ces quatres expansions ganglionnaires qui s'étendent loin vers l'arrière, dans le segment céphalique. Les expansions les plus latérales fusionnent avec les petites racines dorsales des connectifs périoesophagiens. Ces caractères sont comparés à ceux des autres Protodrilidés et les nouvelles autapomorphies révélées par ce travail démontrent que *P. taenioides* est une forme dérivée. L'ensemble des résultats confirme les relations prélablement établies au sein des Protodrilida.

INTRODUCTION

The Protodrilida are interstitial polychaetes characterized by a long and slender body, reduced or absent parapodia, a pair of prostomial appendages (palps), and a pygidium generally with two adhesive lobes. The about 60 known species of the taxon belong to only four genera: *Saccocirrus* Bobretzky, 1871, *Protodrilus* Hatschek, 1880, *Protodriloides* Jouin, 1966 and *Parenterodrilus* Jouin, 1992. Electron microscopic investigations were conducted to clarify the functional morphology of selected organs as well as to test the proposed monophyly of the Protodrilida and their subordinate taxa, to evaluate their relationship and to find synapomorphies with their supposed sister group, the Spionida (e.g., PURSCHKE & JOUIN, 1988; PURSCHKE, 1990a, 1993). In contrast to the small body size and the apparently simple organization of these polychaetes, their sense organs and the central nervous system turned out to be rather complex structures when investigated by electron microscopy (EAKIN *et al.*, 1977; PURSCHKE, 1990a, 1990b, 1990c, 1992, 1993; PURSCHKE & JOUIN-TOULMOND, 1993). Therefore, these structures provide numerous characters which might be useful for phylogenetic considerations.

Sense organs present in every species are: the palps, the nuchal organs, and various types of unpigmented presumed ocelli. Pigmented ocelli only occur in the *Saccocirrus* species and a few *Protodrilus* species. These structures have now been investigated in species of every genus except the monotypic *Parenterodrilus*, which is so far only known from sublittoral coral sands of the island of Moorea, French Polynesia. *Parenterodrilus taenioides* is especially remarkable because it is the only known polychaete possessing a vestigial alimentary canal, without mouth and digestive cavity (JOUIN, 1979, 1992). Thus, the main purpose of the present investigation was to clarify the functional morphology of the sense organs and the central nervous system of this rare species, in order to use these supplementary data for a comprehensive phylogenetic discussion of the Protodrilida. The present findings fit very well into a dendrogram showing the presumed relationship of the subordinate taxa of the protodrilidans which has previously been suggested (PURSCHKE & JOUIN, 1988) and which can now be based on an even larger number of characters.

MATERIAL AND METHODS

Specimens of *P. taenioides* were collected by the junior author in sublittoral sands of the barrier reef at the type locality in Moorea, French Polynesia (JOUIN, 1979). After relaxation in a mixture of equal parts of sea water and 7.7 % $MgCl_2$, specimens were fixed in a cacodylate buffered (0.2 M, pH 7.4) solution of 2 % glutaraldehyde, adjusted with NaCl to about 1,300 mosM for 1 h. They were rinsed in the same buffer, postfixed in buffered 1% OsO_4, dehydrated in an ethanol series, and embedded in Epon. Ultrathin sections of two specimens were cut with a diamond knife on a Reichert Ultracut E microtome and ribbons of sections were collected on single slot grids coated with pioloform support film in order to obtain complete series of ultrathin sections. They were stained in an

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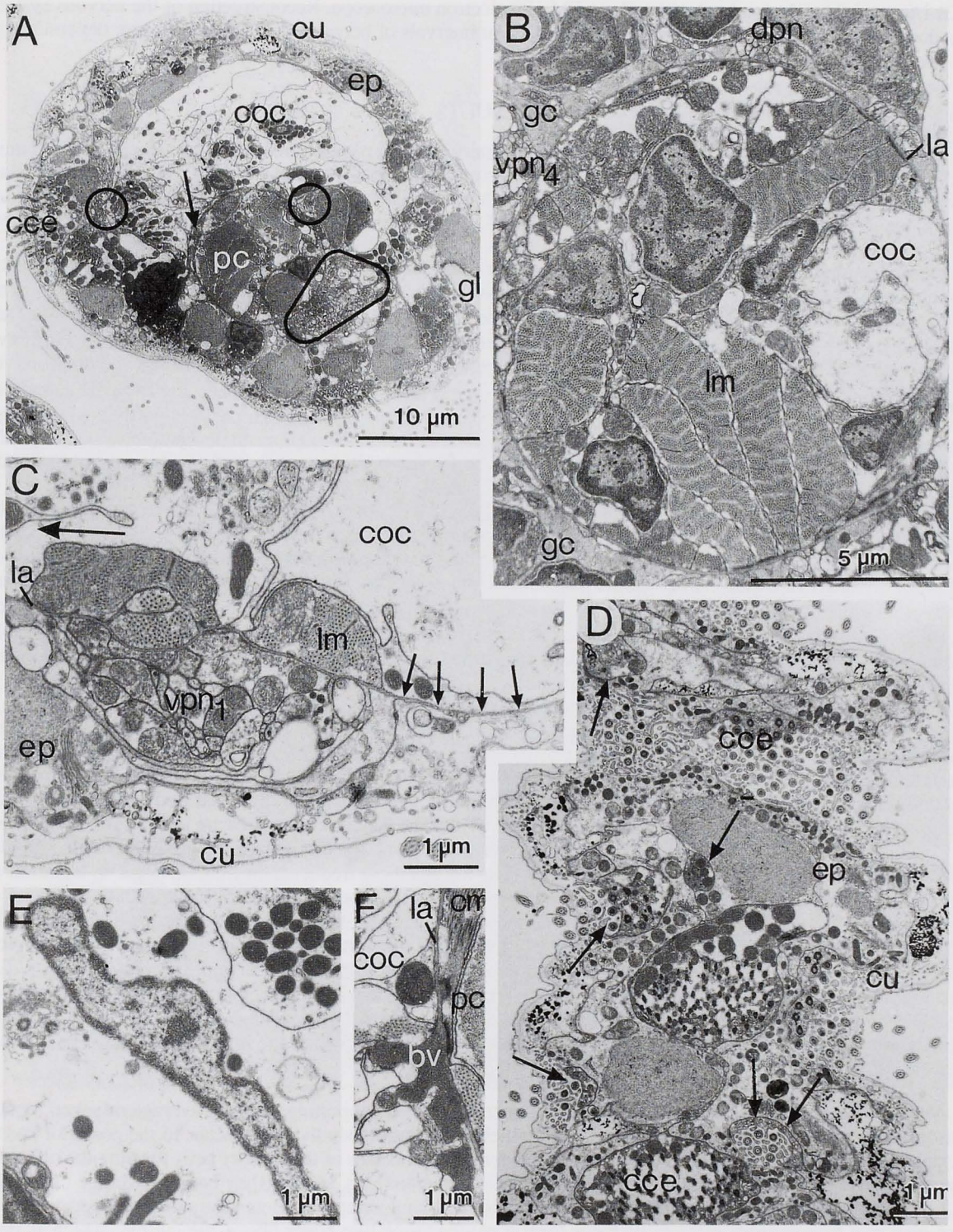
FIG. 1A-F. — *Parenterodrilus taenioides*. Palps. A. Low power TEM micrograph of cross section appr. 25 µm above the palp base; center occupied by palp canal (*pc*) and coelenchyme cells (*coc*); palp nerves encircled; arrow points to position of blood vessel. B. Cross section of palp canal. C. Ventral palp nerve *vpn 1* and longitudinal muscle fibres; note disappearance of extracellular lamina (*la*) between coelenchyme and epidermal cells lateral to *vpn 1* (*small arrows*); the *large arrow* points to position of palp canal. D. Tangential section of ventral side with ciliated cells (*cce*), epidermal supporting cells (*ep*) and sensory cells (*arrows*). E. Coelenchyme cell with nucleus. F. Blood vessel (*bv*). - *cce* ciliated cell, *cm* circular muscle fibre, *coc* coelenchyme cell, *cu* cuticle, *dpn* dorsal palp nerve, *ep* epidermal supporting cell, *gc* glial cell, *gl* gland cell, *la* extracellular lamina, *lm* longitudinal muscle cell, *pc* palp canal, *vpn 1, 4* ventral palp nerve 1,4.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LKB Ultrostainer and examined with a Zeiss EM 109 electron microscope. Reconstruction of the nervous system was done from low power electron micrographs taken at intervals of between 0.7 µm and 3.5 µm, depending on the structures observed.

RESULTS

In *Parenterodrilus taenioides* the palps arise in an anterior-lateral position from the prostomium. The ciliation of the anterior end is very well developed; in addition to numerous sensory cilia, the palps, prostomium and head segment (= peristomium) bear mobile cilia as well. The nuchal organs are heavily ciliated, rounded areas of about 25 µm diameter at the posterior end of the prostomium. Unpigmented ocelli are not visible with light microscopy.

Palps. The palps are circular to oval in cross section. They are composed of cuticle, epidermis, sensory cells, intraepithelial nerves, a palp canal, a small blood vessel, and so-called coelenchyme cells (Fig. 1A-F). The epidermis is comprised of supporting cells, with glandular and ciliated cells distributed among them. The latter are restricted to the ventral side where they are arranged in bands. There are three palp nerves: the medial nerve (*vpn*$_4$; see PURSCHKE, 1993 for terminology) is the largest and contains about 330 nerve fibres; the other nerves are considerably smaller and consist of 15 (*dpn*) and 35 (*vpn*$_1$) fibres. Small branches of these longitudinal nerves form a network of nerve cell processes ventrally, and around the palp canals. Each nerve is partly enveloped by glial cells (Fig. 1B). In the nerve fibres clear vesicles with a diameter of 40-60 nm and dense-cored vesicles of 70-95 nm diameter are present (Fig. 1C). Neuroneuronal and neuromuscular synapses were frequently observed within the nerve tracts.

Each palp has a small canal, 10-15 µm in diameter (Fig. 1A-C, E-F). The canals are situated ventrally in the palps and unite behind the neuropile of the brain. They are filled with muscle cells and a few coelenchyme cells, surrounded by an extracellular lamina. There are only a few small muscle fibres outside the palp canals, most of which are situated close to the small ventral palp nerve (*vpn*$_1$: Fig. 1C). Besides these longitudinal fibres there are a few small circular fibres in the palp canals. The canals are covered dorsolaterally by coelenchyme cells, which are electron-lucent with only very few organelles and an irregular outline (Fig. 1A, C, E). Although of presumably mesodermal origin, this coelenchyme tissue is not separated from the epidermis by a basal lamina on all sides; extracellular material was only detectable between the palp canal and the small palp nerve (Fig. 1C). Each palp is supplied by a small blind-ending blood vessel which is situated at the palp canal opposite to the main palp nerve.

Three types of bipolar sensory cells have been found on the palps and the prostomium (Fig. 2A-F). The monociliary type-1 sensory cells are so-called collar receptors (e.g. SCHLAWNY *et al.*, 1991): the cilium passes through the cuticle and is surrounded by 10 modified microvilli (Fig. 2A-B). A cylinder of electron-dense material lies below the microvilli. It is connected to the ciliary rootlet just underneath the basal body. Proximally, thin filaments originate from this cylinder and enter the microvilli. The dendritic processes are about 1 µm in diameter and contain 3-4 long mitochondria (Fig. 2A). The second type of sensory cell is multiciliary, with 3-9 cilia penetrating the cuticle (Fig. 2C-D). These sensory cells are the most frequent; they either occur in isolation or grouped in two adjacent sensory cells forming a ciliary tuft. The cilia are of different lengths and may be up to 15 µm long. They usually arise from a slight depression of the cell apex, which creates a raised rim at the periphery of the sensory cell (Fig. 2D). The cilia are surrounded by short microvilli and anchored by long rootlets (Fig. 2C). Sensory cells of the third type have non-penetrative (intracuticular) cilia and they may be isolated or clustered in groups of up to 9 sensory cells (Fig. 2E-F). Their long dendritic processes extend above the level of the adjacent epidermal cells and bear one or two horizontal cilia (Fig. 2E). The cilia are about 4 µm long and have a 9x2+0 axoneme (Fig. 2E, inset). Usually they divide in branches in which the microtubules are successively lost.

Nuchal organs. The nuchal organs consist of numerous ciliated supporting cells, an average of seven bipolar sensory cells, and a retractor muscle (Fig. 3A-D), which runs ventromedially and attaches to the posterior end of the palp canal. Ciliated supporting cells surround the dendritic processes of the sensory cells forming the olfactory chamber (3.5-4 µm in diameter) in the middle of the ciliated area (Figs 3A, 4). They bear an average of 35 cilia (3.2 cilia per µm^2), which are anchored by basal bodies and long striated rootlets. The ciliated supporting cells give also rise to numerous microvilli; these form a paving-stone-like cover above the cuticle, which is only penetrated by the cilia of these cells (Fig. 3B-C). This layer also covers the olfactory chamber. The dilated microvillar tips are cubic in shape, only 20 nm apart and interconnected by fibrillar material (Fig. 3C). Numerous clear vesicles, coated vesicles, coated pits and lysosomes indicate a considerable degree of endo- or exocytosis in

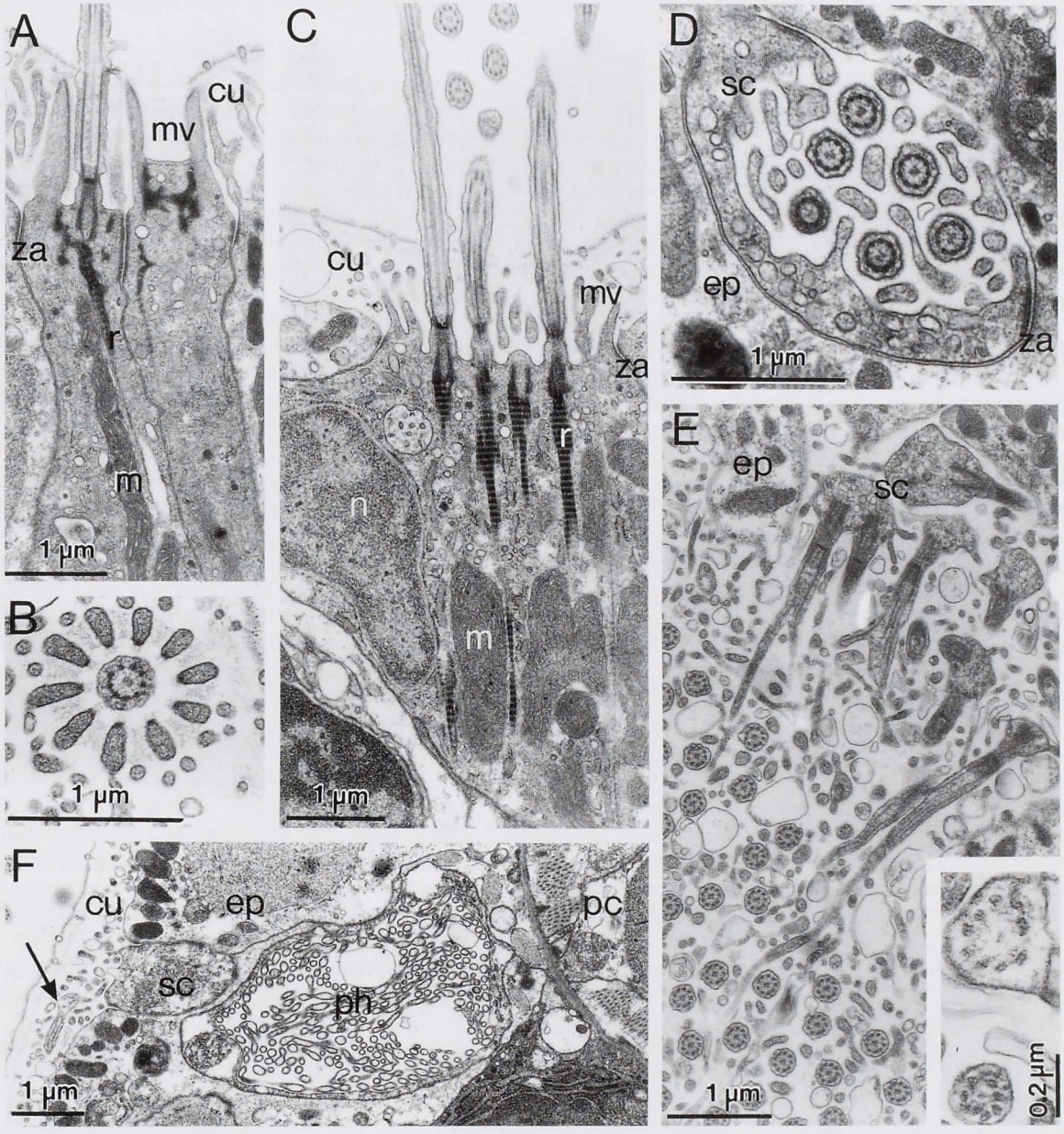


FIG 2A-F. — *Parenterodrilus taenioides*. Sensory cells of palps. A. Collar receptors. B. Cilium and microvilli of collar receptor in cross section. C. Multiciliary sensory cell; nucleus (*n*) situated laterally. D. Cross section of apex of multiciliary sensory cell (*sc*); note clear vesicles accumulating in sensory cell. E. Group of sensory cells with intracuticular cilia; cross sectioned cilia belong to ciliated epidermal cell; inset: sensory cilia in cross section. F. Presumed ocellus with phaosome (*ph*). The *arrow* points to a sensory cell with intracuticular cilium. - *cu* cuticle, *ep* epidermal cell, *m* mitochondrion, *mv* microvillus, *n* nucleus, *pc* palp canal, *ph* phaosome, *r* rootlet, *sc* sensory cell, *za* zonula adhaerens.

these cells (Fig. 3A-B). Each sensory cell bears one cilium with a 9x2+0 axoneme and a few microvilli (Fig. 3A, D). The ciliary rootlets are vestigial: 0.5 µm long and 0.04 µm thick. The ciliary shafts branch. In the branches the microtubules are successively lost, resulting in structures indistinguishable from regular microvilli (Fig. 3D). Microvilli and ciliary branches extend into the subcuticular space above the supportive cells outside the olfactory chamber (Fig. 3A).

Presumed Ocelli. In each palp four presumed ocelli (type 1) have been found close to the main palp nerve (Fig. 4). They consist of a single sensory cell characterized by an intracellular vacuole (phaosome) containing numerous microvillus-like ciliary branches (Fig. 2F). There are no pigmented or unpigmented ocelli in the prostomium of *P. taenioides*. However, the type-2 and type-3 unpigmented ocelli are located in the peristomium (= head segment) in the lateral posterior ganglionic expansions of the brain (Figs 3E-F, 4). Each ocellus consists of a sensory cell and a supporting cell forming an extracellular cavity. These cavities are completely filled with microvillus-like branches of two cilia in both types. There are two of the minute type-2 ocelli (3x2x2 µm; Fig. 3E) but five of the type-3 ocelli (18x6x4 µm; Fig. 3F) in each specimen investigated. Other differences concern position, branching pattern of cilia and arrangement of microvilli. The ocelli will be described in more detail separately (PURSCHKE & JOUIN-TOULMOND, 1993).

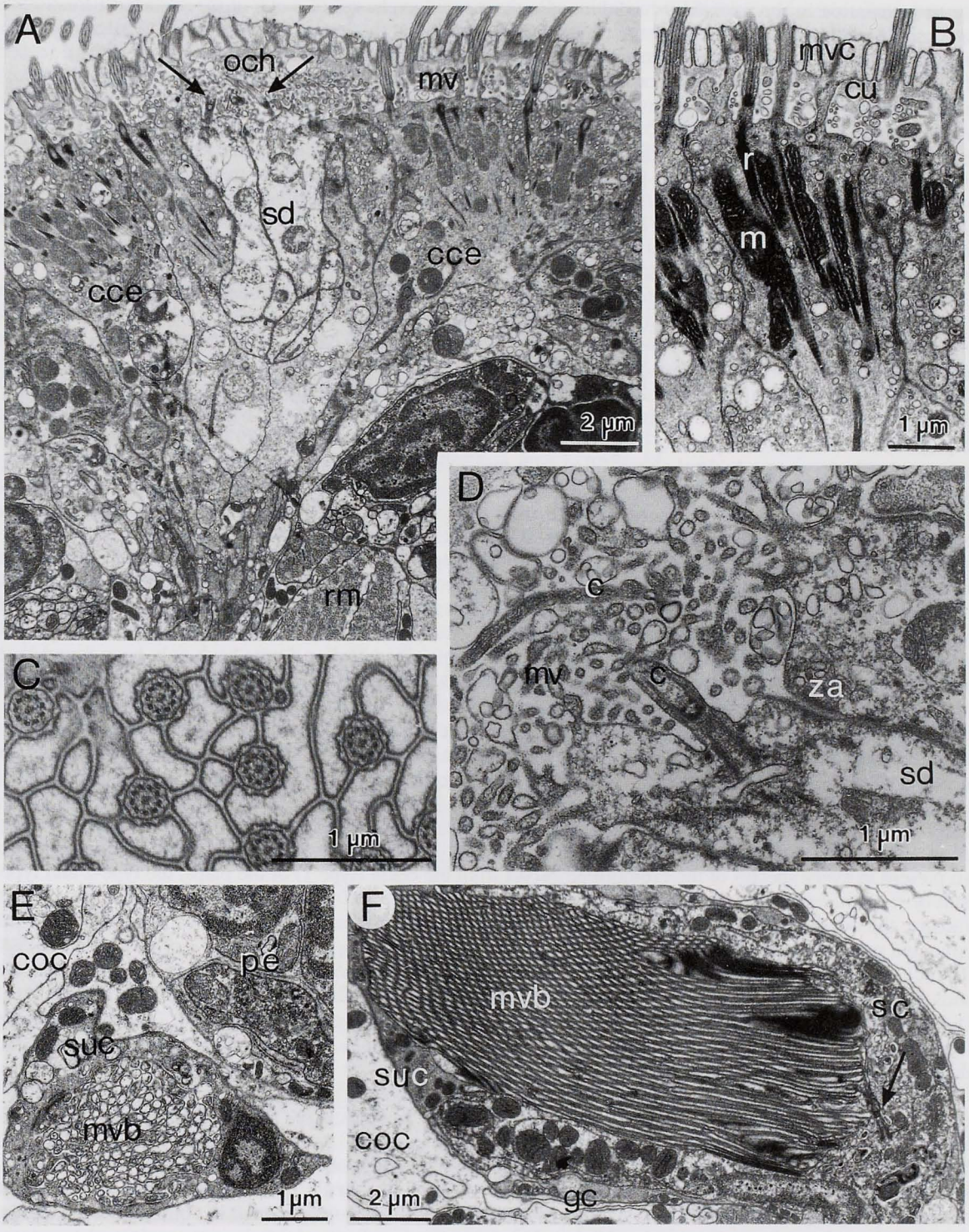
Central nervous system. The neuropile of the brain is situated in the prostomium in the curve formed by the palp canals (Fig. 4). Conspicuous features are two pairs of dorsal expansions (*pe* in Fig. 4) formed by nerve cell processes and, posteriorly, by the perikarya of neurons and glial cells. These expansions extend far into the head segment; the lateral ones contain the presumed ocelli. The ventral nerve cord communicates with the brain through the circumoesophageal connectives (*cc*). Anteriorly, before these nerves turn towards the brain, each connective divides into a ventral (*vrcc*) and a dorsal root (*drcc*). The dorsal roots (*drcc*) and the nerve cell processes of the lateral expansions (*pe*) enter the neuropile together as one nerve. The nuchal nerve (*nn*) very likely emanates from the lateral expansion (*pe*), whereas the medial expansion gives rise to a posteriorly running dorsal nerve (*dn*). Although gut and stomodaeum are residual, the stomatogastric nerves are well-developed and arise ventrally close to the ventral roots of the circumoesophageal connectives (*vrcc*). The main palp nerve (vpn_4) emanates laterally from the anterior part of the brain and receives its fibres from a dorsal and a ventral root. The other palp nerves emerge directly from the roots of the circumoesophageal connectives: the second ventral palp nerve (vpn_1) from the ventral root and the thin dorsal palp nerve (*dpn*) from the common nerve containing the nerve fibres of the lateral posterior expansion and the dorsal root close to the brain.

DISCUSSION

The sense organs and the central nervous system of *P. taenioides* are structurally complex. Although the digestive system is vestigial and not functioning (JOUIN, 1979, 1992), there is no evidence for a reduction of the sensory organs compared with other species of the Protodrilida. However, do these organs provide additional features to elucidate the phylogenetic relationship between them? In a phylogenetic tree previously suggested by PURSCHKE & JOUIN (1988), *Protodrilus* and *Parenterodrilus* were sister groups forming the Protodrilidae which is in turn the adelphotaxon of *Saccocirrus*. Finally, these taxa most likely represent the sister group of *Protodriloides*. Very likely, the taxon Protodrilida is related to the Spionida or one of its subordinate taxa (ORRHAGE, 1974; PURSCHKE & JOUIN, 1988; PURSCHKE, 1993). At present the Protodrilida is still retained, because its sistergroup has not yet been recognized.

The palps of *P. taenioides* are equipped with a variety of sensory cells which allow reception of different sensory stimuli from a wide area around the anterior end. They differ externally from those of *Saccocirrus* and most *Protodrilus* species (except *P. brevis*; see JOUIN, 1970) in the presence of motile cilia (PURSCHKE, 1993). In the Spionida such a ciliation is generally present, located in a groove and used for collecting food particles (DAUER, 1987; FAUCHALD & JUMARS, 1979). Since a mouth is absent in *P. taenioides*, the remaining functions

FIG. 3A-F. — *Parenterodrilus taenioides*. A-D. Nuchal organ. A. Low power micrograph showing entire organ in cross section; *arrows* point to sensory cell cilia; subcuticular space with microvilli (*mv*) and ciliary branches of sensory cells. B. Ciliated cells with cover of microvillar tips (*mvc*). C. Microvillar tips in transverse section. D. Sensory dendrites with cilia (*c*) and microvilli. E-F. Presumed ocelli. E. Small ocellus (type 2). F. Large ocellus (type 3); *arrow* points to sensory cell cilium. - *c* cilium, *cce* ciliated supporting cell, *coc* coelenchyme cell, *cu* cuticle, *gc* glial cell, *m* mitochondrion, *mv* microvillus, *mvb* microvillus-like ciliary branch, *mvc* microvillar cover, *och* olfactory chamber, *pe* posterior expansion of brain, *r* rootlet, *rm* retractor muscle, *sc* sensory cell, *sd* sensory dendrite, *suc* supporting cell, *za* zonula adhaerens.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may be orientation in the interstitial medium and a more rapid exchange of water at the surface of the animal. Since motile cilia are also present on the palps of *Protodriloides*, this character might be a vestige of a more developed ciliation which could be assumed for the last common stem species with the Spionida. The sensory cells with cilia penetrating the cuticle or with non-penetrative cilia are of minor phylogenetic importance, because similar cells have been found in the other Protodrilida and they are not different from sensory cells generally present in annelids (STORCH & SCHLÖTZER-SCHREHARDT, 1988; PURSCHKE, 1993). Among the sensory cells of the palps only the phaosomous ocelli can be considered for phylogenetic considerations. Phaosomes - intracellular cavities containing the presumed light-sensitive organelles - occur only occasionally in polychaetes (PURSCHKE & JOUIN-TOULMOND, 1993,). They are found neither in *Saccocirrus* nor in *Protodriloides* but are present in the palps of several *Protodrilus* species (PURSCHKE, 1993; JOUIN-TOULMOND & MARTIN, unpubl. observ.). These phaosomes are structurally identical with those of *P. taenioides* and, therefore, most likely represent a synapomorphy of *Protodrilus* and *Parenterodrilus*.

With respect to the internal structure, the palps are most similar to those of *Protodrilus*. They differ from those of *Saccocirrus* in the absence of the ampullae, posterior expansions of the palp canals. However, the palp canals are considerably thinner in *P. taenioides*, and the musculature outside the canal and the blood vascular system are reduced compared with *Protodrilus* and *Saccocirrus* (PURSCHKE, 1993). The occurrence of a cord of coelenchyme cells outside the canal and the loss of the external lamina between them and the epidermis are unique for *P. taenioides*. These features are very likely correlated with the absence of podocytes, which form part of the wall of the palp canals in the prostomium of *Protodrilus* and *Saccocirrus* (PURSCHKE, 1993). In these genera the palp canals probably serve as a hydroskeleton filled with movable coelenchyme cells, and the podocytes have been regarded as the site where fluid is introduced into the canals from the blood. Since movable coelenchyme cells, or a fluid-filled lumen, are absent in *P. taenioides*, stiffness of the palps is very likely achieved by the musculature of the palp canals and the external coelenchyme tissue. Consequently, podocytes appear to be redundant.

The nuchal organs of all Protodrilida investigated, including *P. taenioides*, are almost identical in structure and consist of the same types of cells as usually found in polychaetes (PURSCHKE, 1986, 1990a; STORCH & SCHLÖTZER-SCHREHARDT, 1988; RHODE, 1990). In nuchal organs which are not located in deep pits, the ciliated supporting cells generally show structural specialisations which cover and protect the cilia and microvilli of the sensory cells. Paving-stone-like covers of microvillar endings joined by fine fibrils have only been found in the Spionidae *Pygospio elegans* and *Scolelepis squamata* (SCHLÖTZER-SCHREHARDT 1987; RHODE, 1990) and in every species of the Protodrilida, which indicates a high probability of synapomorphy of this character.

The sense organs found in the posterior expansions of the brain in *P. taenioides* show striking similarities to photoreceptors - for example, a great expanse of plasmalemma in the form of microvillus-like cell processes, and the position of the organs beneath the epidermis (EAKIN & HERMANS, 1988). Such presumed ocelli without shading pigment have repeatedly been reported for polychaetes and many species possess at least one type of these ocelli, often in addition to pigmented ones (PURSCHKE, 1992). Their great structural diversity, however, makes it likely that unpigmented ocelli evolved convergently several times in annelids. Unpigmented ocelli are also present in every species of the Protodrilida. Apart from the ocelli (type 1) of the palps, the type-2 and type-3 ocelli of *P. taenioides* are completely different to any ocellus of *Protodrilus*. Due to their different position and structure, the ocelli of *P. taenioides* are not homologous to the so-called statocysts, to the phaosomes or to the pigmented eyes occurring in the prostomium of various *Protodrilus* species (EAKIN *et al.*, 1977; PURSCHKE, 1990b,c). There are also no similarities to the presumed ocelli of *Protodriloides* (unpubl. observ.). On the other hand, there is a certain probability of homology with the type-1 ocelli of *Saccocirrus* (PURSCHKE & JOUIN-TOULMOND, 1993). Since the sister group relationship between *Parenterodrilus* and *Protodrilus* is well established by several synapomorphies, this character may be regarded as a symplesiomorphy taken from the stem species of saccocirrids and protodrilids.

The structure of the central nervous system and the innervation of the anterior end have great potential in phylogenetic reconstruction (ORRHAGE, 1990, 1991). As shown previously, the brain with its nerves and the palp anatomy of *Protodriloides*, *Protodrilus* and *Saccocirrus* give strong evidence for a relationship to the Spionida (PURSCHKE, 1993). As was to be expected, the central nervous system of *P. taenioides* is very similar to that of *Protodrilus* and *Saccocirrus* and corroborates the general pattern observed: e.g., the roots of the circumoesophageal connectives, the stomatogastric nerves and the palp nerves arise in corresponding positions, the main palp nerve vpn_4 has a ventral and a dorsal root, and the dorsal root of the circumoesophageal connectives is much smaller than the ventral root. However, there are only three palp nerves, which means, that the nerves vpn_2 and vpn_3 very likely have been lost; furthermore, there is only one dorsal nerve and the posterior ganglionic expansions of the brain are unknown in the other taxa. The nuchal nerve probably also has a different position,

though the nuchal nerves may have different positions in the Spionida as well (ORRHAGE, 1964, SCHLÖTZER-SCHREHARDT, 1987). The most exceptional features are the ganglionic expansions, which are situated in an area occupied by the foregut in *Protodrilus*. Since they are unkown in the other Protodrilida, with a high degree of probability these characters represent autapomorphies of *P. taenioides*.

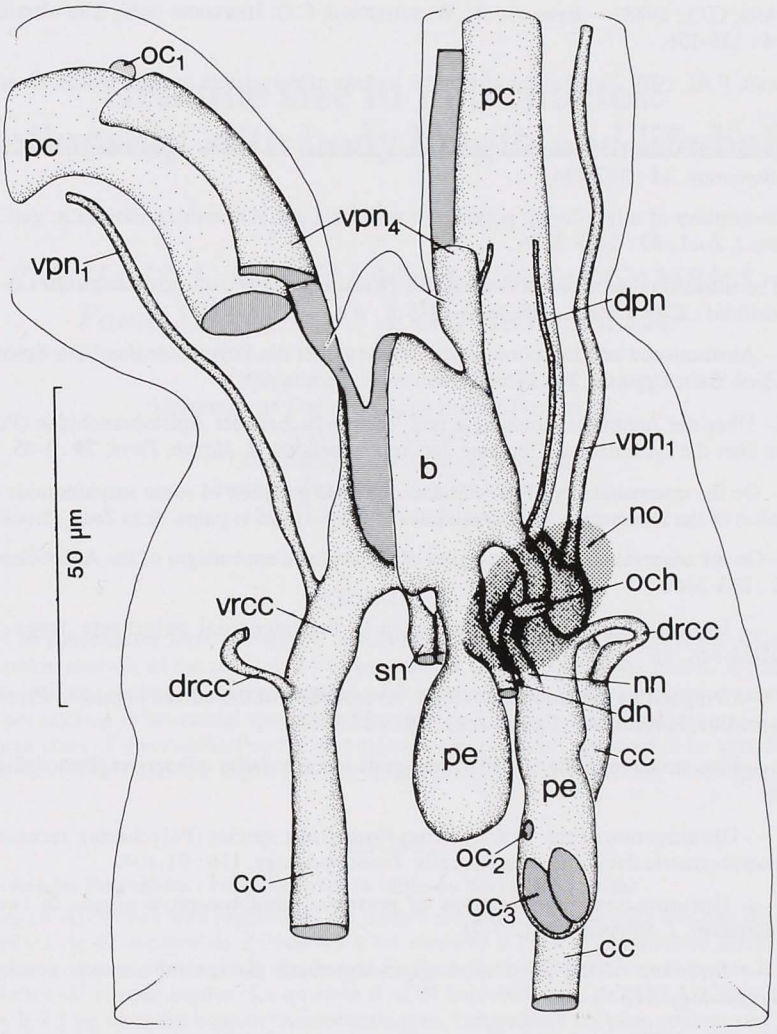

FIG. 4. — *Parenterodrilus taenioides*. Neuropile of the brain (*b*) and associated nerves. Dorsal view; on the left side the dorsal part of the central nervous system has been omitted; reconstruction from electron microscopic observations. *cc* circumoesophageal connective, *dn* dorsal nerve, *dpn* dorsal palp nerve, *drcc* dorsal root of *cc*, *nn* nuchal nerve, *no* nuchal organ, $oc_{1, 2, 3}$ presumed type-1, type-2 and type-3 ocelli; *och* olfactory chamber, *pc* palp canal, *pe* posterior ganglionic expansion of brain, *sn* stomatogastric nerve, $vpn_{1, 4}$ ventral palp nerve 1,4, *vrcc* ventral root of *cc*.

In conclusion, the present findings on *P. taenioides* corroborate its presumed relationship with the other Protodrilida. Its sister group relationship to *Protodrilus* can be sustained by newly found synapomorphies: loss of the ampullae of the palp canals and presence of tentacular phaosomes. Several additional autapomorphies clearly show the derived position of *P. taenioides*: e.g., coelenchyme cells present outside the palp canal, loss of podocytes in the canal, brain with posterior ganglionic expansions, loss of the palp nerves vpn_2 and vpn_3 and loss of the pigmented ocelli. Other characters are likely to be plesiomorphies and allow a better understanding of the relationship of the Protodrilida.

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