Phil. Trans. R. Soc. Lond. B **314**, 1–340 (1986) [1]
Printed in Great Britain

THE STRUCTURE OF THE NERVOUS SYSTEM OF THE NEMATODE *CAENORHABDITIS ELEGANS*

By J. G. WHITE, E. SOUTHGATE, J. N. THOMSON and S. BRENNER, F.R.S.

Laboratory of Molecular Biology, Medical Research Council Centre, Hills Road, Cambridge CB2 2QH, U.K.

(*Received* 9 *August* 1984 – *Revised* 12 *November* 1984)

CONTENTS

The structure and connectivity of the nervous system of the nematode *Caenorhabditis elegans* has been deduced from reconstructions of electron micrographs of serial sections. The hermaphrodite nervous system has a total complement of 302 neurons, which are arranged in an essentially invariant structure. Neurons with similar morphologies and connectivities have been grouped together into classes; there are 118 such classes. Neurons have simple morphologies with few, if any, branches. Processes from neurons run in defined positions within bundles of parallel processes, synaptic connections being made *en passant*. Process bundles are arranged longitudinally and circumferentially and are often adjacent to ridges of hypodermis. Neurons are generally highly locally connected, making synaptic connections with many of their neighbours. Muscle cells have arms that run out to process bundles containing motoneuron axons. Here they receive their synaptic input in defined regions along the surface of the bundles, where motoneuron axons reside. Most of the morphologically identifiable synaptic connections in a typical animal are described. These consist of about 5000 chemical synapses, 2000 neuromuscular junctions and 600 gap junctions.

Introduction

The functional properties of a nervous system are largely determined by the characteristics of its component neurons and the pattern of synaptic connections between them. Although great progress has been made this century in understanding the manner in which information is coded within a neuron and the process of information transmission between neurons via synapses, little is currently known about the detailed connectivity of networks of neurons. The reason for this is simply that a nervous system is an enormously complex organ. In the vertebrate cerebellum alone, it has been estimated that there are more than 10^{10} neurons (Braitenberg & Atwood 1958) each making many thousands of synaptic contacts.

We have undertaken a complete reconstruction of a nervous system from electron micrographs of serial sections. We have been able to do this by using a very simple, small nervous system, that of the soil nematode *Caenorhabditis elegans*. The simplicity and consistency of structure of the nematode's nervous system attracted the attention of several neuroanatomists at the turn

of the century. Richard Goldschmidt was perhaps the most notable of these; he attempted to reconstruct the nervous system of the large parasitic nematode *Ascaris lumbricoides* from serially sectioned material. Goldschmidt and his contemporaries produced detailed and accurate descriptions of the sensilla, the ganglia and the process tracts (Chitwood & Chitwood 1974), but the limited resolution of the light microscope prevented them from unambiguously resolving individual processes within bundles. Goldschmidt was convinced that neuron processes anastomosed extensively and that nervous tissue was therefore a syncytial network. He presented a set of intriguing diagrams representing the layout of processes in the *Ascaris* nervous system in support of his view of the structure of nervous tissue, a view that he vigorously defended (Goldschmidt 1908, 1909). The alternative viewpoint considered that neurons are mononucleate branched structures and that their processes do not anastomose. It is now clear that this alternative viewpoint, as espoused by his contemporary critics, such as Cajal (1972), was correct. More recent anatomical studies with the electron microscope have finally laid to rest the reticularists' view of the nervous system. We have therefore not tried to interpret Goldschmidt's connectivity diagrams, although we have retained some of the names, given to the sensilla and ganglia, that were used by him and his contemporaries.

In recent years, *C. elegans* has become an object of intense developmental and genetical study. The highly reproducible sequence of cell divisions that takes place during the development of this organism has allowed the complete cell lineage to be determined from the fertilized zygote to the mature adult (Sulston 1983; Sulston *et al.* 1983). Each differentiated cell type that is produced at the terminal twigs on the lineage tree is now known. Laser ablation studies have given some insight into the degree of cell autonomy that is involved in determining the pattern of cell divisions and differentiations that occur. Generally it seems that, in *C. elegans*, cells behave fairly autonomously during development, although there are several well-defined instances where regulative cell–cell interactions have been demonstrated (Sulston & White 1980; Kimble 1981).

C. elegans was originally selected as an organism worthy of extensive developmental studies, partly because it is readily amenable to genetic analysis. Many mutants have been isolated and mapped (Brenner 1974). The mutants that have been isolated exhibit a wide variety of phenotypes: some are morphological, some affect various aspects of development and many exhibit aberrant behaviour. Some of the behavioural mutants have been shown to have defects in muscles (Waterston *et al.* 1980), but many probably have alterations in the nervous system (Lewis & Hodgkin 1977; Chalfie & Sulston 1981; Hedgecock *et al.* 1984). It is hoped that a detailed knowledge of the structure of the wild-type nervous system of *C. elegans* will facilitate the interpretation of the changes that occur in such mutant nervous systems. This may in turn shed some light on the genetic control of the developmental processes that ultimately give rise to the specifically interconnected group of neurons that make up a nervous system.

The reconstructions that are presented in this paper describe the connectivity of all the neurons in the nervous system of the *C. elegans* hermaphrodite except those in the pharynx, which have been described by Albertson & Thomson (1976). The detailed morphologies of the sensilla in the head have been described by Ward *et al.* (1975), Ware *et al.* (1975) and Wright (1980); the structure of the ventral cord has been described by White *et al.* (1976) and an independent reconstruction of the tail ganglia has been described by Hall (1977). Together these papers give a fairly complete description of the connectivity, topography and ultrastructure of the nervous system in the hermaphrodite. The *C. elegans* male has a more extensive nervous

system than that of the hermaphrodite; most of the 'extra' nervous tissue is situated in the tail. A partial reconstruction of the nervous system in the male tail has been described by Sulston *et al.* (1980).

The structure of the ventral cord of *Ascaris* has been deduced from reconstructions of light micrographs of serial sections (Stretton *et al.* 1978). In spite of the enormous difference in size between these two nematodes (10 cm as against 1 mm for *C. elegans*), the motoneurons in the ventral cord turn out to be remarkably similar, and it has been possible to identify equivalent motoneuron classes in the two animals. The large size of *Ascaris* enables electrophysiological techniques to be used in the study of its nervous system. Such studies have identified inhibitory and excitatory classes of motoneuron and have shown that acetylcholine is the neurotransmitter used by the excitatory motoneurons (Johnson & Stretton 1980). The small size of *C. elegans* precludes such electrophysiological studies but, by analogy, these results may be related to the equivalent neurons in *C. elegans* and so provide clues as to their functional properties.

Although reconstructions of nervous tissue from electron micrographs can in principle identify all focal synaptic contacts, it is unlikely that the pattern of connectivity obtained would exactly represent the functional synaptic connections between neurons. There is evidence that synaptic transmission mediated by some peptide transmitters acts over a considerable range (Jan *et al.* 1983), suggesting that these types of synapses may not be localized at discrete focal contacts and therefore would not be seen in electron micrographs. There are other routes by which transmission of information could occur between neurons which are not apparent from reconstructions. Neurohumoral transmission is probably used for transmission over long distances and where many targets may be involved; a good candidate for a neurosecretory neuron has been found in the pharynx (Albertson & Thomson 1976). Short-range transmission may occur by means of electrical leakage currents or by capacitive coupling between processes that run alongside each other for long distances. However, in spite of these limitations, high-resolution reconstructions provide a wealth of information on the synaptic contacts between neurons. Thus, of all the currently available techniques, such reconstructions probably provide the most comprehensive picture of the synaptic circuits of a nervous system such as that of *C. elegans*.

Because of the large amount of information that is involved in presenting the connectivity data, we have tried to organize its presentation in such a way as to facilitate quick access. The structure of a 'canonical' nervous system is presented, which is in fact a mosaic of several nervous systems. A general description is first given of the structure of *C. elegans* and some of the salient features of the nervous system. This is followed by a detailed description of each of the neuron classes arranged in alphabetical order in Appendix 1. These descriptions are fairly self-contained and include morphological as well as synaptic data. There are many references in the first section to illustrations in Appendix 1. These appear as the class name followed by a letter, e.g. ASE-a. The lower case letter indicates the diagram referred to in the description of the neuron class ASE.

Materials and methods

The reconstructed nervous systems described in this study were all derived from the nematode *Caenorhabditis elegans* (var. Bristol); these were cultured on lawns of *E. coli* grown on agar Petri plates (Brenner 1974).

Electron microscopy

Worms were rinsed off Petri plates and fixed in 1% osmium tetroxide in 0.1 M sodium phosphate, pH 7.4 for one hour at 20 °C. Pre-fixing in glutaraldehyde was not done in this work because, although this method gives better preservation of fine structure, we found that osmium alone gave better contrast to cell membranes, and this facilitated the resolution of process outlines in regions of dense neuropile.

After fixation, the worms were spread on a thin layer of 1% agar and cut in half. The cut worms were covered with a drop of molten 1% agar, and blocks of agar containing a single half worm were cut out. These were dehydrated through a graded series of alcohols to propylene oxide, then to propylene oxide plus Araldite (CY 212 resin, CIBA Ltd.) and then into Araldite at room temperature overnight. The following day they were transferred to fresh Araldite and polymerized in gelatin capsules overnight at 60 °C.

An LKB ultratome III was used with a diamond knife to cut transverse serial sections of approximately 50 nm thickness. Ribbons of sections were generally picked up on Formvar coated 75-mesh copper grids. The sections in the region of the head, where most of the nervous system is situated, were picked up on slot grids, as it was found to be necessary to have every section in this region for successful reconstructions. Grids were stained with a 5% aqueous solution of uranyl acetate for 10 min at 60 °C and then with lead citrate for 5 min at room temperature according to the procedure of Reynolds (1963). Sections were photographed on cut film with an AEI 6B or an AEI 802 electron microscope. Most reconstructions were done directly from prints of micrographs of nervous tissue. In the region of the nerve ring, four-way montages were necessary; in other regions, single prints were sufficient. Every section was photographed in the region of the nerve ring and other areas of dense neuropile: photographs of every third section usually sufficed for following process bundles. Some use was made of a computer-aided reconstruction system described by White (1974) and Stevens & White (1979), but most of the reconstructions were done by hand from a total of about 8000 prints.

Small groups of processes were given arbitrary labels, which were written onto the prints with Rotring drafting pens. These labels were carried through all the pictures in which the associated processes were present, and this procedure was repeated until all process profiles were labelled. Processes could then be joined to other processes where branches had occurred, or ultimately be assigned to particular neurons if their cell bodies were within the scope of the reconstruction. When all the labelling was completed, each process was individually followed through every section in which it appeared, and a list was compiled of all the synaptic contacts that it made. In this way all synaptic contacts were recorded twice, once for each member of an interacting pair of processes. This provided a useful check on synapse scoring as any synaptic contact that was only scored once was reappraised.

The reconstructions were done piecemeal with data from five overlapping series; these were designated N2T, N2U, JSH, N2Y and JSE (figure A1, Appendix 1). The structure was found to be sufficiently invariant for equivalent processes and cell bodies to be identified in the region of overlap of two series. The N2T series was the first extended series to be cut in the head; the reconstructions of the head sensilla described by Ward *et al.* (1975) were based on this series. Although this series extended through the nerve ring and into the ventral cord, mesh grids were used and it was found that the inevitable occasional section loss, through obscuration by grid bars, allowed only a limited reconstruction to be done of these regions. The N2U series was

from an old hermaphrodite that gave good quality pictures. It was sectioned on slot grids through the nerve ring and anterior ventral cord and a complete reconstruction of this region was obtained. This series also covered more than half the body length of the animal and enabled the anterior ventral and dorsal cords to be reconstructed. The JSH animal was a fourth stage (L4) larva, which was sectioned on slot grids. A complete reconstruction of the nervous system in the nerve ring and anterior ventral cord was obtained from this animal. This allowed the structure deduced from the N2U series to be validated in these regions, which are the most difficult to reconstruct because they contain dense neuropile with many processes that run close to the plane of sectioning. Few significant differences in structure that could be age-related were seen between the N2U and JSH series. The tail ganglia and some of the posterior ventral and dorsal cord were covered in the JSE reconstruction. The region between the anterior extremity of the JSE series and the posterior extremity of the N2U series has not been reconstructed in a hermaphrodite. A long series that overlapped at both ends, designated N2Y, was obtained from a male animal (Sulston *et al.* 1980, in which it was referred to as series 4). The motoneurons of the ventral cord and the cells from the posterior lateral ganglion were reconstructed from this animal. The motoneurons (with the exception of the sex-specific VCn class) exhibited essentially the same synaptic behaviour as their anterior counterparts in the hermaphrodite. As there was also no reason to expect any sex-related differences in the cells of the posterior lateral ganglia, these data were incorporated to enable a complete reconstruction of the whole nervous system to be obtained. The structure that is described is a composite that has been derived from all these series except JSH.

Reliability of data

The biggest problem that was encountered in the course of the reconstruction work was the location of errors. Errors were generally made in one of three ways. (1) The most prevalent was human error, which would occur when following long featureless process bundles and which typically resulted in switches in process labels. (2) Many processes run close to the plane of sectioning in the vicinity of the nerve ring, with the result that the membranes of these processes would often be cut obliquely and give indistinct images. This made process identification very difficult in such situations, leading to the second most prevalent source of errors. (3) Similar errors of process identification also occurred in regions of poor image quality caused by dirt on sections or loss of sections on grid bars although, surprisingly, this was the least prevalent source of errors.

Errors generally manifested themselves by the appearance of an improbable structure, such as a process that was joined to more than one cell body or conversely not joined to any at all. Much of the nervous system was found to be bilaterally symmetrical; some of the sensory receptors in the head have higher levels of symmetry. Any deviations that were seen from expected symmetries were considered suspect. Errors were located either by exhaustive searching of every section that contained the process that was in question, or by looking at the reconstructions for discontinuities in synaptic behaviour, and then closely checking the regions of the process where the discontinuities occurred. In this way a complete, self-consistent structure was built up. The structures of the major regions of neuropile have been validated by separate reconstructions; the JSH series in the case of the nerve ring and the N2S series in the case of the ventral cord (White *et al.* 1976). Hall has undertaken an independent reconstruction of the tail ganglia; the structure that he describes is essentially the same as the structure that we describe here (Hall 1977).

We are reasonably confident that the structure that we present is substantially correct and gives a reasonable picture of the organization of the nervous system in a typical *C. elegans* hermaphrodite. It is likely that in the elaboration of a structure of this complexity that a few small errors might have crept in, but we feel that these may be quite limited because of the amount of cross-checking that was done. A few minor ambiguities still exist, however, which would require a considerable effort to clear up. These are described in Appendix 2.

Nomenclature

We have adopted a uniform system of nomenclature for naming the neurons and associated cells of *C. elegans*. Unfortunately it was not practicable to make such a system compatible with the various nomenclatures that have been used up till now. Appendix 3 lists the equivalences between these systems and the one used in this study.

Neurons are given arbitrary names consisting of three upper case letters. The last letter can alternatively be a number of up to two digits. Additional symmetry descriptors are added to the name in the cases of groups of cells that are in the same class and related to each other by simple geometric symmetries. These descriptors are D or V (dorsal or ventral) and L or R (left or right). A group of cells with six-fold symmetry, such as IL1, has as its members: IL1DL, IL1DR, IL1L, IL1R, IL1VL and IL1VR. The members of the classes of motoneuron in the ventral cord do not have these symmetrical relations with each other. In these cases, the third digit of the class name is a numeral, which represents the anterior or posterior location of the neuron relative to its fellow class members; for example, VA3 is the third VA motoneuron. The use of the three-letter name without descriptors implies all members of the class if there is more than one. For the motoneurons, a lower case n is used in the third digit position to represent the generic name for all class members (for example, VAn).

A slight modification of this system is used to describe the associated cells of sensilla, i.e. the sheath and socket cells. A sheath cell is designated by 'sh' and a socket cell 'so'. Thus in the case of the right sub-dorsal cephalic sensillum, the neuron is referred to as CEPDR, the sheath cell as CEPshDR and the socket cell as CEPsoDR.

General description of *C. elegans*

C. elegans is a small, free-living, soil nematode worm. It has a generation time of about 3.5 d and grows to a length of 1.3 mm and a diameter of 80 μm if there is a plentiful supply of food. It is a self-fertilizing hermaphrodite, one animal generally giving rise to about 300 offspring. Occasionally, at a frequency of about 1 in 10^3, a male is produced, which is capable of mating with the hermaphrodites. *C. elegans* can easily be cultured in the laboratory on bacterial lawns grown on an agar substrate. Mutations may be readily produced by a variety of mutagens and will segregate out as homozygous clones without having to set up back-crosses. These characteristics make the animal very amenable to genetic analyses, and many behavioural and morphological mutants have been mapped (Brenner 1974; Swanson *et al.* 1984).

Behaviour

The animals pass through four larval stages before reaching adulthood: L1, L2, L3 and L4. Each stage is terminated by a moult. If food is scarce, animals can go through an alternative developmental sequence in which a resistant 'dauer' larval form is produced at the L2 to L3 moult. Dauers can survive extreme conditions (desiccation and lack of food) for long periods

until conditions improve and food becomes available, at which time they will moult and become normal adults (Cassada & Russell 1975; Riddle *et al.* 1981). Several structural changes occur on entering the dauer stage, including alterations to the endings of some sensory receptors (Albert & Riddle 1983).

C. elegans normally inhabits the interstices between damp soil particles or in rotting vegetation. It lives in a film of water and is held to solid surfaces by surface tension. Locomotion is achieved by dorso-ventral flexures of the body, which give rise to sinusoidal wave propagation along the length of the body. This can either be in the anterior-to-posterior direction, giving rise to forward motion, or in the posterior-to-anterior direction, giving backward motion. The head has an extra degree of freedom, in that it can make lateral as well as dorso-ventral movements. The dorso-ventral flexures (with the consequential sinusoidal posture of the body), combined with the surface tension forces, constrain the animals to lie on their sides. The L1, dauer and adult stages have longitudinal lateral ridges of cuticle, the alae, which may act to increase lateral friction and minimize sideslip. The thickness of the water film is quite critical; too thin or no water film results in the animals' becoming desiccated and dying, whereas if the film is greater than their diameter they are not held down to the surface and are unable to make any progress. *C. elegans* can move well on an agar surface even though this must be quite different from its normal habitat. If there is no food available locally it will move forward for quite long periods with occasional short intermissions of reversing. When it locates food it starts eating and stops moving, except for short foraging excursions forwards and backwards. Eggs tend to be laid only when the hermaphrodites have a plentiful food supply.

C. elegans responds in a regulated manner to a number of sensory stimuli: it will chemotax up a gradient of chemical attractant or down a gradient of repellant (Ward 1973; Dusenbery 1974); it will avoid regions of high osmolarity (Culotti & Russell 1978); it will actively maintain itself at an optimum temperature in a temperature gradient (Hedgecock & Russell 1975) and it will respond to light touch by moving away from the point of stimulation (Chalfie & Sulston 1981). In addition to these responses, the worm presumably uses its mechanosensory system to navigate through the interstices between soil particles in its natural habitat. Mating-specific behaviour is exhibited only by the male (Hodgkin 1983), which has additional neural circuitry in the tail for controlling copulation (Sulston *et al.* 1980).

Structure

The animal is ensheathed in a tough impermeable elastic cuticle, which is laid down by a system of underlying hypodermal cells. The body cavity (the pseudocoelome) is maintained at a high hydrostatic pressure relative to the outside; it is this pressure, acting on the elastic cuticle, which gives the animal its rigidity (the so-called hydrostatic skeleton (Crofton 1966)).

There are four longitudinal ridges running down the inside of the body cavity: two medial and two lateral. These ridges consist of a ridge of hypodermis adjacent to a bundle of nerve processes, the whole structure being bounded by a basal lamina. Body movements are mediated by four strips of muscle cells running in four quadrants between these longitudinal ridges. Muscle cells have no obvious attachment points at either end and probably have attachments to the hypodermis distributed along their length. They act to deform the cuticle elastically against the stress produced by the turgor pressure.

Food is pumped into the animal and processed by a prominent pharynx. This is a virtually self-contained organ with its own musculature, epithelium and nervous system, and has been described in detail by Albertson & Thomson (1976). The pharynx probably functions as a

largely autonomous unit, although there are two interneurons that originate in the central nervous system and enter it. These interneurons (RIP) are exclusively postsynaptic outside the pharnyx and so probably mediate the overall control of pharyngeal pumping from the central nervous system. The pharynx is used for ingesting food (usually bacteria), concentrating it by filtration and then grinding it, and probably also for secreting digestive enzymes from its gland cells (Albertson & Thomson 1976). The processed food is pumped into the intestine, which has a lumen lined with microvilli. The intestine is connected with the anus; defecation is controlled by three sets of specialized muscles (figure 12).

There is an excretory system, which consists of a single excretory canal cell arranged in an 'H' configuration (Bird 1971). The two arms of the H run longitudinally down the lateral lines. These are joined by a cross bridge, which is connected to the excretory duct on the ventral side; this opens to the outside of the animal via the excretory pore situated on the ventral mid-line. Two ventrally situated 'gland' cells have anteriorly directed processes, which fuse and connect to the lumen of the excretory canal near the pore (Nelson *et al.* 1983). These processes continue running anteriorly on the ventral surface of the ventral nerve cord (figure 16) until the nerve ring is reached, where they terminate. The function of these glands is not yet known.

The adult hermaphrodite reproductive system consists of symmetrical pairs of uteri, oviducts, spermathecae and ovaries, which are joined at the uteri and connect to a vulva. This is situated on the ventral mid-line about halfway down the body (Hirsh *et al.* 1976). During development, sperm are produced before oocytes and are stored for subsequent use. Egg-laying is mediated by a set of sixteen muscle cells, eight of which act to squeeze the contents of the uteri and eight to open the vulval orifice (figure 11).

The male gonad joins the rectum via the vas deferens to form a cloaca in the tail (Sulston *et al.* 1980). The cloaca is surrounded by a large, fan-like, copulatory bursa, which is richly endowed with sensory endings. These endings are derived from male-specific neurons, which are generated post-embryonically along with other neurons in the male. The male also has extra ventral body muscles and muscles that control the copulatory spicules (Sulston *et al.* 1980).

The nervous system

Organization of the nervous system and musculature

There are 302 neurons in the nervous system of *C. elegans*; this number is invariant between animals. Each neuron has a unique combination of properties, such as morphology, connectivity and position, so that every neuron may be given a unique label. Groups of neurons that differ from each other only in position have been assigned to classes. There are 118 classes that have been made using these criteria, the class sizes ranging from 1 to 13. Thus *C. elegans* has a rich variety of neuron types in spite of having only a small total complement of neurons. This is in marked contrast to structures such as the mammalian cerebellum, which contains more than 10^{10} neurons (Braitenberg & Atwood 1958) and yet has only five classes of component neuron (Eccles *et al.* 1967).

Sensory transduction

The bulk of the nervous system of *C. elegans* is situated in the head, which is richly endowed with sensory receptors. These are arranged in groups of sense organs, known as sensilla. The arrangement and structure of sensilla have been described in detail (Ward *et al.* 1975; Ware

et al. 1975; Wright 1980). Each sensillum contains one or a number of ciliated nerve endings and two non-neuronal cells: a sheath cell and a socket cell. A socket cell is effectively an interfacial hypodermal cell acting to join the sensillum to the hypodermis. A sheath cell is a glial-like cell that envelops the endings of neurons. Its inner surface, adjacent to the neural dendrite, is extensively invaginated and large number of secretory-like vesicles are often present in the cytoplasm. The sheath cells of the cephalic sensilla have, in addition, flat sheet-like processes that partly envelop the neuropile of the nerve ring and the anterior extremity of the ventral cord (figure 16). The function of sheath cells is not known, but they probably act to establish a defined extracellular milieu for the receptor endings.

Two large sensilla, the amphids, are located laterally and have internal channels, formed by the sheath and socket cells, which open through the cuticle to the outside. Eight neurons have their ciliated endings in this channel; a further four are associated with the sheath cell. There are two analogous structures, the phasmids, in the tail, but they are simpler in that they only have two neurons ending in the channel. The amphids and phasmids are generally considered to be the main chemoreceptive organs in the animal, because their structure permits a group of nerve endings to be exposed to the external environment of the animal.

The other sensilla in the head are arranged into two concentric rings around the mouth (figure 1). There is an inner ring of six, the inner labial sensilla, each of which has two associated neurones (II1 & IL2). The dendrites of IL2 penetrate the cuticle to the outside of the animal and so they could be chemoreceptors. The other ending (IL1) lies embedded in the cuticle. There is an outer ring of four sensilla, the quadrant outer labials (OLQ), and these are paired with another set of four, the cephalic sensilla (CEP). Two additional lateral outer labial sensilla (OLL) are situated next to the amphid channel openings. The only other sensilla in the hermaphrodite are two pairs of lateral sensilla, the deirids, situated laterally in the anterior body (ADE) and the posterior body (PDE). These sensilla have similar morphologies to the cephalic sensilla in the head (Ward *et al.* 1975).

In addition to the neurons of the sensilla there are other classes of neuron, which, on the basis of their connectivity and morphology, also probably serve a sensory transduction function. The best characterized neurons of this type are the touch receptors ALM, PLM, AVM and PVM. These have specialized, microtubule-filled processes, which run in close apposition to the hypodermis (Chalfie & Sulston 1981).

Disposition of cell bodies and ganglia

Several ganglia have been described and named in the nervous systems of other nematodes (Chitwood & Chitwood 1974). We have retained these names, where appropriate, for the ganglia in *C. elegans*. In several regions, cells are grouped together into well-defined ganglia by the arrangement of the basal lamina in the pseudocoelome. This sometimes results in adjacent cells' being partitioned into different ganglia. The lateral and ventral ganglia are not obviously separated in figure 2, for example, but in fact the cells of the ventral ganglion are a well-defined group (figure 3), being separated from those of the adjacent lateral ganglia by two basal laminae (figure 13). The arrangement of the basal lamina around the pseudocoelome will be discussed later; we will now describe the disposition of the various ganglia.

Most of the neurons of *C. elegans* have their cell bodies situated in the head around the pharynx (figure 2). The pharynx is composed of two prominent bulbs joined by an isthmus. An extensive region of neuropile, the circumpharyngeal nerve ring, encircles the centre region

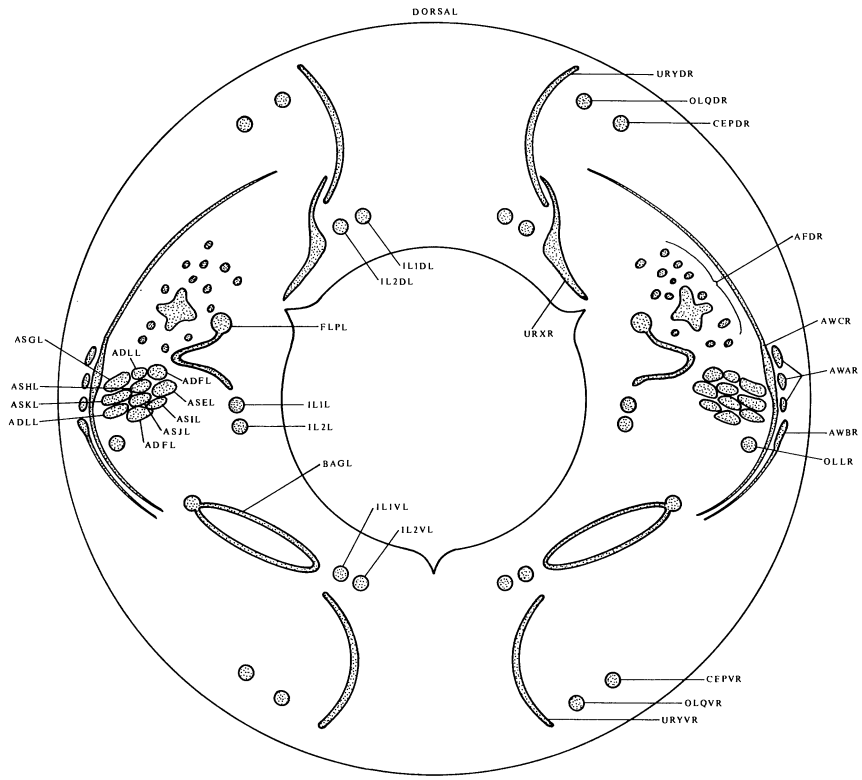
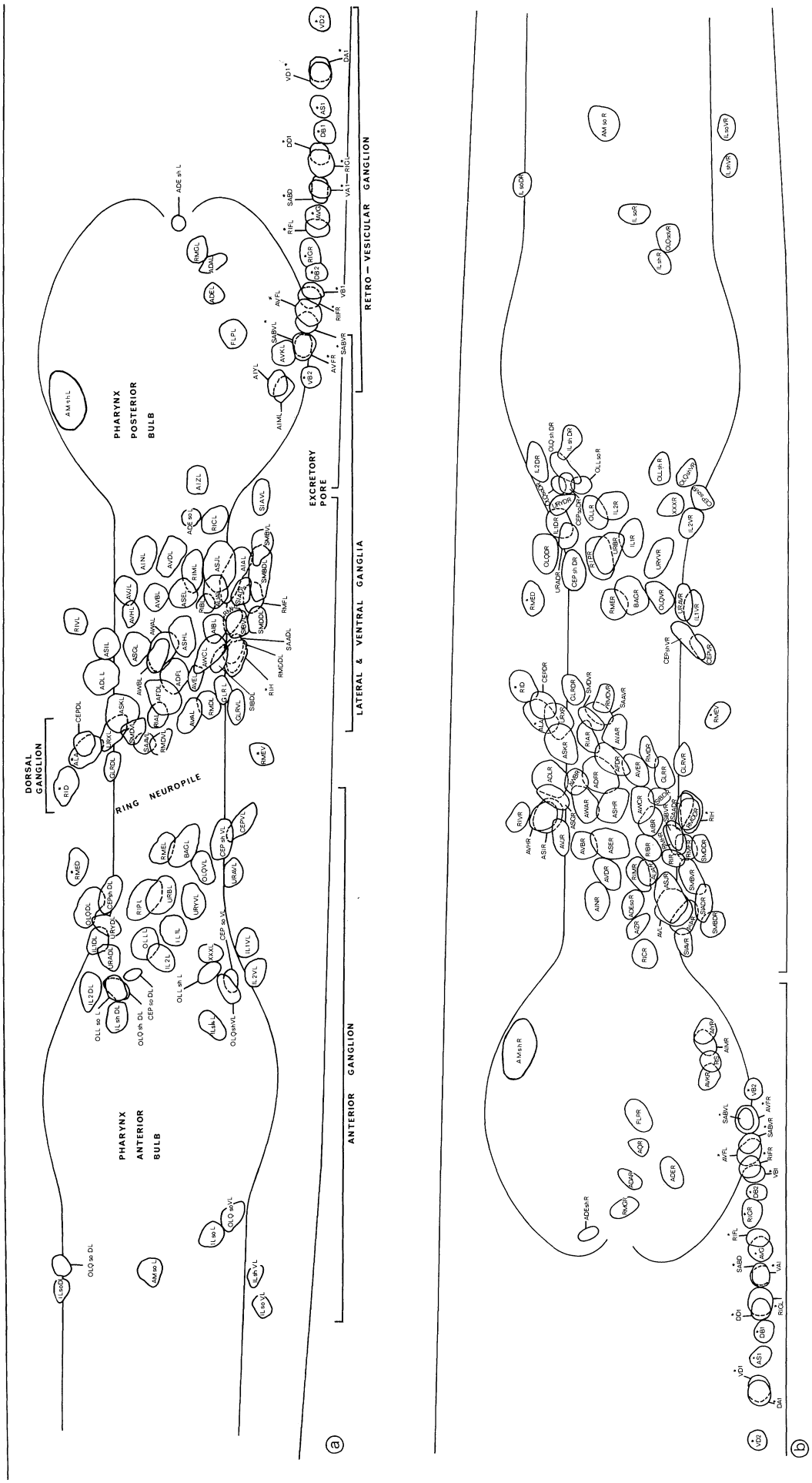


FIGURE 1. Sensory receptors in the head, as seen in an idealized section near the tip of the head. This region is richly endowed with sensory receptors, which are organized in a precise, complex arrangement. Most of the receptors are components of sensilla, and have associated sheath and socket cells. The amphid sensilla are situated in the lateral labia and have channels that are open to the outside with ADL, ADF, ASG, ASH, ASE, ASI, ASJ and ASK entering them. AWA, AWB, AWC and AFD are associated with the amphid sheath cells. There is a single inner labial sensillum in each labium, containing IL1 and IL2 receptor neurons. These sensilla also have channels to the outside, through which the processes of IL2 project. The two dorsal and the two ventral labia each have a single cephalic sensillum with a CEP receptor, and a single outer labial sensillum with an OLQ receptor. The lateral labia also each have an outer labial sensillum but with an OLL receptor. FLP and BAG are ciliated receptors that are free inside the head and are not part of a sensillum. URX and URY are not ciliated but have specialized flattened endings, which insinuate themselves around the inner and outer labial sensilla.

of the isthmus and has cell bodies clustered adjacent to it both anteriorly and posteriorly. There are no obvious subgroupings of the neuron cell bodies anterior to the ring and so these have been lumped together and referred to as the anterior ganglion. The anterior ganglion is mainly made up of the cell bodies of neurons, sheath cells and socket cells from the sensilla that are located in the six labia of the head (figure 1). The relative positions of cell bodies within ganglia are fairly well conserved between animals of the same developmental stage and genotype. There is a certain amount of 'slop', however; the extent of this can be seen by comparing the left and right sides illustrated in figure 2. The most extreme cases of variability in this region arise because the anterior bulb of the pharynx fits fairly tightly in the body cavity and excludes cell bodies from its region of maximum diameter. This leads to some uncertainty in the position of some cell bodies with respect to the bulb; for example, in the N2U reconstruction, OLQsoDL lies anterior to the bulb, whereas its symmetrical partner, OLQsoDR, lies posterior to the bulb (figure 2). In live animals, cells can sometimes be seen to flip from one side of the anterior bulb to the other as the pharynx moves.


DORSAL GANGLION
RING NEUROPILE
PHARYNX ANTERIOR BULB
PHARYNX POSTERIOR BULB
EXCRETORY PORE
LATERAL & VENTRAL GANGLIA
ANTERIOR GANGLION
RETRO-VESICULAR GANGLION
a
b

Posterior to the nerve ring, the basal laminae split the cell bodies adjacent to the ring into four groups (figure 13): a small dorsal ganglion, two lateral ganglia, and a ventral ganglion (figure 3). All receptor neurons of the amphid sensilla have their cell bodies in the lateral ganglia, which also contain cell bodies of motoneurons and interneurons. The dorsal ganglion contains interneurons together with the neurons of the two dorsal cephalic sensilla. The ventral ganglion contains interneurons and motoneurons. The cell bodies of the ventral ganglion are separated into two groups (figure 3) by a mechanical intrusion, as are the cells of the anterior ganglion. In this case it is the excretory duct and canal that displaces the cells.

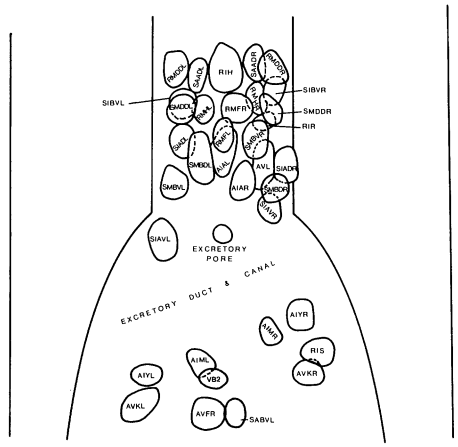


FIGURE 3. View of the ventral ganglion. The cells of the ventral ganglion are bounded by a basal lamina, which separates them from cells of the lateral ganglia even though they are adjacent (figure 2). The posterior region of the ganglion is interrupted by the presence of the excretory duct and excretory canal cells, which exclude the cell bodies of neurons from this region. VB2, AVFR and SABVL are part of the retro-vesicular ganglion and are separated from the cells of the ventral ganglion by a basal lamina. All the cells of the ventral ganglion project into the nerve ring, and several of the cell classes present also have members in the lateral ganglia.

The posterior extremities of the ventral ganglion overlap the anterior of the retrovesicular ganglion, which is situated on the ventral mid-line posterior to the excretory pore (figure 2); however, the two groups of cells are distinct, being separated by basal laminae. A single row of cell bodies runs down the ventral mid-line (figure 4) from the retro-vesicular ganglion to the tail, where it ends in another ganglion, the pre-anal ganglion. There are three extra ganglia in the tail: two laterally symmetric lumbar ganglia and a single, small dorso-rectal ganglion (figure 5). There is a pair of small lateral ganglia in the posterior body, the posterior lateral ganglia, and there are some isolated cells along the body laterally (figure 4).

The anterior ganglion, the ventral ganglion and the dorso-rectal ganglion are completely

---

DESCRIPTION OF FIGURE 2

FIGURE 2. The locations of the cell bodies of all the neurons and their associated cells in the head is shown in left-hand (a) and right-hand (b) views. Cells marked with an asterisk are on or near the centre line and are shown in both views. These diagrams were derived from reconstructions of electron micrographs of one animal and, because of the difficulty of accurately measuring section thickness, there may be some longitudinal distortion. This is not excessive, however, as the overall longitudinal scale was normalized to views taken from the light microscope. The anterior bulb of the pharynx fits tightly in the body hypodermis and excludes cell bodies in the region of its maximum diameter. Cell bodies that are in this region are sometimes indeterminate as to which side of the bulb they reside, as in OLQsoDL/R. The neuropile of the nerve ring also excludes cell bodies and gives rise to the bare region around the isthmus of the pharynx.

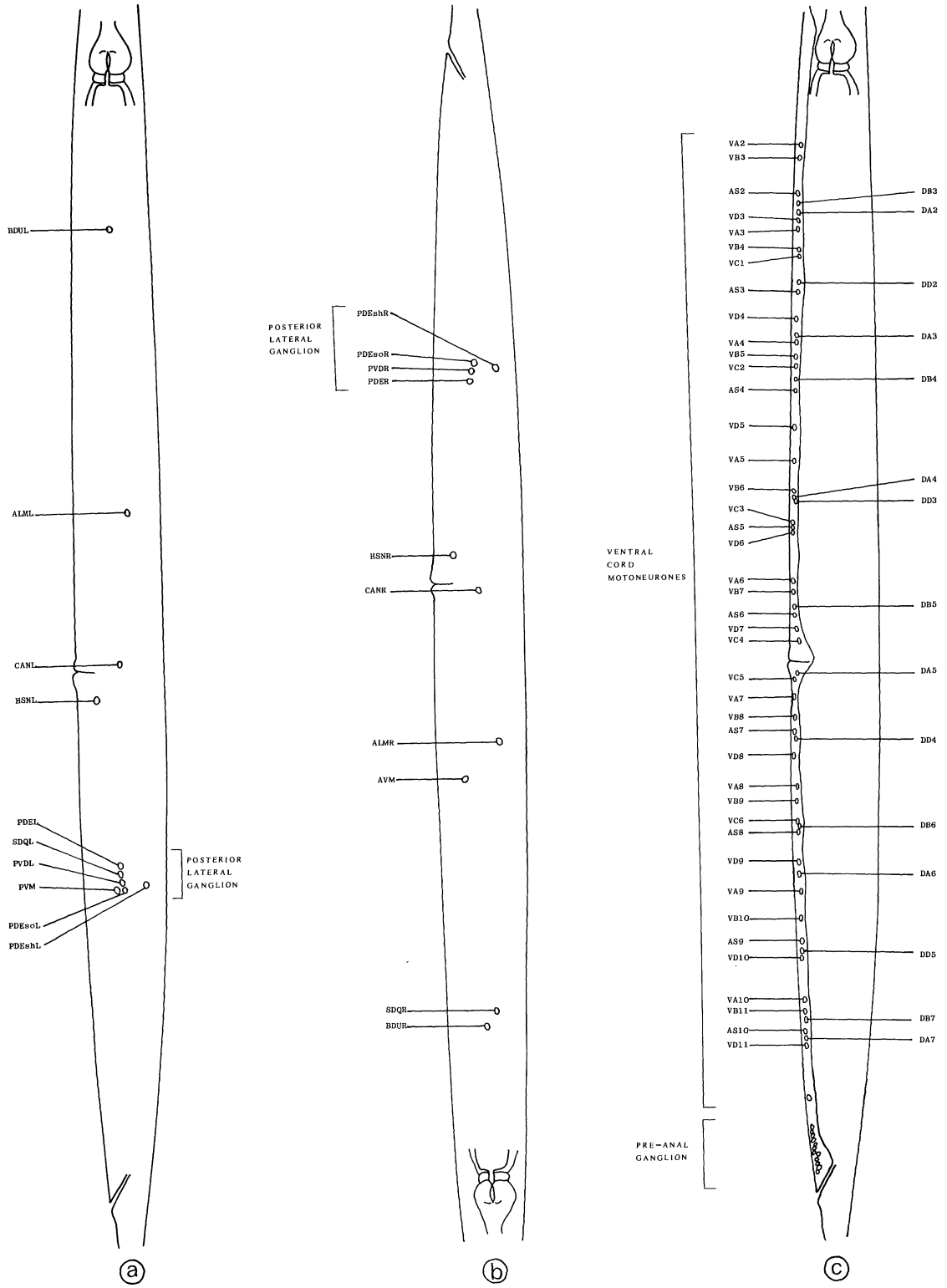
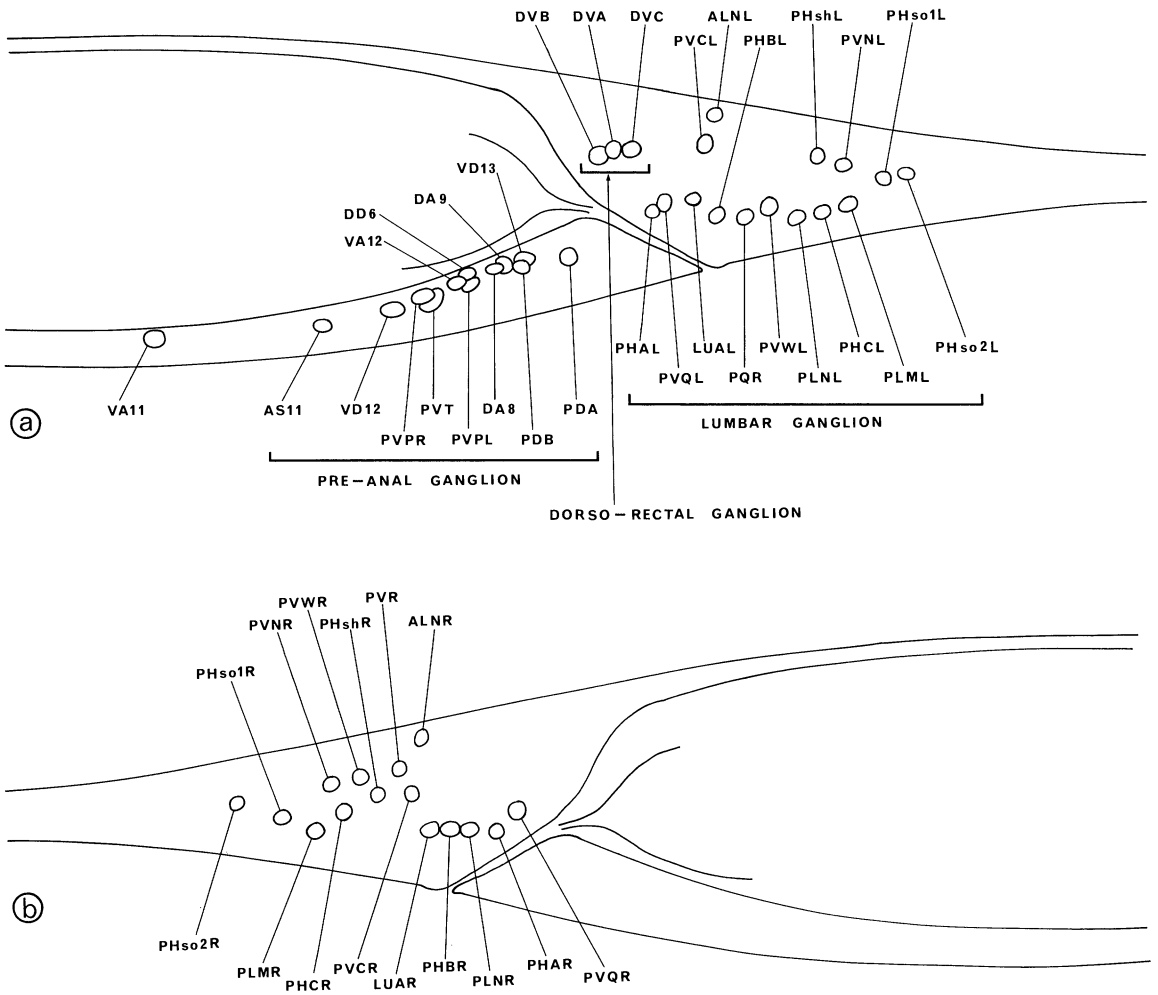


FIGURE 4. For description see opposite.



bounded; that is, they have clear structurally defined limits to their extents. The others are 'open' in that there are no specific boundaries at one end. The retrovesicular ganglion is open and continuous with the region containing the motoneurons of the ventral cord, which in turn is open and continuous with the pre-anal ganglion. Similarly, the lateral ganglia are open and continuous with the isolated cells on the lateral lines, the posterior lateral ganglia and the

Description of figure 4

Figure 4. The locations of the cell bodies of all the neurons and their associated cells in the body are shown on the left-hand side (a), the right-hand side (b) and the middle (c). These diagrams were derived from light microscope observations (Sulston & Horvitz 1977). The asymmetries in the positions of SDQL/R, AVM and PVM are a consequence of the different migration patterns of the initially bilaterally symmetric precursor cells QL and QR. The ventral cord motoneurons shown in (c) can be separated into those that are present at hatching, shown by the labels on the right, and those that develop postembryonically, shown by the labels on the left. The anterior–posterior sequence of cell types in these two groups is always the same, but there is some slight variation in the way the two groups intercalate, giving some variation in the combined adult sequence.

lumbar ganglia. Thus the body has three main compartments where neuron cell bodies are located, two lateral and one ventral.

There seem to be no functional correlates to the groupings of cells into particular ganglia. Often cells are more analogous, in structure and connectivity, to cells in other ganglia than to cells in the same ganglia. Ganglia simply seem to be local groupings of cell bodies brought about by extraneous mechanical factors.

Disposition of process tracts

The nervous system of *C. elegans* is made up of a set of interconnected parallel process bundles. These run either longitudinally or circumferentially, adjacent to hypodermal tissue (figures 6 and 7). The two sub-dorsal and the two sub-ventral labia at the tip of the head each have a single process bundle associated with them. This is made up of processes from the sensilla in the labium, together with other processes that terminate near the sensilla but have no differentiated endings. The lateral labia have similar process bundles but, in addition, each has a larger process bundle made up of processes of the neurons of the amphid sensilla. Most of the processes in the six non-amphidial bundles have associated cell bodies, which are situated in front of the nerve ring in the anterior ganglion. Individual processes peel away from the bundle to join their (bipolar) cell bodies. A second, posteriorly directed process emanates from the cell body and rejoins the process bundle, running in the same region of the bundle as its anteriorly directed counterpart. The six labial process bundles run posteriorly past the outside of the nerve ring and then turn to enter the nerve ring near its posterior face (figure 6). The processes in the amphid bundle bypass the ring completely and run to their (bipolar) cell bodies, situated in the lateral ganglia. Axonal processes from these cell bodies, along with processes from monopolar cell bodies of interneurons and motoneurons, enter the nerve ring via two main routes. Cells in the ventral region of the lateral ganglia have processes that join the amphidial commissures; these run circumferentially round the animal, between muscle and hypodermis, to the ventral mid-line, where they turn and enter the nerve ring. Cells in the dorsal regions of the lateral ganglia do not take this somewhat circuitous route but enter the nerve ring directly sub-dorsally.

The circumpharyngeal nerve ring is the most extensive region of neuropile in the animal and consists of a large toroidal bundle of processes, most of which have entered the ring from the process tracts described above. The processes in the nerve ring are derived from the sensory receptors in the head, interneurons, and motoneurons that innervate head muscles via neuromuscular junctions (NMJs) situated on the inside surface of the ring. The cell bodies of both the interneurons and the motoneurons are situated in the lateral and ventral ganglia.

A large process bundle, the ventral nerve cord (figures 6–8 and 18), runs along the ventral mid-line extending from the ventral region of the nerve ring. The cord enlarges in this region because additional processes are joining it from the amphid and deirid commissures (figure 6). The excretory duct splits the process bundle of the cord into two nearly equal parts as it opens to the outside of the posterior end of the ventral ganglion. A single line of motoneuron cell bodies is situated along the ventral mid-line (figure 4), closely apposed to the process bundle (figure 18). These motoneurons innervate body muscles; some innervate ventral muscles and others innervate dorsal muscles. This latter class send processes round to the dorsal mid-line via commissures (figure 7). These then turn either anteriorly or posteriorly and together make up another process bundle on the dorsal mid-line, the dorsal cord (figures 7 and 19). The dorsal

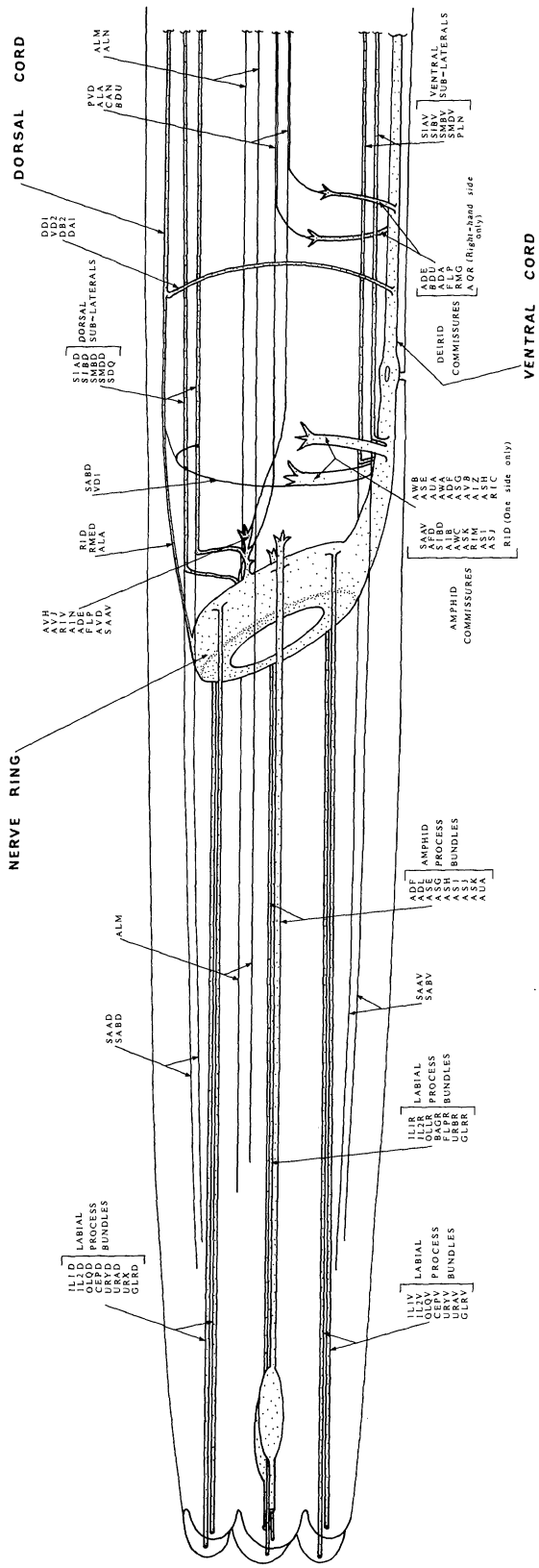


FIGURE 6. Process tracts in the head. A process from a neuron generally runs in a bundle along with the processes of other neurons. These process bundles either run longitudinally or as commissures circumferentially. The six labia at the tip of the head are richly endowed with sensory receptors. Processes from these receptors, along with those from some additional neurons, run along the labial process bundles to their cell bodies, which are situated anteriorly to the nerve ring. Posteriorly directed processes from these bipolar cell bodies rejoin the process bundles and pass along the outside surface of the nerve ring. They then turn and enter the posterior regions of the ring neuropile and move to the inside surface of the ring, and, turning again, they run to the anterior regions of the ring neuropile, where they disperse and have most of their synaptic interactions. Each lateral labium also has an amphid sensillum, and process bundles from its component neurons run posteriorly past the nerve ring to their bipolar cell bodies in the lateral ganglia. Most of these neurons send processes into the ventral cord via the amphid commissures, which then project into the nerve ring. The deirid receptors, along with several other neurons with cell bodies in the posterior regions of the lateral ganglia, send processes into the ventral cord via the deirid commissures. The ventral cord (figure 18) is the main process bundle that emanates from the nerve ring and contains processes of interneurons and motoneurons. Most of the processes in the dorsal cord originate in the ventral cord and enter the dorsal cord via commissures. There are four sub-lateral process bundles, made up of processes from motoneurons and interneurons that come from the nerve ring. These run anteriorly and posteriorly from the nerve ring and eventually end (figure 8).

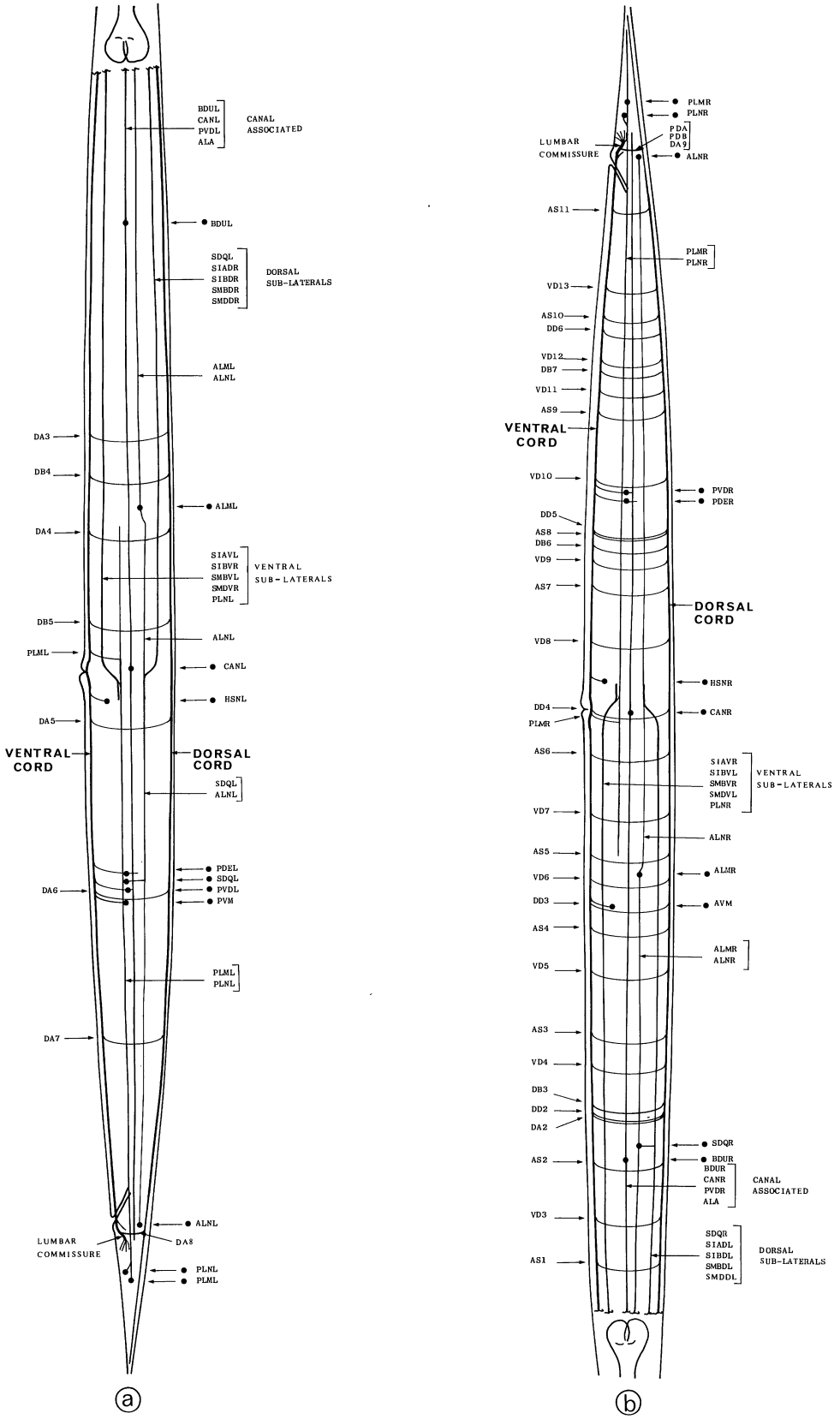


FIGURE 7. For description see opposite.

cord is predominantly made up of these motoneuron axons but, in addition, has two processes (from ALA and RID), which originate in the nerve ring and enter the dorsal cord at its anterior extremity (figure 6). The nerve ring and the ventral and dorsal cords are the only process bundles in which there are significant numbers of synaptic connections. The other distinguishing feature of these process bundles is that they all run adjacent to ridges of hypodermis (figures 13, 18 and 19). Because the hypodermal ridge is situated on the left of the process bundle, it may present a barrier on that side to commissures leaving the cord. This may be the reason why most of the commissures run round the right-hand side of the animal.

In the anterior body there are four sub-laterally situated process bundles that run underneath the body muscles (figure 6). They run in a straight line approximately corresponding to the junction of the two rows of muscles in each quadrant. There are five processes in the sub-lateral cords behind the nerve ring, and two in each of the cords in front of the ring (figure 8). The processes in the anterior cords peter out in the head; those in the posterior cord move to a more lateral position near the middle of the body, where most of them end (figure 7).

Three nerve processes run for much of the length of the animal, closely associated with the excretory canal (CAN-a). These processes run into the nerve ring at the anterior end (figure 6) and peter out posteriorly in the tail.

The only remaining process bundles in the body are those made by the lateral touch receptor neurons, ALM and PLM, and their associated neurons, ALN and PLN. The anterior touch receptors, ALM, run in close association with ALN near the dorsal margin of the lateral hypodermal ridges, whereas the posterior receptors, PLM, run along with PLN near the ventral margin of the lateral hypodermal ridges. The processes of ALN maintain their dorso-lateral location in the posterior part of the body although they are not in close association with ALM in this region.

Musculature

Nematode body muscles are unusual in that their sarcomeres have an oblique conformation with the actomyosin filaments, aligned at an angle of about 10° to the Z lines, rather than being orthogonal to them. This type of arrangement has been referred to as obliquely striated muscle (Rosenbluth 1965; Waterston *et al.* 1980). The Z lines consist of longitudinally oriented lines of discrete structures (dense bodies), which are darkly staining in electron micrographs (figure 18). These structures are roughly conical in shape; the base of the cone is adjacent to

---

DESCRIPTION OF FIGURE 7

FIGURE 7. Left-hand (a) and right-hand (b) process tracts in the body. The main process tracts are the ventral cord, the dorsal cord, the excretory canal associated processes and the posteriorly directed sub-lateral processes. The ventral cord consists of processes of interneurons and processes and cell bodies of motoneurons (figures 4 and 18). The ventral cord bifurcates at the anus and runs up to the lumbar ganglia via the lumbar commissures. The dorsal cord (figure 19) is predominantly made up of motoneuron processes that have come from the ventral cord via circumferential commissures, which are distributed along the length of the body. Most of the processes in the posterior sub-lateral cords are derived from the nerve ring. These process bundles run sub-laterally under the body muscles (figure 8) anteriorly, but move laterally to each side of the lateral hypodermal ridges where most of the processes end. Processes from SDQ and PLN run into these cords from the opposite direction from laterally situated cell bodies. The processes of CAN, ALA, PVD and also (in the anterior of the animal) BDU, run together alongside the excretory cell for most of its length. The anterior touch receptors, ALM, together with their associated neurons, ALN, run anteriorly near the dorsal side of the lateral hypodermal ridges; their posterior counterparts, PLM and PLN, run anteriorly near the ventral side of the ridges.

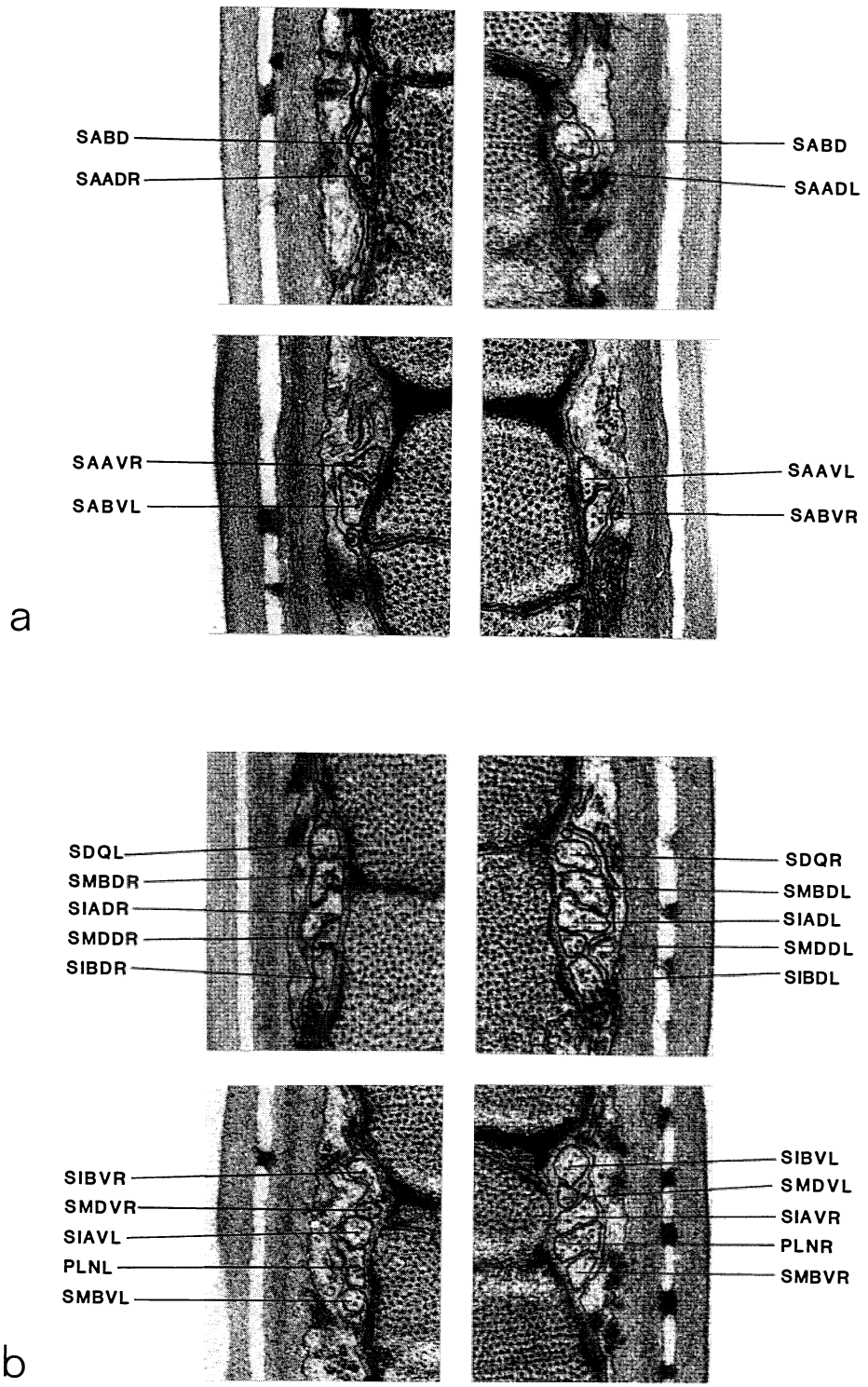


FIGURE 8. Most of the sub-lateral processes originate from the nerve ring and run longitudinally underneath the muscle quadrants close to the line of apposition of the two muscle rows. Apart from a single NMJ, no synapses have been seen on these processes. There are two processes in each of the sub-lateral cords anterior to the ring (a) and five in each of the cords posterior to the ring (b). The individual processes run in fixed positions within the cords. The posterior cords include processes from PLN and SDQ, which must have grown in the opposite direction to the others, as their cell bodies are situated laterally in the body (figure 7). Apart from the processes of these cells, the sublateral processes eventually peter out (figures 6 and 7).

the cell membrane, which is in turn adjacent to the hypodermis and cuticle. The body muscles probably have attachments to the elastic cuticle distributed along their length, since no specialized focal attachment points are seen at the end of these muscle cells.

Body muscles are rhomboid-shaped and are arranged as two parallel rows in each quadrant (figure 10). There are 95 muscle cells in the adult; the left ventral quadrant contains 23 and the other quadrants each contain 24 (Sulston & Horvitz 1977). The muscles in the body can be divided up into three groups on the basis of their source of synaptic input: the anterior group of four muscles in each quadrant, innervated by motoneurons in the nerve ring, the next group of four, which is dually innervated by motoneurons in the nerve ring and ventral cord, and the remaining muscles, which are innervated solely by the motoneurons of the ventral cord (figure 10; see also Ware *et al.* (1975)).

Motoneurons of the ventral cord innervate either both dorsal or both ventral quadrants of muscle. The body can therefore only propagate dorso-ventral waves during locomotion. The head, on the other hand, can make lateral as well as dorso-ventral movements when the animal is foraging. This is probably because the motoneurons in the nerve ring do not synapse onto two quadrants of muscles, but instead are restricted to two adjacent rows (not necessarily in the same quadrant). This would allow differential activation of muscles in adjacent quadrants and possibly even in adjacent rows.

Nematode muscles are unusual in that they have neuron-like processes that run from the muscle bellies to the neuron process bundles in which motoneuron axons reside (figures 9 and 18). Neuromuscular junctions (NMJs) are made by axons running along the surface of their process bundle, through the bounding basal lamina of the bundle and onto muscle arms (see, for example, VDn-a). Muscle arms interdigitate extensively and crowd round regions where NMJs occur; there are often gap junctions between the arms in these regions. Muscle arms in the body converge at the dorsal and ventral mid-lines, where they interdigitate and contact the dorsal and ventral cords (figure 9). Arms from the head muscles, which receive their innervation from motoneurons in the nerve ring, run down past the outside of the ring and then turn and run anteriorly, closely apposed to the inner surface of the ring. Here they sort out in such a way that arms from each muscle row make an arc of about 45° (figure 15). Thus there is a mapping by the muscle arms of the spatial organization of the muscle cells onto the inner surface of the nerve ring. Motoneuron axons run adjacent to the inside surface of the ring and are arranged in a well-ordered pattern (figure 14). The inside surface of the muscle-arm complex in the region of the NMJs is lined by the thin sheet-like processes of the GLR cells (figures 14 and 15). No chemical synapses are seen on these cells, so they are probably not neuronal; however, they do make gap junctions to muscle arms and to RME motoneurons (figure 15).

There are sixteen sex-specific muscles in the hermaphrodite; eight are associated with the uterus and eight with the vulva (figure 11). Unlike the body muscles, these muscles have focal attachment points at their ends and do not have obliquely oriented sarcomeres. The hermaphrodite gonad has twofold rotational symmetry, the axis of symmetry passing through the centre of the vulva. The uterine muscles distal to the vulva, um2, wrap round the uterus, whereas the uterine muscles proximal to the vulva, um1, attach to the lateral lines. Both sets of muscles consist of a pair of muscles that are joined at the ventral mid-line. There are two sets of four vulval muscles, vm1 and vm2. The vm1 muscles are attached to the body wall sub-ventrally, insinuating themselves between the rows of body muscles, and are attached at

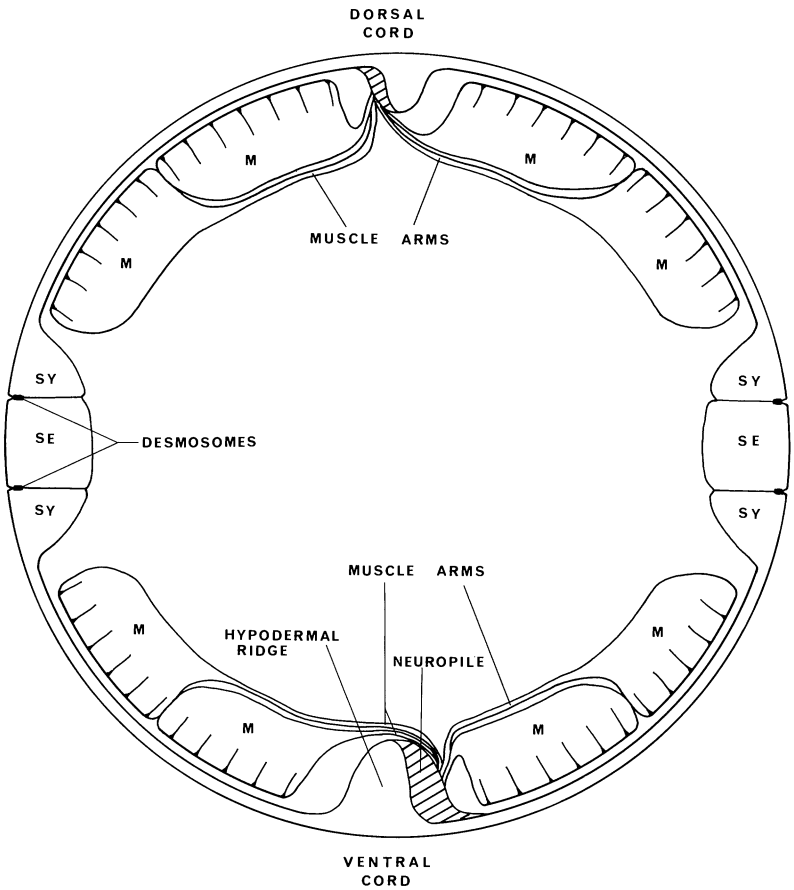


FIGURE 9. The body consists of a tube of hypodermal tissue made up of two cell types: the syncytial cell (SY), which makes up the dorsal and ventral hypodermis, and the lateral seam cells (SE), which are also syncytial in the adult and are joined to the syncytial cell by desmosomes. Longitudinal ridges of hypodermis run down the body on the lateral, dorsal and ventral lines. Process bundles that make up the dorsal and ventral cords run alongside the dorsal and ventral hypodermal ridges and are separated from the pseudocoelome by a basal lamina. The body musculature consists of four quadrants of obliquely striated muscles. Each quadrant consists of two closely apposed rows of muscle cells. The motoneurons that innervate body muscles have longitudinal unbranched processes which are confined to the dorsal and ventral cords. Muscle cells send out processes to the nerve cords, where motoneurons synapse onto them through the basal lamina at NMJs.

their proximal ends to the hypodermal lips of the vulva. The vm2 muscles attach to the body more ventrally, at the ventral margin of the muscle quadrants, and are attached at their proximal ends to the opening in the uterus, which connects to the vulva. Most of the synaptic input to the vulval muscles comes from VCn and HSN neurons and is directed onto the vm2 muscles (figure 11*c*). The other muscles are either directly or indirectly connected to vm2 via gap junctions. The vm1R muscles send a muscle arm down to the ventral cord, where it receives a small amount of synaptic input from ventral cord motoneurons.

Defecation is controlled by three sets of muscles: the anal depressor muscle, the sphincter muscle and two laterally symmetric intestinal muscles (figure 12). The anal depressor muscle is a large H-shaped muscle, which lifts the roof of the anus when it contracts. The sphincter muscle is a circular muscle that closes off the end of the gut. The intestinal muscles have longitudinally oriented filaments, which are situated in the ventral regions of the cells. The dorsal regions flatten into thin sheets, which wrap round the posterior ventral regions of the

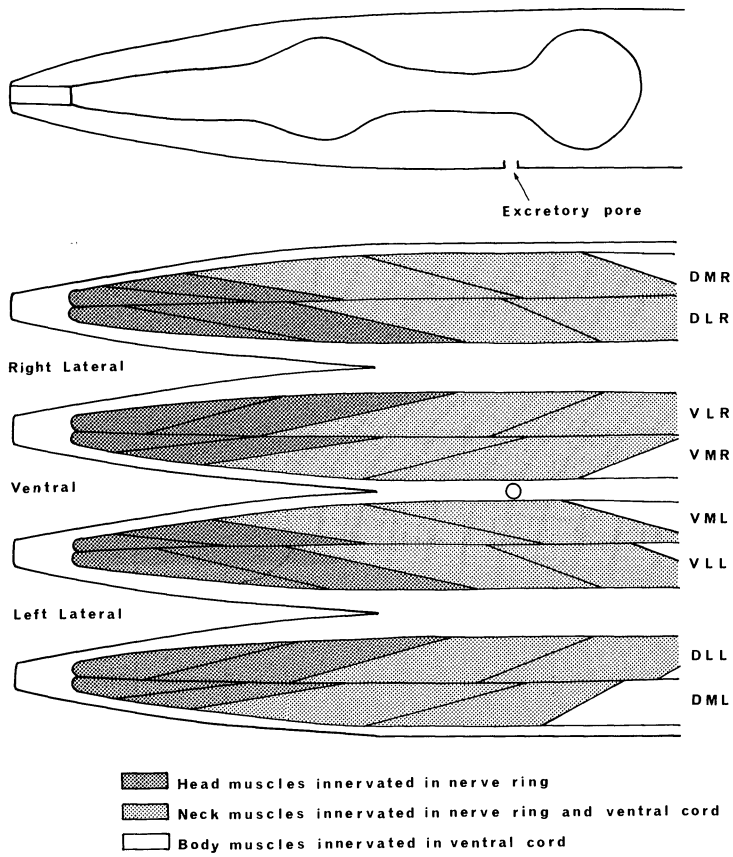


FIGURE 10. 'Orange peel' projection of muscles in the head. The reconstruction was derived from electron micrographs. The muscles are organized as longitudinal strips in each of the four body quadrants (figure 9). Each quadrant has two adjacent rows of muscle cells. The muscles are obliquely striated and packed diagonally so that the sarcomeres are oriented longitudinally. The first two muscle cells in the two ventral and two dorsal rows are smaller than their lateral counterparts, giving a stagger to the packing of the two rows of cells in a quadrant. The first four muscles in each quadrant are innervated exclusively by motoneurons in the nerve ring. The second block of four muscles is dually innervated, receiving synaptic input from motoneurons in the nerve ring and the anterior ventral cord. The rest of the muscles in the body are exclusively innervated by NMJs in the dorsal and ventral cords (figure 9). The eight muscle rows have been labelled dorso-medial right (DMR), dorso-lateral right (DLR), ventro-lateral right (VLR), ventro-medial right (VMR), ventro-medial left (VML), ventro-lateral left (VLL), dorso-lateral left (DLL) and dorso-medial left (DML).

intestine and are probably attached to it. Muscle arms from these three sets of muscles run into the pre-anal ganglion and are coupled together via gap junctions. Surprisingly little synaptic input was found to be present on the defecation muscles, with only a single NMJ being made by DVB.

Basal lamina

The pseudocoelomic cavity is lined with a thin (20 nm) basal lamina, which effectively separates the muscles from the hypodermal and nervous tissues. This lamina has an anisotropic structure, as parallel striations with a spacing of 30 nm can be seen when it is sectioned obliquely (White *et al.* 1976). The gonad and the gut are ensheathed by similar basal laminae; the pharynx is ensheathed by its own, rather thicker (45 nm) basal lamina (Albertson & Thomson 1976). The dorsal and ventral nerve cords, together with their respective hypodermal ridges, are bounded by the pseudocoelomic basal lamina (figures 18 and 19); the lateral

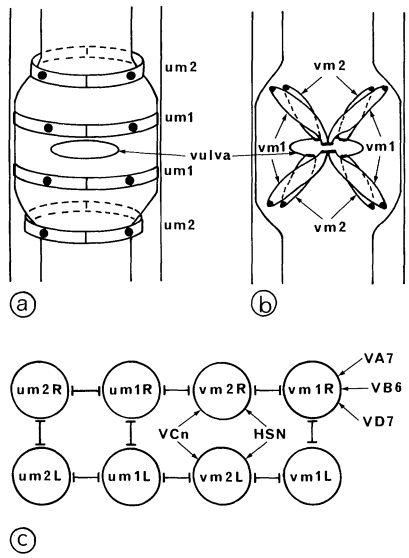


FIGURE 11. Egg laying is controlled by a set of sixteen muscle cells in the hermaphrodite, eight of which act to squeeze the uterus (a) and eight to open the vulva (b). The distal uterine muscles, um2, form circumferential bands of muscle round the distal regions of the uterus. The um1 muscles attach to the lateral hypodermis and wrap round the proximal ventral regions of the uterus. The vm1 muscles attach to the body hypodermis at the ventro-lateral body muscle margins and at the vulval opening. The vm2 muscles attach to the body hypodermis sub-laterally, insinuating themselves between the body muscles, and to the uterus at the vulval opening. The vulval and uterine muscles have gap junctions to each other, as shown in (c). The main synaptic input is onto the vm2 muscles and comes from VCn (*a) and HSN (*a). The NMJs are dorsal to the main part of the ventral cord (VCn-a). vm1R sends an arm down into the ventral cord and receives single synapses from VD7, VB6 and VA7.

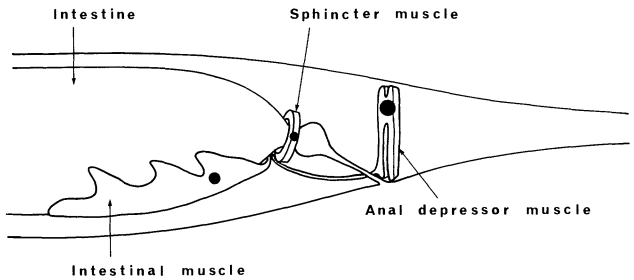


FIGURE 12. There are three muscles directly involved in defecation: the anal depressor muscle, the anal sphincter muscle and the two intestinal muscles. The anal depressor muscle is a large H-shaped cell, which lifts the posterior dorsal surface of the rectum so as to open it and discharge its contents. The intestinal muscles have longitudinally oriented contractile filaments and attach to the body hypodermis at the ventral muscle margin and to the intestine via several distributed contacts on its ventral surface. The intestinal and depressor muscles send muscle arms to the posterior regions of the pre-anal ganglion, where they receive synaptic input from DVB (*c).

hypodermal ridges and the laterally located ganglia are similarly bounded. The boundary curves smoothly, suggesting that the lamina may be under tension in these regions.

All the nervous system is situated to one side of the pseudocoelomic basal lamina, with the exception of the cell bodies of URX, CEPD and GLR. The processes of URX and CEPD run together on each side as they leave the ring sub-dorsally. They are surrounded by, and eventually penetrate, the basal lamina in these regions before reaching their cell bodies, which are situated in the pseudocoelomic cavity. The basal lamina may also be penetrated in four places on the inside of the nerve ring by muscle arms (figure 14 and RIM-d). This enables

a motoneuron (RIM), which has its axon buried in the interior of the ring neuropile, to make NMJs.

Nerve processes seem to be constrained to run alongside the lamina. Processes that run from the ventral to the dorsal cord, for example, run round the animal, travelling underneath the muscle quadrants instead of taking a more direct internal route. In the main part of the body cavity the dorsal and ventral ridges are quite small, consisting of a ridge of hypodermis and an adjacent process bundle (figure 13*d*). As the head is approached, the dorsal, ventral and lateral ridges enlarge as they become filled with the cell bodies of their respective ganglia (figure 13*c*). Eventually the basal laminae bounding the four ridges meet and fuse (figure 13*b*). An internal tract is now opened up and processes course round it inside the muscle quadrants forming the nerve ring. This organization is maintained up to the tip of the head with the four muscle quadrants running in tubes of basal laminae (figure 13a). The central ring of lamina left after the ridges have fused ends in the vicinity of the nerve ring. It appears to terminate on the cylinder that is made up of the sheet-like processes of the GLR cells. This structure is situated on the inside of the nerve ring between the pharynx and the muscle arms.

The arrangement of the basal lamina lining the pseudocoelome suggests that it may be instrumental in the establishment of the general topography of process tracts in the nervous system. Processes from neurons have been shown to grow preferentially along ordered fibrillar arrays (Weiss 1934). The striated structure may likewise serve to guide initial process outgrowths, thereby establishing the antero-posterior and circumferential system of process bundles that are a feature of the nervous system of *C. elegans*.

Neurons

Branching structure

The component neurons of the nervous system of *C. elegans* have simple, unbranched morphologies. Few neurons have more than two processes, and many are monopolar with only a single process (see, for example, AIA). Processes of neurons run in parallel bundles except in the immediate vicinity of their cell bodies, where they join the bundle. This region is not extensive, however, as cell bodies are generally situated close to the bundle into which they project. Branching typically occurs when a neuron has a process that leaves the main bundle to run out as a commissure (see, for example, VDn), or at a discontinuity, where one bundle joins another (as in AQR where it leaves the ventral cord and enters the nerve ring).

Neurons with a branched structure generally have very similar patterns of branching in different animals; however, there are a few interesting cases where differences occur between animals, or between sides of the same animal. The interneuron RID lies on the dorsal mid-line and sends a process round the left-hand side of the nerve ring in the N2U animal and round the right-hand side in the JSH animal. The nerve ring has a high degree of bilateral symmetry and the process of RID runs in a similar position relative to the neighbouring processes whether it runs on the left or the right.

The interneuron PVN is the most highly branched class of neuron in *C. elegans*. The main processes of PVN run up the ventral cord and enter the nerve ring on the right-hand side, travelling round it in an anticlockwise direction. PVNL has an additional branch, which separates from the main process at a point behind the excretory duct. This branch enters the ring on the left-hand side, travelling round it in a clockwise direction. This process (which is not present on PVNR) runs in the same region of neuropile as do the main processes of both

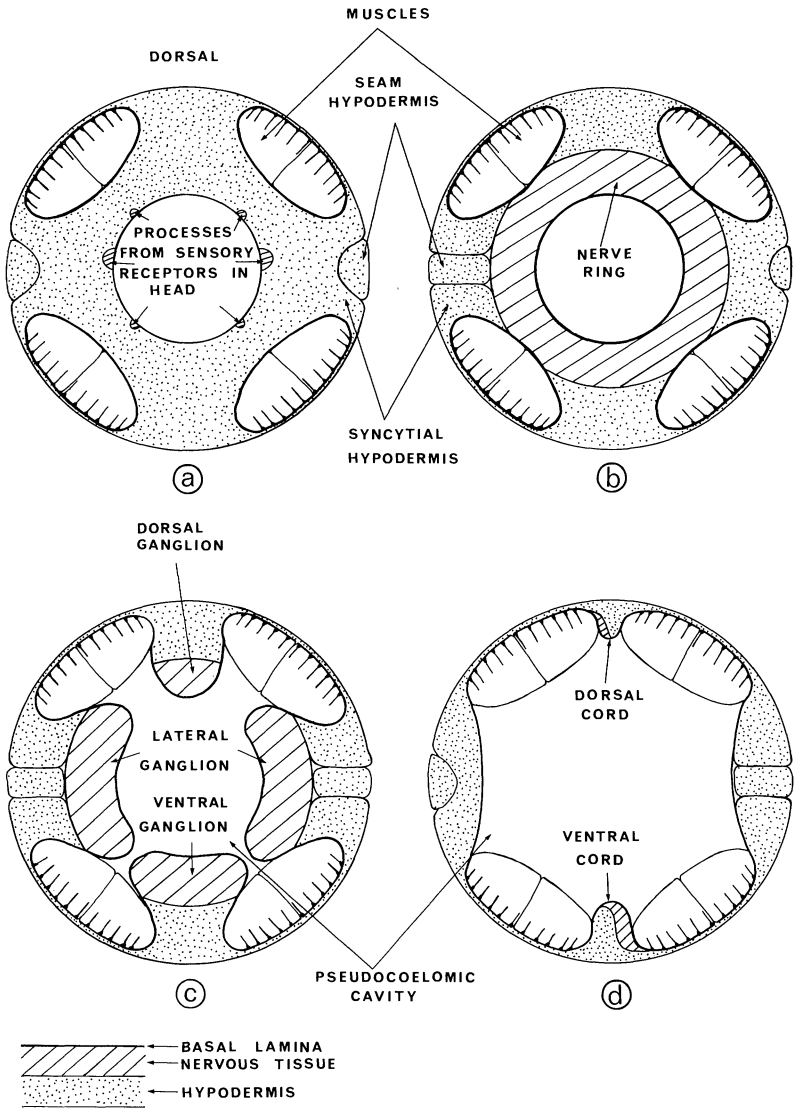


FIGURE 13. The pseudocoelome in the body is bounded by a basal lamina, which covers all the hypodermal and nervous tissue (d). The muscles are in the pseudocoelomic cavity. Processes of neurons do not, in general, cross the basal lamina. Commissures between the dorsal and ventral cords pass underneath the muscle quadrants and do not enter the pseudocoelomic cavity. As the ring is approached, the dorsal, ventral and lateral cords enlarge where they are filled with cell bodies of the respective ganglia (c). There is no direct route between the ganglia at this point, however, and cell bodies in the lateral ganglia send processes into the ventral cord via the amphidial commissures (figure 6). At the level of the nerve ring, the lobes of the basal lamina fuse inside the muscle quadrants (*b*) allowing the processes in the nerve ring to run round without having to pass underneath the muscle quadrants. The processes of the nerve ring, like those of the nerve cords, run alongside a ridge of hypodermis (*a*), which is anterior to the neuropile. The nerve ring seals off the anterior end of the pseudocoelomic cavity and there is no basal lamina bounding the hypodermal and nervous tissue in the head, except for that bounding the pharynx.

PVNR and PVNL, which are travelling in the opposite direction; they also make similar synaptic contacts. Other examples of such conservative variation in branching patterns have previously been noted in the cephalic receptor neurons, CEP (Sulston *et al.* 1975). These observations suggest that, irrespective of branching structure or even direction of growth, a process is capable of locating its appropriate neighbourhood within the neuropile and forming its characteristic synaptic connections.

A few examples of non-conservative changes in branching pattern have been seen. A fairly major branch is missing on RMFR in the N2U animal but is present on its contralateral partner and is also present on RMFR in the JSH animal. As the missing process has all the NMJs made by this motoneuron, such a change must have a profound effect on the function of RMFR in this instance. It seems reasonable to consider such incidences of branching failures as developmental errors in the construction of the nervous system, which could perhaps give rise to non-genetically related variations in behaviour between animals.

Branch termination

The processes of many classes of neuron terminate at the point of contact with a process from a neighbouring member of the same class. There is usually a gap junction at this point (as in ASI on the dorsal mid-line), although there is one case where processes touch and terminate with no gap junction (RIF). There are also a few cases where such contact terminations can occur between heterologous classes (e.g. between processes of ALM and AVM in the nerve ring). The most striking examples of contact termination are exhibited by the DDn and the VDn motoneurons of the ventral cord. There are six DDns and thirteen VDns evenly distributed along the length of the cord. Each of these classes has processes in both ventral and dorsal cords. Together, their processes make an unbroken line of non-overlapping processes in each cord (White *et al.* 1976). This behaviour seems to be an intrinsic property of certain classes of neuron; other classes of neuron make contacts and gap junctions with members of their own class but do not terminate at the site of initial contact and may have considerable overlap (see, for example, ASE, AIN).

Gap junctions

Gap junctions are organelles that mediate electrical and metabolic coupling between cells (Bennett 1977). They are seen in *C. elegans* as regions where the membranes from two adjacent cells are closely apposed and appear more darkly staining than surrounding regions (as in VBn-c). When gap junctions are sectioned transversely, a gap of about 8 nm can be seen separating the membranes. The region of close apposition is usually in the form of a plaque of about 350 nm diameter. The membranes at the junction are notably flatter than those of the surrounding regions. The gap junctions seen in *C. elegans* resemble those described by Pappas & Waxman (1972).

Gap junctions are seen between muscle cells and between neurons. Apart from a couple of possible exceptions (RMD-h and VCn-f), gap junctions are not seen between muscle cells and neurons, probably because there is usually a basal lamina separating the two. The glial-like cells, GLR, are unique in that they make gap junctions to both muscles (GLR-c) and neurons (GLR-d). They do not, however, make gap junctions to themselves. The arrangement of these gap junctions is shown in figure 15.

Muscle arms from muscles in the head have a striking arrangement of gap junctions where they interdigitate at the inside of the nerve ring. Arms make gap junctions with arms from muscle cells in adjacent quadrants but not with arms from muscle cells in the same quadrant, even though both sets of arms are equally accessible (figure 15). Muscles in the same quadrant are, however, connected by gap junctions, but the connections are situated in the region of the muscle cell bellies, well away from the arms. Thus it seems as though muscle arms, when they grow into the nerve ring, can discriminate between the arms of muscle cells that are already connected to themselves via gap junctions and those that are not.

Chemical synapses

Chemical synapses in *C. elegans* occur *en passant* between neighbouring parallel processes. The presynaptic process has a vesicle-filled varicosity and a specialized, darkly staining region in the membrane adjacent to the point of contact with the postsynaptic elements (see, for example, BAG-a). A considerable variation in the size of the presynaptic regions was found (compare OLQ-a with PVN-a). The presynaptic specializations also vary in prominence between different classes of synaptic contact in a way that does not necessarily correspond to the size or the number of vesicles in the presynaptic process. The extremes of this variation are represented by RIP, on the one hand, which has structures that look like presynaptic specializations but with no associated synaptic vesicles (RIP-a); and, on the other, by DVA, which has large vesicle-filled varicosities but rather small presynaptic specializations (DVA-b). There is also considerable variation in the number of chemical synapses between pairs of interacting processes. There are many cases where there is only a single synapse present. At the other end of the scale, the largest number of synapses seen between processes is nineteen (AVDL onto AVAR); more typically it is around five. Some of the single synapses that are seen are small, with few synaptic vesicles or indistinct presynaptic specializations. Synapses of this type are also rather variable, in that they are not present in some individuals and therefore probably not very significant. On the other hand, some single synapses are large, with many vesicles and unambiguous presynaptic specializations. These synapses are seen in all individuals and so are probably significant. This latter type of synapse seems to occur when the layout of the two interacting processes is such that they are only adjacent for a limited extent. In these cases there may only be room for a single synapse in the region where the two processes are adjacent.

Although the fixation and staining procedures that were used are not optimal for the preservation and visualization of vesicle morphology, several classes of vesicle can be clearly distinguished. The most ubiquitous vesicles are spherical, 35 nm in diameter, and have lightly staining interiors (see, for example, RIA-a). Some classes of neuron, including most of the amphid receptors, have a second class of vesicle coexisting with vesicles of this first type. These vesicles are larger and have darkly staining cores (as in ASK-a); the relative proportions of the two types of vesicle varies with cell class. There is a certain amount of variation in the staining properties of these dark-cored vesicles between classes; the sizes also vary, ranging from 37 nm (ASE) to 53 nm (ASK). The dark-cored vesicles seem generally to be excluded from the region immediately adjacent to the presynaptic specialization, which contains only the smaller type of vesicle. A similar segregation of vesicle types is exhibited by DVA, which has a large process in the nerve ring, filled with irregularly shaped vesicles, but has small spherical vesicles next to presynaptic specializations (DVA-a). The neurotransmitters that may be contained in the dark-cored vesicles are not known. Dopamine has been shown to be present in CEP, ADE and PDE neurons (Sulston *et al.* 1975). Acetylcholine is probably used as a neurotransmitter by the ventral cord motoneurons VAn, VBn, DAn, DBn and ASn, as this transmitter has been shown to be used in the equivalent neurons in *Ascaris* (Johnson & Stretton 1980). All these classes of neuron have uniform populations of spherical, 35 nm, synaptic vesicles, with no dark-cored vesicles present (see, for example, CEP-a, VAn-a).

Chemical synapses in *C. elegans* usually have no visible specializations on postsynaptic elements and consequently there is often some ambiguity as to the identities of these elements.

In some cases, the disposition of the processes is such that there clearly can be only one postsynaptic element (as in ASE-a). In many other cases there are two (for example, in ADF-a) or, more rarely, three (for example, in AIY-e) postsynaptic elements, making a dyadic or triadic synapse (Dowling & Boycott 1966). It was difficult to know in these cases whether all the postsynaptic elements are functional (i.e. have an appropriate receptor) or are just neighbouring processes. It seems likely that, in many cases, all the possible postsynaptic elements could be functional, as particular dyadic or triadic combinations are found to occur in many instances (for example, AIA and AIB are often the two postsynaptic elements in a dyadic synapse). Some synaptic pairings are only seen in the context of multiple synapses. Although this may suggest that such a pairing could be non-functional, there are cases where this cannot be so, as the other postsynaptic element of the dyadic synapse is also seen only in the context of a multiple synapse (for example, RIB and AVE are postsynaptic to AUA, and AVE and AIZ are postsynaptic to RIG). This observation raises the interesting possibility that, in some cases, synaptogenesis may be dependent on the simultaneous presence of two particular postsynaptic elements.

Several process pairs are seen to synapse onto each other reciprocally. AVAL/R and PVCL/R synapse onto each other along the length of the ventral cord, for example, but there is no particular spatial relation between the two types of synapse. The reciprocal synapses made by RIA and RMD are usually situated close to each other, however, making a characteristic structure (RIA-e). Such an organization may provide positive or negative feedback in these synaptic connections.

Many classes of neuron are found to have regions of process that are devoid of presynaptic specializations. This could be because the particular class of neuron does not have many synapses in total or that these regions corresponded to regions where there are no suitable postsynaptic partners. In several cases neither of these explanations can be valid. The interneurons AVA, AVB, AVD and AVE are all exclusively postsynaptic in the nerve ring, yet they have extensive synaptic outputs in the ventral cord. Furthermore, AVD, AVE and AVB all have extensive synapses onto AVA along the cord; however, in the nerve ring, processes from these cells do not make such synapses even though they are accessible to AVA (i.e. are adjacent to its processes) for part of their extent within the ring. Thus it appears that certain classes of neuron can localize the regions where they are presynaptic. Those regions of process that are devoid of presynaptic contacts are often more lightly stained than adjacent processes (AVA-a). There seems to be no localization of postsynaptic contacts.

Occasionally, presynaptic elements are seen with no obvious postsynaptic partner, or with a hypodermal cell as the only possible partner. AVB is particularly prone to this behaviour, having six such structures along the length of the ventral cord (see, for example, AVB-a). It is difficult to know how to interpret these structures; they could possibly be functional synapses and control some hypodermal cell function such as cuticle deposition or moulting, or they could be artefacts.

Neuromuscular junctions

Neuromuscular junctions (NMJs) are special cases of chemical synapses where at least one of the postsynaptic elements is muscle. As the muscle and nervous system are situated on opposite sides of the pseudocoelomic basal lamina, NMJs have to pass through the lamina with the presynaptic elements (the motoneuron axons) on one side and the main postsynaptic

elements (the muscle arms) on the other. Because of this arrangement, NMJs are constrained to lie on the two-dimensional surface of the lamina. NMJs usually have several postsynaptic elements. On the inside of the nerve ring, there is a continuous plexus of arms from muscles in the head and a high density of NMJs (figure 14). In the ventral cord, the NMJs are more dispersed and muscle arms crowd round and interdigitate at foci where there are presynaptic elaborations on motoneuron axons (figure 18).

Certain classes of neuron (VDn, DDn, RMD, SMD, RME and RIP) have processes that are postsynaptic at NMJs. These processes are on the same side of the basal lamina as the presynaptic elements and often have a short branch, which dips in and intercepts the NMJ (see, for example, RMD-a). Because of this behaviour, it seems likely that these processes are functional postsynaptic elements. The disposition of the dendritic processes relative to the NMJs that they are intercepting suggests that the NMJs might have formed first and the dendrites might have moved in and insinuated themselves into position later. There is likely to be some specificity as to which NMJs are intercepted by particular dendrites, as dendrites along the ventral cord are not associated with the NMJs of VDn and DDn, but are associated with the NMJs of the other motoneuron classes active in the nerve cord, even though all classes of NMJ are equally accessible to the dendritic processes.

With the exception of RIP, all the classes of neuron that have postsynaptic elements in NMJs are motoneurons themselves and, interestingly, have NMJs on the diametrically opposite side of the animal to the regions where they are postsynaptic. Thus it seems likely that these classes of neuron act as cross-inhibitors, ensuring that muscle contractions in diametrically opposite regions of the animal operate in antiphase. Neurons analogous to VDn and DDn have been identified in the ventral cord of *A. lumbricoides* and have been shown to be inhibitory (Johnson & Stretton 1980).

The arrangement of motoneuron axons around the inside surface of the nerve ring was found to be the most highly ordered region of neuropile in the nervous system (figure 14). The ordering is such that it is often possible to identify many of the processes in this region by their appearance in a single appropriately positioned section. Several of the NMJs in this region are organized as characteristic complexes made up of presynaptic endings clustered around a dendritic process (figure 14). The dendritic processes are from RMD, SMD and RIP. The NMJs made by RMD and SMD are situated diametrically opposite their dendritic processes. The RIP neurons also have processes that cross over to the diametrically opposite side from the dendritic regions, even though they are not motoneurons. These processes eventually enter the pharynx (Ward *et al.* 1975; Albertson & Thomson 1976).

The arms from each row of head muscles are arranged around the inside surface of the nerve ring such that arms from each row occupy a well-defined arc. This arc is positioned in an equivalent location to that of the muscle row from which the arms originated (figure 15). There is thus a fairly precise mapping of the circumferential positions of the muscle rows, by the muscle arms, onto the motor endplate region. The ordering of the motoneuron axons on one side of the basal lamina and the muscle arms on the other is highest at the regions immediately adjacent to the lamina but is less apparent away from it.

The flattened processes of the GLR cells cover the inside surface of the plexus of muscle arms inside the nerve ring and are seen to have gap junctions with adjacent muscle arms (figure 15). The processes of GLR are found to be aligned with the arcs of muscle arms from each row (figure 14). The sub-dorsal and sub-ventral sets (GLRDL/R and GLRVL/R) are each

associated with muscle arms from one row, whereas the lateral pair (GLRL/R) are larger in circumference and are each associated with two muscle rows. The points of contact between adjacent GLR processes are closely aligned with the points of contact of the arcs of muscle arms, except in the case of the muscle rows lying either side of the lateral lines. In these, there is no GLR process junction and a certain amount of mixing of the muscle arms at the point of contact of adjacent arcs occurs, whereas there is no mixing at the points of contact that have an associated GLR process junction. These observations suggest that the GLR processes may act to guide muscle arms and confine them to their appropriate territories on the inside of the nerve ring.

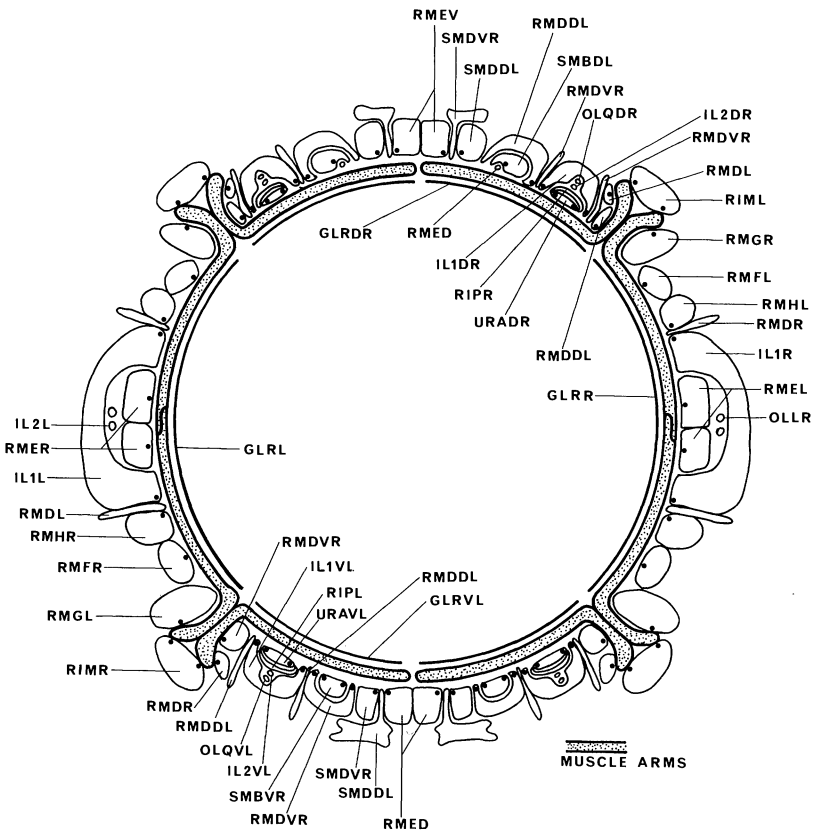


FIGURE 14. Neuromuscular junctions in the nerve ring. The eight rows of muscles in the head and neck (figure 10) have muscle arms that project onto the inside surface of the nerve ring in a highly ordered way (figure 15). They are sandwiched between the thin sheet-like processes of GLR cells on the inside and the motoneurons of the nerve ring on the outside. Four spurs of muscle arm penetrate into the anterior neuropile of the ring sub-laterally and receive synaptic inputs from RIM, which runs in the interior of the ring neuropile. The other classes of motoneuron form complex, but well-defined, structures adjacent to the inner surface of the nerve ring. Most NMJs are dyadic, with dendrites of other motoneuron classes or RIP as the corecipients. The dots in the processes show the locations of the presynaptic specializations.

One motoneuron, RIM, is unusual in that it does not have its axon adjacent to the inside surface of the nerve ring. Instead it forms NMJs onto four spurs of muscle arms that invade the neuropile of the ring (figure 14). It is difficult to visualize the basal lamina in these regions, so it is not clear whether the muscle arms actually penetrate the basal lamina at these points or whether the basal lamina is herniated. The sites of these invaginations again correspond to junctions between GLR processes and are fairly small; muscle arms anterior and posterior to these regions run along the inside surface of the ring.

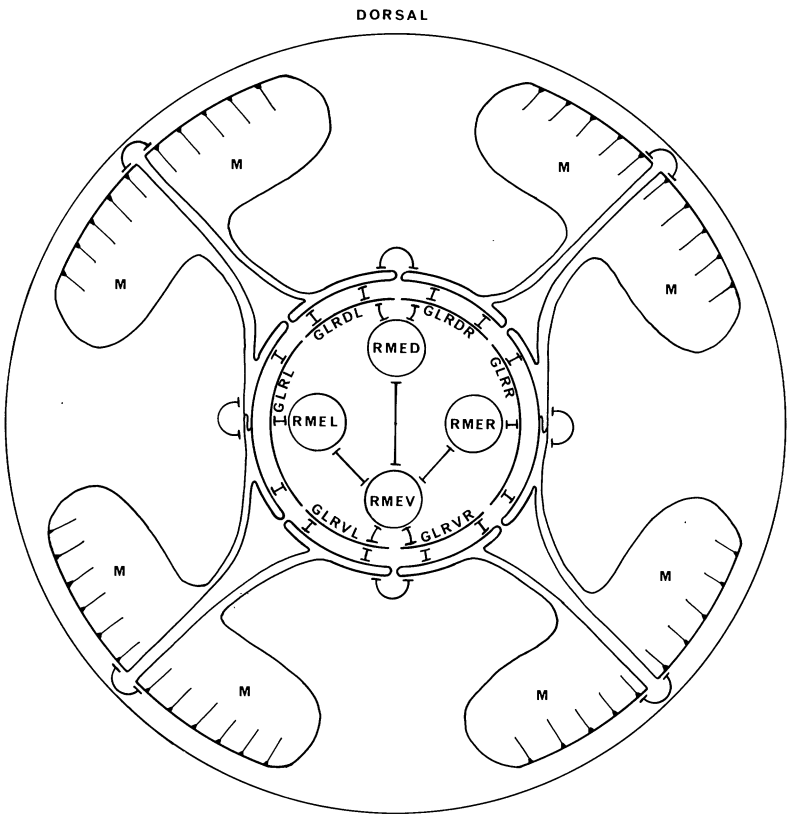


FIGURE 15. Head and neck muscle projections. The muscle arms from the 32 head and neck muscles send arm posteriorly past the outside surface of the nerve ring. These then turn and run anteriorly onto the inside surfac of the ring. The muscle arms are highly ordered in this region and map onto the inside surface according to the circumferential location of the muscle bellies. Muscle arms have gap junctions to arms from adjacent muscles in neighbouring quadrants and to GLR cells. RME motoneurons also have gap junctions to GLR cells in the arrangement shown. There are gap junctions between the muscle bellies of muscles in adjacent rows of the same quadrant but, interestingly, none are seen between the arms from these muscles, even though they interdigitate extensively.

There are seven main classes of motoneuron in the ventral cord: VAn, DAn, VBn, DBn, ASn, VDn and DDn. Members of each class are evenly distributed along the length of the cord (White *et al.* 1976). Within each class there are sharply defined transition points where one axon becomes synaptically active, having many NMJs along the cord, and the adjacent axon becomes inactive, having no more NMJs. These transition points occur in slightly different positions for each class; such observations suggest that there might be intraclass competition for territory along the ventral cord (White *et al.* 1976). Similar intraclass competitions for territories have been shown to occur in two dimensions for classes of ganglion cell in the vertebrate retina (Wässle *et al.* 1981). In the nerve ring, many of the motoneuron classes have NMJs at discrete points around the motor endplate region and so it seems unlikely that intraclass competition has a role in establishing NMJ territories in these cases. The RMDD/V motoneurons have NMJs around the whole circumference of the ring, however, with abrupt transitions between adjacent class members, which each have NMJs over a 45° arc. Thus it seems possible that, in this case, intraclass competition may be used to partition out territory for NMJs to the class members.

The organization of processes within bundles

The process bundles in *C. elegans* are spatially ordered, with processes running in characteristic positions within the bundle and maintaining their locations relative to their immediate neighbours over long distances. This ordering is independent of the size of the process bundle. For example, the four anterior sub-lateral cords, which are made up of only two processes, each have the same relative disposition of processes (figure 7). On the other hand, the ventral cord near the junction of the nerve ring is made up of about 170 processes; it is bilaterally symmetric in this region and the degree of order that was found can be seen by comparing the positions of bilaterally symmetrical processes on each side of the cord (figure 16*b*). There is a little more variability seen between the cords of different animals of the same genotype and developmental stage than between each side of the cord in a single animal. Although the order of processes in the cord is maintained over long distances, local mechanical intrusions, such as cell bodies, can disturb the ordering temporarily, but order returns away from these regions.

Processes that must have grown in opposite directions are found to be freely mixed within process bundles. The processes of PVQR and PVPR in the ventral cord, for example, must have grown up from their cell bodies in the tail, yet most of their surrounding processes, such as those of AVAL, HSNR and AVJL (figure 18*b*), have their cell bodies in the head and their processes must therefore have grown in opposite directions to those of PVQ and PVP. The relative positions of adjacent processes that had grown in opposite directions was fairly constant over long distances. Such an organization of processes might conceivably have arisen by rapid and sequential process growth; in other words, each process would grow along the full length of the process bundle before its neighbour growing in the opposite direction started out. A more likely explanation for these observations is that processes can insinuate themselves in between pre-existing processes in a bundle and follow along specific neighbours. The observation that the processes of PVNL in the left sub-dorsal region of the nerve ring must have grown in opposite directions, but nevertheless, ran in the same region of the nerve ring, supports this latter interpretation.

Any individual process in a bundle has a group of adjacent processes that immediately surround it at any point. We refer to such a group as the neighbourhood of the process. Neighbourhoods are generally fairly constant over the length of processes, reflecting the ordered arrangement of processes within bundles. Certain neighbours are found to be much more persistent than others, however, always remaining adjacent, whereas others move in and out of direct adjacency along the length of the process (White *et al.* 1983). In some instances, groups of processes are seen to be closely associated together; the most striking example of this behaviour is shown by the dendritic regions of RMD motoneurons, which are clustered around the processes of RIA (RMD-d). In this particular case there are extensive synaptic interactions between RIA and RMD, but in other cases, such as the close association of ALM and ALN on the lateral lines (ALN-d), there are no synaptic interactions between the associated processes.

Many processes make abrupt changes of neighbourhood at certain points. The processes of AIB are closely associated with those of AIA on the ipsilateral side, but at the point where the latter terminate, on the dorsal mid-line, the processes of AIB turn and run across the process bundle. They then run for a short distance anteriorly before turning again and continuing on their trajectories round the ring; they are now in a different neighbourhood, where they run

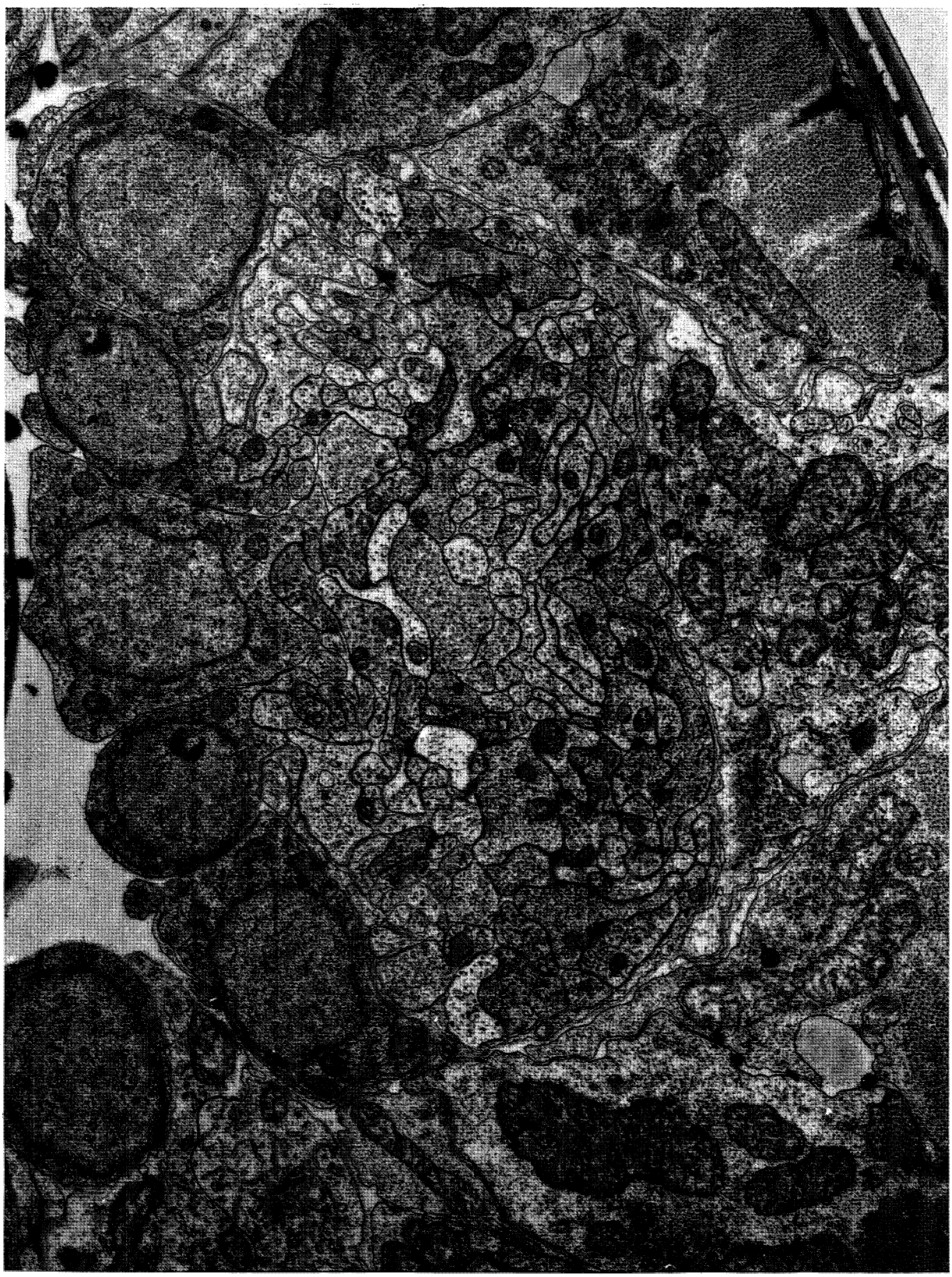


FIGURE 16 (a). For description see opposite.

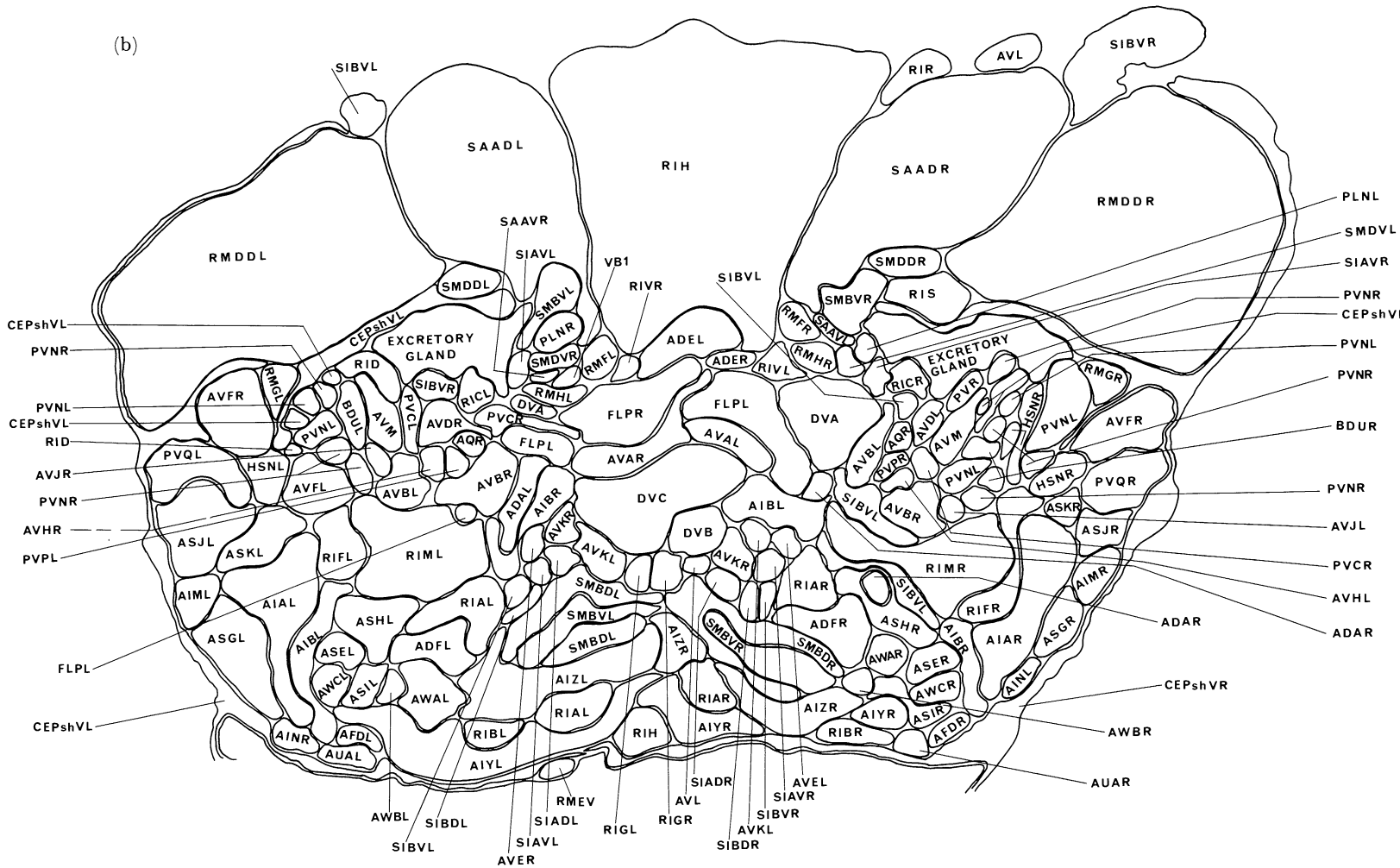


FIGURE 16. Transverse sections through the anterior regions of the ventral ganglion (a) and process identification (b). The ventral cord enlarges at its anterior end and contains some of the neuropile of the cells of the ventral ganglion. Several of the processes in this region have characteristic shapes and synapses; these differences facilitate their identification. Processes of SMB flatten out and sandwich each other; AIY makes characteristic dyadic and triadic synapses onto RIB, AIZ and RIA; FLP makes prominent synapses onto AVA; RIGL/R run near the centre of the neuropile making extensive gap junctions to each other; the processes of AIA enlarge and make several synapses to AIB and RIF. The neuropile in this region is bounded on the ventral and lateral sides by thin sheet-like processes from CEPsh. Processes from the excretory glands run along the dorsal surface of the neuropile and eventually end in the ventral regions of the nerve ring. The four cell bodies above the neuropile are always in this configuration and can be readily identified. The rest of the cell bodies in the ventral ganglion are more variable in their relative positions.

in close association with the processes of RIM (White *et al.* 1983). Such major changes of neighbourhood obviously have considerable functional significance for a neuron as they provide an extended set of possible synaptic partners. Perhaps, more significantly, they also facilitate direct communication between non-adjacent neighbourhoods.

In many (but not all) cases, there are external discontinuities at the transition points between neighbourhoods. The greatest numbers of neighbourhood transitions are seen to occur at the junction of two process bundles. In the region where the amphid commissure (figure 17) joins the anterior ventral cord (figure 16b), most processes from the commissure make transitions of neighbourhood (as in ASG) although some neighbours are maintained (as in AIB/AWC). The same type of behaviour occurs at the junction of the ventral cord and the nerve ring (figures 16 and 20), with some processes maintaining their neighbourhoods (see, for example, ASJ/PVQ/ASK) while others (e.g. ASH) switch. A discontinuity of a different type is seen on the dorsal mid-line of the nerve ring, which corresponds to the points where AIB, AVE and AVD make abrupt transitions of neighbourhood. In this case the discontinuity is apparently due to the termination of many processes in this region (notably the amphid receptor neurons), usually in gap junctions to their symmetrical analogues (e.g. ASJ-c). AIB and AVE are both closely associated with processes that terminate in this way in one of their neighbourhoods. In AVD, the associated processes are not obvious and it appears that the processes of AVD may have been deflected by a process emanating out of the cell body of RID (AVD-e).

Motoneurons are generally found to inhabit two neighbourhoods. One corresponds to the region where the motoneuron is predominantly or exclusively postsynaptic, usually in the interior of a process bundle, and the other is the region where NMJs are situated, at the surface of a process bundle adjacent to the basal lamina. The transitions between these neighbourhoods are not accompanied by obvious external discontinuities in most cases, except for a similar transition occurring in an adjacent motoneuron of the same class.

Groups of processes that are fasciculated together have been shown to share a common antigenic determinant in the leech (Hockfield & McKay 1983) and the grasshopper (Raper *et al.* 1983). It is possible that such antigens are neighbourhood-specific adhesion molecules. Such specific adhesion molecules, or perhaps a single ubiquitous molecule, such as CAM, which is spatially and temporally regulated (Edelman 1983), may be the basis for the close associations of groups of processes seen in the nervous system of *C. elegans*. It is interesting to consider the abrupt changes in neighbourhood exhibited by some neurons in the context of inter-process adhesivity. In the switches in neighbourhood that occur at process bundle junctions, it seems likely that mechanical disturbances have mixed the processes, introducing them to novel neighbours. Some of these neighbours may have high adhesive affinities for the newly introduced processes and act to guide and establish the processes in their new territory. Such a notion carries the implication that specific neighbourhoods are not uniquely attractive for a particular process, but rather that there may be several neighbourhoods in which a process could equally well reside, the one selected being dependent on the initial placement of the process in the bundle. In general there are few directed movements of neurons relative to their neighbours after they are born (Sulston 1983). It therefore seems that the initial placement of a neuron at birth is the major factor that determines which neighbourhood is finally selected out of the set of neighbourhoods in which its process could equally well reside.

The neighbourhood transitions exhibited by motoneurons seem to be mediated by factors that are intrinsic to the neuron. Other neurons, such as AVA and AVB, show a clear

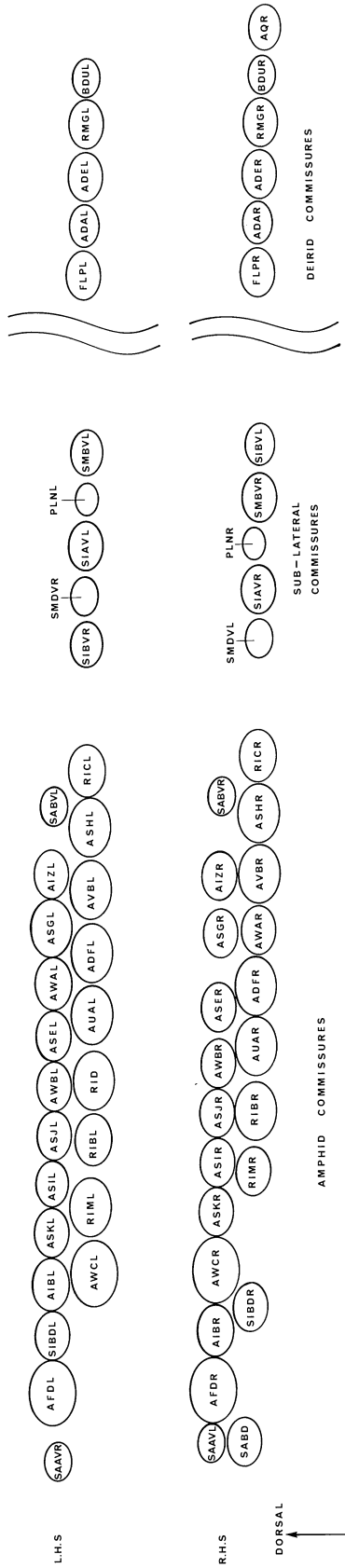


FIGURE 17. Diagram showing the disposition of processes within the amphid, sub-lateral and deirid commissures on each side of the animal.

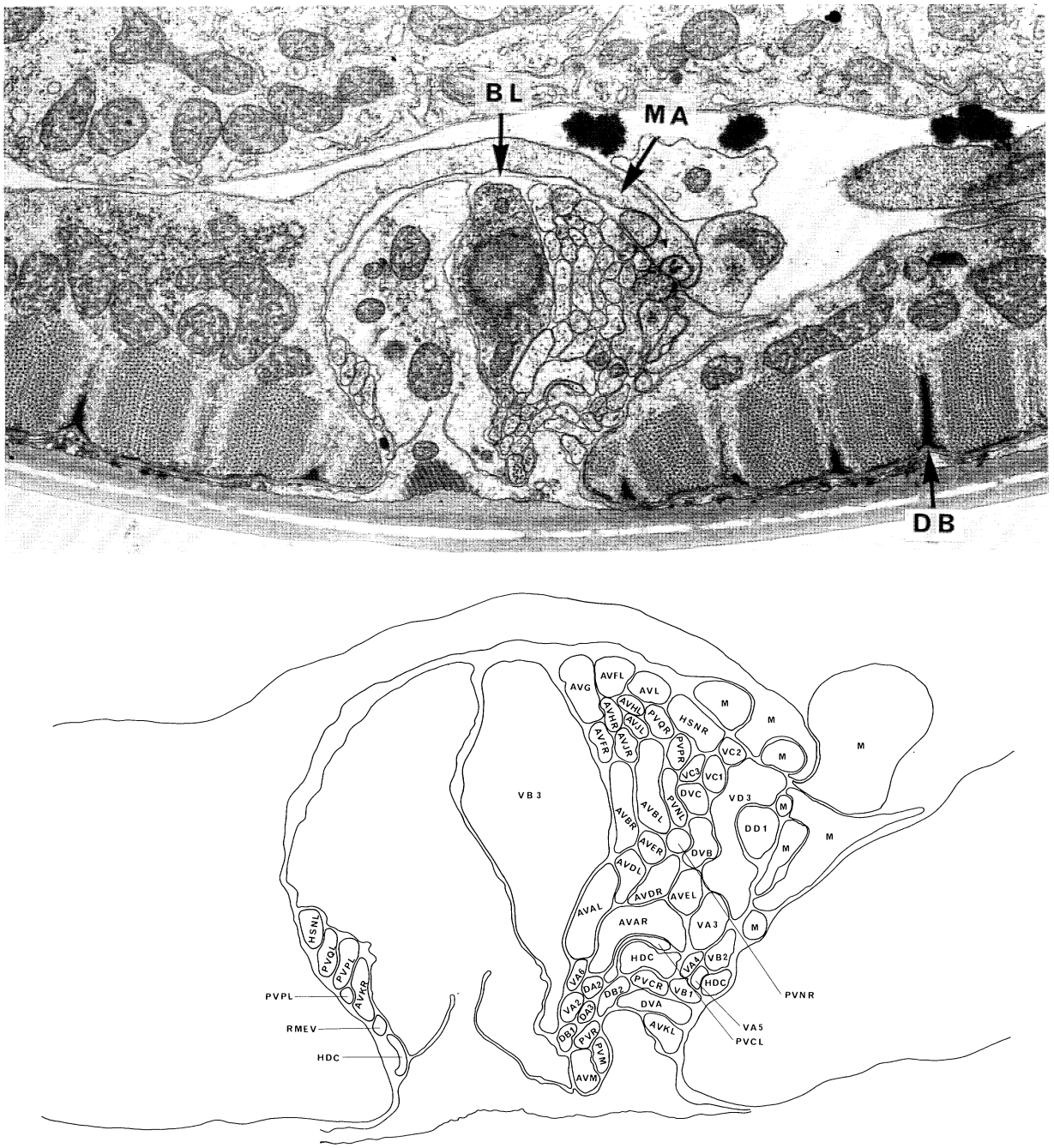


FIGURE 18. Transverse section through the ventral cord (above) and process identifications (below). The ventral cord consists of a process bundle that runs alongside a longitudinal ridge of hypodermis; the whole structure is bounded by a thin basal lamina (BL). Axons of motoneurons arrange themselves next to the basal lamina on the right-hand side of the cord in a fixed arrangement. The usual sequence of motoneuron classes from dorsal to ventral is VCn, VDn, DDn, VAn, and VBn. NMJs are made in this region (one from a VD3 is seen in this section); the motoneurons synapse through the basal lamina onto muscle arms (MA) from both left and right ventral muscle quadrants. The NMJs of a motoneuron are in a well-defined region along its process; outside this region, the process moves away from the basal lamina to the ventral regions of the process bundle. The VDn and DDn neurons are an exception in that their processes terminate abruptly outside the NMJ regions. The cell bodies of the motoneurons that innervate body muscles are arranged in a linear sequence in the ventral cord (figure 4). The ventral cord also contains the interneurons that synapse onto these motoneurons and other interneurons with little or no synaptic activity in the cord. The arrangement of processes in the cord is fairly consistent along the length of the cord, although there may be local distortions. Fingers of hypodermis (HDC) often project from hypodermal cells and run along the cord for short distances. Muscle cells have darkly staining, conical, dense bodies (DB) in the Z bands.

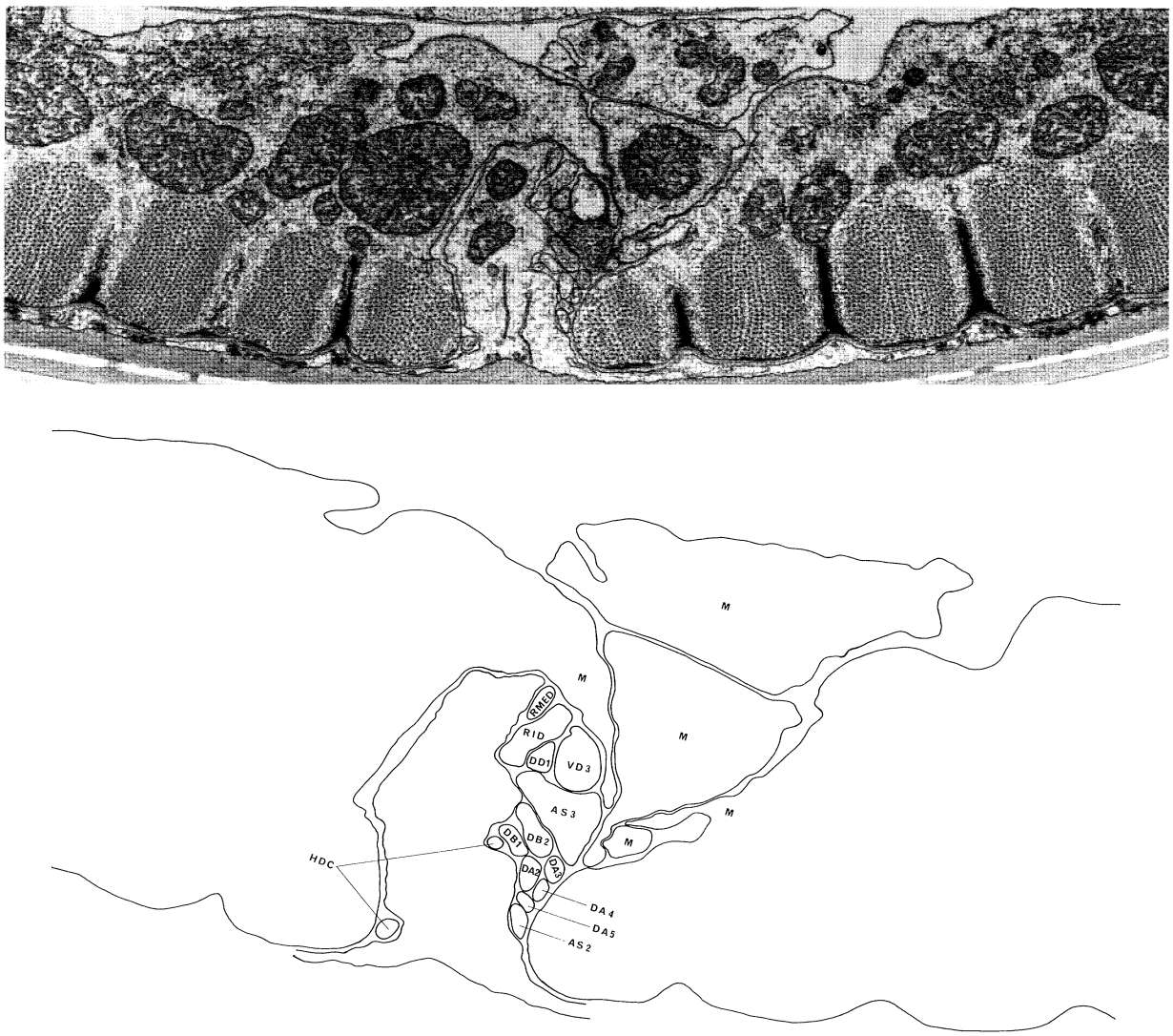


FIGURE 19. Transverse section through the dorsal cord (above) and process identifications (below). The dorsal cord is similar in overall structure to the ventral cord but is much simpler, as it has fewer processes and no cell bodies. The processes in the dorsal cord are all motoneuron axones except for the processes of VDn and RMED. DAn, DBn, ASn, DDn and VDn all have processes in the dorsal cord that originate from cell bodies in the ventral cord via circumferential commissures (figure 7). RID sends a process along the length of dorsal cord from its cell body, which is situated in the dorsal ganglion.

differentiation of their processes into regions that are both pre- and postsynaptic, and regions that are exclusively postsynaptic. In the case of motoneurons it is not clear whether there are no synapses made by the axon when it is in the interior of the process bundle because there are no suitable postsynaptic targets (muscle arms) available in the neighbourhood, or whether this region of the process is intrinsically incapable of supporting synapses. If this latter interpretation is correct, it may be that particular adhesion factors are also associated with these differentiated regions of the process. A factor that was localized in presynaptic regions that conferred an adhesive affinity with the basal lamina could, for example, serve to constrain the process to run alongside the basal lamina in these regions.

(a)

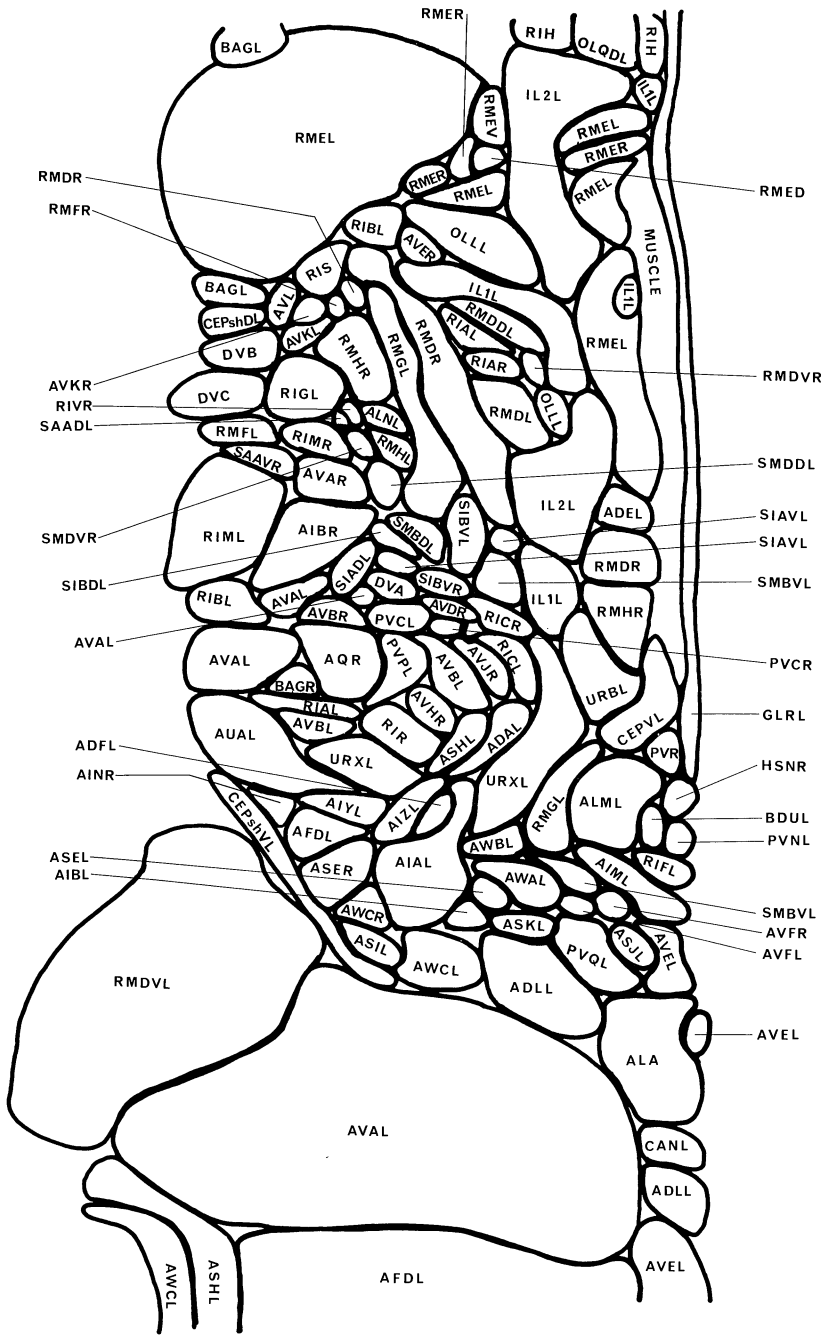


FIGURE 20. Reconstructed cross sections of neuropile of nerve ring; (a) left lateral, (b) right lateral, (c) dorsal and (d) ventral. These drawings were obtained by reconstructing pictures of transverse sections of the nerve ring, so there are no single corresponding electron micrographs. The large outlines peripheral to the neuropile are cell bodies. The relative disposition of processes in the nerve ring is relatively constant; several processes can usually be identified directly from an electron micrograph by their morphology and position in the process bundle. The axonal regions of motoneurons are situated adjacent to the anterior inner surface of the nerve ring and synapse onto muscle arms through a basal lamina. The processes of GLR cells flatten out in this region and form a cylinder on the inside of the muscle arms. The neuropile of the ring is fairly regionalized; the amphid receptors and their associated interneurons have processes in the posterior of the ring, the neurons that make up the sub-lateral cords have their processes in the centre and the mechanoreceptors tend to have processes in the anterior regions.

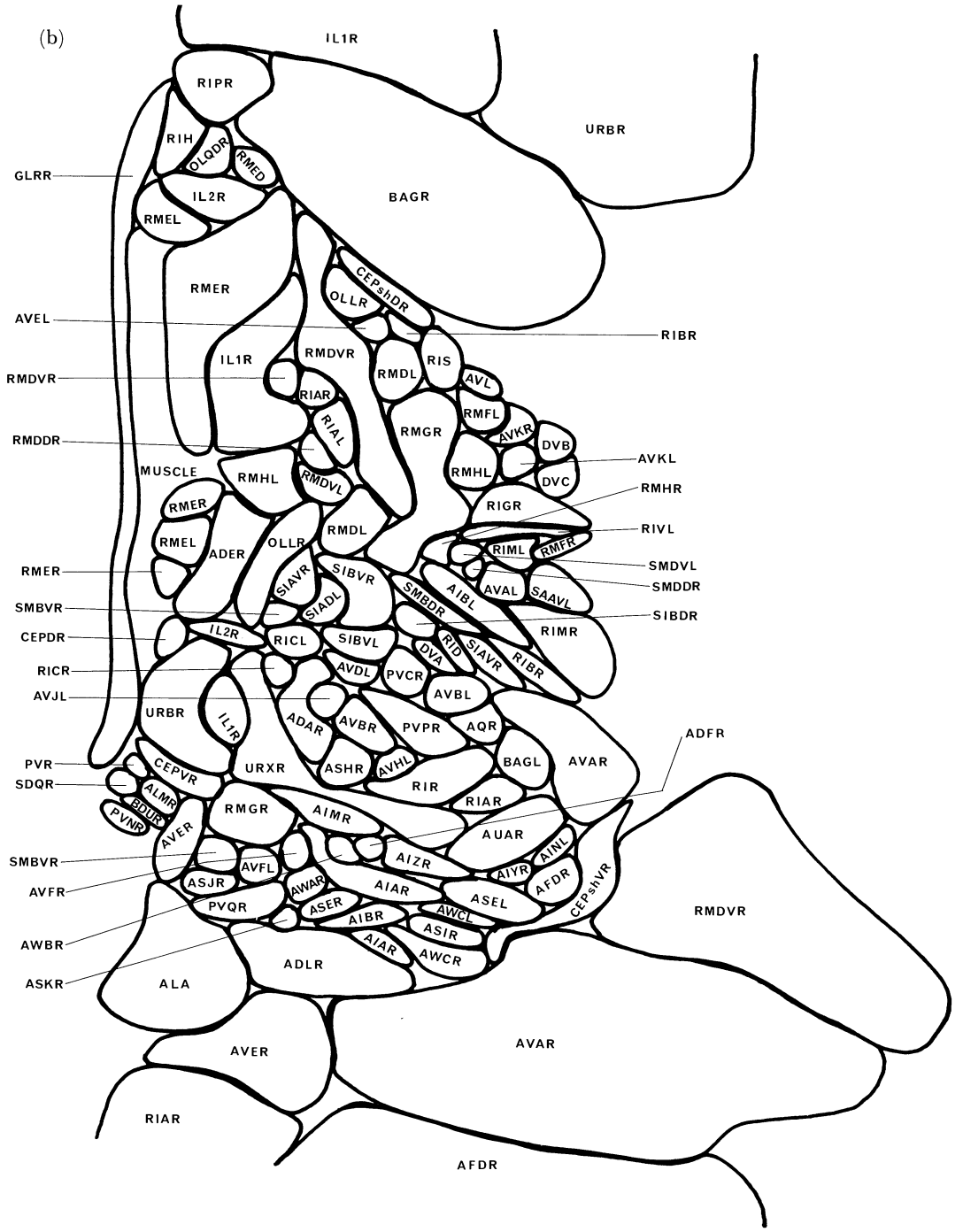


FIGURE 20 (b). For description see opposite.

Circuitry

We have summarized the connectivity data of the neurons detailed in Appendix 1 into a set of connectivity diagrams (figure 21 a–f). In these diagrams, we have lumped together all members of a class and considered the connectivity of the class as a whole. Connectivity was used as one of the main criteria for grouping neurons into classes and so, by definition, all

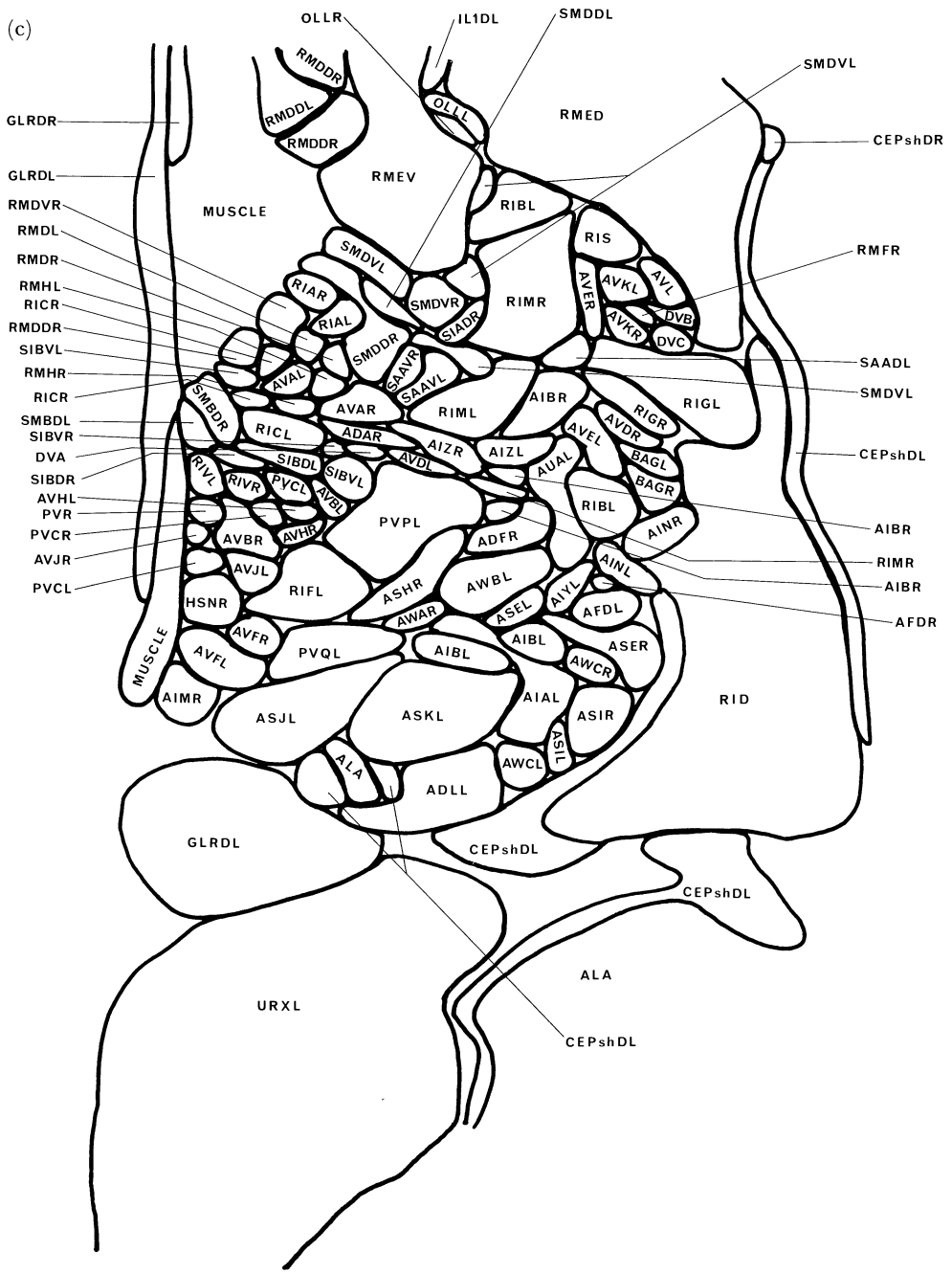


FIGURE 20 (c). For decription see page 40.

neurons within a class have the same, or very similar, patterns of connectivity to members of other classes. Thus such class groupings considerably simplify the circuit diagrams but at the expense of obscuring intraclass differences in synaptic connectivity. Such differences do not break class rules but specify which particular member of a class synapses to which particular member of another class.

The connections between classes that are shown are those that are considered to be

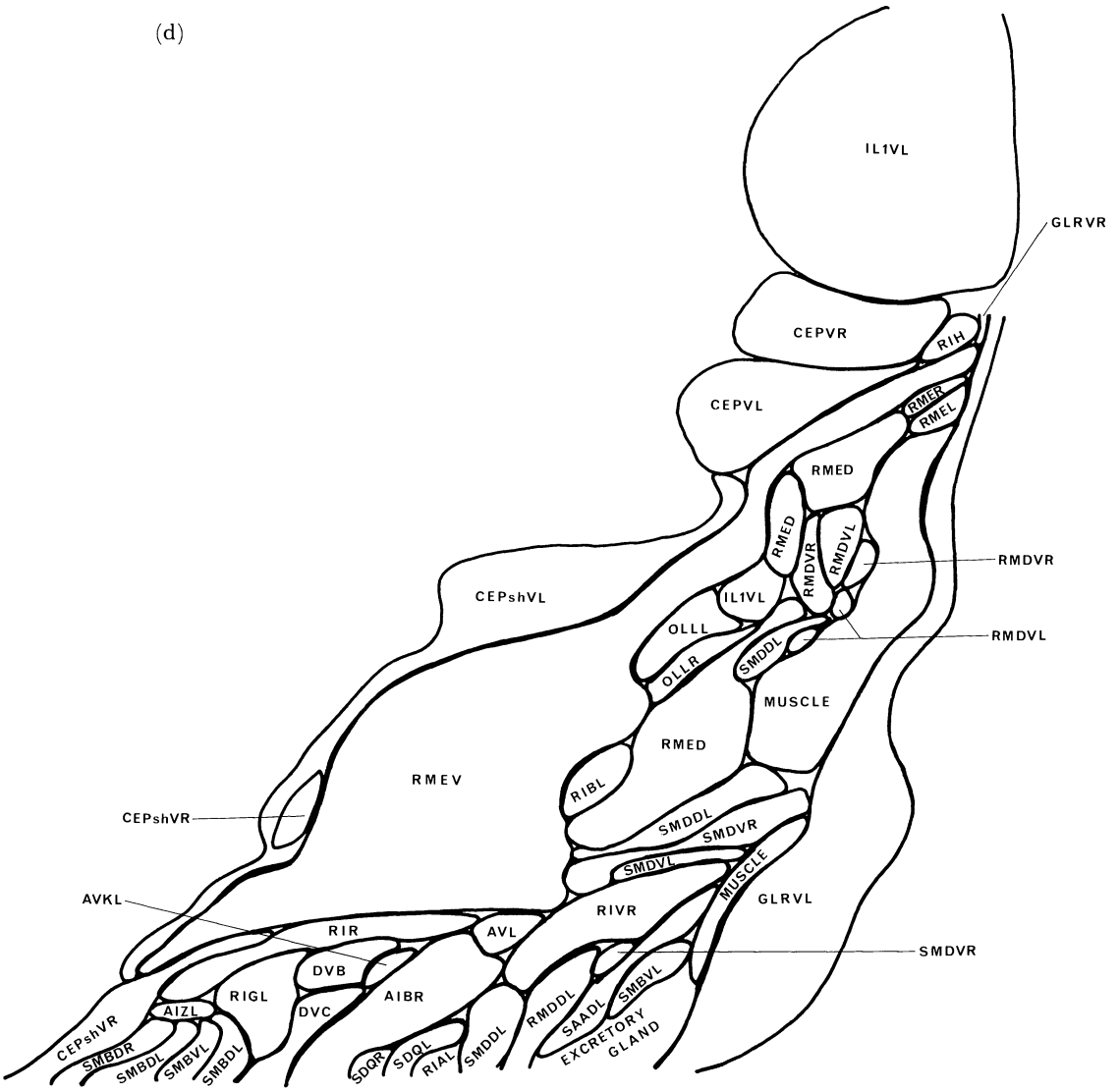


FIGURE 20(d). For description see page 40.

significant. In addition, some indication has been given of the relative prominence of chemical synapses. A number of criteria were considered when making these judgements. For chemical synapses, the numbers and sizes of the synapses in a particular connection were taken into account. In marginal cases, where there were only one or a few small synapses, consideration was also given as to whether the synaptic contacts were all dyadic (with the consequent ambiguities in the identification of the functional postsynaptic partners) and whether they were

DESCRIPTION OF FIGURE 21 (OVERLEAF)

FIGURE 21. Circuit diagrams of nervous system. Diagrams show the pattern of connections made via gap junctions (T) and via chemical synapses (arrows) between classes of neuron. Sensory neuron classes are represented by triangles, interneurons by hexagons and motoneurons by circles. Chemical synaptic connections are graded according to their prominence on a scale of 1 to 4 (cross-hatches on arrows). Most neuron classes have been included in the diagrams; some have been included in more than one diagram for clarity.

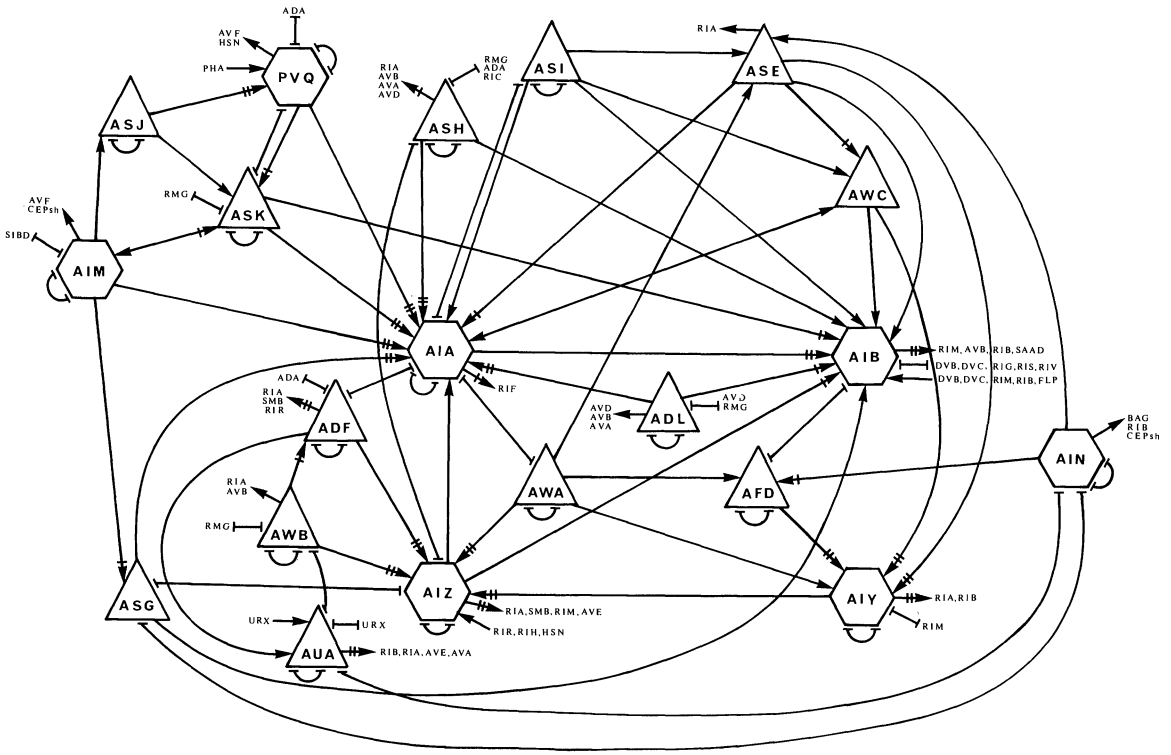


FIGURE 21. (a) Circuitry associated with amphids.

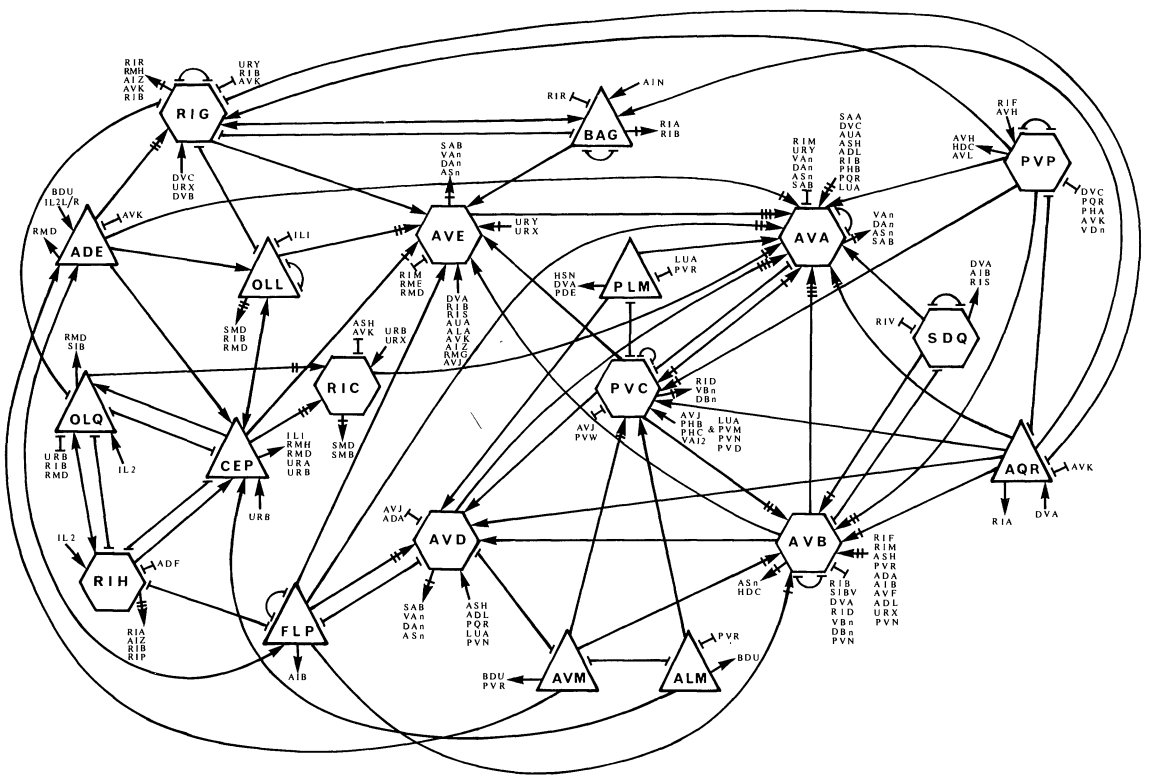


FIGURE 21. (b) Circuitry associated with other sensory receptors in the head.

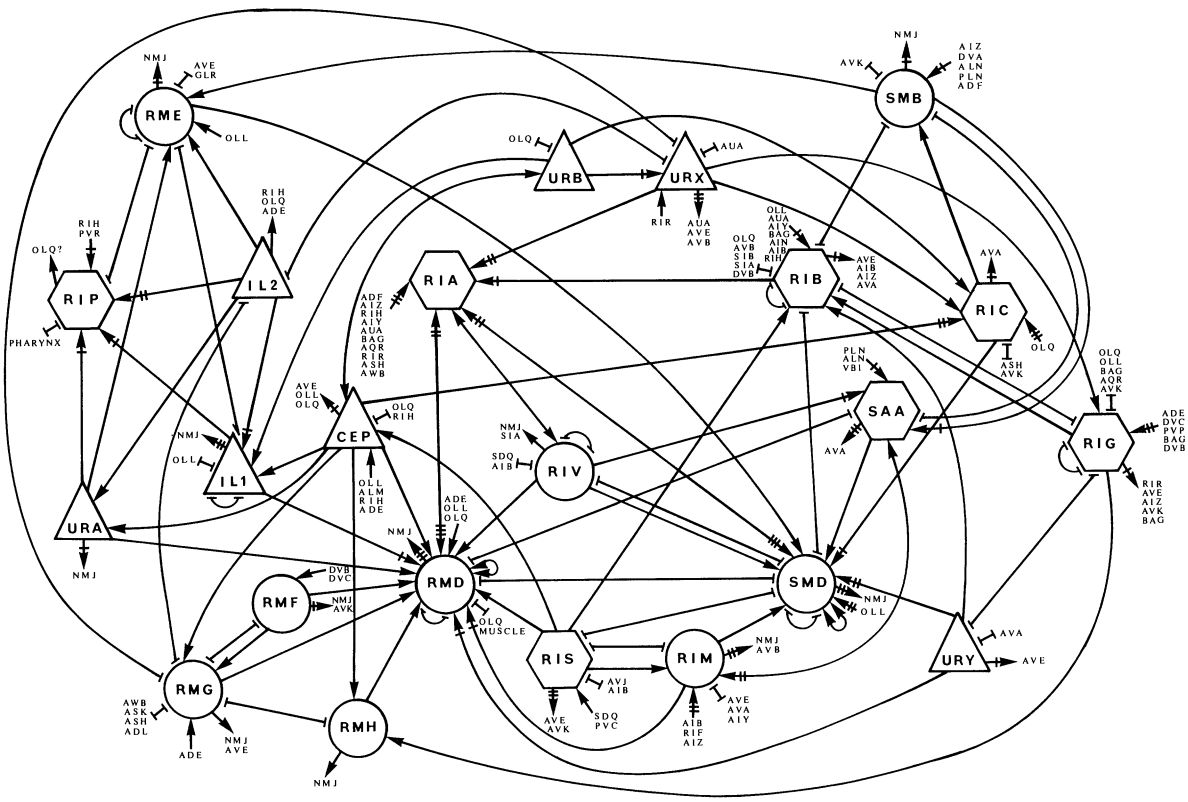


FIGURE 21. (c) Circuitry associated with the motoneurons in the nerve ring.

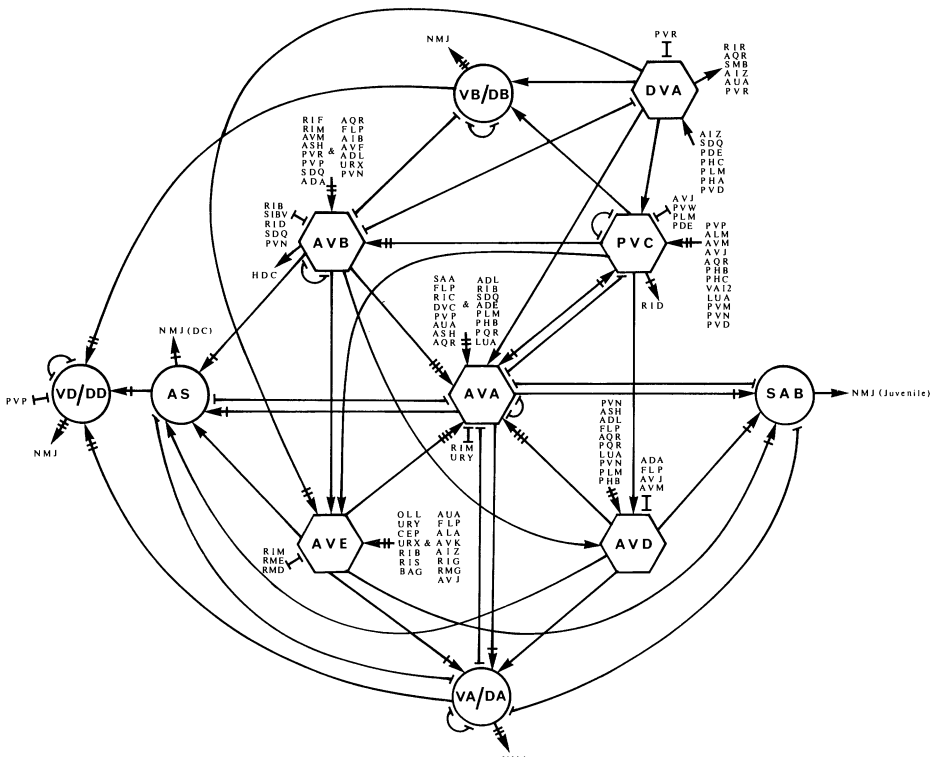


FIGURE 21. (d) Circuitry associated with the motoneurons of the ventral cord.

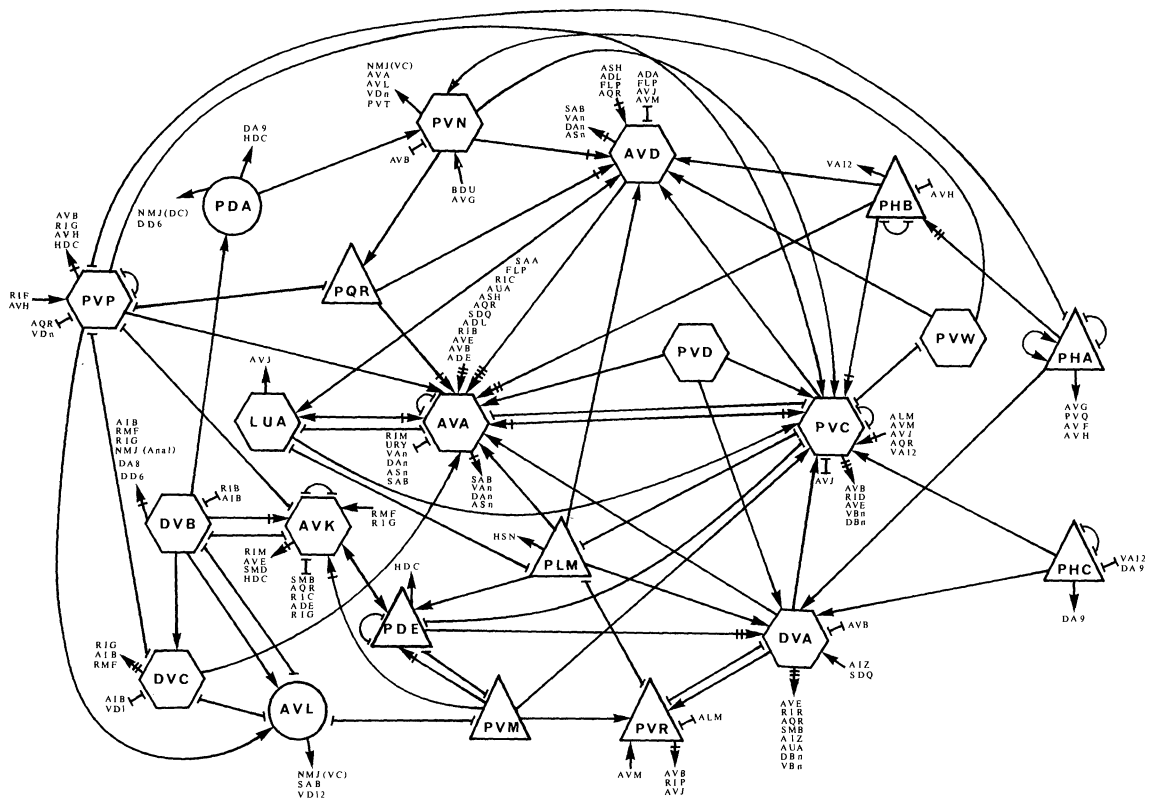


FIGURE 21. (e) Circuitry associated with neurons in the tail ganglia.

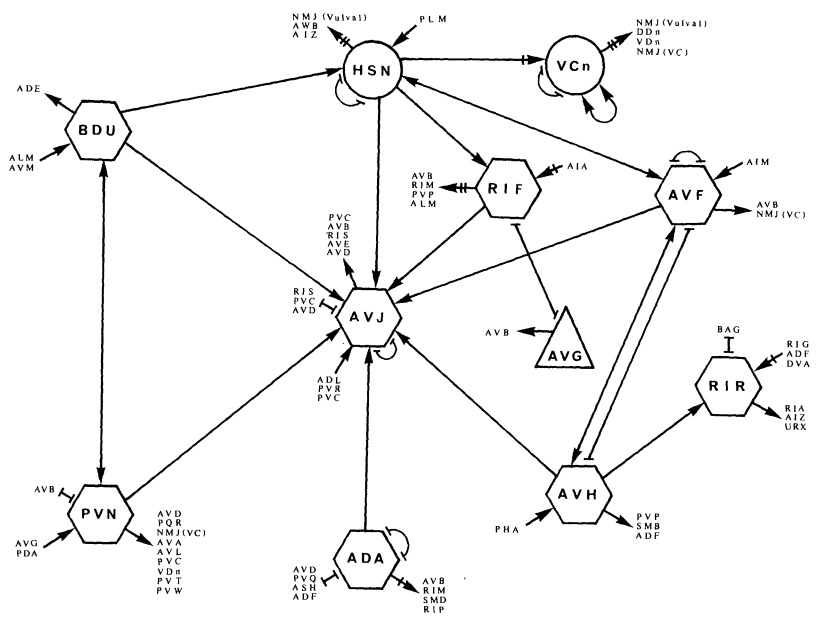


FIGURE 21. (f) Egg-laying circuitry.

present on symmetrical analogues, or corresponding cells in another animal. In the case of gap junctions, the main criteria were the area of contact and darkness of staining of the structures, and again whether they were present between analogous partners in the same or in other animals.

Triangular patterns of connectivity

One of the striking features of the connectivity diagrams is the high incidence of triangular connections linking three classes. These structures may occur frequently as a consequence of the organization of the neuropile. A typical neuron in *C. elegans* is accessible (i.e. adjacent) to a fairly limited subset of the total complement of neurons but is fairly highly locally connected within this subset (White *et al.* 1983). Thus, if a neuron has synaptic contacts with two partners, these two partners must be neighbours to the neuron and therefore are likely to be neighbours themselves. It is therefore quite probable, given the high level of local connectivity, that there will be a synaptic contact between them, which will close the triangle. The abundance of triangular connections in the nervous system of *C. elegans* may thus simply be a consequence of the high levels of connectivity that are present within neighbourhoods.

Gap junction circuitry

Of the 104 classes of neuron in the main (i.e. non-pharyngeal) nervous system, 92 have gap junctions. Many of these classes make gap junctions to members of their own class if they are accessible to them (48 classes form such intraclass junctions). This is in marked contrast to the chemical synapses, where unambiguous synapses between members of the same class are extremely rare. Gap junctions are the presumed mediators of electrical coupling between cells, and so it seems likely that the gap junctions seen between members of a class may act to smooth discontinuities of electrical activity between adjacent class members. This may be important for classes such as the ventral cord motoneurons, for example, where marked differences in activity of adjacent motoneurons may be inimical to the smooth wave propagation required for locomotion.

Many neurons have a process that terminates at its point of contact with a process from a neuron of the same class. Most of the neurons of the amphid sensilla behave in this way, as do the DDn and VDn motoneurons of the ventral cord. In nearly all the cases where this apparent contact termination of process growth is seen, there is a gap junction at the site of contact. (The processes of RIF on the dorsal mid-line are the one striking counterexample to this general rule.) It seems possible that, in these cases, gap junctions may facilitate intercellular communication of the signals for inhibiting process extension.

Functional classification of neuron classes

The simplest functional groupings of neurons that are usually made are their categorizations as either receptor neurons, interneurons or motoneurons. We have used symbols to represent these neuron types in the connectivity graphs of figure 21. Assignment of a particular class to a group is, however, not straightforward; several neuronal classes have to be assigned to more than one group, because they appear to combine two or more of these basic functions. We will go on to discuss some of the characteristics of neurons in each of these three major groupings.

Sensory receptors

The lack of electrophysiological data on any of the neurons of *C. elegans* makes the identification of sensory receptors and their associated modalities rather tentative. We have, however, selected a set of 39 neurons, which, on the basis of morphology and connectivity, are likely to function as sensory receptors; these have been listed in table 1.

TABLE 1. PUTATIVE SENSORY RECEPTORS

Neuron	sensillum	external access	ciliated	rootlet	differentiated ending
ASE	amphid	+	+	·	·
ASG	amphid	+	+	·	·
ASH	amphid	+	+	·	·
ASI	amphid	+	+	·	·
ASJ	amphid	+	+	·	·
ASK	amphid	+	+	·	·
ADF	amphid	+	+ (dual)	·	·
ADL	amphid	+	+ (dual)	·	·
AFD	amphid	·	+	·	+
AWA	amphid	·	+	·	+
AWB	amphid	·	+	·	+
AWC	amphid	·	+	·	+
PHA	phasmid	+	+	·	·
PHB	phasmid	+	+	·	·
IL2	inner labial	+	+	·	·
IL1	inner labial	·	+	+	·
OLQ	outer labial quadrant	·	+	+	·
OLL	outer labial lateral	·	+	·	·
CEP	cephalic	·	+	·	·
ADE	anterior deirid	·	+	·	·
PDE	posterior deirid	·	+	·	·
BAG	·	·	+	·	+
FLP	·	·	+	·	+
AQR	·	·	+	·	·
PQR	·	·	+	·	·
URX	·	·	·	·	+
URY	·	·	·	·	+
ALM	·	·	·	·	+
PLM	*	·	·	·	+
AVM	·	·	·	·	+
PVM	·	·	·	·	+
URA	†	·	·	·	·
URB	†	·	·	·	·
AUA	†	·	·	·	·
AVG	*	·	·	·	·
ALN	*	·	·	·	·
PLN	*	·	·	·	·
PHC	*	·	·	·	·
PVR	*	·	·	·	·

* Neurons that have undifferentiated processes that run into the tailspike.
† Neurons that have undifferentiated processes that run up to the tip of the head.

The component neurons of sensilla are the neurons that are most likely to have a sensory transduction function (Ward *et al.* 1975). There are two general types of sensillum: those that have channels that open to the outside, exposing some or all of the neurons to the external chemical environment, and those that have no such channel. The former class is generally

considered to be chemosensory and the latter, mechanosensory in function. The component neurons of sensilla are all ciliated and some of the presumed mechanoreceptors also have ciliary rootlets. There are several other classes of neurons that are not components of sensilla but which we suspect may be sensory transducers; these are also listed in table 1. The factors that have been taken as being indicative of a possible sensory function are: the presence of a cilium, the presence of a specialized, morphologically differentiated ending or the presence of a long, morphologically undifferentiated process that projects into the extremities (the tailspike or the tip of the head). In addition to these criteria, all the putative receptors should be exclusively or predominantly presynaptic.

Of the putative receptors listed in table 1, one group has a definitely known modality; another's is known with a fair degree of confidence. Laser ablation studies have shown that ALM, PLM, AVM and probably PVM transduce touch, i.e. light mechanical pressure (Chalfie & Sulston 1981). The amphid sensilla are strongly implicated as being necessary for the chemotaxis response, as several chemotaxis-defective mutants have aberrant amphidial neurones (Lewis & Hodgkin 1977).

Interneurons

The interneurons in *C. elegans* are fairly diverse in their general organization, but some classes are conspicuous in that they are restricted in the classes of neuron with which they interact. The interneurons AIA, AIB, AIY and AIZ, for instance, receive synaptic input predominantly from the neurons of the amphid sensilla (figure 21a), whereas RIC receives its synaptic input from putative mechanoreceptors (figure 21b). Other interneurons do not show such a restriction in sensory modalities and receive synaptic input from many sources (see, for example, AVA).

The only other striking grouping that is seen in interneurones is of the classes whose synaptic outputs are directed primarily to motoneurons. These classes are AVA, AVB, AVD, AVE and PVC, which synapse onto motoneurons in the ventral cord, and RIA, which synapses onto motoneurons in the nerve ring. These interneuron classes are among the most prominent neurons in the whole nervous system. They generally have larger-diameter processes than other neurons and have many synaptic connections.

Motoneurons

Each of the motoneurons in *C. elegans* innervates a specific group of muscle cells. This is particularly noticeable in the head region, where there is a fairly precise mapping of motoneurons onto their target muscles. Body-wall muscles are innervated by motoneurons in both the nerve ring and ventral cord. Each of these regions of neuropile contains its own unique set of motoneuron classes. The body-wall muscles can be logically divided into three regions according to the source of innervation: the head region, which receives innervation from motoneurons in the nerve ring, the neck region, which is dually innervated by motoneurons of the nerve ring and ventral cord, and the rest of the body region, which is innervated by motoneurons of the ventral cord (figure 10).

Each member of a motoneuron class in the nerve ring generally innervates muscle cells in two adjacent rows (table 2). Motoneuron classes with fourfold symmetry innervate all eight rows of muscle with no overlap, whereas motoneurons with sixfold symmetry have fields of innervation that overlap with each other by one row on each side but not across the

dorso-ventral mid-line (table 2). Most of the classes of motoneuron with bilateral symmetry innervate only the lateral four rows; the exception is RIV, which only innervates ventral rows (table 2).

In addition to the intraclass circumferential mapping shown by the ring motoneurons there is also some anteroposterior mapping between classes; some motoneuron classes only innervate head muscles, some only neck muscles, while others innervate both (tables 2 and 3).

TABLE 2. MUSCLES INNERVATED BY MOTONEURONS IN THE NERVE RING

	DLM	DLL	VLL	VLM	VRM	VRL	DRL	DRM
IL1DL	A, B	A	·	·	·	·	·	·
IL1L	·	B, A	A	·	·	·	·	·
IL1VL	·	·	A	A	·	·	·	·
IL1VR	·	·	·	·	A	A	·	·
IL1R	·	·	·	·	·	A, B	A, B	·
IL1DR	·	·	·	·	·	·	A	A
RIML	·	·	·	·	·	C	C	·
RIMR	·	C, D	C, D	·	·	·	·	·
RIVL	·	·	·	·	C, D	C	·	·
RIVR	·	·	C	C, D	C	·	·	·
RMDDL	·	·	·	·	·	A	A, B	A
RMDL	·	B, C	·	·	·	A, B, C	A, B	·
RMDVL	·	·	·	·	A, C, D	A	·	·
RMDVR	·	·	A, B	A, D	C	·	·	·
RMDR	·	B, C	C	·	·	·	·	·
RMDDR	A, B	A, B	A	·	·	·	·	·
RMED	·	·	·	A, B, C	A, B	·	·	·
RMEL	·	·	·	·	·	A, B	A, B	·
RMEV	A, B, C	·	·	·	·	·	·	A, B
RMER	·	A, B	A	·	·	·	·	·
RMFL	·	·	·	·	·	A, B	B	·
*RMFR	·	·	·	·	·	·	·	·
RMGL	·	C	C	·	·	·	·	·
RMGR	·	·	·	·	·	C, D	C	·
RMHL	·	·	·	·	·	A	A, B	·
RMHR	·	A, B, C	A	·	·	·	·	·
SMBDL	·	·	·	·	·	·	A, B,	A, B, C
SMBVL	·	·	A, B	A, B, C	·	·	·	·
SMBVR	·	·	·	·	A, B, C	A, B	·	·
SMBDR	A, B, C	B	·	·	·	·	·	B
SMDDL	B, C	·	·	·	·	·	B	B, C
SMDVL	·	·	·	·	A	B		
SMDVR	·	·	B	B	·	·	·	·
SMDDR	B, C	C	·	·	·	·	·	·
URADL	A, B	B	·	·	·	·	·	·
URAVL	·	·	A	A, B	·	·	·	·
URAVR	·	·	·	·	A, B	A, B	·	·
URADR	·	·	·	·	·	·	A, B	A

DLM ≡ dorsal left medial, VRL ≡ ventral right lateral, etc.
* Branch to NMJ region not present on this cell in N2U animal.
A, B, C, D – sequences of muscle cells in each row, anterior to posterior.

The muscles in the main part of the body are not so precisely mapped by motoneurons as those in the head. The ventral cord motoneurons either innervate dorsal muscles or ventral muscles (table 3), there being no finer circumferential divisions. The members of each class are evenly distributed along the length of the cord and so give rise to a longitudinal mapping onto the body muscles.

The vulval muscles are innervated by two main classes of motoneuron, VCn and HSN. The

TABLE 3. MAJOR MOTONEURON CLASSES

motoneuron class	muscles innervated: head	neck	body	vulval	anal	postsynaptic at NMJs	extended distal processes	processes in sub-lateral cords
IL1	+	·	·	·	·	·	·	·
RIM	·	+	·	·	·	·	·	·
RIV	·	+V	·	·	·	·	·	·
RMD	+	+	·	·	·	+	·	·
RME	+	+	·	·	·	+	·	·
RMF	+	·	·	·	·	·	·	·
RMG	·	+	·	·	·	·	·	·
RMH	+	·	·	·	·	·	·	·
SMB	+	+	·	·	·	·	+	+
SMD	+	+	·	·	·	+	+	+
URA	+	·	·	·	·	·	·	·
DAn	·	+*D	+D	·	·	·	+	·
VAn	·	+*V	+V	·	·	·	+	·
DBn	·	+*D	+D	·	·	·	+	·
VBn	·	+*V	+V	·	·	·	+	·
DDn	·	+*D	+D	·	·	+	·	·
VDn	·	+*V	+V	·	·	+	·	·
ASn	·	+*D	+D	·	·	·	·	·
HSN	·	·	·	+	·	·	·	·
VCn	·	·	+V	+	·	·	·	·
DVB	·	·	+	·	+	·	·	·

D, dorsal muscles only; V, ventral muscles only; otherwise both.
*, only the most anterior members of the class make these NMJs.

VCn motoneurons also innervate the ventral body muscles but the HSNs never do this, synapsing exclusively onto the vulval muscles. The other classes of motoneuron that innervate ventral body muscles (VAn, VBn and VDn) also have a few synapses onto the vulval muscles (figure 11); thus the HSNs appear to be the only neurons that are specific for these muscles.

The only motoneuron class that has been seen to synapse onto the set of muscles that mediate defecation is DVB, but only via a single synapse onto the intestinal muscles. The defecation muscles are all coupled together via gap junctions, so it is possible that this single synapse from DVB is the route by which defecation is controlled from the central nervous system. DVB also makes a few synapses onto body muscles.

Several motoneuron classes have long, apparently undifferentiated processes, distal to the regions where NMJs are situated, before they eventually terminate (table 3). It has been suggested in the case of the ventral cord motoneurons VA, DA, VB and DB, that these regions may function as stretch receptors (L. Byerly and R. L. Russell, personal communication). These processes will be stretched when the body bends. This arrangement of the stretch-receptive region adjacent to the NMJ region will therefore result in body curvature's being transduced into motor activity in an adjacent region. This will mediate the translation of the region of curvature along the body. The ring motoneurons have processes that run circumferentially around the nerve ring. Two classes of motoneuron in the nerve ring have processes that leave the nerve ring distally from the region where their NMJs are situated (SMB and SMD). These processes turn and run longitudinally down the sub-lateral cords. Running in these locations, these processes are ideally situated to monitor bend in the anterior body, if these processes have a stretch-transducing function. This would not be the case, however, if they ran round the nerve ring following on from their proximal regions.

Several classes of motoneuron have processes that are postsynaptic at the NMJs of other

neuron classes (table 3), and have their NMJs diametrically opposite these postsynaptic regions. There is nearly always another neuron present, of the same or similar class, which has the converse arrangement of postsynaptic and presynaptic regions, i.e. it has NMJs where its partner is postsynaptic and is itself postsynaptic in the diametrically opposite region where its partner has NMJs (the DDn neurons in the L1 are notable exceptions to this generalization – White *et al.* 1978). This reciprocal arrangement of pairs of such neurons suggests that they may act as reciprocal inhibitors, picking up excitatory synaptic input to muscles from other classes of neuron and relaying this round to the other side of the animal as an inhibitory input to the diametrically opposite muscles, ensuring that they work in antiphase. The postsynaptic regions of these putative cross-inhibitor classes often receive a few synapses from their contralateral partners (RMD has rather more of these connections than other motoneuron classes of this type). If these synapses are inhibitory, as is assumed to be the case for the NMJs, then they could add a certain amount of positive feedback to the system. This would have the effect that when the other (i.e. non-cross-inhibitor) neuron classes are activated, the system would act as a bi-stable switch with one side activated and the other inhibited. If the cross-inhibitors have a time dependent component in their response to stimulation, then the system could oscillate, one side being activated after the other in succession.

Two classes of motoneuron that have their NMJs in the nerve ring, IL1 and URA, are also probably sensory receptors. The IL1 neurons are components of the inner labial sensilla; they may respond to mechanical stimulation at the extreme tip of the head. Presumably such a simple connection acting directly on to muscles can only mediate a simple withdrawal response. The function of URA is not clear; it is probably a sensory receptor as it is predominantly presynaptic in the ring and sends processes to the tip of the head, but the appearance and disposition of these presumed sensory endings gives no indication as to their sensory modality.

Connectivity

The availability of the complete connectivity data for a nervous system generates an almost irresistible desire to speculate extensively on the function of such a structure. We will, however, try to resist this temptation and leave such speculations for future work, when we hope that they can be backed up by corroborative experimental data. We will, therefore, try to confine our comments to the general features of the connectivity, some of which may not be obvious from the connectivity diagrams, and to the functional aspects of those parts of the circuitry for which there is some relevant experimental data.

Amphids (*figure* 21*a*)

The neurons of the amphid sensilla have synaptic outputs that are predominantly focused onto four interneurons: AIA, AIB, AIY and AIZ. Most of the receptors that are situated in the amphid channel synapse onto the AIA–AIB pair, whereas most of the accessory neurons that are associated with the amphid sheath cells synapse onto AIY–AIZ. The amphid channel receptor, ASJ, is unusual in that it alone synapses onto none of the four main amphid associated interneuron classes, but instead synapses onto PVQ, an interneuron class that has cell bodies in the tail. PVQ also receives synaptic input from the phasmid receptor neurons, PHA, in the tail, and synapses onto AIA, thereby providing an indirect route from ASJ onto the major interneurons.

The interneurons AIA and AIB generally receive a common synaptic input from their presynaptic partners. These are usually (but not exclusively) mediated by dyadic synapses,

with the closely associated processes of AIA and AIB being the postsynaptic elements. There is generally a bias to AIA, in that receptor neurons often have additional monadic synapses to AIA or dyadic synapses to AIA with an alternative co-recipient. The main synaptic output of AIA is onto AIB, and this closes the triangles made by all the neurons that synapse onto both AIA and AIB. The output from these triangular subcircuits is derived from AIB and is mainly directed to the nerve ring motoneurons, RIM, and the ventral cord interneurons, AVB.

The interneurons AIY and AIZ do not make as many triangular connections as are seen on AIA and AIB, although AIY synapses onto AIZ in an analogous way to the synapse from AIA onto AIB. The main synaptic outputs of both AIY and AIZ are onto RIA interneurons, which in turn synapse onto the putative cross-inhibitor motoneurons of the nerve ring, RMD and SMD.

Several of the receptor neurons make direct synaptic contacts with some of the other major interneurons, thereby bypassing the AIA–AIB–AIY–AIZ system. Most notable of these are the connections made by ASH and ADF onto RIA and the somewhat less prominent connections made by ASH and ADL onto the ventral cord interneurons AVA, AVB and AVD.

There are several instances of receptor neurons synapsing directly onto other receptor neurons. Some of these synapses are quite striking (that of ASE onto AWC, for example) and some receptors synapse onto more than one other receptor. These receptor–receptor synapses are not peculiar to the amphid receptors as they are seen between many different classes of receptor neuron, although the amphid receptors predominantly synapse onto other amphid receptors. It seems likely that such receptor–receptor connections facilitate the modulation of the activity of one receptor by another.

Other receptors in the head and their associated interneurons (figure 21 b)

Many of the putative sensory receptors in the head, apart from those of the amphid sensilla, have connections either directly or indirectly to the five major classes of ventral cord interneuron that innervate body muscles (AVA, AVB, AVD, AVE and PVC). OLL and CEP synapse directly onto AVE; CEP and OLQ synapse onto RIC, which in turn synapses onto AVA, for example. There are also connections to the motoneurons in the nerve ring, such as the direct connections made by OLL onto SMD or the connections made to SMD and SMB by OLQ and CEP indirectly via RIC. Most of the putative sensory receptors are not exclusively postsynaptic but receive synaptic input primarily from other sensory receptors; however, these receptor–receptor connections are not as prominent as receptor–interneuron or receptor–motoneuron connections. The only receptors with a well characterized sensory modality are the touch receptors ALM, PLM and AVM (Chalfie & Sulston 1981). ALM and AVM have long, differentiated processes that run in the anterior regions of the body, whereas the processes of PLM span the posterior regions. Stimulation of the anterior neurons, by gently stroking animals with a fine hair, causes animals to move backwards; stimulation of the posterior neurons causes the animals to move forwards. Laser ablation studies have shown that these responses are primarily mediated by the connections made to AVA, AVD, PVC and AVB (Chalfie *et al.* 1984).

Motoneurons in the nerve ring (figure 21 c)

Two prominent motoneuron classes, RMD and SMD, are probable cross-inhibitors in the nerve ring. RMD receives extensive synaptic input from most of the motoneurons of the ring (including itself) at dyadic NMJs. Each of the SMD neurons has only one dendritic process

that enters the NMJ region of the ring; this is postsynaptic to RME and the contralateral SMD. The dorsal and ventral RMEs (RMED and RMEV) have dendritic processes that are postsynaptic at the NMJs made by SMB. The lateral RMEs have no such processes, however, and so it is not clear whether this class should be considered to be a cross-inhibitor.

The putative cross-inhibitors of the nerve ring receive extensive synaptic input from interneurons. This is quite unlike their counterparts in the ventral cord (DDn and VDn), which are only postsynaptic to ventral cord motoneurons at NMJs. The RIP interneurons, which provide the only connection between the central nervous system and the pharyngeal nervous system, have several of the features of cross-inhibitor motoneurons; they are postsynaptic at the NMJs made by the receptors IL1 and URA, and have axonal processes that cross over to the contralateral side. It seems likely that they may act to inhibit pharyngeal pumping on receipt of an appropriate stimulus from IL1, URA or IL2.

The major source of synaptic input to the RMD and SMD cross-inhibitors comes via extensive synapses from RIA interneurons. These connections are reciprocal; the reverse connections are quite significant although not as numerous as the forward connections. RIA is one of the most prominent interneurons in the nerve ring and receives extensive synaptic input from the RIB interneurons, neurons associated with the amphid sensilla and other putative sensory receptors with no obvious modality. RIB is also a fairly prominent interneuron, which makes synaptic connections with diverse partners.

The putative receptors IL1 and URA are both fairly prominent motoneurons in the nerve ring. They behave as other motoneurons, and make quite extensive NMJs, which are also presynaptic to cross-inhibitor neurons. They also receive synaptic input from other putative receptor neurons, notably IL2 and CEP. The IL2 receptors share the same inner labial sensilla as the IL1 receptors or motoneurons, but unlike the IL1 receptors they are open to the outside and so are probably chemoreceptive.

The SAA interneurons have long, anteriorly directed, undifferentiated processes that run in the sub-lateral cords. These processes could possibly act as stretch receptors monitoring the posture of the tip of the head. The main synaptic output of SAA is directed to the major ring motoneurons, RIM, and the ventral cord interneurons, AVA. There is synaptic input from the SMB motoneurons and the VB1 ventral cord motoneurons. Thus SAA interacts with the body and the head motor systems and, given its possible head-posture transducing function, it seems likely that these interneurons could function to couple and coordinate head and body movements. Such coupling seems to occur during forward locomotion, as there are no discontinuities between head and body movements in this situation.

Motoneurons of the ventral cord (*figure* 21*d*)

The ventral and dorsal body muscles are innervated by their own sets of motoneurons. Both sets of motoneurons have cell bodies that reside in the ventral cord (figure 4) and receive their synaptic inputs from interneurons that have processes that run along the cord. The motoneurons that innervate dorsal muscles have axons that run in the dorsal cord and join up to their cell bodies in the ventral cord via circumferential commissures (figure 7).

There are four classes of motoneuron that innervate ventral muscles (VAn, VBn, VDn, and VCn), and four that innervate dorsal muscles (DAn, DBn, DDn and ASn). Of these, the VAn and DAn classes are similar and should probably be considered to be the same class, as both have forward-directed axons and both have the same pattern of synaptic input from

interneurons in the cord. In an analogous way, VBn and DBn should probably be considered as one class, as again both have the same pattern of synaptic input and the same direction of axon projection, only in this case they are posteriorly directed. All four of these classes have long, undifferentiated distal regions on their axons, in contrast to the processes of VDn and DDn motoneurons, which end abruptly at the point of contact with the process of an adjacent neuron of the same class.

The VDn and DDn motoneurons receive their synaptic input solely from the other motoneuron classes on one side of the animal, usually at dyadic NMJs, and have their own NMJs on the opposite side. On the dorsal side, DDn has NMJs and VDn is postsynaptic; on the ventral side, VDn has NMJs and DDn is postsynaptic. The VDn and DDn could again be considered as a single class; the disposition of their processes and axons suggests that they probably are cross-inhibitors. The DDn neurons have been shown to rewire in the course of larval development (White *et al.* 1978). In the L1 (first stage) larva their polarity is reversed from that of the adult, having NMJs on the ventral side and being postsynaptic to DAn and DBn motoneurons on the dorsal side. The DAn, DBn, SAB and DDn are the only classes of motoneuron present in the L1 ventral cord; the other classes develop post-embryonically (Sulston & Horvitz 1977).

The SAB neurons have no synaptic outputs in the adult and L4 larval stages, but in the first stage (L1) larva the three neurons of this class innervate anterior ventral body muscles (SAB-b). The only other motoneurons that are seen to innervate ventral body muscles at this stage are the putative cross-inhibitors DDn. This perhaps suggests that the SAB motoneurons may provide some excitatory inputs to the ventral body muscles during this stage. In several ways SAB neurons resemble VAn–DAn neurons. They have the same pattern of synaptic input as these classes and also have long undifferentiated distal endings to their anteriorly directed processes. These processes run in the sub-lateral cords, unlike the distal processes of VAn–DAn, which run ventrally.

The two remaining classes, ASn and VCn, are quite distinct and are less prominent with respect to their innervation of body muscles than the other classes. The ASn motoneurons innervate dorsal muscles and are somewhat similar to DAn motoneurons in morphology and synaptic input. The VCn motoneurons are primarily motoneurons for the vulval muscles (figure 11), but also innervate ventral body muscles.

There are five main classes of interneuron that provide synaptic input to the motoneurons of the ventral cord: AVA, AVB, AVD, AVE and PVC. All have cell bodies anteriorly in the lateral ganglia, except for PVC, which has its cell bodies in the lumbar ganglia in the tail. The classes AVD and AVE have identical patterns of synaptic output although they have quite different patterns of synaptic input. The processes of AVE terminate in the mid-body region, whereas the processes of all the other interneuron classes run the whole length of the ventral nerve cord. AVA, AVD and AVE make chemical synapses onto the VAn–DAn motoneurons; AVA also makes gap junctions to them. The dorsal motoneuron class, ASn, has all the classes of synaptic partner that VAn–DAn motoneurons have, and indeed makes gap junctions with them, but it receives an additional chemical synapse from AVB.

The VBn–DBn motoneurons are predominantly innervated by gap junctions from AVB and chemical synapses from PVC together with a few chemical synapses from DVA. Laser ablation experiments have demonstrated that, in the first stage larva, the DBn motoneurons are necessary for forward locomotion (backward-propagating body waves), and the DAn moto-

neurons are necessary for backward locomotion (forward-propagating body waves) (Chalfie *et al.* 1984). Because of their similar structure and identical patterns of synaptic input, it seems likely that VAn motoneurons have similar functions to DAn motoneurons, and likewise VBn motoneurons have similar functions to DBn motoneurons. Considering the sources of synaptic input to these classes of motoneuron, it seems likely that the AVB–PVC interneurons are used for forward movement and the AVA–AVD–AVE interneurons are used for backward movement. There is some evidence for this from laser ablation studies (Chalfie *et al.* 1984).

Circuitry associated with neurons in the tail (*figure* 21*e*)

The tail region of *C. elegans* contains a number of classes of receptor neuron, interneuron and motoneuron that are specific to this region. Most of these neurons project into the neuropile of the pre-anal ganglion, which is situated at the posterior extremity of the ventral cord. In general, synapses made by neurons in the tail are smaller and less numerous than those seen in the nerve ring or anterior ventral cord. Some classes of neuron, such as PVT, PVW and PDB, make very few synaptic contacts. The major interneurons in the tail circuitry are the ventral cord neurons, AVA, AVD and PVC, and two interneuron classes with cell bodies in the tail, DVA and LUA.

The tail has two pairs of sensilla, the phasmids and the posterior deirids. The phasmids are probably chemosensory, as their component neurons are open to the outside in a similar arrangement to the neurons of the amphid sensilla. There are two neurons in each sensillum, PHA and PHB. PHA is unusual; virtually all its synaptic output is directed onto the other phasmid neuron, PHB. This in turn synapses mainly onto AVA and PVC.

The posterior deirid sensilla are similar in structure to the anterior deirids, and both have been shown to contain the neurotransmitter dopamine (Sulston *et al.* 1975). The cell bodies of the single receptor neuron (PDE) and the accessory cells of the sensilla are situated in the lateral, mid-posterior regions of the body. The synaptic output of PDE is quite different from that of the anterior deirid receptor neuron, ADE; its main postsynaptic partner is DVA. The putative receptor neuron PVM has a cell body in the right-hand posterior lateral ganglion and has a differentiated ultrastructure that is very similar to that of the anterior touch receptor neuron, AVM (Chalfie & Sulston 1981). Its synaptic output is quite different from that of AVM, however, being directed mainly to PDE. This neuron does not seem to be involved in the touch response (Chalfie *et al.* 1984) as is AVM.

The posterior body of the hermaphrodite tapers down into a long thin tailspike. Seven classes of neuron have long, undifferentiated processes that run nearly to the end of this tailspike (AVG, ALN, PLN, PHC, PVR, PLM and PDB). It seems likely that these neurons are sensory and that the tailspike is, in fact, a large sense organ, although it does not have the sheath and socket cells that are components of sensilla. The neurons of the tailspike are quite diverse in their synaptic connections. PHC has short processes and synapses predominantly onto DVA and PVC; PVR has a process that traverses the length of the ventral cord and synapses onto AVB and RIP in the nerve ring. AVG is the only tailspike class that does not have a posteriorly located cell body; it has a single, rather large cell body in the retrovesicular ganglion. The main synaptic output of AVG seems to be via extensive gap junctions to the two RIF interneurons also situated in the retrovesicular ganglion.

The other classes of neuron with processes in the tailspike, ALN, PLN and PLM, probably have a sensory function in other regions as well as in the tailspike. PLM are the posterior touch

neurons and span the whole of the posterior region of the body. ALN and PLN are two classes that have processes that run alongside, and are closely associated with, the transducing regions of the processes of ALM and PLM respectively. They project into the nerve ring and it seems probable that they are also involved with the touch system in some way.

The motoneuron PDB has a proximal process that runs into and out of the tailspike *en route* from the ventral to the dorsal cord. No synaptic input is seen onto this neuron; however, it makes a few NMJs onto dorsal body muscles. It is possible that, in contrast to other motoneurons with long distal processes, the long proximal process of PDB may have some transducing function in the tailspike. PDA is another single motoneuron like PDB; both have cell bodies situated in the pre-anal ganglion. PDA also innervates dorsal muscles but sends its process to the dorsal cord by a more direct route via a lumbar commissure. It receives some synaptic input from the interneuron/motoneuron DVB. The only synaptic input to the defecation muscles is provided by DVB, which therefore (presumably) controls defecation. PDA may mediate the contractions of the posterior body, which are associated with defecation (Crofton 1966), via its connection with DVB.

The ventral cord motoneurons, DA8, DA9 and VA12, have rather different patterns of synaptic connections from the more anterior members of their classes. Although they still retain the synaptic inputs from AVA and AVD that are characteristic of these classes, DA9, DA8 and VA12 have several additional sources of synaptic input: VA12 from PHC; DA9 from PHC and PHB; and DA8 from DVB. In addition VA12 synapses onto DB7, DA8 and DA9. None of the other VAn motoneurons is seen to synapse convincingly onto other motoneuron classes except VDn and DDn, and so this feature is probably indicative of an intrinsic difference between VA12 and the other VAns. The synaptic inputs from PHC and PHB, on the other hand, may be restricted to the posterior members of the VAn and DAn classes simply because of the limited extent of the axons of PHB and PHC in the ventral cord. This would not necessarily require an intrinsic difference in DA8, DA9 and VA12 compared with the other members of their class.

The egg-laying circuitry (*figure* 21*f*)

The vulval and uterine muscles are predominantly innervated by two classes of motoneuron, HSN and VCn. The VCn motoneuron class has six members, which are distributed along the central regions of the ventral cord. They synapse onto ventral body muscles as well as vulval muscles. The only significant synaptic input that was seen on to them comes from HSN. These synapses are in close proximity to the NMJs made by the VCns onto the vulval muscles, suggesting that they could perhaps be mediating a presynaptic inhibition of the VCns. Various pharmacological agents, including acetylcholine agonists, serotonin analogues and an octopamine blocking agent, have been shown to stimulate egg laying (Horvitz *et al.* 1984).

Laser ablation experiments have shown that the HSN neurons are essential for egg laying (Trent *et al.* 1983). The circuitry associated with HSN is rather ambiguous. It is predominantly presynaptic and only receives a few synapses back from its postsynaptic partner, BDU, and a single synapse from each PLM. This type of behaviour suggests that HSN is not simply a motoneuron but may have some sensory transduction function that provides the primary signal for the activation of the vulval muscles. There is, however, no obvious feature of its structure which suggests such a function.

The same arguments can be applied to the VCn neurons because of their apparent lack of

presynaptic partners, although it is not yet known whether the VCns are essential for egg laying. Another possibility is that the main inputs for HSN and VCn come via humoral neurotransmitters rather than by focal synaptic contacts. The sensory integration required to determine the appropriate moment for egg laying could then be executed in other regions of the nervous system, with no morphologically distinguishable connections being made to the vulval muscle motoneurons.

Conclusions

There are, perhaps, two fundamental questions in the field of neurobiology: how neurons organize themselves during development into specifically interconnected networks, and how such a network functions. A knowledge of the detailed structure of a nematode's nervous system does not in itself provide any answers to these questions, but it does at least provide a framework within which it is possible to pose rather more specific questions.

The development of a nervous system can be divided into three separate phases. The first is the generation of a group of differentiated neurons; the second is the outgrowth and guidance of processes from these neurons and the third is the establishment of connections between processes. The structural data on the nervous system provides information that is most pertinent to the last two phases. This is because the final structure represents the ultimate consequences of the execution of these two processes. We will go on to discuss how these two developmental processes, together with the question of nervous system function, may be further explored in *C. elegans*.

Process placement

One of the most striking features of the nervous system of *C. elegans* is the precision with which processes are positioned relative to their neighbours within process bundles. Synaptic contacts are made *en passant* between adjacent processes; the set of possible synaptic partners that a neurone may have is therefore limited to the set of processes that are neighbours. Given the unbranched nature of nematode neurons, this set is usually a relatively small subset of the total complement of neurons that make up the nervous system. Within this neighbourhood, however, neurons are fairly highly connected, making connections to nearly half their neighbours on average (White *et al.* 1983). Furthermore, there is circumstantial evidence that this level of connectivity may be independent of neighbourhood, i.e. that a given neuron may make synaptic connections to more or less the same percentage of its neighbours no matter what class they may be (White *et al.* 1983). Thus process placement must be a major determinant in the establishment of the patterns of connectivity within the nervous system of *C. elegans*.

It seems likely that there may be two aspects of process placement: substrate guidance of pioneering processes to establish process tracts (Berlot & Goodman 1984), and the positioning of processes relative to their neighbours within bundles once process tracts have become established. A distinctive feature of the organization of processes within bundles is the close associations that are seen between specific processes, or between a process and the basal lamina. Such associations are probably the consequence of selective adhesive affinities between the associating entities. Given the probable importance of selective adhesivity in determining connectivity, it is worth considering, within the context of the nematode's nervous system, how such phenomena may be further investigated.

Many behavioural mutants have been isolated in *C. elegans*; it is likely that most of their phenotypes are the consequence of alterations in the nervous system. It is also likely that some of these alterations could take the form of misplaced processes. Up to now, relatively few behavioural mutants have been analysed at the ultrastructural level. This is mainly because of the considerable effort that is required to reconstruct a significant portion of the nervous system from electron micrographs. Recently, staining techniques have been developed that allow the visualization of specific processes or process bundles in whole mounts of *C. elegans* when viewed with the light microscope. In one of these techniques, sensory process tracts are labelled by dye filling (Hedgecock *et al.* 1984). In another, processes of certain neuron classes are labelled with monoclonal antibodies and viewed by immunofluorescence in whole mounts (Okamoto & Thomson 1984). Such techniques will facilitate the pre-screening of behavioural mutants for those that have abnormalities in process placement. Selected mutants may then be subjected to a full ultrastructural analysis.

With the dye uptake technique, certain mutants have been found to have abnormal projections from sensory receptors (Hedgecock *et al.* 1984); such mutants could be candidates for substrate guidance. The defects in these mutants could either be located in the neurons, or in the substrate upon which they grow. It may be possible to distinguish between these two possibilities by means of mosaic analysis (Herman 1984).

Of the mutants that have been analysed by serial section reconstruction, one (*unc-30*) has been found to have misplaced processes on the VDn and DDn motoneuron classes (J. G. White, S. Brenner & R. Durbin, unpublished observations). The disposition of the processes of the other motoneuron classes in the ventral cord appears normal. It seems possible that such a mutant could be defective in the class-specific expression of an adhesion factor. The molecular analysis of genes that affect process placement may provide a route to an eventual understanding of the function and deployment of region-specific adhesion molecules. Another route to the same end may be taken by directly looking for putative adhesion molecules. Candidate molecules would be expected to be common to a group of processes that are closely associated together. Such a molecule could be sought either directly by using antibodies, or indirectly by looking for species of messenger RNA that show the appropriate neuronal distribution.

Synaptic specificity

Although we have played down the role of synaptic specificity in the generation of the pattern of connections within the nervous system of *C. elegans* to a certain extent, it is clear that there has to be some level of specificity. On average, a neuron is presynaptic to about 15% of its neighbours (unpublished observations). The subset of neighbours that are postsynaptic to a given neuron is fairly constant from animal to animal, and so is presumably actively selected. It is likely that synaptogenesis is initiated by a cell–cell recognition event. Such an event may involve the binding of a surface receptor molecule on one cell to a matching 'label' molecule on another cell. If all cell classes had single distinguishing label and receptor types, then the set of synaptic partners of a given cell class could never intersect with that of another. Such intersections are, in fact, the general rule in the nervous system. Therefore, if such a label–receptor system is the basis of synaptic specificity, then the labels (and/or receptors) have to be arranged combinatorially.

It is probably not reasonable to assume that the pattern of connections seen between processes in a particular neighbourhood is solely the consequence of the intrinsic specificities

of the neurons involved. There are suggestions that interactions between synapses may act to modify certain patterns of synaptic connection that might otherwise form as a consequence of specific neuron–neuron recognition. There are slight differences in connectivity between the dorsal and ventral members of the classes SMB, SAA, OLQ and RMD. These differences are manifested as reciprocal substitutions of gap junctions for chemical synapses and chemical synapses for gap junctions. This behaviour may suggest that there are interactions between these types of connection in these circumstances, and that these interactions result in a mutual exclusivity of chemical synapses and gap junctions.

We have used the criteria of morphology and connectivity to define the 118 classes of neuron that have been described. Given that a particular neuron can only select synaptic partners from its neighbourhood, it is probable that there are classes that we have defined that have the same intrinsic synaptic potential; in other words, if placed in the same neighbourhood they would select the same subset of neighbours as synaptic partners. Therefore, the number of classes that we have defined (118) is almost certainly an overestimate of the number of neuron types that are intrinsically different in their specificities. It is strongly suspected, on the basis of morphology, that AQR and PQR are members of a single class, as are ALM and PLM, ALN and PLN, and AVM and PVM. It is probable that there are other class equivalences that are not so obvious, particularly among the interneurons, which often do not have distinguishably different morphologies. It may be possible to identify such 'superclasses' by a neighbourhood analysis. If the neighbourhoods from two classes are compared and common neighbours are identified, then it is possible that the two classes may be members of a superclass, if the pattern of synaptic connections made to the common neighbours is the same in each case. By considering all pairwise combinations of classes, and then reiterating the process considering all members of putative superclasses as equivalent, it may be possible to arrive at a logically consistent set of superclasses. These superclasses will define groups of cells that have intrinsically identical synaptic specificities. Such an endeavour may not just be an idle intellectual exercise, as a knowledge of such 'supergroups' could facilitate the identification of mutants that have altered labels or receptors. Such mutations would be expected to have pleiotropic consequences, affecting all the members of a supergroup. Thus mutants that affect connectivity of all the members of a particular supergroup are candidates for mutants with altered labels and/or receptors. An analysis of such mutants may provide a possible route towards an understanding of the molecular basis of synaptic specificity.

Nervous system function

The relative simplicity of the structure of the nervous system of *C. elegans* provides a challenge to determine how it functions. The main disadvantage of this nervous system from the point of view of functional studies is that the small size of the component neurons precludes the use of electrophysiological recording techniques. Such techniques can, however, be used with *Ascaris*. There are considerable homologies between the ventral cord motoneurons of *Ascaris* and *C. elegans* (Stretton *et al.* 1978); more recently, similar homologies have been seen in the interneurons of the retro-vesicular ganglion (Donmoyer, Angstadt and Stretton, personal communication). The neurotransmitter dopamine has been shown to be present in the same classes of cells in the two animals (Sulston *et al.* 1975). It seems likely that such structural and biochemical similarities may indicate an underlying functional similarity, justifying the extrapolation of data obtained from one animal to the other. Electrophysiological studies on homologous cells in *Ascaris* suggest that the DAn, DBn, and ASn motoneurons of *C. elegans* are

excitatory, whereas the DDn and VDn motoneurons are inhibitory (Johnson & Stretton 1980). Further work may yield information about the role of the interneurons of the ventral cord in activating the motoneurons.

The functional aspects of the nervous system of *C. elegans* may be studied directly by characterizing the behavioural consequences of specific lesions in the nervous system. Lesions may be produced by laser microsurgery (Sulston & White 1980), a technique that is capable of removing any cell or small group of cells within the nervous system. As an alternative, use may be made of lesions produced as a consequence of mutations. For example, one mutant, *unc-30*, specifically affects the organization of the VDn and DDn motoneurons in the ventral cord, leaving the other motoneuron classes relatively unaffected (J. G. White, S. Brenner & R. Durbin, unpublished observations). This mutant is uncoordinated in forward and backward locomotion. When stimulated by a tap on the head, instead of backing away, these animals shorten by simultaneously activating both their ventral and their dorsal muscles. This behaviour is what one would predict if cross-inhibition between the dorsal and ventral sides were lacking. This observation reinforces the suggestion, originally made on morphological criteria, that the VDn and DDn classes function as cross-inhibitors.

The combined techniques of laser microsurgery, mutants and tests for drug responsiveness have been used to produce detailed models for the function of the circuitry associated with the touch response (Chalfie *et al.* 1984), and the circuitry that controls egg-laying (Horvitz *et al.* 1984). Other areas of the nervous system should be equally amenable to such methodologies, particularly the chemosensory system. This system is particularly attractive, as the chemotactic response has been characterized (Ward 1973; Dusenbery 1974) and many mutants that are defective in chemotaxis have been isolated (Dusenbery *et al.* 1975; Lewis & Hodgkin 1977).

We would like to thank our colleagues who, over the years, have offered advice and encouragement for this work. We would particularly like to mention Donna Albertson, Martin Chalfie, Richard Durbin, Edward Hedgecock, Robert Horvitz and John Sulston for the many stimulating discussions that we have had together, and also Donna Albertson, Leon Nawrocki and John Sulston for reading and commenting on the manuscript.

References

Albert, P. S. & Riddle, D. L. 1983 Developmental alterations in the sensory neuroanatomy of the *C. elegans* dauer larva. *J. comp. Neurol.* **219**, 416–481.

Albertson, D. G. & Thomson, J. N. 1976 The pharynx of *Caenorhabditis elegans*. *Phil. Trans. R. Soc. Lond.* B **275**, 299–325.

Bennett, M. L. V. 1977 Electrical transmission: a functional analysis and comparison to chemical transmission. In *The handbook of physiology. Section 1: the nervous system.* (ed. J. M. Brookhart & V. B. Mountcastle), pp. 357–416. Bethesda, Maryland: American Physiological Society.

Berlot, J. & Goodman, C. 1984 Guidance of peripheral pioneer neurones in the grasshopper: an adhesive hierarchy of epithelial and neuronal surfaces. *Science, Wash.* **223**, 293–295.

Bird, A. F. 1971 *The structure of nematodes.* New York: Academic Press.

Boycott, B. B. & Dowling, J. E. 1969 Organization of the primate retina: Light microscopy. *Phil. Trans. R. Soc. Lond.* B **255**, 109–184.

Braitenberg, V. & Atwood, R. P. 1958 Morphological observations on the cerebellar cortex. *J. comp. Neurol.* **109**, 1–34.

Brenner, S. 1974 The genetics of *Caenorhabditis elegans*. *Genetics, Princeton* **77**, 71–94.

Cajal, R. 1972 *Histologie du système de l'homme et des vertébrés.* Madrid: C.S.I.C.

Cassada, R. C. & Russell, R. L. 1975 The dauer larva, a postembryonic developmental variant of the nematode *Caenorhabditis elegans*. *Devl Biol.* **46**, 326–342.

Chalfie, M. & Sulston, J. 1981 Developmental genetics of the mechanosensory neuron of *Caenorhabditis elegans*. *Devl Biol.* **82**, 358–370.

Chalfie, M., Sulston, J. E., White, J. G., Southgate, E., Thomson, J. N. & Brenner, S. 1984 The neural circuits for touch sensitivity in *Caenorhabditis elegans*. *J. Neurosci.* **5**, 956–964.

Chalfie, M. & Thomson, J. N. 1982 Structural and functional diversity of neuronal microtubules of *Caenorhabditis elegans*. *J. Cell Biol.* **93**, 15–23.

Chitwood, B. G. & Chitwood, M. B. 1974 *Introduction to nematology*. Baltimore: University Park Press.

Crofton, H. D. 1966 *Nematodes*. London: Hutchinson.

Culotti, J. G. & Russell, R. L. 1978 Osmotic avoidance defective mutants of the nematode, *Caenorhabditis elegans*. *Genetics, Princeton* **90**, 243–256.

Dowling, J. E. & Boycott, B. B. 1966 Organisation of the primate retina: electron microscopy. *Proc. R. Soc. Lond.* B **166**, 80–11.

Dusenbery, D. B. 1974 Analysis of chemotaxis in the nematode *Caenorhabditis elegans* by countercurrent separation. *J. exp. Zool.* **188**, 41–47.

Dusenbery, D. B., Sheridan, R. E. & Russell, R. L. 1975 Chemotaxis defective mutants of the nematode, *Caenorhabditis elegans*. *Genetics, Princeton* **80**, 297–309.

Eccles, J. C., Ito, M. & Szentágothai, J. 1967 *The cerebellum as a neuronal machine*. Berlin: Springer-Verlag.

Edelman, G. M. 1983 Cell adhesion molecules. *Science, Wash.* **219**, 450–457.

Goldschmidt, R. 1908 Das Nervensystem von *Ascaris lumbricoides* und *megalocephela*, I. *Z. wiss. Zool.* **90**, 73–136.

Goldschmidt, R. 1909 Das Nervensystem von *Ascaris lumbricoides* und *megalocephela*, II. *Z. wiss. Zool.* **92**, 306–357.

Hall, D. H. 1977 The posterior nervous system of *Caenorhabditis elegans*. Ph.D. thesis, California Institute of Technology.

Hedgecock, E. M. & Russell, R. L. 1975 Normal and mutant thermotaxis in the nematode, *Caenorhabditis elegans*. *Proc. natn. Acad. Sci. U.S.A.* **72**, 4061–4065.

Hedgecock, E. M., Culotti, J. G., Thomson, J. N. & Perkins, L. A. 1985 Axonal guidance mutants of *Caenorhabditis elegans* identified by filling identified neurons with fluorescein dyes. *Devl Biol.* **111**, 158–170.

Herman, R. K. 1984 Analysis of genetic mosaics in *Caenorhabditis elegans*. *Genetics, Princeton* **108**, 165–180.

Hirsh, P., Oppenheim, D. & Klass, M. 1976 Development of the reproductive system of *Caenorhabditis elegans*. *Devl Biol.* **49**, 200–219.

Hockfield, S. & McKay, R. 1983 Monoclonal antibodies demonstrate the organisation of axons in the leech. *J. Neurosci.* **3**, 369–375.

Hodgkin, J. A. 1983 Male phenotypes and mating efficiency in *Caenorhabditis elegans*. *Genetics, Princeton* **103**, 43–64.

Horvitz, H. R., Trent, C., White, J. G. & Sulston, J. E. 1986 Structure and function of the egg-laying system of the nematode *Caenorhabditis elegans*. (In preparation.)

Jan, Y. N., Bowers, C. W., Branton, D., Evans, L. & Jan, L. Y. 1983 Peptides in neural function: Studies using frog autonomic ganglia. *CSH Symp. quant. Biol.* **48**, 363–374.

Johnson, C. D. & Stretton, A. O. W. 1980 Neural control of locomotion in *Ascaris*: Anatomy, electrophysiology and biochemistry. In *Nematodes as biological models* (ed. B. Zukerman) New York and London: Academic Press.

Kimble, J. 1981 Alterations in cell lineage following laser ablation of cells in the somatic gonad of *Caenorhabditis elegans*. *Devl Biol.* **87**, 286–300.

Lewis, J. A. & Hodgkin, J. A. 1977 Specific neuroanatomical changes in chemosensory mutants of the nematode, *Caenorhabditis elegans*. *J. comp. Neurol.* **172**, 489–509.

Nelson, F. K., Albert, P. S. & Riddle, D. L. 1983 Fine structure of the *Caenorhabditis elegans* secretory-excretory system. *J. Ultrastruct. Res.* **82**, 156–171.

Okamoto, H. & Thomson, J. N. 1984 Monoclonal antibodies which distinguish certain classes of neuronal and supporting cells in the nervous system of *C. elegans*. *J. Neurosci.* **5**, 643–653.

Pappas, G. D. & Waxman, S. G. 1972 *Structure and function of synapses*. New York: Raven Press.

Raper, J. A., Bastiane, M. & Goodman, C. S. 1983 Pathfinding by neural growth cones in grasshopper embryos. *J. Neurosci.* **3**, 31–41.

Reynolds, E. S. 1963 The use of lead citrate at high pH as an electron opaque stain in electron microscopy. *J. Cell Biol.* **17**, 208–213.

Riddle, D. L., Swanson, M. M. & Albert, P. S. 1981 Interacting genes in nematode dauer larva formation. *Nature, Lond.* **290**, 668–671.

Rosenbluth, J. 1965 Ultrastructural organisation of obliquely striated muscle fibres in *Ascaris lumbricoides*. *J. Cell Biol.* **25**, 495–515.

Stevens, B. J. & White, J. G. 1979 Computer reconstruction of mitochondria from yeast. *Meth. Enzym.* **56**, 718–728.

Stretton, A. O. W., Fishpool, R. M., Southgate, E., Donmoyer, J. E., Walrond, J. P., Moses, J. E. & Kass, I. S. 1978 Structure and physiological activity of the motoneurones of the nematode *Ascaris*. *Proc. natn. Acad. Sci. U.S.A.* **75**, 3493–3497.

Sulston, J. E. 1983 Neuronal cell lineages in the nematode *Caenorhabditis elegans*. *CSH Symp. quant. Biol.* **48**, 443–452.

Sulston, J. E., Albertson, D. G. & Thomson, J. N. 1980 The *Caenorhabditis elegans* male: Postembryonic development of non-gonadal structures. *Devl Biol.* **78**, 542–576.

Sulston, J., Dew, M. & Brenner, S. 1975 Dopaminergic neurons in the nematode, *Caenorhabditis elegans*. *J. comp. Neurol.* **163**, 215–226.

Sulston, J. E. & Horvitz, H. R. 1977 Post-embryonic lineages of the nematode, *Caenorhabditis elegans*. *Devl Biol.* **56**, 110–156.
Sulston, J. E., Schierenberg, E., White, J. G. & Thomson, J. N. 1983 The embryonic cell lineage of the nematode, *Caenorhabditis elegans*. *Devl Biol.* **100**, 64–119.
Sulston, J. E. & White, J. G. 1980 Regulation and cell autonomy during postembryonic development of *Caenorhabditis elegans*. *Devl Biol.* **78**, 577–597.
Swanson, M. M., Edgley, M. L. & Riddle, D. L. 1984 In *Genetic maps 1984* (ed. S. J. O'Brien), pp. 286–300. New York: Cold Spring Harbor Laboratory.
Trent, C., Tsung, N. & Horvitz, H. R. 1983 Egg-laying defective mutants of the nematode, *Caenorhabditis elegans*. *Genetics, Princeton* **104**, 619–647.
Wässle, H., Peichl, L. & Boycott, B. B. 1981 Dendritic territories of cat retinal ganglion cells. *Nature, Lond.* **292**, 344–345.
Ward, S. 1973 Chemotaxis by the nematode, *Caenorhabditis elegans*: Identification of attractants and analysis of the response by the use of mutants. *Proc. natn. Acad. Sci. U.S.A.* **70**, 817–821.
Ward, S., Thomson, N., White, J. G. & Brenner, S. 1975 Electron microscopal reconstruction of the anterior sensory anatomy of the nematode, *Caenorhabditis elegans*. *J. comp. Neurol.* **160**, 313–338.
Ware, R. W., Clark, C., Crossland, K. & Russell, R. L. 1975 The nerve ring of the nematode, *Caenorhabditis elegans*. *J. comp. Neurol.* **162**, 71–110.
Waterston, R. H., Thomson, J. N. & Brenner, S. 1980 Mutants with altered muscle structure in *Caenorhabditis elegans*. *Devl Biol.* **77**, 271–302.
Weiss, P. 1934 *In vitro* experiments on the factors determining the course of the outgrowing nerve fibre. *J. exp. Zool.* **68**, 393–448.
White, J. G. 1974 Computer aided reconstruction of the nervous system of *C. elegans*. Ph.D. thesis, University of Cambridge.
White, J. G., Albertson, D. G. & Aness, M. A. R. 1978 Connectivity changes in a class of motoneurone during the development of a nematode. *Nature, Lond.* **271**, 764–766.
White, J. G., Southgate, E., Thomson, J. N. & Brenner, S. 1976 The structure of the ventral cord of *Caenorhabditis elegans*. *Phil. Trans. R. Soc. Lond.* B **275**, 327–348.
White, J. G., Southgate, E., Thomson, J. N. & Brenner, S. 1983 Factors that determine connectivity in the nervous system of *Caenorhabditis elegans*. *CSH Symp. quant. Biol.* **48**, 633–640.
Wright, K. A. 1980 Nematode sense organs. In *Nematodes as biological models* (ed. B. Zukerman), pp. 237–293. New York: Academic Press.

Appendix 1. Connectivity data

In this section, all the detailed connectivity data for each of the neuron classes are presented. The neuron classes are arranged in alphabetical order; the data for each class are fairly self-contained. Some classes have been grouped together because they share many common features; PLM is listed with ALM, PLN with ALN, PVM with AVM and PQR with AQR.

The data that are presented were derived primarily from three reconstructed animals; the N2T series, the N2U series and the JSE series. Together these series covered the whole of the animal except for a region in the posterior body (figure A 1). This region was covered by a partial reconstruction of a male (N2Y series). Data from this animal provided information on the neurons of the posterior lateral ganglia and the motoneurons of the posterior ventral cord. The neuropile of the nerve ring and anterior ventral cord was also reconstructed from an L4 larva (JSH series, figure A 1). These data were mainly used as a check on the N2U

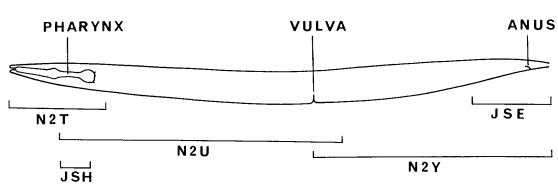


Figure A 1. The regions covered by the five separate reconstructions. The N2T, N2U and JSE series were adult hermaphrodites, the JSH series was an L4 larva and the N2Y series was an adult male.

reconstructions, which covered this region and are not shown, except in the case of RMF, where there was a significant difference between the two series.

Neuron topographies are shown in semidiagrammatic form for simplicity in presentation. Processes of neurons in *C. elegans* have few, if any, branches and tend to run in parallel process bundles. It is therefore possible to give a reasonably accurate impression of their three-dimensional structure by means of such diagrams. Neurons that inhabit the regions of the nerve ring and anterior ventral cord are plotted out in diagrams on templates of the form shown in figure A 2. Similarly, neurons that have processes in the posterior ventral cord are plotted out in diagrams on templates of the form shown in figure A 3. Additional diagrams show the disposition of the cell bodies and processes of the class members within the animal, as seen from a lateral viewpoint. The nerve ring or anterior ventral cord diagrams are drawn as if from a dorsal viewpoint of an animal in which the nerve ring has been flattened so as to lie in the same plane as the ventral cord. The diagrams of neurons in posterior regions are again drawn from a dorsal viewpoint, but in this case an imaginary cut has been made along the dorsal mid-line and the animal opened out flat so that the ventral mid-line runs along the centre of the diagrams (figure A 3).

Processes that run in the regions covered by these types of diagram have been drawn out with all their synaptic connections listed. Synaptic connections mediated by chemical synapses are depicted by arrows. The direction in which the arrow points relative to the process indicates

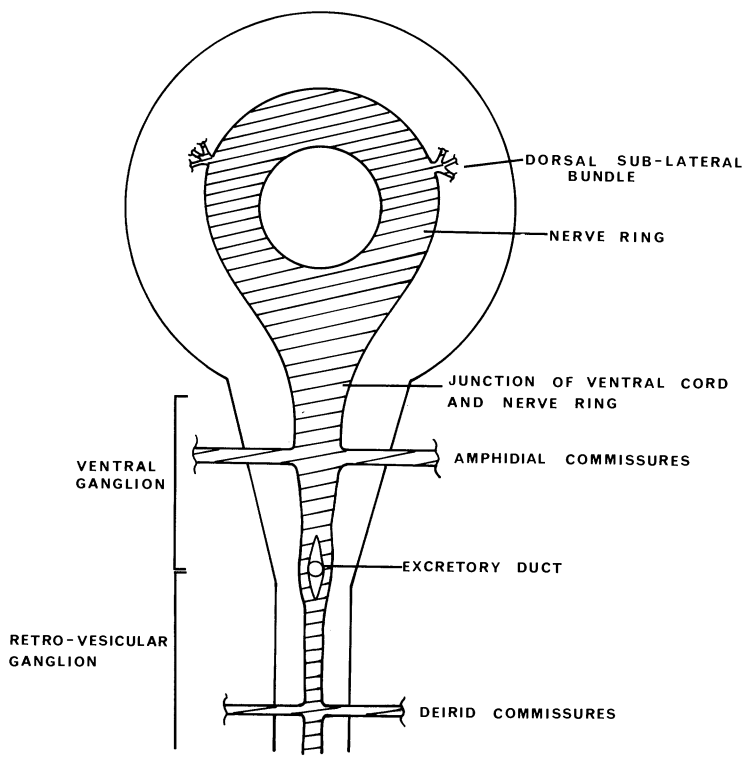


FIGURE A 2. Diagram of the projection and template used for the plots of processes that run in the nerve ring and ventral cord. The nerve ring has been flattened out to lie in the same plane as the ventral cord, so that the posterior face of the nerve ring and the dorsal face of the ventral cord are directed out of the page. The shaded region indicates the extent of the neuropile in these regions. The isthmus of the pharynx passes through the hole in the middle of the nerve ring. The disposition of the major process tracts that join this region of neuropile are shown.

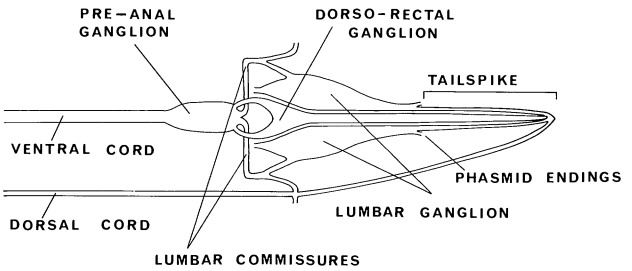
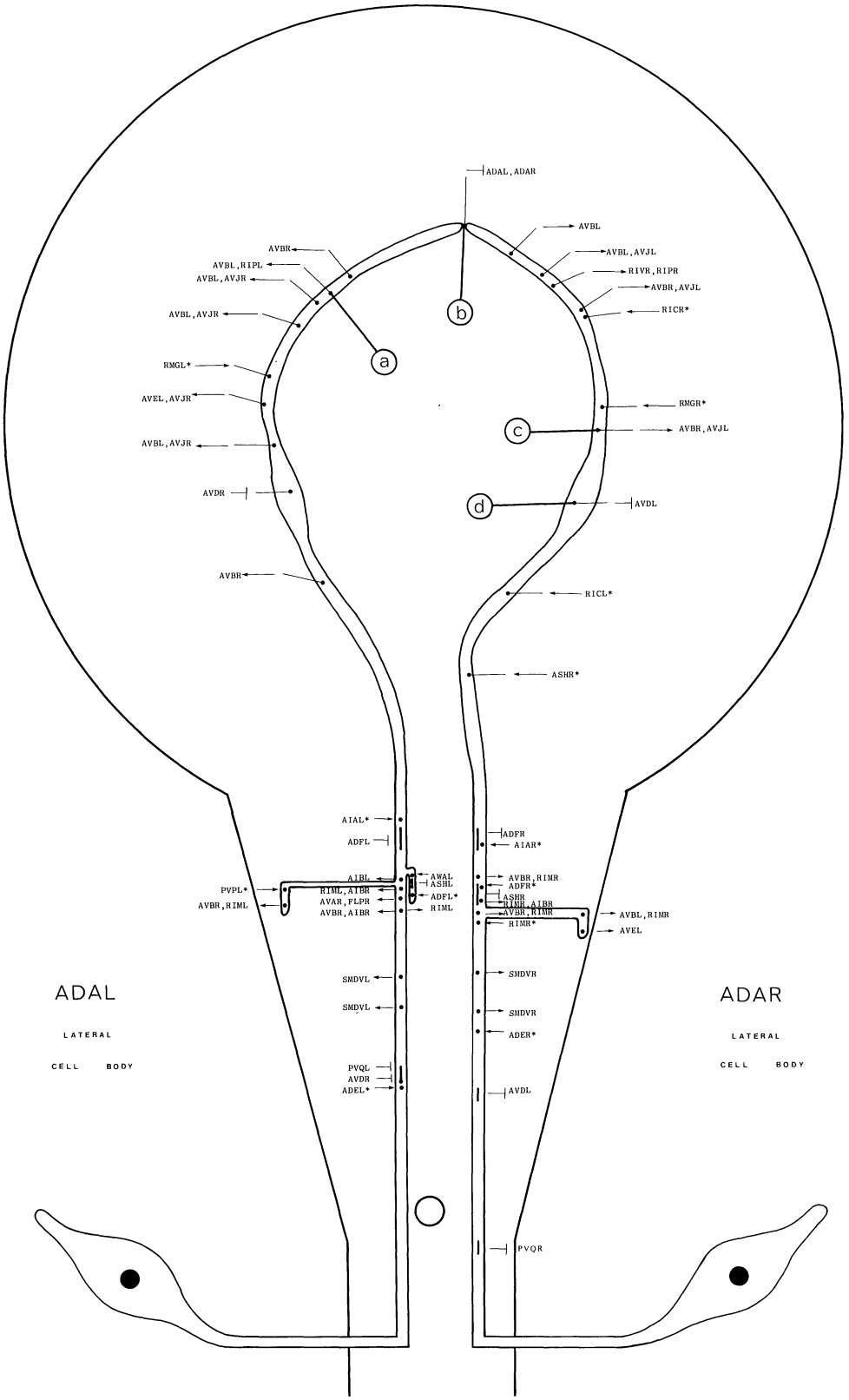


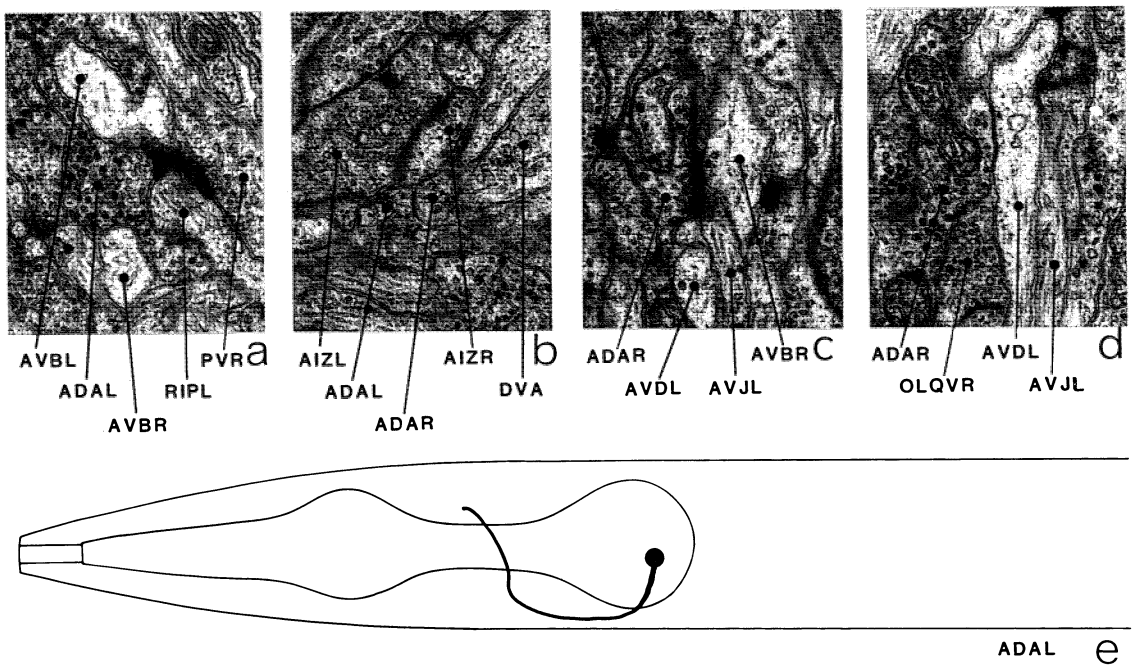
FIGURE A 3. Diagram of the projection and template that is used for the plots of processes in the tail region. This is a dorsal view of the projection obtained by making an imaginary cut along the dorsal mid-line and then opening and flattening the animal. The outlines indicate the dispositions of the process tracts and ganglia. The rectum passes through the hole in the middle.

whether the process is presynaptic or postsynaptic for that particular contact. Synaptic contacts in which the process is one of several that are postsynaptic to a single presynaptic element are marked with an asterisk. All possible postsynaptic partners of contacts in which the process is presynaptic are shown. Gap junctions only appear between two elements and are marked with a T; no directionality is implied.

Certain synaptic connections have additional labels. These labels refer to a set of electron micrographs, which illustrate these connections. Many illustrations were taken from the JSH series because of the better quality of the pictures that were obtained from this series. Although the diagrams refer to connections seen in the other series, it was nevertheless possible to use these illustrations, because in most cases synaptic connections equivalent to those indicated in the diagrams could be found in the JSH series. References to illustrations of synaptic contacts are made by an index letter. These refer to the set of illustrations that is associated with the neuron class currently under discussion. If the index letter is preceded by an asterisk then the index letter refers to the set of illustrations associated with the class being referenced.

The two diagram formats described above do not cover the central body region, particularly the region of the ventral cord in which there are many synaptic contacts. Data from this region are presented in two ways: either as a table of synaptic contacts, in the case of interneurons which have processes that enter the region, or as individual diagrams, for motoneurons that are totally contained within the region. The motoneurons of the ventral cord have up to thirteen members in each of the classes, compared with a maximum of four members for all the other neuron classes in the animal. Only one 'typical' member of each of the ventral cord motoneuron classes is plotted, together with any atypical members that there may be in the class.


ADAL,ADAR
AVBL
AVBR
AVBL,AVJL
AVBL,RIPL
RIVR,RIPR
AVBL,AVJR
AVBR,AVJL
AVBL,AVJR
RICR*
RMGL*
AVEL,AVJR
RMGR*
AVBR,AVJL
AVBL,AVJR
AVDR
AVDL
AVBR
RICL*
ASHR*
AIAL*
ADFR
ADFL
AIAR*
AIBL
AWAL
ASHL
AVBR,RIMR
ADFR*
PVPL*
RIML,AIBR
ADFL*
ASHR
AVBR,RIML
AVAR,FLPR
RIML
RIMR,AIBR
AVBR,AIBR
AVBR,RIMR
AVBL,RIMR
RIMR*
AVEL
SMDVL
SMDVR
SMDVL
SMDVR
ADER*
PVQL
AVDR
ADEL*
AVDL
PVQR
ADAL
LATERAL
CELL BODY
ADAR
LATERAL
CELL BODY

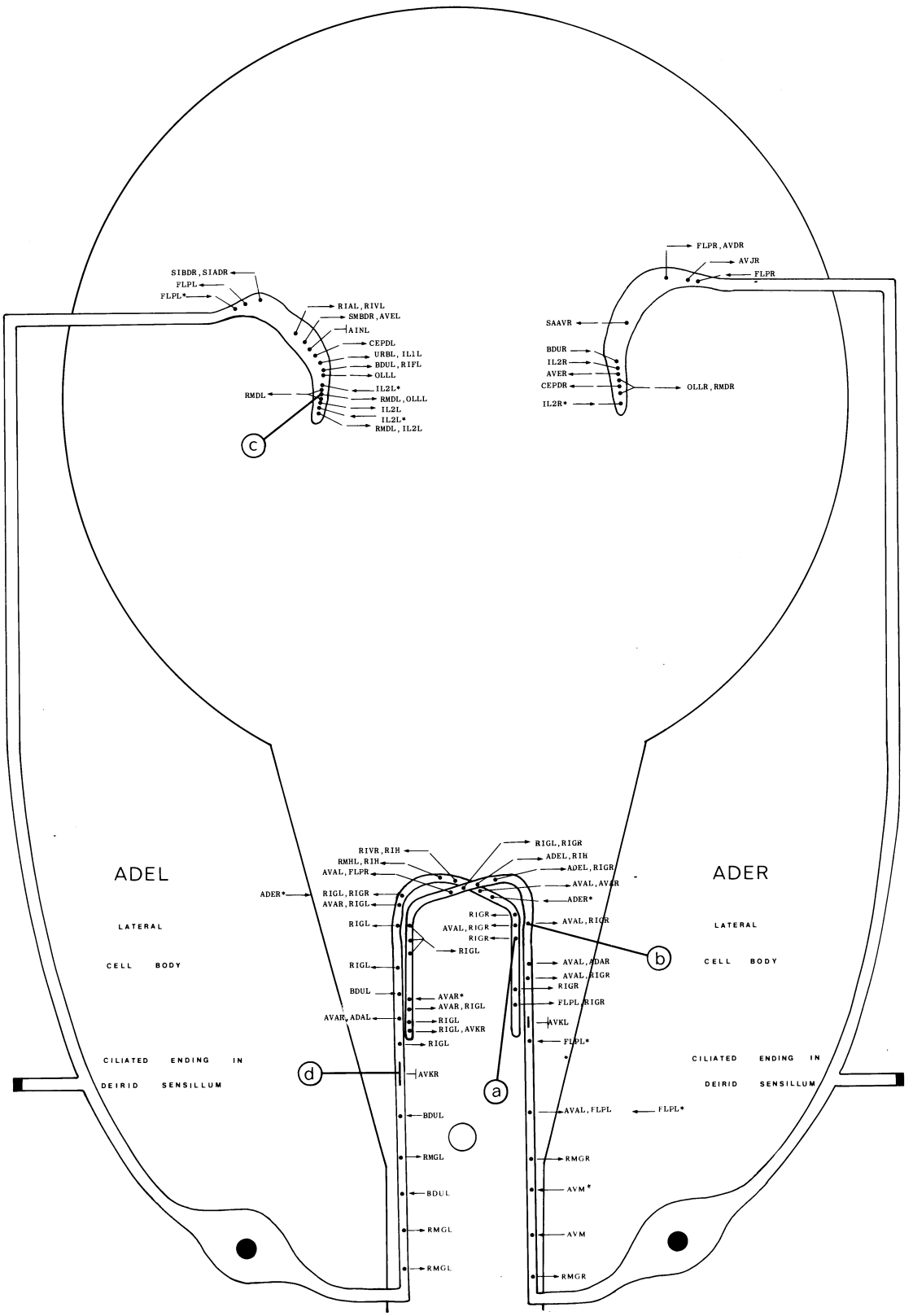


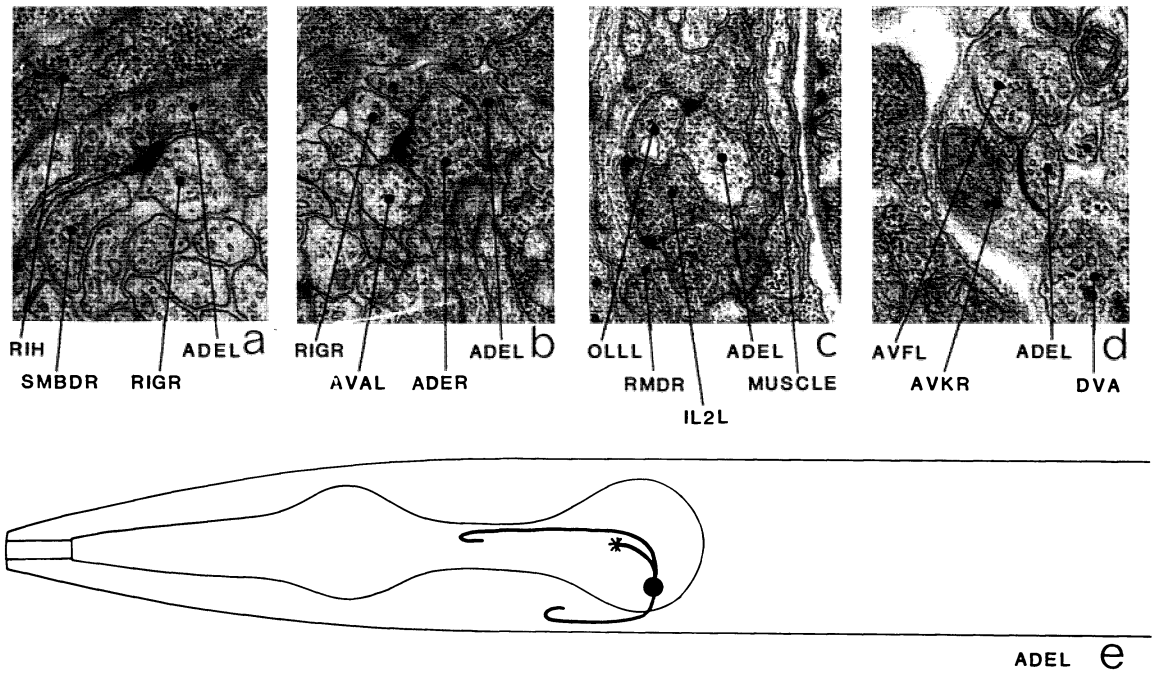
ADA

Members: ADAL, ADAR.

ADA is a set of two interneurons with cell bodies situated laterally at the level of the second bulb of the pharynx. Processes enter the neuropile of the retro-vesicular ganglion via the deirid commissures and run anteriorly into the nerve ring. They then run round the nerve ring and end in a gap junction to their contralateral partners (b). The processes of ADA are rather small and run near the centre of the neuropile of the ring, adjacent to the processes of AVA, much of the time. Synaptic endings are generally small and have large dark vesicles (a). The main synaptic output is to AVB (a, c), with a few synapses also being made to AVJ (c), RIM, SMD and RIP (a). There are gap junctions to itself (b), AVD (d), PVQ, ASH and ADF.

Magnifications: (a–d) × 25500.


SIBDR, SIADR
FLPL
FLPL*
RIAL, RIVL
SMBDR, AVEL
AINL
CEPDL
URBL, IL1L
BDUL, RIFL
OLLL
IL2L*
RMDL
RMDL, OLLL
IL2L
IL2L*
RMDL, IL2L
c
FLPR, AVDR
AVJR
FLPR
SAAVR
BDUR
IL2R
AVER
CEPDR
IL2R*
OLLR, RMDR
ADEL
LATERAL
CELL BODY
CILIATED ENDING IN
DEIRID SENSILLUM
RIVR, RIH
RMHL, RIH
AVAL, FLPR
ADER*
RIGL, RIGR
AVAR, RIGL
RIGL
RIGL
BDUL
AVAR, ADAL
AVAR*
AVAR, RIGL
RIGL
RIGL, AVKR
RIGL
AVKR
BDUL
RMGL
BDUL
RMGL
RMGL
d
RIGL, RIGR
ADEL, RIH
ADEL, RIGR
AVAL, AVAR
ADER*
AVAL, RIGR
RIGR
AVAL, RIGR
RIGR
b
AVAL, ADAR
AVAL, RIGR
RIGR
FLPL, RIGR
AVKL
FLPL*
a
AVAL, FLPL
FLPL*
RMGR
AVM*
AVM
RMGR
ADER
LATERAL
CELL BODY
CILIATED ENDING IN
DEIRID SENSILLUM

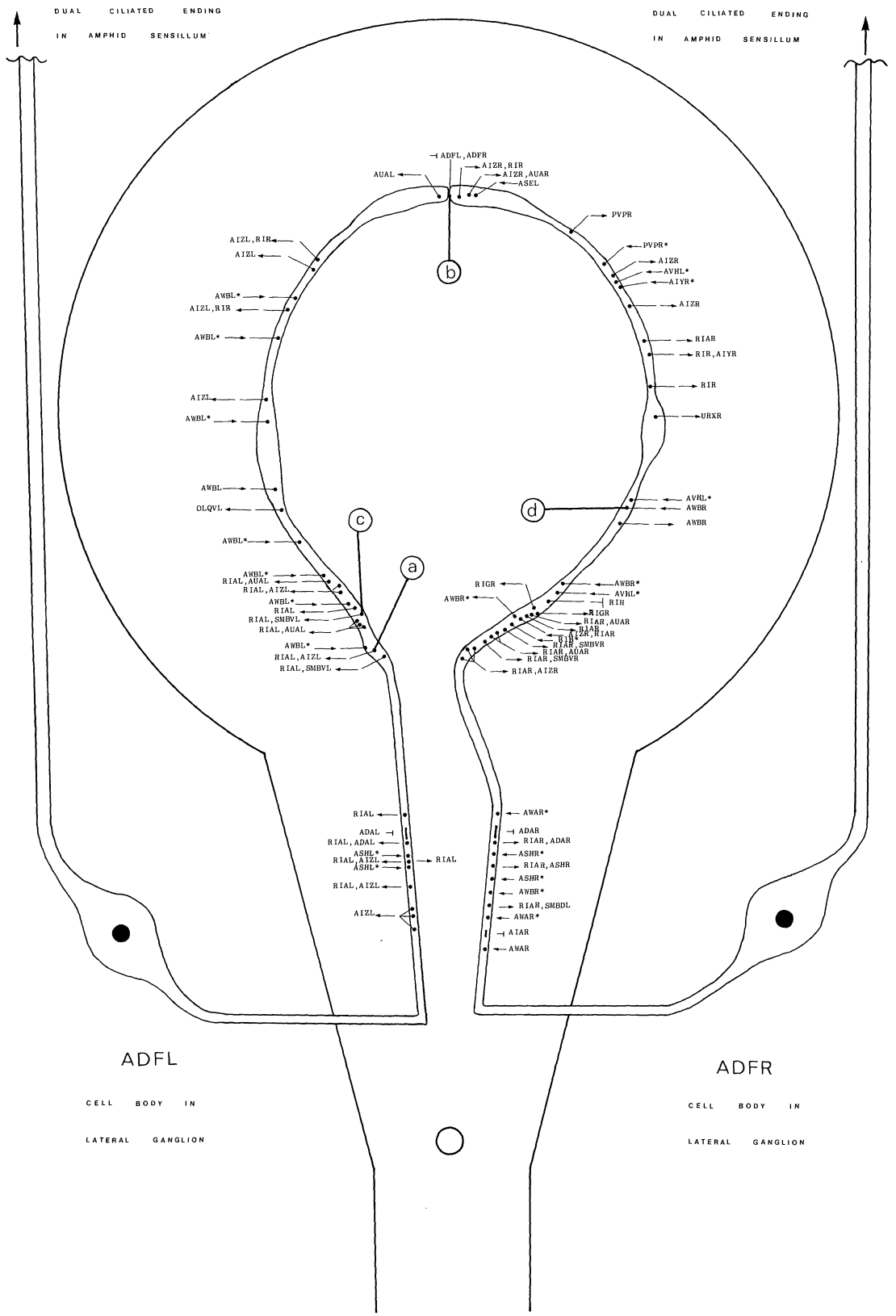


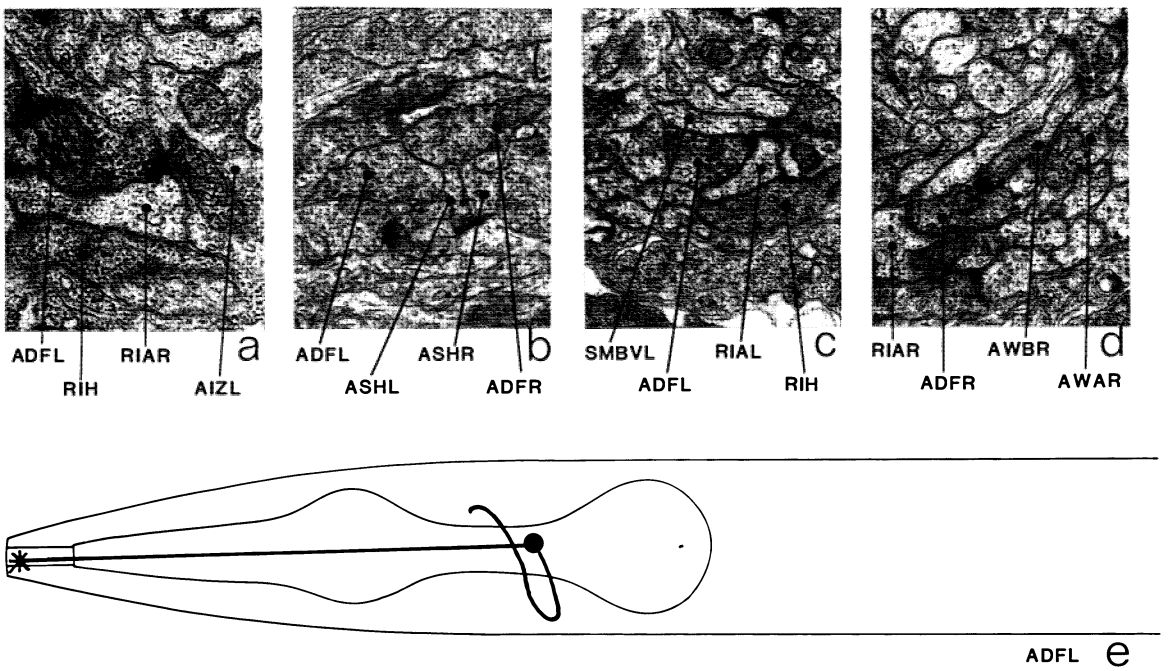
ADE

Members: ADEL, ADER.

ADE is a set of two ciliated neurons with endings in the deirid sensilla, which are situated in the alae on the lateral lines. The cell bodies of ADE are part of a small group of cells situated laterally behind the second bulb of the pharynx. Processes enter the retro-vesicular ganglion via the deirid commissures and then run anteriorly in the ventral ganglion (e). Here they cross over to the contralateral side and run posteriorly for a short distance before ending. Most of the synaptic output is situated in this region and is predominantly to RIG (a) and RIG in association with AVA (b) although there is usually a bias towards RIG in these dyadic synapses. The process to the ciliated ending has a branch, which enters the ring neuropile laterally, running anteriorly through the ring neuropile and making some rather small synapses to diverse partners; OLL, RMD (c), CEP and FLP are the most prominent synaptic partners in this region. ADE receives some synaptic input from BDU (*b), FLP (*c), AVM(*) and IL2L/R. It has gap junctions to AVK (d) in the neuropile of the ventral ganglion. ADE neurons have been shown to contain dopamine (Sulston *et al.* 1975).

Magnifications: (a, c, d) ×25500, (b) ×12750.


DUAL CILIATED ENDING IN AMPHID SENSILLUM
DUAL CILIATED ENDING IN AMPHID SENSILLUM
ADFL, ADFR
AIZR, RIR
AIZR, AUAR
AUAL
ASEL
PVPR
PVPR*
AIZR
AVHL*
AIYR*
AIZR
RIAR
RIR, AIYR
RIR
URXR
AVHL*
AWBR
AWBR
AIZL, RIR
AIZL
AWBL*
AIZL, RIR
AWBL*
AIZL
AWBL*
AWBL
OLQVL
AWBL*
AWBL*
RIAL, AUAL
RIAL, AIZL
AWBL*
RIAL
RIAL, SMBVL
RIAL, AUAL
AWBL*
RIAL, AIZL
RIAL, SMBVL
RIGR
AWBR*
AWBR*
AVHL*
RIH
RIGR
RIAR, AUAR
RIAR
RIAR, RIAR
RIAR, SMBVR
RIAR, AUAR
RIAR, SMBVR
RIAR, AIZR
a
b
c
d
RIAL
ADAL
RIAL, ADAL
ASHL*
RIAL, AIZL
ASHL*
RIAL, AIZL
AIZL
RIAL
AWAR*
ADAR
RIAR, ADAR
ASHR*
RIAR, ASHR
ASHR*
AWBR*
RIAR, SMBDL
AWAR*
AIAR
AWAR
ADFL
CELL BODY IN LATERAL GANGLION
ADFR
CELL BODY IN LATERAL GANGLION



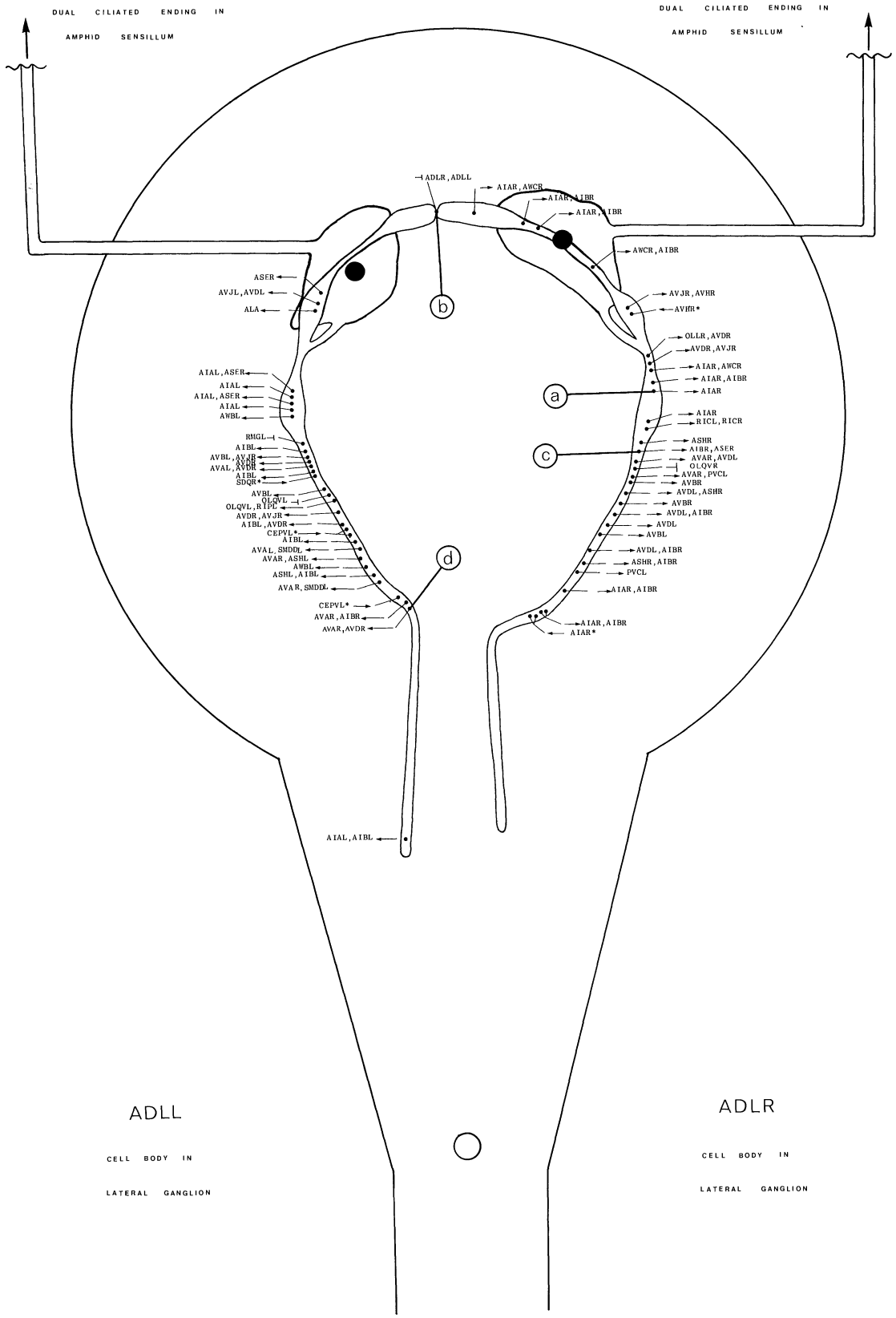
ADF

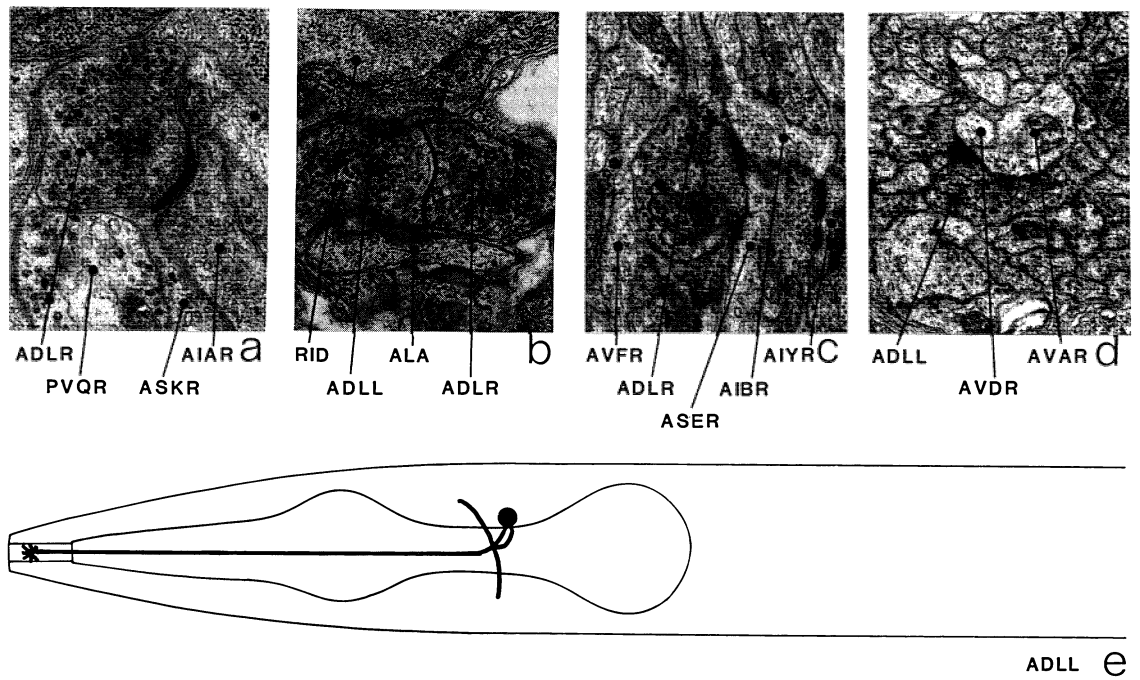
Members: ADFL, ADFR.

ADF is a set of two neurons that have dual ciliated endings in the amphid sensillum. The endings are in the amphid channel, which is open to the outside (figure 1). Processes from lateral cell bodies enter the ventral cord via the amphidial commissures and turn anteriorly to enter the nerve ring. The processes of ADF run near the outside surface and posterior face of the ring, in close association with those of AIZ. They meet at the dorsal mid-line and terminate; there is a gap junction at the point of contact (b). The main synaptic output is to RIA and AIZ (a); there are also synapses to SMB (c), AUA and RIR, usually in dyadic combinations with RIA or AIZ. AWB synapses onto ADF in several places (d, *a) and there are gap junctions to RIH, ADA and AIA.

Magnifications: (a) ×25500, (b)–(d) ×12750.

ADL


DUAL CILIATED ENDING IN AMPHID SENSILLUM
DUAL CILIATED ENDING IN AMPHID SENSILLUM
ADLR, ADLL
AIAR, AWCR
AIAR, AIBR
AIAR, AIBR
AWCR, AIBR
ASER
AVJL, AVDL
ALA
AVJR, AVHR
AVHR*
OLLR, AVDR
AVDR, AVJR
AIAR, AWCR
AIAR, AIBR
AIAR
AIAR
RICL, RICR
ASHR
AIBR, ASER
AVAR, AVDL
OLQVR
AVAR, PVCL
AVBR
AVDL, ASHR
AVBR
AVDL, AIBR
AVDL
AVBL
AVDL, AIBR
ASHR, AIBR
PVCL
AIAR, AIBR
AIAR, AIBR
AIAR*
AIAL, ASER
AIAL
AIAL, ASER
AIAL
AWBL
RMGL
AIBL
AVBL, AVJR
AVAR
AVAL, AVDR
AIBL
SDQR*
AVBL
OLQVL
OLQVL, RIPL
AVDR, AVJR
AIBL, AVDR
CEPVL*
AIBL
AVAL, SMDDL
AVAR, ASHL
AWBL
ASHL, AIBL
AVAR, SMDDL
CEPVL*
AVAR, AIBR
AVAR, AVDR
AIAL, AIBL
a
b
c
d
ADLL
CELL BODY IN LATERAL GANGLION
ADLR
CELL BODY IN LATERAL GANGLION

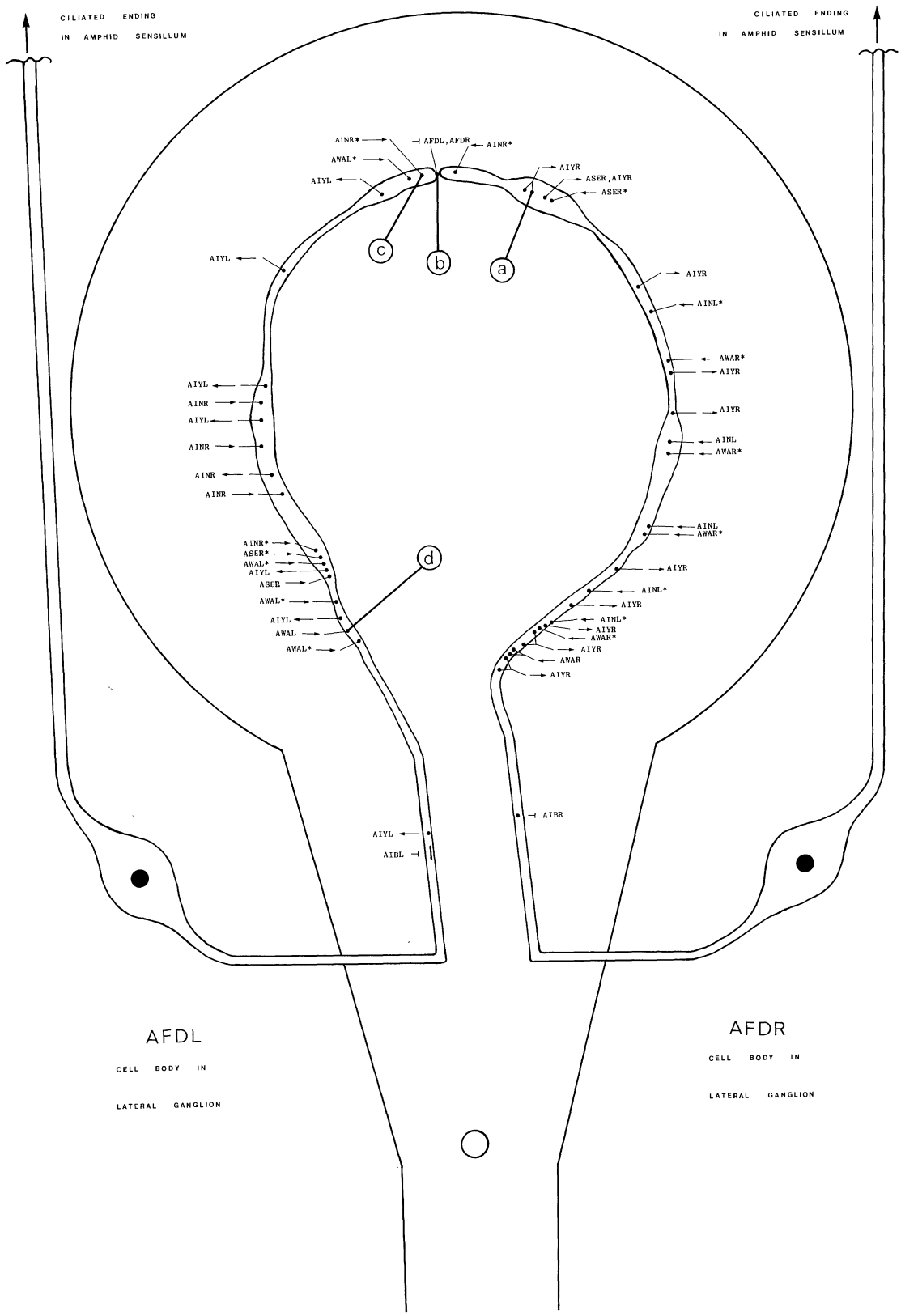


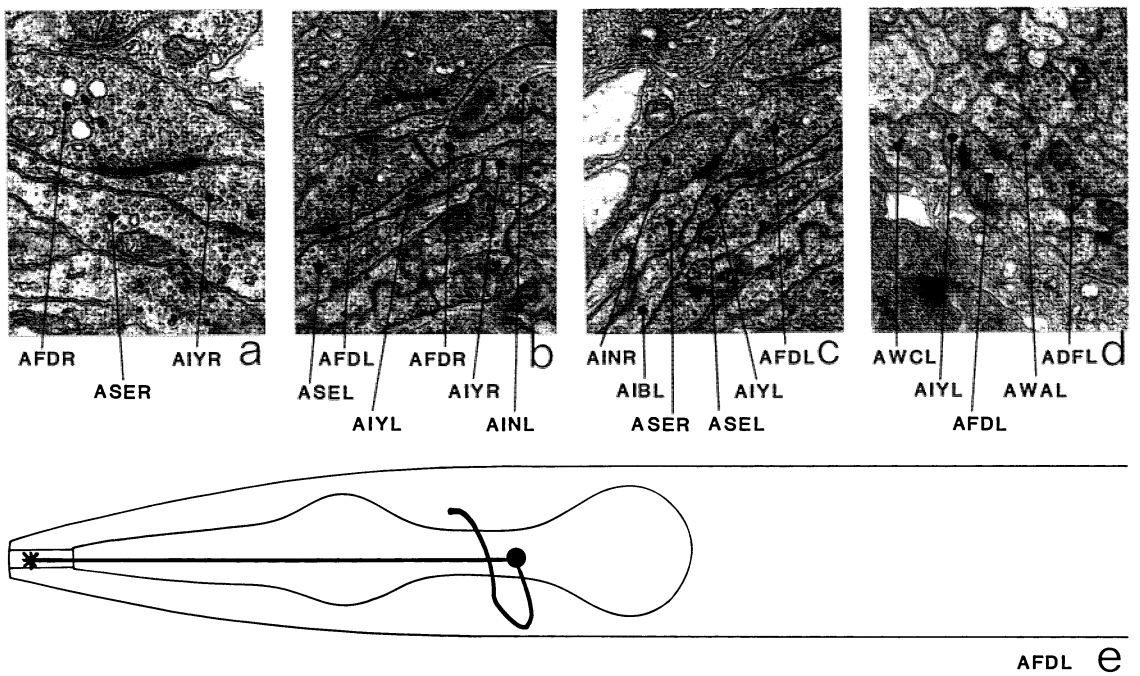
ADL

Members: ADLL, ADLR.

ADL is a set of two neurons that have dual ciliated endings in the amphid sensillum. The endings are in the amphid channel, which is open to the outside (figure 1). Cell bodies are situated in the dorsal regions of the lateral ganglia and have processes that enter the nerve ring laterally, unlike the other amphid neurons, which enter the ventral cord via the amphidial commissures. The processes split as they enter the nerve ring and one process runs dorsally round to the mid-line on the posterior face of the nerve ring, where it meets its contralateral partner and terminates with a gap junction (b). The other process runs ventrally and eventually peters out in the ventral ganglion. The general disposition of the processes in the nerve ring is much like those of the other amphid neurons (such as ASK, alongside which it runs for much of its length) yet the route from the cell body is completely different. The processes are large; they run in close association with those of AIB and are filled with vesicles, many of which are dark-cored (a). The processes are predominantly presynaptic, synapsing mainly onto AIA (a) and AIB (c) and to a lesser extent onto AVD, AVB and AVA (d). There are gap junctions to OLQ and RMG.

Magnifications: (a) ×25500, (b–d) ×12750.


CILIATED ENDING
IN AMPHID SENSILLUM
CILIATED ENDING
IN AMPHID SENSILLUM
AINR*
AFDL, AFDR
AINR*
AWAL*
AIYL
AIYR
ASER, AIYR
ASER*
c
b
a
AIYL
AIYR
AINL*
AWAR*
AIYR
AIYL
AINR
AIYL
AIYR
AINR
AINL
AWAR*
AINR
AINR
AINL
AWAR*
AINR*
ASER*
AWAL*
AIYL
ASER
d
AIYR
AINL*
AWAL*
AIYR
AIYL
AINL*
AWAL
AIYR
AWAR*
AWAL*
AIYR
AWAR
AIYR
AIBR
AIYL
AIBL
AFDL
CELL BODY IN
LATERAL GANGLION
AFDR
CELL BODY IN
LATERAL GANGLION

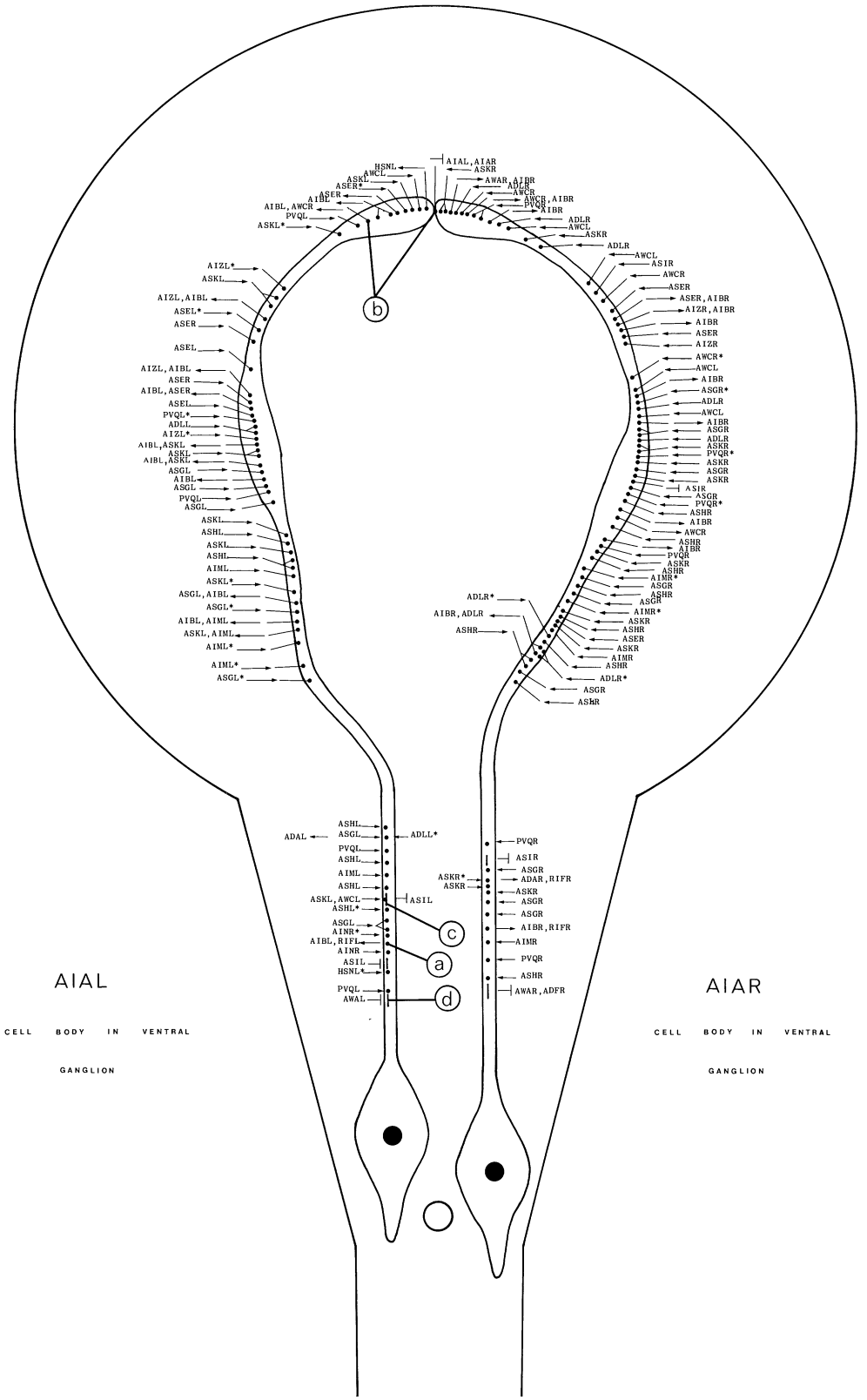


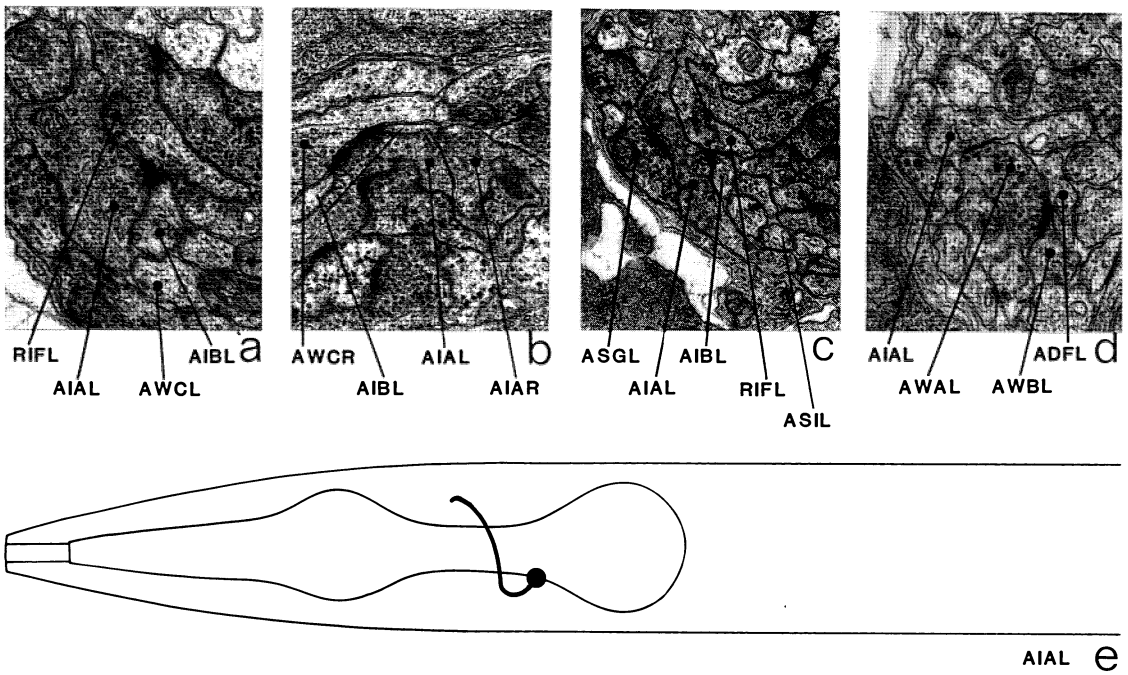
AFD

Members: AFDL, AFDR.

AFD is a set of two ciliated neurons that are part of the amphid sensillum. The endings of AFD have numerous villi, which poke into the amphid sheath cells (figure 1). The cell bodies are situated in the lateral ganglia; processes enter the ventral cord via the amphidial commissures and turn anteriorly to enter the nerve ring. They run round on the outside surface and the posterior face of the nerve ring in close association with the processes of AIY until they meet at the dorsal mid-line, where they terminate. There is a gap junction at the point of contact (b). The only synaptic output is to AIY (a); some dark-cored vesicles are seen in presynaptic terminals (a). There are synaptic inputs from AIN (c) and AWA (d) and small gap junctions to AIB in the ventral ganglion.

Magnifications: (a) $\times 25500$, (b–d) $\times 12750$.


AIAL
CELL BODY IN VENTRAL GANGLION
AIAR
CELL BODY IN VENTRAL GANGLION
HSNL
AWCL
ASKL
ASER*
AIBL
AIBL, AWCR
PVQL
ASKL*
AIAL, AIAR
ASKR
AWAR, AIBR
ADLR
AWCR
AWCR, AIBR
PVQR
AIBR
ADLR
AWCL
ASKR
ADLR
AWCL
ASIR
AWCR
ASER
ASER, AIBR
AIZR, AIBR
AIBR
ASER
AIZR
AWCR*
AWCL
AIBR
ASGR*
ADLR
AWCL
AIBR
ASGR
ADLR
ASKR
PVQR*
ASKR
ASGR
ASKR
ASIR
ASGR
PVQR*
ASHR
AIBR
AWCR
ASHR
AIBR
PVQR
ASKR
ASHR
AIMR*
ASGR
ASHR
ASGR
AIMR*
ASKR
ASHR
ASER
ASKR
AIMR
ASHR
ADLR*
ASGR
ASHR
AIZL*
ASKL
AIZL, AIBL
ASEL*
ASER
ASEL
AIZL, AIBL
ASER
AIBL, ASER
ASEL
PVQL*
ADLL
AIZL*
AIBL, ASKL
ASKL
AIBL, ASKL
ASGL
AIBL
ASGL
PVQL
ASGL
ASKL
ASHL
ASKL
ASHL
AIML
ASKL*
ASGL, AIBL
ASGL*
AIBL, AIML
ASKL, AIML
AIML*
AIML*
ASGL*
ADLR*
AIBR, ADLR
ASHR
b
ASHL
ADAL
ASGL
ADLL*
PVQL
ASHL
AIML
ASHL
ASKL, AWCL
ASHL*
ASIL
ASGL
AINR*
AIBL, RIFL
AINR
ASIL
HSNL*
PVQL
AWAL
ASKR*
ASKR
PVQR
ASIR
ASGR
ADAR, RIFR
ASKR
ASGR
ASGR
AIBR, RIFR
AIMR
PVQR
ASHR
AWAR, ADFR
c
a
d



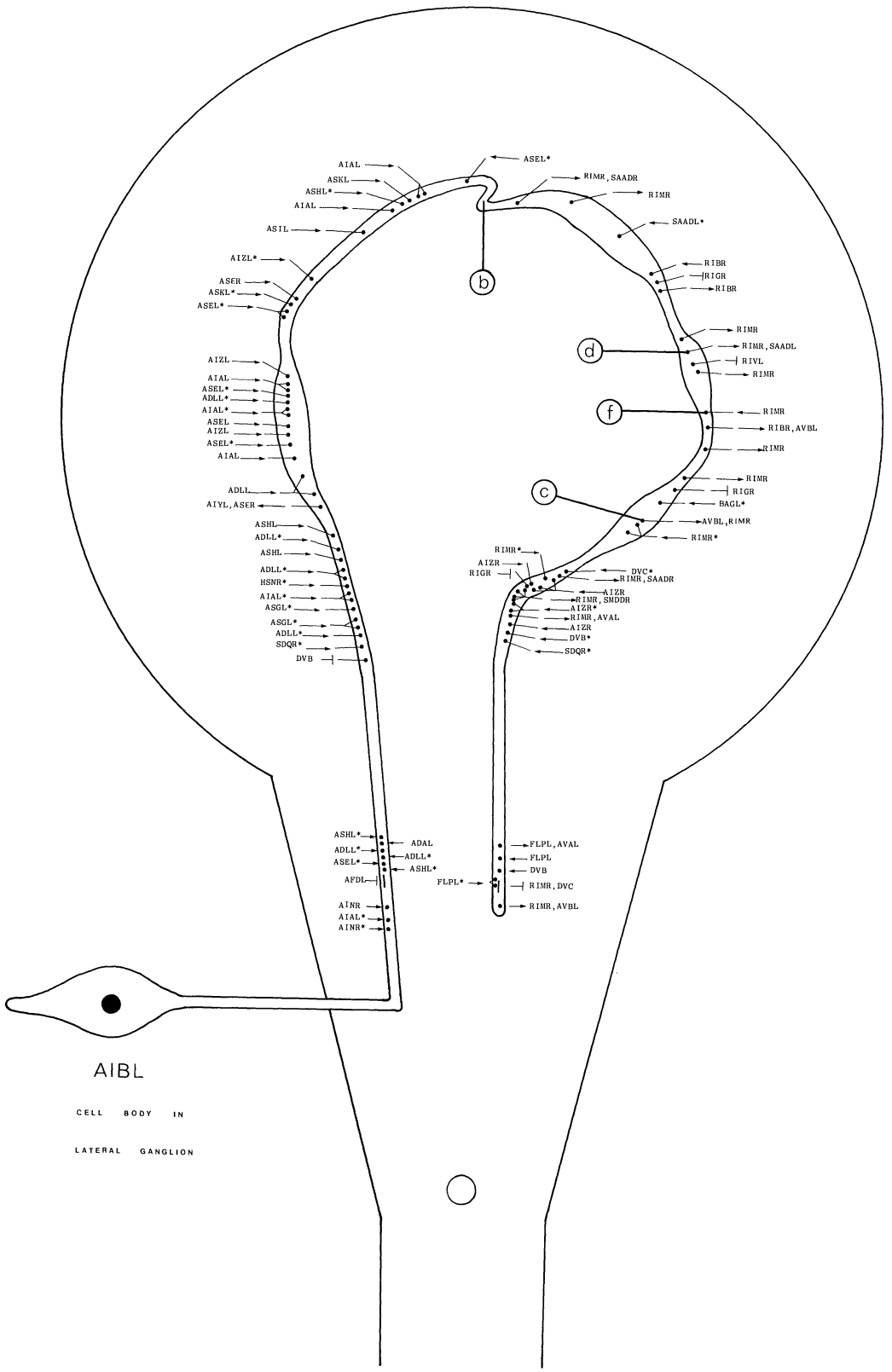
AIA

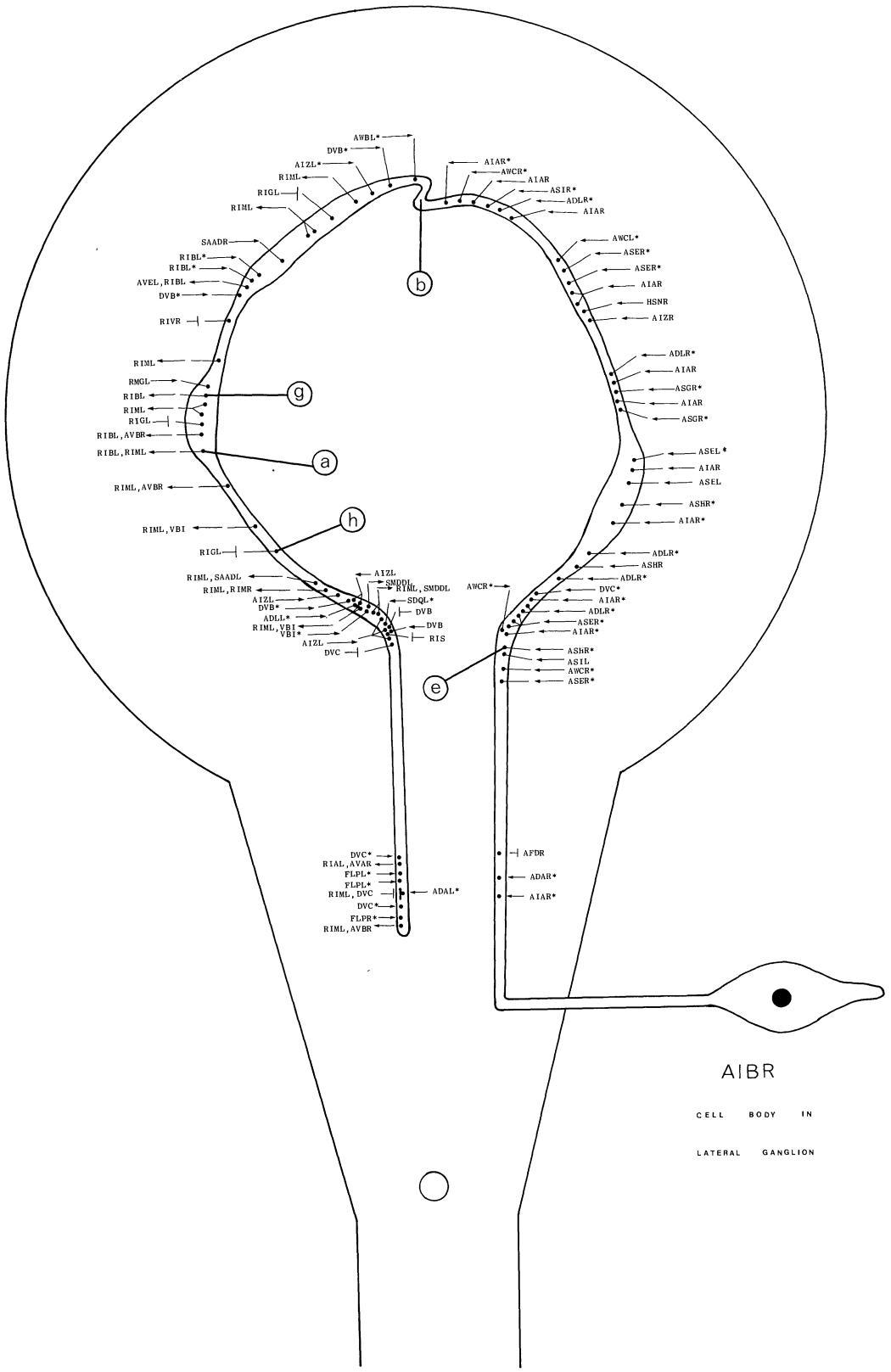
Members: AIAL, AIAR.

AIA is a set of two interneurons with cell bodies situated in the ventral ganglion. Their processes run up the ventral cord, run round the nerve ring close to the posterior face of the neuropile and terminate at the dorsal mid-line with a gap junction to their contralateral partners (b). The processes of AIA run in close association with the proximal regions of the processes from AIB (a). AIA is one of the main classes of integrating neuron for the neurons of the amphid sensilla, receiving synaptic inputs predominantly from ASK (*a), ASG (*a), ASH (*a), ADL (*a), PVQ (*a–*d), AIM (*a), ASE (*b), AWC (*c), AIZ and ASI (*a). Most of these synapses are dyadic; AIB is the corecipient. The main synaptic output is to AIB, often as a dyadic with RIF (a) or AWC (b) as the corecipient. AIA has gap junctions to ASI (c), AWA (d) and ADF.

Magnifications: (a, d) ×25500, (b, c) ×12750.

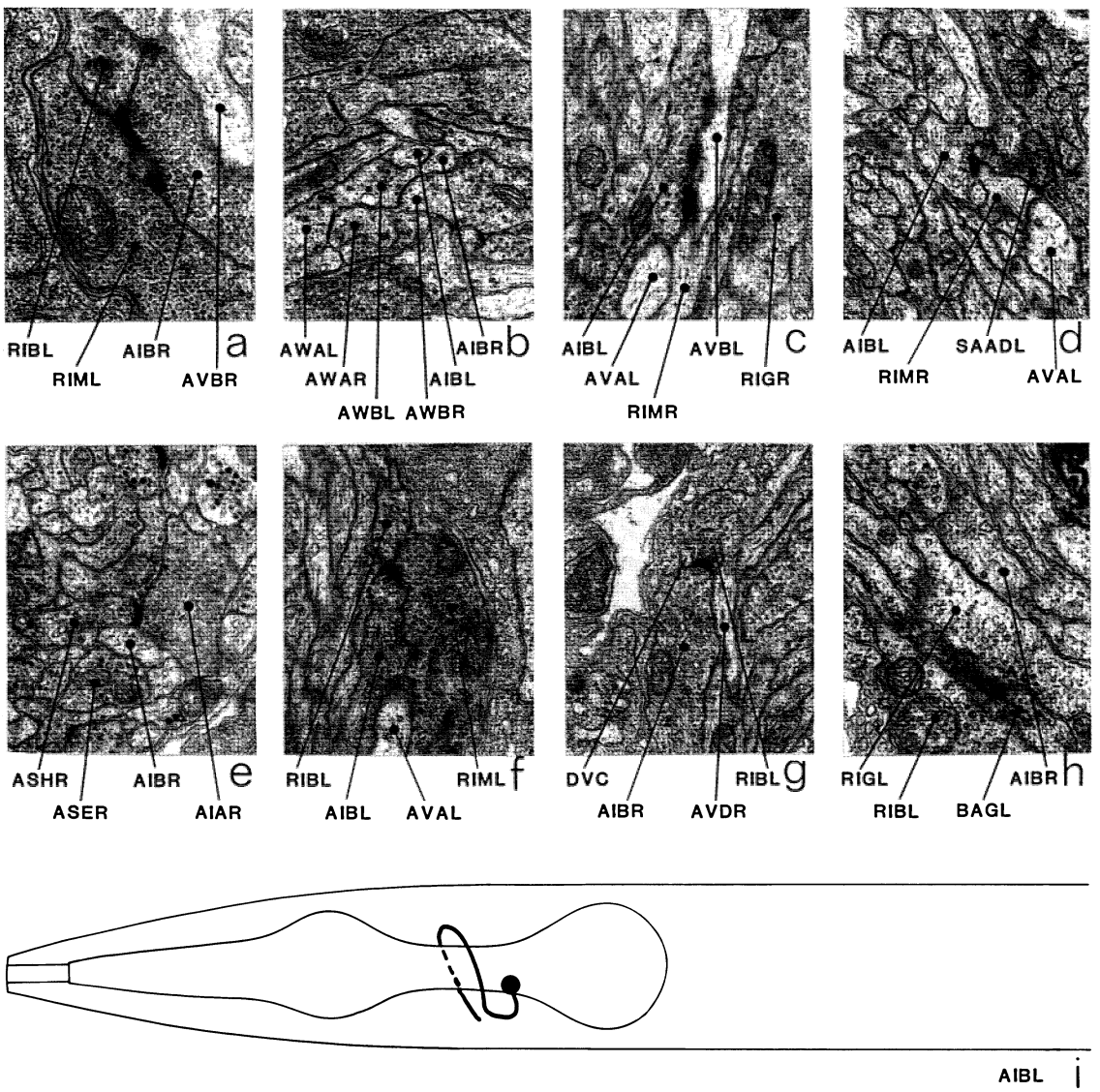
AIB


AIAL
ASKL
ASHL*
AIAL
ASIL
AIZL*
ASER
ASKL*
ASEL*
AIZL
AIAL
ASEL*
ADLL*
AIAL*
ASEL
AIZL
ASEL*
AIAL
ADLL
AIYL, ASER
ASHL
ADLL*
ASHL
ADLL*
HSNR*
AIAL*
ASGL*
ASGL*
ADLL*
SDQR*
DVB
ASEL*
RIMR, SAADR
RIMR
SAADL*
RIBR
RIGR
RIBR
RIMR
RIMR, SAADL
RIVL
RIMR
RIMR
RIBR, AVBL
RIMR
RIMR
RIGR
BAGL*
AVBL, RIMR
RIMR*
RIMR*
AIZR
RIGR
DVC*
RIMR, SAADR
AIZR
RIMR, SMDDR
AIZR*
RIMR, AVAL
AIZR
DVB*
SDQR*
ASHL*
ADLL*
ASEL*
AFDL
AINR
AIAL*
AINR*
ADAL
ADLL*
ASHL*
FLPL*
FLPL, AVAL
FLPL
DVB
RIMR, DVC
RIMR, AVBL
b
d
f
c
AIBL
CELL BODY IN
LATERAL GANGLION



AIBR

CELL BODY IN LATERAL GANGLION



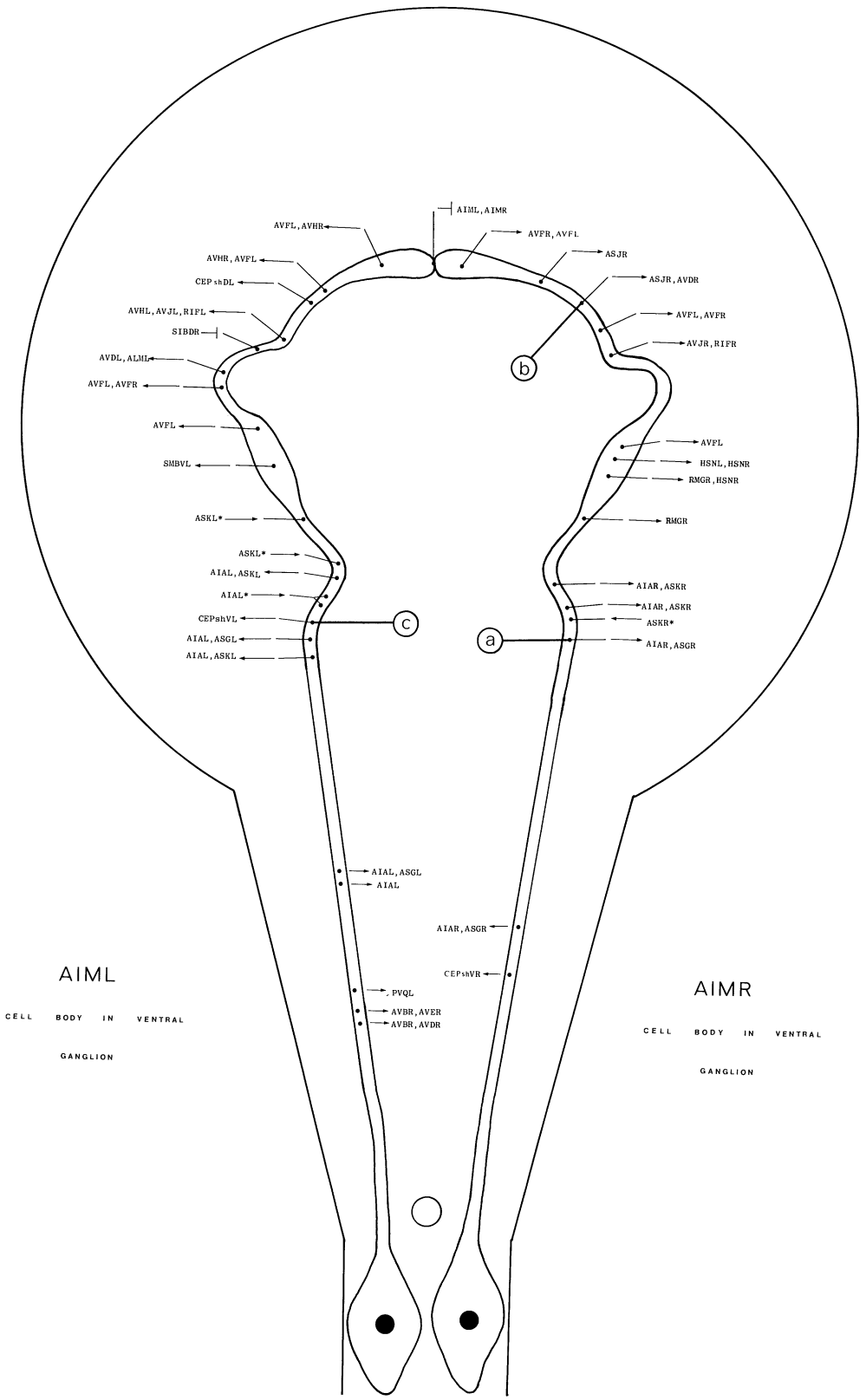
AIB

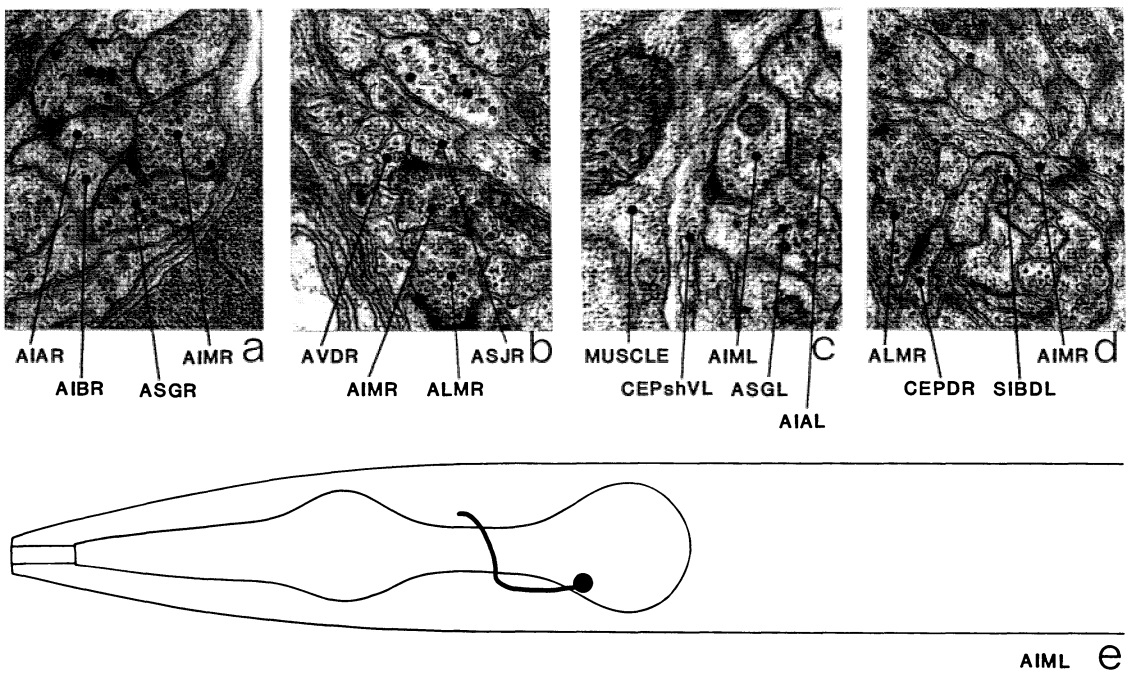
Members: AIBL, AIBR.

AIB is a set of two interneurons with cell bodies situated in the lateral ganglia; it is one of the main classes of integrating neuron for the receptors of the amphid sensilla. Processes enter the ventral cord from the cell bodies via the amphid commissures and project anteriorly into the nerve ring. They then run round the nerve ring close to the posterior face, in close association with the processes of AIA. When they reach the dorsal midline, at the point where the processes of AIA terminate, they turn and run anteriorly for about 2.5 μm at right angles to the orientation of the neighbouring processes in this region (b). They then turn again and continue running round the ring, but now in close association with the proximal processes of RIM near the anterior surface of the ring. They eventually reenter the ventral cord and finally end in the region of the ventral ganglion. AIB is presynaptic only on these distal regions of its processes; the predominant postsynaptic partners are RIM (a, c, d), AVB (c), RIB (a, g)

and SAAD (d). Because of the unusual shift of position that occurs on the dorsal mid-line, the distal and proximal regions of AIB reside in different regions of the ring neuropile and the synaptic inputs are, therefore, different for these two regions. The proximal regions receive essentially the same synaptic input as AIA (except for synapses from AIA), with AIB being the second postsynaptic element in dyadic synapses. Most of the synapses appear to be symmetrical, although some have a bias towards AIA (e). The main synaptic inputs in these proximal regions are from AIA (*a, *b), ASE, ADL (*c), ASH, AWC (*b), ASG (*b), AIZ (*g), ASK (*d) and ASI. The main synaptic inputs on the distal branch are from AIZ (*e, *f), DVB (*a), DVC (*c), RIM (f), RIB and FLP. AIB has gap junctions to DVB, DVC, RIG (h), AFD, RIS and RIV (*h).

Magnifications: (a, h) $\times 25500$, (b–g) $\times 12750$.


AIML, AIMR
AVFL, AVHR
AVFR, AVFL
AVHR, AVFL
ASJR
CEPshDL
ASJR, AVDR
AVHL, AVJL, RIFL
AVFL, AVFR
SIBDR
AVJR, RIFR
AVDL, ALML
b
AVFL, AVFR
AVFL
AVFL
HSNL, HSNR
SMBVL
RMGR, HSNR
ASKL*
RMGR
ASKL*
AIAL, ASKL
AIAR, ASKR
AIAL*
AIAR, ASKR
CEPshVL
ASKR*
c
a
AIAL, ASGL
AIAR, ASGR
AIAL, ASKL
AIAL, ASGL
AIAL
AIAR, ASGR
CEPshVR
PVQL
AVBR, AVER
AVBR, AVDR
AIML
CELL BODY IN VENTRAL GANGLION
AIMR
CELL BODY IN VENTRAL GANGLION

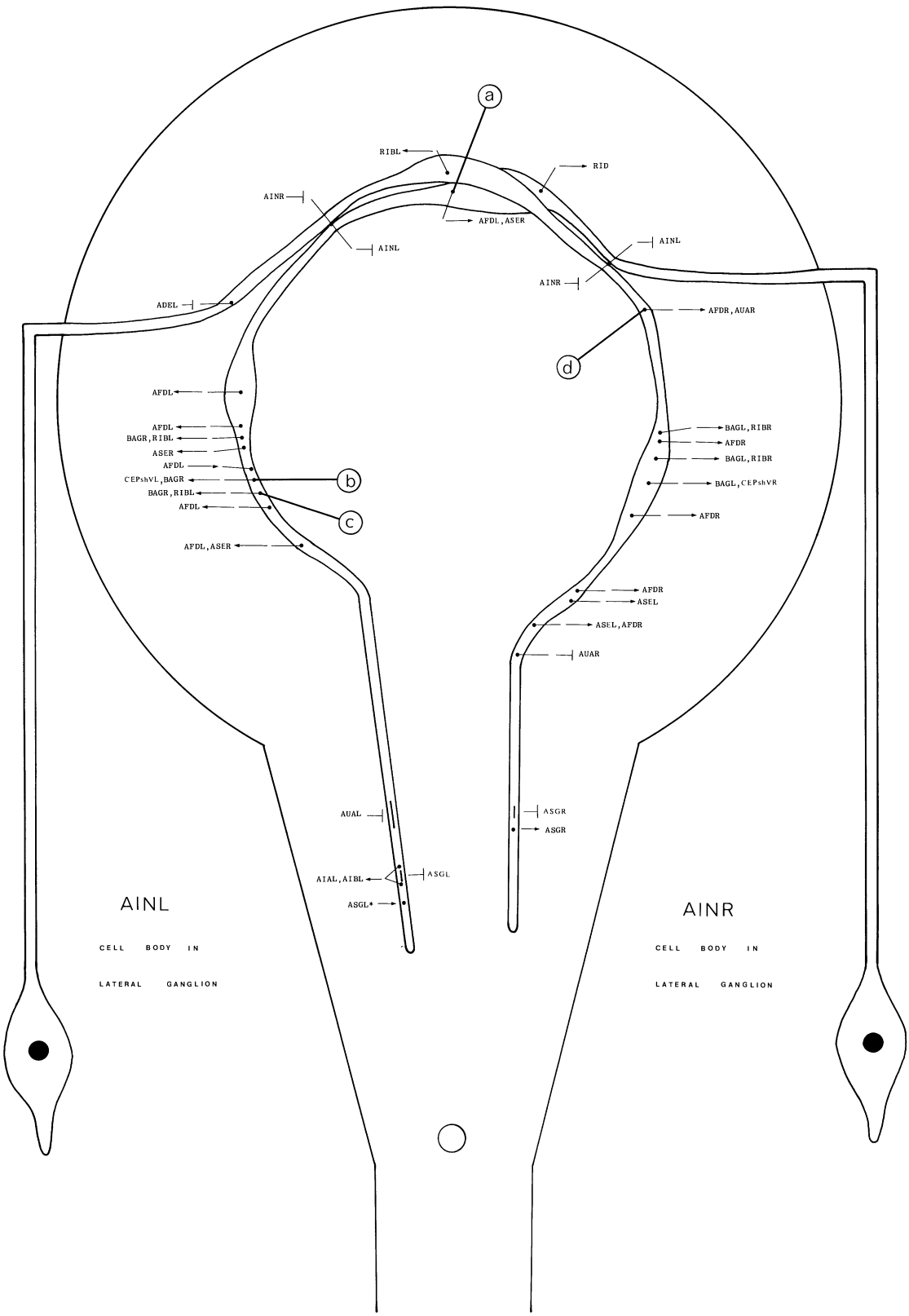


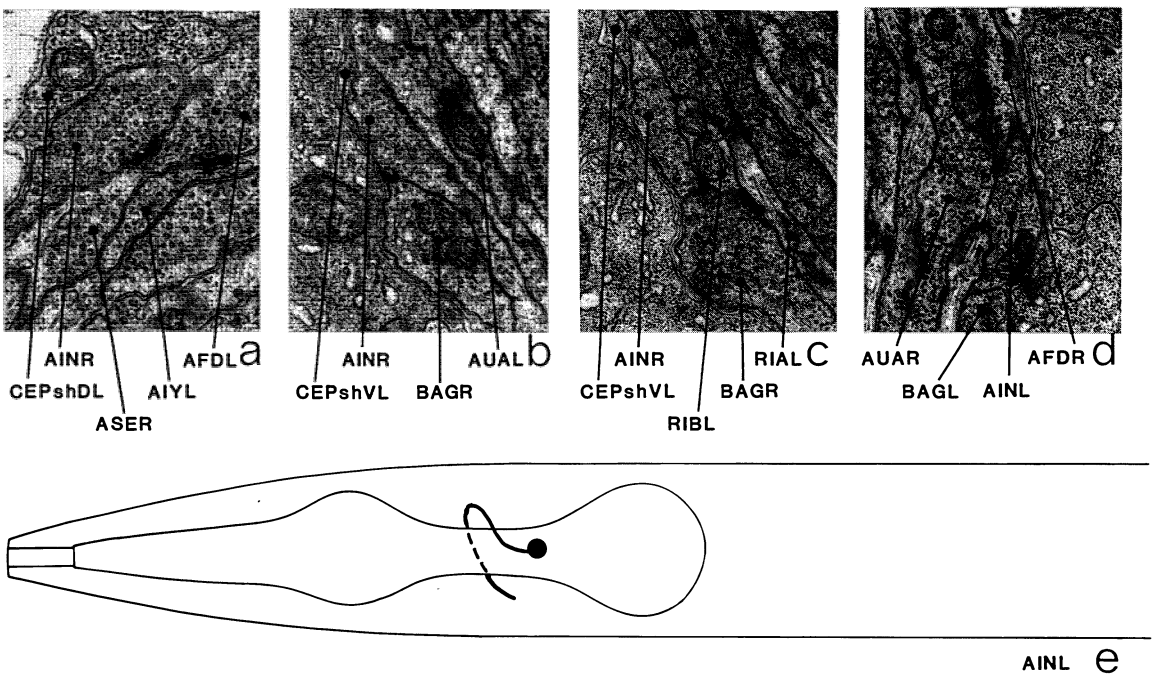
AIM

Members: AIML, AIMR.

AIM is a set of two interneurons with cell bodies in the ventral ganglion behind the excretory duct. Processes run anteriorly from the cell bodies, adjacent to the lateral surfaces of the ventral cord. On entering the nerve ring they move round to the inside surface until they reach a sub-dorsal position, where they loop out into the middle of the neuropile and then return to the inner surface until the processes meet and terminate with a gap junction on the dorsal mid-line. The main synaptic output is to AIA, usually in association with ASG (a) or ASK as dyadic partners. Synapses are also made to ASJ (b), AVF, the cephalic sheath cells (c) and a few other minor partners. There is not much synaptic input except for a few synapses from ASK (*c). There are gap junctions to SIBD (d) (there was only one present in the U series but there is one on each side in the H series).

Magnifications: (a–d) ×25500.


a
RIBL
RID
AINR
AFDL, ASER
AINL
AINL
AINR
ADEL
AFDR, AUAR
d
AFDL
AFDL
BAGR, RIBL
ASER
AFDL
CEPshVL, BAGR
BAGR, RIBL
AFDL
b
c
AFDL, ASER
BAGL, RIBR
AFDR
BAGL, RIBR
BAGL, CEPshVR
AFDR
AFDR
ASEL
ASEL, AFDR
AUAR
AUAL
ASGR
ASGR
AIAL, AIBL
ASGL
ASGL*
AINL
CELL BODY IN
LATERAL GANGLION
AINR
CELL BODY IN
LATERAL GANGLION



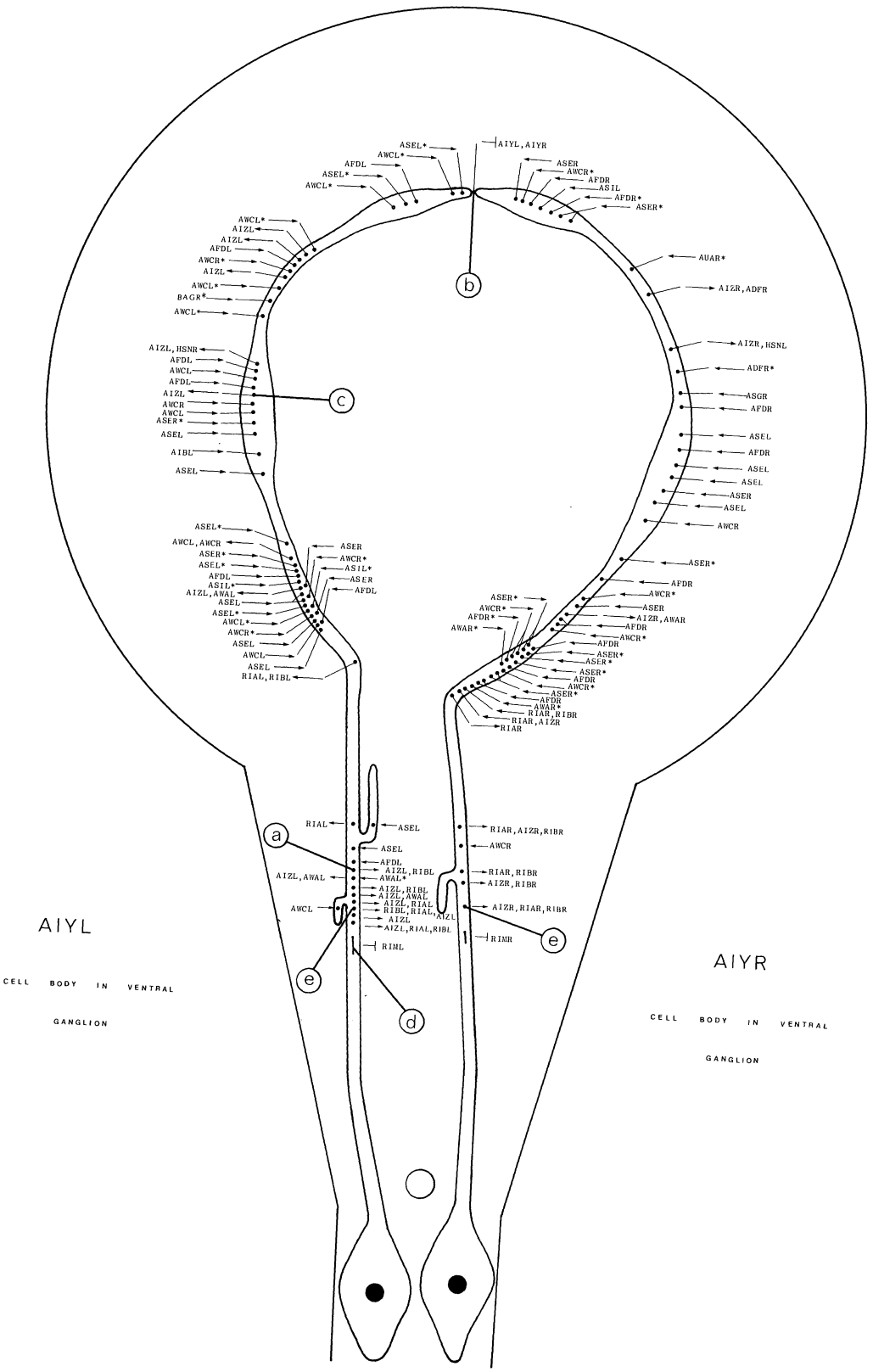
AIN

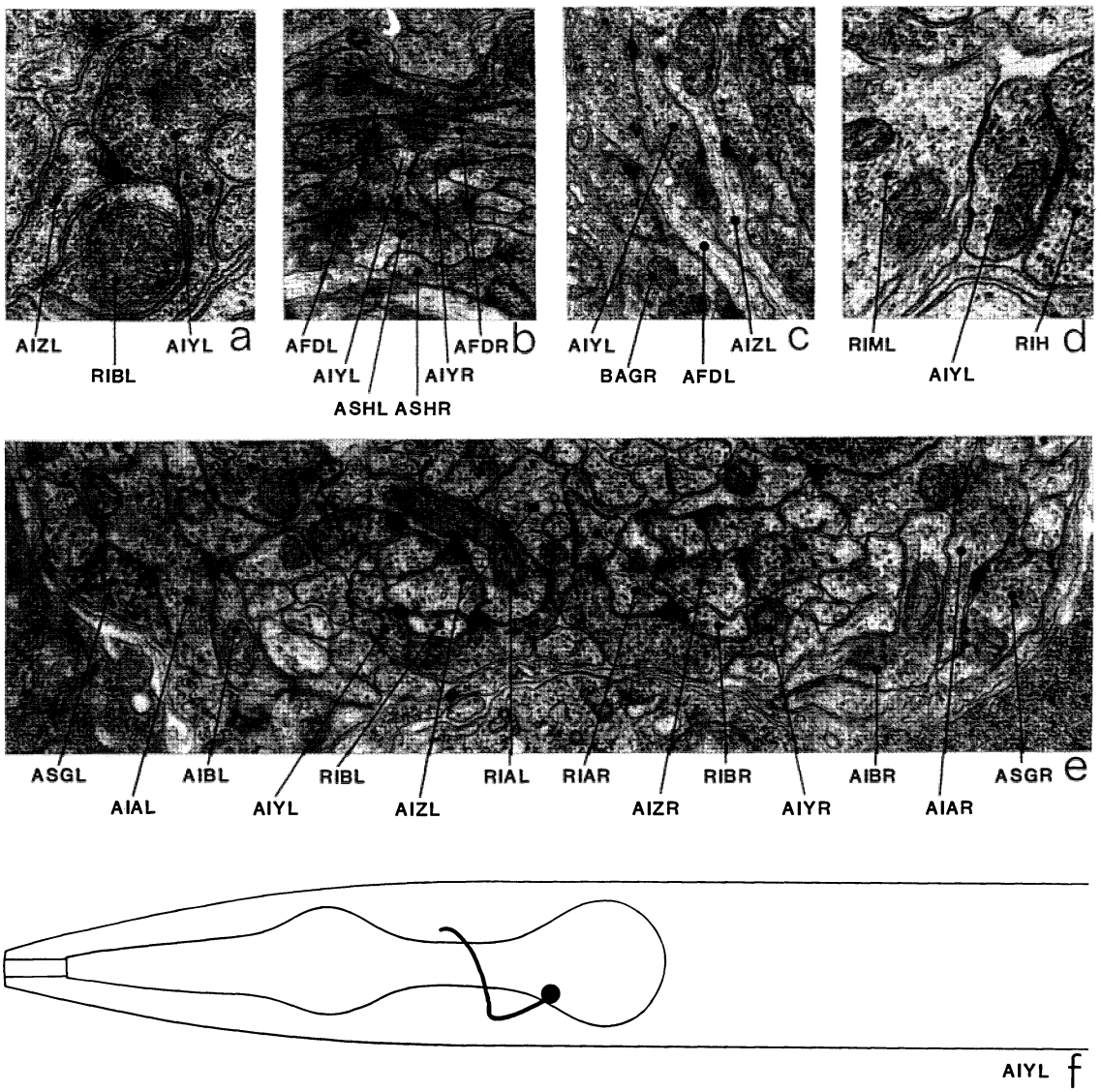
Members: AINL, AINR.

AIN is a set of two interneurons with cell bodies situated in the lateral ganglia. Processes project anteriorly and enter the nerve ring sub-dorsally. They run round the ring to the contralateral side on the outside surface and then enter the ventral cord, eventually petering out in the region of the ventral ganglion. The main synaptic output is to AFD (a, d), BAG (b), RIB (c), and ASE (a). The cephalic sheath cells may also be receiving synaptic input from AIN at dyadic synapses (b). AIN has no significant synaptic inputs but has gap junctions with ASG, AUA (*d) and itself.

Magnifications: (a) ×25500, (b–d) ×12750.

AIY


ASEL*
AWCL*
AFDL
ASEL*
AWCL*
AIYL, AIYR
ASER
AWCR*
AFDR
ASIL
AFDR*
ASER*
AWCL*
AIZL
AIZL
AFDL
AWCR*
AIZL
AWCL*
BAGR*
AWCL*
AUAR*
AIZR, ADFR
AIZL, HSNR
AFDL
AWCL
AFDL
AIZL
AWCR
AWCL
ASER*
ASEL
AIBL
ASEL
AIZR, HSNL
ADFR*
ASGR
AFDR
ASEL
AFDR
ASEL
ASEL
ASER
ASEL
AWCR
ASEL*
AWCL, AWCR
ASER*
ASEL*
AFDL
ASIL*
AIZL, AWAL
ASEL
ASEL*
AWCL*
AWCR*
ASEL
AWCL
ASEL
RIAL, RIBL
ASER
AWCR*
ASIL*
ASER
AFDL
ASER*
AWCR*
AFDR*
AWAR*
ASER
AIZR, AWAR
AFDR
AWCR*
AFDR
ASER*
ASER*
ASER*
AFDR
AWCR*
ASER*
AFDR
AWAR*
RIAR, RIBR
RIAR, AIZR
RIAR
RIAL
ASEL
ASEL
AFDL
AIZL, RIBL
AIZL, AWAL
AWAL*
AIZL, RIBL
AIZL, AWAL
AIZL, RIAL
RIBL, RIAL, AIZL
AIZL
AIZL, RIAL, RIBL
AWCL
RIML
RIAR, AIZR, RIBR
AWCR
RIAR, RIBR
AIZR, RIBR
AIZR, RIAR, RIBR
RIMR
a
b
c
d
e
e
AIYL
CELL BODY IN VENTRAL GANGLION
AIYR
CELL BODY IN VENTRAL GANGLION

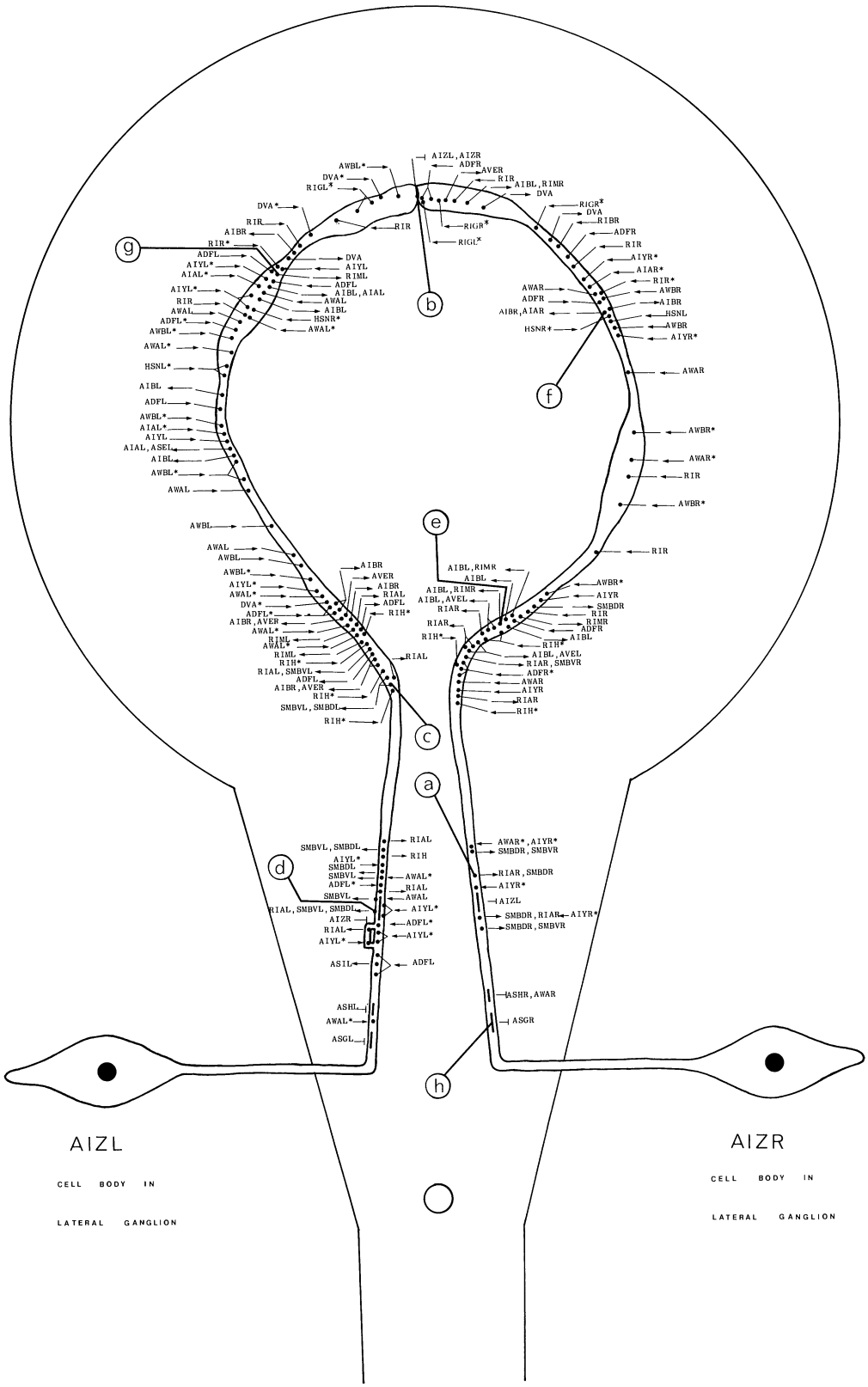


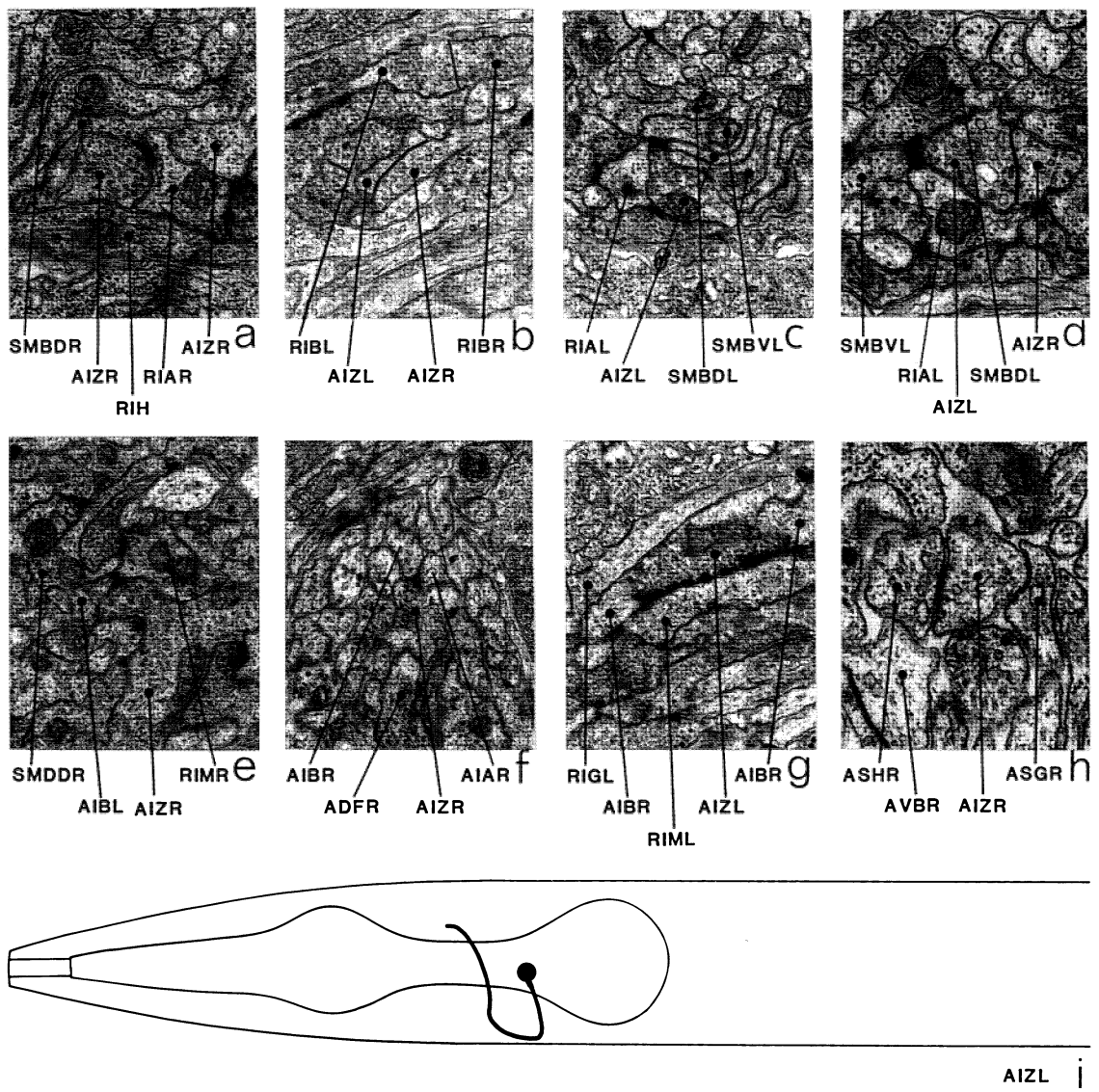
AIY

Members: AIYL, AIYR.

AIY is a set of two interneurons with cell bodies situated in the ventral ganglion behind the excretory duct. AIY is one of the main classes of integrating neuron for the receptors of the amphid sensilla. Processes run up the ventral cord from the cell bodies, forming characteristic structures in the ventral region of the neuropile of the ventral ganglion (e). The processes then run round the nerve ring in the posterior region of the neuropile, meeting and terminating at the dorsal mid-line with a gap junction (b). The main synaptic output from AIY is to AIZ, RIA and RIB. These synapses are mainly in the region of the ventral ganglion and are usually dyadic (a) or triadic (e). There are also a few smaller synapses to AIZ laterally in the nerve ring (c). Synaptic input is predominantly from ASE (*a), AWC (*c), AFD (*a) and AWA (*c). Gap junctions are made to RIM (d).

Magnifications: (a, d) ×25500, (b, c, e) ×12750.


AIZL
CELL BODY IN
LATERAL GANGLION
AIZR
CELL BODY IN
LATERAL GANGLION

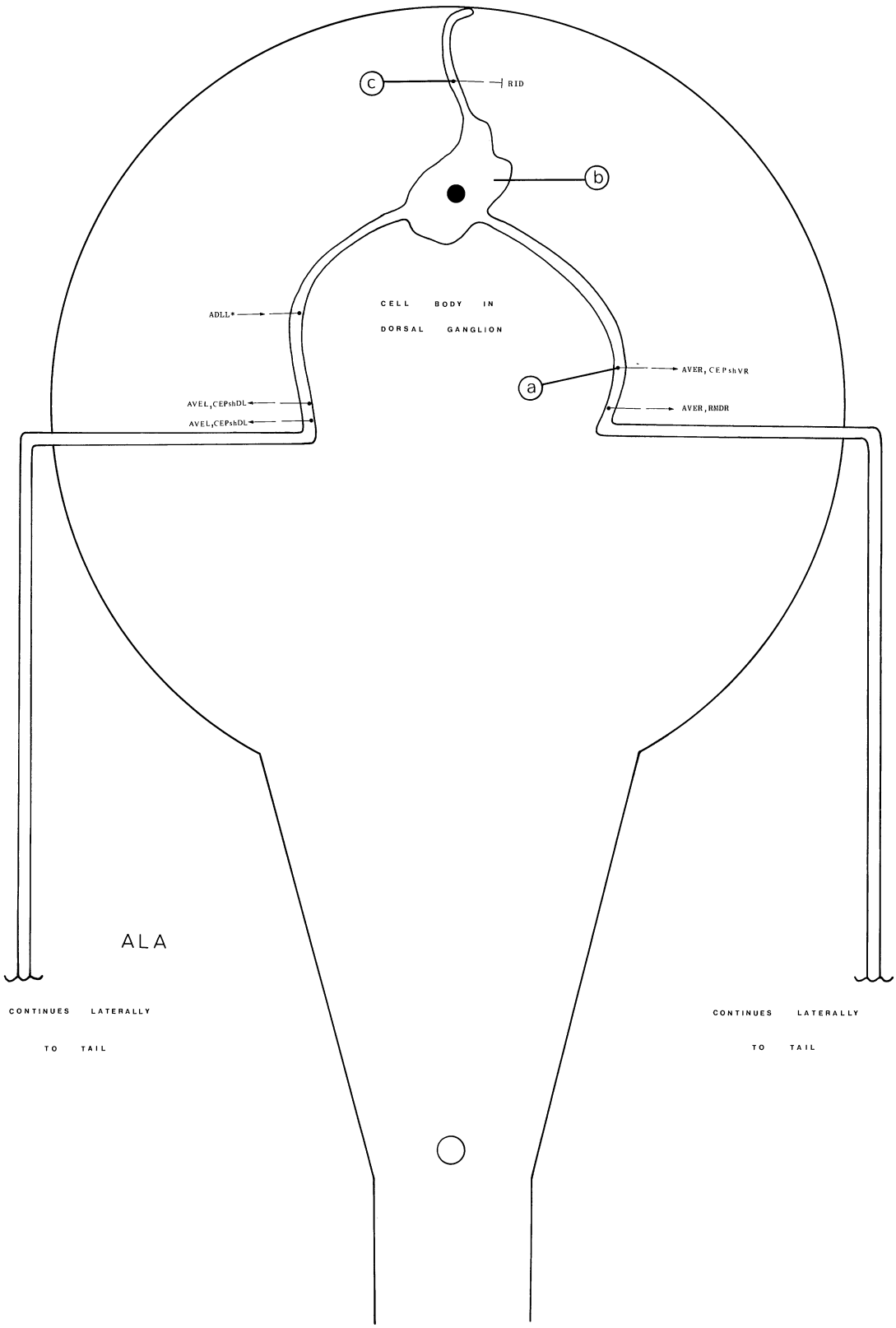


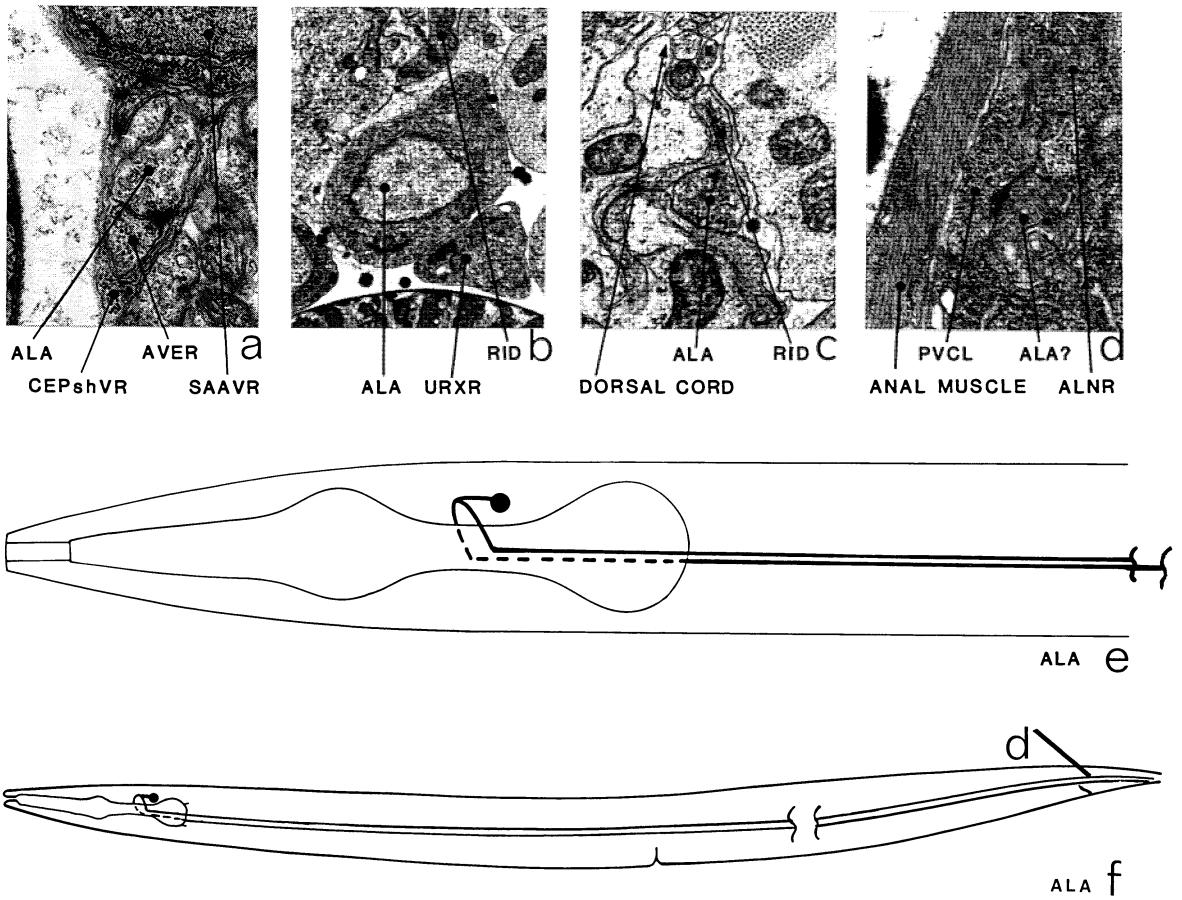
AIZ

Members: AIZL, AIZR.

AIZ is a set of two interneurons with cell bodies situated in the lateral ganglia. AIZ is one of the main classes of integrating neuron for the receptors of the amphid sensilla. Processes enter the ventral cord via the amphid commissures and run anteriorly near the ventral surface of the neuropile. Most of the synaptic output is in the region of the neuropile of the ventral ganglion. The processes then enter the nerve ring and run round it in close association with the processes of ADF near the middle of the neuropile. They move slightly anteriorly on the dorsal side of the nerve ring and meet and terminate at the dorsal mid-line with a gap junction between them (b). The main synaptic outputs are to RIA (a, c, d), SMB (a, c, d), AIB (e, f, g), RIM (e, g), AIY (f) and AVE. The main synaptic inputs are from ADF (*a), AWA (*a), AIY (*a, *c, *e), RIR (*c), AWB (*a), RIH (*a) and HSN (*f). Gap junctions are made to ASH and ASG (h) near the amphid commissures.

Magnifications: (a, h) ×25500, (b–g) ×12750.


c
RID
b
CELL BODY IN
DORSAL GANGLION
ADLL*
AVEL, CEPshDL
AVEL, CEPshDL
a
AVER, CEPshVR
AVER, RMDR
ALA
CONTINUES LATERALLY
TO TAIL
CONTINUES LATERALLY
TO TAIL

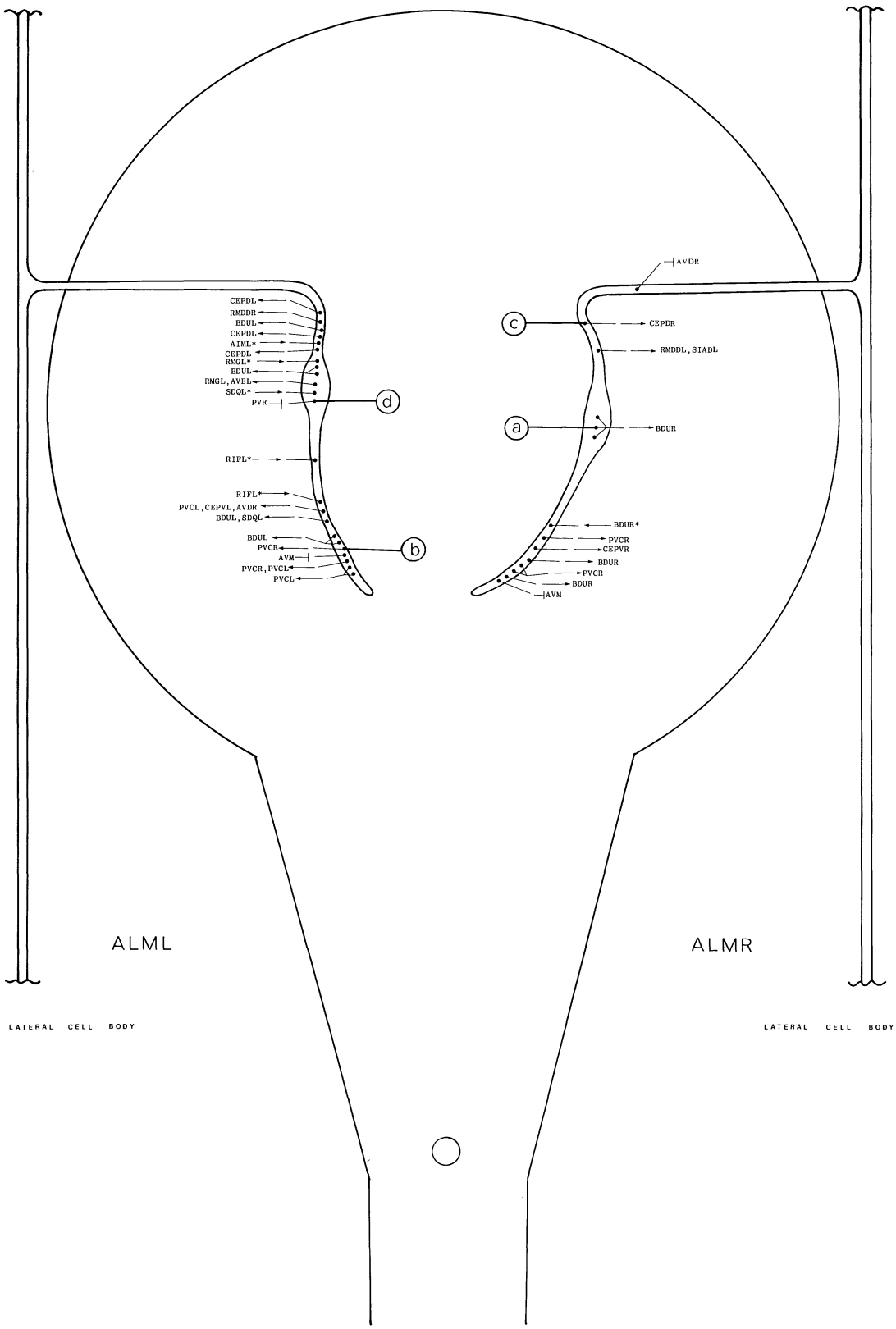


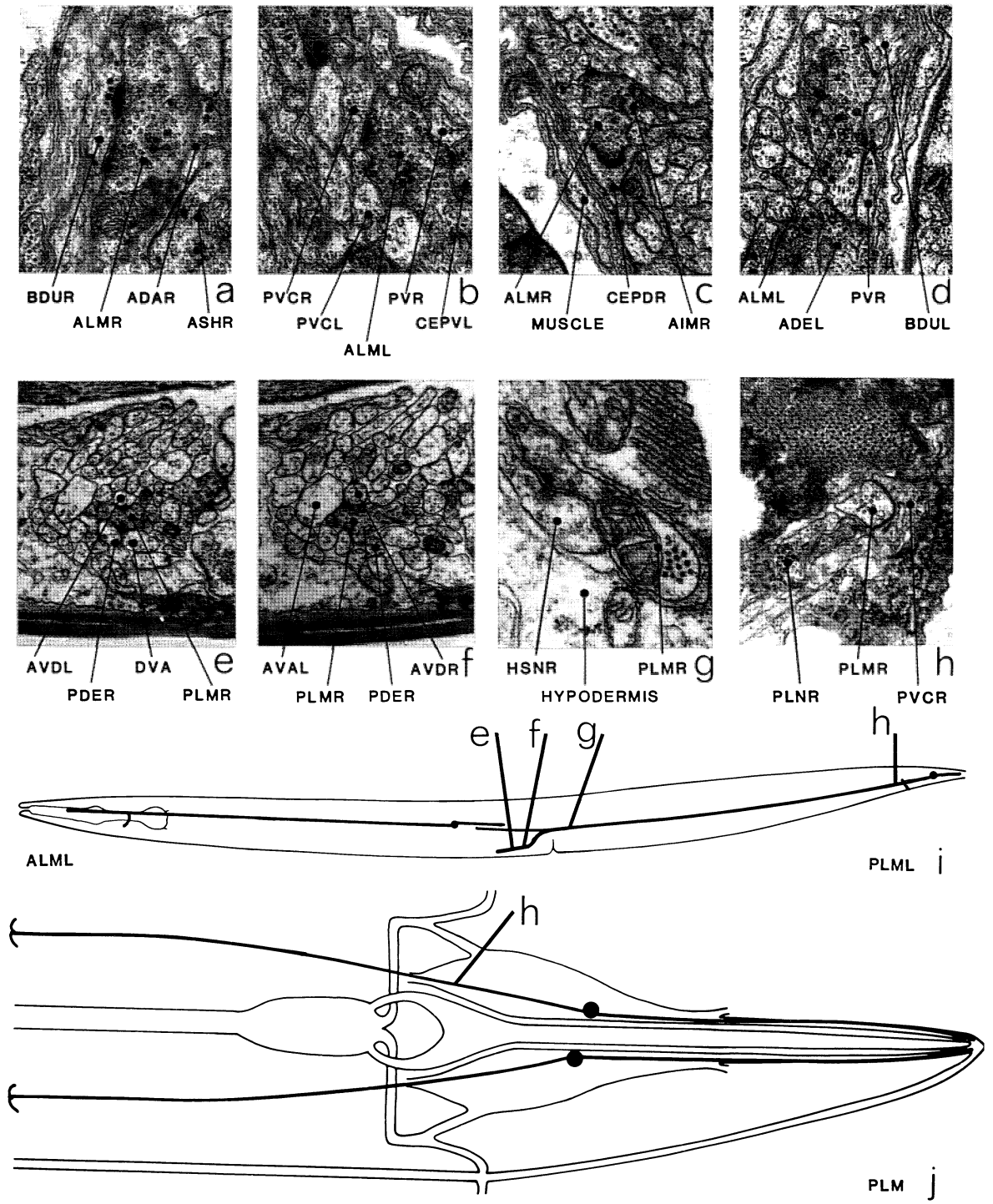
ALA

Member: ALA.

ALA is a single cell situated in the dorsal ganglion just behind the nerve ring (b). A short process enters the dorsal cord and then peters out. Two larger, bilaterally symmetrical processes leave the cell body and run right and left round the ring, leaving it laterally and running down the length of the animal, adjacent to the excretory canal and alongside the processes of CAN and PVD. This group of three processes, which run in close association to the excretory canal, has not been followed completely along the length of the animal although it has been sampled in several places. No synapses have been seen from this group except for one small synapse to the lateral hypodermis (CAN-c). Two of the three processes end at about the level of the anus and one enters the lumbar ganglion and synapses onto PVC (d). In the nerve ring, ALA has a few synapses to AVE (a) and possibly CEPsh (a) and a gap junction to RID (c) in the dorsal cord.

Magnifications: (a, d) ×25500, (b) ×6375, (c) ×12750.


CEPDL
RMDDR
BDUL
CEPDL
AIML*
CEPDL
RMGL*
BDUL
RMGL, AVEL
SDQL*
PVR
d
RIFL*
RIFL*
PVCL, CEPVL, AVDR
BDUL, SDQL
BDUL
PVCR
AVM
PVCR, PVCL*
PVCL
b
AVDR
c
CEPDR
RMDDL, SIADL
a
BDUR
BDUR*
PVCR
CEPVR
BDUR
PVCR
BDUR
AVM
ALML
ALMR
LATERAL CELL BODY
LATERAL CELL BODY



ALM AND PLM

Members: ALML, ALMR; PLML, PLMR.

ALM and PLM are two sets of two sensory neurons that transduce touch stimuli (Chalfie & Sulston 1981). Both ALM and PLM have long lateral processes, closely apposed to the

cuticle, which contain large, darkly staining microtubules (g) (Chalfie & Thomson 1982). Microtubules with the same appearance are seen in AVM and PVM, which are also part of the touch-transducing system.

ALM

The cell bodies of ALM are situated laterally in the mid-body (i). Anteriorly directed processes leave the cell bodies and run near the dorsal edge of the lateral hypodermal ridges in close association with the processes of ALN (*d). Each process sends off a branch, which enters the nerve ring sub-dorsally; this then runs ventrally round the ring near the inside surface, ending soon after it meets a process of AVM. The processes of ALM are predominantly presynaptic in the nerve ring and synapse onto BDU (a), PVC (b) and CEP (c). There are gap junctions to AVM (*d) and PVR (d).

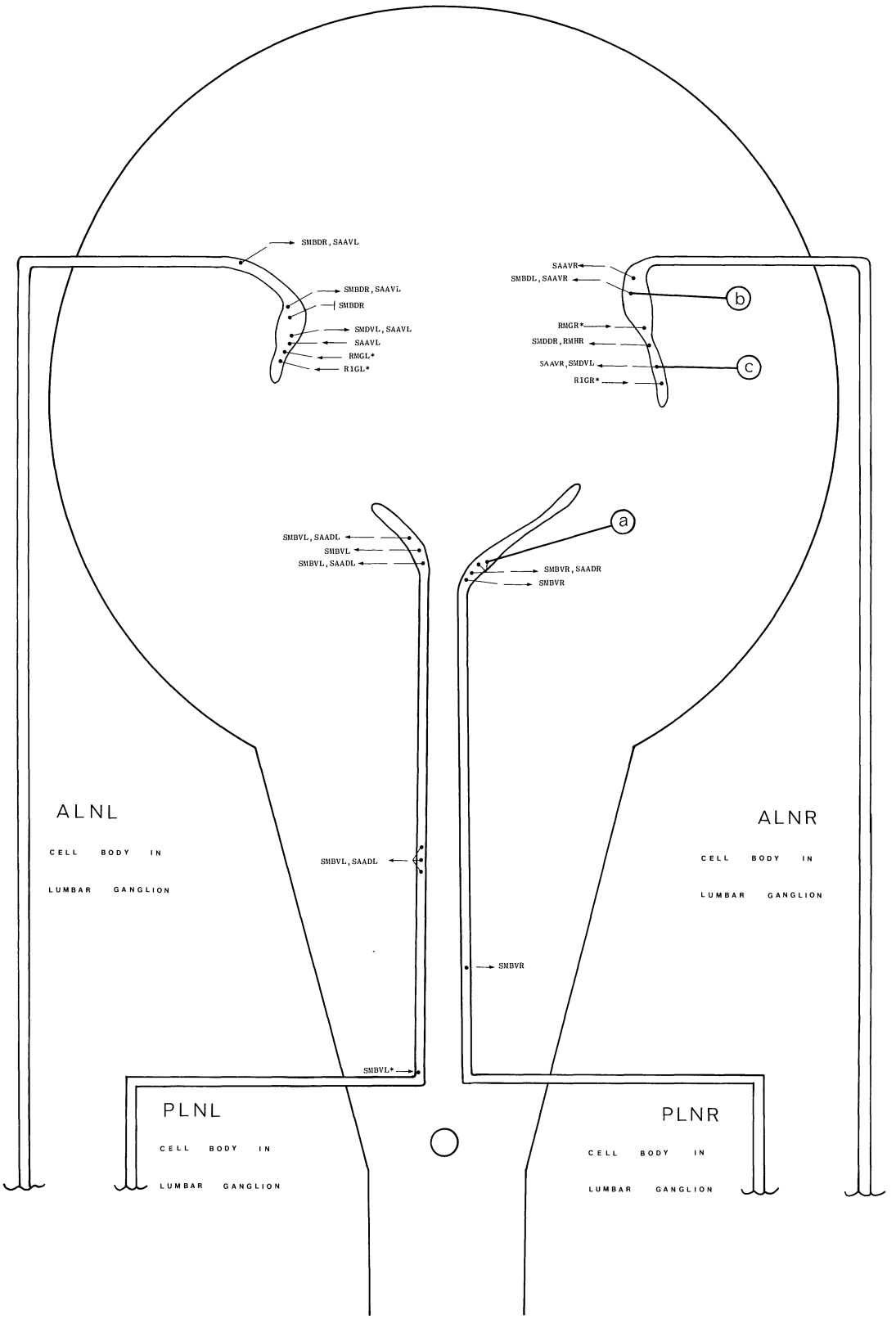
PLM

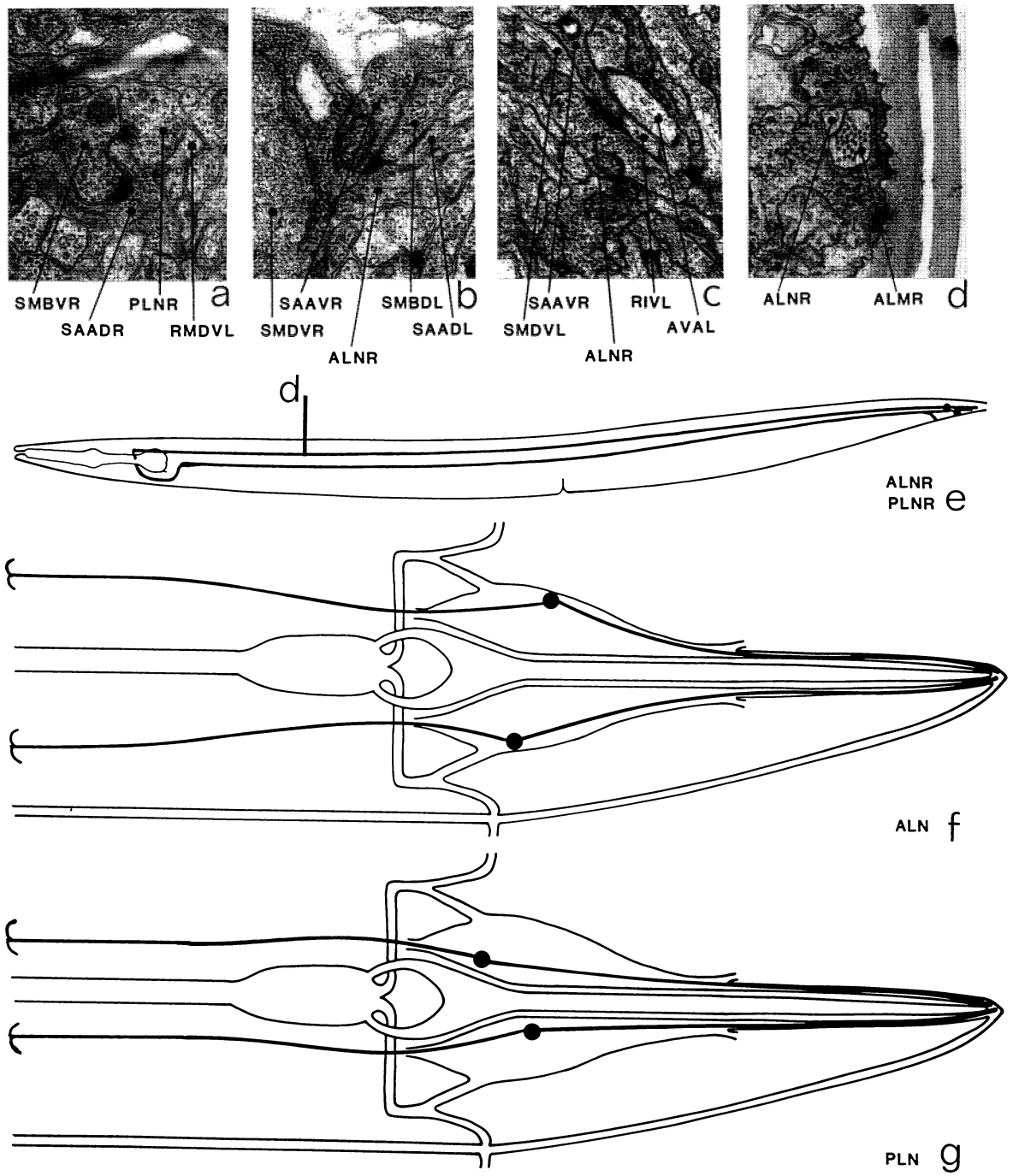
The cell bodies of PLM are situated in the lumbar ganglia (j). Anteriorly and posteriorly directed processes emanate from the cell bodies and run near the ventral edge of the lateral hypodermal ridges (g) in close association with the processes of PLN for part of their length. Gap junctions are made to PVC (h), LUA (*d), and PVR where the processes of PLM cross the lumbar commissures (j). Each HSN sends out a short ventral branch, which receives a single synapse from the lateral PLM processes (g). The processes of PLM turn and enter the ventral cord via a commissure near the vulva. The process of PLML does not get over the hypodermal ridge (which is rather wide at this point due to the proximity of the vulva) and has no synapses. The process of PLMR runs along the neuropile of the cord for a short distance and synapses onto DVA (e), AVA (f), PDE (e) and AVD (e, f).

Magnifications: (a, b, d, g, h) ×25500, (c, e, f) ×12750.

PLM VENTRAL CORD SYNAPSES

partners	gap junctions	synapses from	synapses to and corecipients
DVA	—	—	5PDE
PDE	—	—	5DVA
AVA	—	—	1, 3AVD, PVC
AVD	—	—	1, 3AVA
HSN	—	—	2
PVC	2	—	AVA
LUA	2	—	—
PVR	2	—	—
PHC	1	—	—
AVJ	—	1	—


SMBDR, SAAVL
SMBDR, SAAVL
SMBDR
SMDVL, SAAVL
SAAVL
RMGL*
RIGL*
SAAVR
SMBDL, SAAVR
b
RMGR*
SMDDR, RMHR
SAAVR, SMDVL
c
RIGR*
a
SMBVL, SAADL
SMBVL
SMBVL, SAADL
SMBVR, SAADR
SMBVR
ALNL
CELL BODY IN
LUMBAR GANGLION
ALNR
CELL BODY IN
LUMBAR GANGLION
SMBVL, SAADL
SMBVR
SMBVL*
PLNL
CELL BODY IN
LUMBAR GANGLION
PLNR
CELL BODY IN
LUMBAR GANGLION



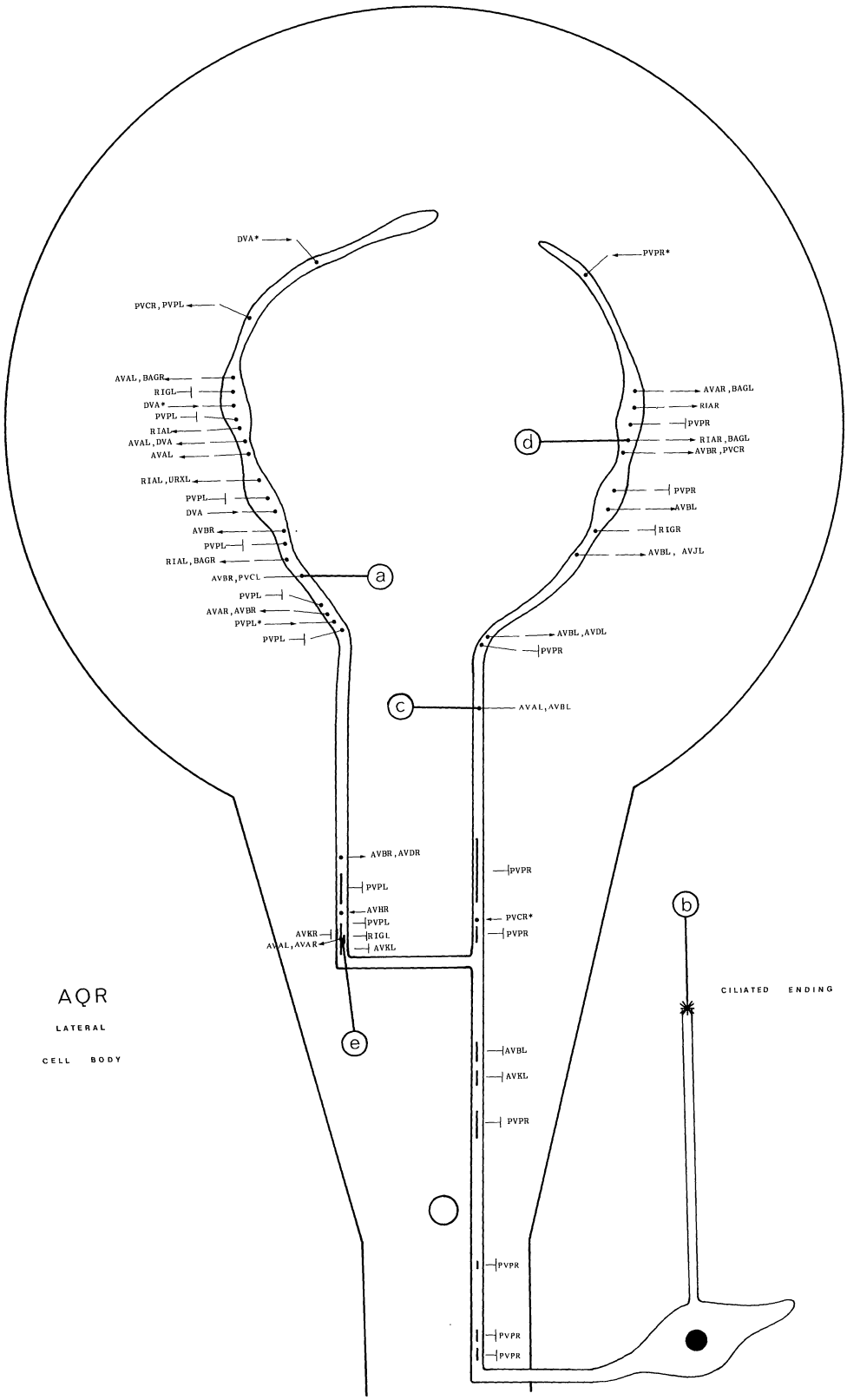
ALN AND PLN

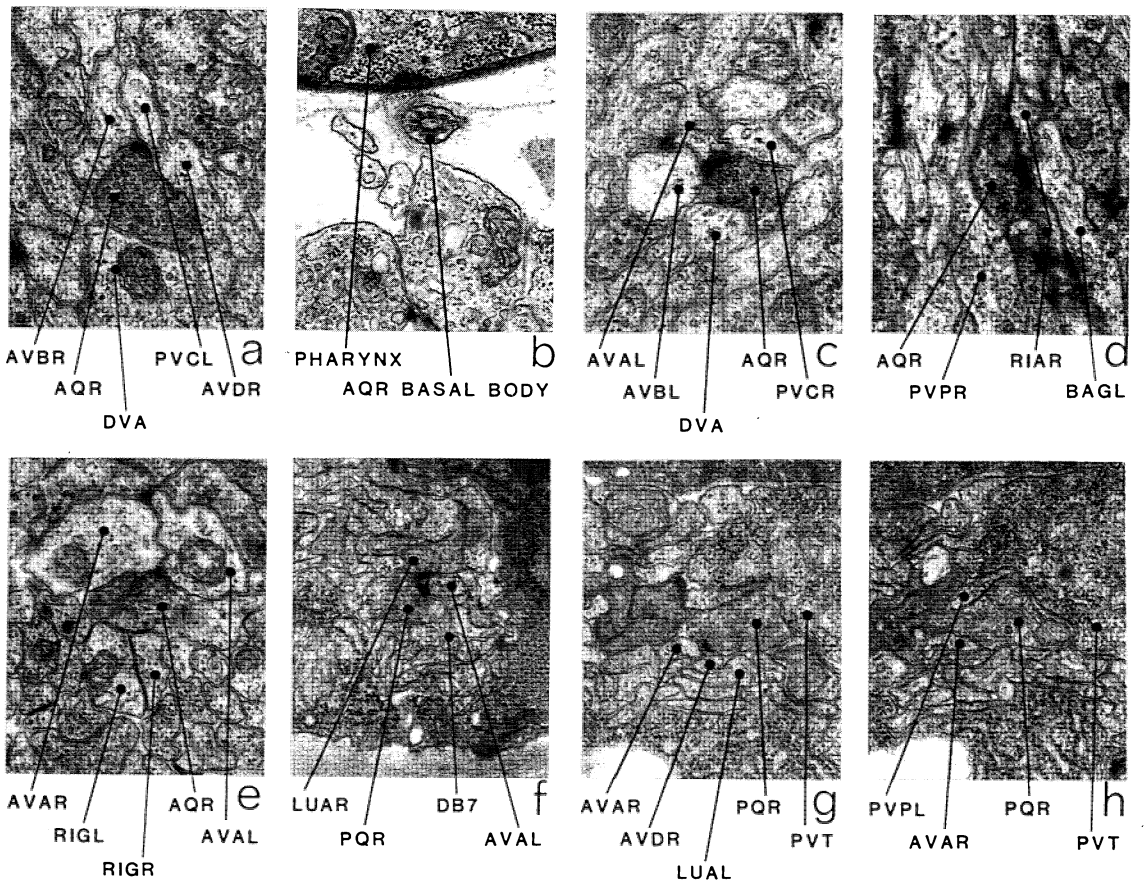
Members: ALNL, ALNR, PLNL, PLNR.

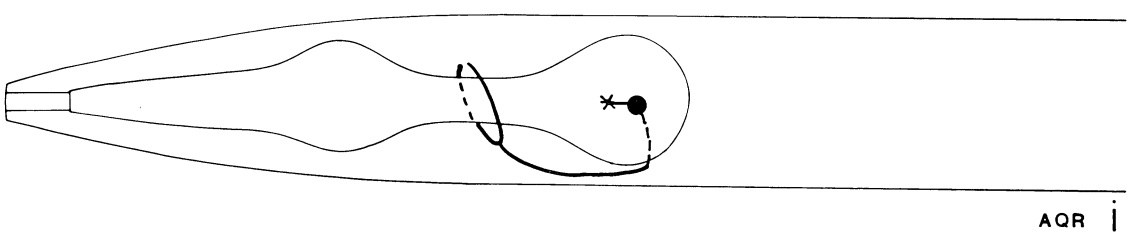
ALN and PLN are two sets of two neurons with cell bodies situated in the lumbar ganglion (e, f, g). All four send processes anteriorly, which eventually enter the nerve ring; they also have posteriorly directed processes that run into the tailspike. The processes of ALN run laterally and become closely associated with those of ALM in the anterior half of the animal

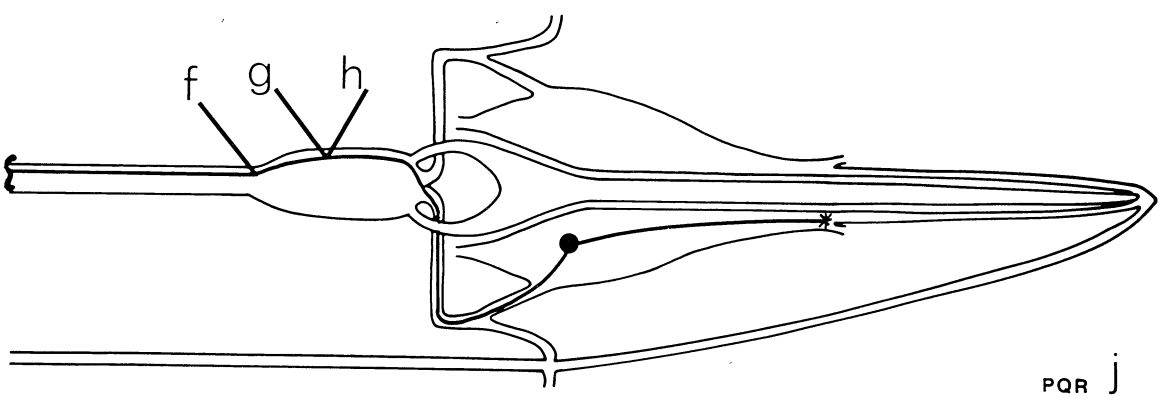
(d). They then enter the nerve ring sub-dorsally and run ventrally round the ring for a short distance. The processes from PLN are closely associated with those of PLM in the posterior half of the animal, although the association is not as striking as that of ALN with ALM. The processes of PLN join the ventral sub-lateral cords in the anterior of the animal and from there enter the ventral cord via the amphidial commissures. The processes of PLN then enter the nerve ring and run dorsally for a short distance. The main synaptic outputs of both ALN and PLN are dyadic synapses to SMB and SAA (a, b) and a few synapses to SMD (c).

Magnifications: (a, b, d) $\times 25500$, (c) $\times 12750$.


DVA*
PVCR, PVPL
AVAL, BAGR
RIGL
DVA*
PVPL
RIAL
AVAL, DVA
AVAL
RIAL, URXL
PVPL
DVA
AVBR
PVPL
RIAL, BAGR
AVBR, PVCL
PVPL
AVAR, AVBR
PVPL*
PVPL
a
PVPR*
AVAR, BAGL
RIAR
PVPR
RIAR, BAGL
AVBR, PVCR
d
PVPR
AVBL
RIGR
AVBL, AVJL
AVBL, AVDL
PVPR
c
AVAL, AVBL
AVBR, AVDR
PVPR
PVPL
AVHR
PVPL
RIGL
AVKL
AVKR
AVAL, AVAR
PVCR*
PVPR
b
e
AVBL
AVKL
PVPR
PVPR
PVPR
PVPR
AQR
LATERAL
CELL BODY
CILIATED ENDING


AVBR
AQR
DVA
PVCL
AVDR
a
PHARYNX
AQR BASAL BODY
b
AVAL
AVBL
DVA
AQR
PVCR
c
AQR
PVPR
RIAR
BAGL
d
AVAR
RIGL
RIGR
AQR
AVAL
e
LUAR
PQR
DB7
AVAL
f
AVAR
AVDR
LUAL
PQR
PVT
g
PVPL
AVAR
PQR
PVT
h


AQR i


f
g
h
PQR j

AQR AND PQR

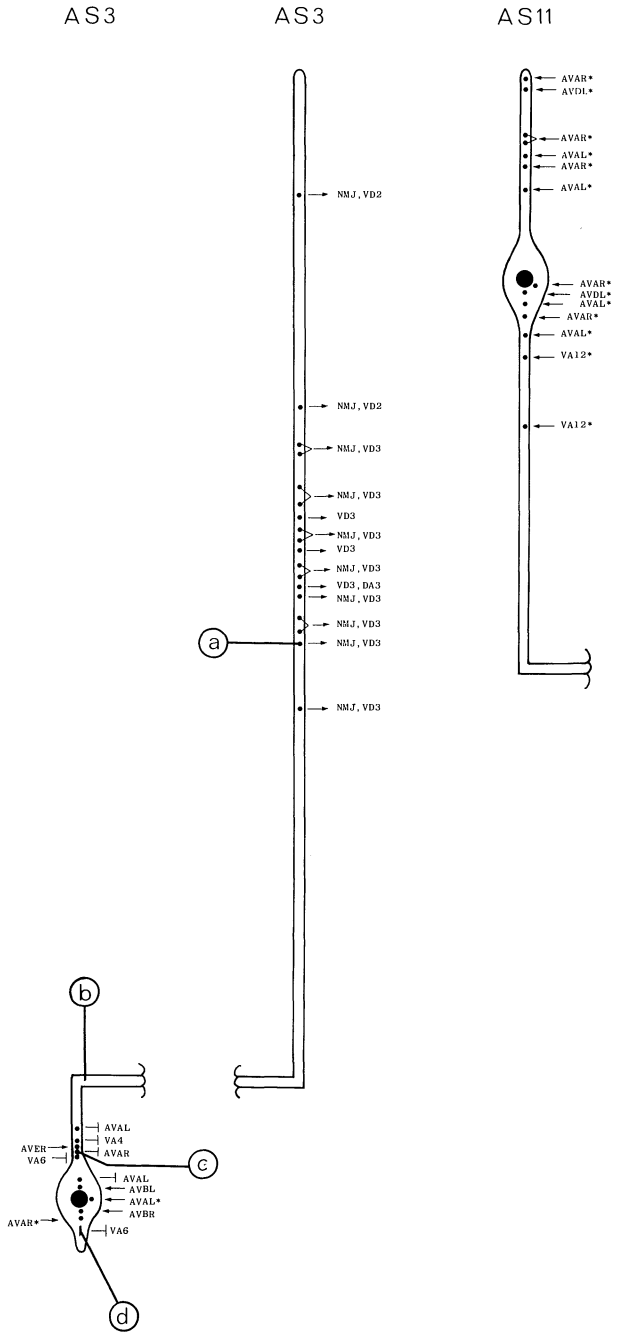
Members: AQR, PQR.

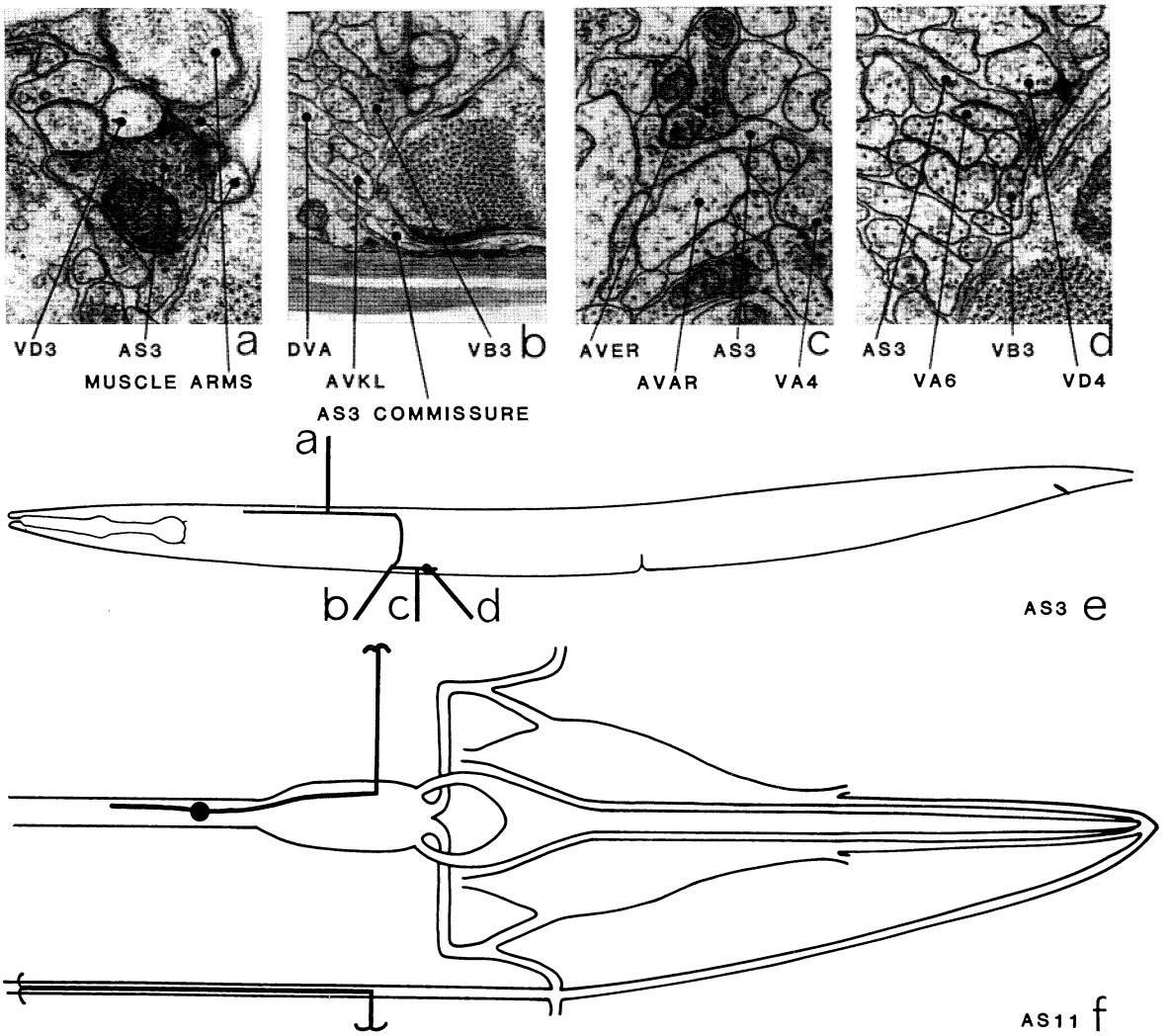
Although AQR and PQR have been given different class names, they have several features in common and so have been grouped together. Each is derived from an equivalent position on bilaterally symmetrical lineages (Sulston & Horvitz 1977) and each has a small cilium, which is not part of a sensillum but is free in the body cavity (b). The cell body of AQR is situated laterally on the right-hand side near the posterior bulb of the pharynx. The cilium is on a small process emanating from the cell body (i). The cell body of PQR is in the left lumbar ganglion and its cilium is near the end of a posteriorly directed process (j). The main process of AQR enters the ventral cord via the right-hand deirid commissure and runs anteriorly. It splits near the nerve ring and the two branches run round each side of the nerve ring, near the middle of the ring neuropile and in close association with the process of DVA. The processes of AQR end without meeting near the dorsal mid-line. The main synaptic output is to AVB (a, c), AVA (c, e), RIA (d), BAG (d), PVC (a) and AVD. AQR has noticeably denser clusters of vesicles presynaptically than most of the other classes of neuron. There is some synaptic input from DVA (*c) and many gap junctions to PVP and also some to AVK (*f) and RIG. PQR sends an anteriorly directed process that enters the pre-anal ganglion and runs anteriorly in the ventral region of the process bundle, eventually ending somewhere in the posterior half of the ventral cord. The main synaptic output of PQR is directed to AVA (f, g) and AVD (g), usually in dyadic combinations. There are also gap junctions to PVP (h) and there is some synaptic input from PVN (*c).

Magnifications: (a–c, e, f) ×25500, (d) ×12750, (g, h) ×38250.

PQR VENTRAL CORD SYNAPSES

partners	gap junctions	synapses from	synapses to and corecipients
AVA	—	—	11AVD, 2AVA, LUA
AVD	—	1	11AVA, AVD, PVN
AVG	—	—	1
LUA	—	1 m	AVA
PVN	—	3 m	AVD
PVP	4	—	—


AS3
AS3
AS11
NMJ, VD2
NMJ, VD2
NMJ, VD3
NMJ, VD3
VD3
NMJ, VD3
VD3
NMJ, VD3
VD3, DA3
NMJ, VD3
NMJ, VD3
NMJ, VD3
NMJ, VD3
AVAR*
AVDL*
AVAR*
AVAL*
AVAR*
AVAL*
AVAR*
AVDL*
AVAL*
AVAR*
AVAL*
VA12*
VA12*
a
b
c
d
AVAL
VA4
AVAR
AVER
VA6
AVAL
AVBL
AVAL*
AVBR
AVAR*
VA6

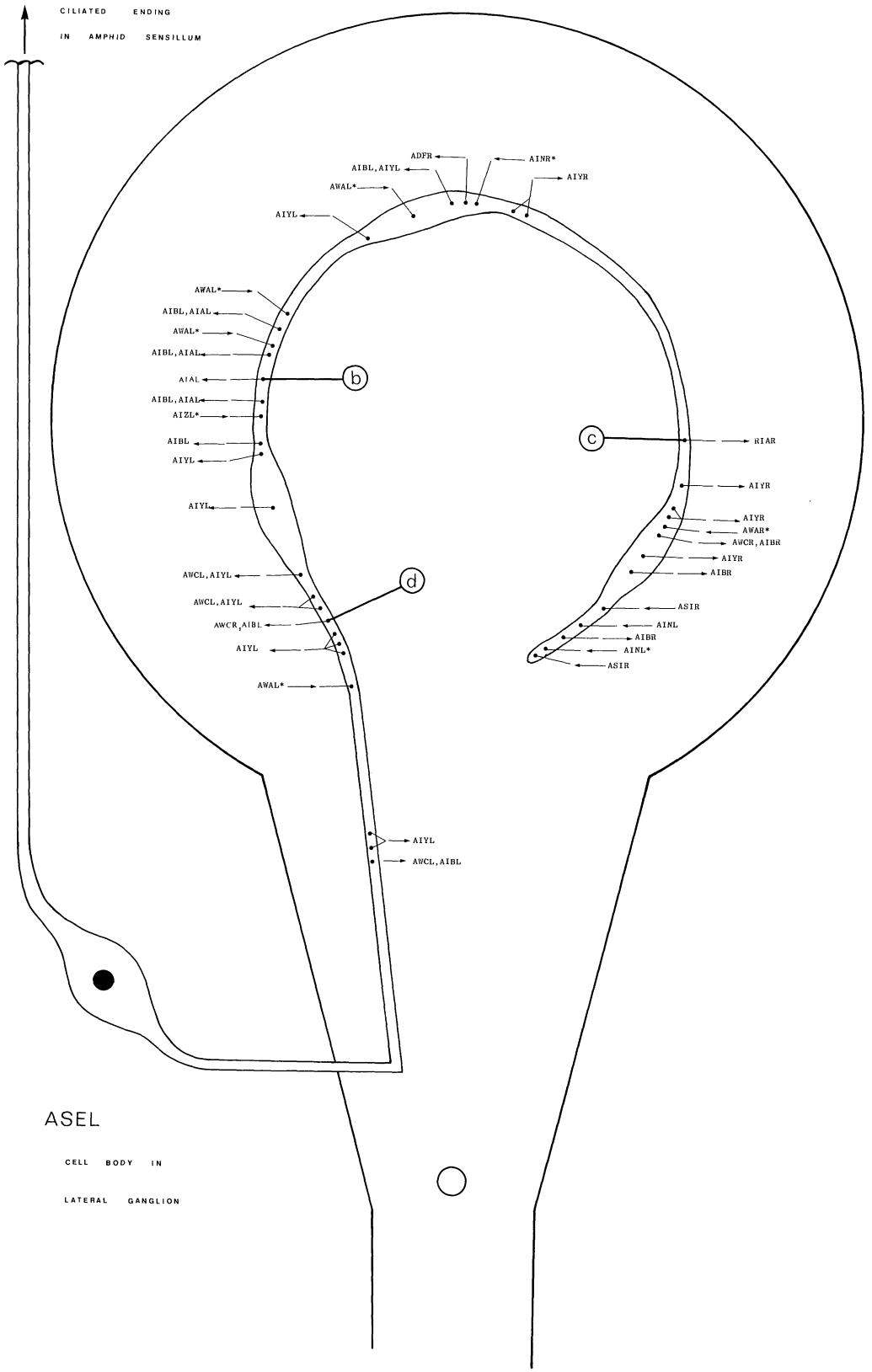


ASn

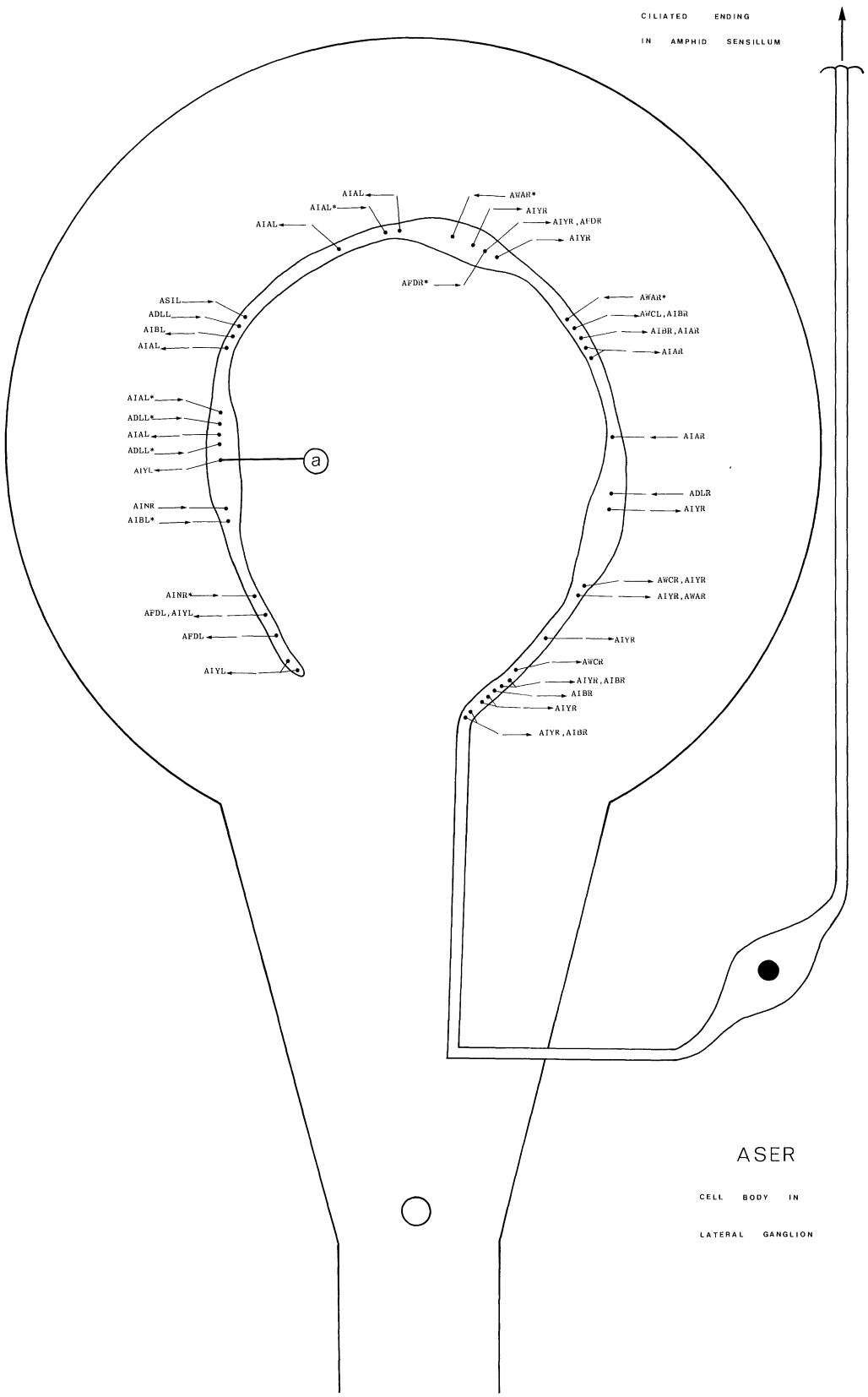
Members: AS1 to AS11.

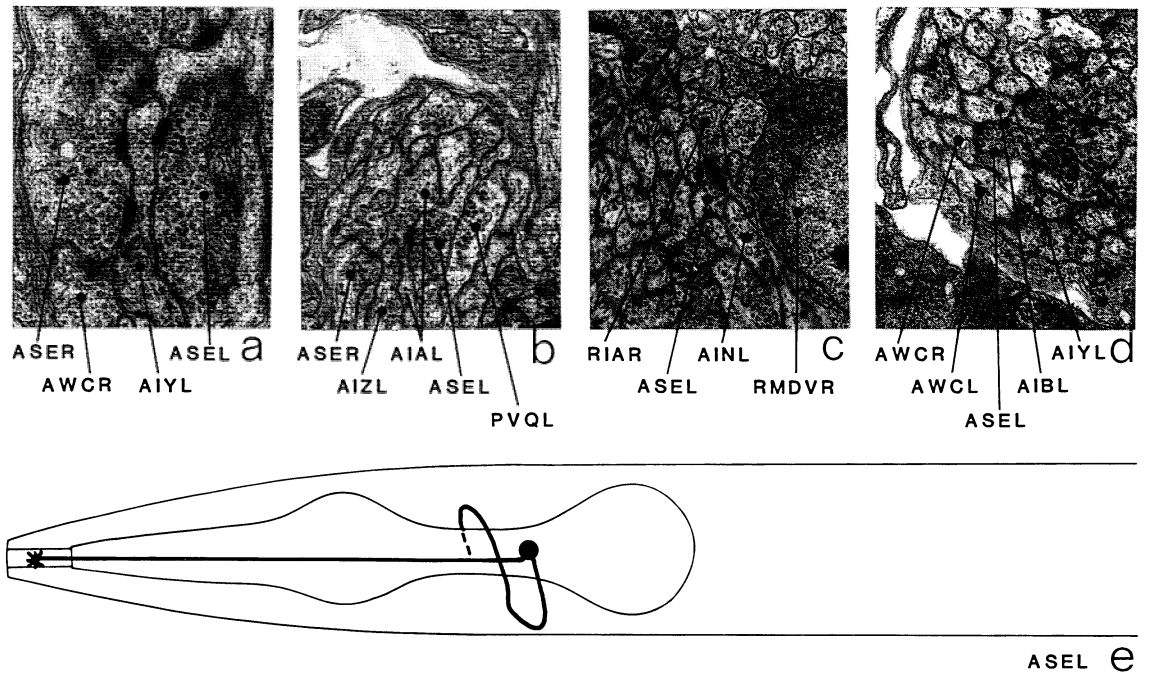
ASn is a set of eleven motoneurons, with cell bodies in the ventral cord, which innervate dorsal muscles. A typical ASn (e.g. AS3 (e)) has rather short processes in the ventral cord on either side of its cell body. These are exclusively postsynaptic and receive synaptic input from AVB (*c), AVA (*e) and AVD (*d). In addition AS1 to AS3 receive some synaptic input from AVE (*f). There are often gap junctions to AVA (c) and VAn (d) in this region also. The anterior process (except AS11 (f)) leaves the ventral cord and runs round to the dorsal cord as a commissure (b). All eleven ASn commissures run round the right-hand side of the body. The process of an ASn turns and runs anteriorly in the dorsal cord, running for part of the time adjacent to the basal lamina. There are dyadic NMJs in this region with VDn being the corecipient (a and figure 19). The processes of ASn in the dorsal cord are similar to those of DAn except that they are shorter and have fewer NMJs.

Magnifications: (a, c, d) $\times 25500$, (b) $\times 17000$.


CILIATED ENDING
IN AMPHID SENSILLUM
ADFR
AINR*
AIBL, AIYL
AIYR
AWAL*
AIYL
AWAL*
AIBL, AIAL
AWAL*
AIBL, AIAL
AIAL
b
AIBL, AIAL
AIZL*
AIBL
AIYL
AIYL
c
RIAR
AIYR
AIYR
AWAR*
AWCR, AIBR
AIYR
AIBR
ASIR
AINL
AIBR
AINL*
ASIR
AWCL, AIYL
d
AWCL, AIYL
AWCR, AIBL
AIYL
AWAL*
AIYL
AWCL, AIBL
ASEL
CELL BODY IN
LATERAL GANGLION

ASE


CILIATED ENDING
IN AMPHID SENSILLUM
AIAL
AIAL*
AIAL
AWAR*
AIYR
AIYR,AFDR
AIYR
AFDR*
ASIL
ADLL
AIBL
AIAL
AWAR*
AWCL,AIBR
AIBR,AIAR
AIAR
AIAL*
ADLL*
AIAL
ADLL*
AIYL
a
AIAR
ADLR
AIYR
AINR
AIBL*
AWCR,AIYR
AIYR,AWAR
AINR*
AFDL,AIYL
AFDL
AIYL
AIYR
AWCR
AIYR,AIBR
AIBR
AIYR
AIYR,AIBR
ASER
CELL BODY IN
LATERAL GANGLION

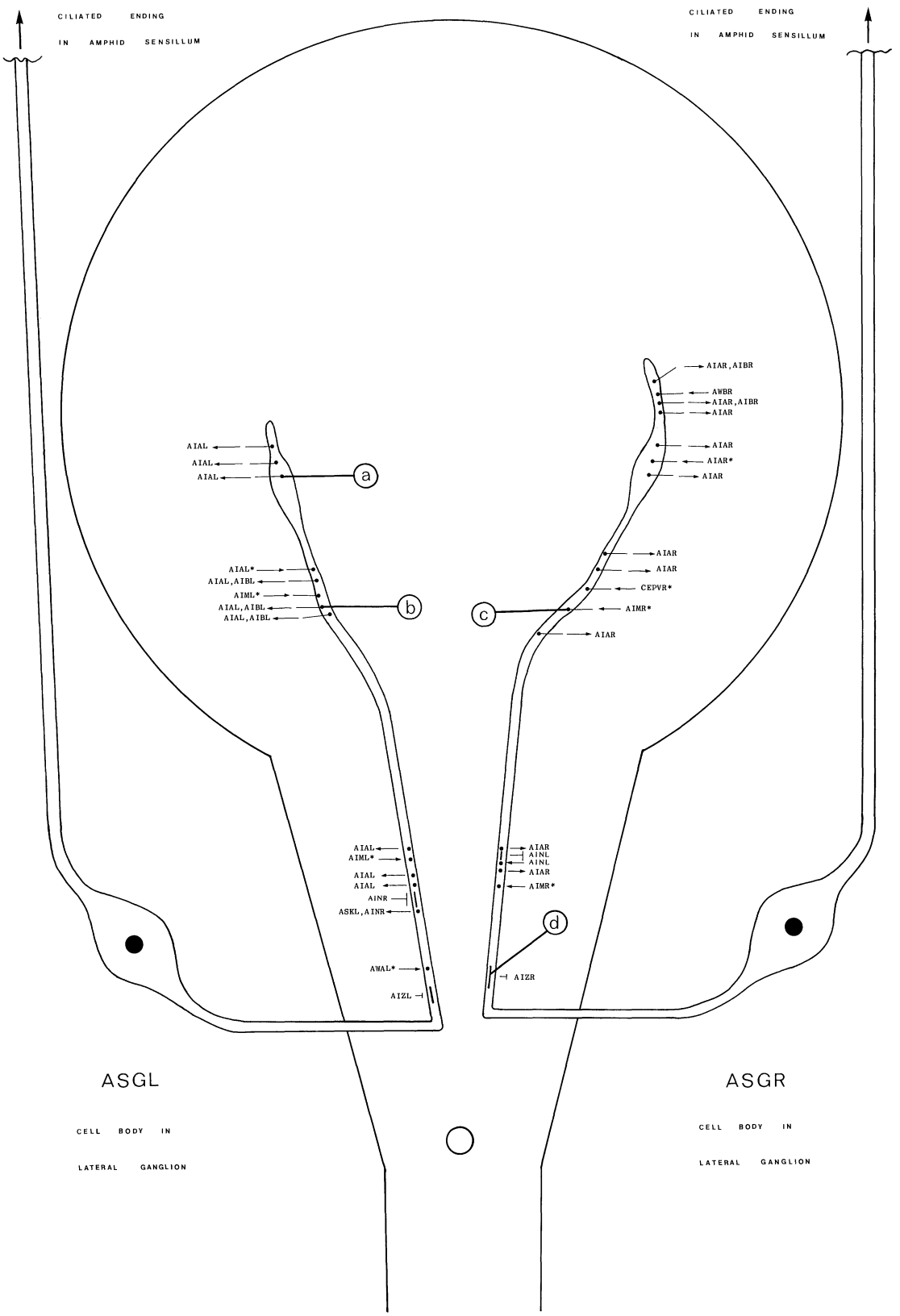


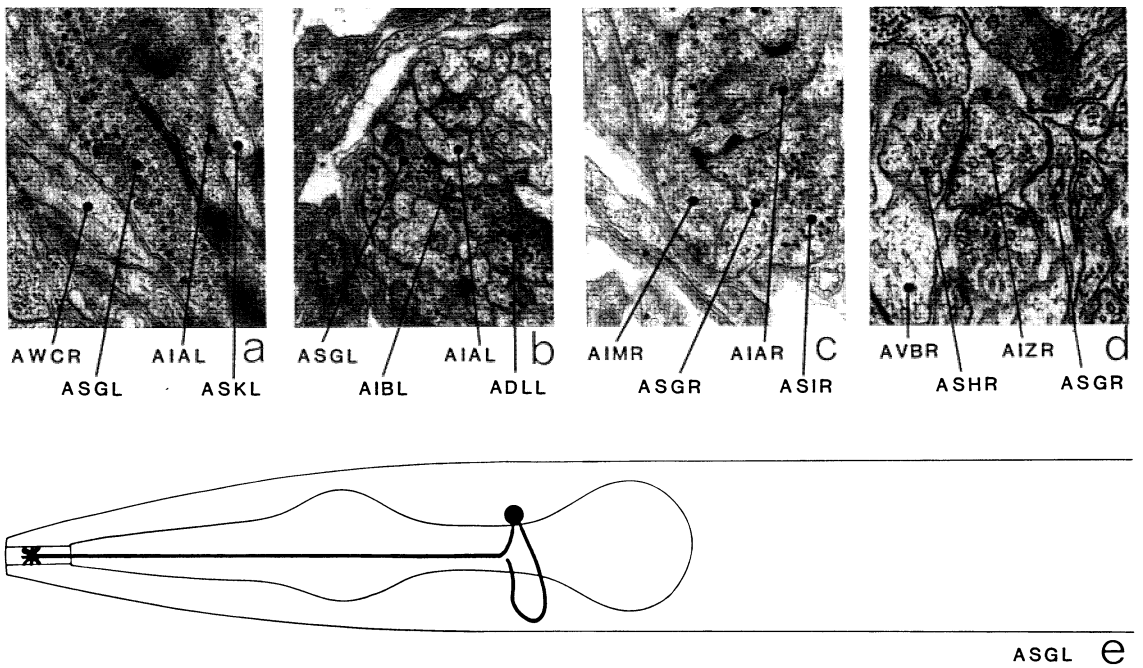
ASE

Members: ASEL, ASER.

ASE is a set of two ciliated neurons that are part of the amphid sensilla. The endings are in the amphid channel, which is open to the outside (figure 1). Cell bodies are situated in the lateral ganglia and have processes which enter the ventral cord via the amphidial commissures. From here they run anteriorly into the nerve ring and then run round it in the posterior regions of the neuropile, in close association with the processes of AIY. The distal region of each process runs outside the proximal region of the contralateral process. These two processes sandwich processes of AIY, which is the most prominent postsynaptic partner (a). Synapses are also made onto AIA (b), RIA (c) and AIB, usually in association with AWC (d). There are synaptic inputs from AIN (*a), AWA and ASI.

Magnifications: (a) ×25500, (b–d) ×12750.


CILIATED ENDING IN AMPHID SENSILLUM
CILIATED ENDING IN AMPHID SENSILLUM
AIAL
AIAL
AIAL
a
AIAL*
AIAL,AIBL
AIML*
AIAL,AIBL
AIAL,AIBL
b
AIAL
AIML*
AIAL
AIAL
AINR
ASKL,AINR
AWAL*
AIZL
AIAR,AIBR
AWBR
AIAR,AIBR
AIAR
AIAR
AIAR*
AIAR
AIAR
AIAR
CEPVR*
c
AIMR*
AIAR
AIAR
AINL
AINL
AIAR
AIMR*
d
AIZR
ASGL
CELL BODY IN LATERAL GANGLION
ASGR
CELL BODY IN LATERAL GANGLION

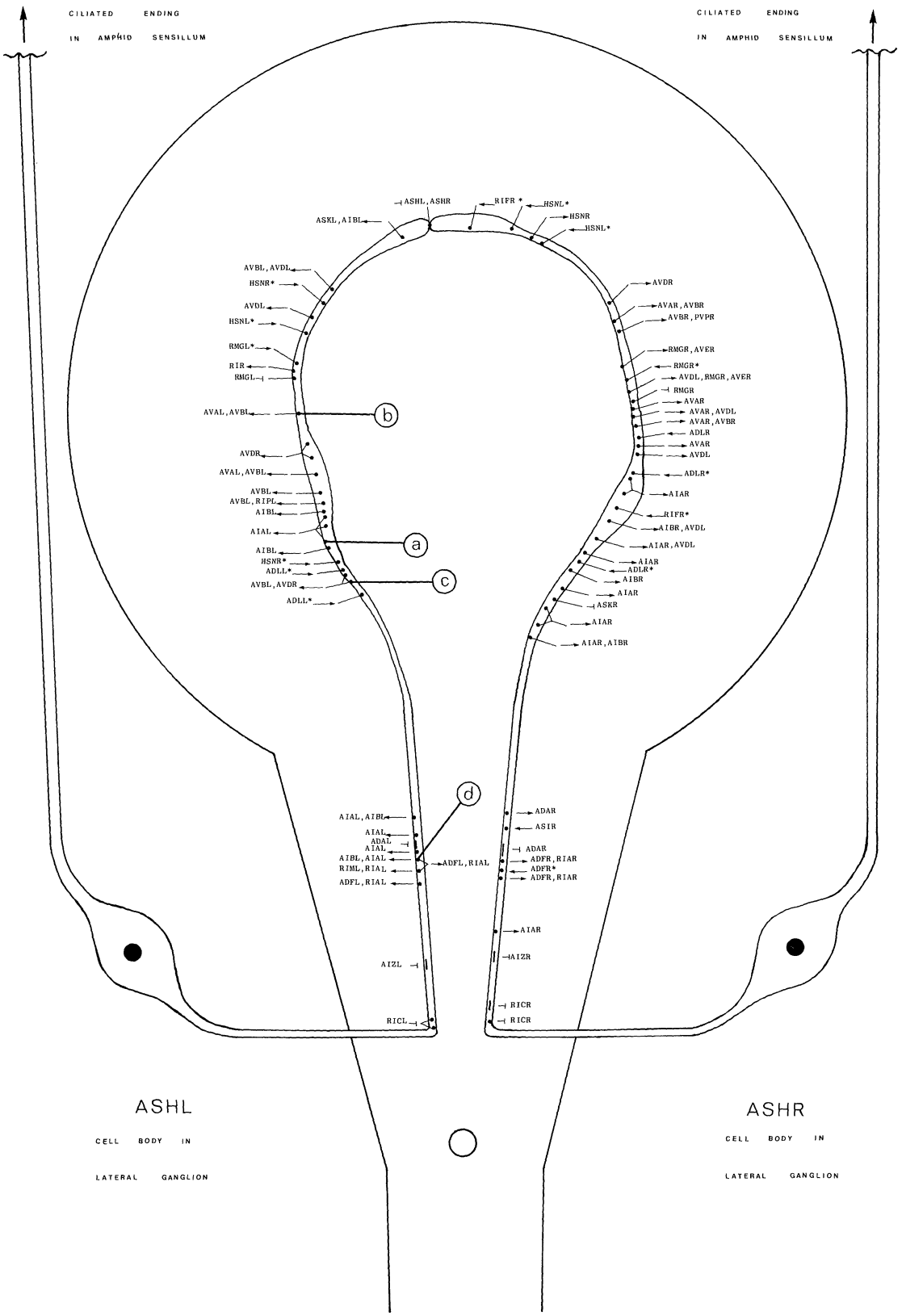


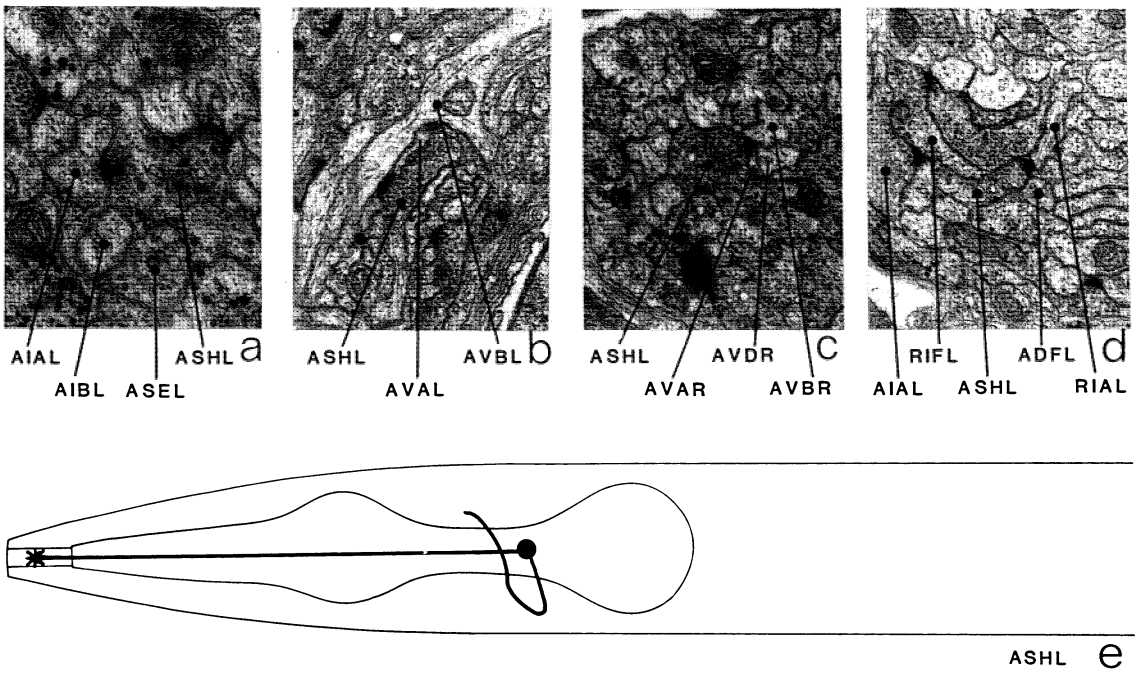
ASG

Members: ASGL, ASGR.

ASG is a set of two ciliated neurons that are part of the amphid sensilla. The endings are in the amphid channel, which is open to the outside (figure 1). Cell bodies are situated in the lateral ganglia and send processes into the ventral cord via the amphidial commissures. The processes run on the outside surface of the neuropile of the ventral ganglion in close association with the processes of AIA. They project into the nerve ring a short distance, ending laterally. Synaptic output is almost exclusively onto AIA (a). Some synapses are also made onto AIB in association with AIA, but AIB always seems to be the minor partner (b). Some of the vesicles in the synaptic terminals have dark cores (a). ASG is postsynaptic to AIM in a few places (c) and has gap junctions with AIZ (d) and AIN.

Magnifications: (a, d) $\times 25500$, (b, c) $\times 12750$.


CILIATED ENDING IN AMPHID SENSILLUM
CILIATED ENDING IN AMPHID SENSILLUM
ASHL, ASHR
RIFR *
HSNL*
ASKL, AIBL
HSNR
HSNL*
AVBL, AVDL
HSNR*
AVDL
HSNL*
RMGL*
RIR
RMGL
AVAL, AVBL
b
AVDR
AVAL, AVBL
AVBL
AVBL, RIPL
AIBL
AIAL
a
AIBL
HSNR*
ADLL*
AVBL, AVDR
c
ADLL*
AVDR
AVAR, AVBR
AVBR, PVPR
RMGR, AVER
RMGR*
AVDL, RMGR, AVER
RMGR
AVAR
AVAR, AVDL
AVAR, AVBR
ADLR
AVAR
AVDL
ADLR*
AIAR
RIFR*
AIBR, AVDL
AIAR, AVDL
AIAR
ADLR*
AIBR
AIAR
ASKR
AIAR
AIAR, AIBR
d
AIAL, AIBL
AIAL
ADAL
AIAL
AIBL, AIAL
RIML, RIAL
ADFL, RIAL
ADFL, RIAL
ADAR
ASIR
ADAR
ADFR, RIAR
ADFR*
ADFR, RIAR
AIAR
AIZR
AIZL
RICR
RICL
RICR
ASHL
CELL BODY IN LATERAL GANGLION
ASHR
CELL BODY IN LATERAL GANGLION

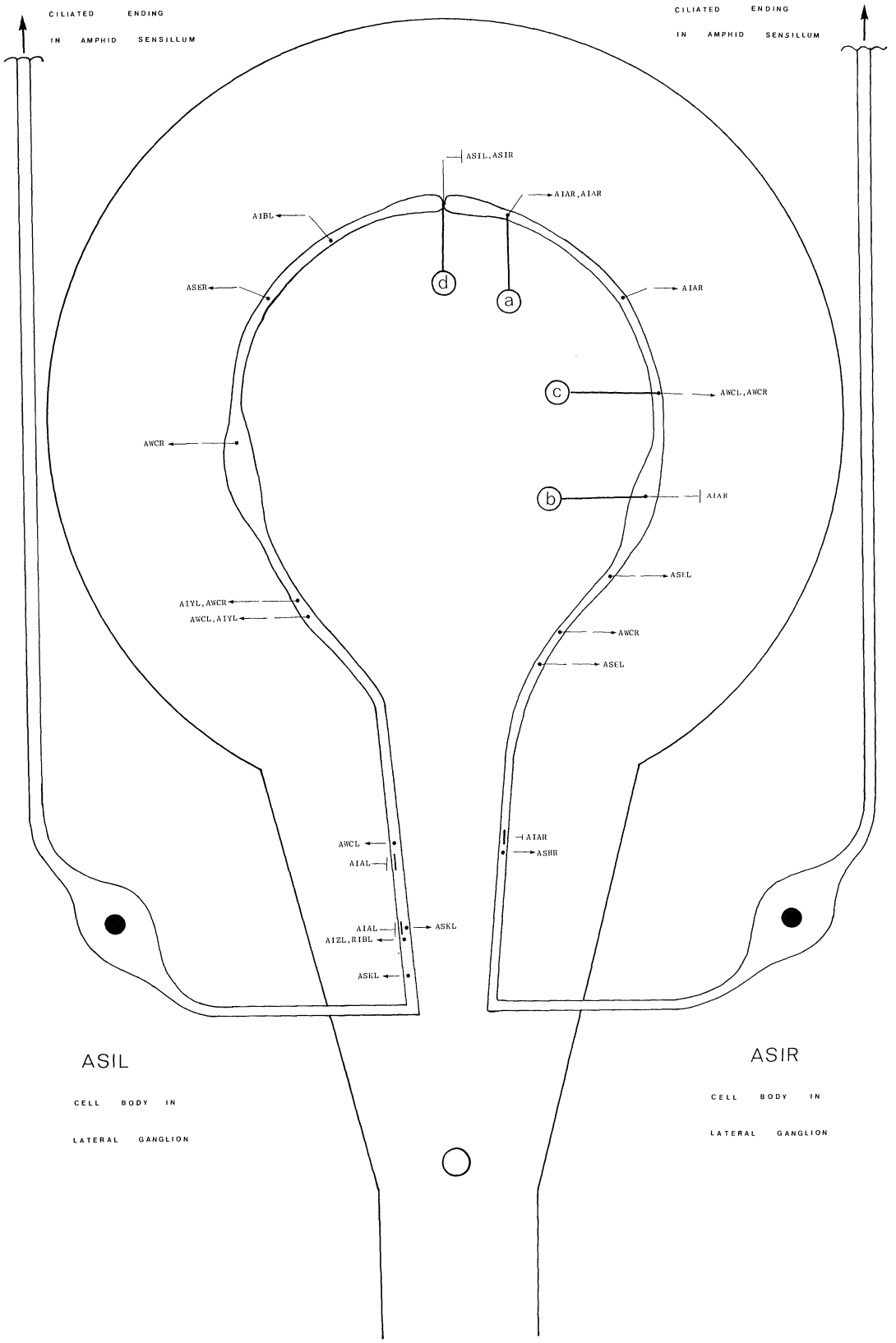


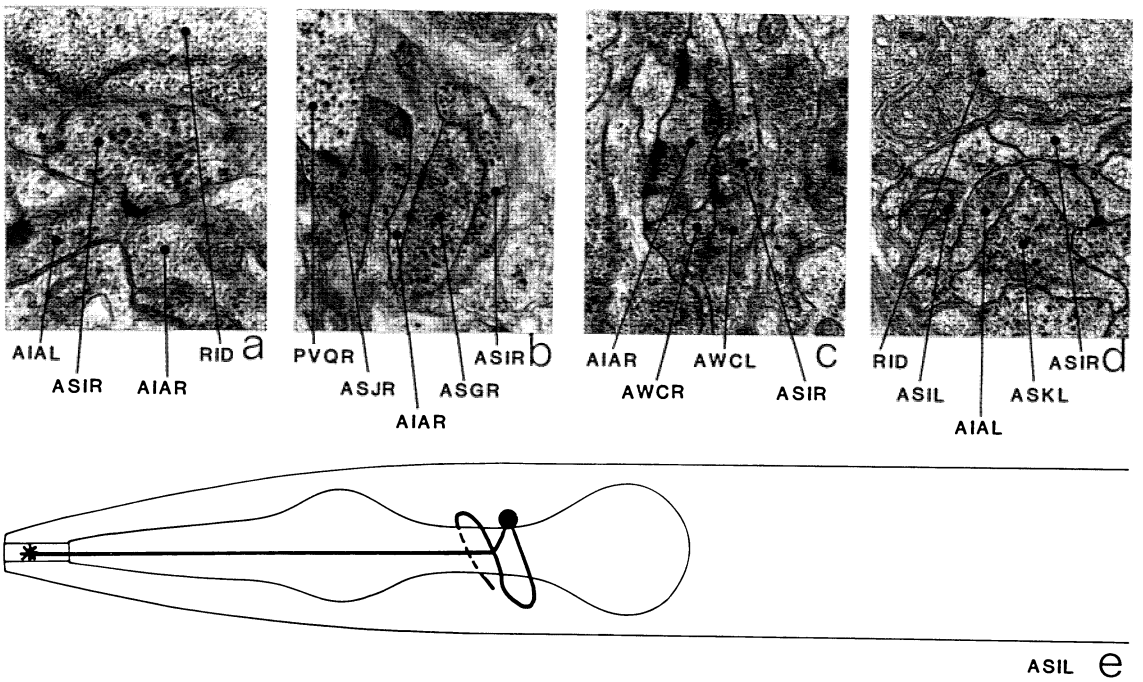
ASH

Members: ASHL, ASHR.

ASH is a set of two ciliated neurons that are part of the amphid sensilla. The endings are in the amphid channel, which is open to the outside (figure 1). Cell bodies are situated in the lateral ganglia and send processes into the ventral cord via the amphidial commissures. From there the two processes pass up into the nerve ring, running near the middle of the neuropile, and meet and terminate at the dorsal mid-line, where there is a gap junction between them. Processes from ASH run in close association with those from AIA in the ventral part of the ring and AVB in the dorsal part of the ring. The main synaptic output is to AIA (a). Synapses are also made to AIB, RIA (d) and to AVB (b) often in association with AVA and AVD (c). Some of the vesicles in the synaptic terminals have dark cores (a). There are gap junctions to AIZ, RIC, ADA and RMG.

Magnifications: (a) ×25500, (b–d) ×12750.


CILIATED ENDING IN AMPHID SENSILLUM
CILIATED ENDING IN AMPHID SENSILLUM
ASIL,ASIR
AIAR,AIAR
AIBL
ASER
AIAR
d
a
c
AWCL,AWCR
AWCR
b
AIAR
ASEL
AIYL,AWCR
AWCL,AIYL
AWCR
ASEL
AWCL
AIAL
AIAR
ASHR
AIAL
ASKL
AIZL,RIBL
ASKL
ASIL
CELL BODY IN LATERAL GANGLION
ASIR
CELL BODY IN LATERAL GANGLION

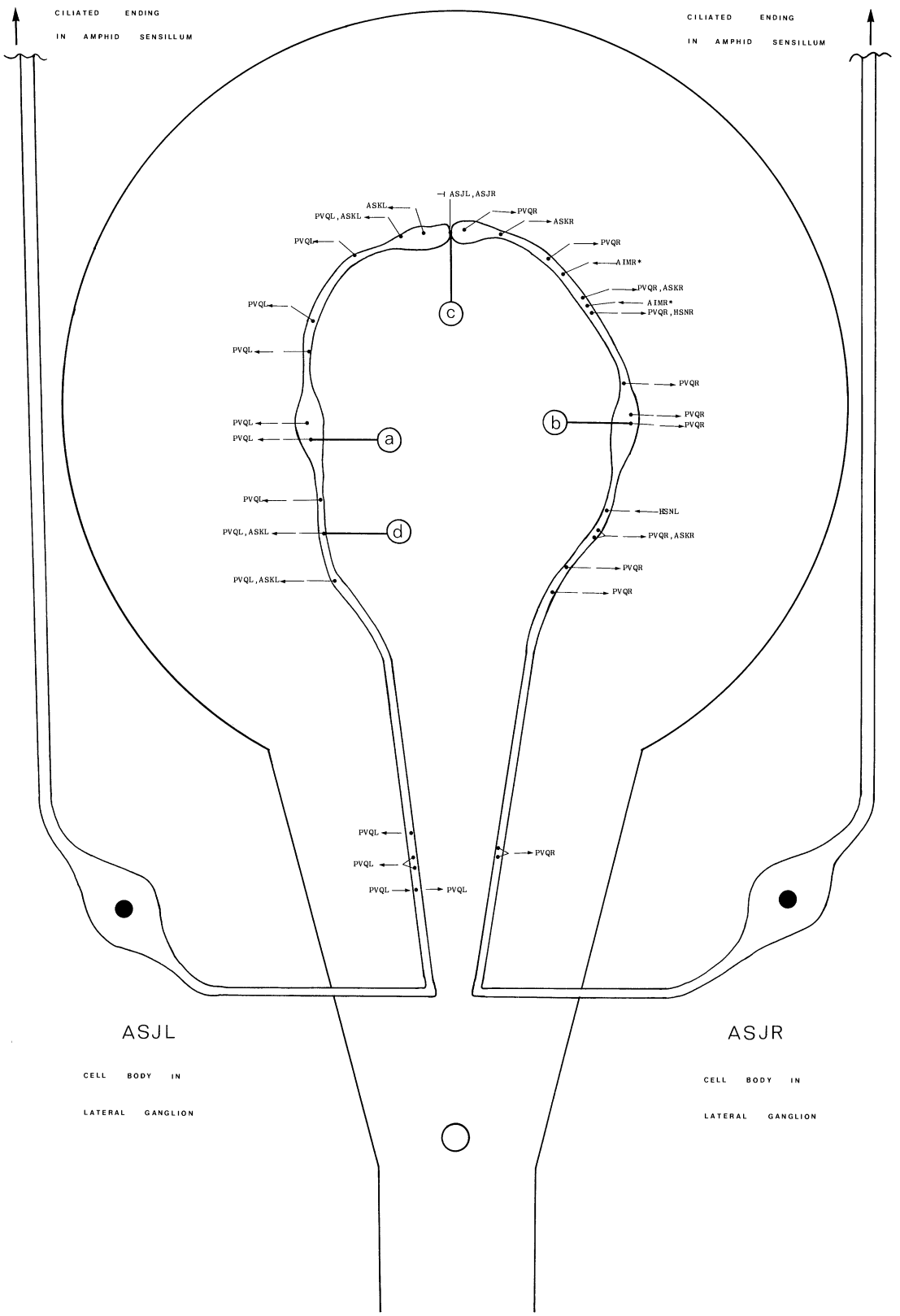


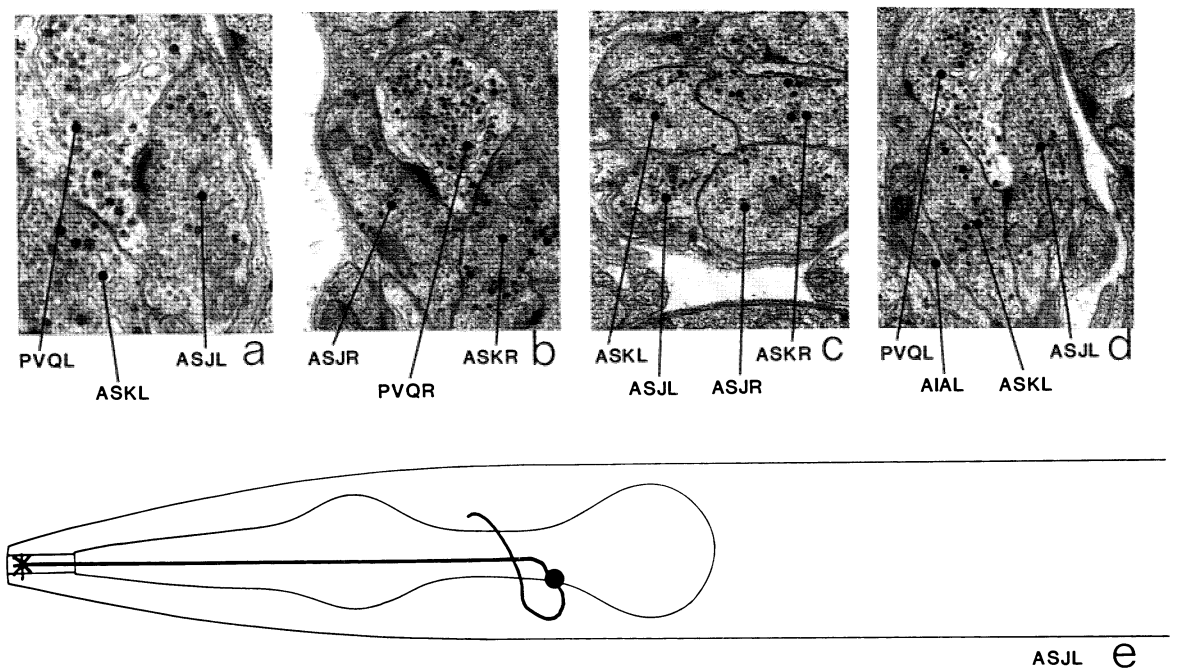
ASI

Members: ASIL, ASIR.

ASI is a set of two ciliated neurons that are part of the amphid sensilla. The endings are in the amphid channel, which is open to the outside (figure 1). Cell bodies are situated in the lateral ganglia and send processes into the ventral cord via the amphid commissures, which project anteriorly into the nerve ring. They run round the nerve ring near the outside surface and meet and terminate at the dorsal mid-line with a gap junction between them (d). The processes are smaller than those of the other amphid neurons and fewer synapses are seen. The main synaptic output is to AIA (a) to which they also make gap junctions (b). There are also some smaller synapses onto AIB, AWC (c) and ASE. Some of the vesicles in the synaptic terminals have dark cores (a).

Magnifications: (a) ×25500, (b–d) ×12750.


CILIATED ENDING IN AMPHID SENSILLUM
CILIATED ENDING IN AMPHID SENSILLUM
ASJL, ASJR
ASKL
PVQL, ASKL
PVQL
PVQR
ASKR
PVQR
AIMR*
PVQR, ASKR
AIMR*
PVQR, HSNR
PVQL
PVQL
PVQR
PVQR
PVQR
PVQL
PVQL
a
b
PVQL
HSNL
PVQL, ASKL
d
PVQR, ASKR
PVQR
PVQL, ASKL
PVQR
PVQL
PVQR
PVQL
PVQL
ASJL
CELL BODY IN LATERAL GANGLION
ASJR
CELL BODY IN LATERAL GANGLION

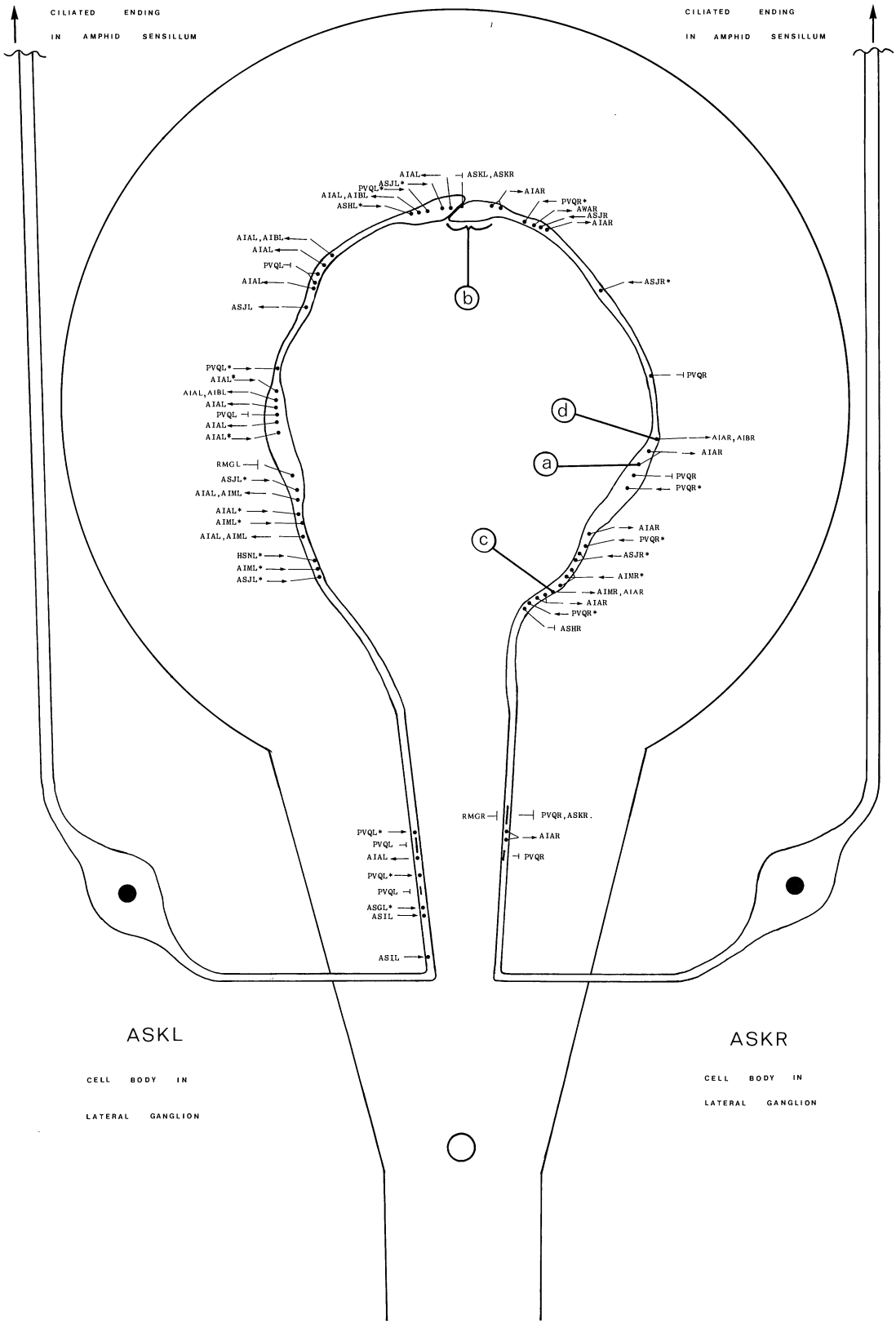


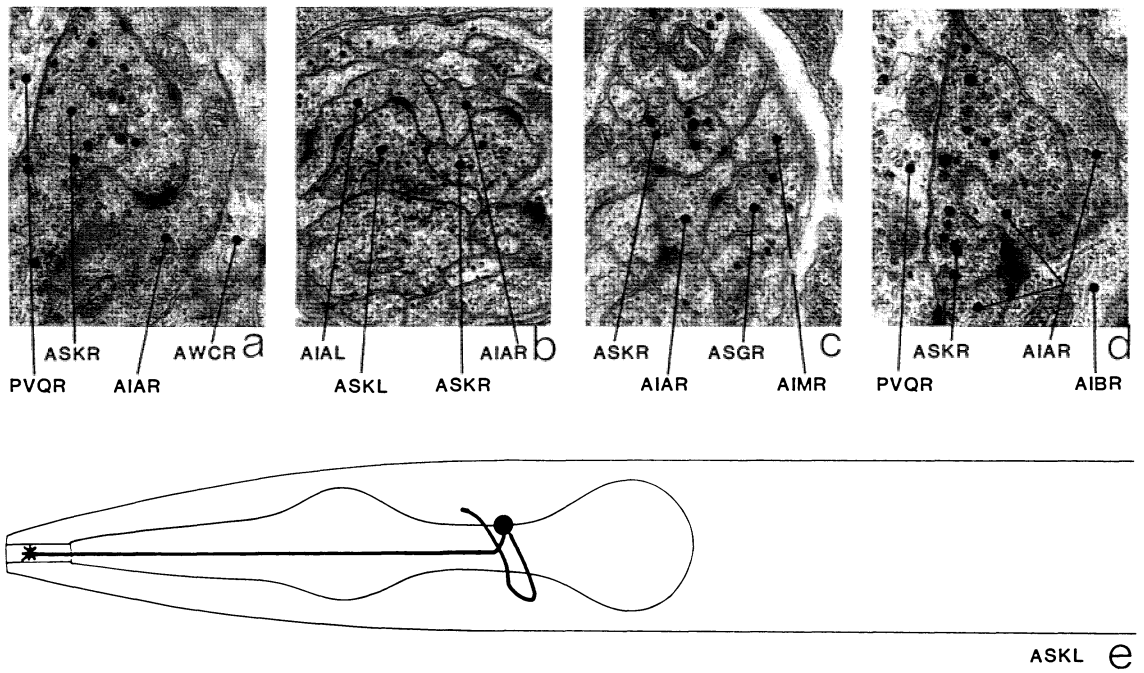
ASJ

Members: ASJL, ASJR.

ASJ is a set of two ciliated neurons that are part of the amphid sensilla. The endings are in the amphid channel, which is open to the outside (figure 1). Cell bodies are situated in the lateral ganglia and send processes into the ventral cord via the amphid commissures. These processes run anteriorly near the lateral extremities of the ventral cord and then project into the nerve ring where they run near the inner surface. At all times the processes of ASJ run in close association with those of PVQ onto which they synapse extensively and almost exclusively (a, b). The processes of ASJ meet and terminate at the dorsal mid-line with a gap junction between them (c). A few of the vesicles in synapses have dark cores (a) but these are less prominent than those seen in the other amphidial neurons. Some synapses are made onto ASK but usually in association with PVQ (d). There is some synaptic input from AIM (*b).

Magnifications: (a) $\times 25500$, (b–d) $\times 12750$.


CILIATED ENDING IN AMPHID SENSILLUM
CILIATED ENDING IN AMPHID SENSILLUM
AIAL
ASKL, ASKR
ASJL*
PVQL*
AIAL, AIBL
ASHL*
AIAR
PVQR*
AWAR
ASJR
AIAR
AIAL, AIBL
AIAL
PVQL
AIAL
ASJL
ASJR*
b
PVQR
PVQL*
AIAL*
AIAL, AIBL
AIAL
PVQL
AIAL
AIAL*
d
AIAR, AIBR
AIAR
a
PVQR
PVQR*
RMGL
ASJL*
AIAL, AIML
AIAL*
AIML*
AIAL, AIML
c
AIAR
PVQR*
ASJR*
AIMR*
AIMR, AIAR
AIAR
PVQR*
ASHR
HSNL*
AIML*
ASJL*
RMGR
PVQR, ASKR.
AIAR
PVQR
PVQL*
PVQL
AIAL
PVQL*
PVQL
ASGL*
ASIL
ASIL
ASKL
CELL BODY IN LATERAL GANGLION
ASKR
CELL BODY IN LATERAL GANGLION

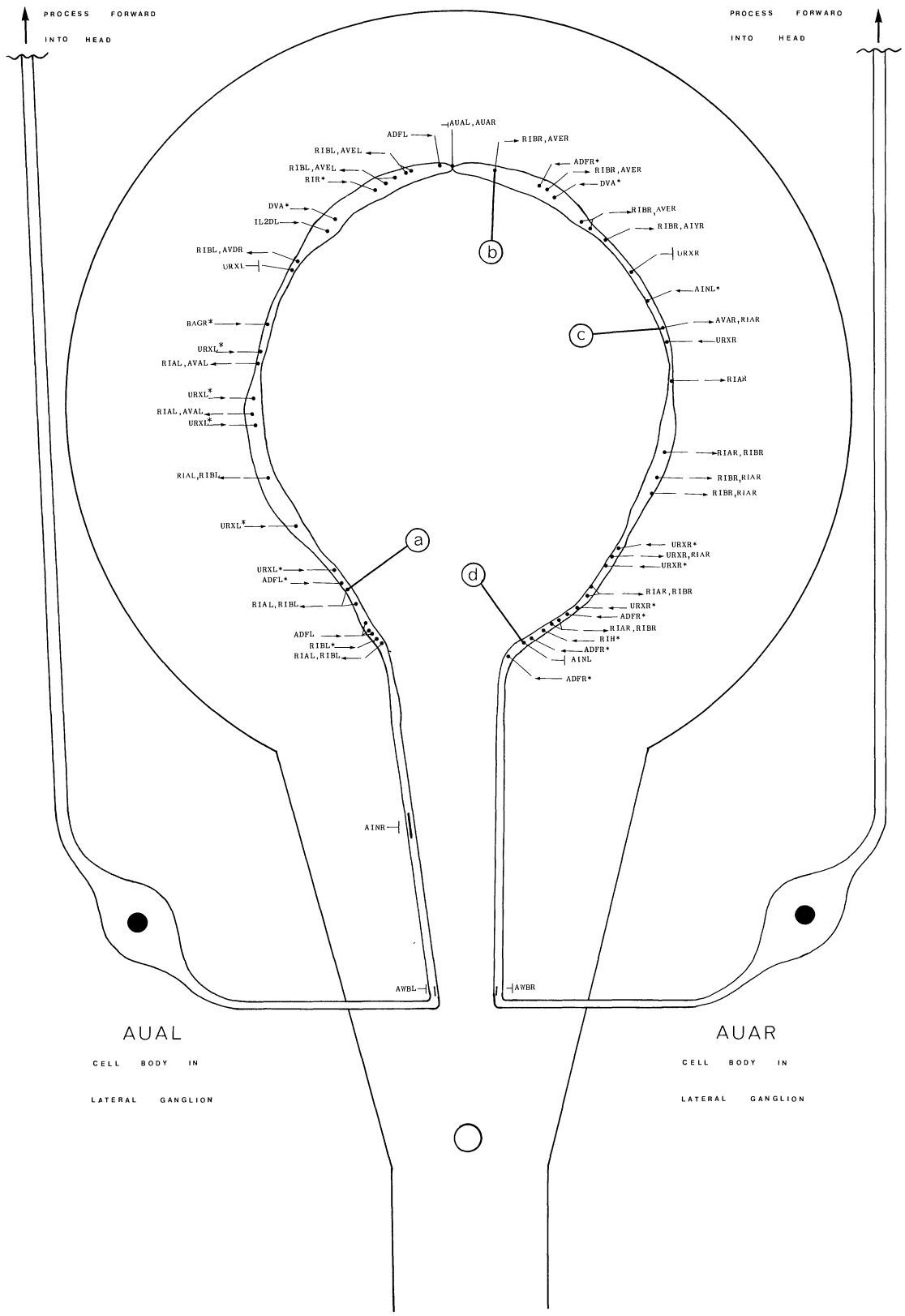


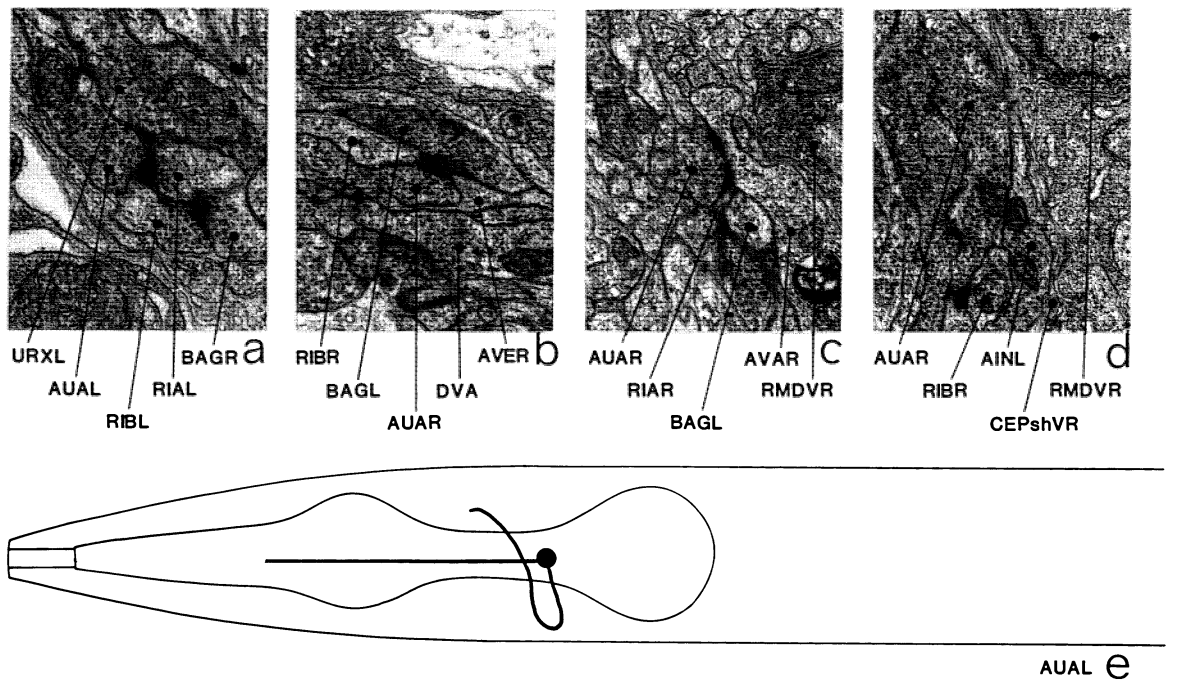
ASK

Members: ASKL, ASKR.

ASK is a set of two ciliated neurons that are part of the amphid sensilla. The endings are in the amphid channel, which is open to the outside (figure 1). Cell bodies are situated in the lateral ganglia and send processes into the ventral cord via the amphid commissures. These processes run anteriorly near the lateral extremities of the ventral cord and then project into the nerve ring, where they run near the middle of the neuropile. The processes meet and terminate at the dorsal mid-line with a gap junction between them (b). Some of the vesicles in the synaptic terminals of ASK are large and darkly staining (a). The predominant synaptic output is to AIA (a, b). Some of the AIA synapses also include AIM (c) and AIB (d) as possible partners. There is some synaptic input from ASJ (*d), PVQ and AIM. ASK makes gap junctions with PVQ (a) and RMG.

Magnifications: (a, c, d) ×25500, (b) ×12750.


PROCESS FORWARD
INTO HEAD
PROCESS FORWARD
INTO HEAD
AUAL,AUAR
ADFL
RIBL,AVEL
RIBL,AVEL
RIR*
DVA*
IL2DL
RIBL,AVDR
URXL
RIBR,AVER
ADFR*
RIBR,AVER
DVA*
RIBR,AVER
RIBR,AIYR
URXR
AINL*
AVAR,RIAR
URXR
RIAR
RIAR,RIBR
RIBR,RIAR
RIBR,RIAR
URXR*
URXR,RIAR
URXR*
RIAR,RIBR
URXR*
ADFR*
RIAR,RIBR
RIH*
ADFR*
AINL
ADFR*
BAGR*
URXL*
RIAL,AVAL
URXL*
RIAL,AVAL
URXL*
RIAL,RIBL
URXL*
URXL*
ADFL*
RIAL,RIBL
ADFL
RIBL*
RIAL,RIBL
a
b
c
d
AINR
AWBL
AWBR
AUAL
CELL BODY IN
LATERAL GANGLION
AUAR
CELL BODY IN
LATERAL GANGLION



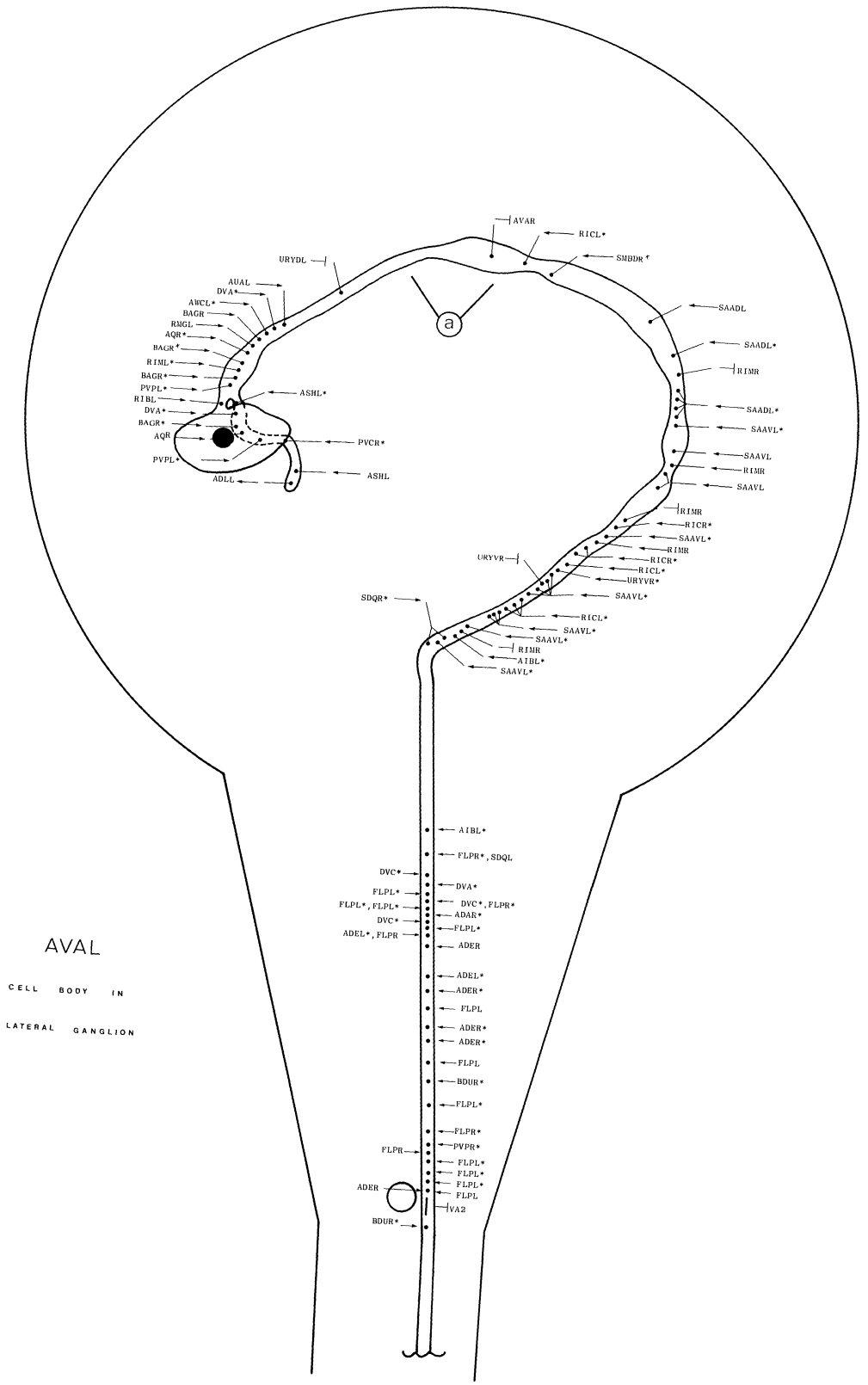
AUA

Members: AUAL, AUAR.

AUA is a pair of neurons with cell bodies situated in the lateral ganglia. Anteriorly directed processes leave the cell bodies and run along with the bundles of processes from the amphid sensilla until they peter out, with no terminal specializations, just in front of the first bulb of the pharynx (e). A second process comes out of each cell body and enters the ventral cord via the amphidial commissures; it then turns and runs anteriorly on the ventral surface of the cord. The processes of AUA then enter and run round each side of the ring, close to the outside surface, eventually meeting and terminating in a gap junction on the dorsal mid-line. The main synaptic output is to RIB (a, b), RIA (a, c), AVE (b) and AVA (c) in various dyadic combinations. The main synaptic input is from URX (*a) and ADF. There are gap junctions to URX, AWB and AIN (d).

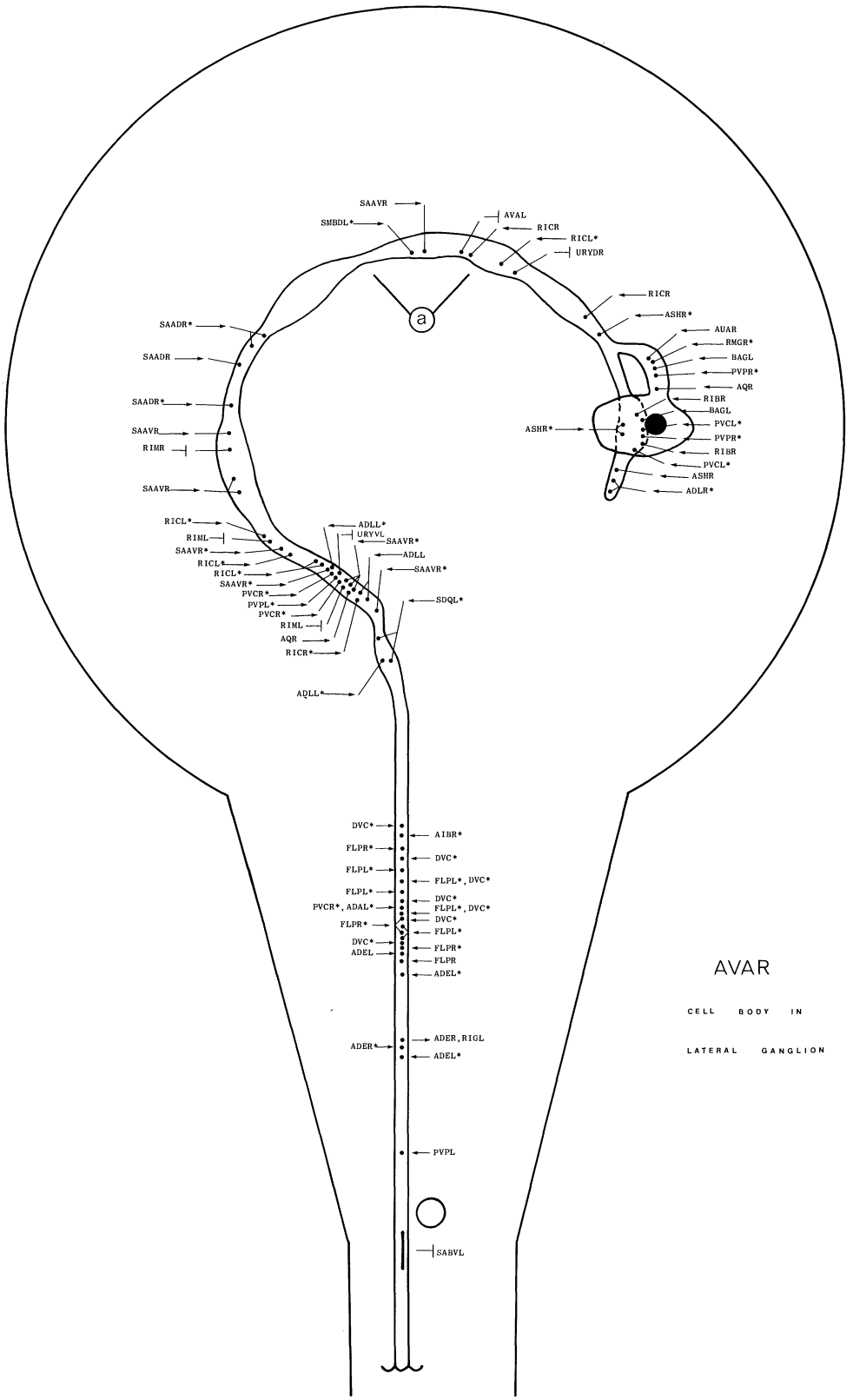
Magnifications: (a) ×25500, (b–d) ×17000.

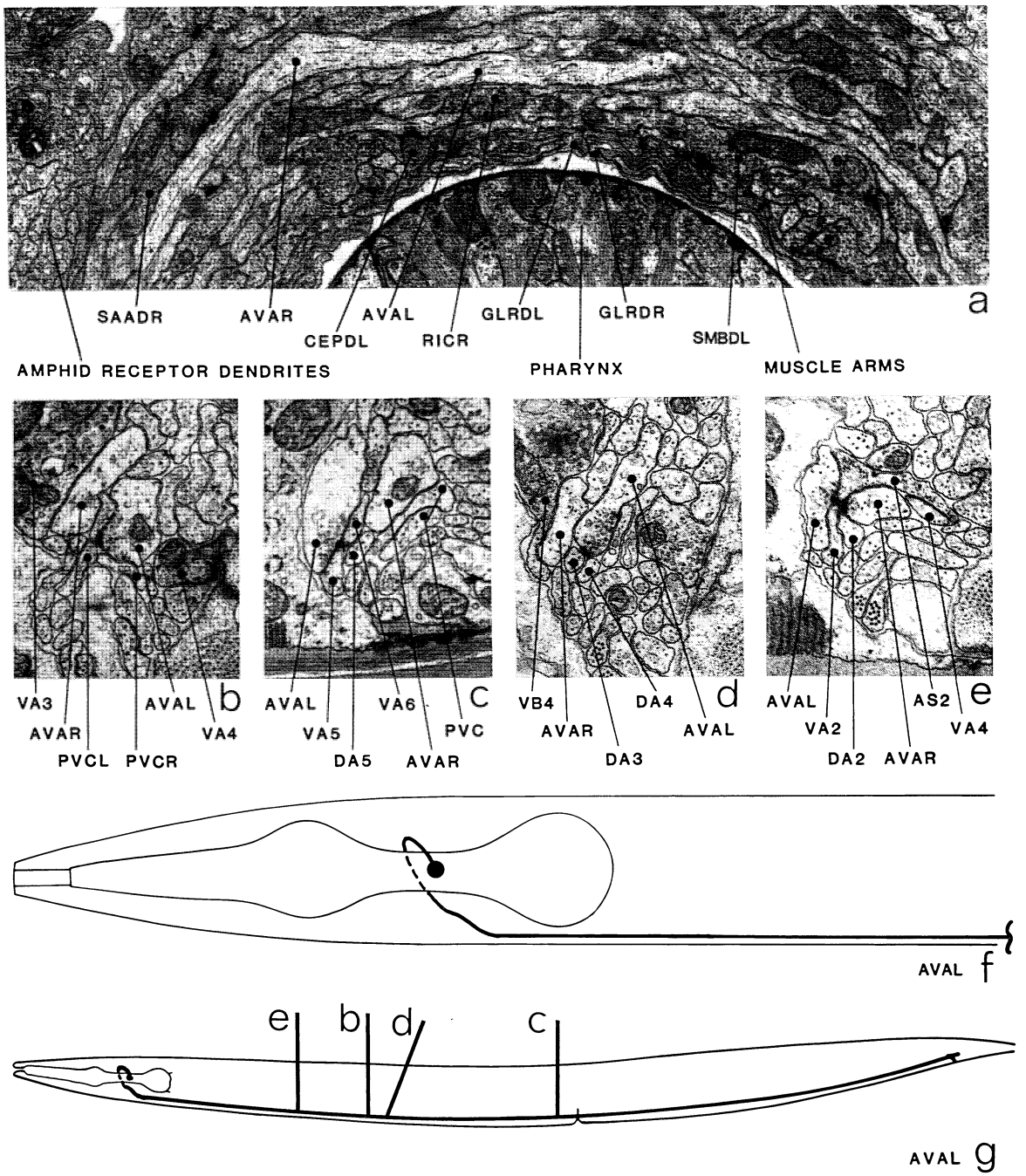
AVA



AVAL

CELL BODY IN LATERAL GANGLION


SAAVR
SMBDL*
AVAL
RICR
RICL*
URYDR
a
RICR
ASHR*
AUAR
RMGR*
BAGL
PVPR*
AQR
RIBR
BAGL
PVCL*
PVPR*
RIBR
PVCL*
ASHR
ADLR*
ASHR*
SAADR*
SAADR
SAADR*
SAAVR
RIMR
SAAVR
RICL*
RIML
SAAVR*
RICL*
RICL*
SAAVR*
PVCR*
PVPL*
PVCR*
RIML
AQR
RICR*
ADLL*
URYVL
SAAVR*
ADLL
SAAVR*
SDQL*
ADLL*
DVC*
FLPR*
FLPL*
FLPL*
PVCR*, ADAL*
FLPR*
DVC*
ADEL
AIBR*
DVC*
FLPL*, DVC*
DVC*
FLPL*, DVC*
DVC*
FLPL*
FLPR*
FLPR
ADEL*
ADER*
ADER, RIGL
ADEL*
PVPL
SABVL
AVAR
CELL BODY IN
LATERAL GANGLION



AVA

Members: AVAL, AVAR.

AVA is a pair of interneurons with cell bodies situated in the lateral ganglia adjacent to the neuropile of the nerve ring. Processes from the cell bodies enter the nerve ring laterally and run round it, near the outside and posterior faces, to the contralateral side, eventually leaving the ring ventrally and entering the ventral cord. They then run the length of the cord positioned near the centre of the process bundle (figure 18), ending near the posterior extremity

of the cord in the pre-anal ganglion. The processes of AVA are rather large and lightly staining (a); together with those of AVB they are the most prominent interneurons in the ventral cord. In the nerve ring they are exclusively postsynaptic and receive extensive synaptic input. The main presynaptic partners in this region are: SAA (*b), FLP (*a), RIC (*a), DVC (*c), PVP (*c), AUA (*c), ASH (*b), AQR (*c), ADL (*d), SDQ (*b), DVA (*c) and RIB (*g); there are gap junctions to RIM, URY and itself (a). In the ventral cord AVA is both pre- and postsynaptic, although the chemical synapses that it makes have rather few vesicles (b, c, d, e). The main synaptic output is to the ventral cord motoneurons: VAn (c), DAn (d), ASn (e) and also to PVC (b) and SAB. PVC (*g), VAn (*b), DAn (*c), ASn (*c) and SAB (*c) have gap junctions with AVA. There is considerable synaptic input from AVD (*a), AVE (*a) and AVB (*b) distributed along the length of the cord as well as some less extensive input from PVC (*f), ADE (*b) and PLM (*f). In the pre-anal ganglion, AVA receives synapses from PHB (*a), PQR (*g) and LUA (*a).

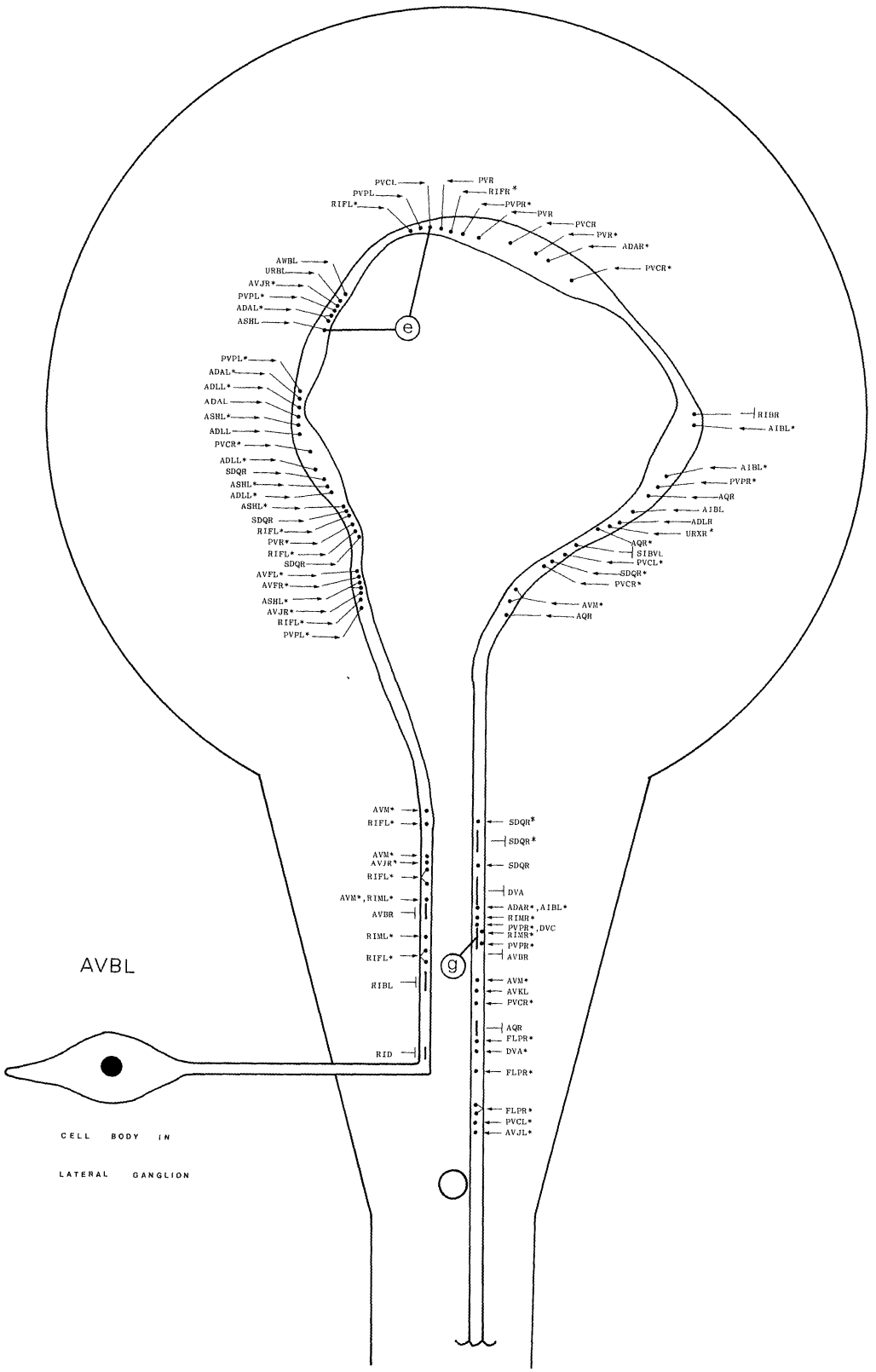
Magnifications: (a–e) ×17000.

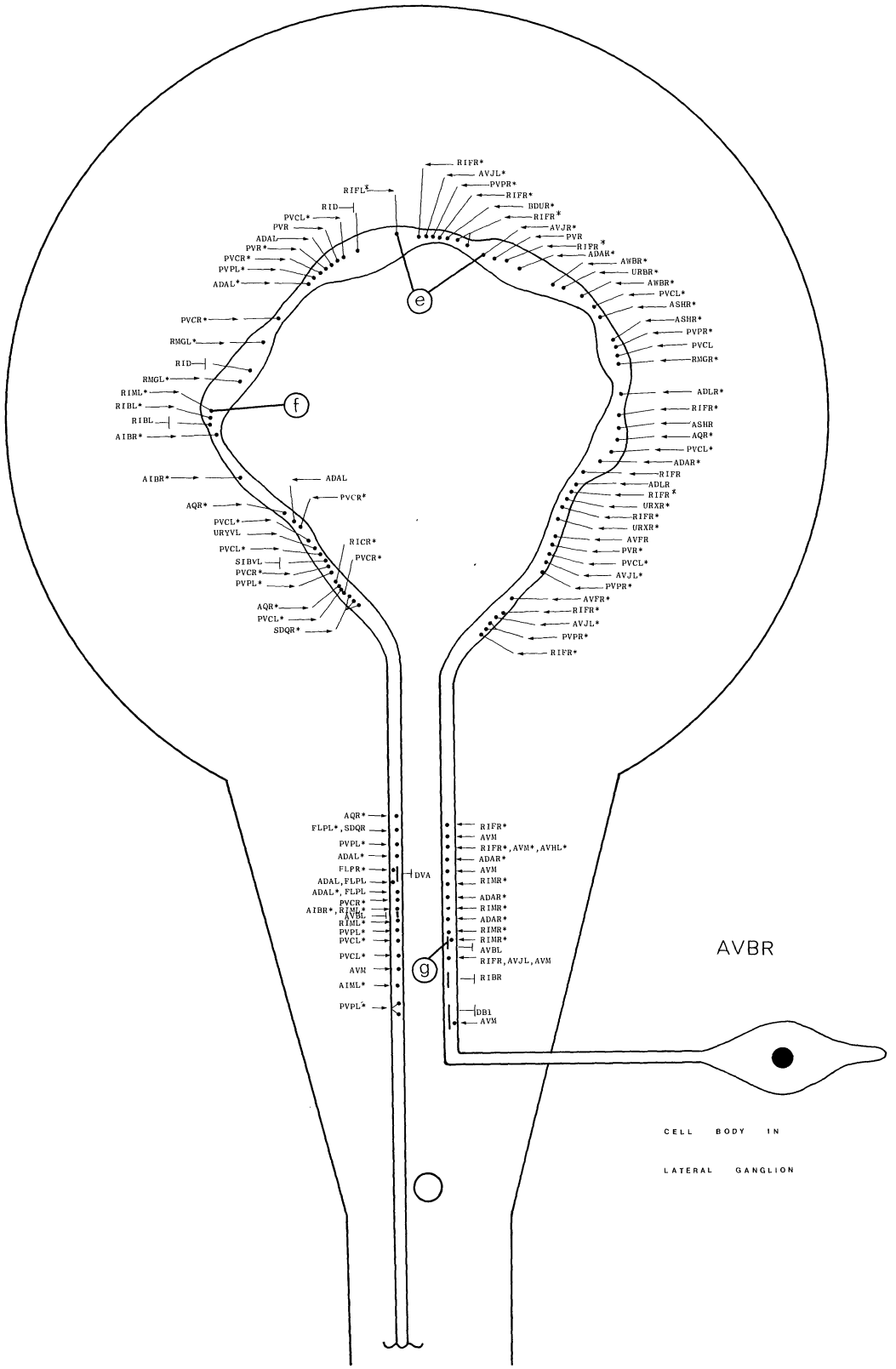
AVA VENTRAL CORD SYNAPSES

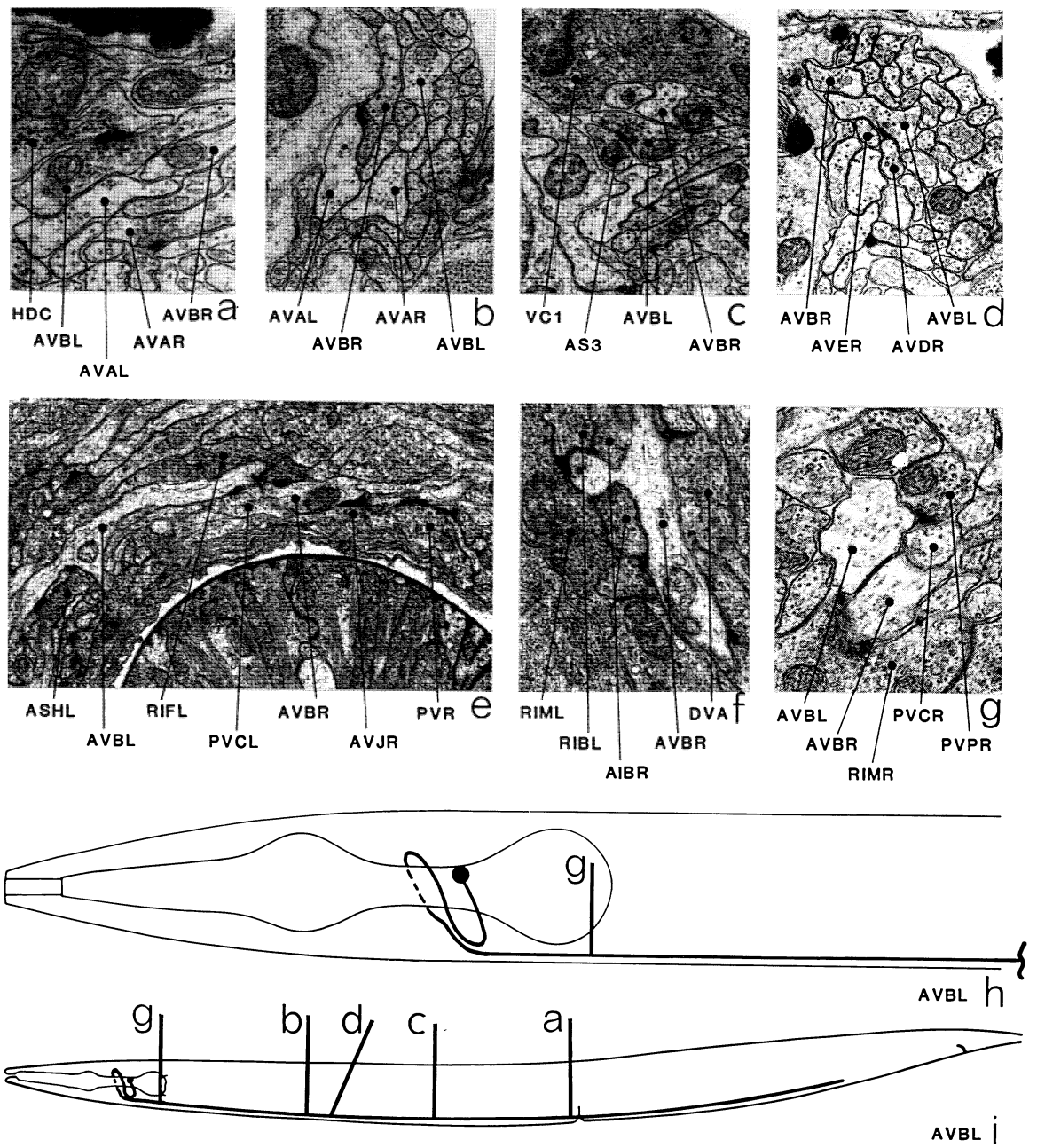
partners	gap junctions	synapses from	synapses to and corecipients
PVC	10	3+11 m	7, 5LUA, 4PVC, 4DA8, 2PDE, VA10, DB5, VA4, DB3, DA7, DA5
VA11	8	—	6AS11, 3DA8, 2DA9, VA12, VA10, VD13
DA8	1	—	4PVC, 3VA11, 2AS11, VA12, DA7, DA9, VA10, VD13
DA4	5	—	3, 4DA3, 2DA5, 2VA3, VA4
VA10	2	—	1, 3AS10, 2DA7, PVC, VA11, AS11, DA8
DA5	5	—	2, 3VA5, 2DA4, PVC, DA6
DA3	2	—	2, 4DA4, 2DA2, VA3
AS11	—	—	6VA11, 2DA8, VA10
DA7	2	—	2AVA, 2VA10, AS10, DA8, PVC
VA5	6	—	3DA5, VA6, AS6, DA6
LUA	—	1+19 m	5PVC
DA9	—	—	2, 2VA11, DA8
AS5	2	—	3VA6, AVB
DA1	8	—	2, AVA, SABD
AS10	1	—	3VA10, DA7
VA4	3	—	PVC, DA4, AS4, DB3
DA2	3	—	1, 2DA3, AVE
VA6	5	—	3AS5, VA5
VA3	3	—	1, 2DA4, DA3
AVE	—	8+30 m	2AS3, AS1, DA2
AVA	4	3 m	2DA7, DA1
VA2	3	—	1, 2AS2
AS2	—	—	1, 2VA2
AVD	—	7+56 m	SABV, AS6
DB5	2	—	1, PVC
VA12	1	—	DA8, VA11
SABV	4	—	1, AVD
AS6	2	—	VA5, AVD
AS4	—	—	1, VA4
VD13	—	2 m	DA8, VA11
DB3	—	—	PVC, VA4
DA6	—	—	DA5, VA5
PDE	—	—	2 PVC
AVB	—	21+6 m	1, AS5
AS3	3	—	2AVE
SABD	4	—	DA1
AS1	4	—	AVE

AVA VENTRAL CORD SYNAPSES (*cont.*)

partners	gap junctions	synapses from	synapses to and corecipients
PHB	—	21 m	—
PQR	—	5+14 m	—
FLP	—	3+14 m	—
PLM	—	1+4 m	—
PVN	—	2+4 m	—
AVJ	2	2 m	—
PVD	—	3 m	—
VD11	—	2	—
AVG	—	1+1 m	—
VA7	5	—	—
VA1	2	—	—
VA5	1	—	—
DA2	1	—	—
VA8	1	—	—
BDU	—	2 m	—


PVCL
PVPL
RIFL*
PVR
RIFR*
PVPR*
PVR
PVCR
PVR*
ADAR*
PVCR*
AWBL
URBL
AVJR*
PVPL*
ADAL*
ASHL
e
PVPL*
ADAL*
ADLL*
ADAL
ASHL*
ADLL
PVCR*
ADLL*
SDQR
ASHL*
ADLL*
ASHL*
SDQR
RIFL*
PVR*
RIFL*
SDQR
AVFL*
AVFR*
ASHL*
AVJR*
RIFL*
PVPL*
RIBR
AIBL*
AIBL*
PVPR*
AQR
AIBL
ADLR
URXR*
AQR*
SIBVL
PVCL*
SDQR*
PVCR*
AVM*
AQR
AVM*
RIFL*
AVM*
AVJR*
RIFL*
AVM*,RIML*
AVBR
RIML*
RIFL*
RIBL
RID
SDQR*
SDQR*
SDQR
DVA
ADAR*,AIBL*
RIMR*
PVPR*,DVC
RIMR*
PVPR*
AVBR
g
AVM*
AVKL
PVCR*
AQR
FLPR*
DVA*
FLPR*
FLPR*
PVCL*
AVJL*
AVBL
CELL BODY IN
LATERAL GANGLION


RIFR*
AVJL*
PVPR*
RIFR*
BDUR*
RIFR*
AVJR*
PVR
RIFR*
ADAR*
AWBR*
URBR*
AWBR*
PVCL*
ASHR*
ASHR*
PVPR*
PVCL
RMGR*
ADLR*
RIFR*
ASHR
AQR*
PVCL*
ADAR*
RIFR
ADLR
RIFR*
URXR*
RIFR*
URXR*
AVFR
PVR*
PVCL*
AVJL*
PVPR*
AVFR*
RIFR*
AVJL*
PVPR*
RIFR*
RIFL*
RID
PVCL*
PVR
ADAL
PVR*
PVCR*
PVPL*
ADAL*
e
PVCR*
RMGL*
RID
RMGL*
RIML*
RIBL*
RIBL
AIBR*
f
AIBR*
ADAL
PVCR*
AQR*
PVCL*
URYVL
PVCL*
SIBVL
PVCR*
PVPL*
RICR*
PVCR*
AQR*
PVCL*
SDQR*
AQR*
FLPL*,SDQR
PVPL*
ADAL*
FLPR*
ADAL,FLPL
ADAL*,FLPL
PVCR*
AIBR*,RIML*
AVBL
RIML*
PVPL*
PVCL*
PVCL*
AVM
AIML*
PVPL*
DVA
g
RIFR*
AVM
RIFR*,AVM*,AVHL*
ADAR*
AVM
RIMR*
ADAR*
RIMR*
ADAR*
RIMR*
RIMR*
AVBL
RIFR,AVJL,AVM
RIBR
DB1
AVM
AVBR
CELL BODY IN
LATERAL GANGLION



AVB

Members: AVBL, AVBR.

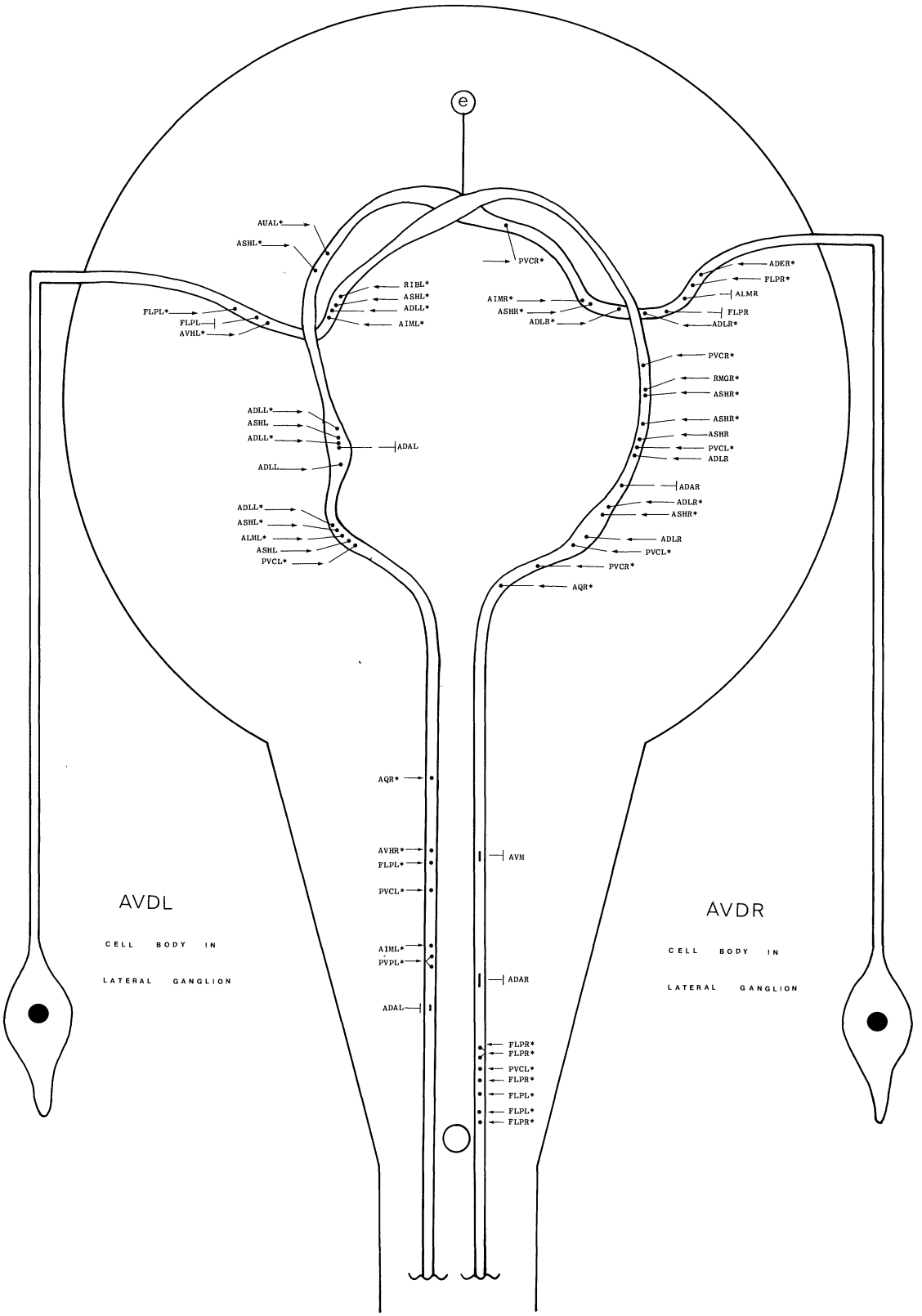
AVB is a pair of interneurons with cell bodies situated in the lateral ganglia. Processes leave the cell bodies and enter the ventral cord via the amphidial commissures (h). They then turn, run anteriorly into the nerve ring and run right round it near the middle of the neuropile, in close association with the processes of PVC and AVJ. They reenter the ventral nerve cord on the contralateral side and run along it in the dorsal region of the process bundle (figure 18), ending in the posterior body before the pre-anal ganglion is reached (i). AVB, together with AVA, are the most prominent interneurons of the ventral cord. The processes of AVB are large

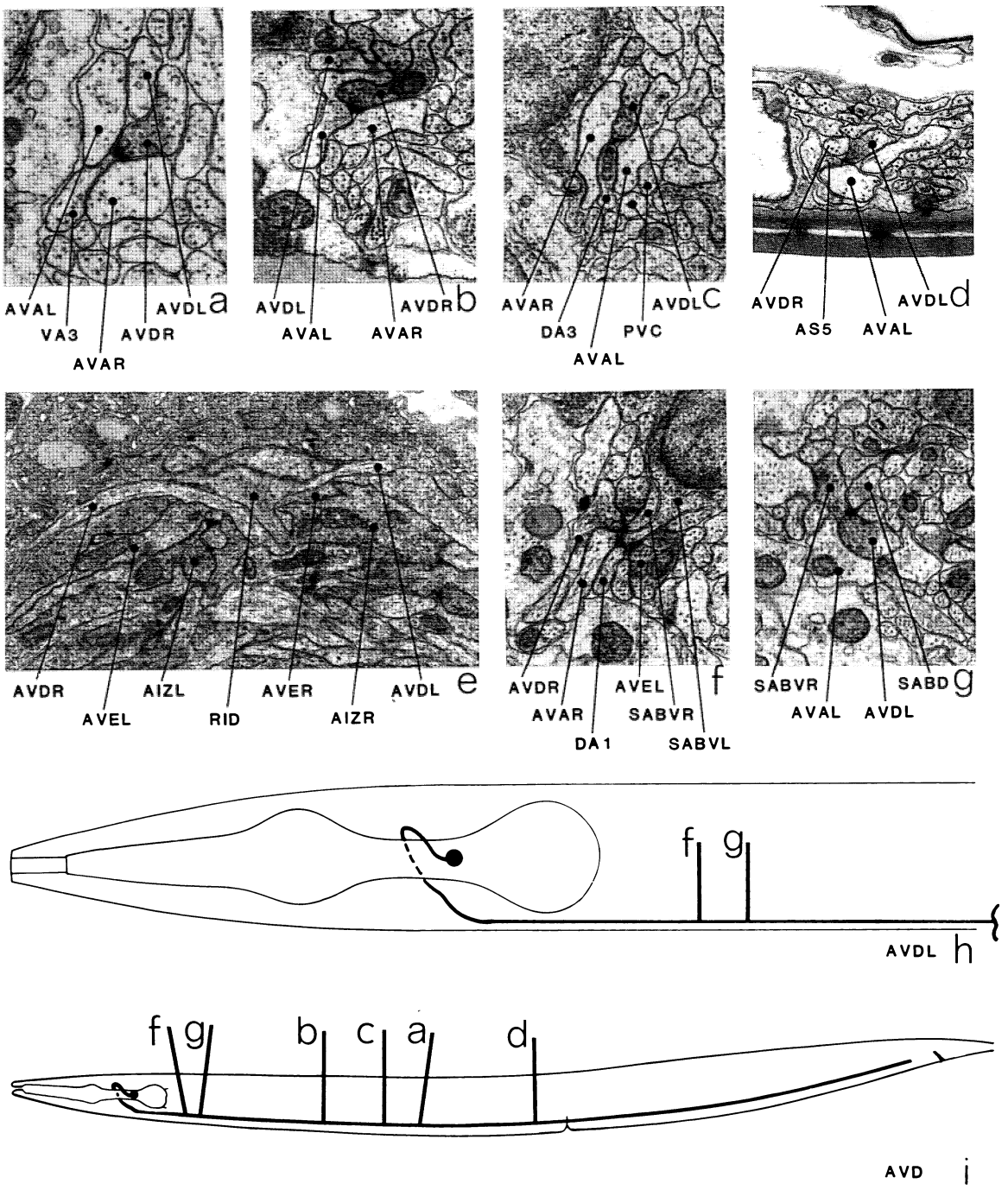
and lightly staining (e, f, g) and have several short projections emanating from them in the nerve ring (e, f). AVB is entirely postsynaptic in the nerve ring, where it receives many synaptic inputs. These come mainly from RIF (*b), RIM (*f), AVM (*a), PVC (*b), ASH (*b), PVR (*a), PVP (*a), SDQ (*a), ADA (*a), AQR (*a), FLP (*b), AIB (*c), AVF (*c), ADL and URX. There are also gap junctions to RIB (*g), SIBV (*d), DVA (*g), RID (*c), SDQ and itself (g) in the nerve ring. AVB is predominantly presynaptic in the ventral cord, where it synapses mainly onto AVA (b), ASn (c) and the hypodermis (HDC) (a) together with a few small synapses onto AVD (d) and AVE (d). There are gap junctions to all the VBn (*c) and DBn (*c) motoneurons, usually in the vicinity of their cell bodies. AVB has little synaptic input in the ventral cord; what there is comes from AVF (*c), PVN (*c) and PVC.

Magnifications: (a, f, g) ×25500, (b–d) ×17000, (e) ×12750.

AVB VENTRAL CORD SYNAPSES

partners	gap junctions	synapses from	synapses to and corecipients
AVA	—	1+1 m	21, 2AVA, DA5, AVD
HDC	—	—	6
AVD	—	1	AVA, AVB, AVE
AVE	—	—	1, AVD, VA4
AS3	—	—	2
AVB	1	2 m	VD3, AVD
AS10	—	—	2
AS4	—	—	2
AS6	—	—	2
AS5	—	—	1
VA10	—	—	1
AVL	—	—	1
VA7	—	—	1
AS1	—	—	1
HSN	—	—	1
VA4	—	—	AVE
VD3	—	—	AVB
DA5	—	—	AVA
FLP	—	1+5 m	—
AVG	—	3+1 m	—
AVF	—	1+3 m	—
PVN	2	1+2 m	—
PVC	—	3 m	—
AVJ	—	1	—
AVH	—	1 m	—
VC4	—	1 m	—
DB3	5	—	—
VB7	4	—	—
DB7	3	—	—
VB11	3	—	—
VB4	2	—	—
DB5	2	—	—
VB8	2	—	—
DB1	2	—	—
VB5	1	—	—
DB4	1	—	—
DB2	1	—	—
VB1	1	—	—
VB3	1	—	—


e
AUAL*
ASHL*
PVCR*
RIBL*
ASHL*
ADLL*
AIML*
AIMR*
ASHR*
ADLR*
ADER*
FLPR*
ALMR
FLPR
ADLR*
FLPL*
FLPL
AVHL*
PVCR*
RMGR*
ASHR*
ASHR*
ASHR
PVCL*
ADLR
ADAL
ADAR
ADLR*
ASHR*
ADLR
PVCL*
PVCR*
AQR*
ADLL*
ASHL
ADLL*
ADLL
ADLL*
ASHL*
ALML*
ASHL
PVCL*
AQR*
AVHR*
FLPL*
PVCL*
AVM
AIML*
PVPL*
ADAR
ADAL
FLPR*
FLPR*
PVCL*
FLPR*
FLPL*
FLPL*
FLPR*
AVDL
CELL BODY IN
LATERAL GANGLION
AVDR
CELL BODY IN
LATERAL GANGLION



AVD

Members: AVDL, AVDR.

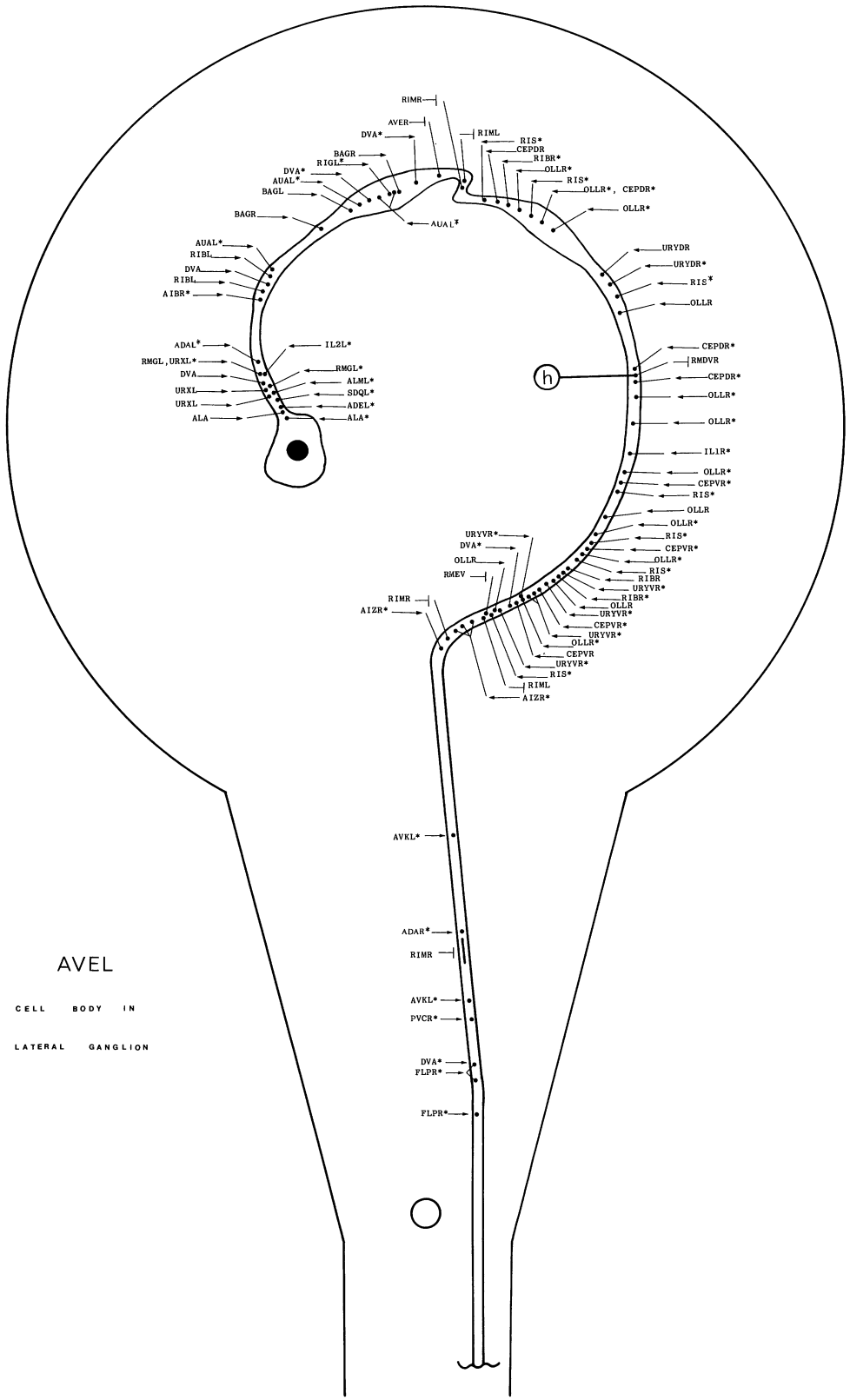
AVD is a pair of interneurons with cell bodies situated in the lateral ganglia. Anteriorly directed processes leave the cell bodies and enter the ring sub-dorsally, where they initially run near the inside surface of the neuropile. They move out near the outside surface as the processes cross over on the dorsal mid-line (e) and move back to the middle of the neuropile as they carry on round the ring. They then enter the ventral cord where they run near the middle of the process bundle (figure 18), eventually ending in the pre-anal ganglion. The processes

of AVD are exclusively postsynaptic in the nerve ring and are lightly staining. The main synaptic input in this region is from ASH (*c), ADL (*d), FLP (*b), PVC (*c) and AQR. There are gap junctions to ADA (*d) and FLP. AVD is predominantly presynaptic in the ventral cord having the same post-synaptic partners as AVE. It makes many synapses to AVA (a, b, c, d) and several to SAB (f, g), VAn (a), DAn (c) and ASn (d), usually in various dyadic combinations. There are some striking synaptic complexes in the vicinity of the cell bodies of the SAB neurons, where two presynaptic specializations from AVD and/or AVE (and sometimes also AVA) occur in the same region with the processes of SAB, DA1 and VA1 sandwiched in between (f). The main synaptic input to AVD in the ventral cord is from PQR (*g), LUA (*a), PVN (*b) and PLM (*f), there are also minor inputs from AVB (*b), PHB (*c) and possibly PVW (*c). There are gap junctions to AVJ, AVM (*e) and FLP in the cord.

Magnifications: (a) ×25500, (b–d, f, g) ×17000, (e) ×12750.

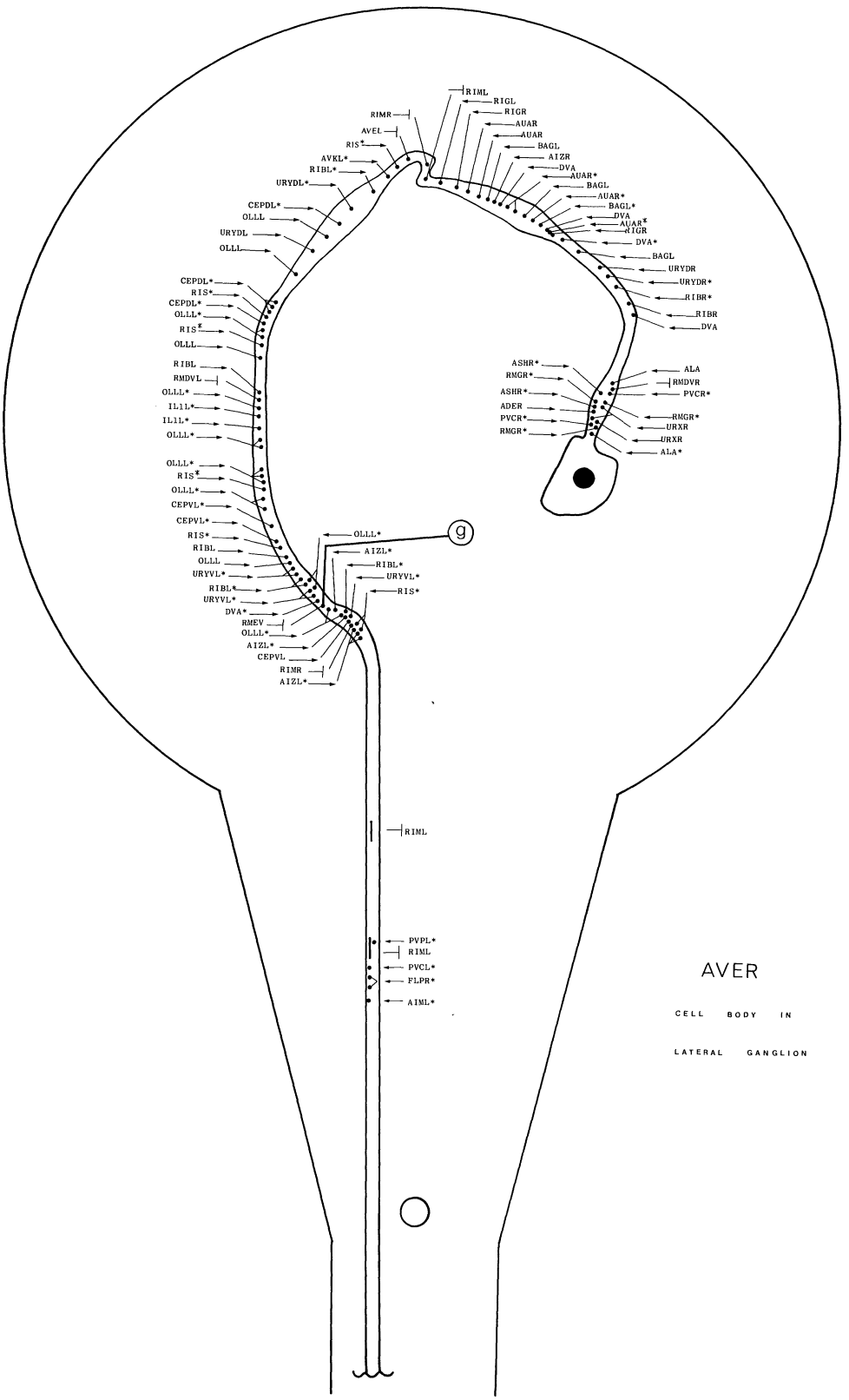
AVD VENTRAL CORD SYNAPSES

partners	gap junctions	synapses from	synapses to and corecipients
AVA	—	2	7, 33AVA, 4SABV, 3DA1, 3LUA, 2DA4, 2AS11, 2SABD, 2AVD, VA6, DA5, PVC, AS4, AS10, VA5, VA11, DA8, PQR, VA3, DB4, DA3
DA3	—	—	5, AVA
SABV	—	—	4AVA, 2SABV
DA4	—	—	2, 2AVA
LUA	—	7 m	3AVA
SABD	—	—	1, 2AVA
DA1	—	—	3AVA
DA5	—	—	2, AVA
VA3	—	—	2, AVA
AS11	—	—	2AVA
AVD	—	—	2AVA
DA2	—	—	2
VA6	—	—	1, AVA
AS10	—	—	1, AVA
PQR	—	12 m	AVA
PVN	—	6 m	—
DA8	—	—	AVA
PVC	—	3 m	AVA
AS1	—	—	1
AS4	—	—	AVA
AVB	—	3 m	1
DA9	—	—	1
VA2	—	—	1
DVC	—	—	1
AS5	—	—	1
DB4	—	—	AVA
VA11	—	—	AVA
VA5	—	—	AVA
FLP	1	2+18 m	—
PLM	—	1+4 m	—
AVJ	4	4 m	—
PHB	—	3 m	—
HSN	—	3 m	—
AVG	—	1	—
VA4	—	1	—
PHA	—	1 m	—
PVW	—	1 m	—
AVE	—	1 m	—
AVM	1	—	—



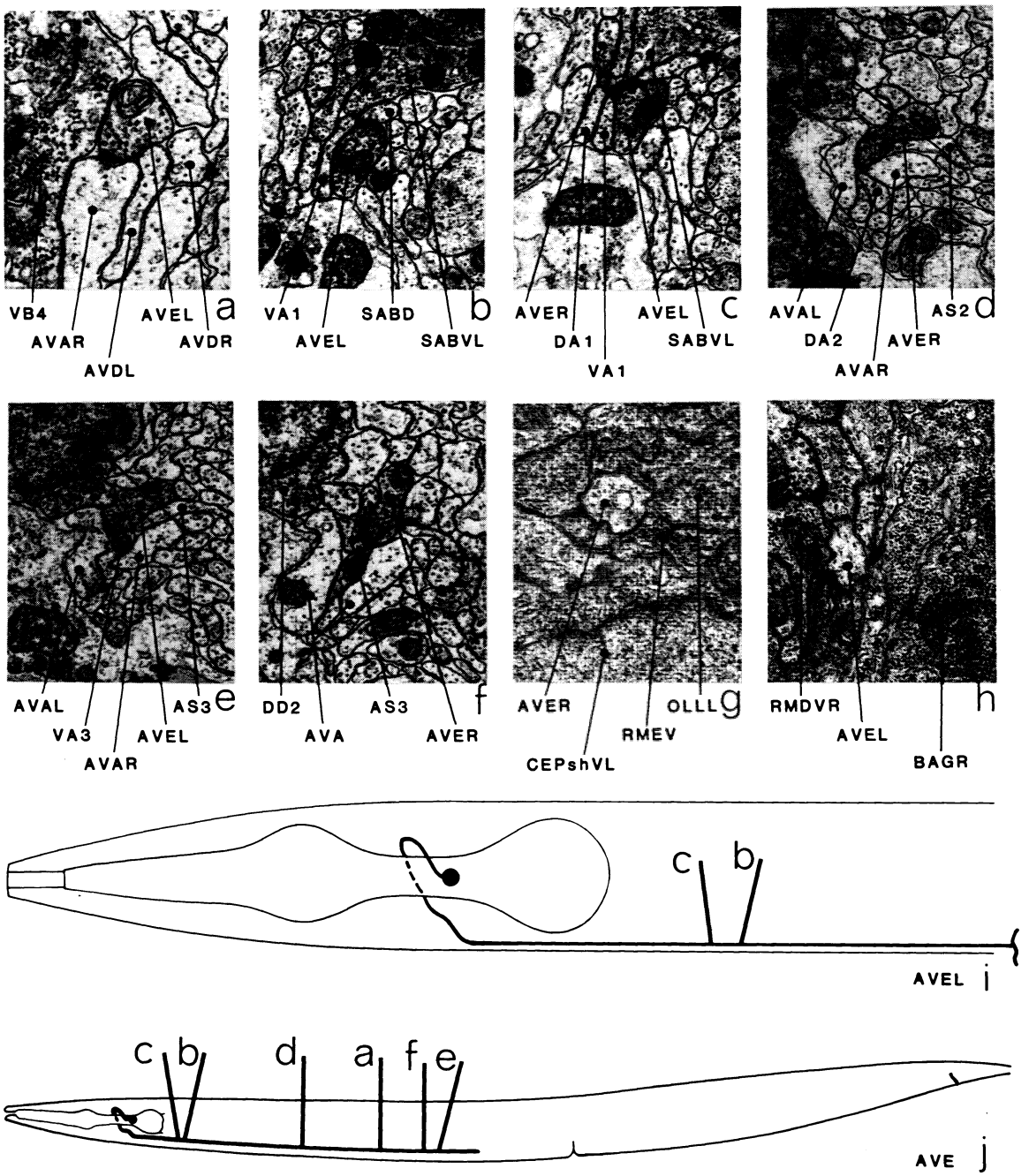
AVEL

CELL BODY IN LATERAL GANGLION



AVER

CELL BODY IN LATERAL GANGLION



AVE

Members: AVEL, AVER.

AVE is a pair of interneurons with cell bodies situated in the lateral ganglion close to the ring neuropile. Processes from the cell bodies enter the ring laterally and run anteriorly through the neuropile until they are near the anterior surface. They then turn dorsally and start running round the ring in close association with the processes of AIB. When the processes of AVE reach the dorsal mid-line they turn and run anteriorly for a short distance until the anterior surface

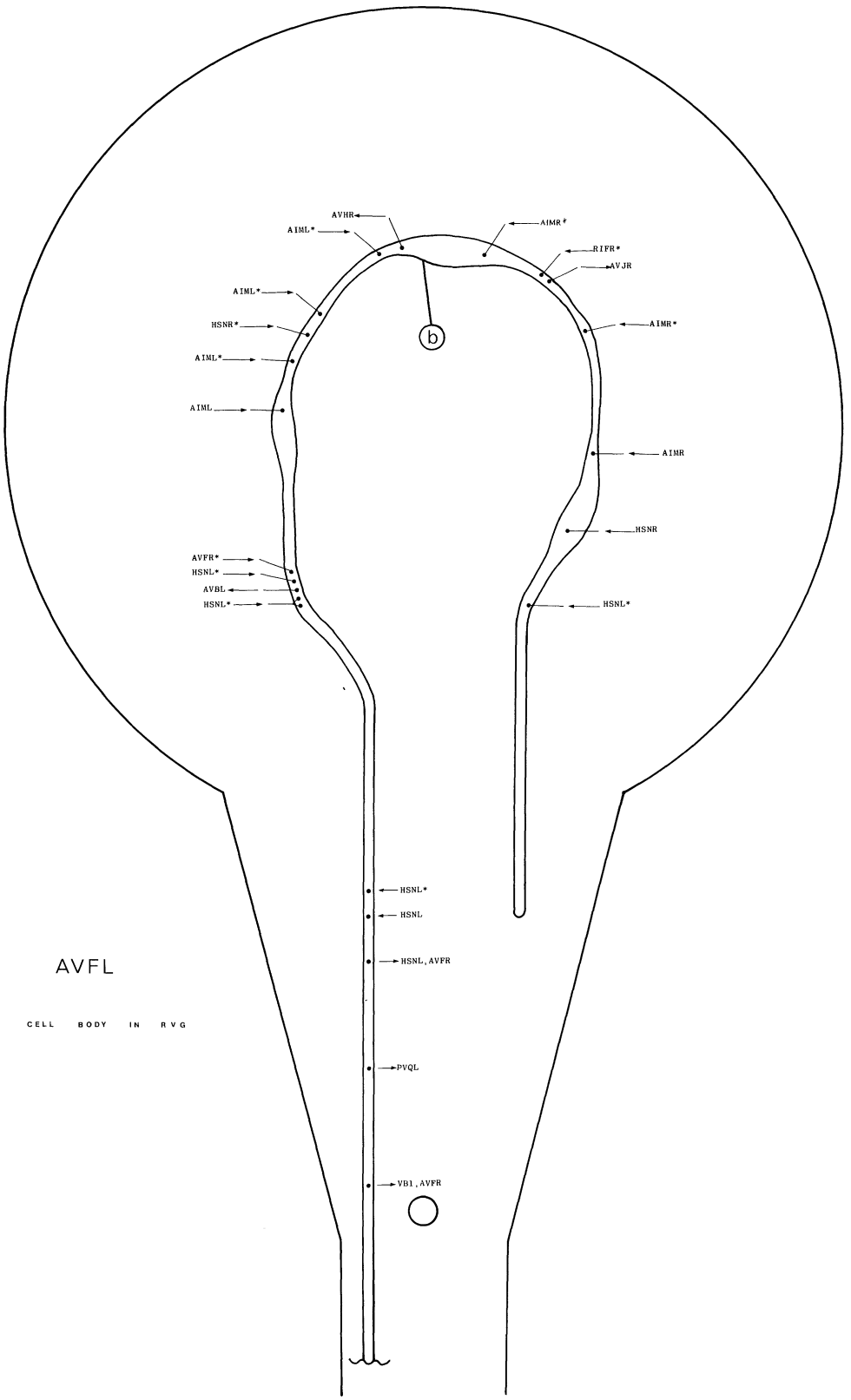
is reached, where they turn again and carry on round the ring in close association with the processes of RIB, until they leave the ring ventrally and enter the ventral cord. They run near the centre of the nerve cord (figure 18) and eventually end before the vulva is reached (j). The processes of AVE are exclusively postsynaptic in the nerve ring and are lightly staining in this region. They receive many synapses, particularly from the mechanosensory system. The main synaptic input is from OLL (*a), URY (*b), CEP (*d), URX (*b), DVA (*a), RIB (*h), RIS (*a), BAG (*c) and AUA (*b); there are also a few synapses from FLP (*b), ALA (*a), AVK (*a), AIZ, RIG, PVC (*a) and RMG. There are gap junctions to RIM (*h), RME (g) and RMD (h) in the ring. AVE is predominantly presynaptic in the ventral cord and has the same postsynaptic partners as AVD. It makes many synapses onto AVA (a) and also several onto SAB (b, c), VAn (c, e), DAn (d) and ASn (f), usually in various dyadic combinations. There are some striking synaptic complexes in the vicinity of the SAB cell bodies, where both AVEL and AVER have presynaptic specializations in the same region with processes of SAB, VA1 and DA1 sandwiched in between (c). There is some synaptic input from AVJ (*d) and AVB (*d) in the ventral cord.

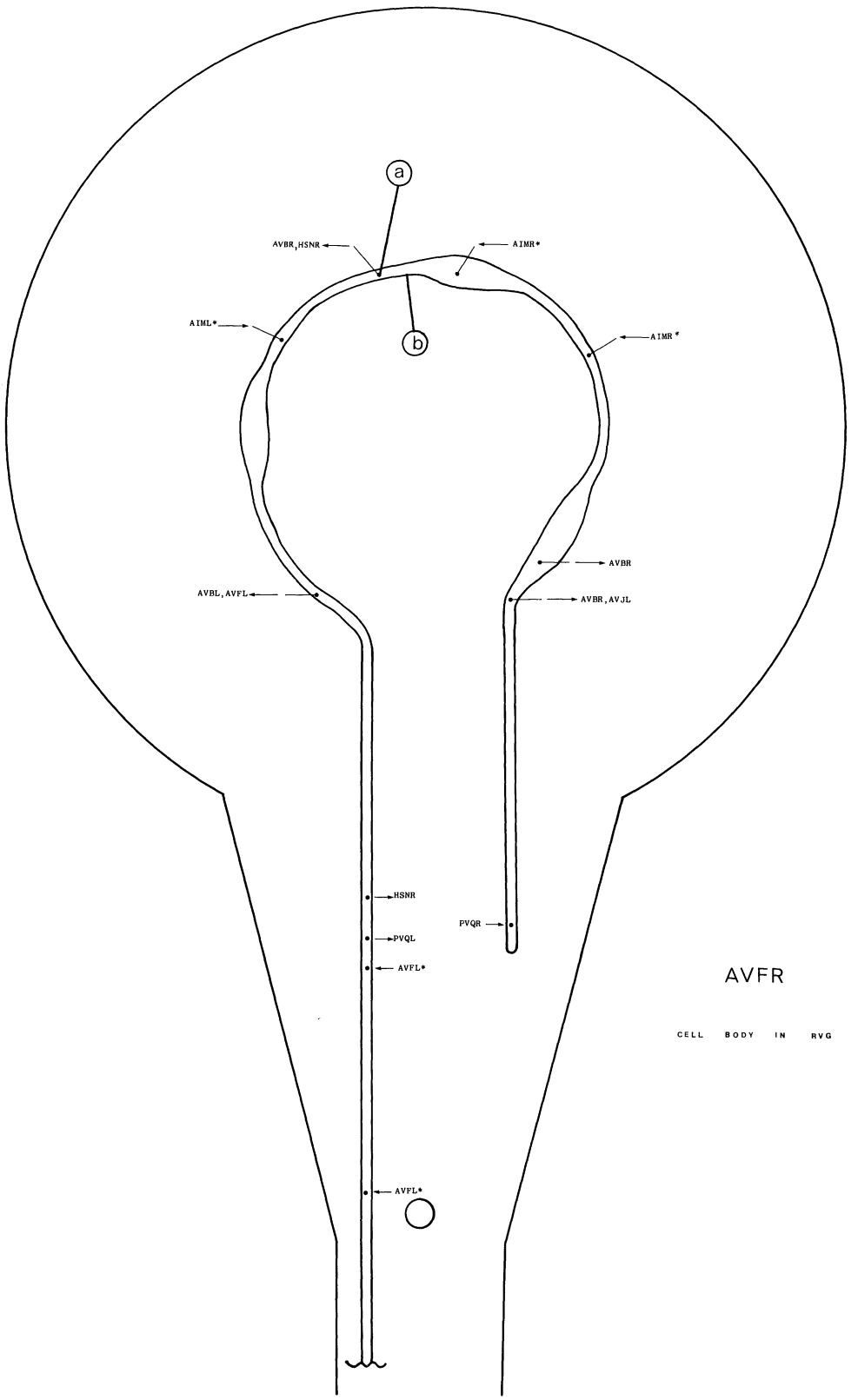
Magnifications: (a, g, h) ×25500, (b–f) ×17000.

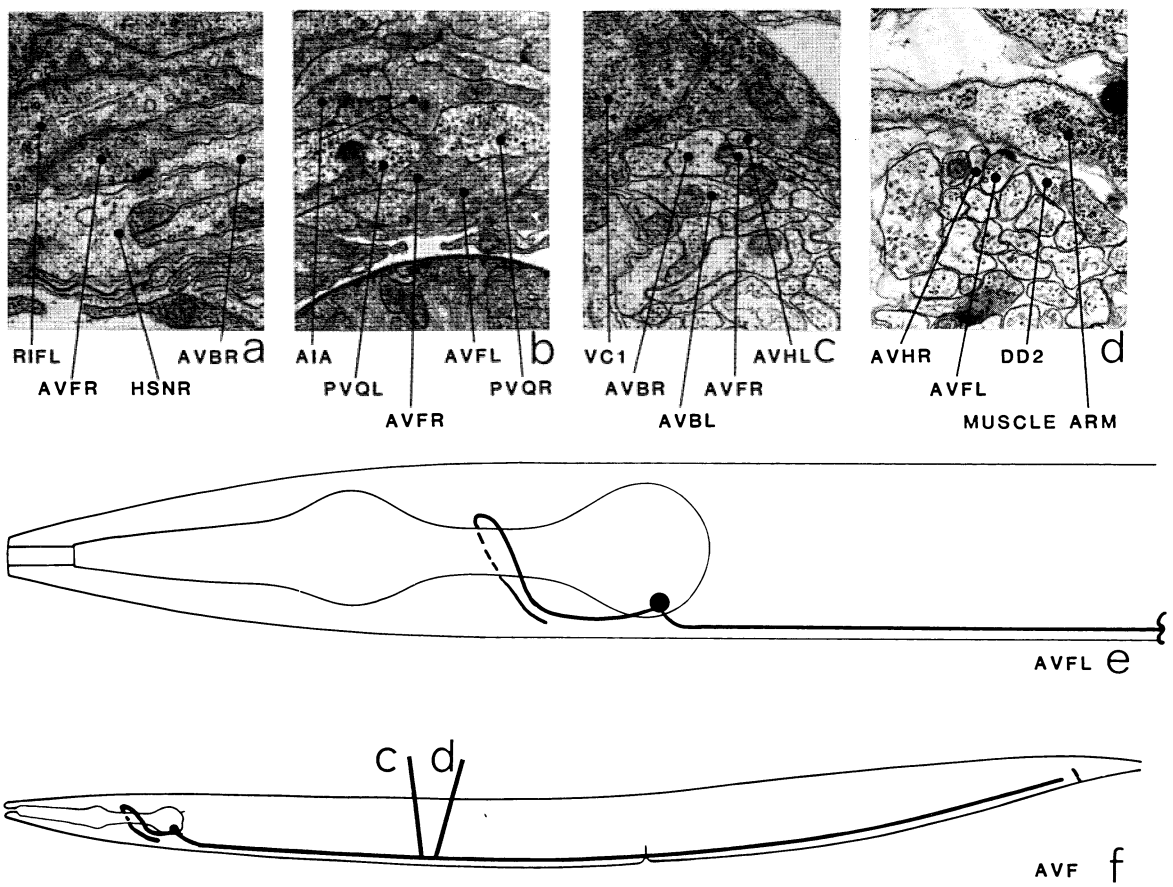
AVE VENTRAL CORD SYNAPSES

partners	gap junctions	synapses from	synapses to and corecipients
AVA	—	3 m	8, 6DA1, 5DA2, 4SABV, 4AS1, 4AVA, 2DA3, 2AS2, 2DB3, 2VA2, PVC, VA3, DA4, AVD, 1VA4
SABV	—	—	4SABD, 4AVA, 4DA1, 3VA1, 2SABV
DA1	—	—	6AVA, 4SABV, 2SABD
SABD	—	—	4SABV, 2VA1, 2DA1
VA1	—	—	3SABV, 2SABD, VA3
VA3	—	—	3, AVA, VD3, VA1
DA2	—	—	1, 5AVA
AS1	—	—	1, 4AVA
DA3	—	—	2, 2AVA
DB3	—	—	2AVA
AS2	—	—	2AVA
VA2	—	—	2AVA
PVC	—	1 m	AVA
DVB	—	—	VD2
VD2	—	—	DVB
VD3	—	—	VA3
DA4	—	—	AVA
AVD	—	—	AVA
AS3	—	—	1
VA6	—	—	1
VA4	—	—	AVA
AVJ	—	2+2 m	—
AVB	—	1+1 m	—
AVG	—	2 m	—
AVL	—	1 m	—

AVF


AVHR
AIML*
AIMR*
RIFR*
AVJR
AIML*
HSNR*
AIML*
AIML
b
AIMR*
AIMR
HSNR
AVFR*
HSNL*
AVBL
HSNL*
HSNL*
HSNL*
HSNL
HSNL, AVFR
PVQL
VB1, AVFR
AVFL
CELL BODY IN RVG


a
b
AVBR,HSNR
AIMR*
AIML*
AIMR*
AVBR
AVBL,AVFL
AVBR,AVJL
HSNR
PVQR
PVQL
AVFL*
AVFR
AVFL*
CELL BODY IN RVG



AVF

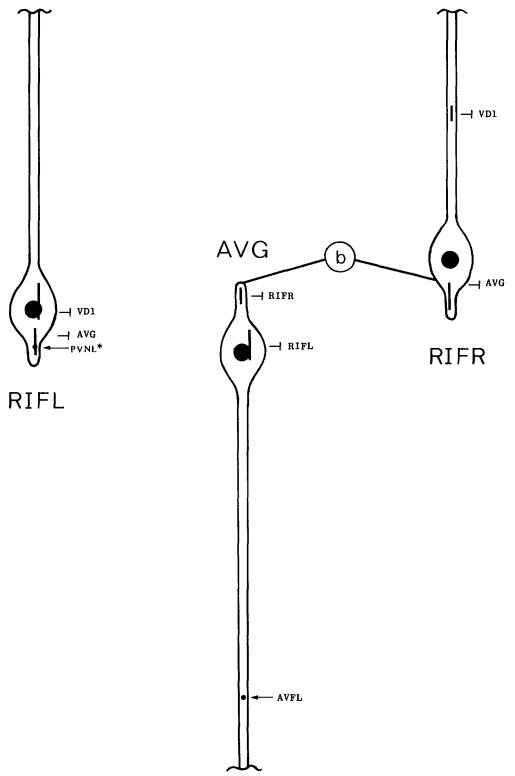
Members: AVFL, AVFR.

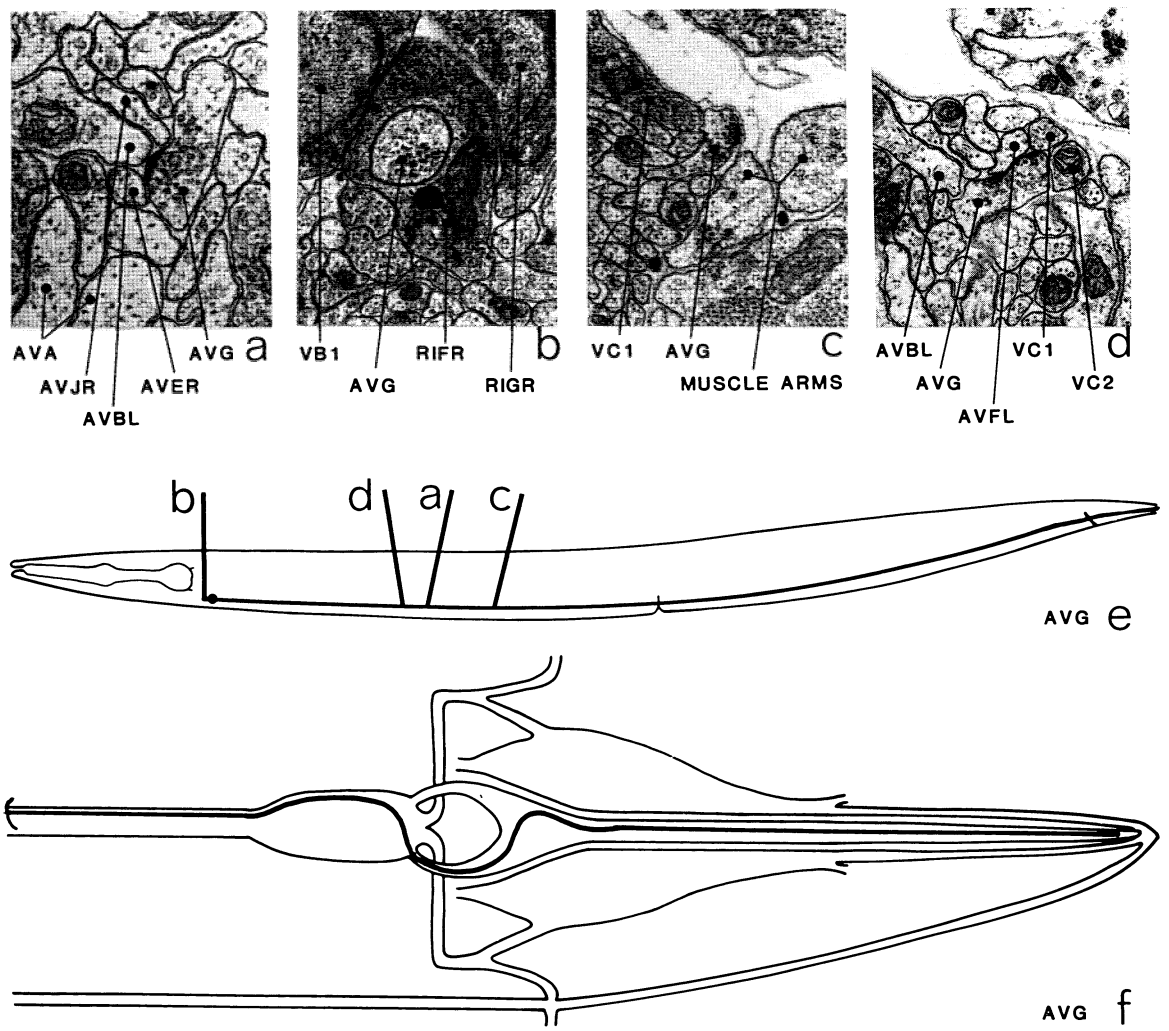
AVF is a pair of interneurons with bipolar cell bodies situated in the retro-vesicular ganglion. Anteriorly directed processes leave the cell bodies and run together round the left side of the excretory duct and then enter the nerve ring. They run right round the nerve ring on a trajectory which is near the inside and posterior surfaces of the neuropile, eventually ending ventrally. The posteriorly directed processes from the cell bodies of AVF run together in the dorsal regions of the ventral cord and end in the pre-anal ganglion. The processes of AVFL and AVFR are at all times closely associated. AVF makes a few rather small synapses, although in the nerve ring there are several regions that have vesicle-filled varicosities with no associated synaptic contacts (b). The main synaptic output in the nerve ring is to AVB (a), HSN (a) and AVJ; the main synaptic input is from AIM and HSN (*c). In the ventral cord there are chemical synapses to and from AVH (c and *d) as well as several gap junctions. There are also a few synapses to AVB (c) and several other synapses including a couple of small NMJs (d) and a few synapses with no obvious postsynaptic partner. There are many rather small gap junctions between AVFL and AVFR along the length of the cord.

Magnifications: (a) ×25500, (b) ×12750, (c, d) ×17000.

AVF VENTRAL CORD SYNAPSES

partners	gap junctions	synapses from	synapses to and corecipients
AVH	8	6 m	1, AVL, AVF, AVB, AVJ
AVB	—	—	1, AVG, AVJ, AVH
AVF	21	1+2 m	1, PVT, AVH
AVJ	1	1 m	1, AVB, AVH
NMJ	—	—	2
AVG	—	1	1, AVB
PVQ	1	—	PDE
PDE	—	—	PVQ
AVL	—	1 m	AVH
VD11	—	—	1
PHA	—	3 m	—
VC5	—	1+1 m	—
PHB	—	1 m	—
VC4	2	—	—


VD1
AVG
PVNL*
RIFL
VD1
AVG
b
AVG
RIFR
RIFL
RIFR
AVFL



AVG

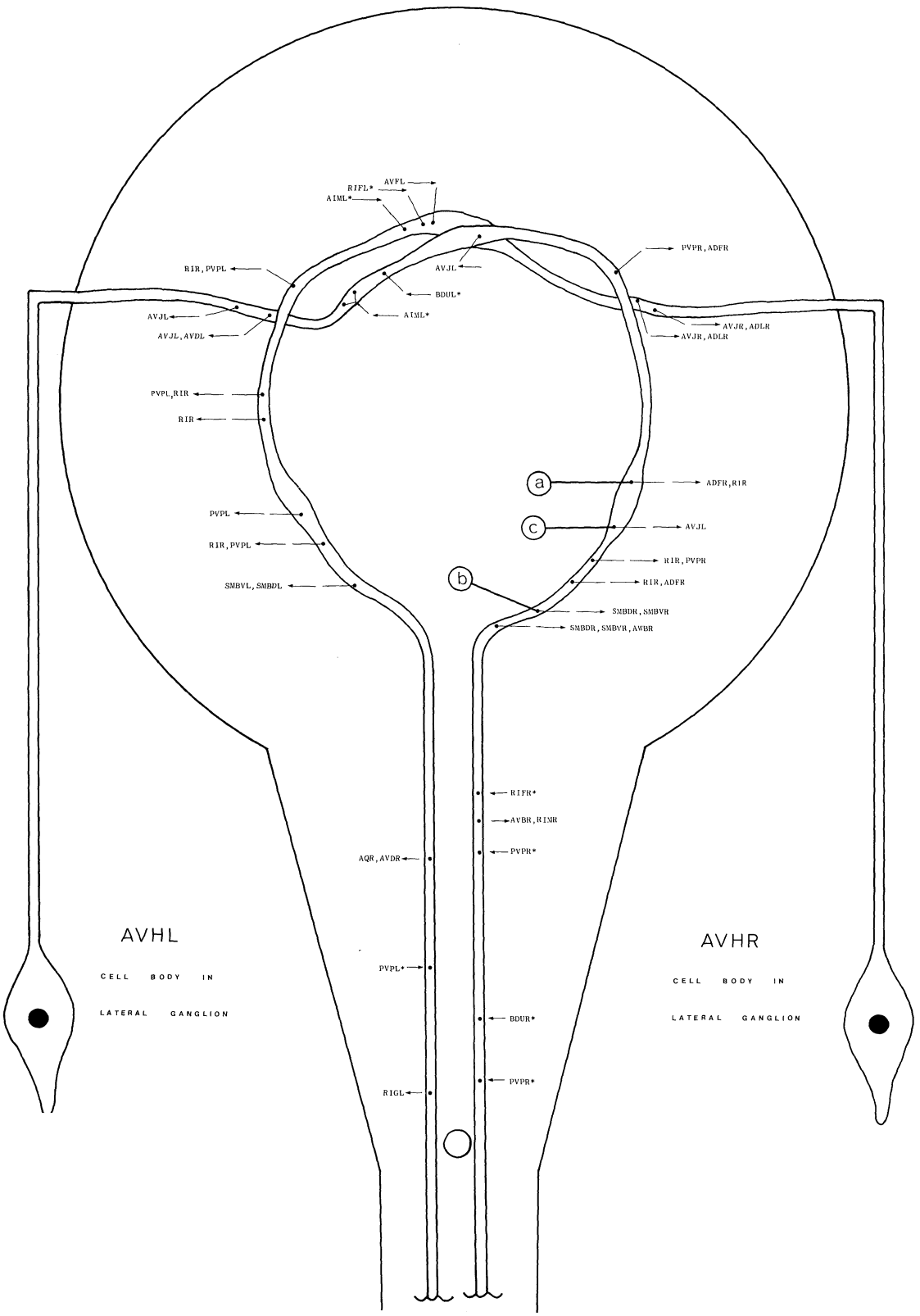
Member: AVG.

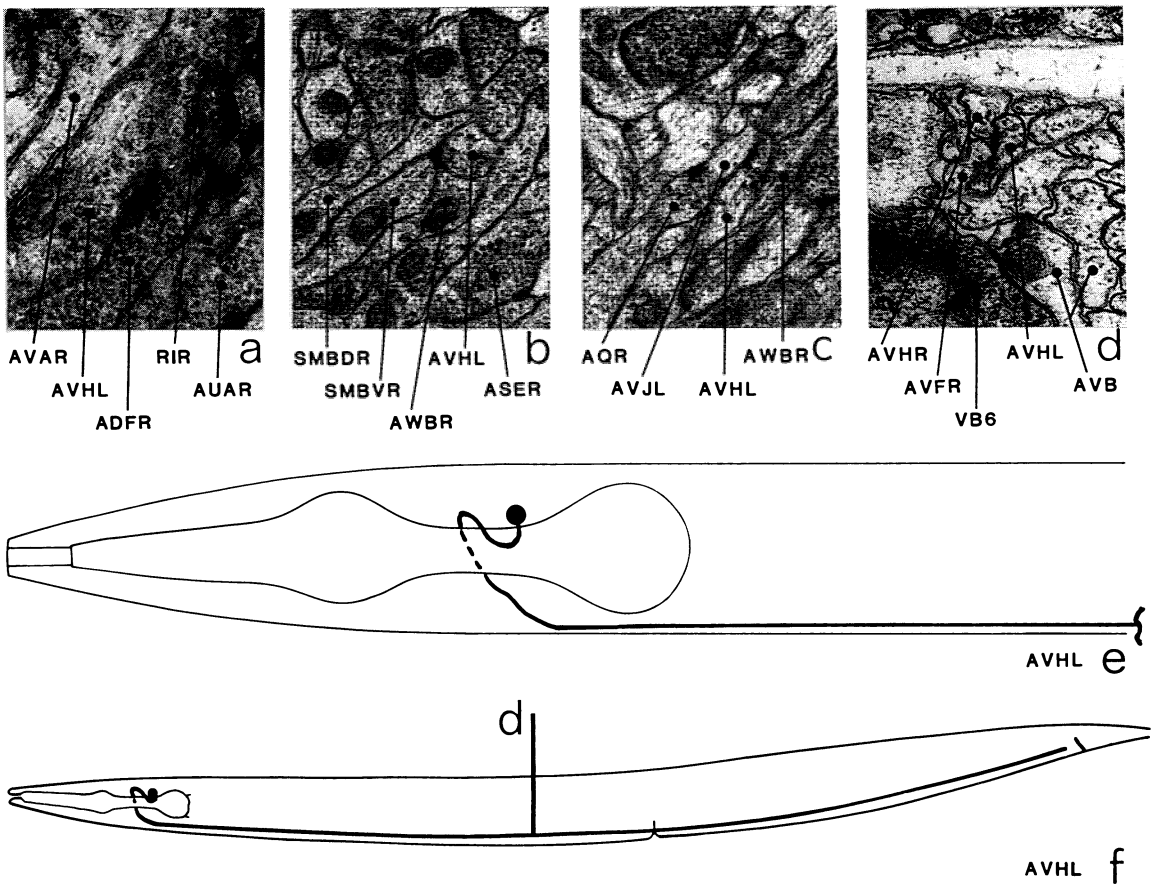
AVG is a single interneuron with its cell body situated in the retro-vesicular ganglion. A posteriorly directed, fairly large process leaves the cell body and runs in the dorsal region of the cord down to the pre-anal ganglion. Here it runs to the left of the anus and enters the dorso-rectal ganglion and from there runs down the dorsal hypodermal ridge to the tip of the tail. The disposition of the posterior extremities of this process suggest that it could be a sensory dendrite. There are a few scattered synapses in the ventral cord (e.g. d) the most prominent of which are some synapses to AVB (a). There are several synapses onto the basal lamina surrounding the nerve cord with no obvious postsynaptic partners (c). The most striking features of AVG are the gap junctions it makes with RIF in the retro-vesicular ganglion (b). A short anteriorly directed process from AVG often pokes into the cell bodies of one of the RIF neurons (b).

Magnifications: (a) ×25500, (b–d) ×17000.

AVG VENTRAL CORD SYNAPSES

partners	gap junctions	synapses from	synapses to and corecipients
AVB	—	—	3, AVJ
AVA	—	—	1, PVC, HSN
PHA	—	2+6 m	PVQ, DA8
AVE	—	—	AVE
AVF	—	1+1 m	1
VA11	—	—	1
AVD	—	—	1
DVB	—	—	1
HDC	—	—	1
DA8	—	—	PHA
PVQ	—	—	PHA
PVC	—	—	AVA
AVJ	—	—	AVB
AVL	—	—	PVP
PVP	—	—	AVL
HSN	—	—	AVA
PQR	—	1	—
RIF	2	—	—
PVN	—	1 m	1, AVA


RIFL*
AVFL
AIML*
PVPR, ADFR
RIR, PVPL
AVJL
BDUL*
AVJL
AIML*
AVJR, ADLR
AVJL, AVDL
AVJR, ADLR
PVPL, RIR
RIR
a
ADFR, RIR
PVPL
c
AVJL
RIR, PVPL
RIR, PVPR
b
SMBVL, SMBDL
RIR, ADFR
SMBDR, SMBVR
SMBDR, SMBVR, AVBR
RIFR*
AVBR, RIMR
AQR, AVDR
PVPR*
AVHL
CELL BODY IN
LATERAL GANGLION
AVHR
CELL BODY IN
LATERAL GANGLION
PVPL*
BDUR*
RIGL
PVPR*



AVH

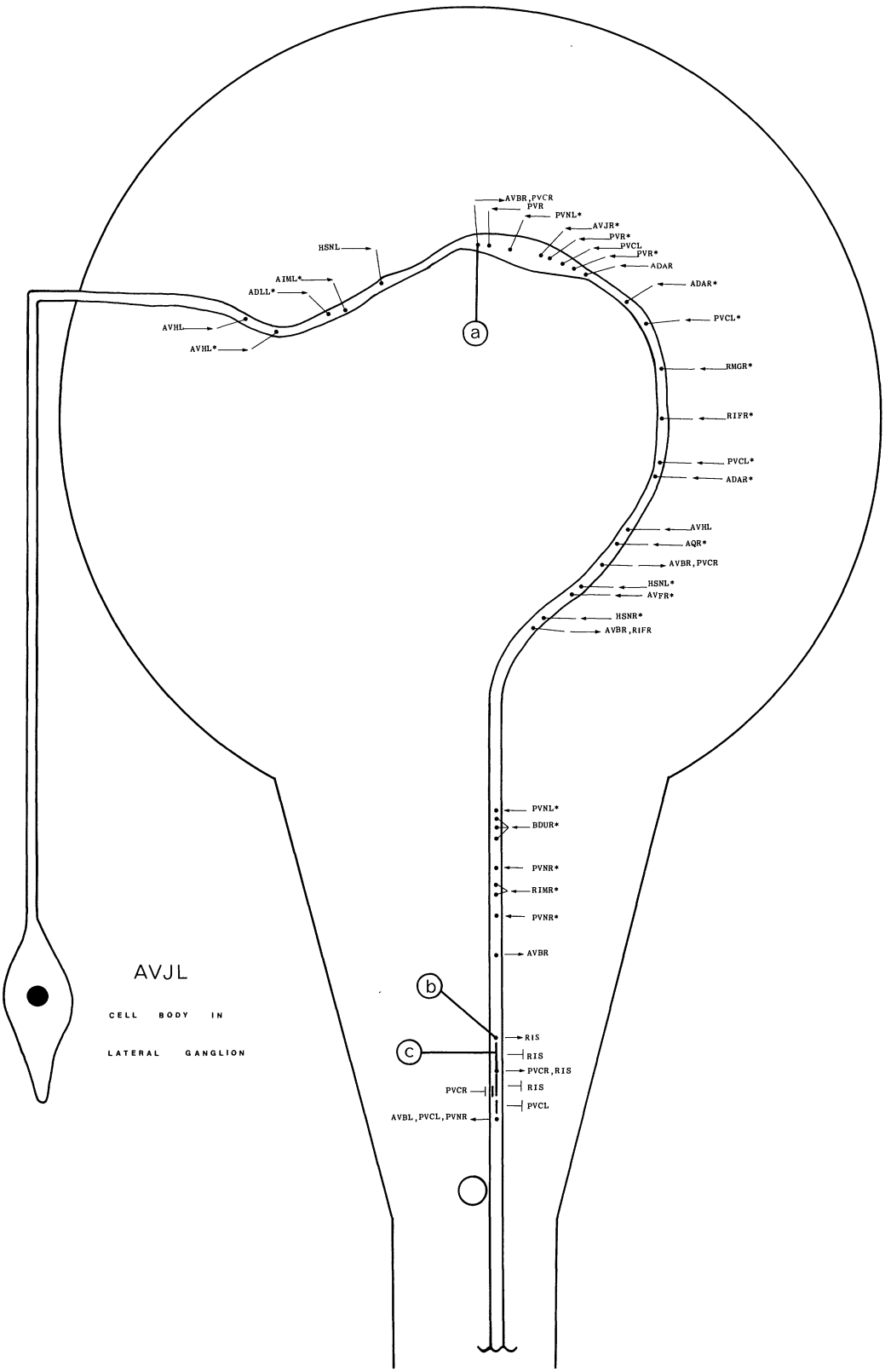
Members: AVHL, AVHR.

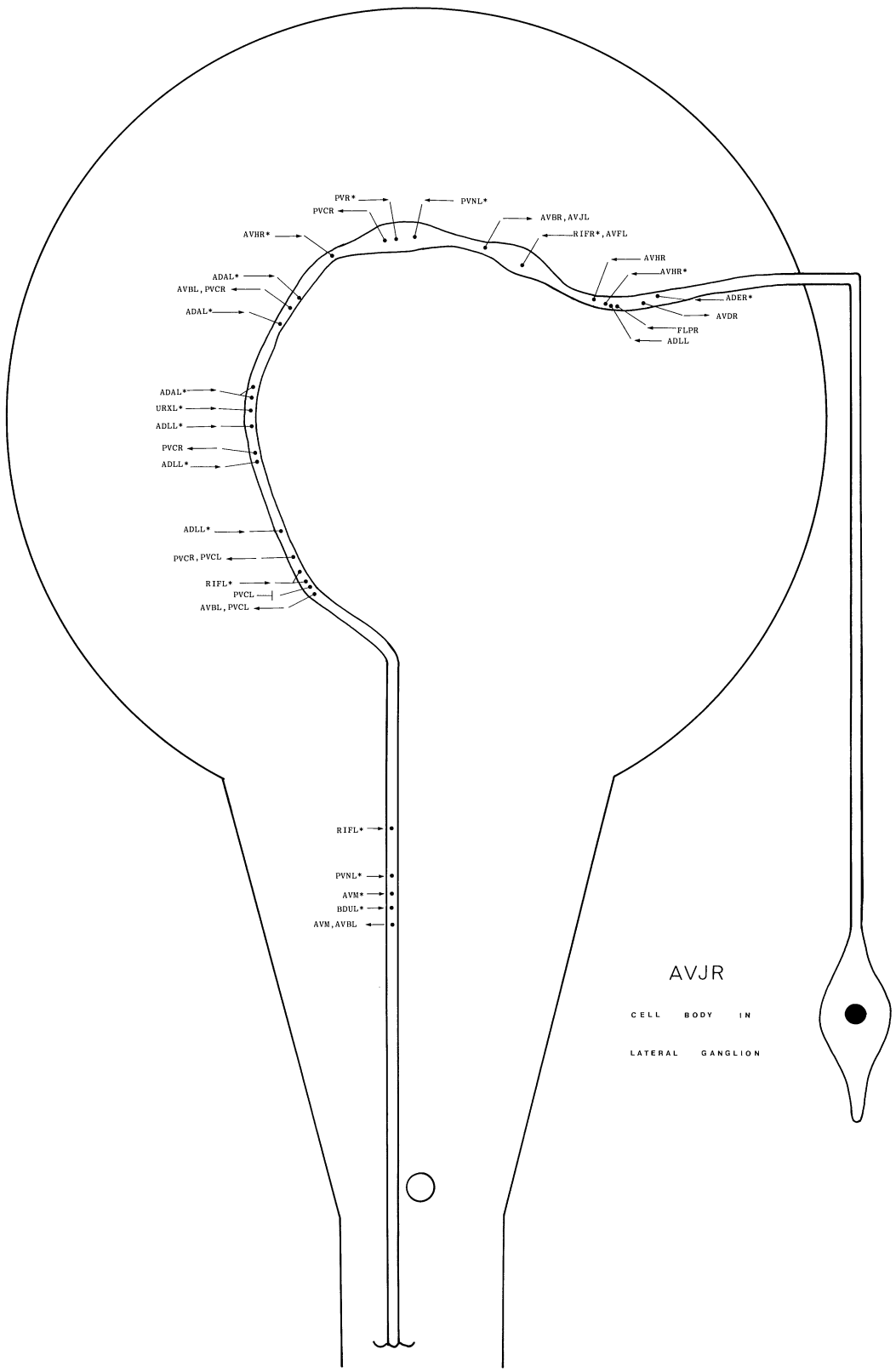
AVH is a pair of interneurons with cell bodies in the lateral ganglia. Processes from the cell bodies enter the nerve ring sub-dorsally and cross over to the contralateral side. They then travel ventrally round the ring, running near the middle of the neuropile, and leave it to enter the ventral cord. The processes of AVH run in the dorsal regions of the cord and end in the pre-anal ganglion. The chemical synapses made by AVH are rather small, with few synaptic vesicles. The main synaptic outputs are to AVJ (c), PVP, SMB (b), ADF (a) and RIR (a) in the nerve ring. In the ventral cord there are synapses to and from AVF (d, *c) as well as gap junctions to AVF and also a few synapses from PHA.

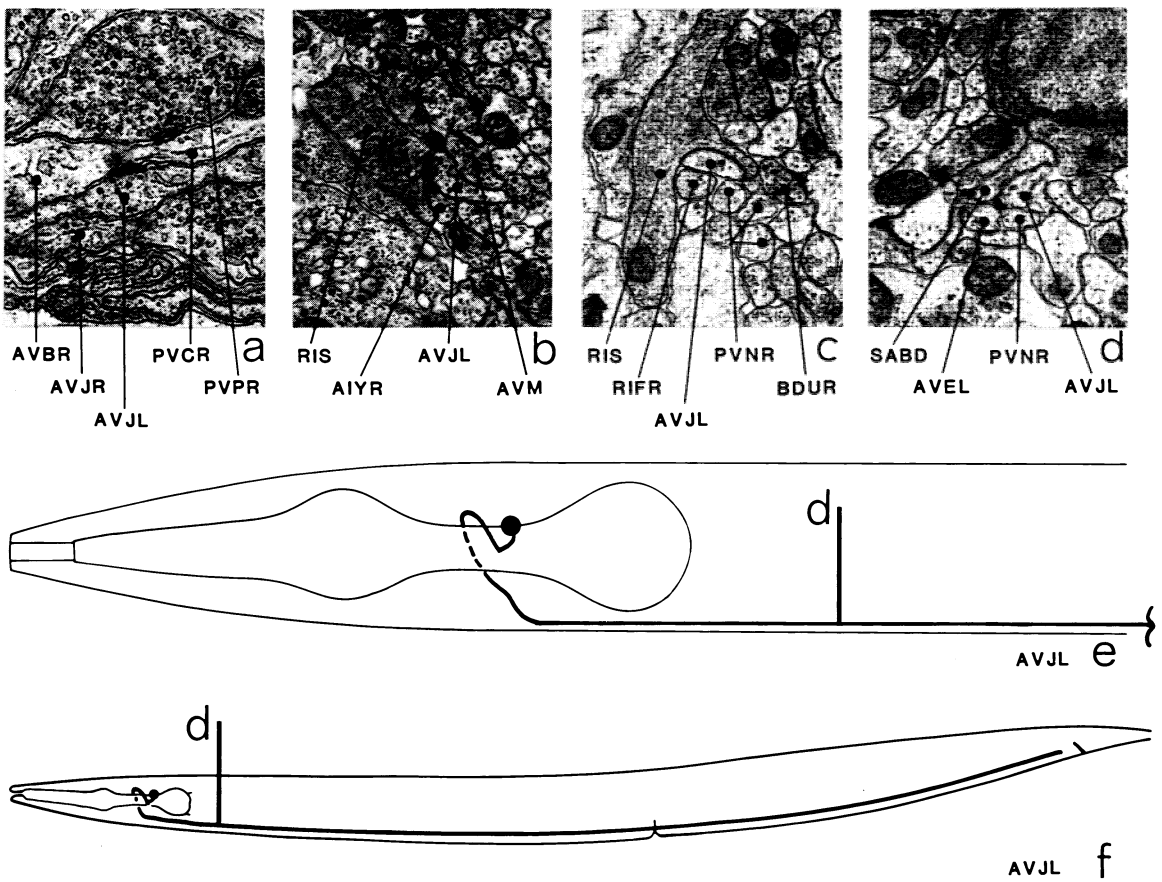
Magnifications: (a) ×25500, (b–d) ×17000.

AVH VENTRAL CORD SYNAPSES

partners	gap junctions	synapses from	synapses to and corecipients
AVF	8	3+5 m	2AVH, 2AVF, PVQ
PVQ	—	—	AVF, VD1
AVH	1	2 m	2AVF
VD1	—	—	PVQ
AVJ	—	1 m	AVB
AVB	—	—	AVJ
PHB	1	—	—
PHA	—	3 m	—
PVP	—	1 m	—
AVA	—	1 m	—
PHC	—	1 m	—
VC4	—	1 m	—


AVBR,PVCR
PVR
PVNL*
AVJR*
PVR*
PVCL
PVR*
ADAR
ADAR*
PVCL*
RMGR*
RIFR*
PVCL*
ADAR*
AVHL
AQR*
AVBR,PVCR
HSNL*
AVFR*
HSNR*
AVBR,RIFR
HSNL
AIML*
ADLL*
AVHL
AVHL*
a
PVNL*
BDUR*
PVNR*
RIMR*
PVNR*
AVBR
b
c
RIS
RIS
PVCR,RIS
RIS
PVCL
PVCR
AVBL,PVCL,PVNR
AVJL
CELL BODY IN
LATERAL GANGLION


PVR*
PVCR
PVNL*
AVBR, AVJL
AVHR*
RIFR*, AVFL
AVHR
AVHR*
ADAL*
AVBL, PVCR
ADER*
ADAL*
AVDR
FLPR
ADLL
ADAL*
URXL*
ADLL*
PVCR
ADLL*
ADLL*
PVCR, PVCL
RIFL*
PVCL
AVBL, PVCL
RIFL*
PVNL*
AVM*
BDUL*
AVM, AVBL
AVJR
CELL BODY IN
LATERAL GANGLION



AVJ

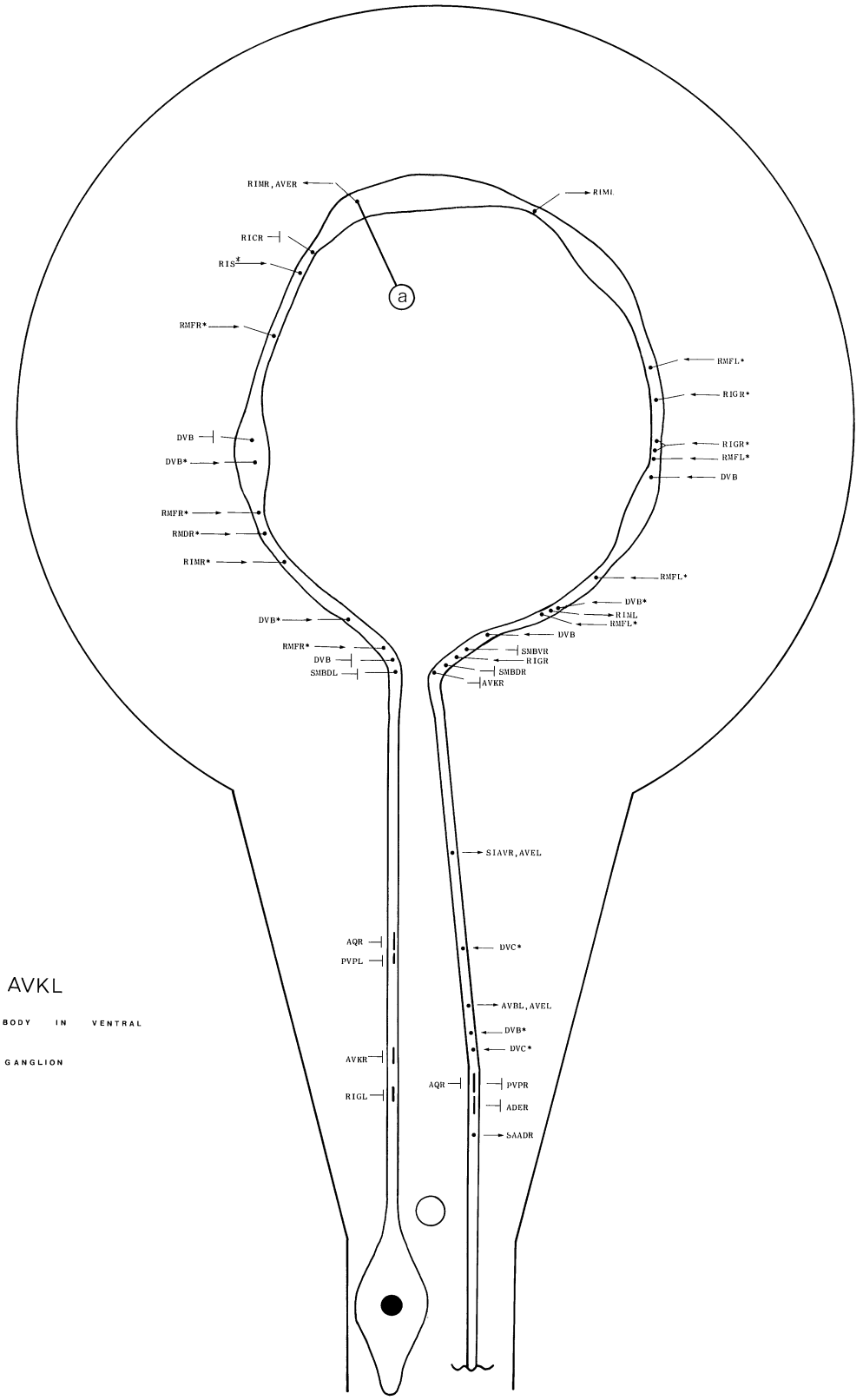
Members: AVJL, AVJR.

AVJ is a pair of interneurons with cell bodies in the lateral ganglion. Processes from the cell bodies enter the ring sub-dorsally and then run round it to the contralateral side near the centre of the neuropile, in close association with the processes of AVB. The processes of AVJ then leave the ring ventrally and traverse the length of the ventral cord, running immediately adjacent and dorsal to the processes of AVB and eventually petering out in the pre-anal ganglion. There are few synapses from AVJ; and those that are present are rather small and have some dark-cored vesicles. The main synaptic output is directed to PVC (a), AVB (a) and RIS (b) in the nerve ring, and to AVE (d) and AVD in the ventral cord. The main synaptic input is from BDU (*a), AVH (*c), ADA (*c), ADL, PVR (*b), RIF (*b), HSN and PVC in the nerve ring and PVN (*b) and AVF in the nerve ring and ventral cord. AVJ has a prominent gap junction with RIS in the neuropile of the ventral ganglion (c); RIS sends a short branch down into the neuropile of the cord in this region. There are gap junctions to PVC (*h) in the nerve ring and to AVD, PVC and itself in the ventral cord.

Magnifications: (a) ×25500, (b–d) ×17000.

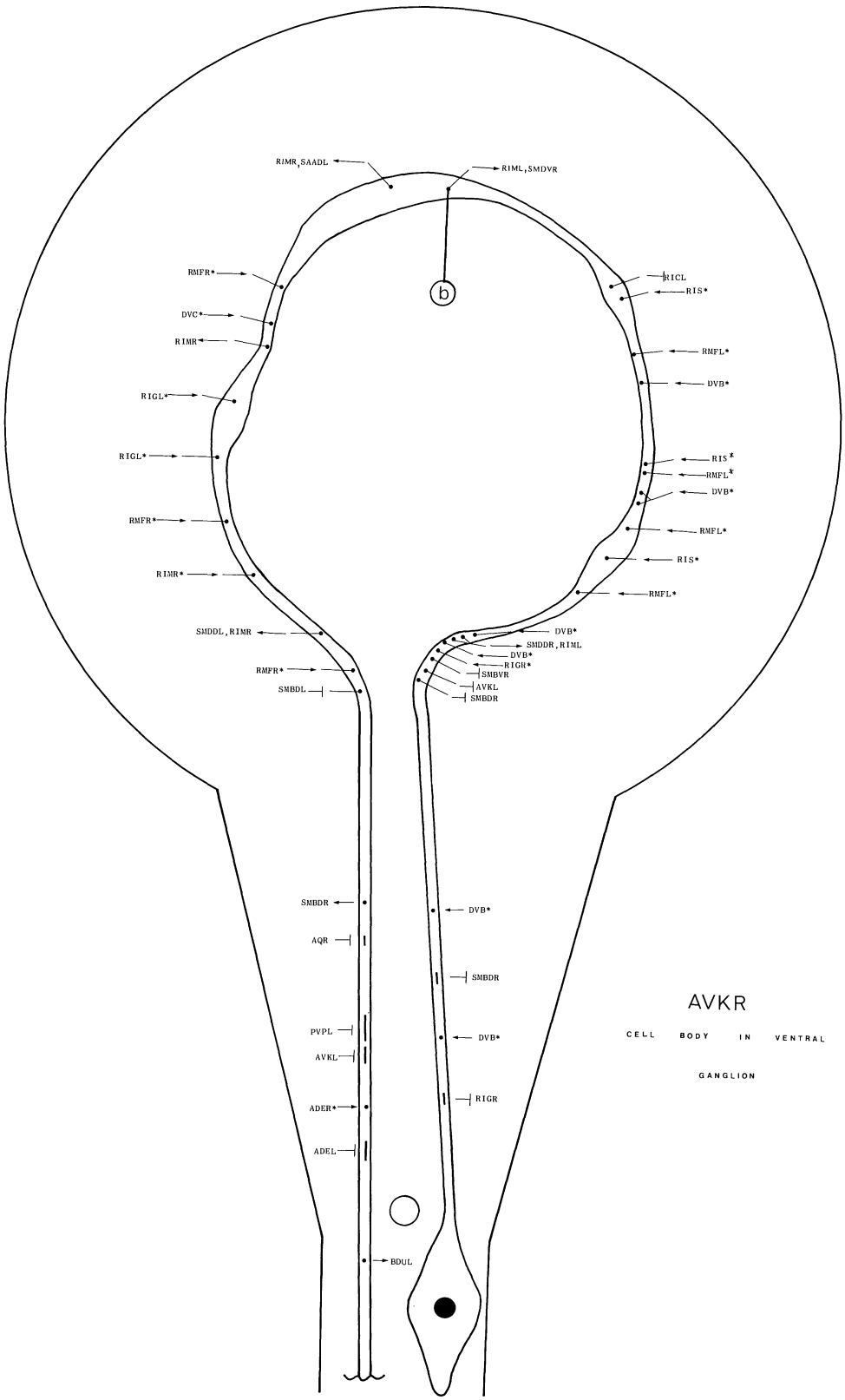
AVJ VENTRAL CORD SYNAPSES

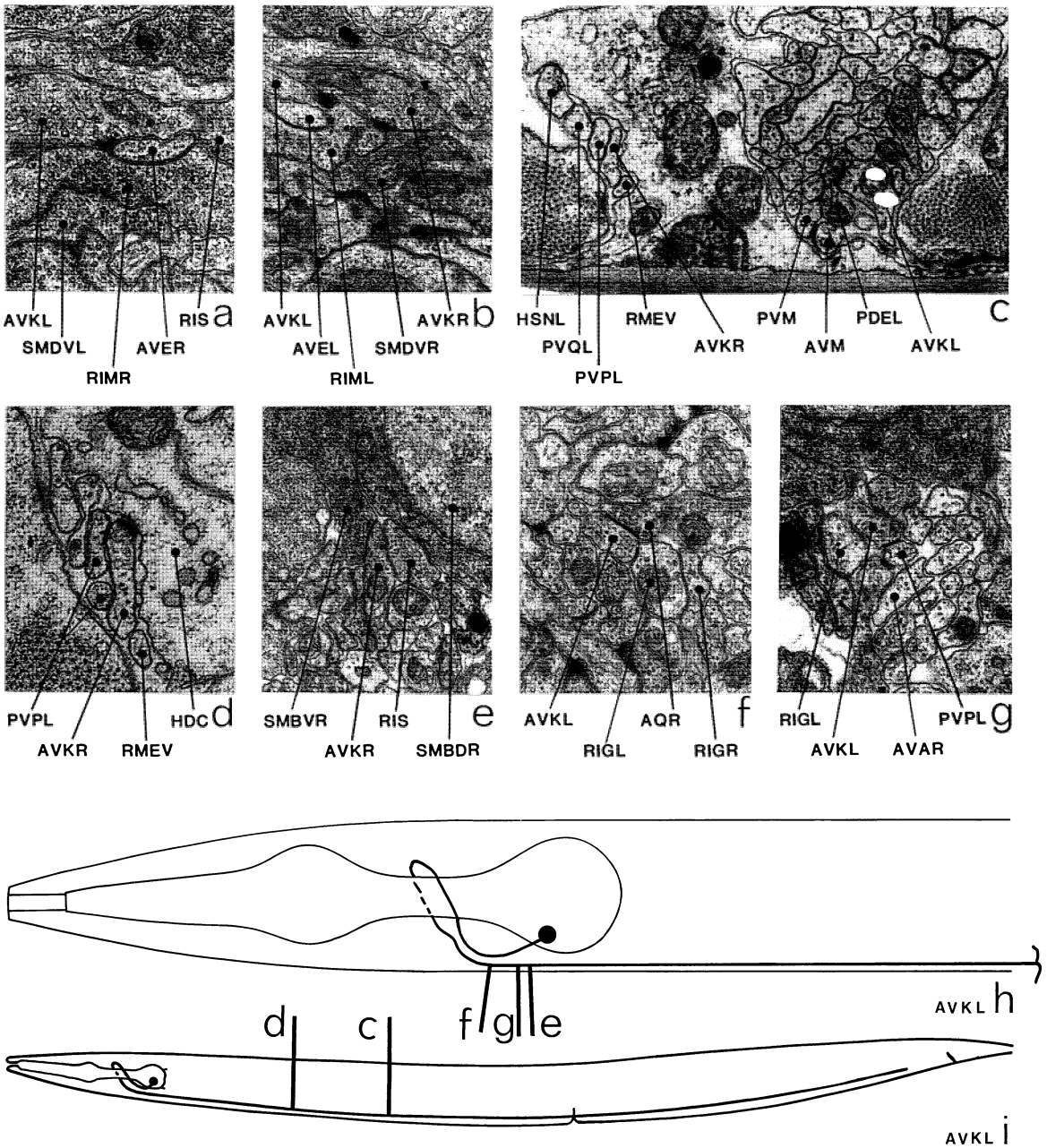
partners	gap junctions	synapses from	synapses to and corecipients
AVE	—	—	2, 2AVD
AVD	2	—	2AVE, AVA
AVA	—	—	AVD, SABV
HSN	—	—	1
PVN	—	2+4 m	1
AVB	—	—	1
PVQ	—	—	1
AVF	—	1+2 m	AVH
AVH	—	1 m	AVF
SABV	—	—	AVA
LUA	—	2 m	—
PVW	—	1 m	—
AVG	—	1 m	—
AVJ	4	—	—
PVC	2	—	—



AVKL

CELL BODY IN VENTRAL GANGLION


RIMR,SAADL
RIML,SMDVR
RMFR*
DVC*
RIMR
RIGL*
RIGL*
RMFR*
RIMR*
SMDDL,RIMR
RMFR*
SMBDL
RICL
RIS*
RMFL*
DVB*
RIS*
RMFL*
DVB*
RMFL*
RIS*
RMFL*
DVB*
SMDDR,RIML
DVB*
RIGR*
SMBVR
AVKL
SMBDR
SMBDR
AQR
PVPL
AVKL
ADER*
ADEL
BDUL
DVB*
SMBDR
DVB*
RIGR
AVKR
CELL BODY IN VENTRAL GANGLION



AVK

Members: AVKL, AVKR.

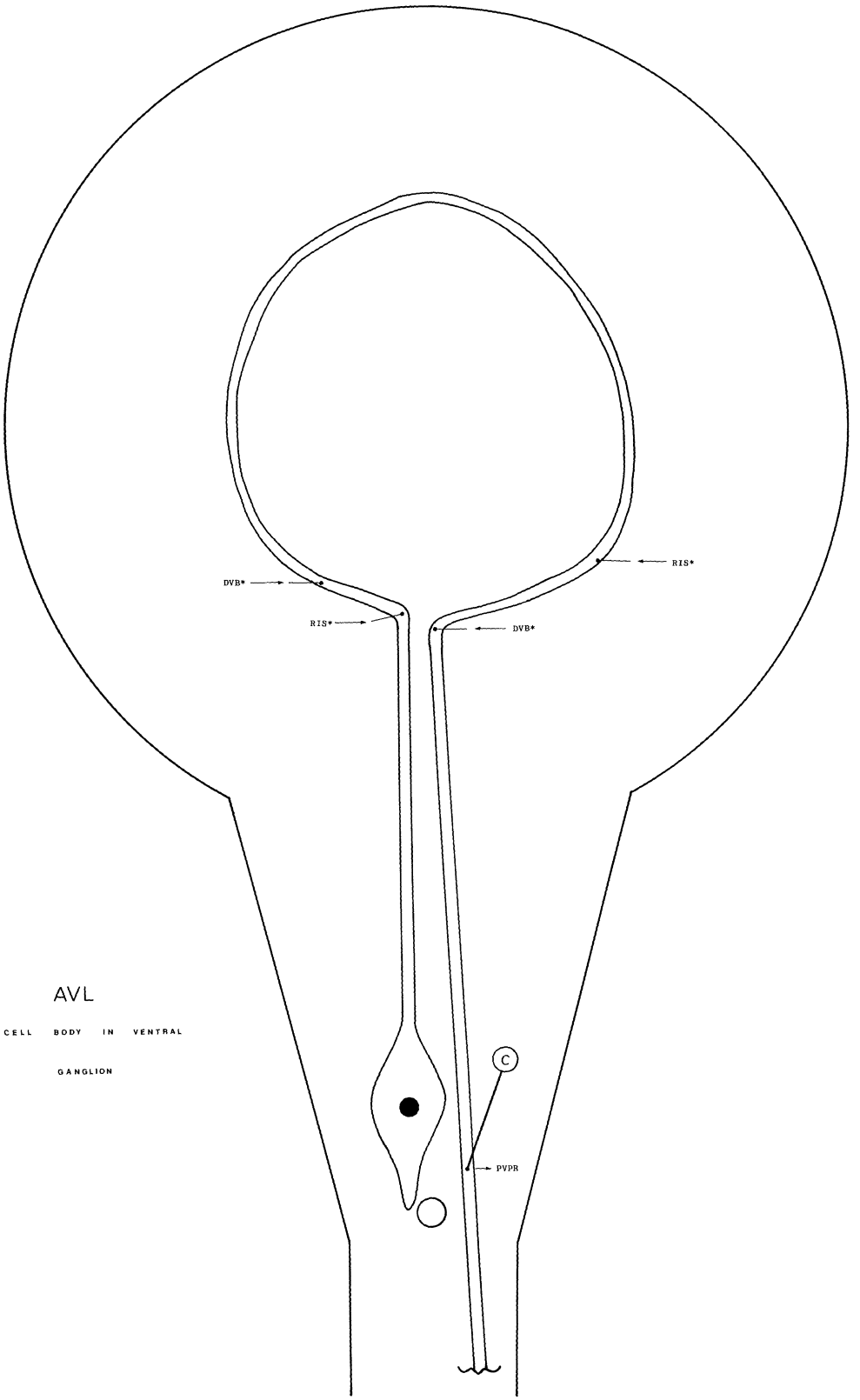
AVK is a pair of interneurons with cell bodies situated in the ventral ganglion behind the excretory duct. Anteriorly directed processes leave the cell bodies and run near the centre of the neuropile. They move ventrally as the nerve ring is approached and then run right round the ring near the outside surface, emerging on the contralateral side adjacent to the processes of their partners. At all times, in the regions of overlap, the processes of AVK run in close association with those of their contralateral partners. The processes travel down the length of the ventral cord running in the ventral regions of the process bundles on either side of the

hypodermal ridge (c), eventually petering out in the pre-anal ganglion. The main synaptic output in the nerve ring is on the dorsal side and is directed to RIM (a, b), AVE (a) and SMD (b). Synapses are received mainly from DVB (*b), RMF (*e) and RIG (*f). AVK has gap junctions to several partners, namely itself, SMB (e), AQR (f), DVB, PVP (g), RIC, ADE (*d) and RIG. In the ventral cord there are a few small synapses to hypodermal cells (HDC) (d) and PDE (c). AVK receives synapses from PDE (*b) and PVM (*f). There are also some rather marginal gap junctions to PVP.

Magnifications: (a, d, f, g) ×25500, (b, c, e) ×17000.

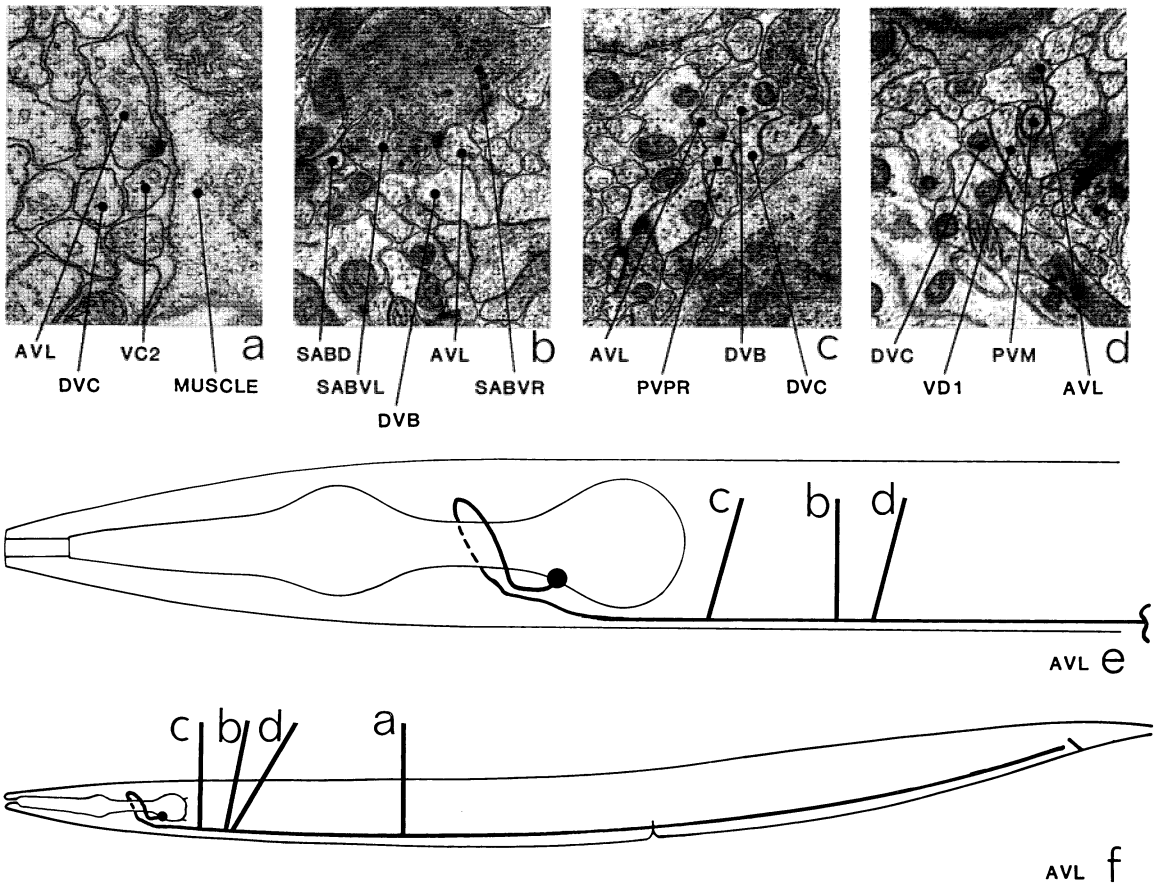
AVK VENTRAL CORD SYNAPSES

partners	gap junctions	synapses from	synapses to and corecipients
HDC	—	—	5, AVM
PDE	—	1+10 m	2, 2PDE
PVM	—	7+4 m	1
DVA	—	—	1
PVQ	—	1	1
AVM	—	—	HDC
PVP	5	—	—



AVL

CELL BODY IN VENTRAL GANGLION



AVL

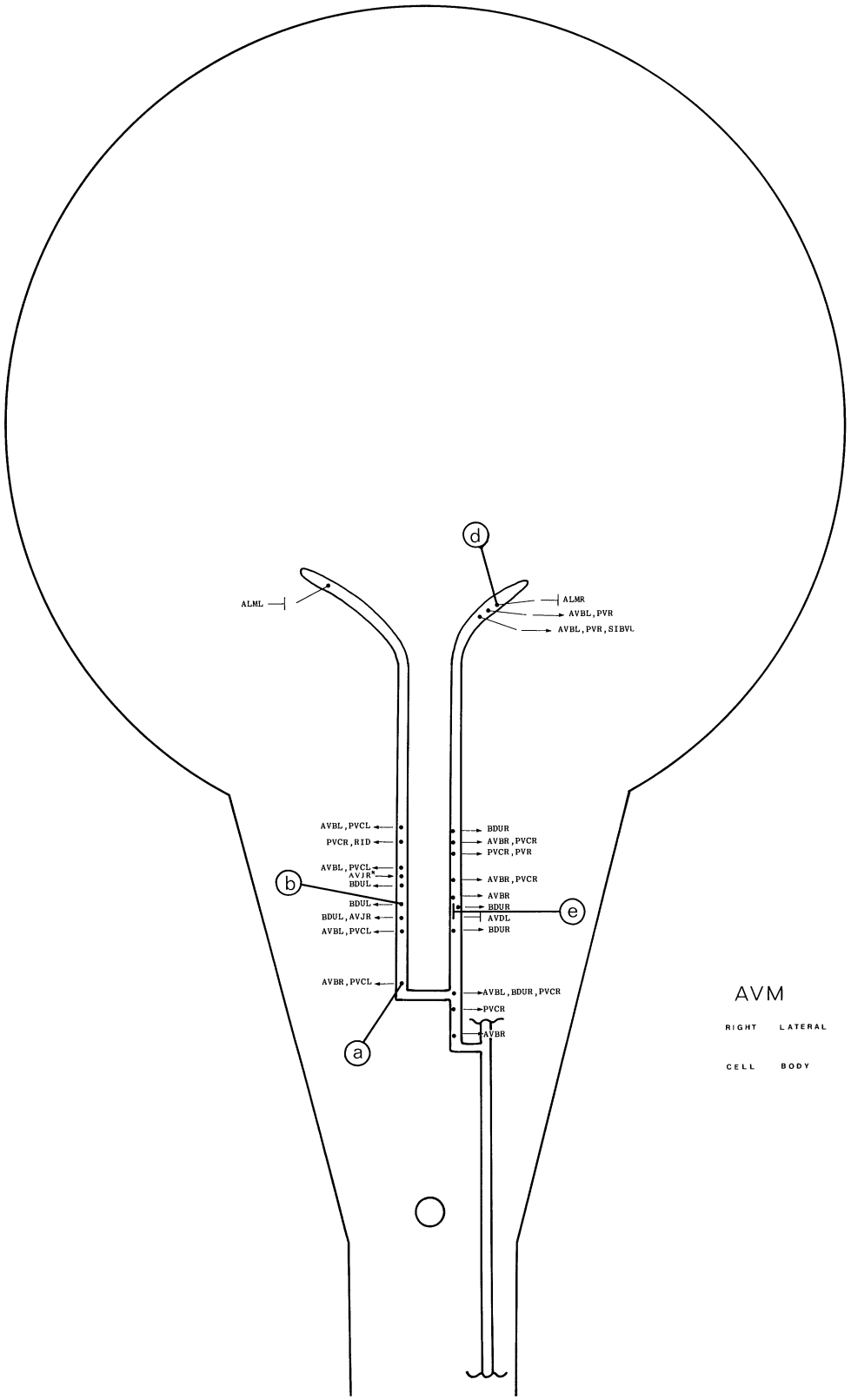
Member: AVL.

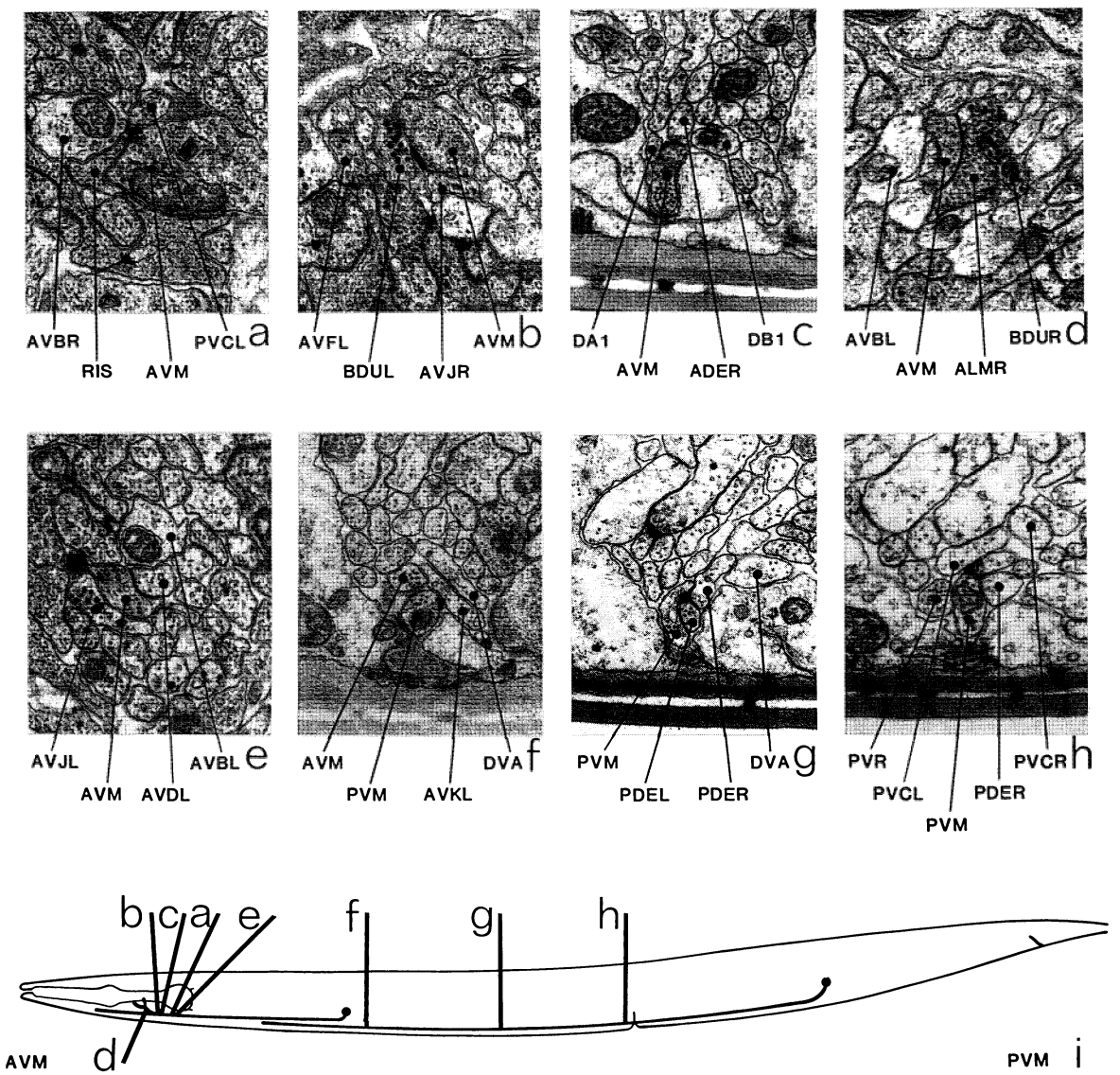
AVL is a motoneuron/interneuron with its cell body situated in the ventral ganglion. An anteriorly directed process runs in the mid-line on the dorsal surface of the neuropile of the ventral ganglion. It enters the ring on the left and makes a complete circuit running near the outside surface and the anterior face. It then re-enters the neuropile of the ventral ganglion and runs posteriorly down the length of the ventral cord running in the ventral regions of the process bundle. AVL has few synaptic connections in the nerve ring. In the ventral cord the synapses are rather small and are onto muscles (a), SAB (b) and VD12. Synapses are received from DVB and PVP (*e). There is a gap junction to PVM (d), DVB and several rather marginal gap junctions to DVC.

Magnifications: (a) 25500, (b–d) ×17000.

AVL VENTRAL CORD SYNAPSES

partners	gap junctions	synapses from	synapses to and corecipients
SABV	—	—	4SABD, 2SABV, AVE
NMJ	—	—	6
SABD	—	—	1, 4SABV
VD12	—	—	2DD6, PVW
DD6	—	—	2VD12
HSN	—	1	—
PVW	—	—	VD12
AVE	—	—	SABV
AS1	—	—	AVF
AVF	—	—	AS1
DA2	—	—	1
DD1	—	—	1
DVB	1	2+3 m	—
PVP	—	1+3 m	—
PVN	—	2 m	—
VC1	—	1 m	—
VC3	—	1 m	—
AVB	—	1	—
PVC	—	1	—
PVQ	—	1	—
AVF	—	1 m	—
AVG	—	1 m	—
DVC	9	—	—
PVM	1	—	—


ALML
ALMR
AVBL, PVR
AVBL, PVR, SIBVL
d
AVBL, PVCL
PVCR, RID
AVBL, PVCL
AVJR
BDUL
BDUL
BDUL, AVJR
AVBL, PVCL
b
AVBR, PVCL
a
BDUR
AVBR, PVCR
PVCR, PVR
AVBR, PVCR
AVBR
BDUR
AVDL
BDUR
e
AVBL, BDUR, PVCR
PVCR
AVBR
AVM
RIGHT LATERAL
CELL BODY



AVM AND PVM

Members: AVM, PVM.

AVM and PVM, although given separate class names, have been grouped together because of their many common features. Both are known to be touch receptors (Chalfie & Sulston 1981) and share with ALM and PLM the large microtubules that are present on the regions of their processes which are adjacent to the cuticle (Chalfie & Thomson 1982). The cell body of PVM is situated laterally, on the left-hand side of the posterior half of the body (i). A process from the cell body enters the ventral cord via a commissure and runs anteriorly along it in an extreme ventral location adjacent to the cuticle. It terminates in the anterior body after making some *en passant* synapses, mainly to AVK (f), PDE (g), PVC (h) and PVR. There are gap junctions to PDE and AVL (*d). The cell body of AVM is situated laterally, on the right-hand side of the anterior half of the body (i). A process leaves the cell body and enters the ventral cord via a commissure, and then runs anteriorly along it in an extreme ventral location, alongside

the process of PVM. It terminates at a position just beyond the first bulb of the pharynx. A branch leaves the main process and enters the neuropile of the ventral ganglion. This splits and the branches enter the nerve ring at each side, but terminate, while still in the ventral half of the ring, with gap junctions to the ends of the processes of ALM. Nearly all the synapses of AVM are on these branches. The main synaptic output is to AVB (a), PVC (a), BDU (b), ADE (c) and PVR. AVM has gap junctions with ALM (d) and AVD (e).

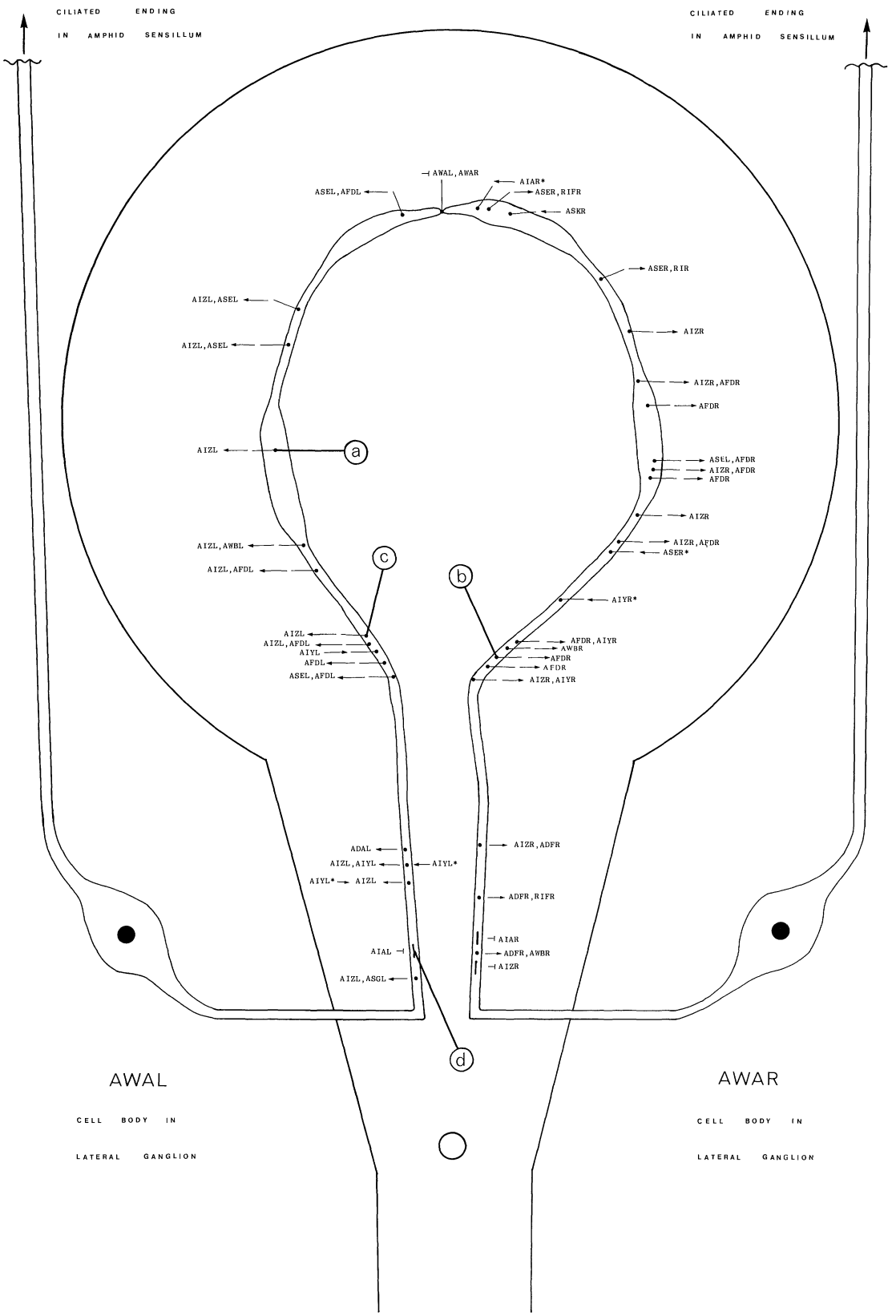
Magnifications: (a, b, d, e) ×25500, (c, f–h) ×17000.

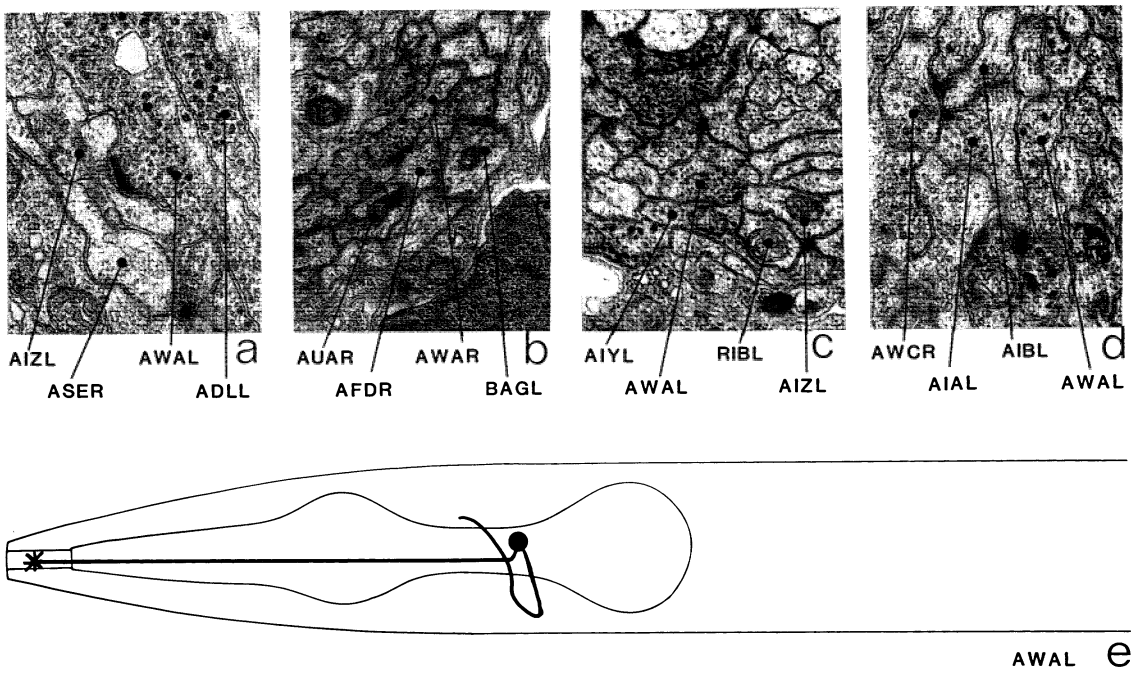
AVM VENTRAL CORD SYNAPSES

partners	gap junctions	synapses from	synapses to and corecipients
ADE	—	—	1, DA1
DA1	—	—	ADE
AVD	1	—	—
PVM	—	1 m	—
AVK	—	1 m	—

PVM VENTRAL CORD SYNAPSES

partners	gap junctions	synapses from	synapses to and corecipients
AVK	—	1	7, AVM, PVR, PDE, DVA
PDE	2	2 m	3, 5PDE, AVK, PVR
DVA	—	—	1, AVK, HDC
PVC	—	—	2
PVR	—	—	PDE, AVK
AVM	—	—	AVK
HDC	—	—	DVA
AVL	1	—	—


CILIATED ENDING IN AMPHID SENSILLUM
CILIATED ENDING IN AMPHID SENSILLUM
AWAL, AWAR
AIAR*
ASEL, AFDL
ASER, RIFR
ASKR
ASER, RIR
AIZL, ASEL
AIZR
AIZL, ASEL
AIZR, AFDR
AFDR
AIZL
a
ASEL, AFDR
AIZR, AFDR
AFDR
AIZR
AIZL, AWBL
AIZR, AFDR
ASER*
AIZL, AFDL
c
b
AIYR*
AIZL
AIZL, AFDL
AIYL
AFDL
ASEL, AFDL
AFDR, AIYR
AWBR
AFDR
AFDR
AIZR, AIYR
ADAL
AIZR, ADFR
AIZL, AIYL
AIYL*
AIYL*
AIZL
ADFR, RIFR
AIAL
AIAR
ADFR, AWBR
AIZR
AIZL, ASGL
d
AWAL
CELL BODY IN LATERAL GANGLION
AWAR
CELL BODY IN LATERAL GANGLION

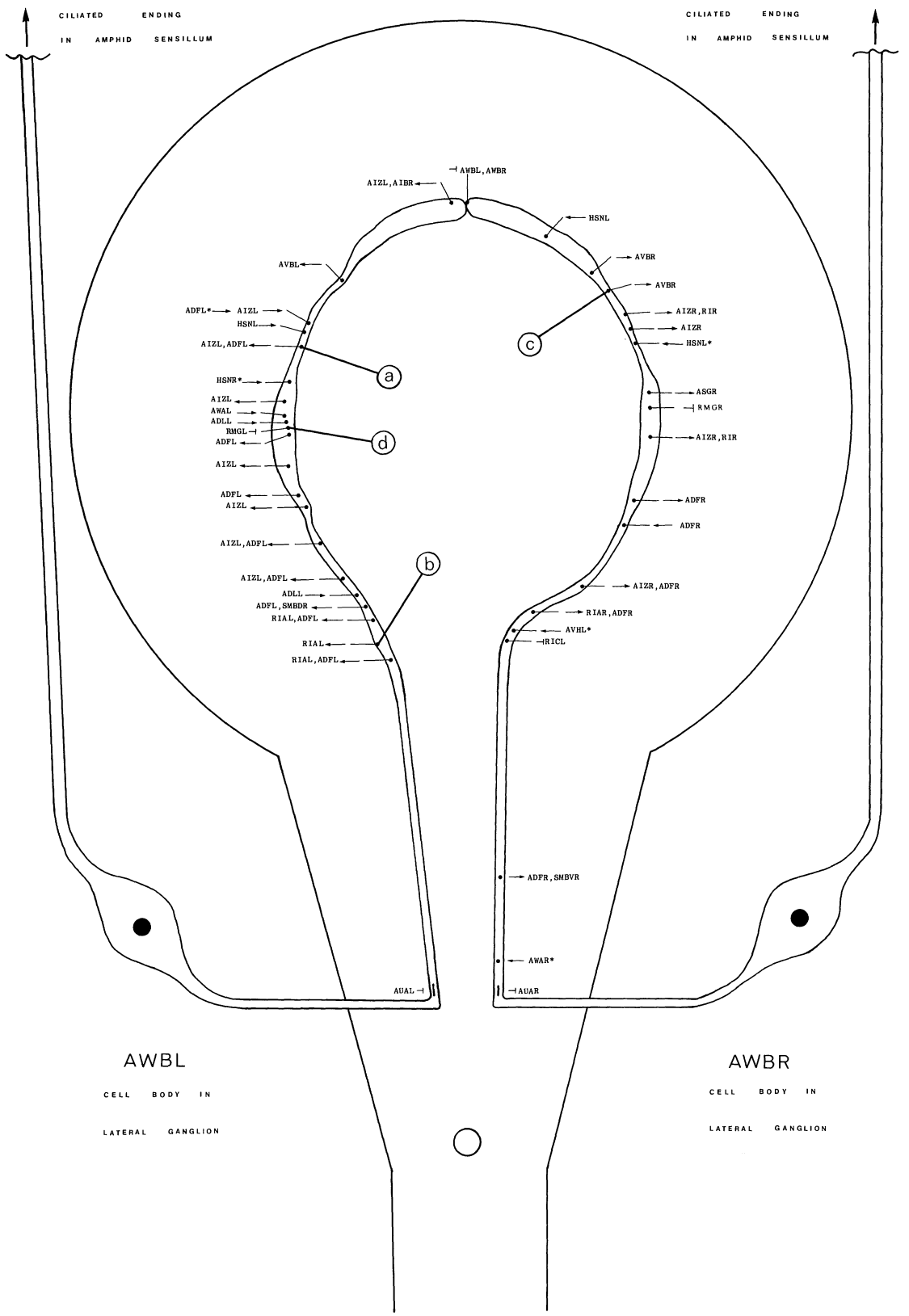


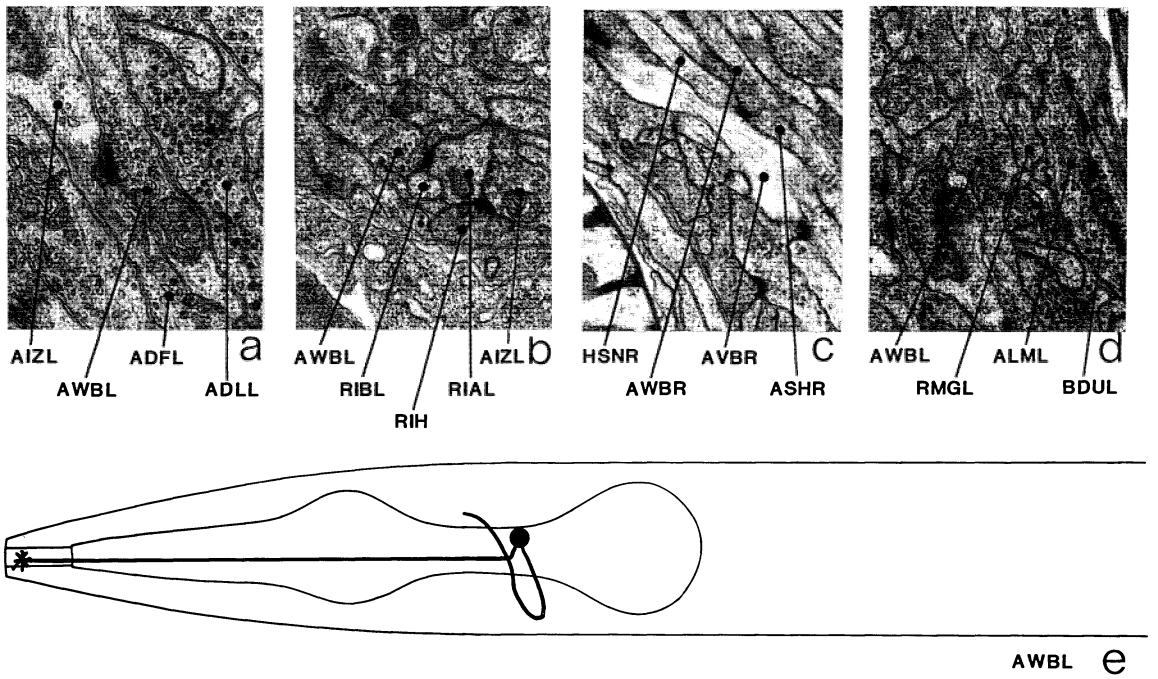
AWA

Members: AWAL, AWAR.

AWA is a set of two ciliated neurons that are associated with the sheath cells of the amphid sensilla (figure 1). The cell bodies of AWA are situated in the lateral ganglia and send processes into the ventral cord via the amphid commissures. The processes run anteriorly in the ventral cord near the ventral surface of the cord and project into the nerve ring, where they run near the middle of the neuropile. The processes of AWA meet and terminate at the dorsal mid-line with a gap junction. The predominant synaptic output is to AIZ (a); there are also some synapses to AFD (b), AIY (c) and ASE usually in dyadic combination with AIZ. A few of the synaptic vesicles are dark cored (a). There are gap junctions to AIA (d).

Magnifications: (a, d) ×25500, (b, c) ×12750.


CILIATED ENDING IN AMPHID SENSILLUM
CILIATED ENDING IN AMPHID SENSILLUM
AWBL, AWBR
AIZL, AIBR
HSNL
AVBL
AVBR
AVBR
ADFL* AIZL
HSNL
AIZL, ADFL
AIZR, RIR
AIZR
HSNL*
c
a
HSNR*
AIZL
AWAL
ADLL
RMGL
ADFL
d
ASGR
RMGR
AIZR, RIR
AIZL
ADFL
AIZL
ADFR
ADFR
AIZL, ADFL
b
AIZL, ADFL
ADLL
ADFL, SMBDR
RIAL, ADFL
RIAL
RIAL, ADFL
AIZR, ADFR
RIAR, ADFR
AVHL*
RICL
ADFR, SMBVR
AWAR*
AUAL
AUAR
AWBL
CELL BODY IN LATERAL GANGLION
AWBR
CELL BODY IN LATERAL GANGLION

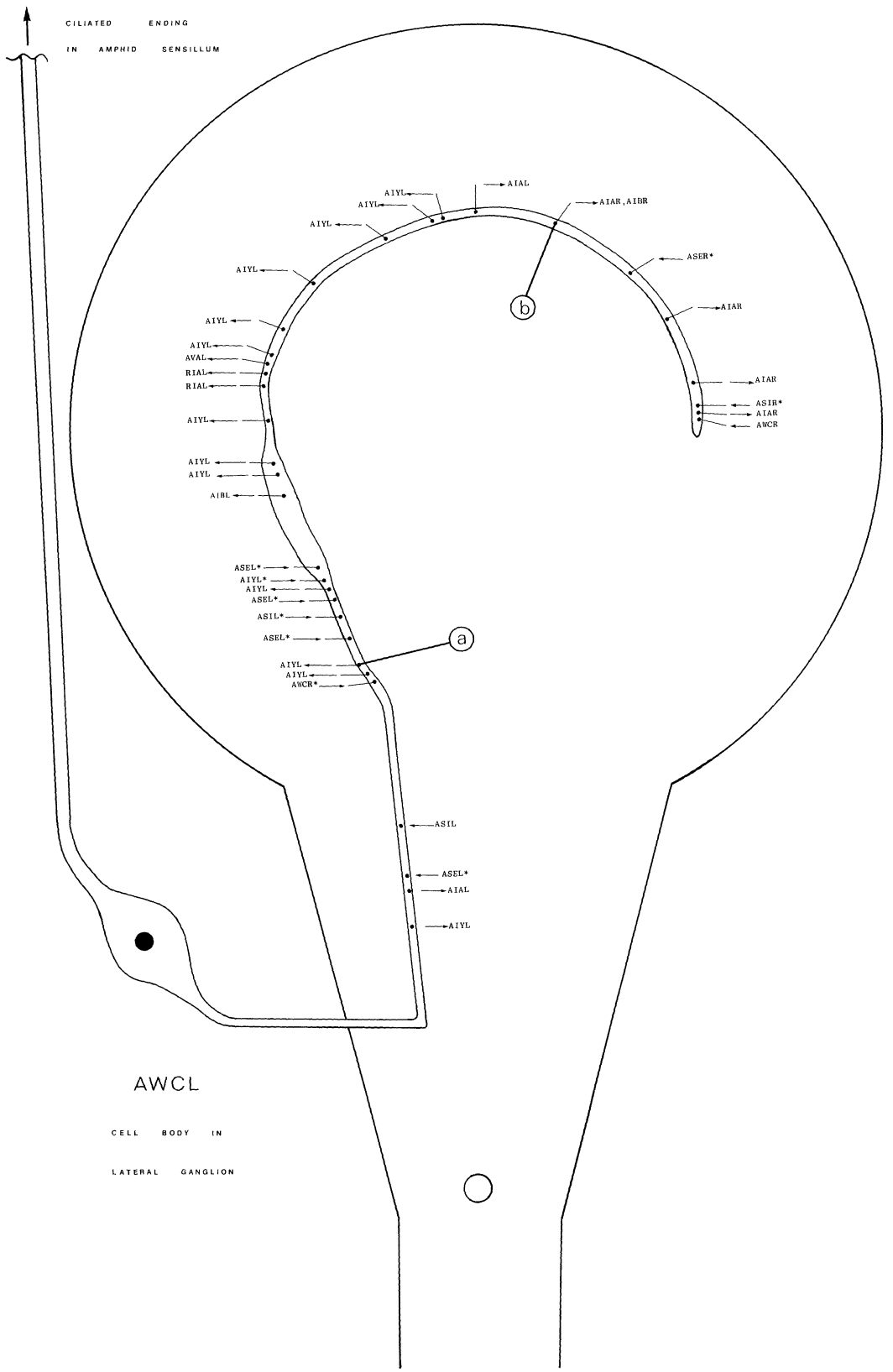


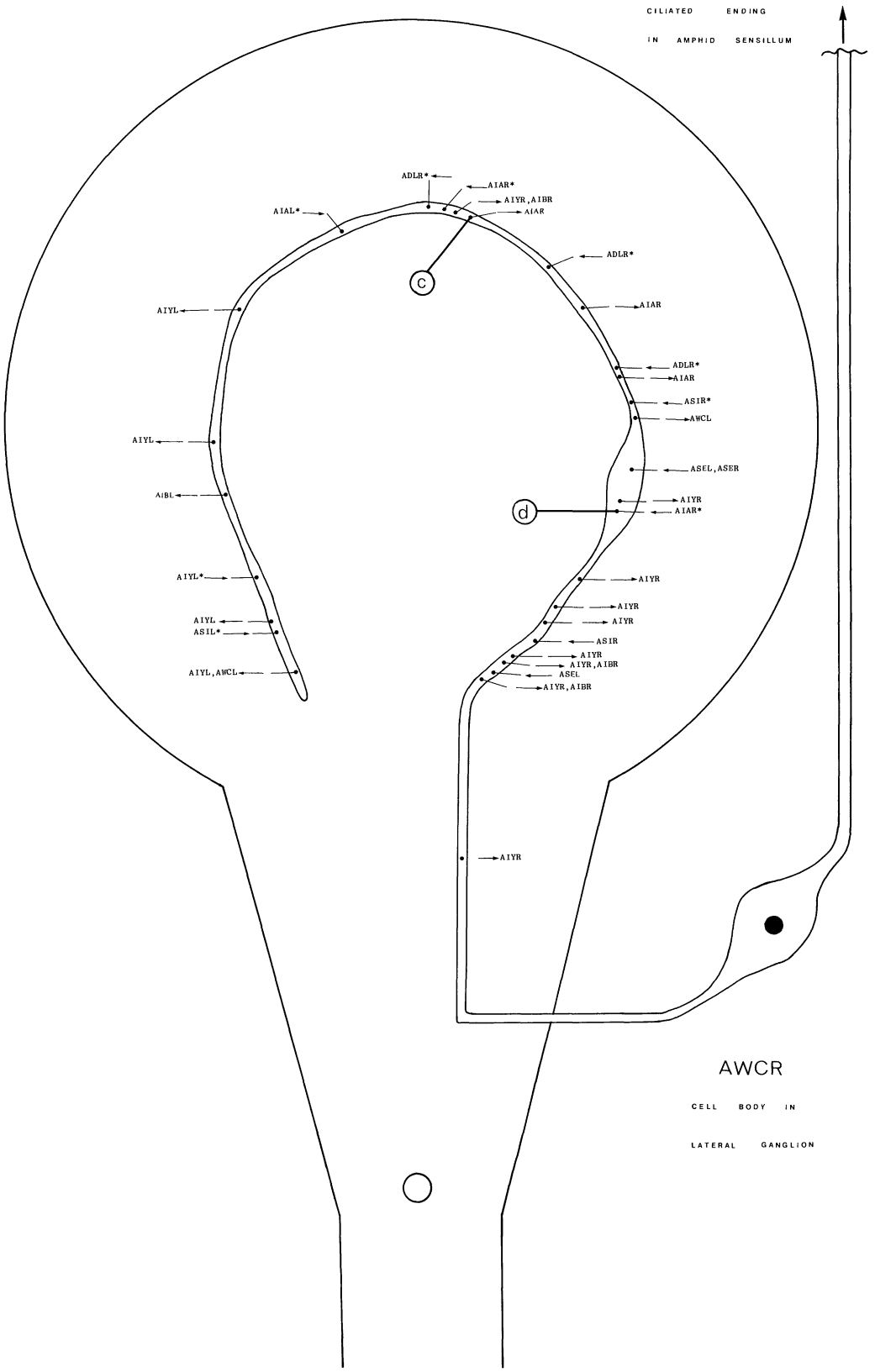
AWB

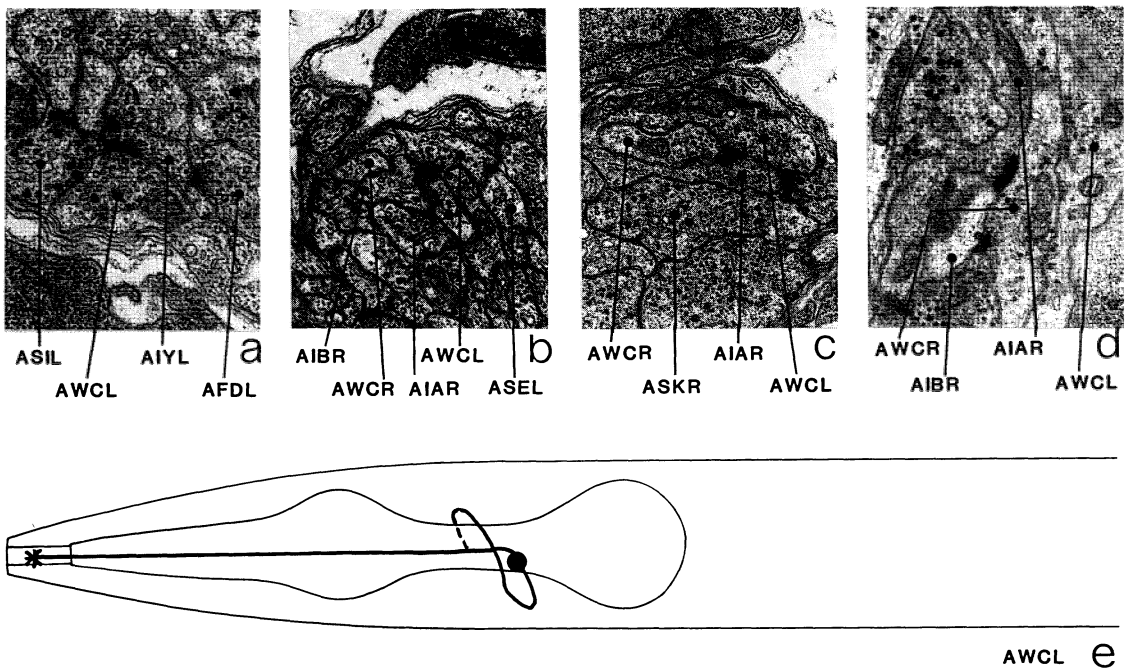
Members: AWBL, AWBR.

AWB is a set of two ciliated neurons with flattened, sheet-like endings that are associated with the sheath cells of the amphid sensilla (figure 1). Cell bodies are situated in the lateral ganglion and send processes into the ventral cord via the amphid commissures. The processes run anteriorly in the ventral part of the nerve cord and project into the nerve ring, where they run near the middle of the neuropile. They meet and stop at the dorsal mid-line with a gap junction. The processes are fairly small and none of the synapses is very large. The main synaptic output is to AIZ and ADF, usually together in a dyadic synapse (a). There are also synapses to RIA (b) and AVB (c). There are gap junctions to RMG (d) and AUA.

Magnifications: (a) ×25500, (b–d) ×12750.


CILIATED ENDING
IN AMPHID SENSILLUM
AIYL
AIAL
AIAR,AIBR
ASER*
AIAR
AVAL
RIAL
ASIR*
AWCR
AIBL
ASEL*
AIYL*
ASIL*
AWCR*
a
b
ASIL
AWCL
CELL BODY IN
LATERAL GANGLION


CILIATED ENDING
IN AMPHID SENSILLUM
ADLR*
AIAR*
AIYR,AIBR
AIAR
AIAL*
ADLR*
c
AIYL
AIAR
ADLR*
AIAR
ASIR*
AWCL
AIYL
ASEL,ASER
AIBL
AIYR
AIAR*
d
AIYL*
AIYR
AIYR
AIYL
AIYR
ASIL*
ASIR
AIYR
AIYR,AIBR
ASEL
AIYL,AWCL
AIYR,AIBR
AIYR
AWCR
CELL BODY IN
LATERAL GANGLION



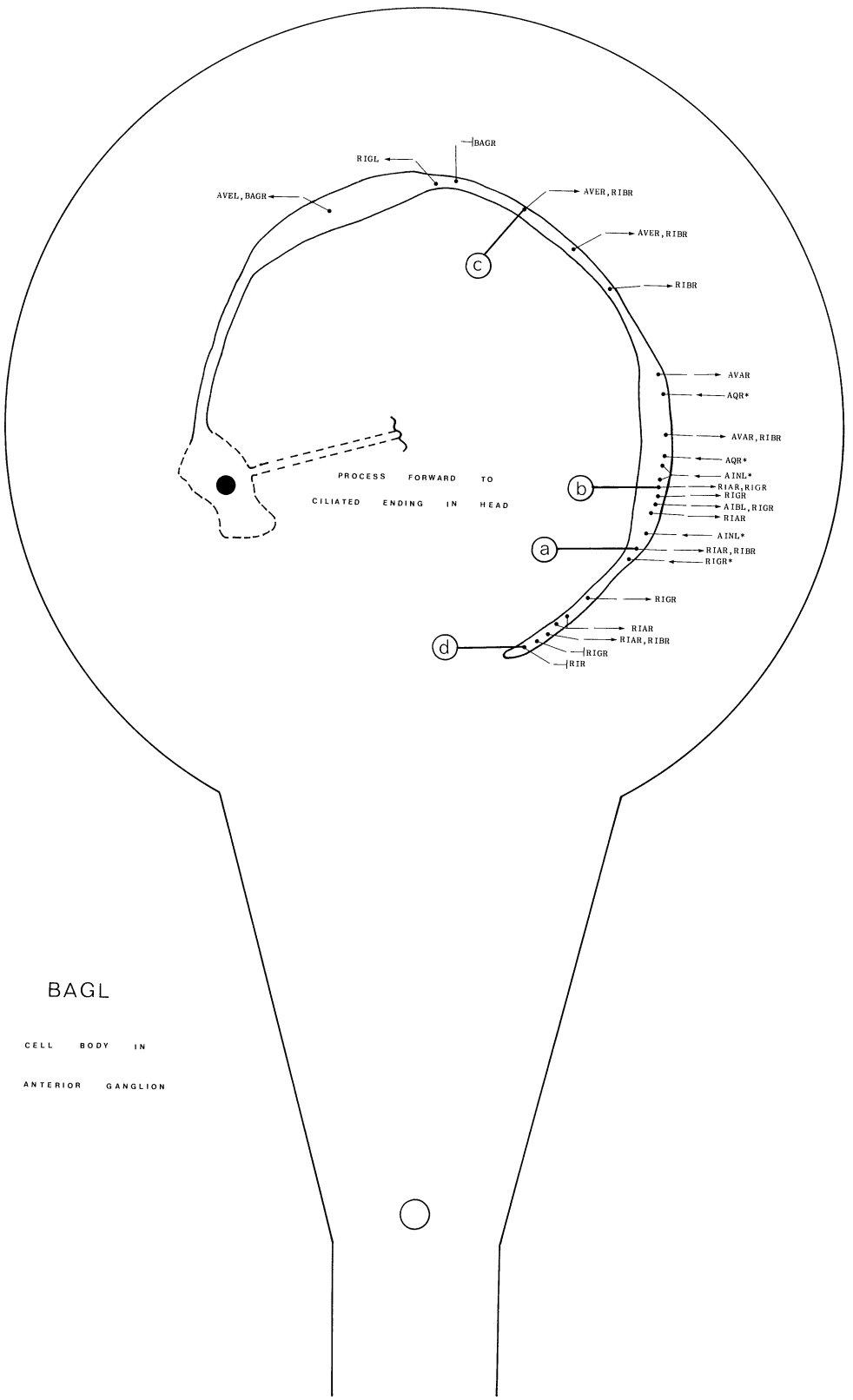
AWC

Members: AWCL, AWCR.

AWC is a set of two ciliated neurons with large, flattened, sheet-like endings that are associated with the sheath cells of the amphid sensilla (figure 1). The cell bodies of AWC are situated in the lateral ganglia and send processes into the ventral cord via the amphid commissures. These turn anteriorly and run near the lateral surfaces of the cord. They then enter the nerve ring which they then run right round adjacent to the posterior surface; finally ending ventrally. The main synaptic output is to AIY (a), AIB (b) and AIA (c) which synapses back to AWC reciprocally (d). AWC also has some synaptic input from ASE (*d) and ASI (*c). Occasional dark vesicles are seen at synapses (a).

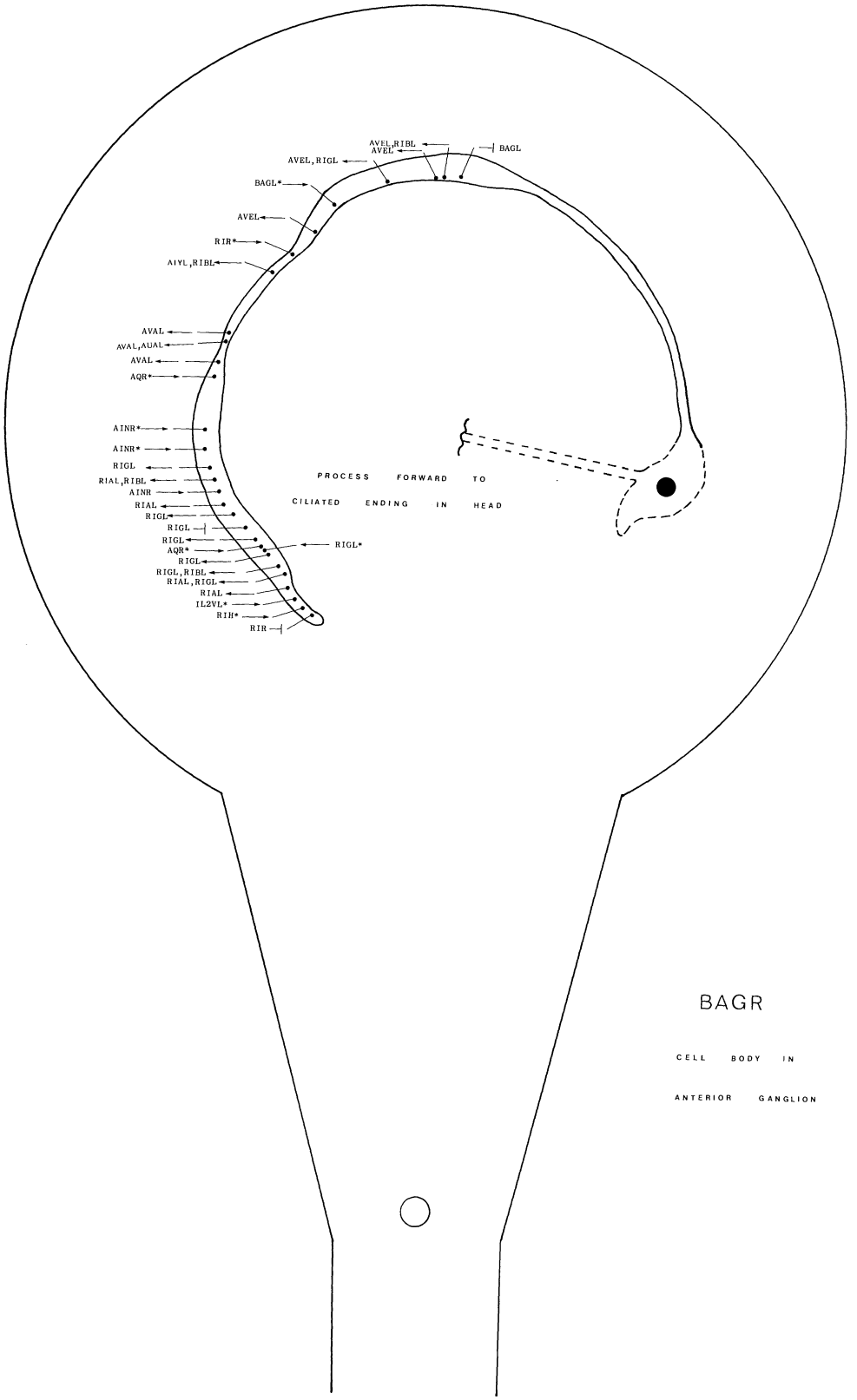
Magnifications: (a) ×25500, (b–d) ×12750.

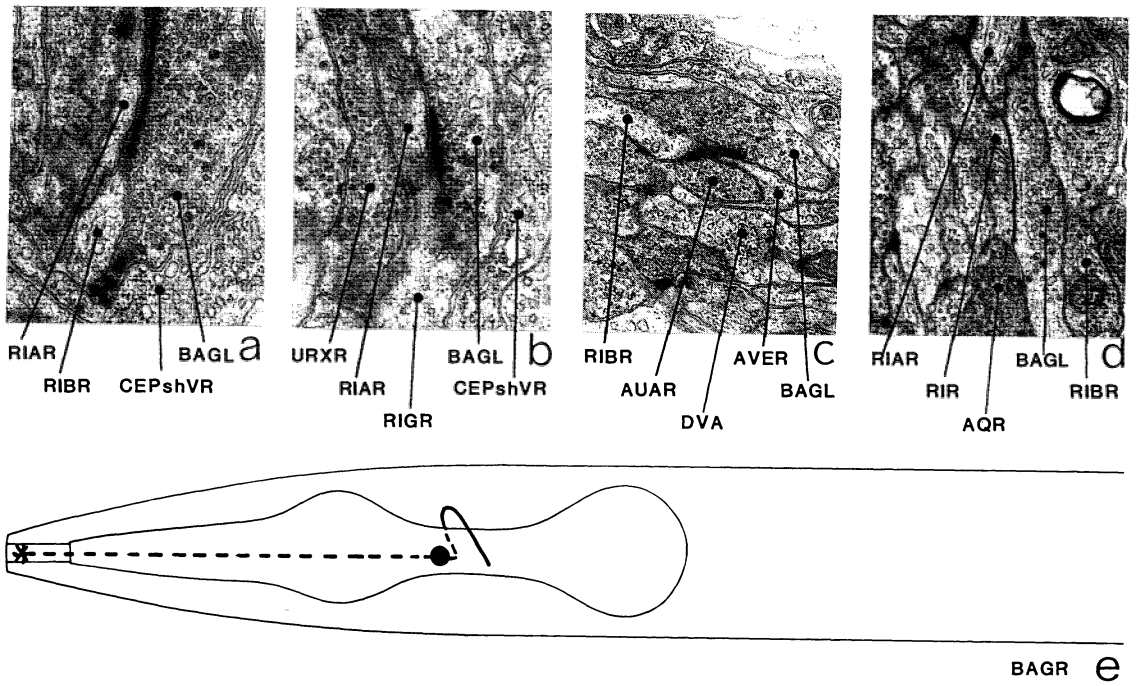
BAG



BAGL

CELL BODY IN ANTERIOR GANGLION


AVEL,RIBL
AVEL
BAGL
AVEL,RIGL
BAGL*
AVEL
RIR*
AIYL,RIBL
AVAL
AVAL,AUAL
AVAL
AQR*
AINR*
AINR*
RIGL
RIAL,RIBL
AINR
RIAL
RIGL
RIGL
RIGL
AQR*
RIGL
RIGL,RIBL
RIAL,RIGL
RIAL
IL2VL*
RIH*
RIR
RIGL*
PROCESS FORWARD TO
CILIATED ENDING IN HEAD
BAGR
CELL BODY IN
ANTERIOR GANGLION

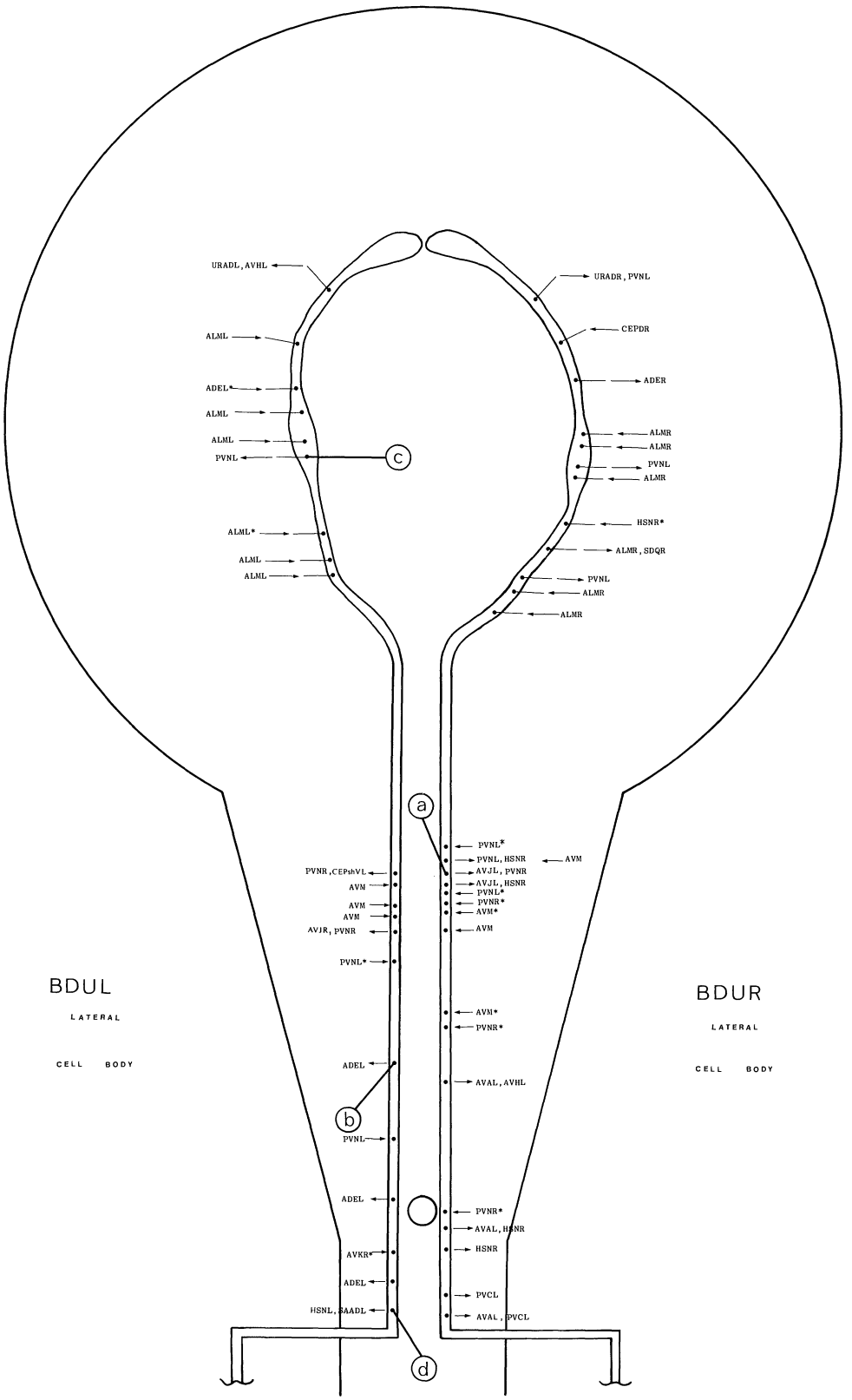


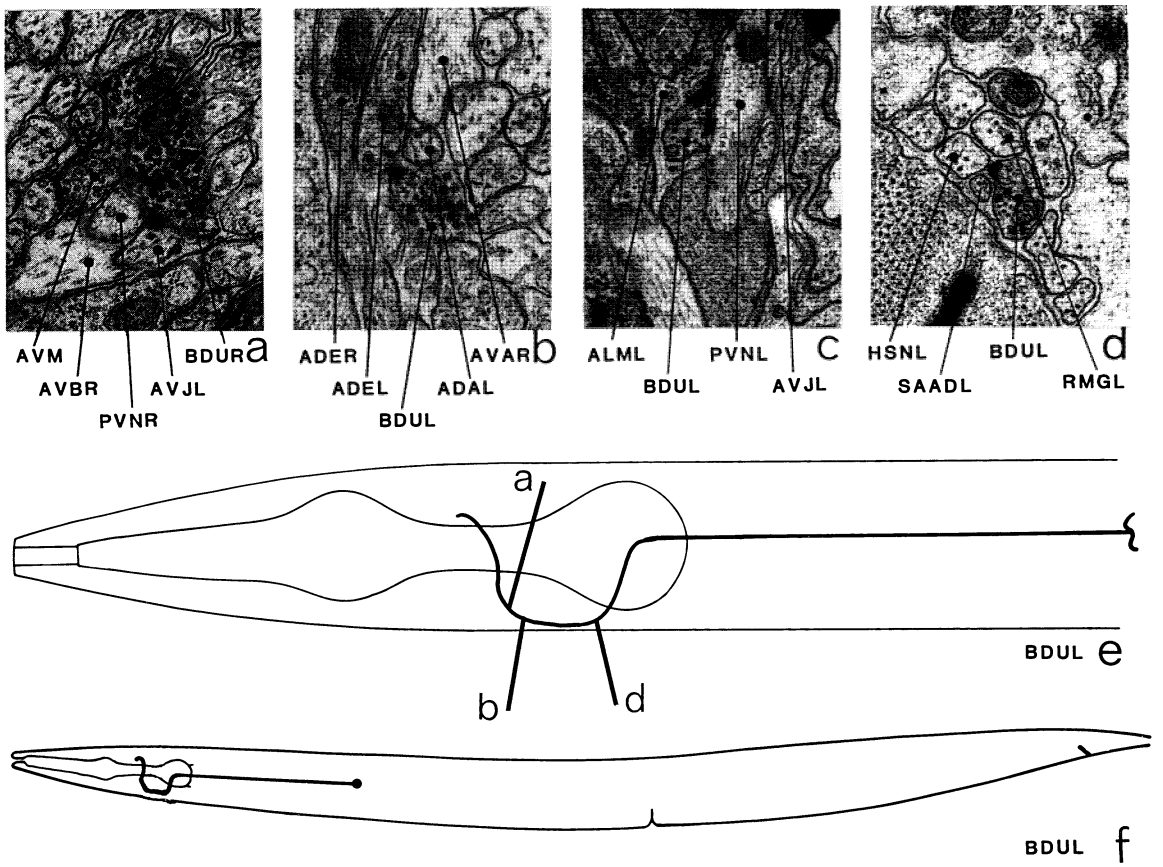
BAG

Members: BAGL, BAGR.

BAG is a set of two neurons with ciliated endings, in the head, with elliptical, closed, sheet-like processes near the cilium, which envelop a piece of hypodermis (figure 1). These endings have no associated sheath and socket cells and so are not directly attached to the hypodermis. The cell bodies are situated anterior to the nerve ring, just ventral of lateral, and send processes anteriorly to the ciliated endings in the head. Posteriorly directed processes enter the nerve ring from the cell bodies and then run round the ring to the contralateral side near the outside surface of the neuropile, eventually ending ventrally. The main synaptic output is to RIA (a, b), RIB (a, c), AVE (c) and RIG (b). There are a few dark-cored vesicles in the synaptic terminals (a). There is some synaptic input from AIN (*b), RIG (*d) and AQR (*d). BAG has gap junctions with itself, RIR (d) and RIG (*h).

Magnifications: (a, b) $\times 25500$, (c, d) $\times 12750$.


URADL, AVHL
URADR, PVNL
CEPDR
ALML
ADER
ADEL*
ALML
ALMR
ALML
ALMR
PVNL
c
PVNL
ALMR
HSNR*
ALML*
ALMR, SDQR
ALML
ALML
PVNL
ALMR
ALMR
a
PVNL*
PVNL, HSNR
AVM
PVNR, CEPshVL
AVJL, PVNR
AVM
AVJL, HSNR
PVNL*
AVM
PVNR*
AVM
AVM*
AVJR, PVNR
AVM
PVNL*
BDUL
LATERAL
CELL BODY
BDUR
LATERAL
CELL BODY
AVM*
PVNR*
ADEL
AVAL, AVHL
b
PVNL
ADEL
PVNR*
AVAL, HSNR
AVKR*
HSNR
ADEL
PVCL
HSNL, SAADL
AVAL, PVCL
d



BDU

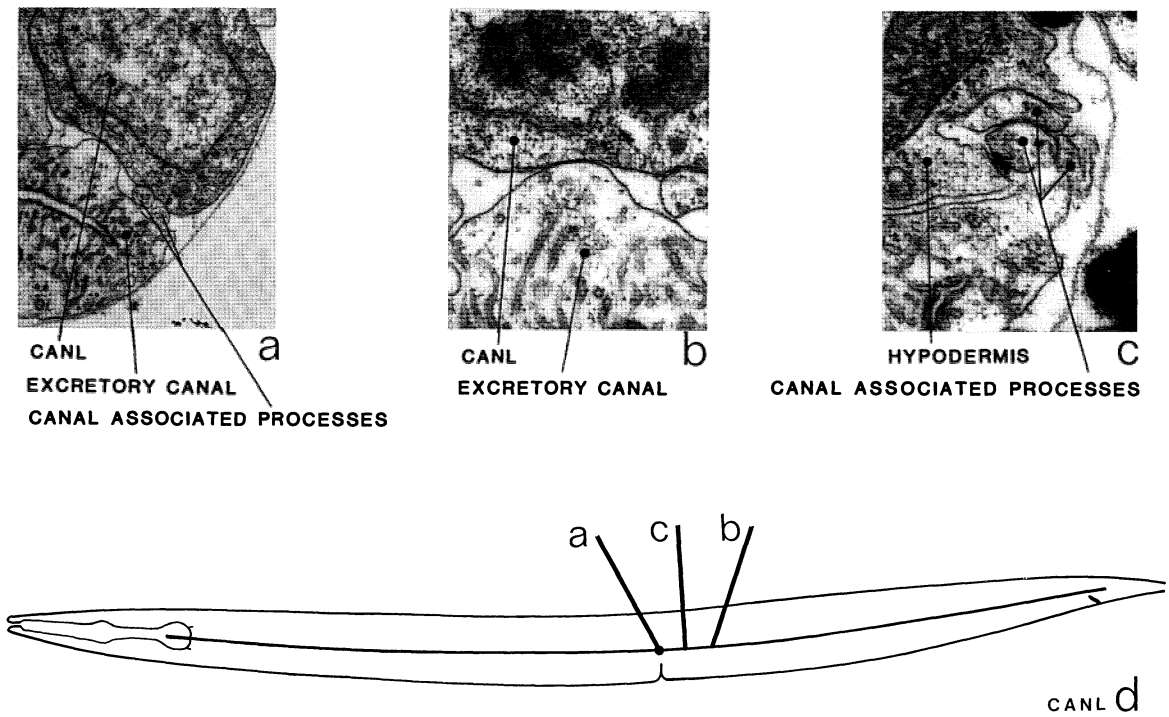
Members: BDUL and BDUR.

BDU is a set of two interneurons with cell bodies situated laterally in the anterior body (f). Single processes project anteriorly from each cell body and run adjacent to the excretory canal, until they enter the retro-vesicular ganglion via deirid commissures. The processes then run anteriorly on either side of the ventral hypodermal ridge until the nerve ring is reached. This they enter, running round near the inside surface of the neuropile in close association with the processes of PVN, finally meeting and terminating on the dorsal mid-line. The presynaptic regions of chemical synapses from BDU are generally rather small but have striking, darkly staining vesicles (a, b, c, d). The main synaptic output of BDU is to AVJ (a), PVN (c), ADE (b) and HSN (d). The main synaptic inputs are from ALM (*a), AVM (*b), HSN (*d) and PVN (*a).

Magnifications: (a–d) ×25500.

BDU VENTRAL CORD SYNAPSES

partners	gap junctions	synapses from	synapses to and corecipients
HSN	—	—	1, AVA, SAAD
AVA	—	—	PVC, HSN
PVC	—	—	1, AVA
ADE	—	—	1
SAAD	—	—	HSN

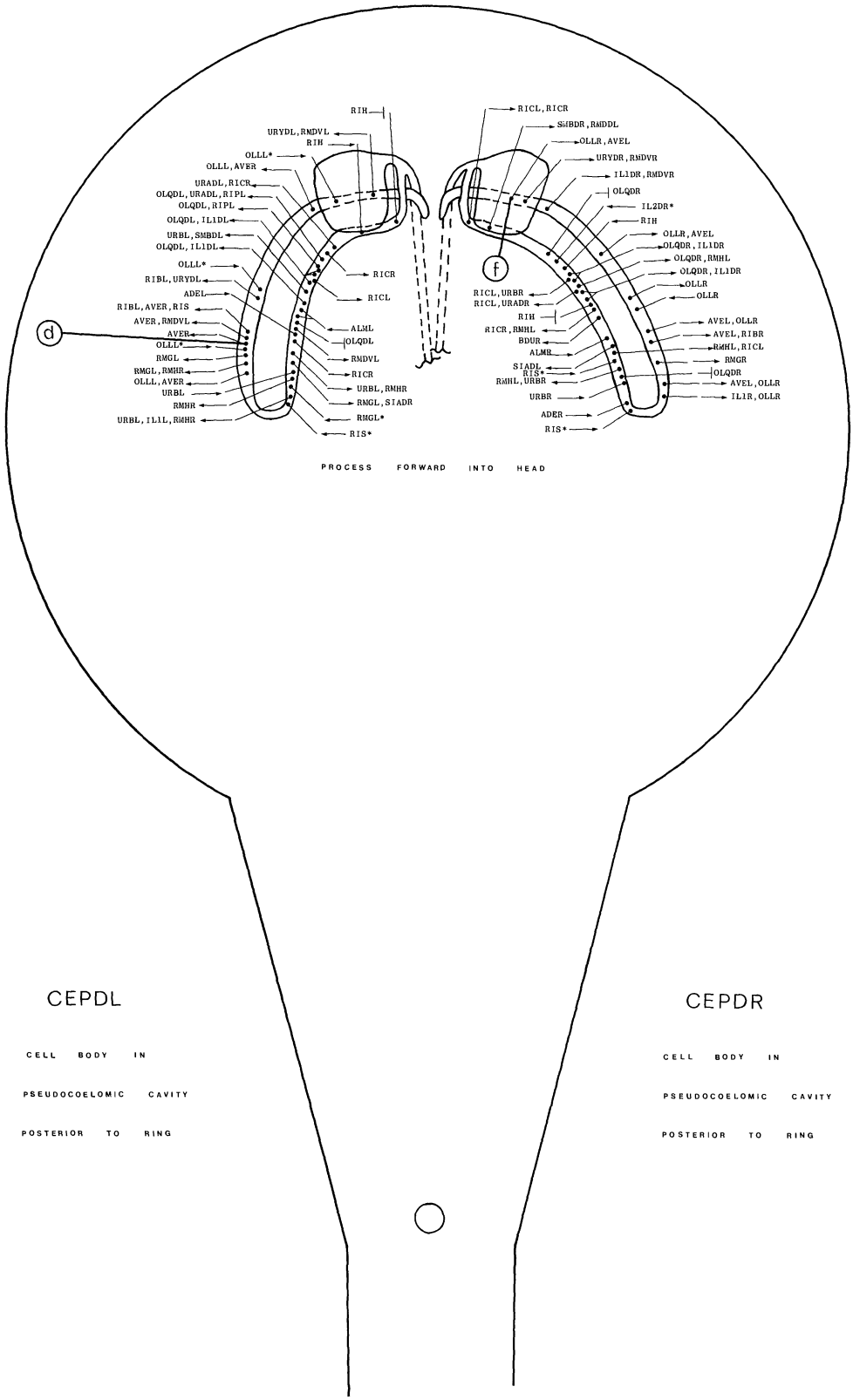


CAN

Members: CANL, CANR.

CAN is a set of two cells that are closely associated with the excretory canal. The cell bodies of CAN are situated adjacent and dorsal to the excretory canal at about the level of the vulva (d). Anteriorly and posteriorly directed processes emanate from the cell bodies and run along the canal in close association with the processes of ALA and PVD. The anterior process of CAN ends just behind the nerve ring (d). The three canal-associated processes on each side, ALA, CAN and PVD, have not been completely reconstructed although they have been sampled in several places. Two of the processes end at about the level of the anus and the third enters the pre-anal ganglia and synapses onto PVC (ALA-d). A single synapse onto the lateral hypodermis has also been seen on one of the processes (c). Apart from a few rather unconvincing gap junctions to the excretory canal (b), no other synapses can be unambiguously assigned to CAN. Laser ablation experiments have, however, shown it to be essential for the survival of the animal (J. Sulston, unpublished observations).

Magnifications: (a) $\times 12750$, (b, c) $\times 25500$.

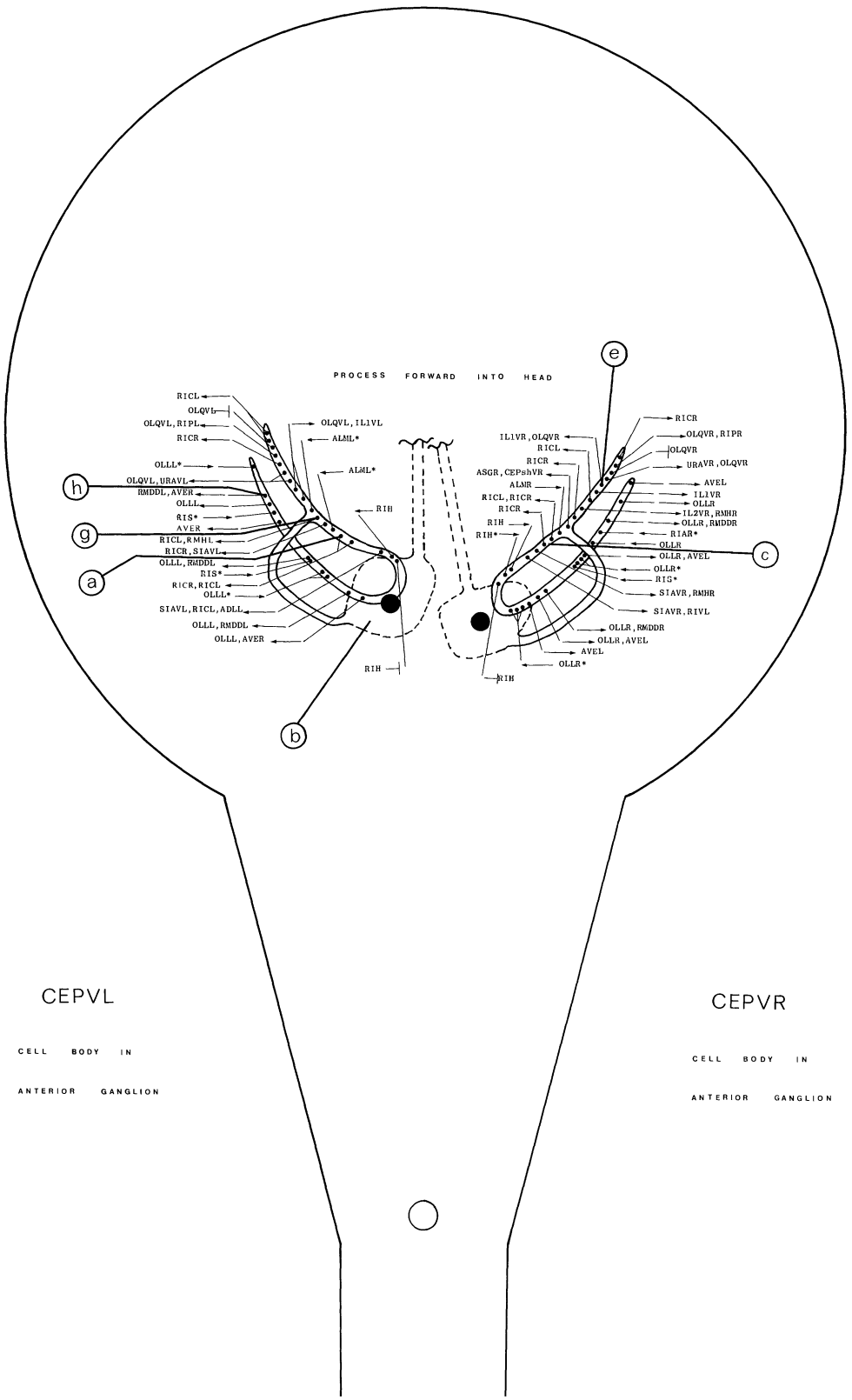


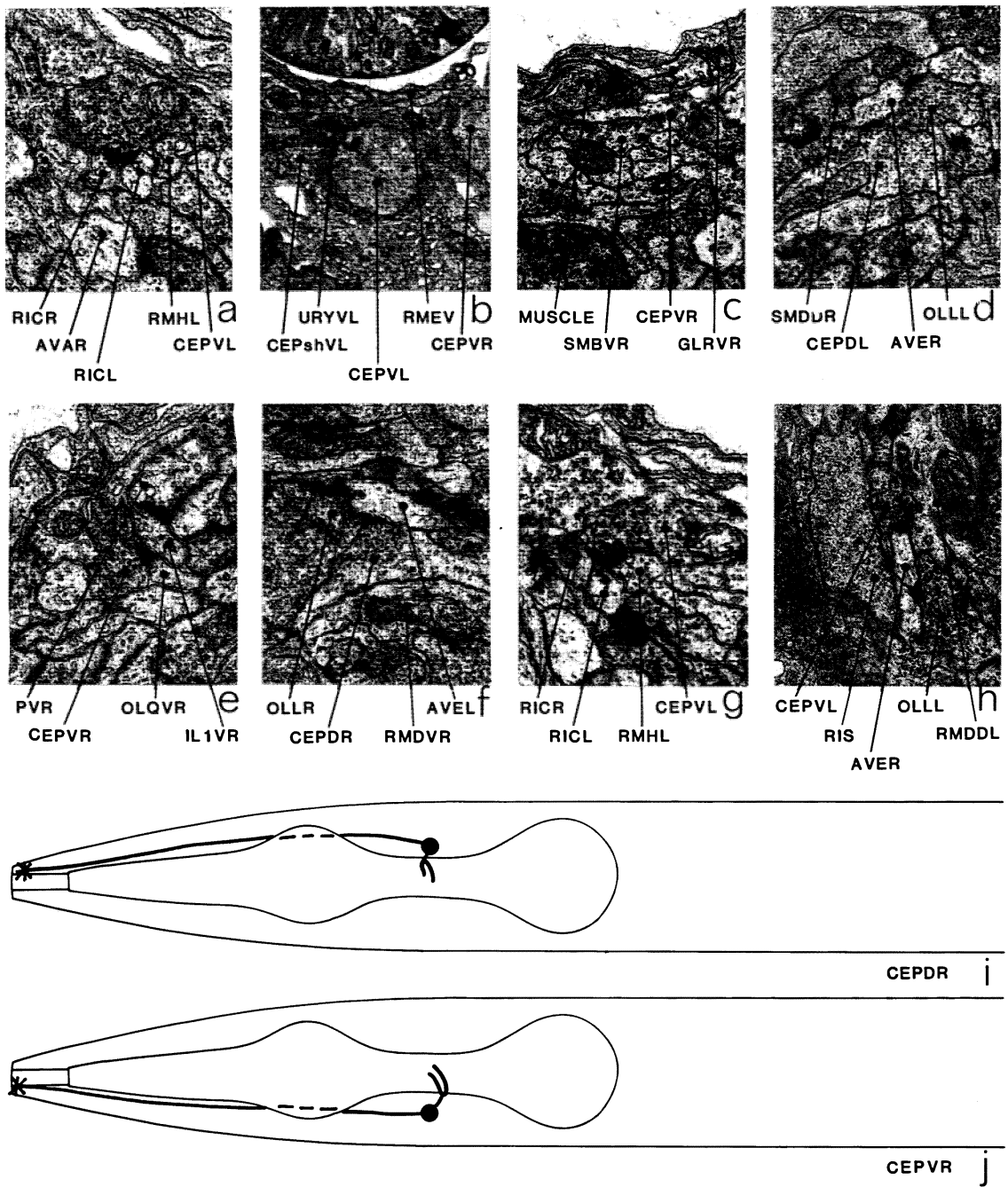
CEPDL

CELL BODY IN PSEUDOCOELOMIC CAVITY POSTERIOR TO RING

CEPDR

CELL BODY IN PSEUDOCOELOMIC CAVITY POSTERIOR TO RING


PROCESS FORWARD INTO HEAD
RICL
OLQVL
OLQVL,RIPL
RICR
OLLL*
OLQVL,URAVL
RMDDL,AVER
OLLL
RIS*
AVER
RICL,RMHL
RICR,SIAVL
OLLL,RMDDL
RIS*
RICR,RICL
OLLL*
SIAVL,RICL,ADLL
OLLL,RMDDL
OLLL,AVER
OLQVL,IL1VL
ALML*
ALML*
RIH
RIH
h
g
a
b
e
c
IL1VR,OLQVR
RICL
RICR
ASGR,CEPshVR
ALMR
RICL,RICR
RICR
RIH
RIH*
RICR
OLQVR,RIPR
OLQVR
URAVR,OLQVR
AVEL
IL1VR
OLLR
IL2VR,RMHR
OLLR,RMDDR
RIAR*
OLLR
OLLR,AVEL
OLLR*
RIG*
SIAVR,RMHR
SIAVR,RIVL
OLLR,RMDDR
OLLR,AVEL
AVEL
OLLR*
RIH
CEPVL
CELL BODY IN
ANTERIOR GANGLION
CEPVR
CELL BODY IN
ANTERIOR GANGLION



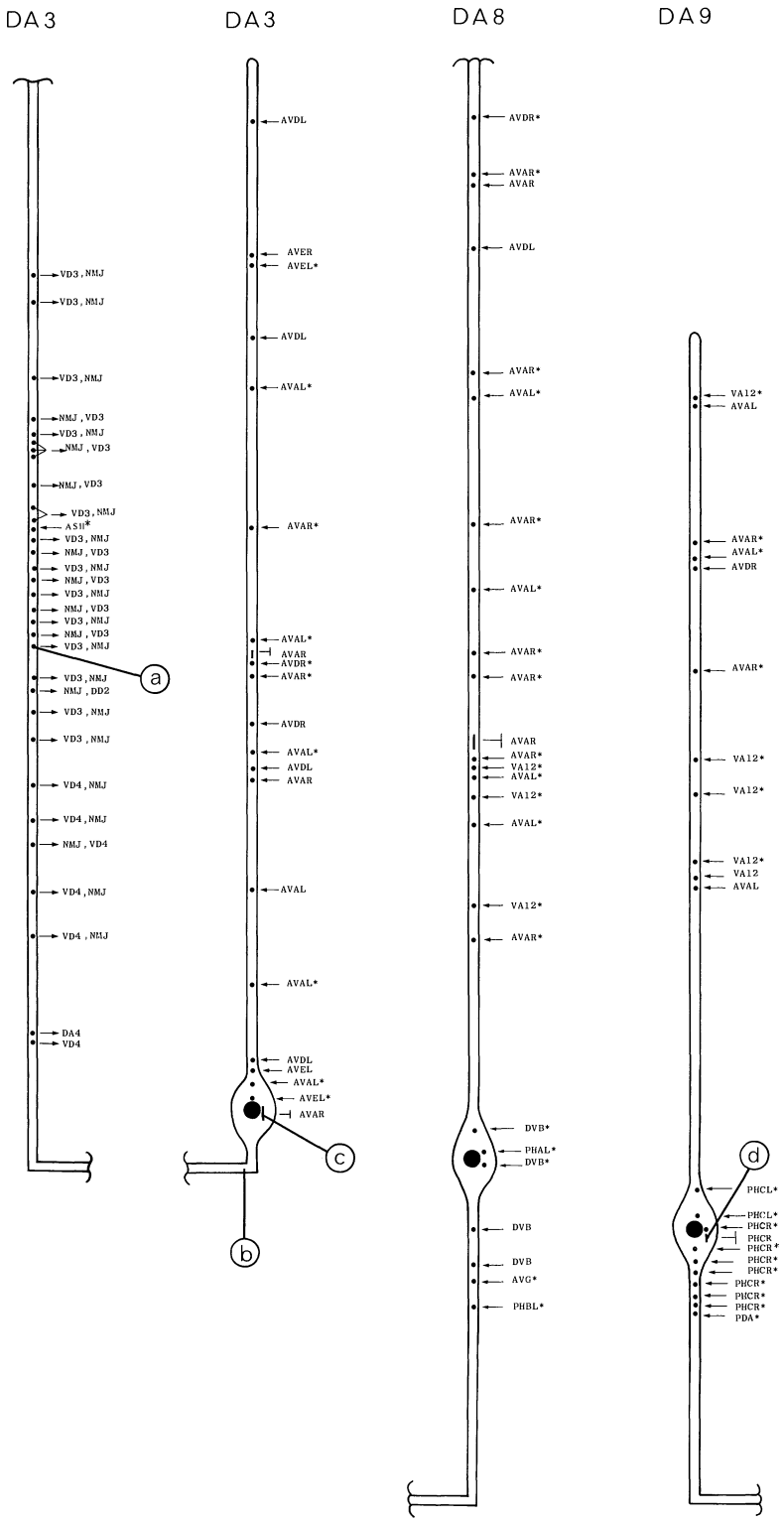
CEP

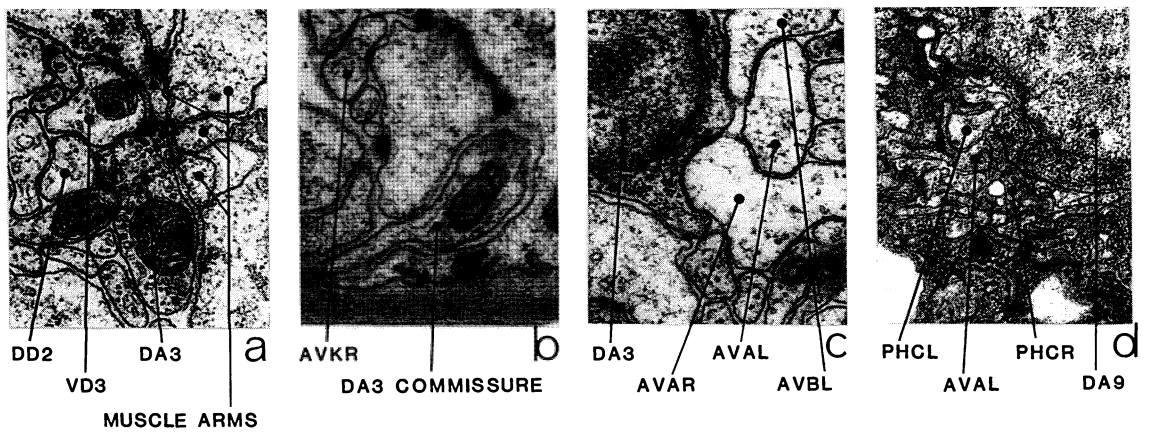
Members: CEPDL, CEPDR, CEPVL, CEPVR.

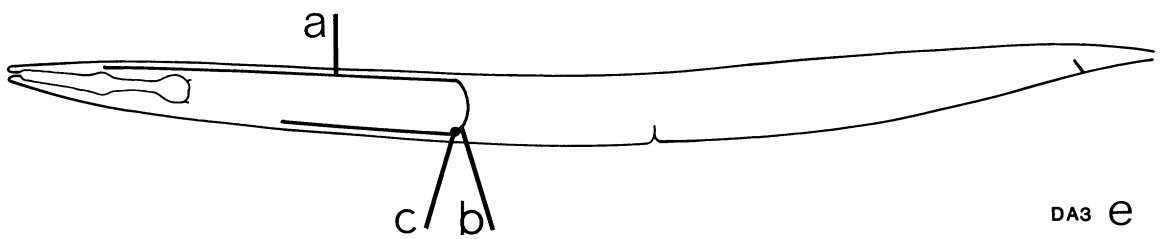
CEP is a set of four neurons with ciliated endings in the cephalic sensilla (figure 1). The dorsal pair of cell bodies is situated in the pseudocoelomic cavity posterior to the nerve ring (along with those of URX). The ventral cell bodies are situated anterior to the ring and closely apposed to the ring neuropile (b). Anteriorly directed processes run in four of the six labial process bundles to the receptor endings in the head. Posteriorly directed processes emanate from the ventral CEP pair and loop round the posterior face of the ring neuropile; they then

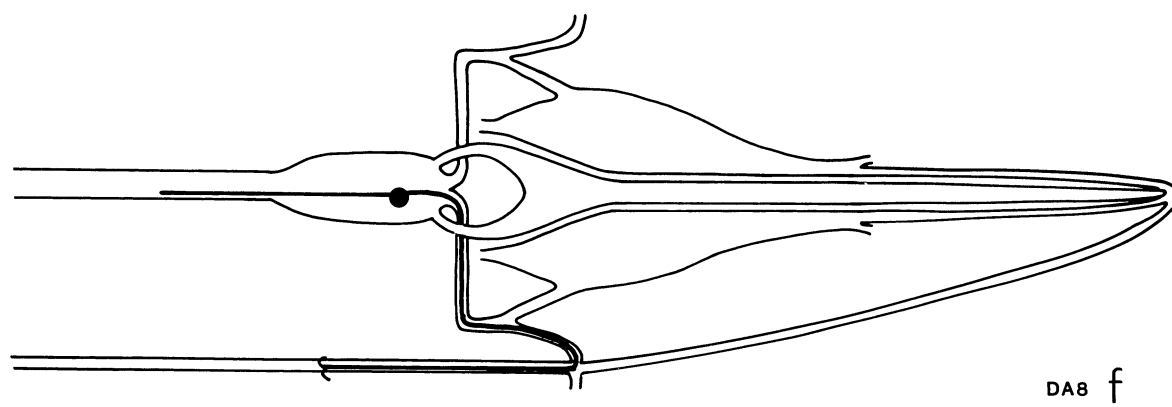
enter it on the inside surface adjacent to the muscle arms (j, c). The processes branch at this point and run both ways round the nerve ring on the inside surface near the posterior face of the ring neuropile. The dorsal branch ends; the ventral branch loops round and runs dorsally in the middle of the anterior regions of the ring neuropile. The dorsal pair of CEP neurons send out anteriorly directed processes, which enter the ring near the dorsal mid-line (i) and then run ventrally on the inside of the ring neuropile adjacent to the muscle arms. These then loop back and run in the middle of the anterior regions of neuropile, eventually moving back to the inner surface, where they end. The main synaptic output is to RIC (a, g), AVE (d, f, h), OLL (f), OLQ (e), IL1 (e), RMH (g), RMD (h), RMG, URA and URB. CEP synapses have been shown to contain the neurotransmitter dopamine (Sulston *et al.* 1975). There is some synaptic input from OLL, ALM (*c), RIH, RIS, and also from URB (*b) and ADE to the dorsal pair only. There are gap junctions to OLQ (*e) and RIH.

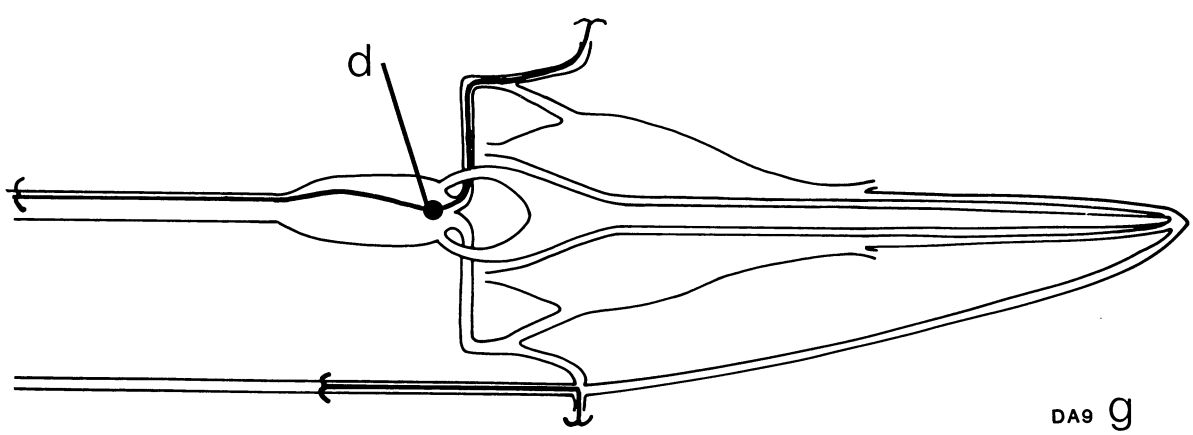
Magnifications: (a, e, g) ×25500, (b) ×6375, (c, d, f, h) ×12750.


DA3
VD3,NMJ
VD3,NMJ
VD3,NMJ
NMJ,VD3
VD3,NMJ
NMJ,VD3
NMJ,VD3
VD3,NMJ
ASH*
VD3,NMJ
NMJ,VD3
VD3,NMJ
NMJ,VD3
VD3,NMJ
NMJ,VD3
VD3,NMJ
NMJ,VD3
VD3,NMJ
a
VD3,NMJ
NMJ,DD2
VD3,NMJ
VD3,NMJ
VD4,NMJ
VD4,NMJ
NMJ,VD4
VD4,NMJ
VD4,NMJ
DA4
VD4
DA3
AVDL
AVER
AVEL*
AVDL
AVAL*
AVAR*
AVAL*
AVAR
AVDR*
AVAR*
AVDR
AVAL*
AVDL
AVAR
AVAL
AVAL*
AVDL
AVEL
AVAL*
AVEL*
AVAR
c
b
DA8
AVDR*
AVAR*
AVAR
AVDL
AVAR*
AVAL*
AVAR*
AVAL*
AVAR*
AVAR*
AVAR
AVAR*
VA12*
AVAL*
VA12*
AVAL*
VA12*
AVAR*
DVB*
PHAL*
DVB*
DVB
DVB
AVG*
PHBL*
DA9
VA12*
AVAL
AVAR*
AVAL*
AVDR
AVAR*
VA12*
VA12*
VA12*
VA12
AVAL
d
PHCL*
PHCL*
PHCR*
PHCR
PHCR*
PHCR*
PHCR*
PHCR*
PHCR*
PHCR*
PDA*


DD2
VD3
DA3
a
MUSCLE ARMS
AVKR
b
DA3 COMMISSURE
DA3
AVAR
AVAL
AVBL
c
PHCL
AVAL
PHCR
DA9
d


a
c
b
DA3 e


DA8 f

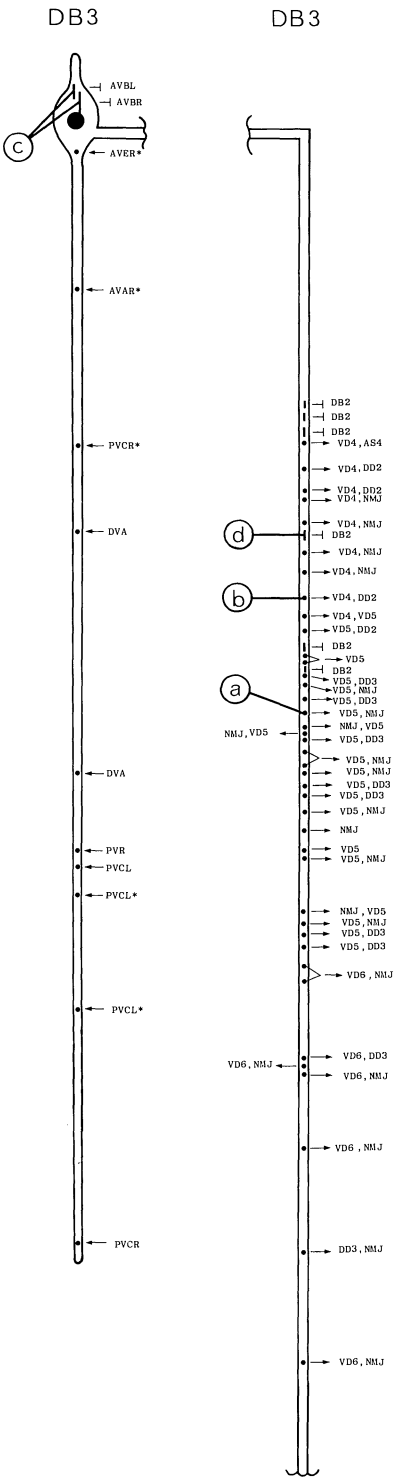

d
DA9 g

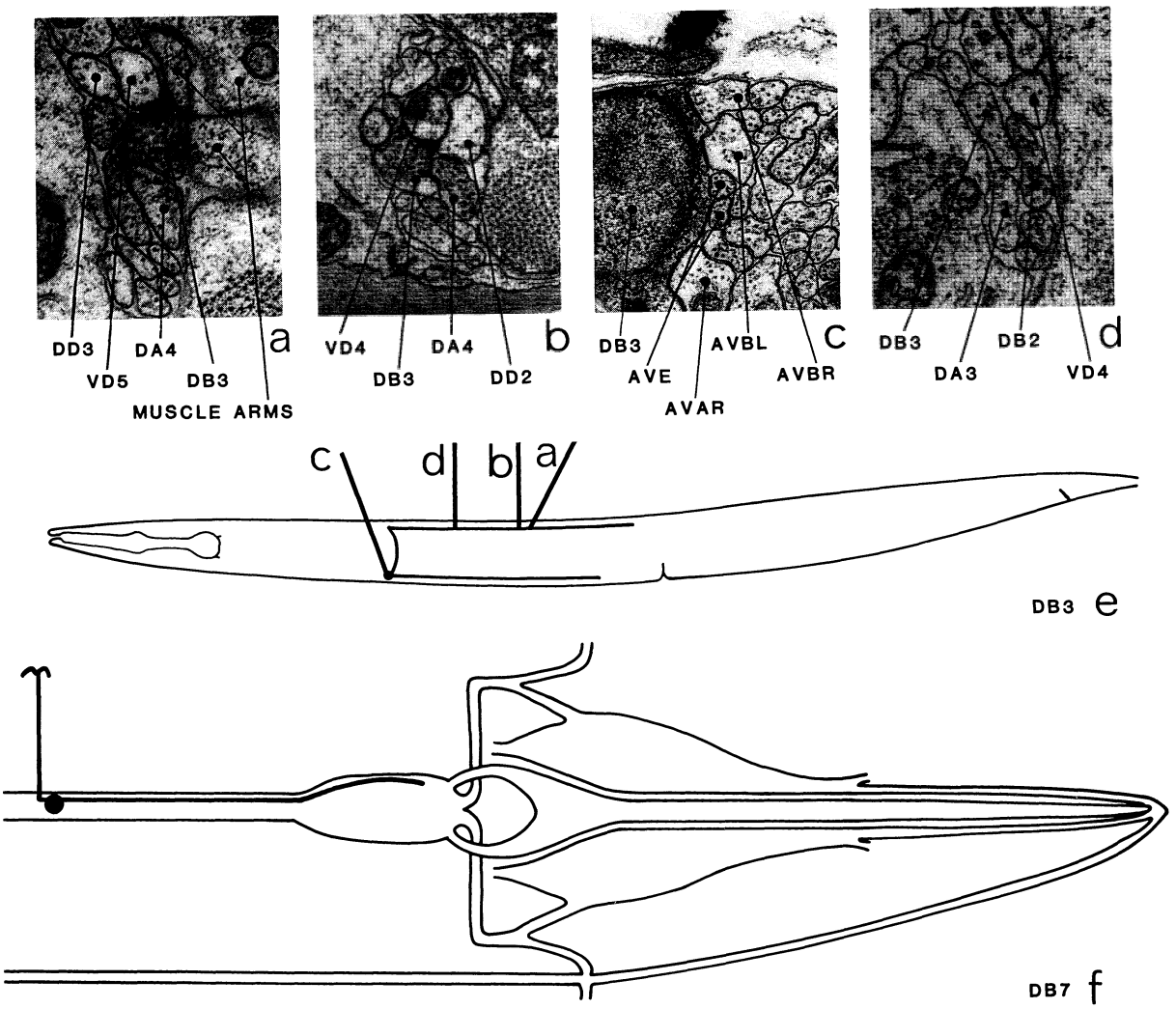
DAn

Members: DA1 to DA9.

DAn is a set of nine motoneurons that innervate dorsal muscles and have cell bodies in the ventral cord. A typical DAn (e.g. DA3 (e)) has an exclusively postsynaptic, anteriorly directed process in the ventral cord that runs in the ventral regions of the cord. It receives synaptic input from AVA (*d) and AVD (*c); in addition, DA1–DA4 receive synaptic input from AVE (*d), DA8 receives input from DVB and DA9 from PHC (*a). There are gap junctions to AVA (c) and occasional gap junctions to VAn. DA1 and DA2 also have gap junctions to SAB and DA9 to PHC (d). A posteriorly directed process from DAn leaves the ventral cord and runs round to the dorsal cord. All except those from DA2 and DA9 go round as a left-hand commissure, passing through the ventral hypodermal ridge (b). The process of DAn runs anteriorly in the dorsal cord with the proximal regions of the process running adjacent to the basal lamina. There are many NMJs in this region, which are nearly all dyadic, with VDn as the corecipient (a). The distal regions of the dorsal DAn processes are generally not adjacent to the basal lamina and have few, if any, synaptic contacts.

Magnifications: (a–d) $\times 25500$.


DB3
DB3
AVBL
AVBR
AVER*
AVAR*
PVCR*
DVA
DVA
PVR
PVCL
PVCL*
PVCL*
PVCR
c
d
b
a
DB2
DB2
DB2
VD4, AS4
VD4, DD2
VD4, DD2
VD4, NMJ
VD4, NMJ
DB2
VD4, NMJ
VD4, NMJ
VD4, DD2
VD4, VD5
VD5, DD2
DB2
VD5
DB2
VD5, DD3
VD5, NMJ
VD5, DD3
VD5, NMJ
NMJ, VD5
NMJ, VD5
VD5, DD3
VD5, NMJ
VD5, NMJ
VD5, DD3
VD5, DD3
VD5, NMJ
NMJ
VD5
VD5, NMJ
NMJ, VD5
VD5, NMJ
VD5, DD3
VD5, DD3
VD6, NMJ
VD6, NMJ
VD6, DD3
VD6, NMJ
VD6, NMJ
DD3, NMJ
VD6, NMJ

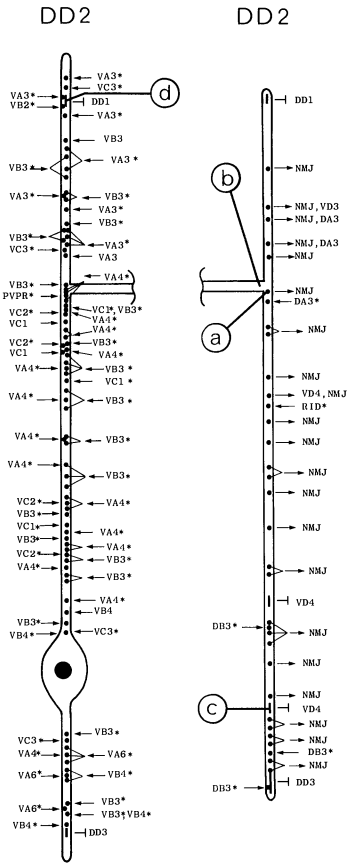


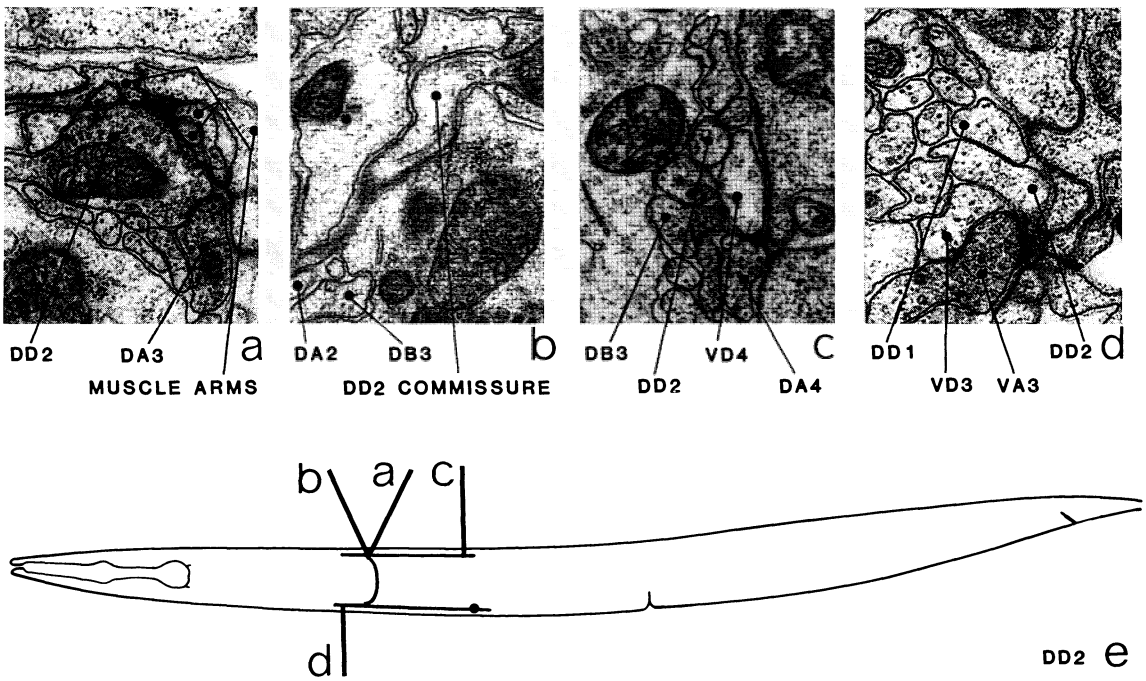
DBn

Members: DB1 to DB7

DBn is a set of seven motoneurons that innervate dorsal muscles and have cell bodies in the ventral cord. A typical DBn (e.g. DB3 (e)) has an exclusively postsynaptic, posteriorly directed process in the ventral cord that runs in the ventral regions of the cord. It receives synaptic input from PVC (*e) and occasionally from DVA (*f). There are prominent gap junctions to AVB, usually situated near the cell body (c). A process, which either comes directly out of the cell body or just anteriorly to it, leaves the ventral cord and runs round to the dorsal cord as a commissure. DB2, DB4 and DB5 run round the left-hand side of the body; the others run on the right. The process of DBn turns and runs posteriorly on reaching the dorsal cord, with the proximal regions of the process running adjacent to the basal lamina. There are many NMJs in this region, most of which are dyadic, with VDn as the corecipient (a). There are also a few dyadic synapses to DDn and VDn (b) and gap junctions to adjacent DBns (d). The distal regions of the dorsal cord processes move away from the basal lamina and are generally devoid of any synaptic contacts.

Magnifications: (a, d) ×25500, (b, c) ×17000.


DD2
DD2
VA3*
VC3*
DD1
VA3*
VB2*
VA3*
VB3
VA3*
VB3*
VA3*
VB3*
VA3*
VB3*
VC3*
VA3*
VA3
VA4*
VB3*
PVPR*
VC1*,VB3*
VC2*
VA4*
VC1
VA4*
VC2*
VB3*
VC1
VA4*
VA4*
VB3*
VC1*
VA4*
VB3*
VA4*
VB3*
VA4*
VB3*
VC2*
VA4*
VB3*
VC1*
VA4*
VB3*
VA4*
VC2*
VA4*
VB3*
VA4*
VB3*
VA4*
VB4
VB3*
VB4*
VC3*
VB3*
VC3*
VA4*
VA6*
VA6*
VB4*
VB3*
VA6*
VB3*
VB4*
VB4*
DD3
d
b
a
c
DD1
NMJ
NMJ,VD3
NMJ,DA3
NMJ,DA3
NMJ
NMJ
DA3*
NMJ
NMJ
VD4,NMJ
RID*
NMJ
NMJ
NMJ
NMJ
NMJ
NMJ
VD4
DB3*
NMJ
NMJ
NMJ
VD4
NMJ
NMJ
DB3*
NMJ
DB3*
DD3

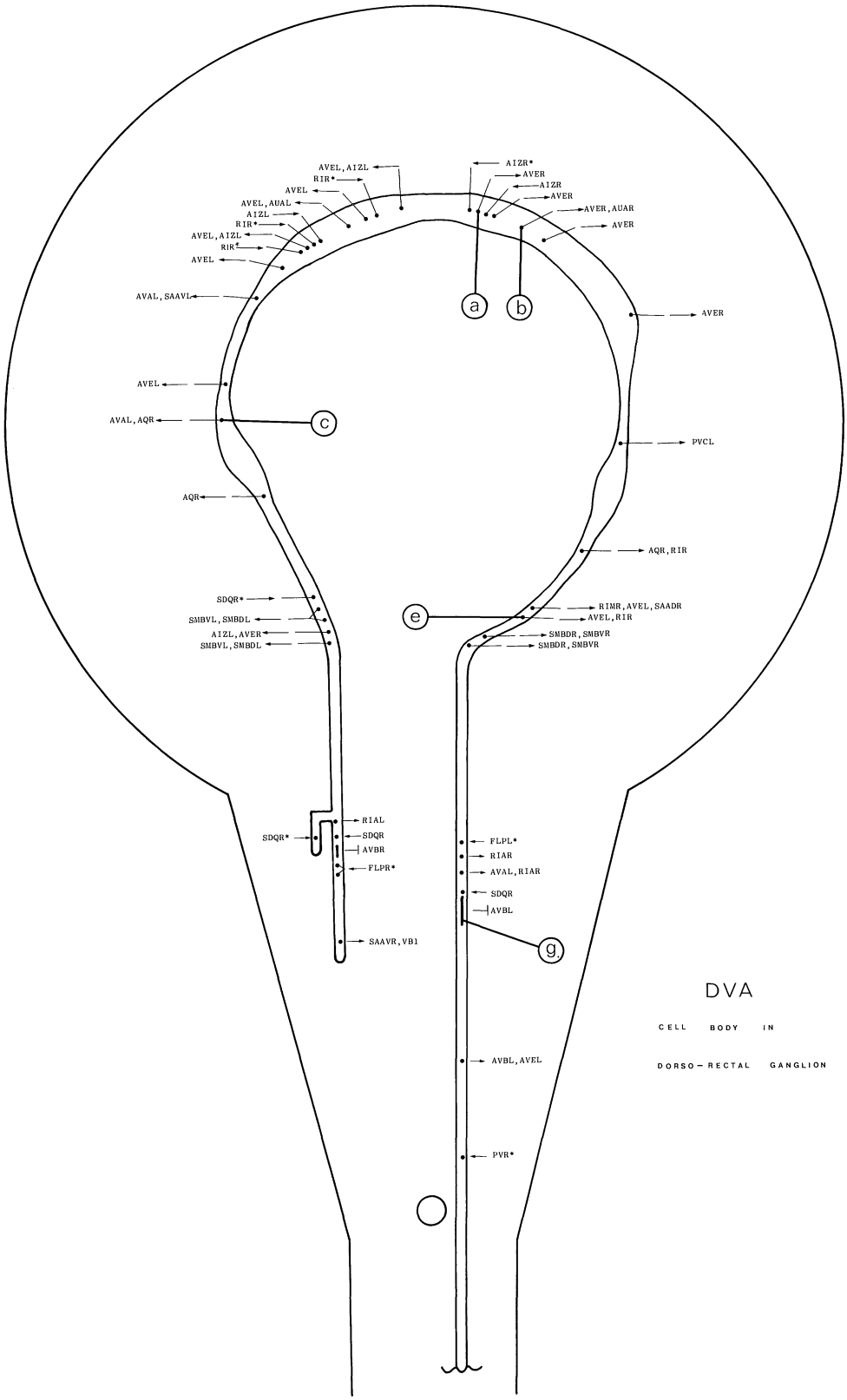


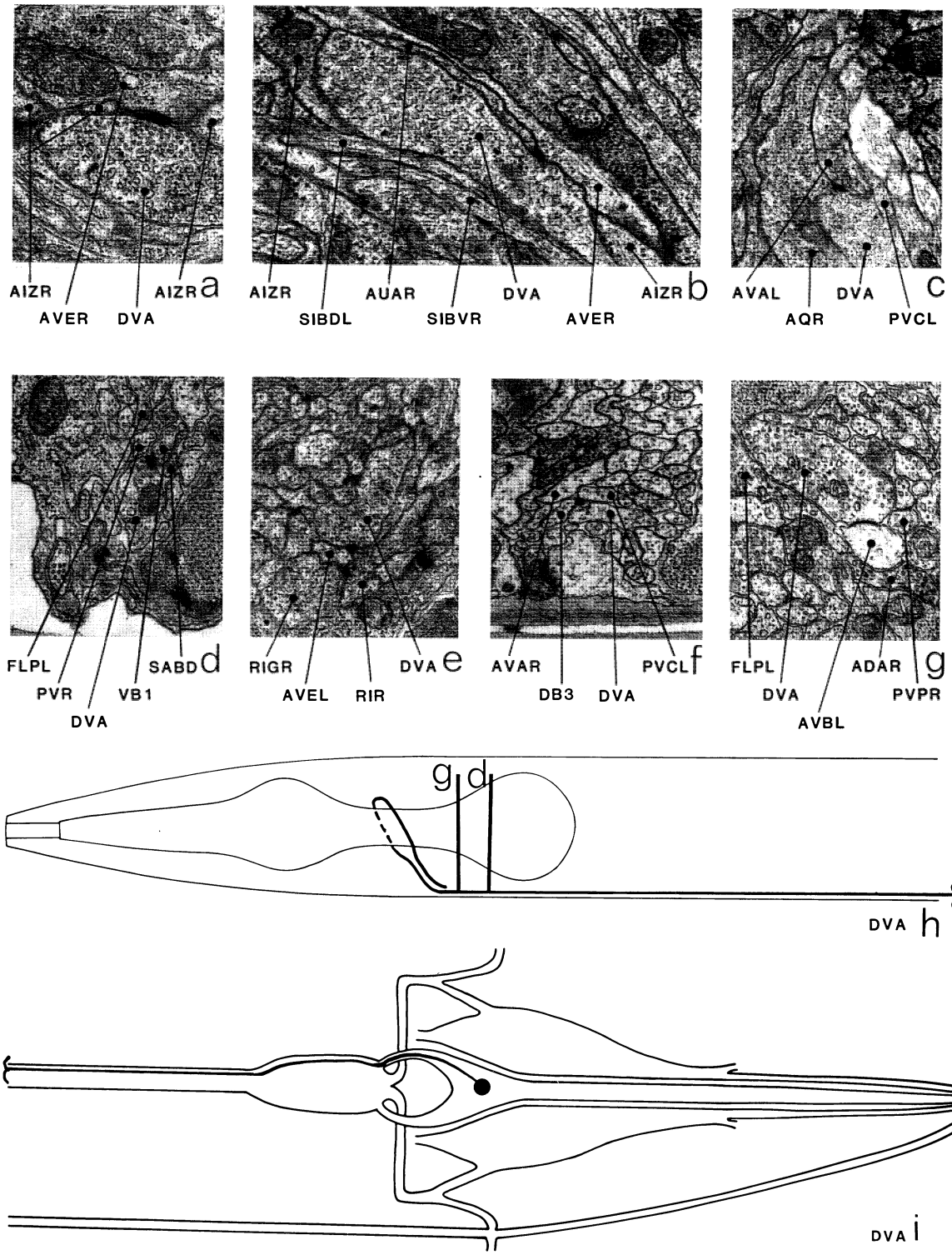
DDn

Members: DD1 to DD6.

DDn is a set of six motoneurons, with cell bodies in the ventral cord, which innervate dorsal muscles. Each cell has a short, posteriorly directed and a longer, anteriorly directed process emanating from its cell body. The anterior process has a branch, which leaves the ventral cord as a commissure and runs round to the dorsal cord. (The DD1 commissure runs to the left, the rest to the right.) The commissures often run through the hypodermal ridge when entering or leaving the nerve cords (b). The commissure splits, as it enters the dorsal cord, into an anteriorly and a posteriorly directed process, which span approximately the same longitudinal region of the body as their ventral counterparts. Both the dorsal and the ventral processes run adjacent to the basal lamina bounding the cord and run in close association with the processes of the VDn neurons. In the ventral cord they run between the more dorsal processes of the VC neurons and the more ventral processes of the VAn and VBn neurons (figure 18). In the dorsal cord they run to ventral of the other motoneuron classes (figure 19). The DDn processes in the ventral cord are exclusively postsynaptic and receive synaptic input from VAn (d), VBn (*a) and VCn (*b) as corecipients at NMJs, often with short dendritic spines intercepting the NMJs (as in VAn-a). The processes in the dorsal cord are predominantly presynaptic and have many NMJs (a), most of which have only muscle as the postsynaptic partner. The role of the dorsal and ventral processes is reversed in the first larval stage and switches round to the adult configuration at about the time of the first moult (White *et al.* 1978). The processes of DDn and VDn do not have extended, apparently undifferentiated, distal regions, as do the other classes of motoneuron; instead, they end abruptly in close proximity to the end of a neighbouring process of the same class and there is usually a gap junction between them (d). There are also a few gap junctions to VDn neurons (c).

Magnifications: (a–d) ×25500.


AVEL, AIZL
RIR*
AVEL
AVEL, AUAL
AIZL
RIR*
AVEL, AIZL
RIR*
AVEL
AVAL, SAAVL
AVEL
AVAL, AQR
AQR
SDQR*
SMBVL, SMBDL
AIZL, AVER
SMBVL, SMBDL
SDQR*
RIAL
SDQR
AVBR
FLPR*
SAAVR, VB1
AIZR*
AVER
AIZR
AVER
AVER, AUAR
AVER
a
b
AVER
c
PVCL
AQR, RIR
e
RIMR, AVEL, SAADR
AVEL, RIR
SMBDR, SMBVR
SMBDR, SMBVR
FLPL*
RIAR
AVAL, RIAR
SDQR
AVBL
g
AVBL, AVEL
PVR*
DVA
CELL BODY IN
DORSO-RECTAL GANGLION


AIZR
AVER
DVA
AIZR a
AIZR
SIBDL
AUAR
SIBVR
DVA
AVER
AIZR b
AVAL
AQR
DVA
PVCL c
FLPL
PVR
DVA
VB1
SABD d
RIGR
AVEL
RIR
DVA e
AVAR
DB3
DVA
PVCL f
FLPL
DVA
AVBL
ADAR
PVPR g
g
d
DVA h
DVA i

DVA

Member: DVA.

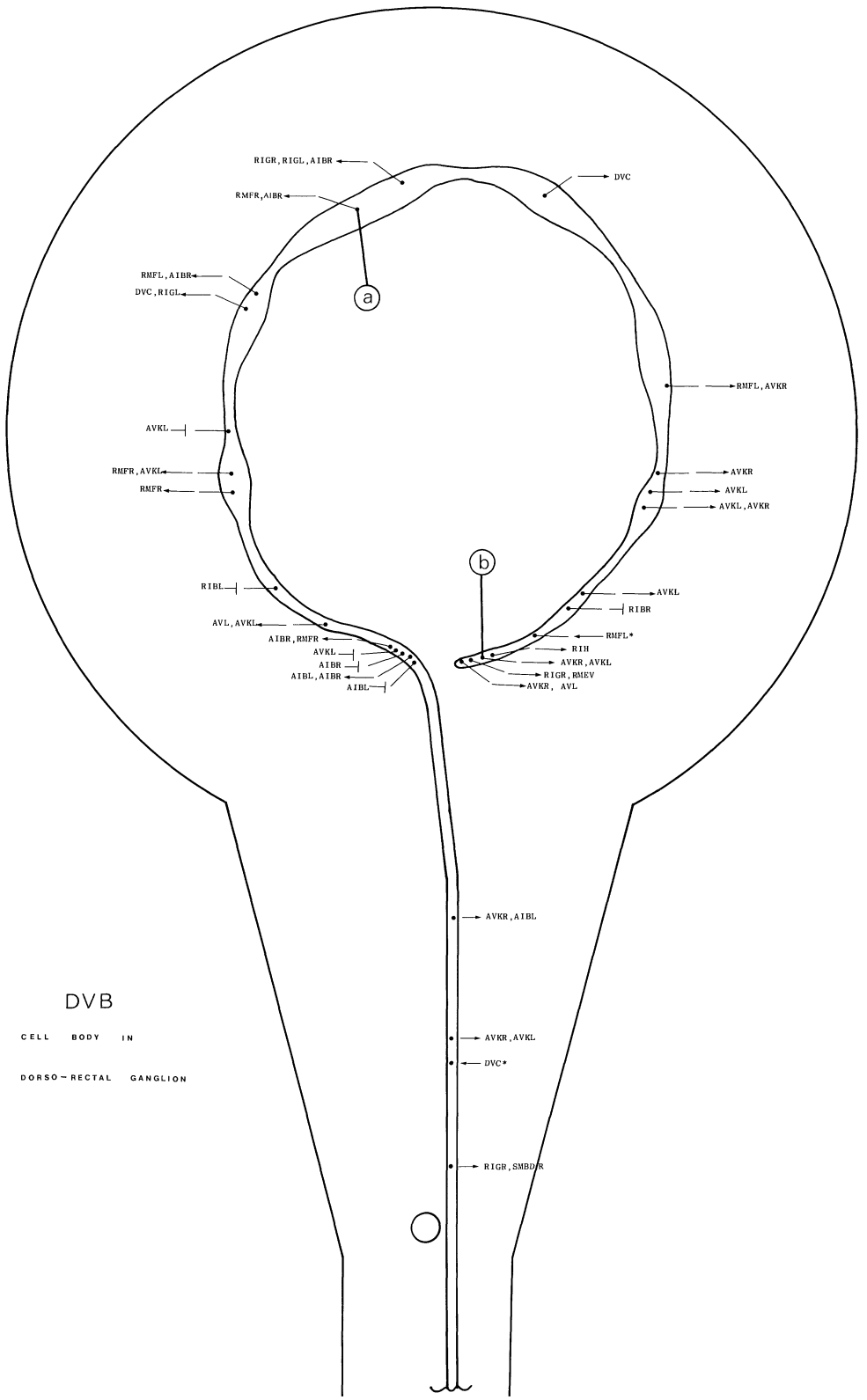
DVA is a single interneuron with its cell body situated in the dorso-rectal ganglion. An anteriorly directed process enters the pre-anal ganglion (i) and runs in the ventral part of the process bundle for the whole length of the ventral cord. It enters the nerve ring on the right-hand side and travels right round it in an anticlockwise direction (h) running near the centre of the neuropile in close association with the process of AQR; it then ends shortly after rejoining the ventral cord on the left hand side. The process of DVA is generally rather large and has large, vesicle-filled varicosities in the nerve ring (b). The vesicles tend to be irregularly shaped, except in the vicinity of the presynaptic specializations, where they are smaller and more spherical (a, b). In the nerve ring the main synaptic output is to AVE (a, b, e); there are some smaller synapses to RIR (e), AVA (c), AQR (c), SMB, AIZ and AUA (b) and there are gap junctions to AVB (g). There is a little synaptic input from AIZ and SDQ (*a). In the ventral cord there are some small synapses to PVC (f), PVR, DBn (f) and VBn (d); there are several synapses from PDE (*a) and some from PHC (*c), PLM (*e), PHA (*a) and PVD (*d); there are gap junctions to PVR.

Magnifications: (a, b, d, g) ×25500, (c, e, f) ×17000.

DVA VENTRAL CORD SYNAPSES

partners	gap junctions	synapses from	synapses to and corecipients
PVC	1	3 m	2DB7, DB5, DB3
PDE	—	22+14 m	1, VB11
PVR	2	—	1, DB2
DB3	—	—	1, PVC
DB7	—	—	2PVC
VB11	—	—	PDE, VA12
DB4	—	—	1
VA12	—	—	VB11
DB2	—	—	PVR
DB5	—	—	PVC
PHC	—	4+7 m	—
PLM	—	5 m	—
PHA	—	1+3 m	—
PVM	—	2+1 m	—
AVK	—	1	—

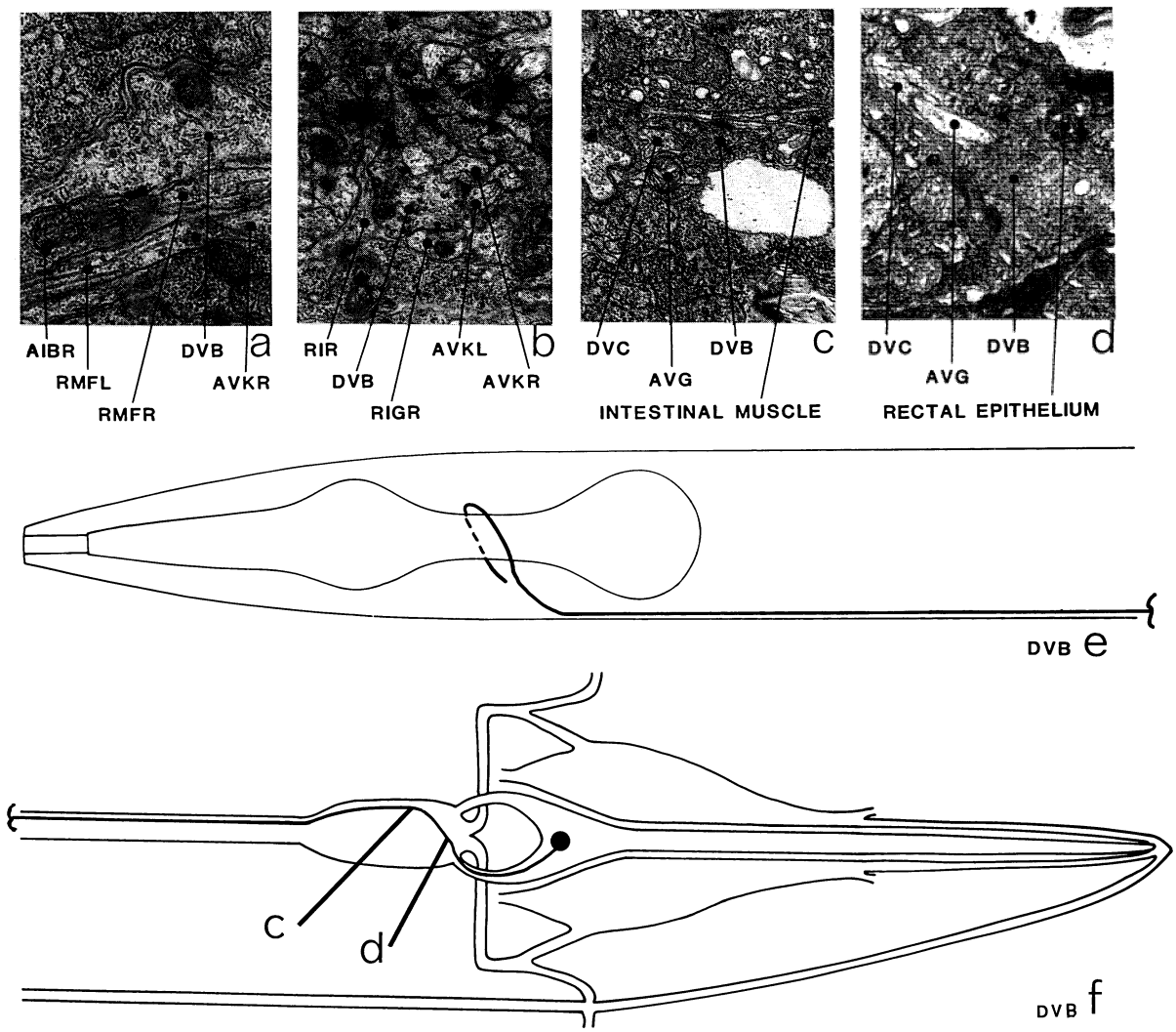
DVB



DVB

CELL BODY IN

DORSO-RECTAL GANGLION



DVB

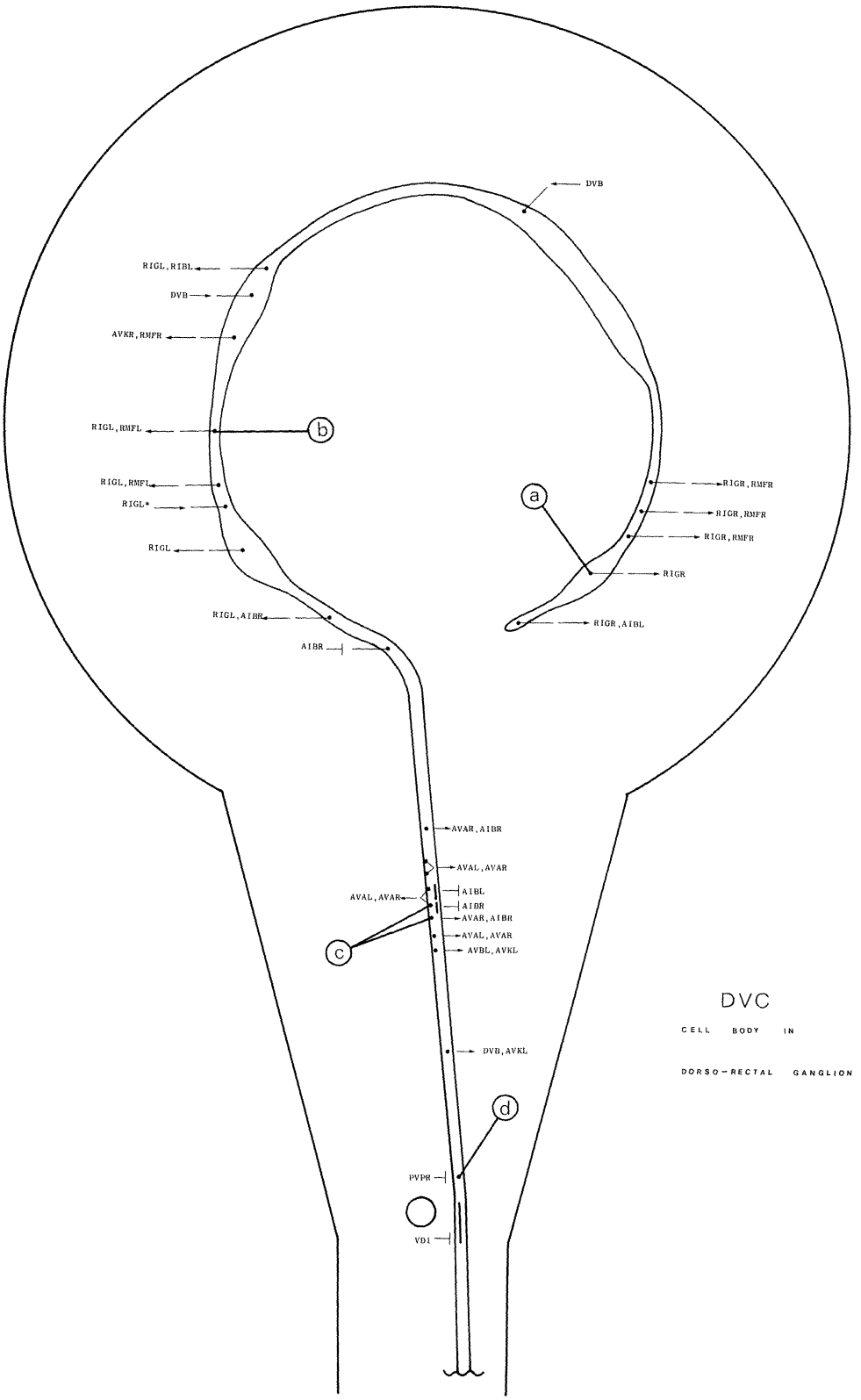
Member: DVB.

DVB is a single interneuron/motoneuron with its cell body situated in the dorso-rectal ganglion. An anteriorly directed process enters the ventral cord and runs in the dorsal regions of the process bundle until the nerve ring is reached. This then enters the nerve ring close to the ventral mid-line and runs right round it in a clockwise direction on the outside surface of the neuropile. At all times along its length, the process of DVB runs in close association with that of DVC. In the nerve ring the main synaptic output is to AVK (b), AIB (a), RMF (a), DVC and RIG and there are gap junctions to AVK, RIB and AIB. The synaptic activity in the ventral cord is restricted to the pre-anal ganglion, where there are NMJs to the intestinal and anal depressor muscles (c), and also synapses to the rectal epithelial cell (d), AVL, DA8, DD6, PDA and DVC. Some of the presynaptic endings in the nerve ring have a few dark-cored vesicles (b). There is a gap junction to AVL.

Magnifications: (a, c, d) $\times 25500$, (b) $\times 17000$.

DVB VENTRAL CORD SYNAPSES

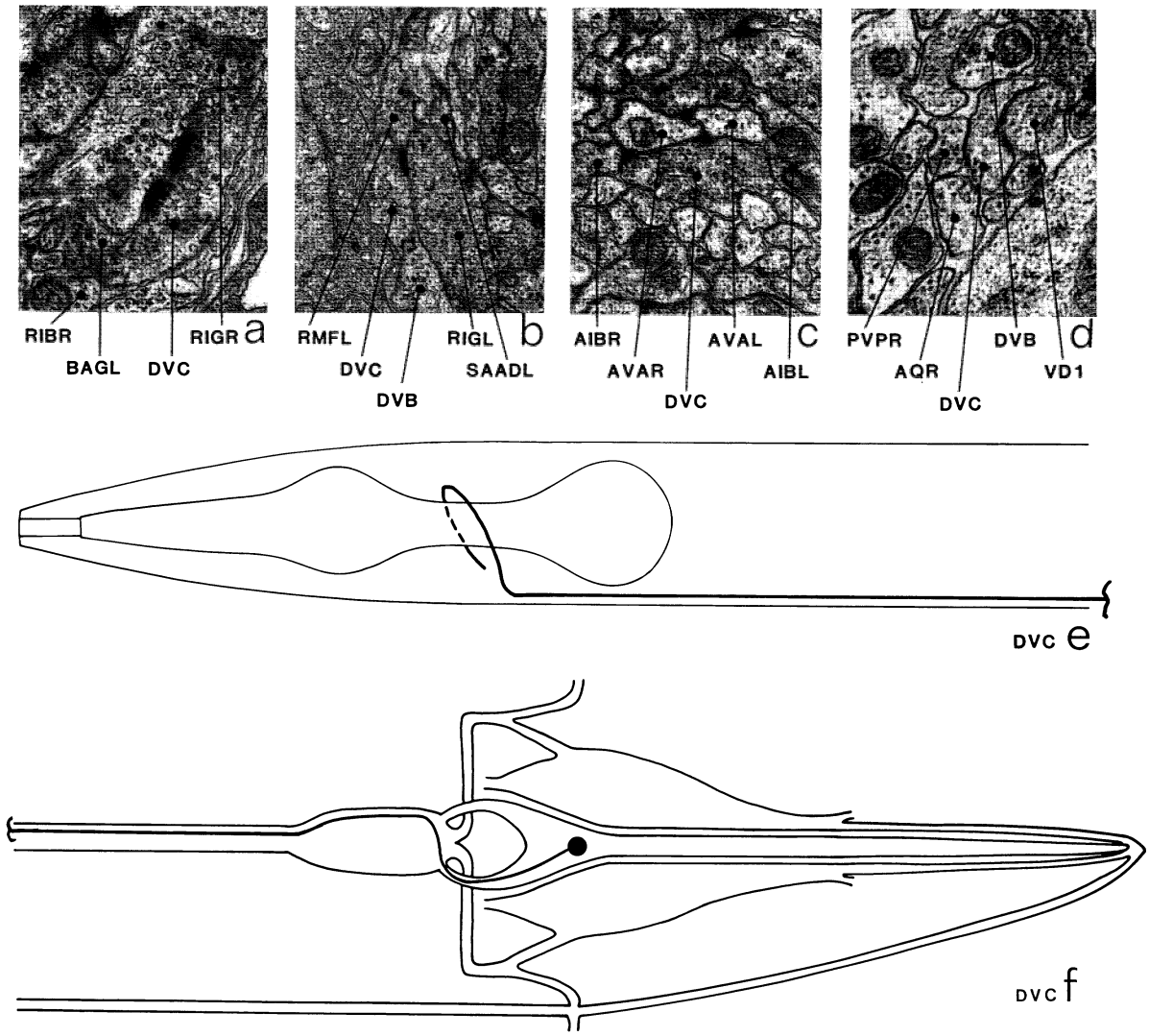
partners	gap junctions	synapses from	synapses to and corecipients
NMJ	—	—	4, DA8
HDC	—	—	2, 3DVC
AVL	1	—	2DD6, PVP
DVC	—	—	3HDC
DD6	—	—	2AVL, DA8
DA8	—	—	DD6, NMJ
PVP	—	—	1, AVL
PDA	—	—	PHC
PHC	—	—	PDA
VC2	—	2 m	—
AVG	—	1	—
VA9	—	1 m	—
AVE	—	1 m	—
VC5	—	1 m	—
PVQ	—	1 m	—



DVC

CELL BODY IN

DORSO-RECTAL GANGLION



DVC

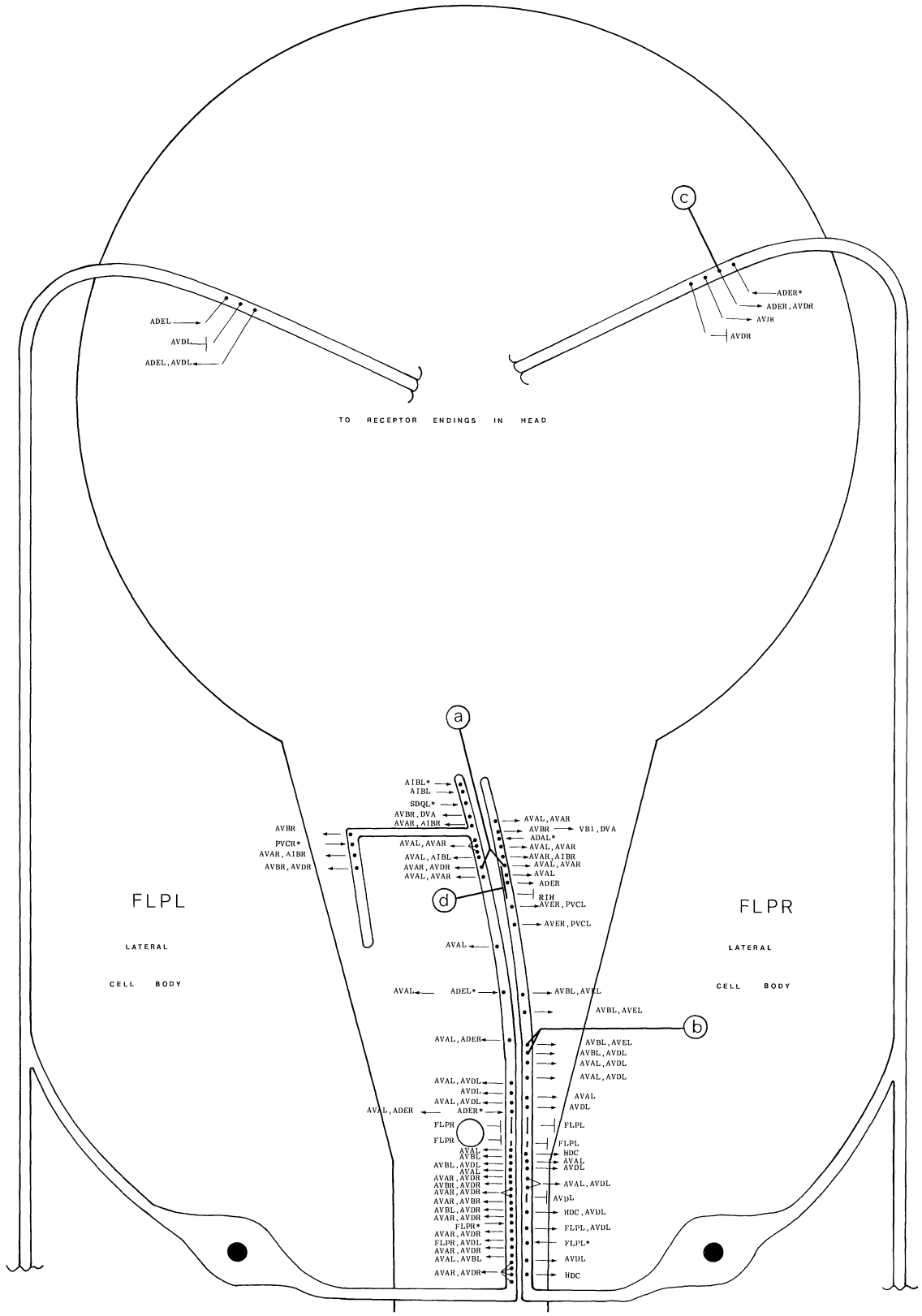
Member: DVC.

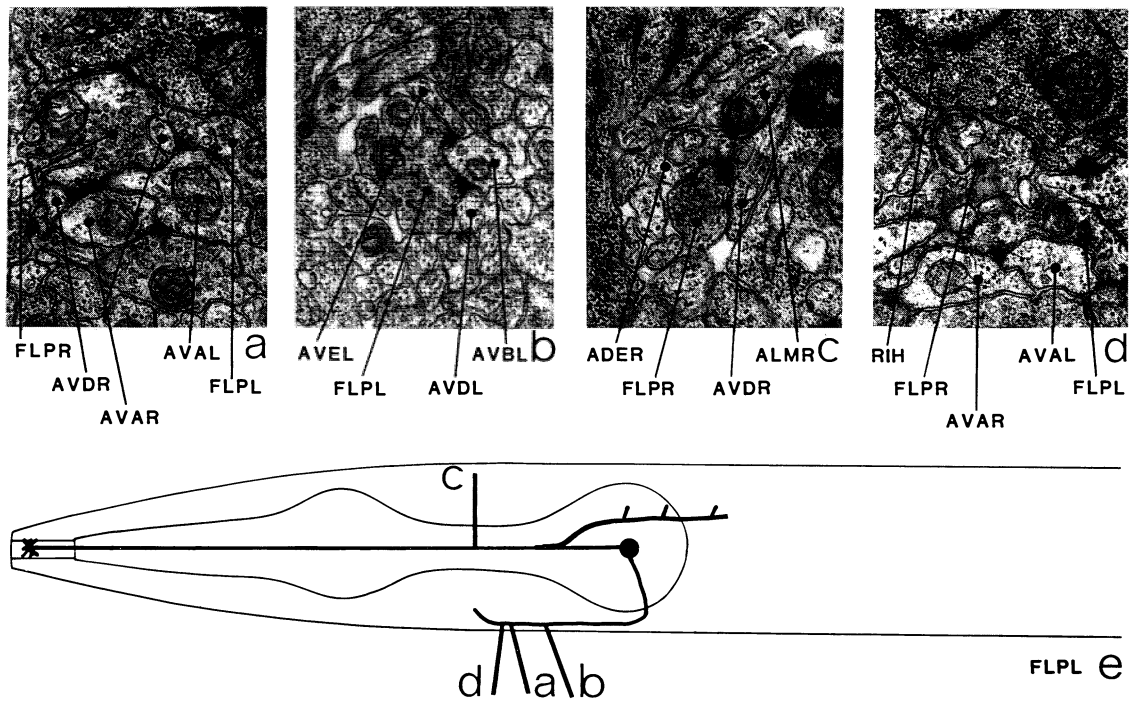
DVC is a single interneuron with its cell body situated in the dorso-rectal ganglion. An anteriorly directed process enters the ventral cord and runs in the dorsal part of the process bundle until the nerve ring is reached. It enters the nerve ring close to the ventral mid-line and then runs right round it in a clockwise direction on the outside surface of the neuropile. At all times along its length, the process of DVC runs in close association with that of DVB. In the nerve ring the main synaptic output is to RIG (a, b), AVA (c), AIB (c) and RMF (b), and there are gap junctions to AIB. In the ventral cord there is some synaptic input from DVB and there are also many gap junctions to PVP (d) and several rather marginal gap junctions to AVL and VD1.

Magnifications: (a, d) ×25500, (b, c) ×17000.

DVC VENTRAL CORD SYNAPSES

partners	gap junctions	synapses from	synapses to and corecipients
PVP	12	1+1 m	—
AVL	9	—	—
VD1	3	—	—
DVB	—	3 m	—
VC5	—	2 m	—
AVD	—	1	—
VC1	—	1 m	—
VC2	—	1 m	—
PVQ	—	1 m	—


c
ADER*
ADER, AVDR
AVJR
AVDR
ADEL
AVDL
ADEL, AVDL
TO RECEPTOR ENDINGS IN HEAD
a
AIBL*
AIBL
SDQL*
AVBR, DVA
AVAR, AIBR
AVAL, AVAR
AVBR
VB1, DVA
ADAL*
AVAL, AVAR
AVAR, AIBR
AVAL, AVAR
AVAL
ADER
RIH
AVER, PVCL
AVER, PVCL
AVBR
PVCR*
AVAR, AIBR
AVBR, AVDR
AVAL, AVAR
AVAL, AIBL
AVAR, AVDR
AVAL, AVAR
d
FLPL
LATERAL
CELL BODY
FLPR
LATERAL
CELL BODY
AVAL
AVAL
ADEL*
AVBL, AVEL
AVBL, AVEL
b
AVAL, ADER
AVBL, AVEL
AVBL, AVDL
AVAL, AVDL
AVAL, AVDL
AVDL
AVAL, AVDL
AVAL, ADER
ADER*
AVAL
AVDL
FLPR
FLPL
FLPR
FLPL
AVAL
AVBL
AVBL, AVDL
AVAL
AVAR, AVDR
AVBR, AVDR
AVAR, AVDR
AVAR, AVBR
AVBL, AVDR
AVAR, AVDR
FLPR*
AVAR, AVDR
FLPR, AVDL
AVAR, AVDR
AVAL, AVBL
AVAR, AVDR
HDC
AVAL
AVDL
AVAL, AVDL
AVDL
HDC, AVDL
FLPL, AVDL
FLPL*
AVDL
HDC

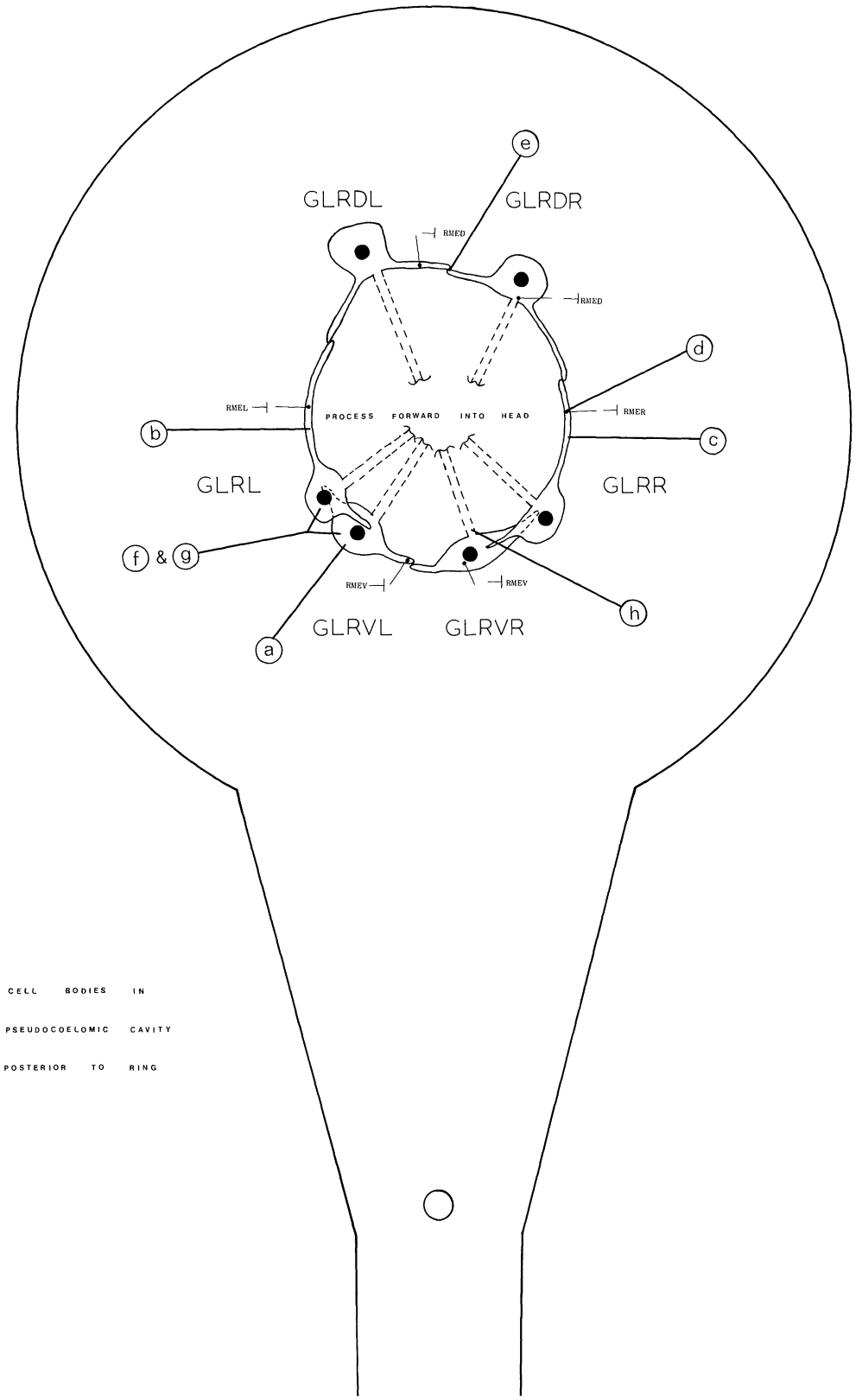


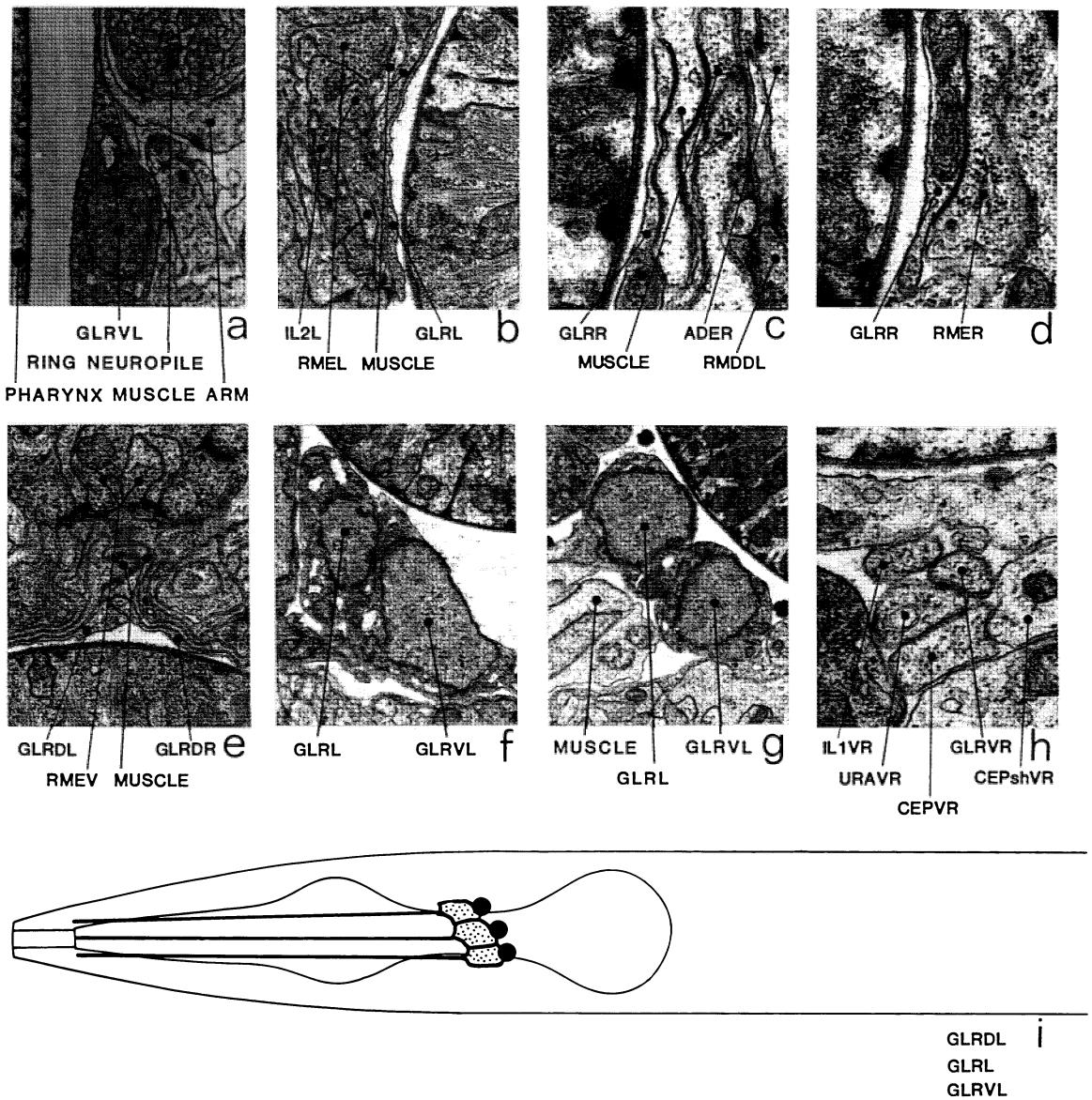
FLP

Members: FLPL, FLPR.

FLP is a set of two neurons, which have ciliated endings situated immediately dorsal to the lateral inner labial sensilla in the head but have no associated sheath or socket cells. They have flattened processes in this region of the cilium (figure 1). The processes from the endings run down in the lateral labial process bundles but do not enter the nerve ring along with the other processes; instead they continue posteriorly and join up with their cell bodies laterally. A branch comes off this process anterior to the cell body and runs backwards alongside the dorsal muscle quadrants. Small processes emanate from this branch and run underneath the muscles for a short distance (e). Processes from the cell bodies enter the retro-vesicular ganglion via the deirid commissures and run together anteriorly, near the middle of the cord, ending before the nerve ring is reached. Most of the synaptic interactions occur in this region of the cord but there are also a few synapses on the lateral processes in the vicinity of the nerve ring (c). The main synaptic outputs are to AVA (a), AVD (a, b), AVB (b), AIB and ADE (c) in various dyadic combinations. There is possibly some synaptic input from ADE. There are gap junctions to RIH (d), AVD and itself.

Magnifications: (a, c, d) $\times 25500$, (b) $\times 17000$.


e
GLRDL
GLRDR
RMED
RMED
d
RMEL
PROCESS FORWARD INTO HEAD
RMER
b
c
GLRL
GLRR
f & g
RMEV
RMEV
h
a
GLRVL
GLRVR
CELL BODIES IN
PSEUDOCOELOMIC CAVITY
POSTERIOR TO RING



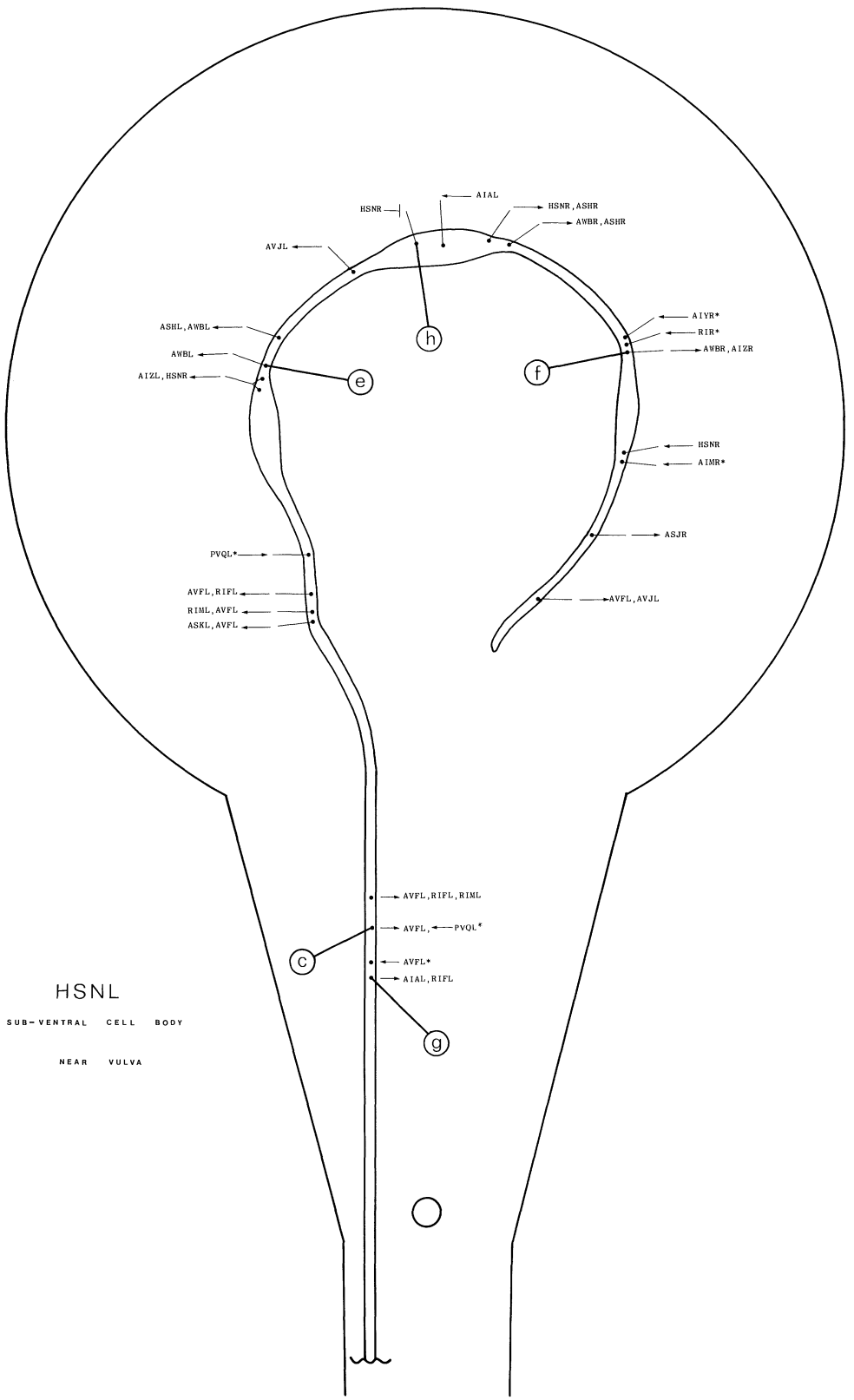
GLR

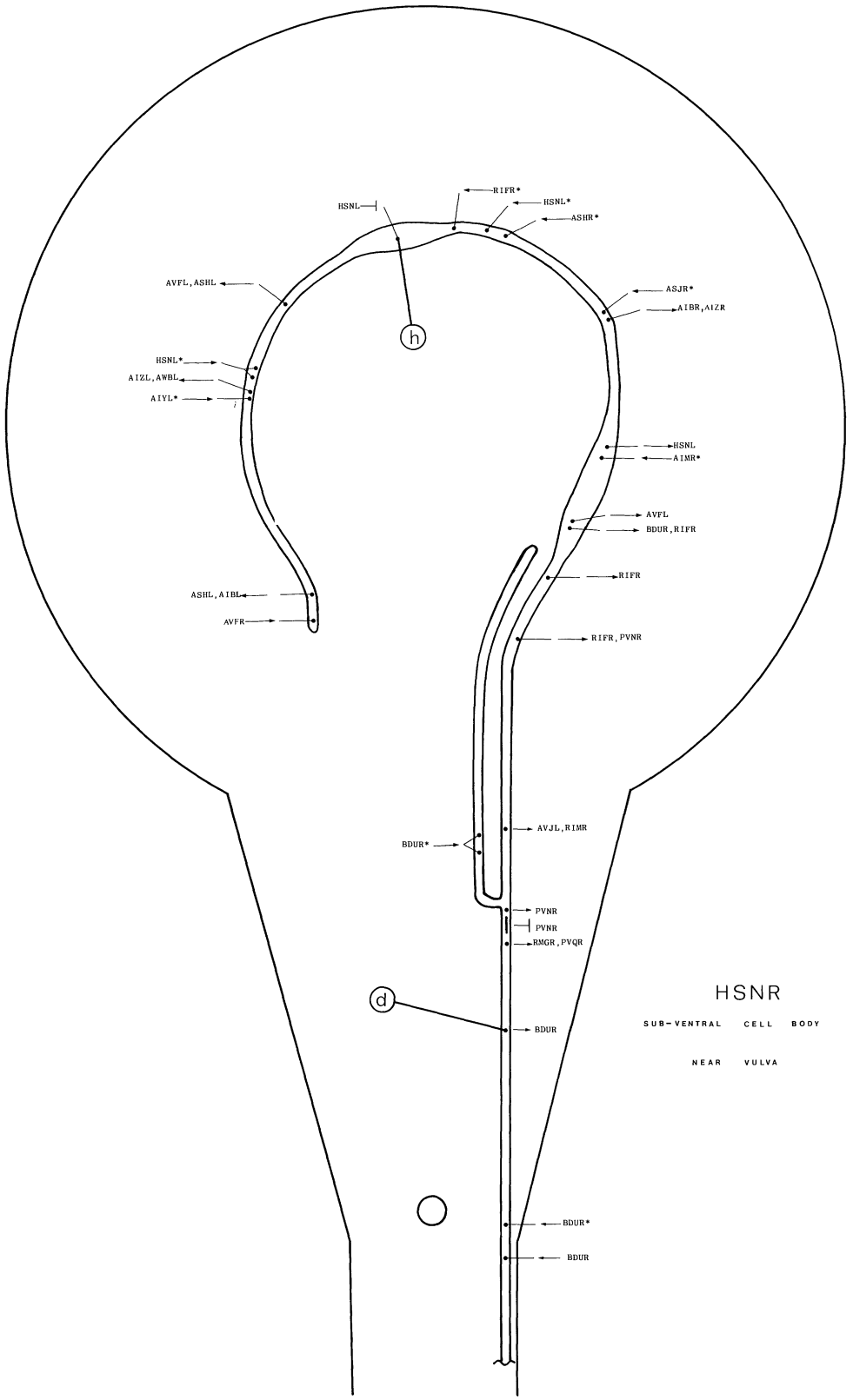
Members: GLRL, GLRR, GLRVR, GLRDL, GLRVL, GLRDR.

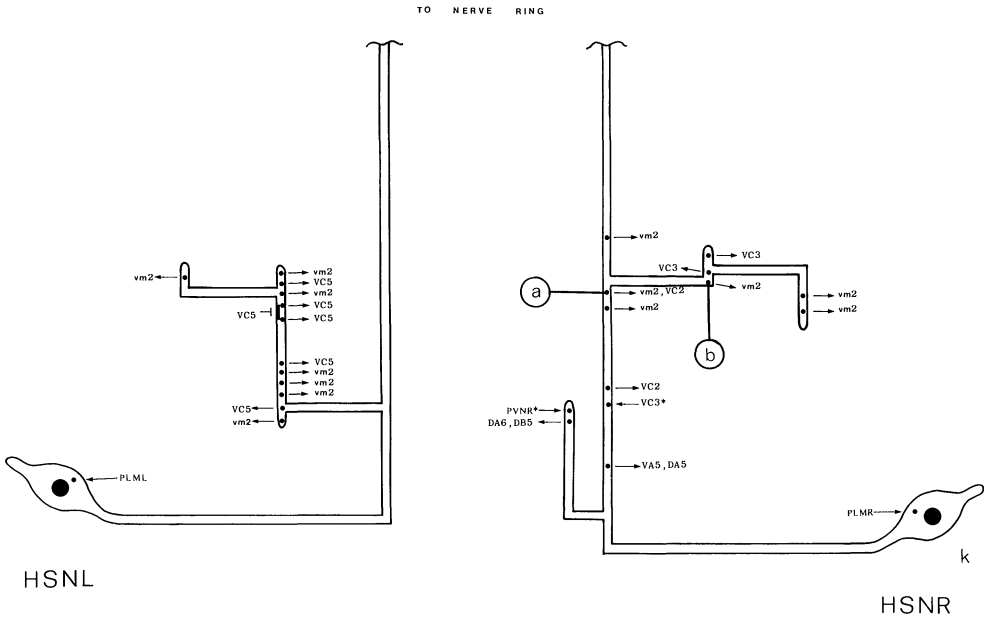
GLR is a set of six cells that are situated posteriorly to the nerve ring, close to the neuropile (a). Cell bodies are situated in a sixfold symmetrical arrangement and send processes that project anteriorly and run adjacent to the pharynx. All six processes peter out and end, with no terminal specializations, at the level of the junction of the pharynx and the buccal cavity. Each process flattens out into a sheet, which touches its neighbour on each side, forming a cylinder as they pass the inside surface of the nerve ring. Muscle arms from the head muscles run posteriorly down the outside of the nerve ring and then turn to run anteriorly, next to the inside surface of the nerve ring, where they are sandwiched between the cylinder of GLR cells and the motor endplate region of the nerve ring (a, b, c). It is in this region that the muscle arms receive their synaptic input from the motoneurons of the nerve ring. The muscle arms

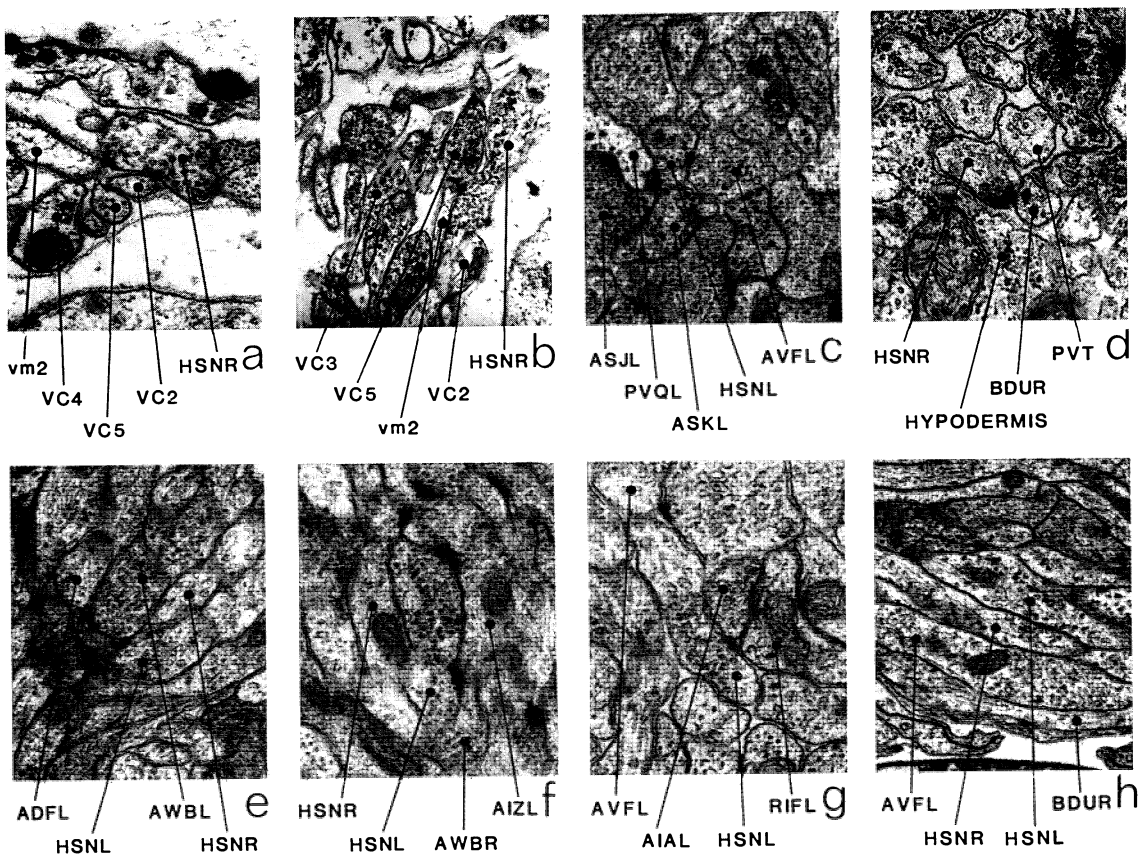
are highly ordered in this region, arms from individual muscle rows running along specific GLR cells (figure 15). Gap junctions are seen between GLR cells and muscle arms (c) and also RME motoneurons (d), but not between adjacent GLR cells even though they touch in this region (e). At the anterior extremity of the ring the GLR processes lose their sheet-like morphology and revert to a small cylindrical form. These processes run anteriorly and are always closely apposed with the IL1 (h) dendrites until they end. The nuclei of the GLR cells are small and the cytoplasm contains large, irregularly shaped, membrane-bound vesicles, which are more prominent in the larva (f) than the adult stages (g). No chemical synapses have been seen either to or from these cells. The disposition and the layout of these cells suggest that they might be glial cells and might act to guide growing muscle arms and the sensory dendrites from each of the labia in the head.

Magnifications: (a, f, g) $\times 8500$, (b, e) $\times 12750$, (c, d, h) $\times 25500$.


AIAL
HSNR
HSNR,ASHR
AWBR,ASHR
AVJL
ASHL,AWBL
AWBL
AIZL,HSNR
h
e
f
AIYR*
RIR*
AWBR,AIZR
HSNR
AIMR*
ASJR
PVQL*
AVFL,RIFL
RIML,AVFL
ASKL,AVFL
AVFL,AVJL
AVFL,RIFL,RIML
AVFL,
PVQL*
AVFL*
AIAL,RIFL
c
g
HSNL
SUB-VENTRAL CELL BODY
NEAR VULVA


RIFR*
HSNL
HSNL*
ASHR*
AVFL,ASHL
ASJR*
AIBR,AIZR
h
HSNL*
AIZL,AWBL
AIYL*
HSNL
AIMR*
AVFL
BDUR,RIFR
RIFR
ASHL,AIBL
AVFR
RIFR,PVNR
BDUR*
AVJL,RIMR
PVNR
PVNR
RMGR,PVQR
d
BDUR
HSNR
SUB-VENTRAL CELL BODY
NEAR VULVA
BDUR*
BDUR


TO NERVE RING
vm2
vm2
VC5
vm2
VC5
VC5
VC5
vm2
vm2
vm2
VC5
vm2
PLML
HSNL
vm2
VC3
VC3
a
vm2, VC2
vm2
vm2
vm2
b
VC2
VC3*
PVNR*
DA6, DB5
VA5, DA5
PLMR
k
HSNR


vm2
VC4
VC5
VC2
HSNR a
VC3
VC5
vm2
VC2
HSNR b
ASJL
PVQL
ASKL
HSNL
AVFL c
HSNR
HYPODERMIS
BDUR
PVT d
ADFL
HSNL
AWBL
HSNR e
HSNR
HSNL
AWBR
AIZL f
AVFL
AIAL
HSNL
RIFL g
AVFL
HSNR
HSNL
BDUR h
HSNL i
b
a
HSNL j

HSN

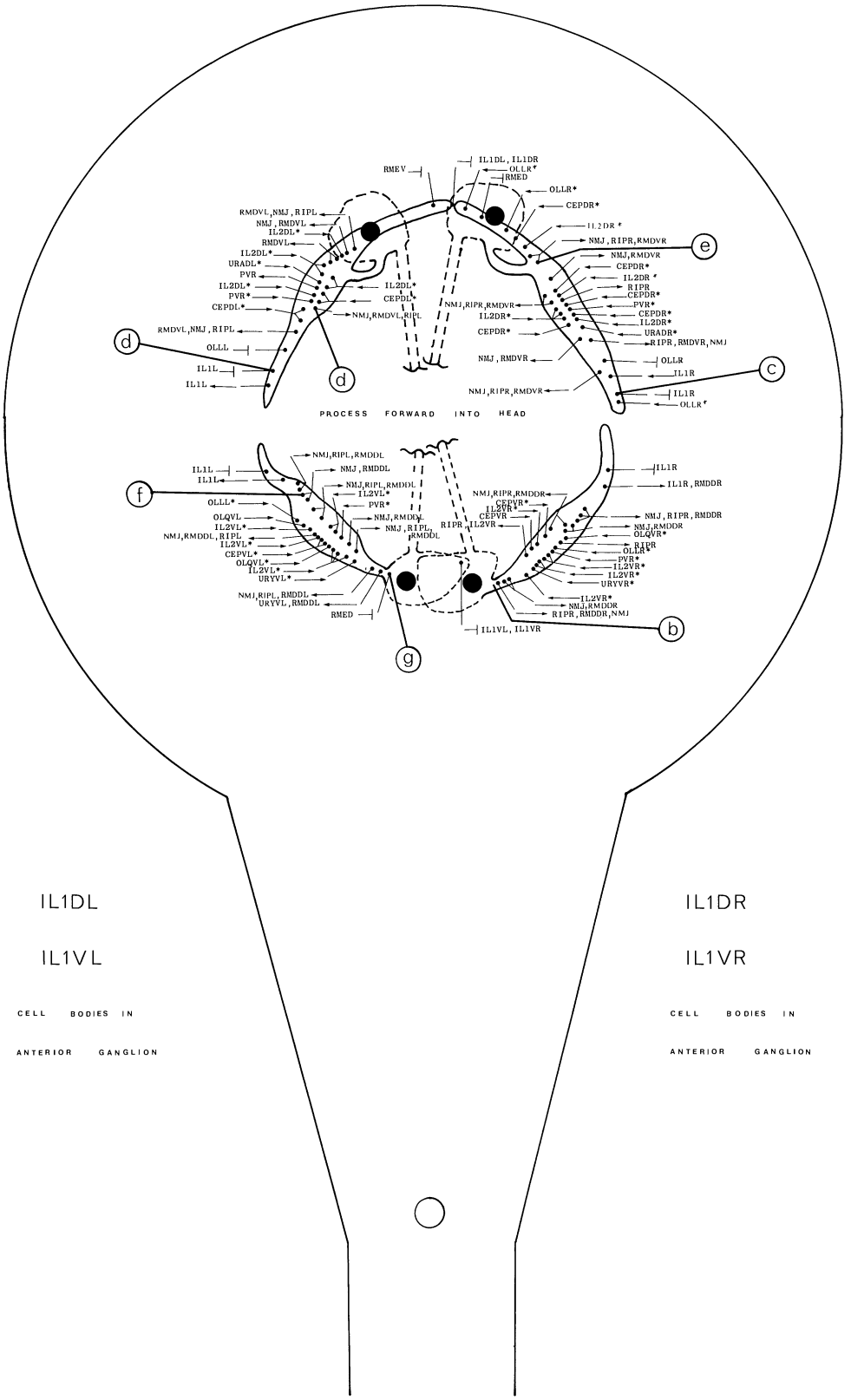
Members: HSNL, HSNR.

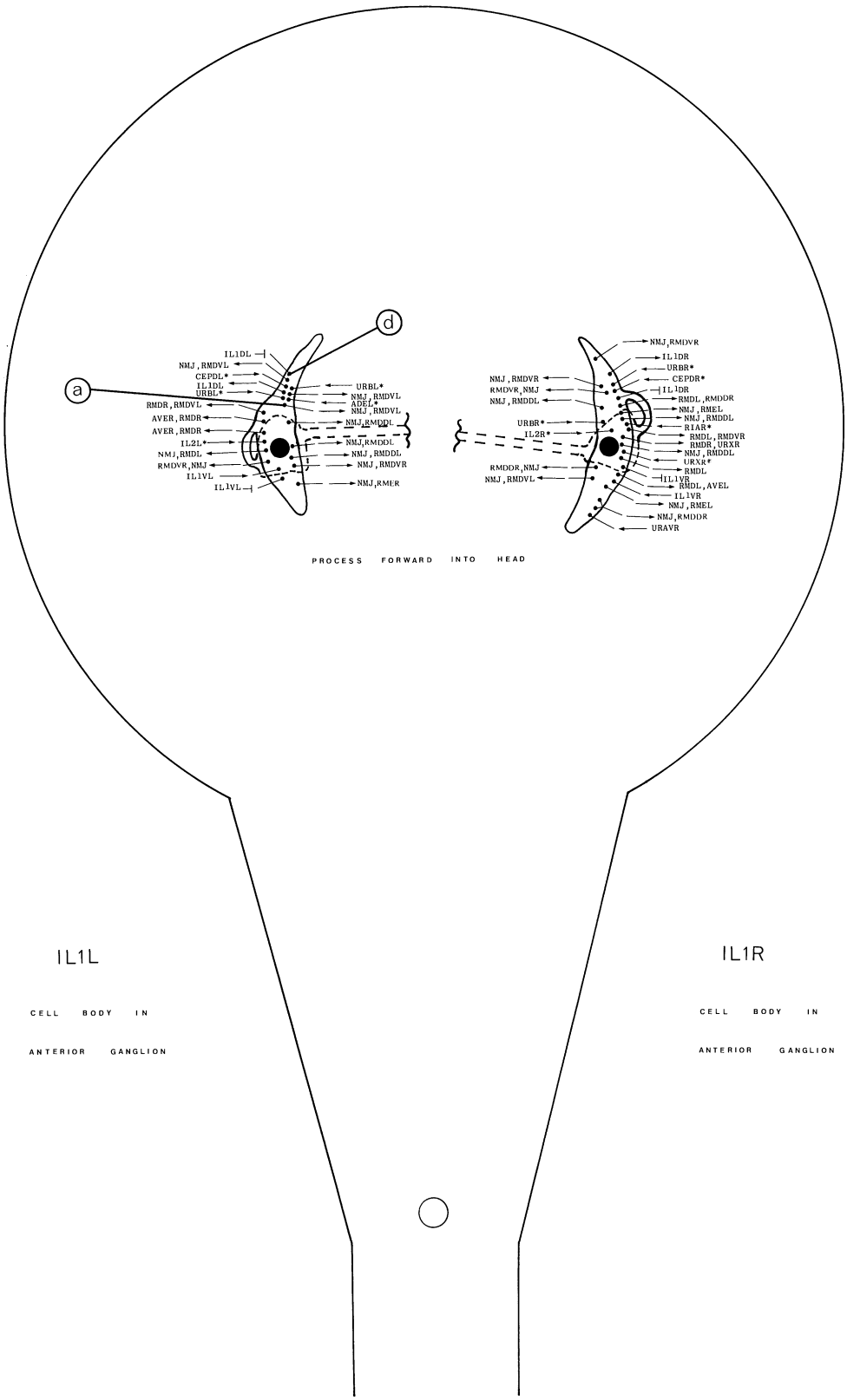
HSN is a set of two motoneurons that innervate vulval muscles in the hermaphrodite. The cell bodies of HSN are situated sub-ventrally just posterior to the vulva. A few short branches come off the processes in the vicinity of the vulva which have several synapses. The main processes enter the ventral cord and run anteriorly on either side of the ventral hypodermal ridge eventually entering the nerve ring. The processes of HSN run right round the ring near the posterior surface and end ventrally. Processes from HSN neurons were not present in the JSH animal and so, presumably, they must grow into the nerve ring sometime during or after the L4 larval stage. The main synaptic output from HSN is on the branches near the cell body. The VCn axons and the processes from HSN separate dorsally from the main body of the cord in this region (VCn-a). There are fairly large NMJs to the vm2 muscles of the vulva and synapses onto VCn (a, b). In the nerve ring the synapses tend to be rather smaller and are directed predominantly to AVF (c), BDU (d), AWB (e, f), RIF (g), AIZ (f) and AVJ. Several neurons make odd synapses onto HSN but none looks particularly significant, except perhaps BDU (*d), AVF (a) and also PLM (*g), which synapses onto HSN near its cell bodies. The processes of HSN have a gap junction between them on the dorsal mid-line (h) although they do not terminate at this point.

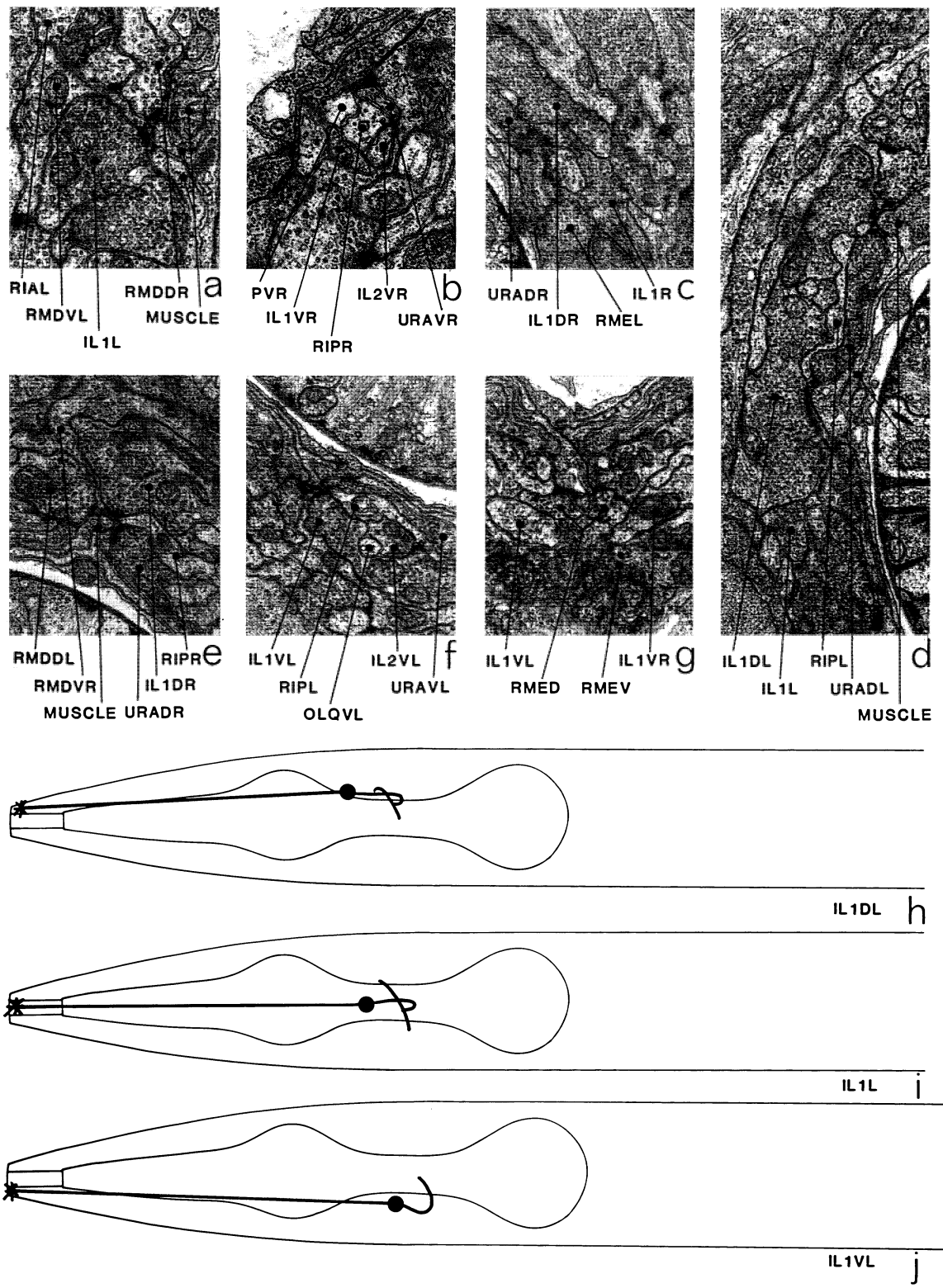
Magnifications: (a, d, g) ×25500, (b, h) ×12750, (c, e, f) ×17000.

HSN VENTRAL CORD SYNAPSES

partners	gap junctions	synapses from	synapses to and corecipients
VUL, NMJ	—	—	15
VC5	—	—	5
NMJ	—	—	2, VC2
SABV	—	—	1, 2AVD
AVD	—	—	2SABV, AVE
BDU	—	1+2 m	—
AVL	—	1	—
SABD	—	—	1
VC2	—	—	NMJ, Vm2
AS5	—	—	1
PLM	—	2	—
AVB	—	1	—
AVJ	—	1	—
PVQ	—	1	—
PVN	—	1 m	—
VA6	—	—	DA5
DA5	—	—	VA6
DA6	—	—	1
AVG	—	1 m	—


IL1DL, IL1DR
RMEV
OLLR*
RMED
OLLR*
CEPDR*
IL2DR*
NMJ, RIPR, RMDVR
e
NMJ, RMDVR
CEPDR*
IL2DR*
RIPR
CEPDR*
PVR*
CEPDR*
IL2DR*
URADR*
RIPR, RMDVR, NMJ
OLLR
IL1R
IL1R
OLLR*
RMDVL, NMJ, RIPL
NMJ, RMDVL
IL2DL*
RMDVL
IL2DL*
URADL*
PVR
IL2DL*
PVR*
CEPDL*
RMDVL, NMJ, RIPL
OLLL
IL1L
IL1L
d
d
IL2DL*
CEPDL*
NMJ, RMDVL, RIPL
NMJ, RIPR, RMDVR
IL2DR*
CEPDR*
NMJ, RMDVR
NMJ, RIPR, RMDVR
c
PROCESS FORWARD INTO HEAD
NMJ, RIPL, RMDDL
IL1L
IL1L
NMJ, RMDDL
NMJ, RIPL, RMDDL
IL2VL*
PVR*
f
OLLL*
OLQVL
IL2VL*
NMJ, RMDDL, RIPL
IL2VL*
CEPVL*
OLQVL*
IL2VL*
URYVL*
NMJ, RIPL, RMDDL
URYVL, RMDDL
RMED
NMJ, RMDDL
NMJ, RIPL, RMDDL
g
IL1VL, IL1VR
IL1R
IL1R, RMDDR
NMJ, RIPR, RMDDR
CEPVR*
IL2VR*
CEPVR
RIPR
IL2VR
NMJ, RIPR, RMDDR
NMJ, RMDDR
OLQVR*
RIPR
OLLR*
PVR*
IL2VR*
IL2VR*
URYVR*
IL2VR*
NMJ, RMDDR
RIPR, RMDDR, NMJ
b
IL1DL
IL1VL
CELL BODIES IN
ANTERIOR GANGLION
IL1DR
IL1VR
CELL BODIES IN
ANTERIOR GANGLION


d
a
IL1DL
NMJ , RMDVL
CEPDL*
IL1DL
URBL*
RMDR , RMDVL
AVER , RMDR
AVER , RMDR
IL2L*
NMJ , RMDL
RMDVR , NMJ
IL1VL
IL1VL
URBL*
NMJ , RMDVL
ADEL*
NMJ , RMDVL
NMJ , RMDDL
NMJ , RMDDL
NMJ , RMDDL
NMJ , RMDVR
NMJ , RMER
PROCESS FORWARD INTO HEAD
NMJ , RMDVR
IL1DR
URBR*
CEPDR*
IL1DR
RMDL , RMDDR
NMJ , RMEL
NMJ , RMDDL
RIAR*
RMDL , RMDVR
RMDR , URXR
NMJ , RMDDL
URXR*
RMDL
IL1VR
RMDL , AVEL
IL1VR
NMJ , RMEL
NMJ , RMDDR
URAVR
NMJ , RMDVR
RMDVR , NMJ
NMJ , RMDDL
URBR*
IL2R*
RMDDR , NMJ
NMJ , RMDVL
IL1L
CELL BODY IN
ANTERIOR GANGLION
IL1R
CELL BODY IN
ANTERIOR GANGLION

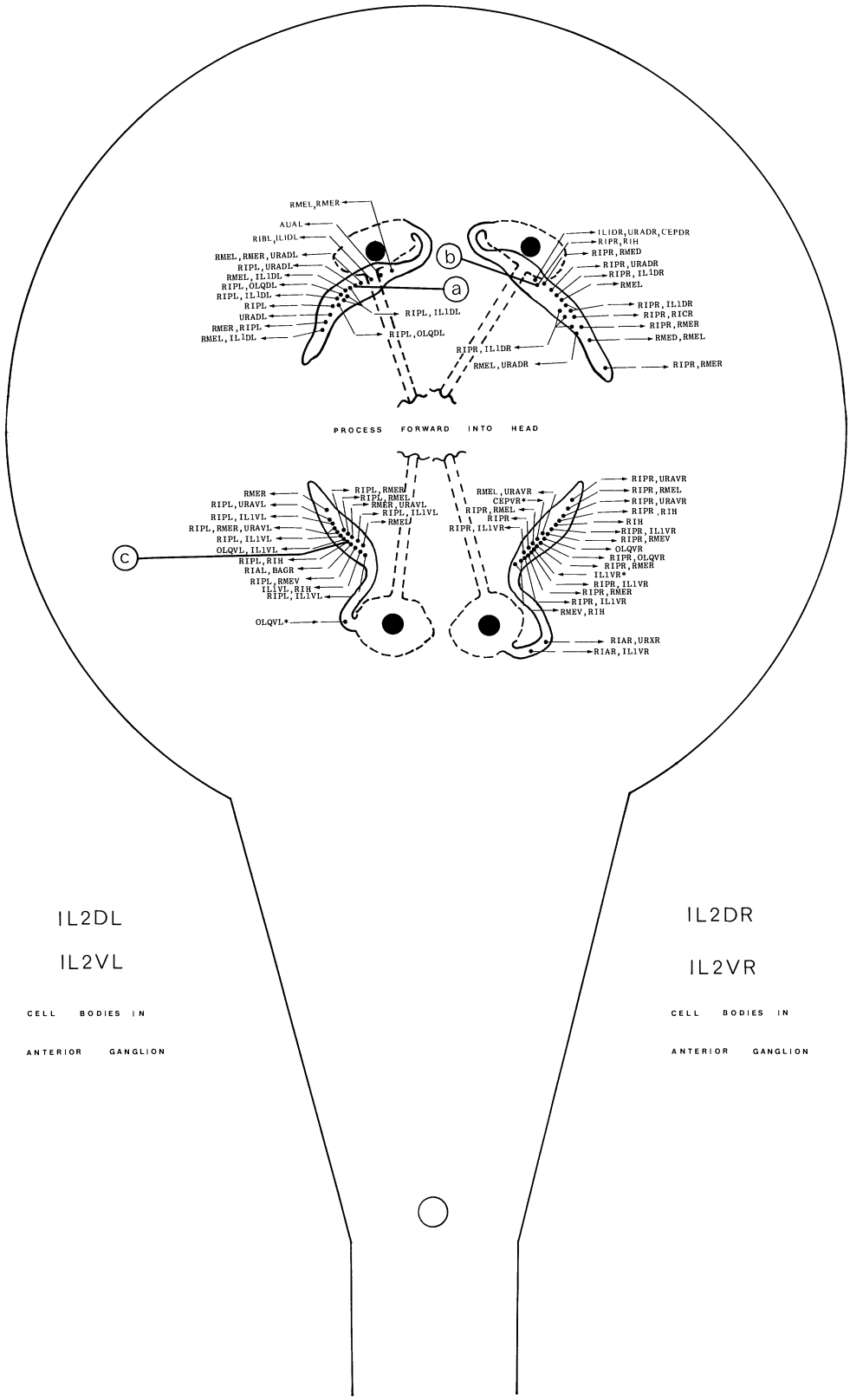

RIAL
RMDVL
IL1L
RMDDR
MUSCLE
a
PVR
IL1VR
RIPR
IL2VR
URAVR
b
URADR
IL1DR
RMEL
IL1R
c
IL1DL
IL1L
RIPL
URADL
MUSCLE
d
RMDDL
RMDVR
MUSCLE
IL1DR
URADR
RIPR
e
IL1VL
RIPL
OLQVL
IL2VL
URAVL
f
IL1VL
RMED
RMEV
IL1VR
g
IL1DL
h
IL1L
i
IL1VL
j

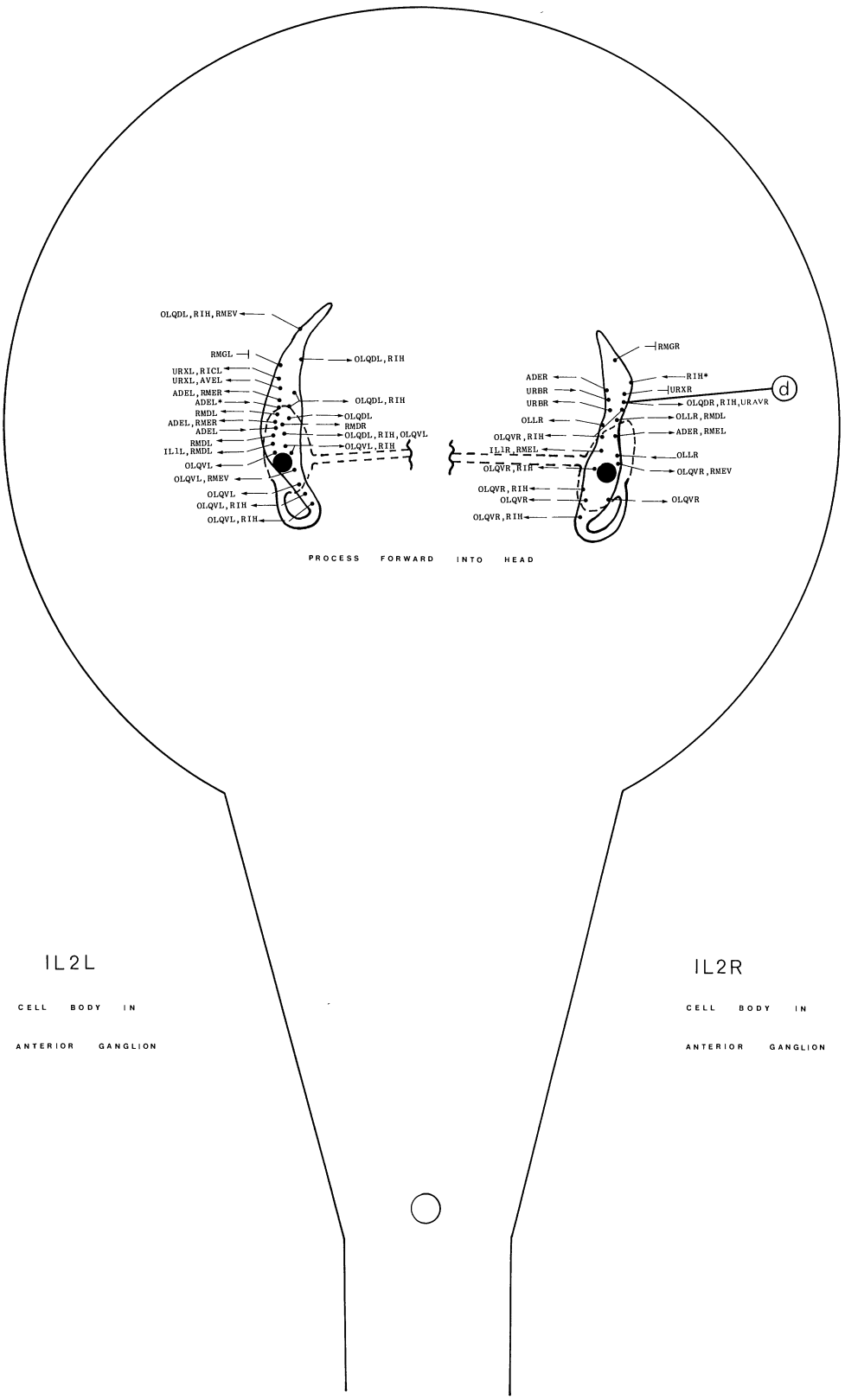
IL1

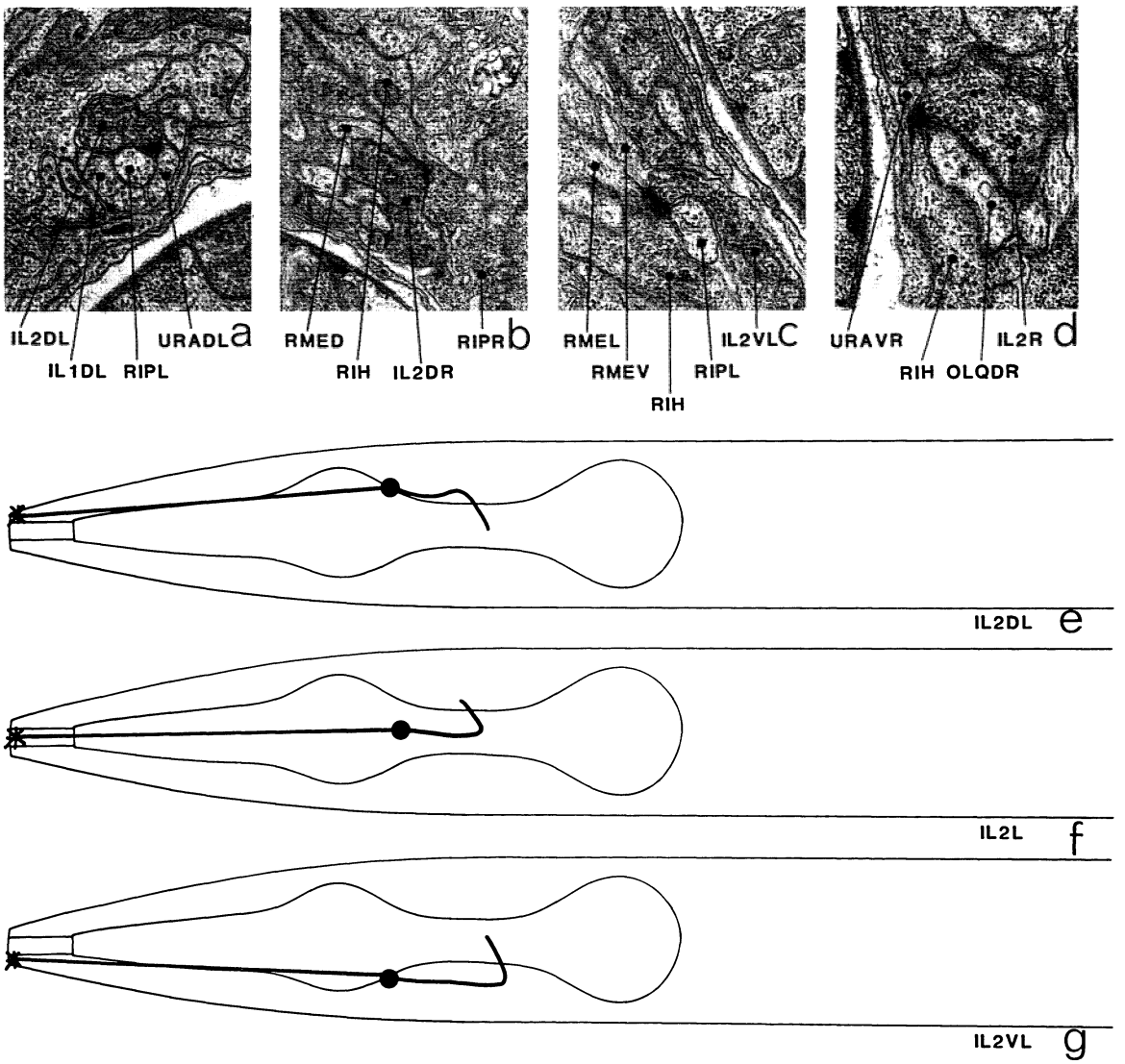
Members: IL1DL, IL1DR, IL1L, IL1R, IL1VL, IL1VR.

IL1 is a set of six ciliated neurons with striated rootlets, each of which is one of the two component neurons of the inner labial sensilla. Unlike IL2, the IL1 dendrite does not protrude through the hole in the socket cell to the outside. Processes of IL1 run posteriorly from the sensilla in each of the six labial process bundles. They run into their cell bodies, which are anterior to the ring; posteriorly directed processes from the cell bodies rejoin the process bundles, which pass down outside the ring, turn, and then run anteriorly near the inside of the ring (b) until the processes disperse in the anterior regions of the neuropile. Each of the IL1 processes runs for about 60° round the ring, terminating with a gap junction to the process of the neighbouring IL1 (c, d); thus the IL1s inhabit most of the circumference of the ring. IL1s are prominent motor neurons in the anterior regions of the ring and form characteristic synaptic complexes with RMD, URA and RIP (d). There are significant differences in the synaptic partners of the lateral IL1s (IL1L/R) from the others. The main synaptic outputs of IL1D/V are triadic NMJs, with RMD and RIP as the corecipients (e, f, d). IL1L/R has dyadic NMJs, with RMD as the corecipient (a). The main synaptic inputs to IL1D/V are IL2D/V and CEP (*e); IL1L/R only receives a few synapses from URB and CEP. IL1D/V have gap junctions to RME (g) and OLL.

Magnifications: (a, b) ×25500, (c–g) ×12750.


RMEL,RMER
AUAL
RIBL,IL1DL
RMEL,RMER,URADL
RIPL,URADL
RMEL,IL1DL
RIPL,OLQDL
RIPL,IL1DL
RIPL
URADL
RMER,RIPL
RMEL,IL1DL
RIPL,IL1DL
RIPL,OLQDL
a
b
IL1DR,URADR,CEPDR
RIPR,RIH
RIPR,RMED
RIPR,URADR
RIPR,IL1DR
RMEL
RIPR,IL1DR
RIPR,RICR
RIPR,RMER
RMED,RMEL
RIPR,RMER
RIPR,IL1DR
RMEL,URADR
PROCESS FORWARD INTO HEAD
RMER
RIPL,URAVL
RIPL,IL1VL
RIPL,RMER,URAVL
RIPL,IL1VL
OLQVL,IL1VL
RIPL,RIH
RIAL,BAGR
RIPL,RMEV
IL1VL,RIH
RIPL,IL1VL
OLQVL*
RIPL,RMER
RIPL,RMEL
RMER,URAVL
RIPL,IL1VL
RMEL
c
RMEL,URAVR
CEPVR*
RIPR,RMEL
RIPR
RIPR,IL1VR
RIPR,URAVR
RIPR,RMEL
RIPR,URAVR
RIPR,RIH
RIH
RIPR,IL1VR
RIPR,RMEV
OLQVR
RIPR,OLQVR
RIPR,RMER
IL1VR*
RIPR,IL1VR
RIPR,RMER
RIPR,IL1VR
RMEV,RIH
RIAR,URXR
RIAR,IL1VR
IL2DL
IL2VL
CELL BODIES IN
ANTERIOR GANGLION
IL2DR
IL2VR
CELL BODIES IN
ANTERIOR GANGLION


OLQDL, RIH, RMEV
RMGL
OLQDL, RIH
URXL, RICL
URXL, AVEL
ADEL, RMER
ADEL*
OLQDL, RIH
RMDL
ADEL, RMER
OLQDL
ADEL
RMDR
OLQDL, RIH, OLQVL
RMDL
IL1L, RMDL
OLQVL, RIH
OLQVL
OLQVL, RMEV
OLQVL
OLQVL, RIH
OLQVL, RIH
PROCESS FORWARD INTO HEAD
RMGR
ADER
RIH*
URBR
URXR
URBR
OLQDR, RIH, URAVR
OLLR
OLLR, RMDL
OLQVR, RIH
ADER, RMEL
IL1R, RMEL
OLLR
OLQVR, RIH
OLQVR, RMEV
OLQVR, RIH
OLQVR
OLQVR
OLQVR, RIH
d
IL2L
CELL BODY IN
ANTERIOR GANGLION
IL2R
CELL BODY IN
ANTERIOR GANGLION



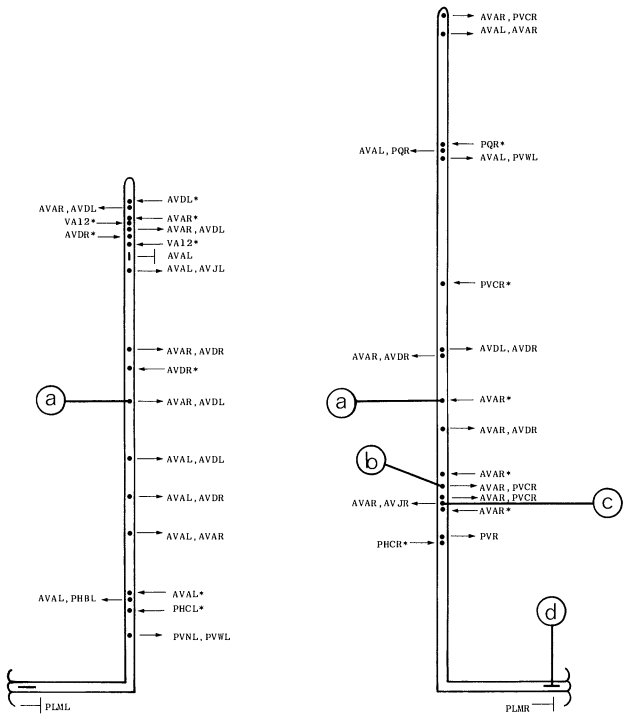
IL2

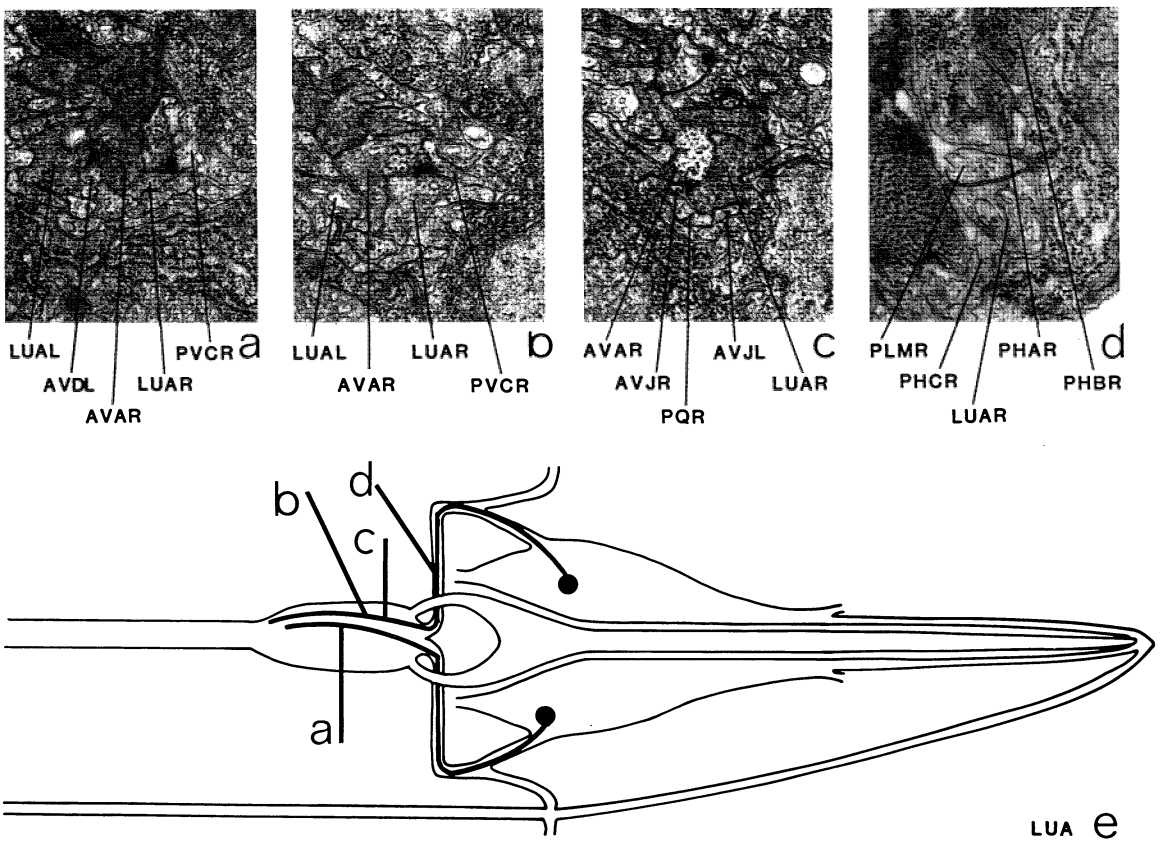
Members: IL2DL, IL2DR, IL2L, IL2R, IL2VL, IL2VR.

IL2 is a set of six ciliated neurons, each of which is one of the two component neurons of the six inner labial sensilla. The socket cell of each sensillum has a hole in it, through which the dendrite of IL2 protrudes. Processes of IL2 run posteriorly from the sensillum in each of the six labial process bundles and join their cell bodies, which are situated anterior to the ring neuropile. Posteriorly directed processes from the cell bodies rejoin the process bundles, which pass down the outside of the ring, turn and then run anteriorly (a) until the fibres disperse in the anterior regions of the neuropile. Here they run round the ring for about 60° until they are in the vicinity of the neighbouring IL2. Thus the processes of all the IL2 inhabit most of the circumference of the ring. There are some differences in the synaptic partners of the lateral IL2 (i.e. IL2L/R) from the others. The main synaptic outputs of IL2D/V are to RIP (a, b), IL1D/V, RME (c), URA (a), RIH (c) and OLQ; the main synaptic outputs of IL2L/R are to OLQ (d), RIH (d), ADE and RME. IL2L/R also have occasional dark-cored vesicles in their synapses (d) and have gap junctions with RMG and URX.

Magnifications: (a, c, d) ×25500, (b) ×12750.

LUAL LUAR


AVDL*
AVAR*
AVAR, AVDL
VA12*
AVAL
AVAL, AVJL
AVAR, AVDR
AVDR*
AVAR, AVDL
AVAL, AVDL
AVAL, AVDR
AVAL, AVAR
AVAL*
PHCL*
PVNL, PVWL
PLML
AVAR, AVDL
VA12*
AVDR*
a
AVAL, PHBL
AVAR, PVCR
AVAL, AVAR
PQR*
AVAL, PVWL
PVCR*
AVDL, AVDR
AVAR*
AVAR, AVDR
AVAR, PVCR
AVAR, PVCR
AVAR*
PVR
PLMR
AVAL, PQR
AVAR, AVDR
AVAR, AVJR
PHCR*
a
b
c
d

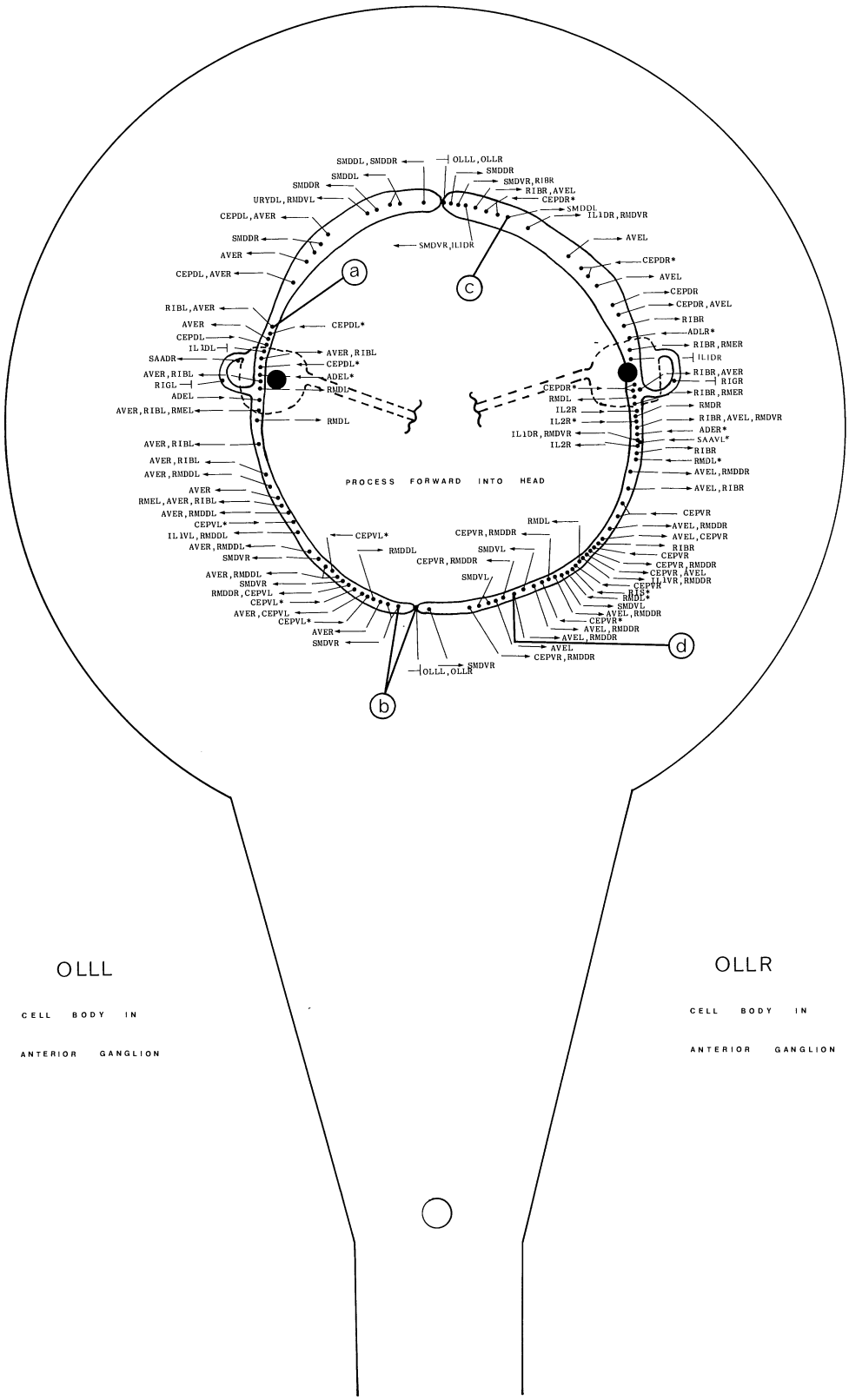


LUA

Members: LUAL, LUAR.

LUA is a set of two interneurons with cell bodies situated in the lumbar ganglia. Anteriorly directed processes leave the cell bodies and enter the pre-anal ganglion via the lumbar commissures (e). The processes of LUA run in the ventral regions of the neuropile of the pre-anal ganglion and terminate at the anterior end of the ganglion. LUA is quite synaptically active; its main postsynaptic partners are AVA (a, b, c) and AVD (a). There are also a few synapses to PVC (b) and AVJ (c). LUA receives some synaptic input from AVA (a) and possibly AVD. There are distinctive gap junctions between LUA and PLM in the lumbar commissures (d) and possibly a gap junction to AVA in the pre-anal ganglion.

Magnifications: (a–d) ×25500.

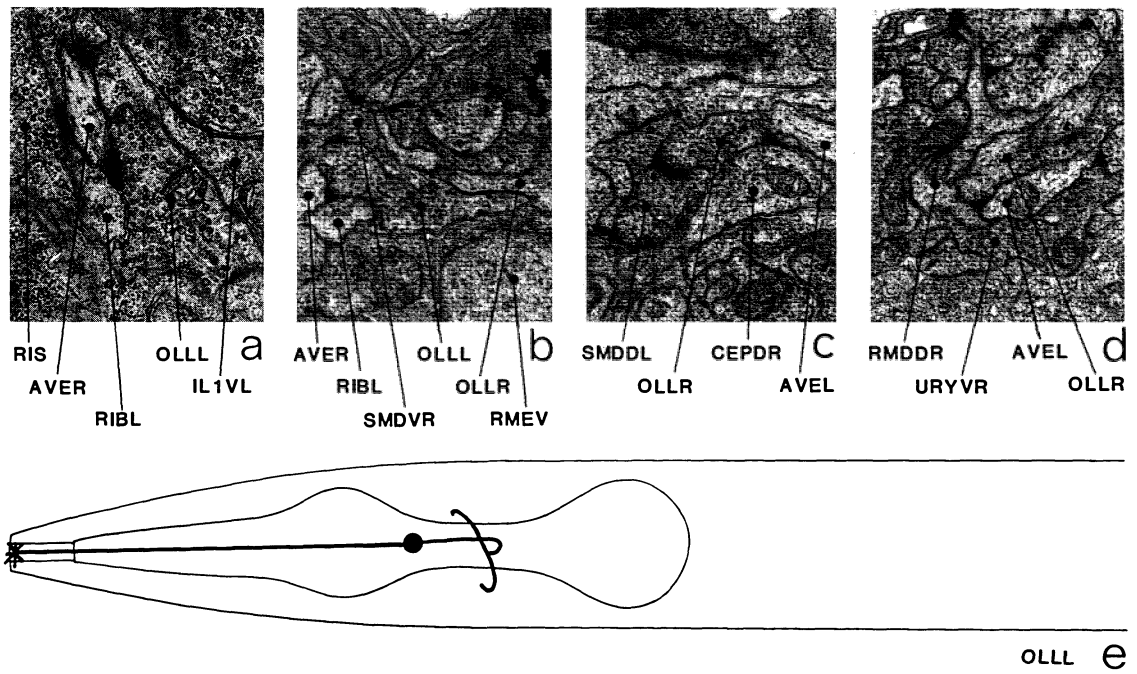


OLLL

CELL BODY IN ANTERIOR GANGLION

OLLR

CELL BODY IN ANTERIOR GANGLION

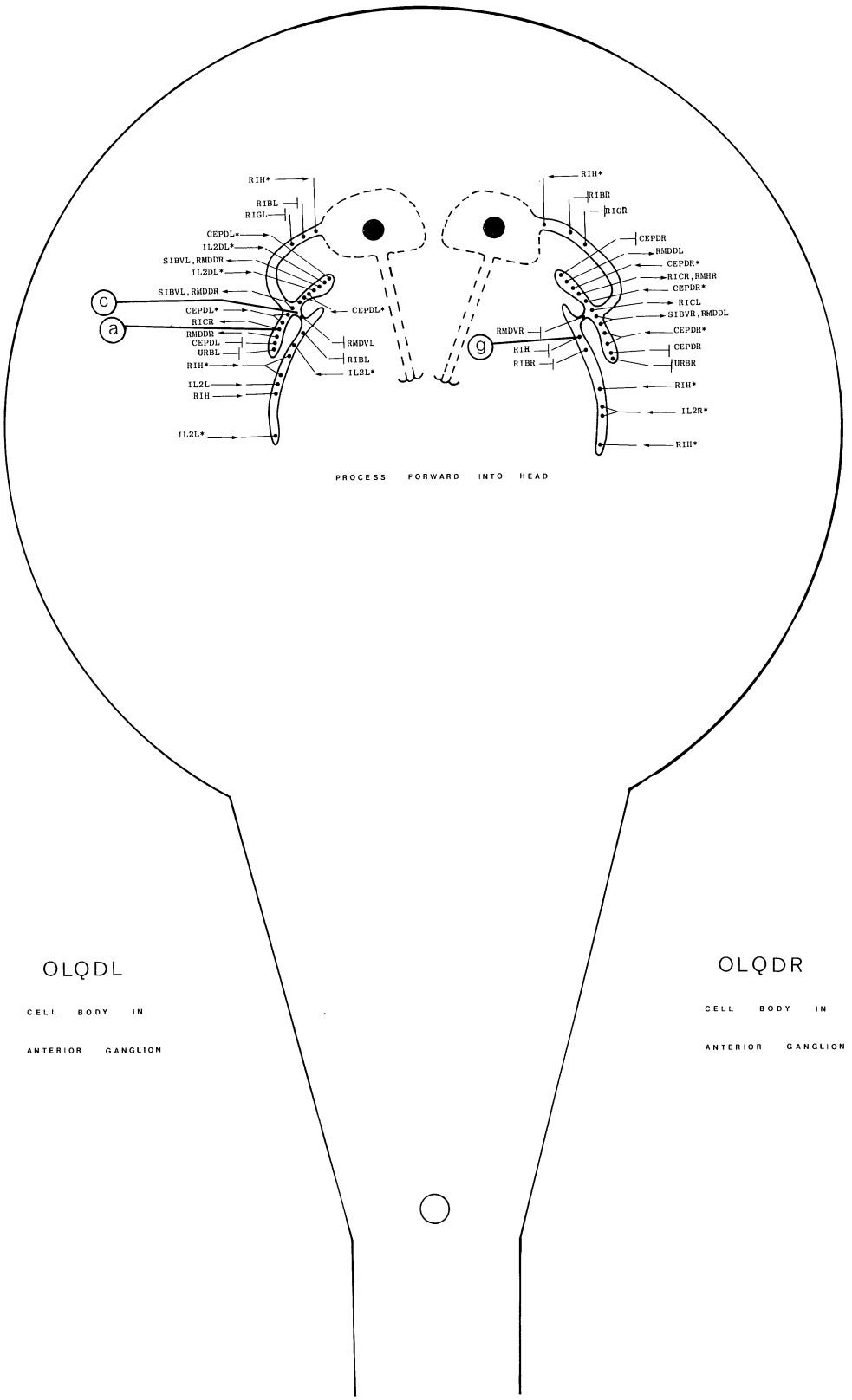


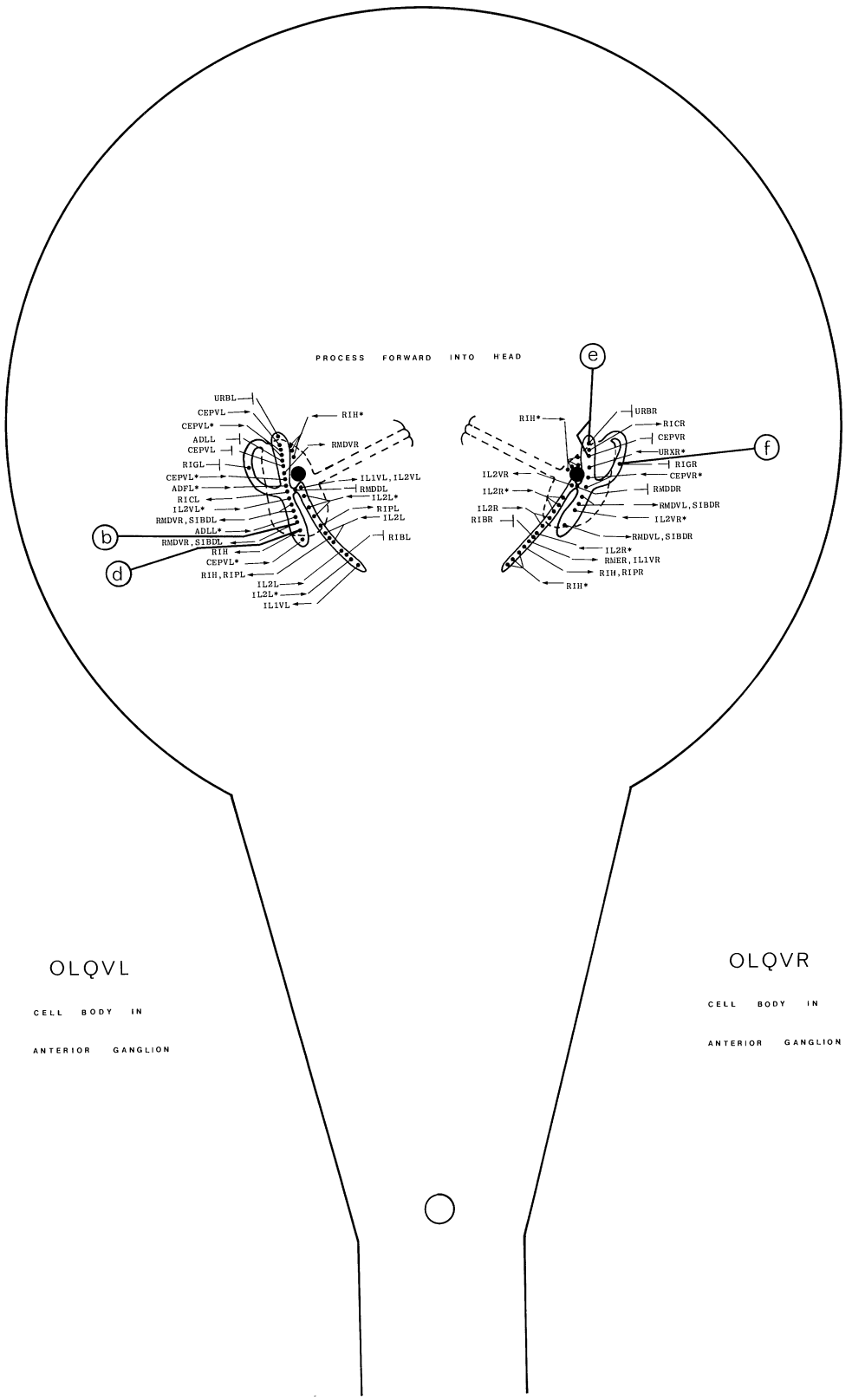
OLL

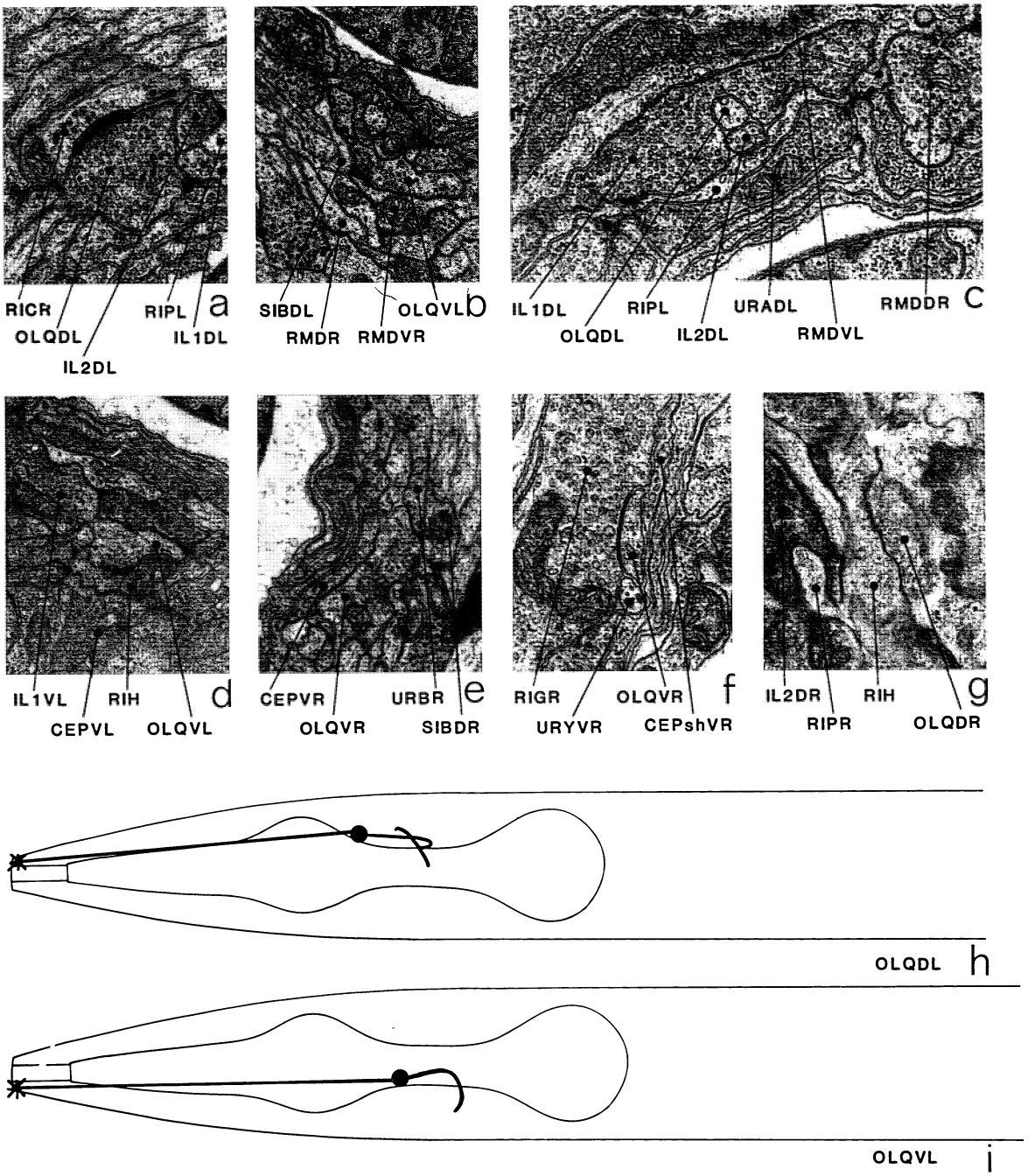
Members: OLLL, OLLR.

OLL is a set of two neurons with ciliated endings in the lateral outer labial sensilla. Cell bodies are situated anteriorly to the nerve ring and have anteriorly directed processes to the ciliated endings, which run in the two lateral labial process bundles. Posteriorly directed processes from the cell bodies rejoin the process bundles, which initially run along the outside of the nerve ring but then turn and run anteriorly near the inner surface. The processes of OLL bifurcate near the anterior surface of the ring; the dorsal and ventral branches run in close association with the processes of AVE and terminate with gap junctions to their symmetrical partners on the dorsal and ventral (b) mid-lines. The main synaptic output of OLL is to SMD (c) and to various dyadic combinations of AVE (a, b), RIB (a, b), RMD (d) and CEP. The main synaptic input is from CEP (*f); there are also a few synapses from ADE. There are gap junctions to RIG (*f) and IL1.

Magnifications: (a) ×25500, (b–d) ×12750.


RIH*
RIBL
RIGL
CEPDL*
IL2DL*
SIBVL,RMDDR
IL2DL*
SIBVL,RMDDR
CEPDL*
RICR
RMDDR
CEPDL
URBL
RIH*
IL2L
RIH
IL2L*
CEPDL*
RMDVL
RIBL
IL2L*
c
a
RIH*
RIBR
RIGR
CEPDR
RMDDL
CEPDR*
RICR,RMHR
CEPDR*
RICL
SIBVR,RMDDL
CEPDR*
CEPDR
URBR
RIH*
IL2R*
RIH*
RMDVR
RIH
RIBR
g
PROCESS FORWARD INTO HEAD
OLQDL
CELL BODY IN
ANTERIOR GANGLION
OLQDR
CELL BODY IN
ANTERIOR GANGLION


PROCESS FORWARD INTO HEAD
URBL
CEPVL
CEPVL*
ADLL
CEPVL
RIGL
CEPVL*
ADFL*
RICL
IL2VL*
RMDVR,SIBDL
ADLL*
RMDVR,SIBDL
RIH
CEPVL*
RIH,RIPL
IL2L
IL2L*
IL1VL
RIH*
RMDVR
IL1VL,IL2VL
RMDDL
IL2L*
RIPL
IL2L
RIBL
b
d
e
f
RIH*
URBR
RICR
CEPVR
URXR*
RIGR
CEPVR*
RMDDR
RMDVL,SIBDR
IL2VR*
RMDVL,SIBDR
IL2R*
RMER,IL1VR
RIH,RIPR
RIH*
IL2VR
IL2R*
IL2R
RIBR
OLQVL
CELL BODY IN
ANTERIOR GANGLION
OLQVR
CELL BODY IN
ANTERIOR GANGLION



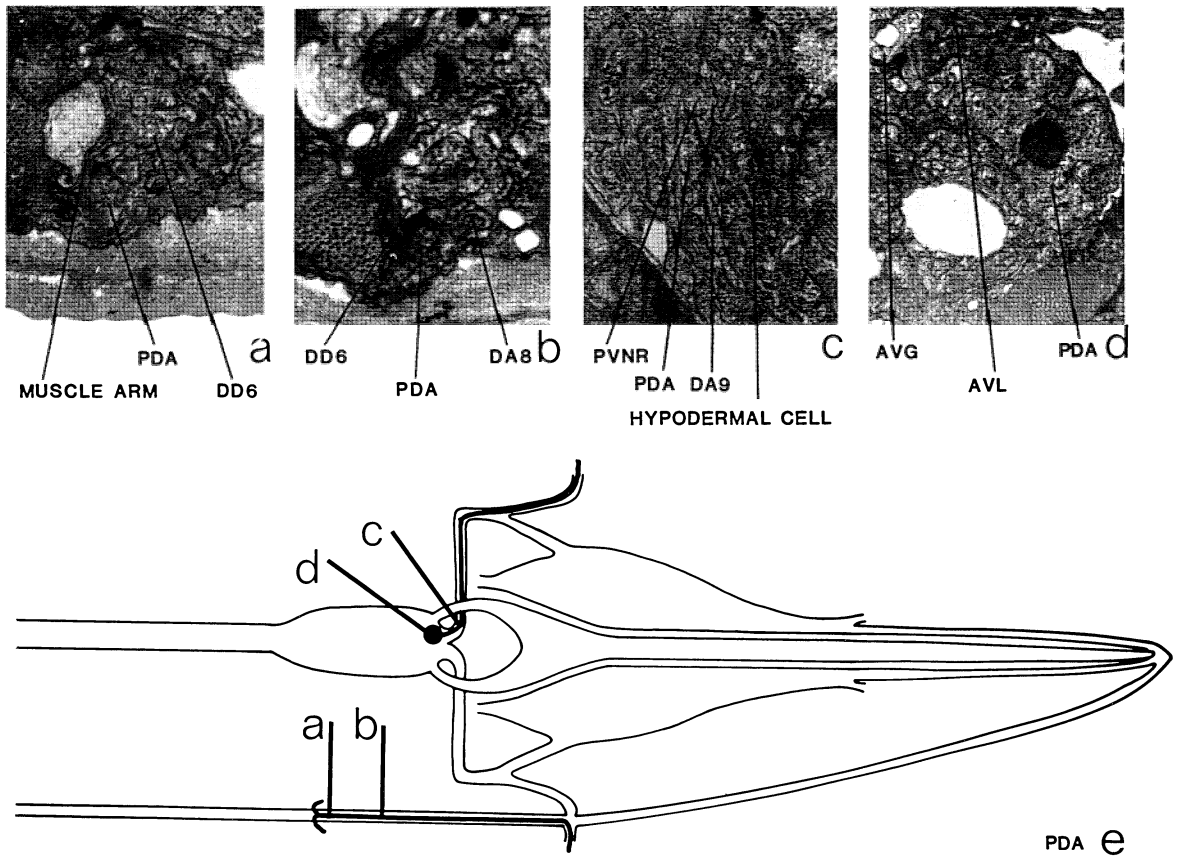
OLQ

Members: OLQDL, OLQDR, OLQVL, OLQVR.

OLQ is a set of four neurons with ciliated endings and striated rootlets in the dorsal and ventral outer labial sensilla. Cell bodies are situated anterior to the nerve ring and have anteriorly directed processes to the endings (h, i), which run in four of the six labial process bundles. Posteriorly directed processes from the cell bodies rejoin the process bundles, which run along the outside of the nerve ring and then turn and run anteriorly near its inner surface. The processes of OLQ enlarge at this point and wrap round the other processes of the bundle

(b). They become small as they pass anteriorly through the NMJ complex made by IL1, URA and so on (c), and then enlarge again and run ventrally on the anterior surface of the nerve ring, in close association with the processes of RIH, until they terminate. The main synaptic output is to RIC (a); although there is only one of these synapses from each OLQ, they are large. There is also synaptic output to RMD (b) and SIB (b), usually in a dyadic combination, and also occasionally to RIH (d). The main synaptic input is from CEP (*e), IL2 (*d) and RIH (*c). There are gap junctions to URB (e), CEP (e), RIG (f), RIH (g), RIB (*c) and RMD.

Magnifications: (a, c, f) $\times 25500$, (b, d, e, g) $\times 12750$.

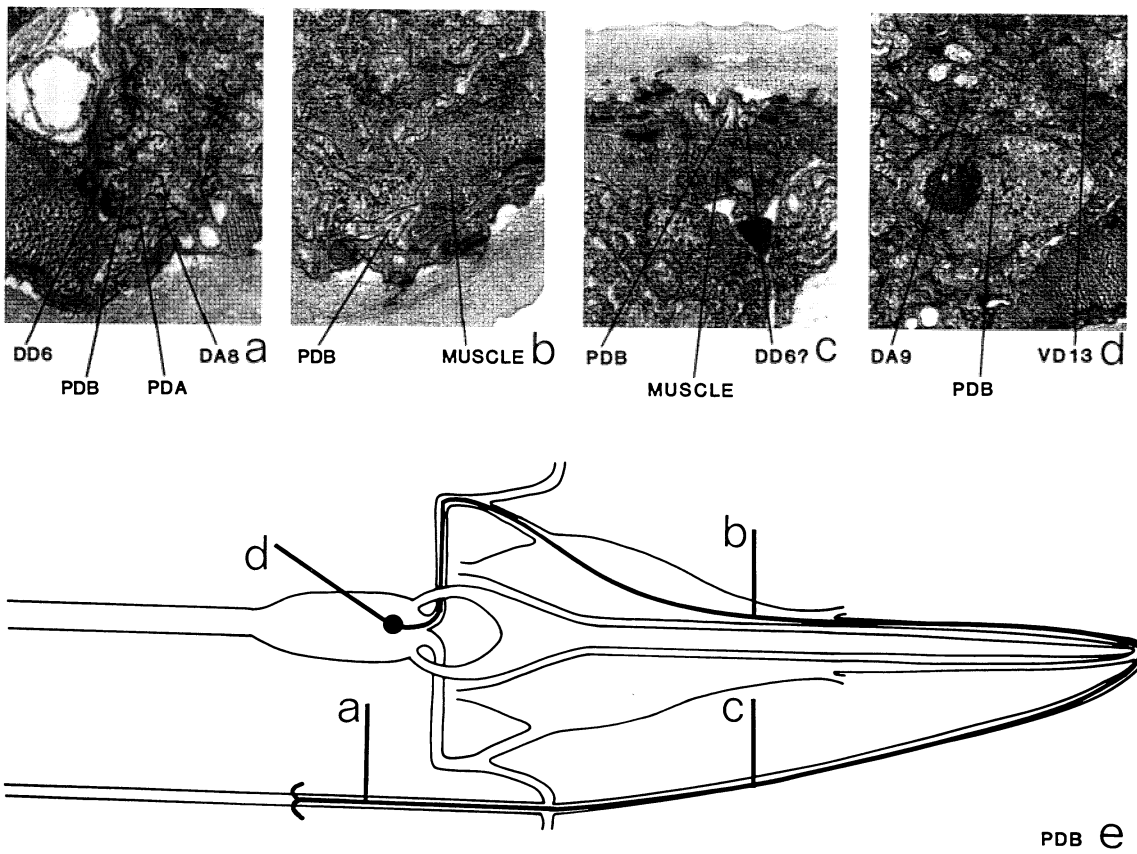


PDA

Member: PDA.

PDA is a single motoneuron that innervates posterior dorsal body muscles. Its cell body is situated at the posterior end of the pre-anal ganglion and has a large amoeboid nucleus (d). A process leaves the cell body and runs round to the dorsal cord via the right hand lumbar commissure (e). This process then runs anteriorly for some distance in the dorsal cord (the location of its end point has not been determined). PDA has few synaptic contacts; in the ventral cord and the commissure region, there is a triadic synapse to PVN, DA9 and a hypodermal cell (c), and in the dorsal cord there are a couple of NMJs (a) and a synapse to DD6 (b). PDA receives a single, but fairly prominent, synapse from DVB.

Magnifications: (a–c) ×25500, (d) ×12750.

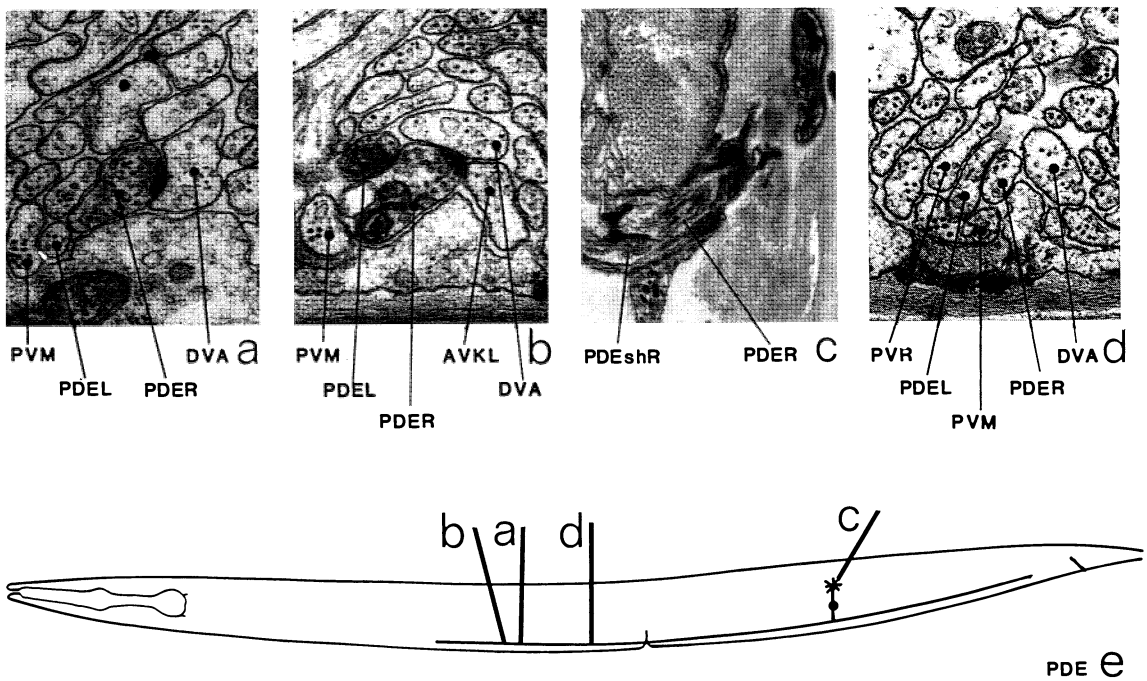


PDB

Member: PDB.

PDB is a single motoneuron that innervates posterior dorsal body muscles. Its cell body is situated in the posterior region of the pre-anal ganglion (d). A posteriorly directed process leaves the pre-anal ganglion via the right hand lumbar commissure (e). This then runs posteriorly, in a sub-ventral location adjacent to the right ventral muscle (b), nearly to the end of the tail. Here it turns and runs anteriorly in a mid-dorsal location (e), becoming part of the dorsal cord (the anterior end point in the dorsal cord has not been determined). The only synapses that have been seen to or from PDB are a couple of small dyadic NMJs, with DD6 as the second postsynaptic element (a).

Magnifications: (a–c) ×25500, (d) ×17000.



PDE

Members: PDEL, PDER.

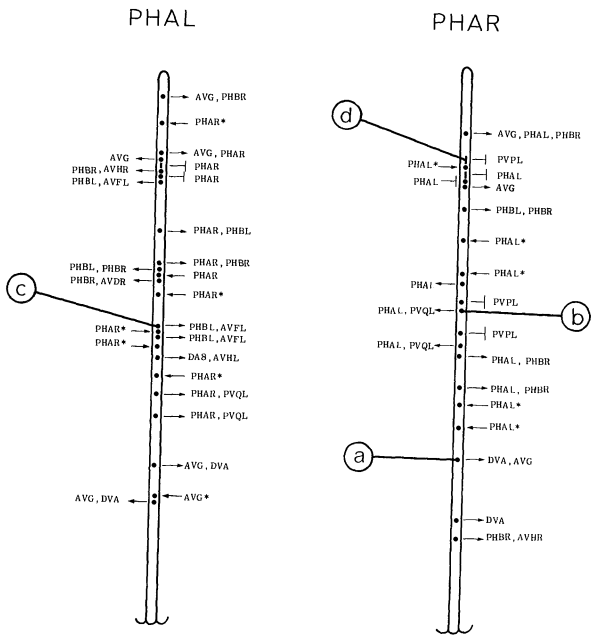
PDE is a pair of neurons with ciliated endings in the posterior deirid sensilla. The cell bodies of PDE are situated sub-ventrally in the posterior body (e). Dorsally directed processes run up to the sensilla, which are not in the alae, as are those of ADE, but dorsal to them, next to the sub-dorsal muscles (c). Ventrally directed processes leave the cell body and enter the ventral cord via a commissure, where they split and run both anteriorly and posteriorly in the ventral region of the cord. PDE neurons have been shown to contain dopamine (Sulston *et al.* 1975). The main synaptic output is to DVA (a, b) and AVK (b); there are also a few synapses to hypodermal cells. The main synaptic input is from PVM (*g), and there is also some from PLM (*e) and AVK (*c). There are gap junctions to itself (d), PVC and PVM.

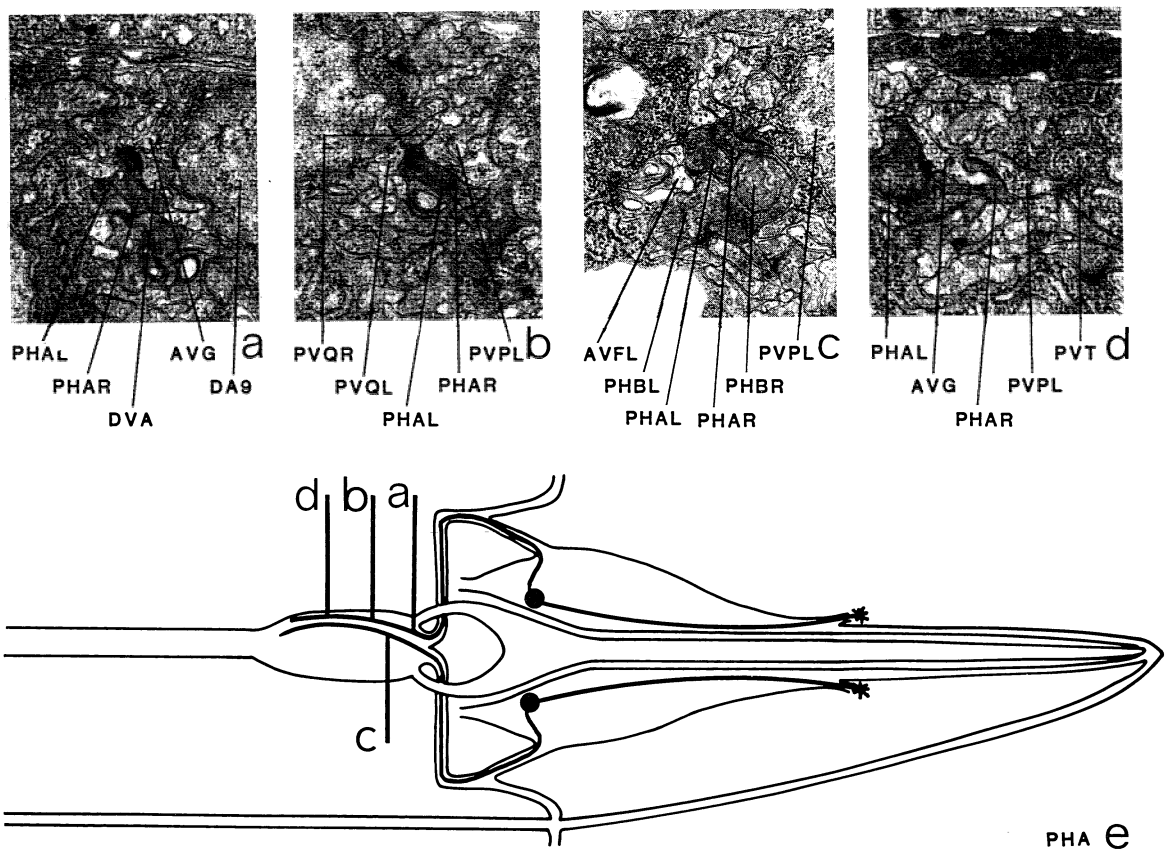
Magnifications: (a, b, d) ×25500, (c) ×17000.

PDE VENTRAL CORD SYNAPSES

partners	gap junctions	synapses from	synapses to and corecipients
DVA	—	1+2 m	37, 20AVK, 2PVR, PDE, PVM
AVK	—	2+2 m	1, 20DVA, HDC
HDC	—	—	2, AVK, VA9
PVC	1	1 m	2
PVR	—	1 m	2DVA
PVM	1	3+12 m	DVA
PDE	3	1 m	DVA
VA9	—	—	HDC
VD9	1	—	—
PLM	—	5 m	—
AVA	—	2 m	—
AVF	—	1 m	—

PHA


PHAL
PHAR
AVG, PHBR
PHAR*
AVG
PHBR, AVHR
PHBL, AVFL
AVG, PHAR
PHAR
PHAR
PHAR, PHBL
PHBL, PHBR
PHBR, AVDR
PHAR, PHBR
PHAR
PHAR*
c
PHAR*
PHAR*
PHBL, AVFL
PHBL, AVFL
DA8, AVHL
PHAR*
PHAR, PVQL
PHAR, PVQL
AVG, DVA
AVG, DVA
AVG*
d
AVG, PHAL, PHBR
PHAL*
PHAL
PVPL
PHAL
AVG
PHBL, PHBR
PHAL*
PHAL*
PHAL
PVPL
PHAL, PVQL
b
PVPL
PHAL, PVQL
PHAL, PHBR
PHAL, PHBR
PHAL*
PHAL*
a
DVA, AVG
DVA
PHBR, AVHR

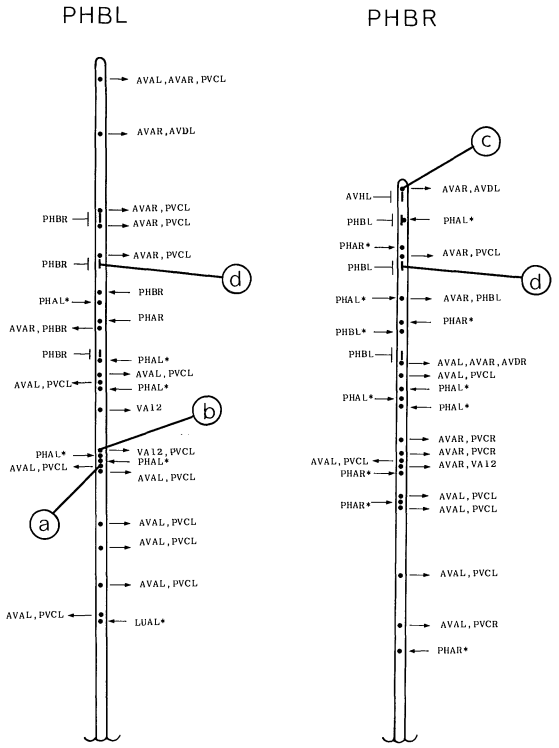


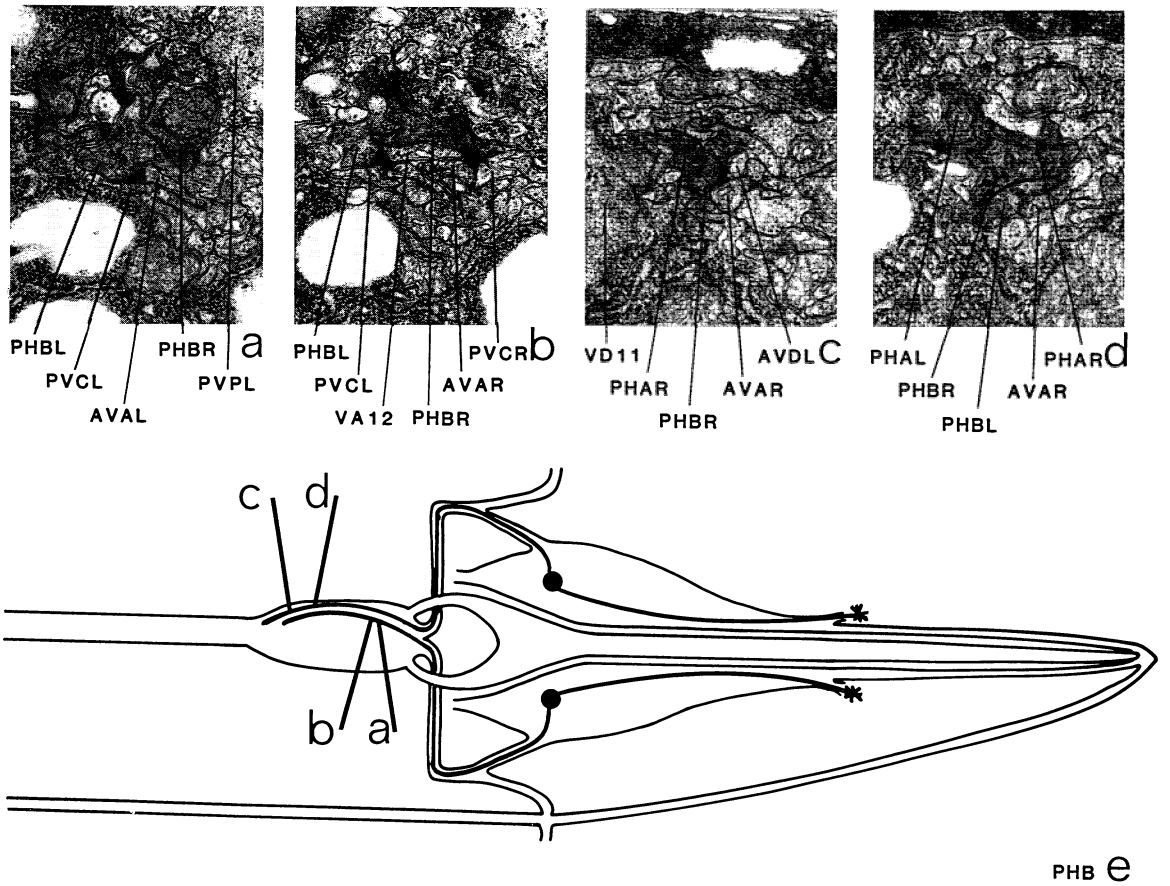
PHA

Members: PHAL, PHAR.

PHA is a set of two ciliated neurons that are components of the phasmid sensilla. Posteriorly directed processes emanate from each cell body in the lumbar ganglia and terminate in a cilium. The basal body of the cilium is ventral to that of PHB, which is also part of the same sensillum. Anteriorly directed processes enter the pre-anal ganglion via the lumbar commissures and run near the middle of the neuropile for the length of the ganglion (e). The main synaptic output is to PHB (c), AVG (a, d), PVQ (b), itself (d), DVA (a), AVF and AVH, usually in various dyadic combinations. PHA also has gap junctions to PVP (d) and itself.

Magnifications: (a–d) ×25500.


PHBL
PHBR
AVAL, AVAR, PVCL
AVAR, AVDL
AVAR, PVCL
AVAR, PVCL
AVAR, PVCL
PHBR
PHBR
PHAL*
PHBR
PHAR
AVAR, PHBR
PHBR
PHAL*
AVAL, PVCL
AVAL, PVCL
PHAL*
VA12
PHAL*
VA12, PVCL
AVAL, PVCL
PHAL*
AVAL, PVCL
AVAL, PVCL
AVAL, PVCL
AVAL, PVCL
LUAL*
a
b
d
AVHL
PHBL
PHAR*
PHBL
PHAL*
PHBL*
PHBL
PHAL*
AVAR, AVDL
PHAL*
AVAR, PVCL
d
AVAR, PHBL
PHAR*
AVAL, AVAR, AVDR
AVAL, PVCL
PHAL*
PHAL*
AVAR, PVCR
AVAR, PVCR
AVAL, PVCL
PHAR*
AVAR, VA12
AVAL, PVCL
PHAR*
AVAL, PVCL
AVAL, PVCL
AVAL, PVCR
PHAR*
c



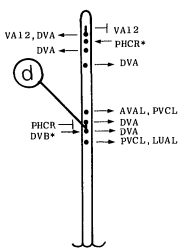
PHB

Members: PHBL, PHBR.

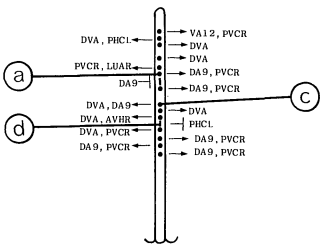
PHB is a set of two ciliated neurons that are components of the phasmid sensilla. Posteriorly directed processes emanate from each cell body in the lumbar ganglia and terminate in a cilium. The basal body of the cilium is dorsal to that of PHA, which is also part of the same sensillum. Anteriorly directed processes enter the pre-anal ganglion via the lumbar commissures and run near the middle of the neuropile for the length of the ganglion (e). The synapses of PHB are generally rather larger than those of PHA. The predominant synaptic output is to AVA and PVC at dyadic synapses (a, b). There are also synapses to AVD (c) and VA12 (b). There are several gap junctions to itself (d) and a small gap junction to AVH. The main synaptic input is from PHA (*c).

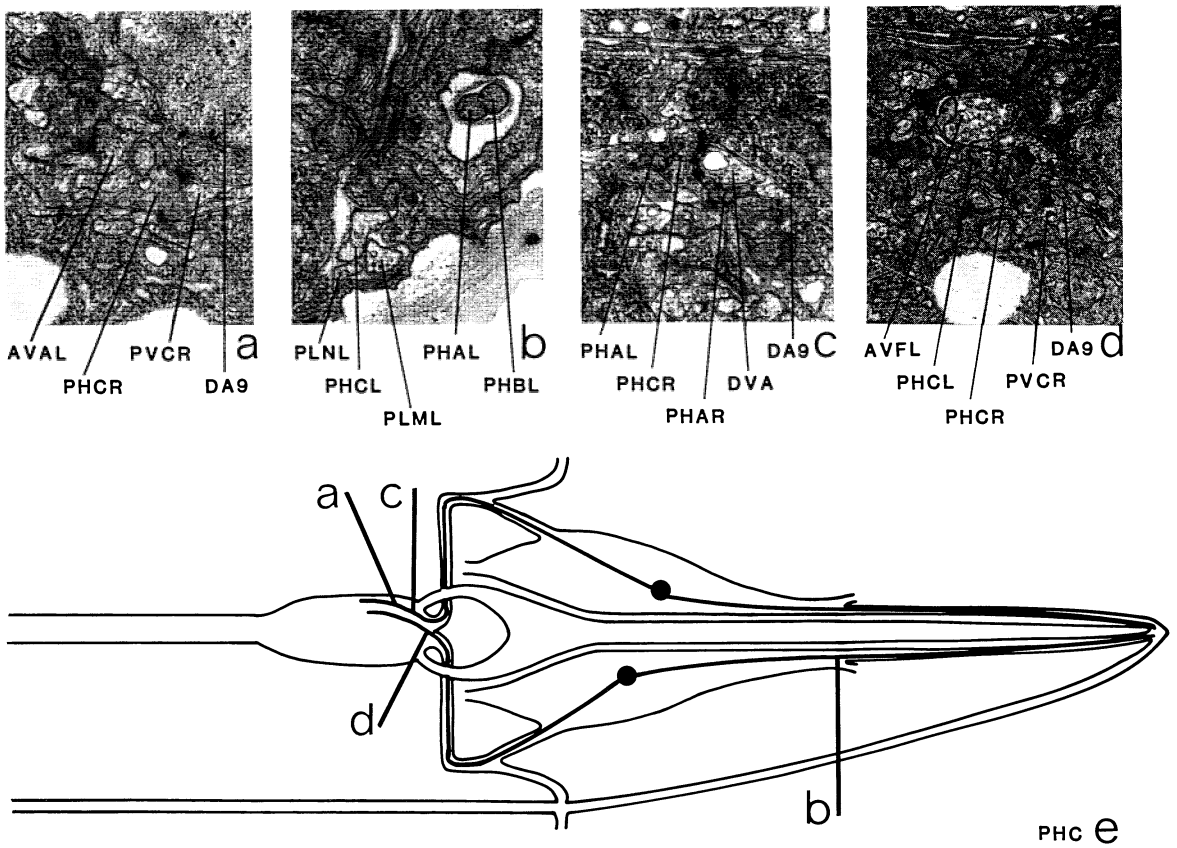
Magnifications: (a–d) ×25500.

PHCL


VA12, DVA
DVA
d
VA12
PHCR*
DVA
AVAL, PVCL
PHCR
DVB*
DVA
DVA
PVCL, LUAL

PHCR


DVA, PHCL
VA12, PVCR
DVA
DVA
a
PVCR, LUAR
DA9
DA9, PVCR
DA9, PVCR
c
DVA, DA9
DVA, AVHR
DVA, PVCR
DA9, PVCR
d
DVA
PHCL
DA9, PVCR
DA9, PVCR

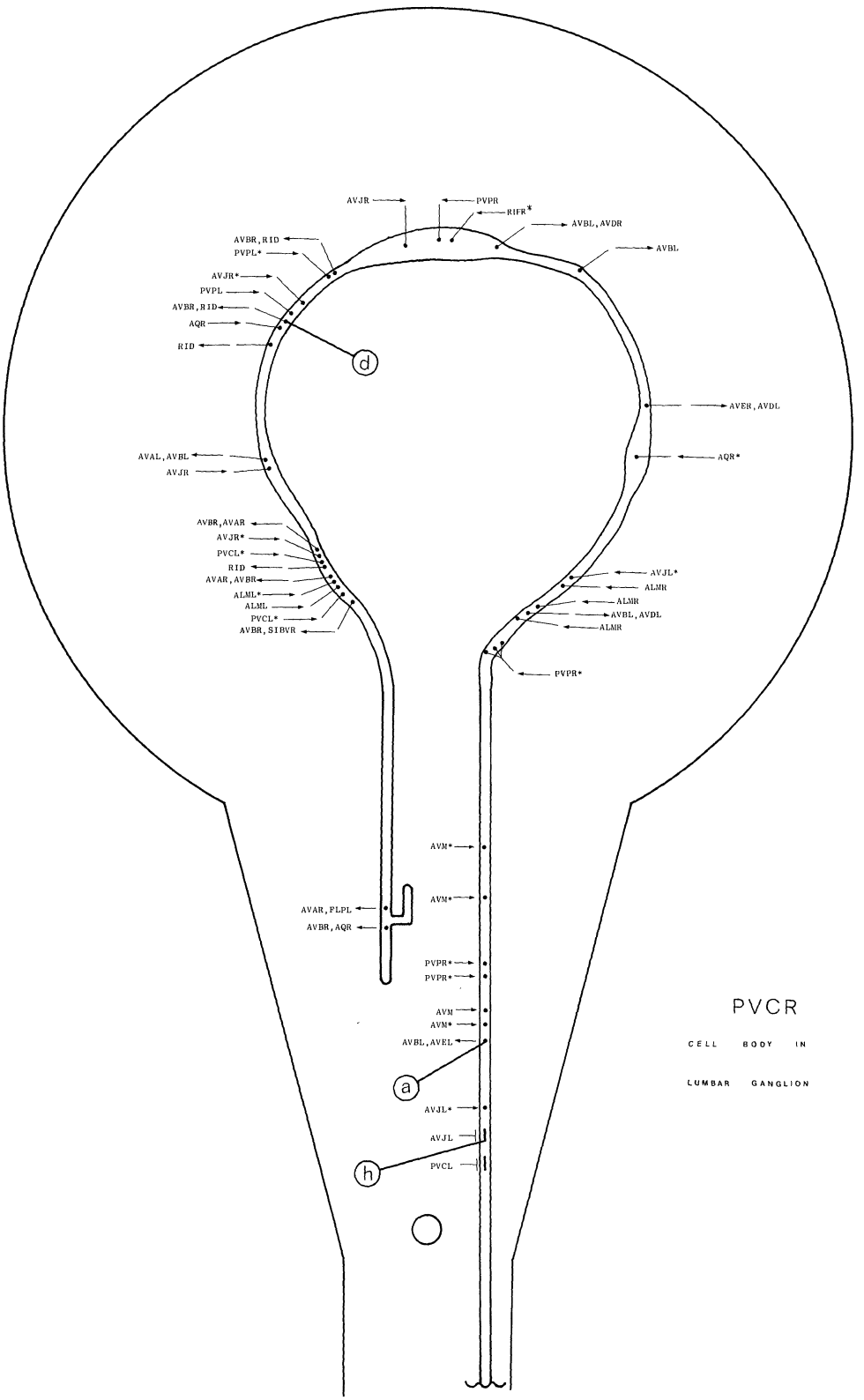


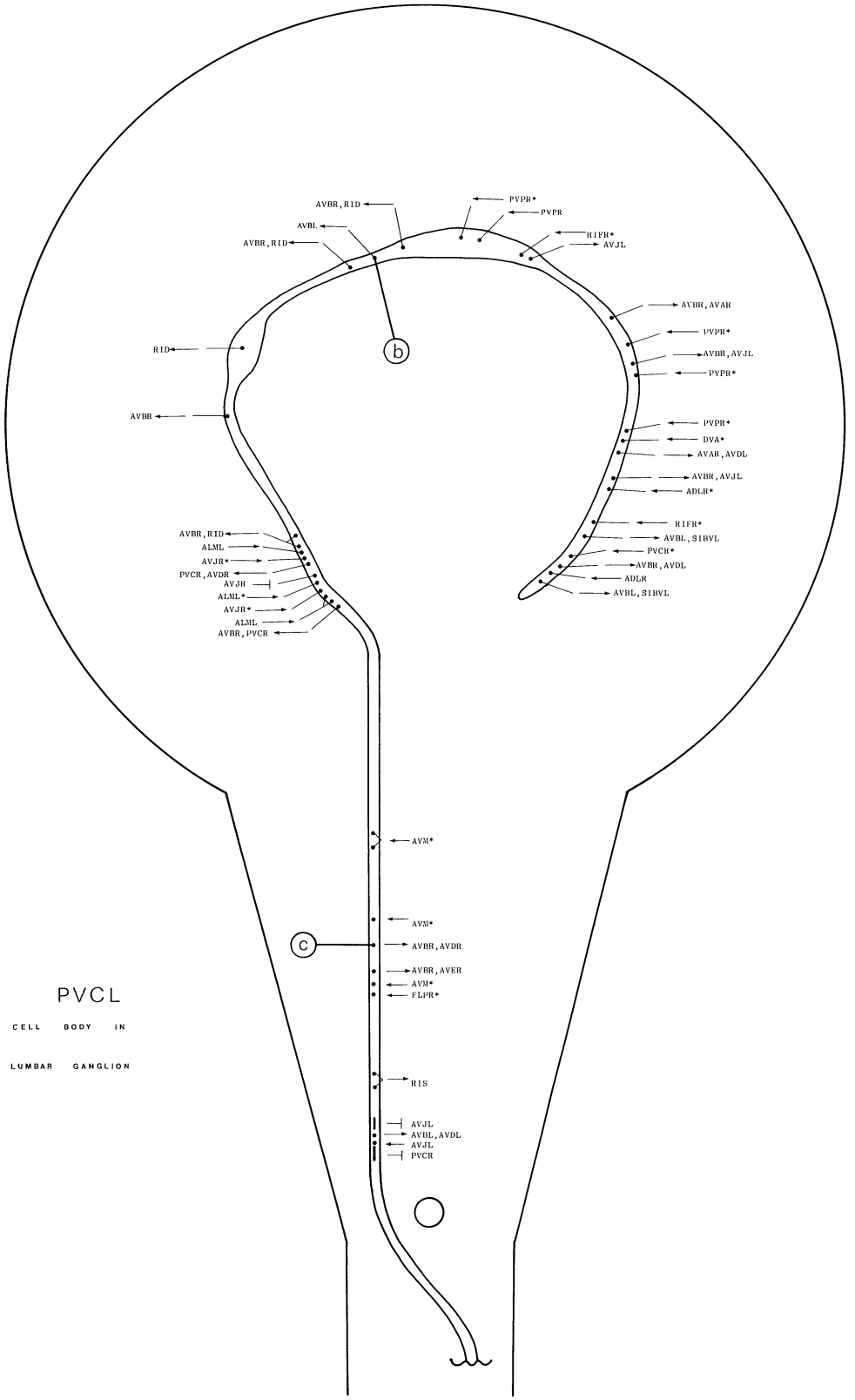
PHC

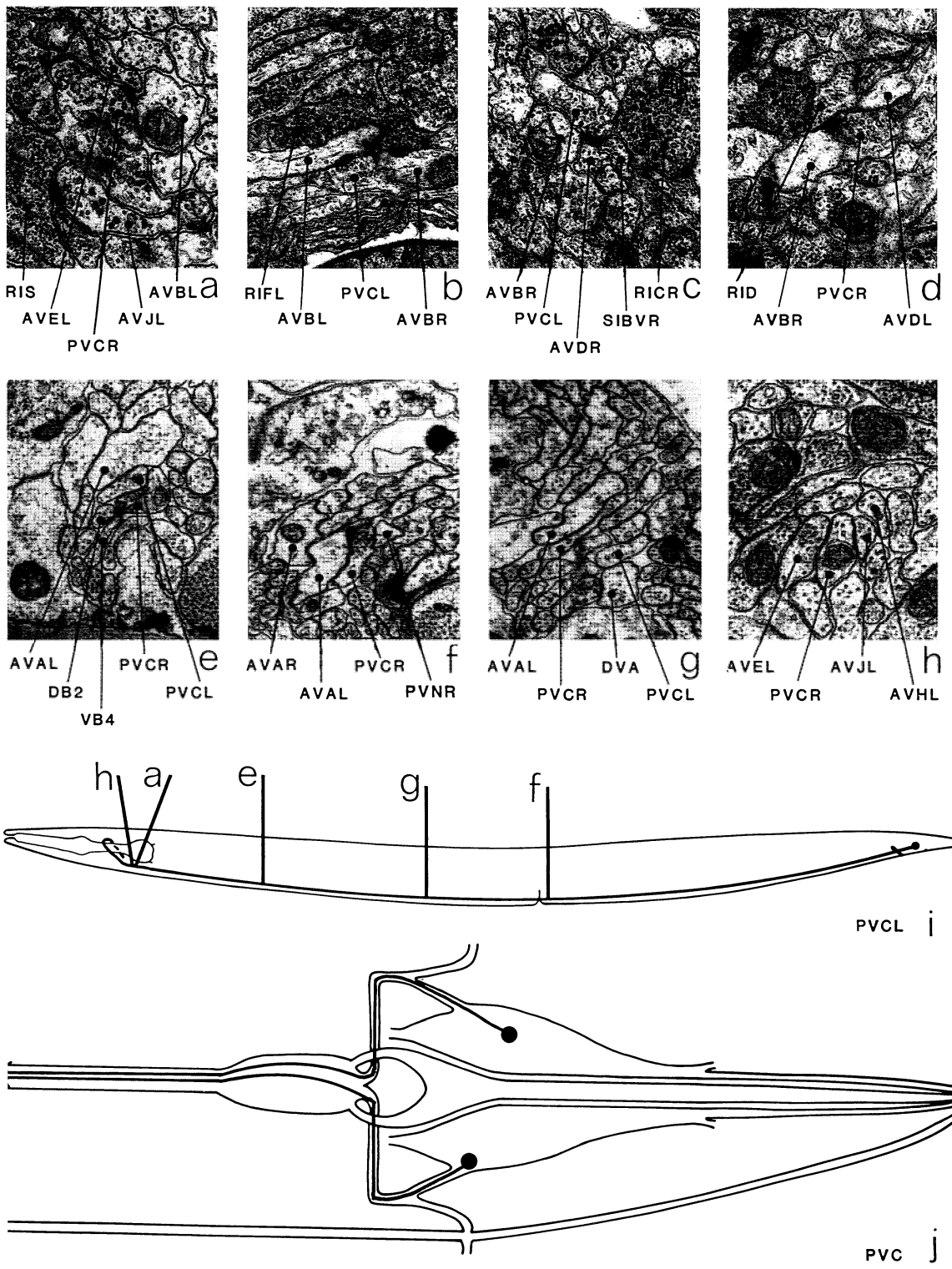
Members: PHCL, PHCR.

PHC is a set of two neurons with cell bodies situated in the lumbar ganglia. Posteriorly directed processes run from the cell bodies into the tailspike (e) running alongside the processes of PLM and PLN. The disposition of these processes suggests that they may be sensory dendrites. Anteriorly directed processes leave the cell body and enter the pre-anal ganglion via the lumbar commissures and run for a short distance near the middle of the neuropile before ending. The main synaptic output is to DVA (c), PVC (a) and DA9 (a). There are gap junctions to itself (d), VA12 and DA9.

Magnifications: (a–d) ×25500.


AVJR
PVPR
RIFR*
AVBL, AVDR
AVBL
AVBR, RID
PVPL*
AVJR*
PVPL
AVBR, RID
AQR
RID
d
AVER, AVDL
AQR*
AVAL, AVBL
AVJR
AVBR, AVAR
AVJR*
PVCL*
RID
AVAR, AVBR
ALML*
ALML
PVCL*
AVBR, SIBVR
AVJL*
ALMR
ALMR
AVBL, AVDL
ALMR
PVPR*
AVM*
AVM*
AVAR, PLPL
AVBR, AQR
PVPR*
PVPR*
AVM
AVM*
AVBL, AVEL
a
AVJL*
AVJL
h
PVCL
PVCR
CELL BODY IN
LUMBAR GANGLION


AVBR, RID
AVBL
AVBR, RID
PVPR*
PVPR
RIFR*
AVJL
b
RID
AVBR
AVBR, AVAR
PVPR*
AVBR, AVJL
PVPR*
PVPR*
DVA*
AVAR, AVDL
AVBR, AVJL
ADLR*
RIFR*
AVBL, SIBVL
PVCR*
AVBR, AVDL
ADLR
AVBL, SIBVL
AVBR, RID
ALML
AVJR*
PVCR, AVDR
AVJR
ALML*
AVJR*
ALML
AVBR, PVCR
AVM*
AVM*
c
AVBR, AVDR
AVBR, AVER
AVM*
FLPR*
RIS
AVJL
AVBL, AVDL
AVJL
PVCR
PVCL
CELL BODY IN
LUMBAR GANGLION


RIS
AVEL
AVJL
AVBL
PVCR
a
RIFL
AVBL
PVCL
AVBR
b
AVBR
PVCL
AVDR
SIBVR
RICR
c
RID
AVBR
PVCR
AVDL
d
AVAL
DB2
VB4
PVCR
PVCL
e
AVAR
AVAL
PVCR
PVNR
f
AVAL
PVCR
DVA
PVCL
g
AVEL
PVCR
AVJL
AVHL
h
h
a
e
g
f
PVCL
i
PVC
j

PVC

Members: PVCL, PVCR.

PVC is a pair of interneurons with cell bodies situated in the lumbar ganglia. Processes leave the cell bodies, enter the nerve-cord via the lumbar commissures and run anteriorly on the right-hand side of the hypodermal ridge, in the ventral region of the cord. The processes of PVC travel the length of the cord and enter the nerve ring, running right round it near the middle of the neuropile and eventually ending ventrally. While in the ring, the processes of PVC run in close association with each other and with those of AVB. In the nerve ring, the main synaptic output is to AVB (a, b, c, d), RID (d) and AVD (c). There are also a few synapses to AVA and AVE (a). The main synaptic input is from PVP (*a), ALM (*b), AVM (*a), AVJ (*a) and AQR (*a); there are also gap junctions to itself and AVJ (h). In the ventral cord, the main synaptic output is to AVA (f), and to VBn (e) and DBn (e) motoneurons; the main synaptic input is from AVA (*b), PHB (*a), PHC (*a), VA12 (*d), LUA (*b), PVM (*h), PVN (*c), DVA (*f) and PVD (*a); there are gap junctions to AVA (g), PVW (*d), PLM (*h), AVJ, PDE and itself.

In the ventral cord, the processes of PVC run adjacent and ventral to the processes of AVA; the processes of AVB run more dorsally, seldom running next to those of PVC. This may explain why there are so few synaptic interactions with AVB in the nerve cord compared with the nerve ring.

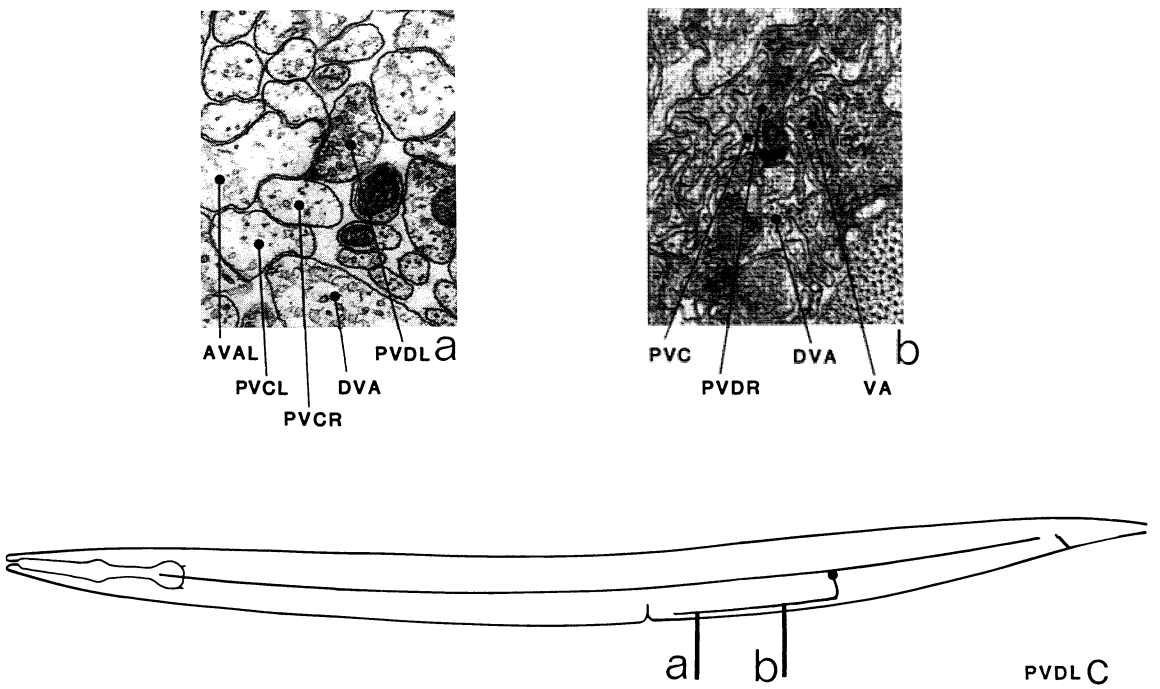
Magnifications: (a, c, d, h) ×25500, (b, e–g) ×17000.

PVC VENTRAL CORD SYNAPSES

partners	gap junctions	synapses from	synapses to and corecipients
AVA	10	7+21 m	3,4AVA, 2AS2, AVB, AVE, AVD, DA2, PVR
DB4	—	—	1, 3VB7, DA5, DB5, VB6
VB6	—	—	2, 2DB3, DB4
DB3	—	—	2, 2VB6, DVA
DB7	—	—	1, 2DVA, PVC
AVB	—	—	2AVD, AVA, AVE
DB2	—	—	2VB4, DVA, VB3
VB4	—	—	2, 2DB2
DVA	1	3	2DB7, DB2, DB3
AVD	—	1 m	2AVB, AVA, AS1
DB5	—	—	2VB8, DB4
VB7	—	—	3DB4
VB8	—	—	2DB5
AVE	—	1 m	AVA, AVB
AS2	—	—	2AVA
LUA	—	3 m	PVW
PDE	1	1	1
PVR	—	1	AVA
VB11	—	1 m	1
PVW	3	1 m	LUA
PVC	4	1 m	DB7
AVL	—	—	1
VB3	—	—	DB2
AS1	—	—	AVD
DA2	—	—	AVA
VB5	—	—	1
DA5	—	—	DB4
PHB	—	22 m	—
PHC	1	10 m	—

PVC VENTRAL CORD SYNAPSES (*cont.*)

partners	gap junctions	synapses from	synapses to and corecipients
VA12	—	5 m	—
PVM	—	2	—
PVD	—	3 m	—
PLM	2	1 m	—
BDU	—	1+1 m	—
PVN	—	1+1 m	—
AVG	—	1 m	—
PVP	—	1 m	—
VD13	—	1 m	—
AVJ	2	—	—



PVD

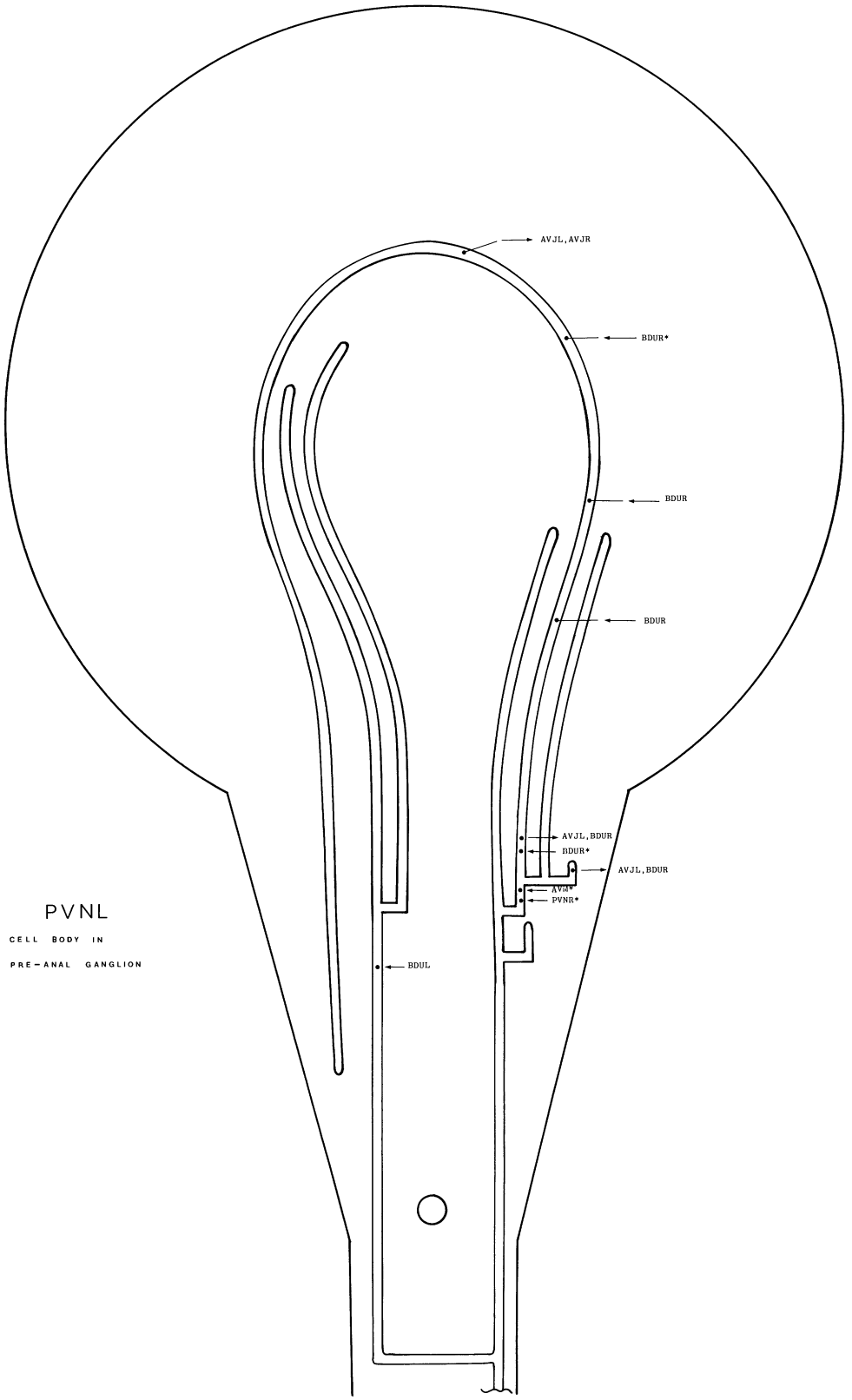
Members: PVDL, PVDR.

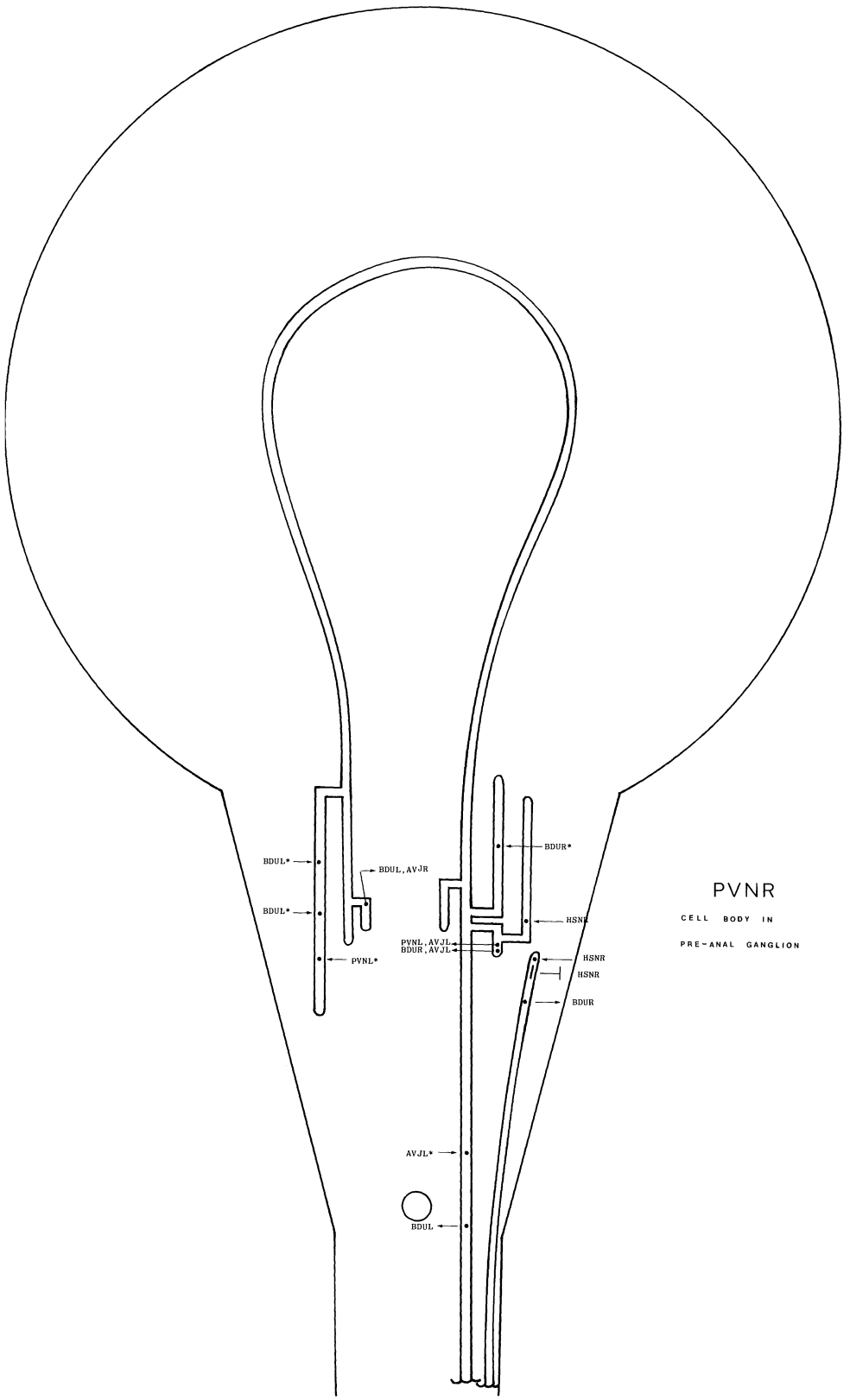
PVD is a set of two interneurons with cell bodies situated laterally in the posterior body. Anteriorly and posteriorly directed processes leave the cell bodies and run alongside the excretory canal in close association with the processes of ALA and CAN. These three processes have not been completely reconstructed in the posterior body, although they have been sampled in several places. Two of the processes end at about the level of the anus; a third enters the lumbar ganglia and synapses onto PVC (ALA-d). A single synapse on the lateral hypodermis has also been seen on one of the processes (CAN-c). PVD neurons send out a third, ventrally directed process, which enters the ventral cord as a commissure. This process runs anteriorly in the ventral part of the cord and has several dyadic synapses to AVA and PVC (a). There are also a few synapses to DVA (b).

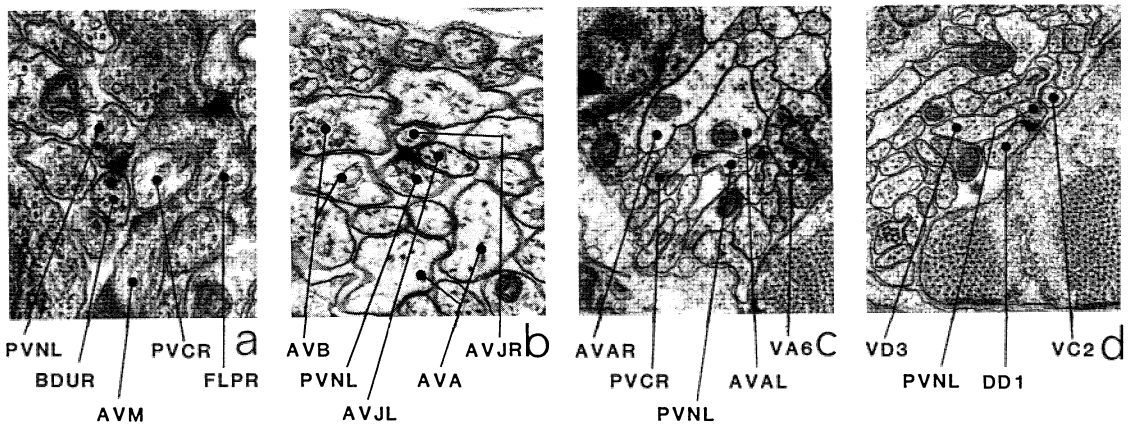
Magnifications: (a, b) ×25500.

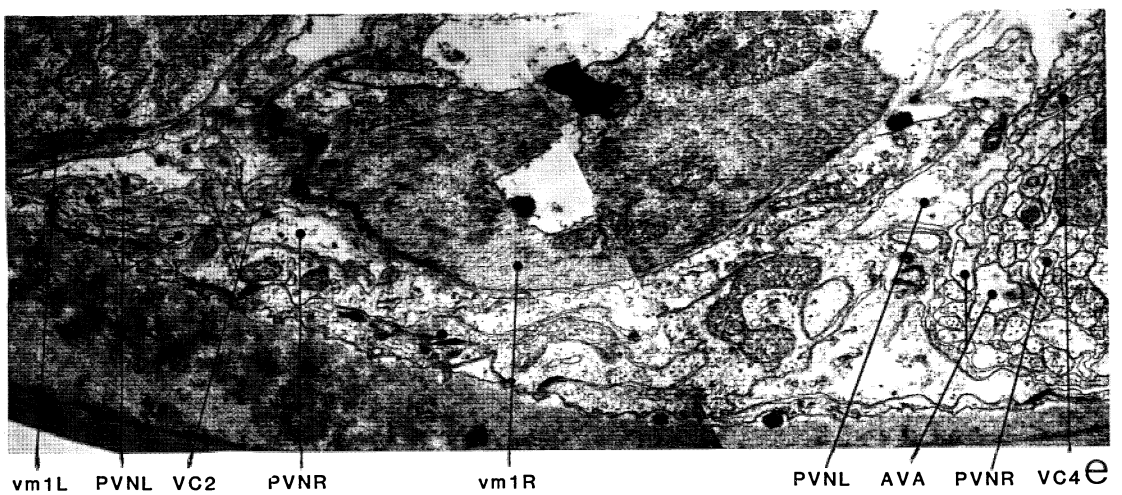
PVD VENTRAL CORD SYNAPSES

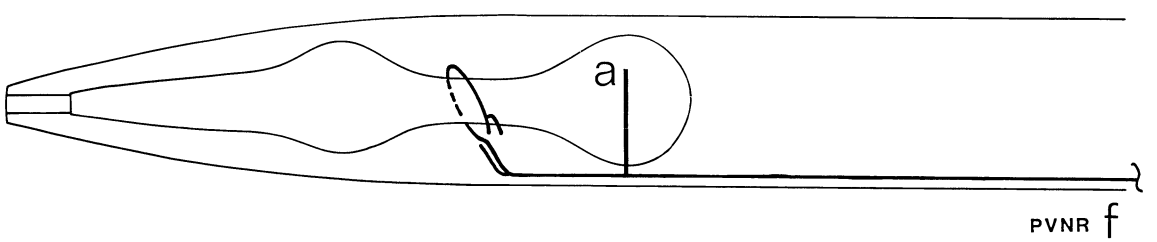
partners	gap junctions	synapses from	synapses to and corecipients
AVA	—	—	22PVC, 4AVA, PVD
PVC	—	1 m	2, 22AVA, 2PVC, DVA, HDC
DVA	—	—	2, PVC
PVD	—	1 m	AVA
HDC	—	—	PVC

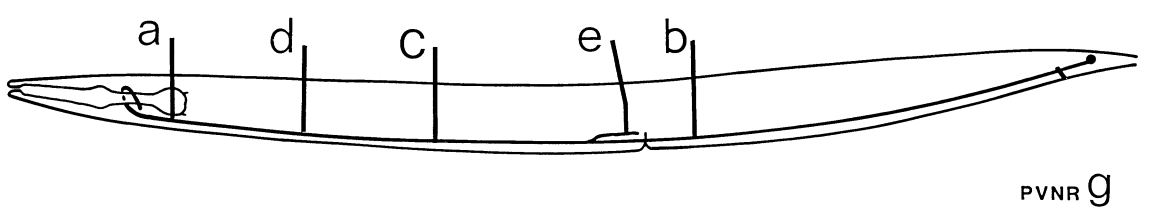

AVJL,AVJR
BDUR*
BDUR
BDUR
AVJL,BDUR
RDUR*
AVJL,BDUR
AVM*
PVNR*
BDUL
PVNL
CELL BODY IN
PRE-ANAL GANGLION


BDUL*
BDUL*
PVNL*
BDUL, AVJR
BDUR*
HSNR
PVNL, AVJL
BDUR, AVJL
HSNR
HSNR
BDUR
AVJL*
BDUL
PVNR
CELL BODY IN
PRE-ANAL GANGLION


PVNL
BDUR
AVM
PVCR
FLPR
a
AVB
PVNL
AVJL
AVA
AVJR
b
AVAR
PVCR
PVNL
AVAL
VA6
c
VD3
PVNL
DD1
VC2
d


vm1L
PVNL
VC2
PVNR
vm1R
PVNL
AVA
PVNR
VC4
e


a
PVNR
f


a
d
c
e
b
PVNR
g

PVN

Members: PVNL, PVNR.

PVN is a set of two interneurons/motoneurons with cell bodies situated in the lumbar ganglia. Anteriorly directed processes enter the pre-anal ganglion via the lumbar commissures and then run alongside each other near the centre of the ventral cord. Prominent lateral branches enter the anterior regions of the vulva (e), running underneath the vm1 vulval muscles. These branches become quite large and contain a few vesicles, although no obvious focal synaptic contacts have been seen. The processes of PVN also branch extensively in the anterior extremities of the ventral cord; PVN is the most highly branched class of neuron in the nervous system. Many of the branches probably develop quite late, as PVN neurons in the JSH series (an L4 larva) had few branches. The branches of PVN tend to stay in the same neighbourhood as the main processes, running alongside them (they have been drawn separated for clarity). The main processes of both PVNL and PVNR enter the nerve ring on the right-hand side and run round it near the inside surface of the neuropile, in close association with the processes of BDU. PVNL has an additional branch, which enters the ring on the left-hand side, travelling in the same neighbourhood as the other branches of PVN. The synapses that are made by PVN are all rather small, with few vesicles in their synaptic terminals. In the nerve ring there are a few synapses to and from BDU (a, *c) and to AVJ (b). In the ventral cord the synapses are more numerous and are mainly onto AVD, NMJs (d), VDn, DDn (d), AVJ and PVW. There is a single gap junction to both HSN and PVQ, and a couple to AVB.

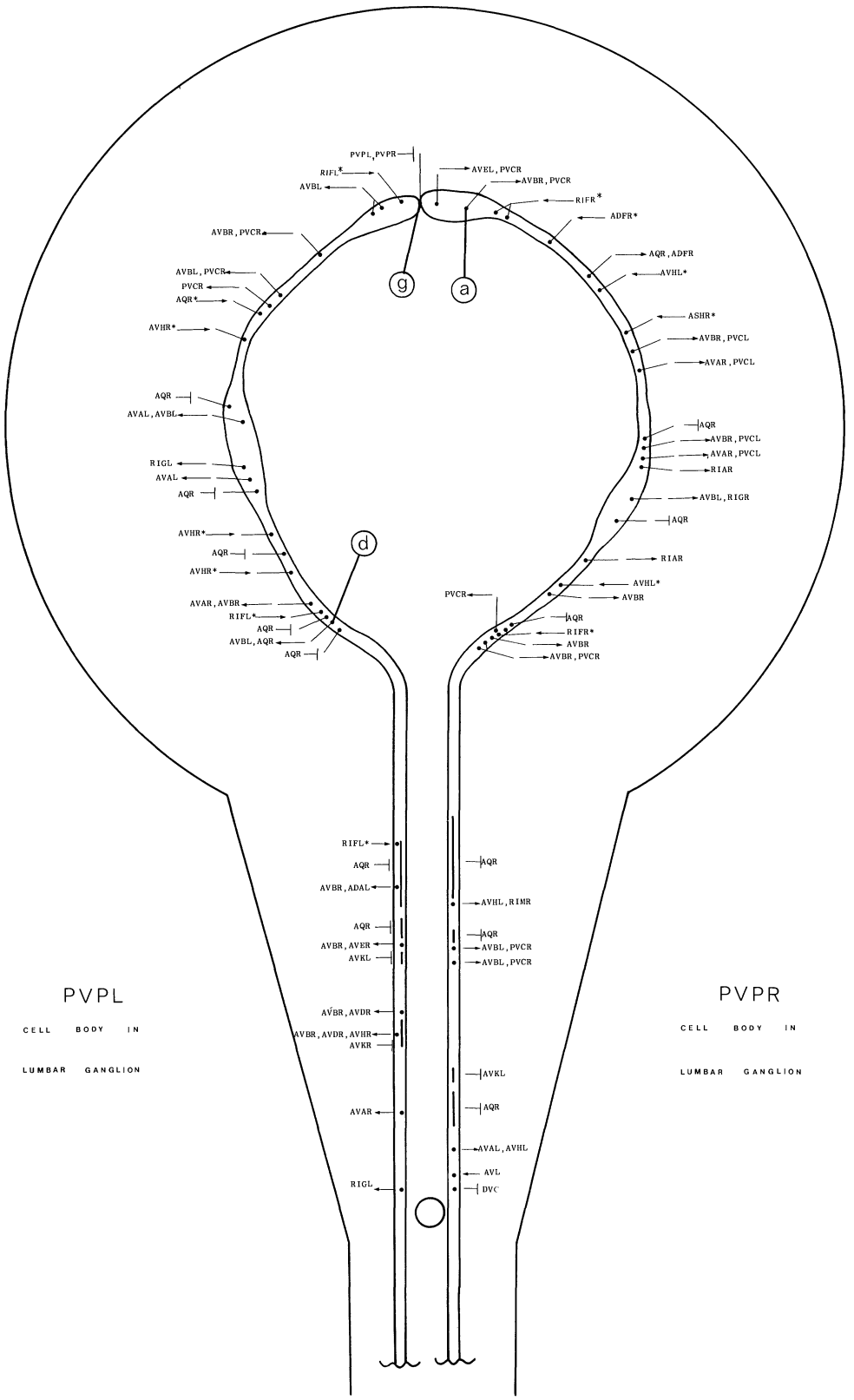
Magnifications: (a, b) ×25500, (c, d) ×17000, (e) ×12750.

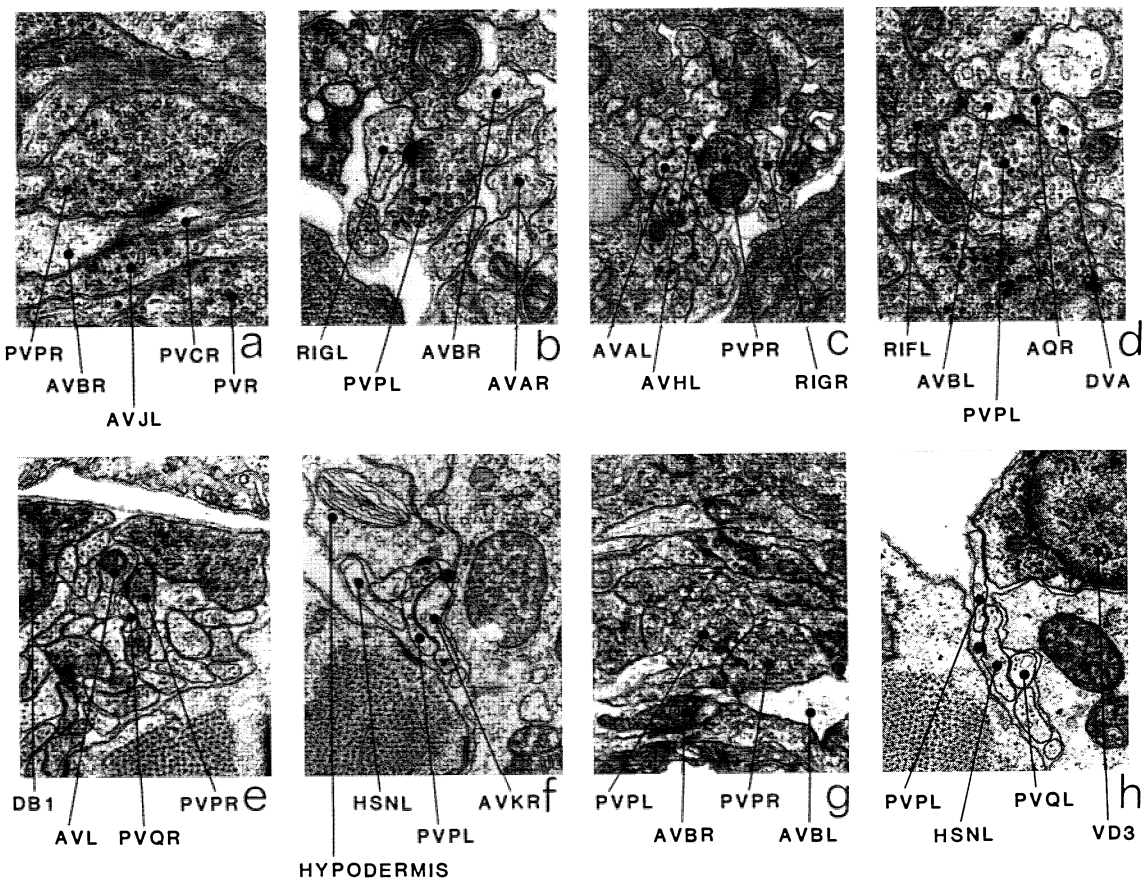
PVN VENTRAL CORD SYNAPSES

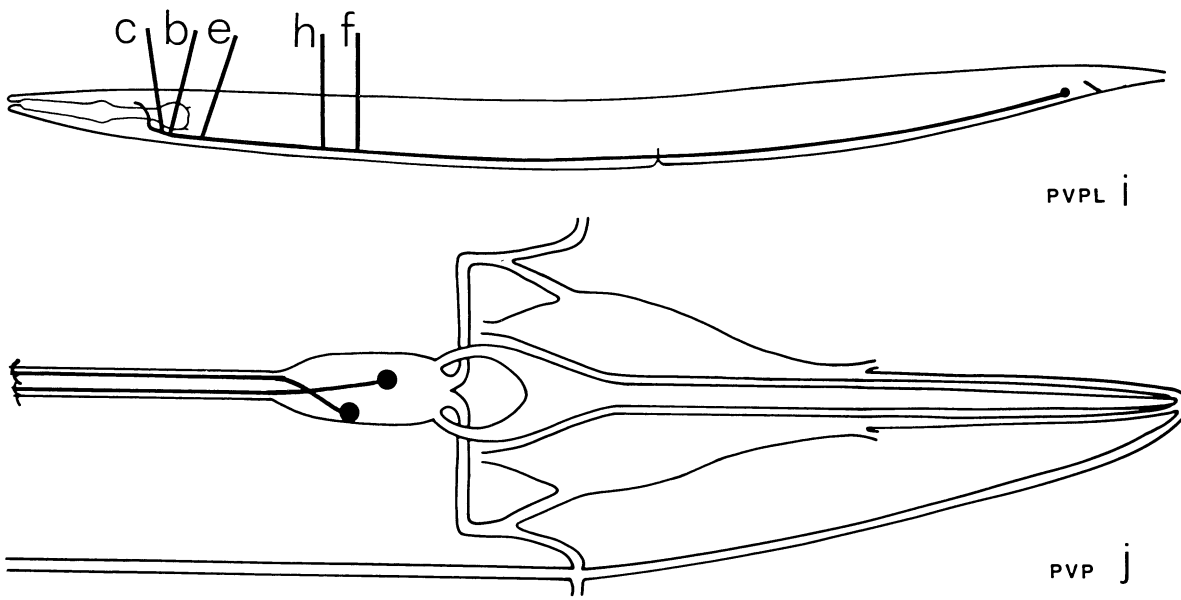
partners	gap junctions	synapses from	synapses to and corecipients
AVD	—	—	2AVD, PQR, AVJ, AVA, AVE
PQR	—	—	AVD, AVB, PVW
NMJ	—	—	3, VD12, 2DD1, VD3
PVW	—	—	PQR, PVN, HDC
AVB	2	1 m	1, PQR, HDC
PVN	—	4 m	AVL, PVW, AVG, VD4
PVT	—	—	1, AVL
AVA	—	—	2, PVC, AVD, VD4, VA6
AVL	—	—	2PVN, PVT, VA6
HDC	—	—	PVW, AVB
AVJ	—	—	2, AVD, AVJ, HSN, BDU
PVC	—	—	1, AVA
VD12	—	—	NMJ
AVG	—	1+1 m	PVN
BDU	—	—	AVJ
AVE	—	—	2, AVD
AVF	—	1 m	RIF
RIF	—	—	AVF
AVH	—	1 m	—
PVQ	1	—	—
DD1	—	—	2NMJ
VD3	—	—	NMJ, DD2
DD2	—	—	VD3
VD4	—	—	2, AVA, PVN
VC2	—	—	1, VC3
VC3	—	1 m	VC2

PVN VENTRAL CORD SYNAPSES (*cont.*)

partners	gap junctions	synapses from	synapses to and corecipients
VA6	—	—	AVL, AVA
DVB	—	—	VD7
VD7	—	—	DVB
HSN	—	—	AVJ
DB3	—	—	1
DD3	—	—	1
LUA	—	1 m	—
VA11	—	2 m	—
VD12	—	—	NMJ
PDA	—	1 m	—


PVPL, PVPR
RIFL*
AVBL
AVEL, PVCR
AVBR, PVCR
RIFR*
ADFR*
AVBR, PVCR
AVBL, PVCR
PVCR
AQR*
AVHR*
AQR, ADFR
AVHL*
ASHR*
AVBR, PVCL
AVAR, PVCL
g
a
AQR
AVAL, AVBL
RIGL
AVAL
AQR
AQR
AVBR, PVCL
AVAR, PVCL
RIAR
AVBL, RIGR
AQR
AVHR*
AQR
AVHR*
d
RIAR
AVHL*
AVBR
PVCR
AVAR, AVBR
RIFL*
AQR
AVBL, AQR
AQR
AQR
RIFR*
AVBR
AVBR, PVCR
RIFL*
AQR
AVBR, ADAL
AQR
AVBR, AVER
AVKL
AVBR, AVDR
AVBR, AVDR, AVHR
AVKR
AVAR
RIGL
AQR
AVHL, RIMR
AQR
AVBL, PVCR
AVBL, PVCR
AVKL
AQR
AVAL, AVHL
AVL
DVC
PVPL
CELL BODY IN
LUMBAR GANGLION
PVPR
CELL BODY IN
LUMBAR GANGLION


PVPR
AVBR
AVJL
PVCR
PVR
a
RIGL
PVPL
AVBR
AVAR
b
AVAL
AVHL
PVPR
RIGR
c
RIFL
AVBL
PVPL
AQR
DVA
d
DB1
AVL
PVQR
PVPR
e
HYPODERMIS
HSNL
PVPL
AVKR
f
PVPL
AVBR
PVPR
AVBL
g
PVPL
HSNL
PVQL
VD3
h


c
b
e
h
f
PVPL i
PVP j

PVP

Members: PVPL, PVPR.

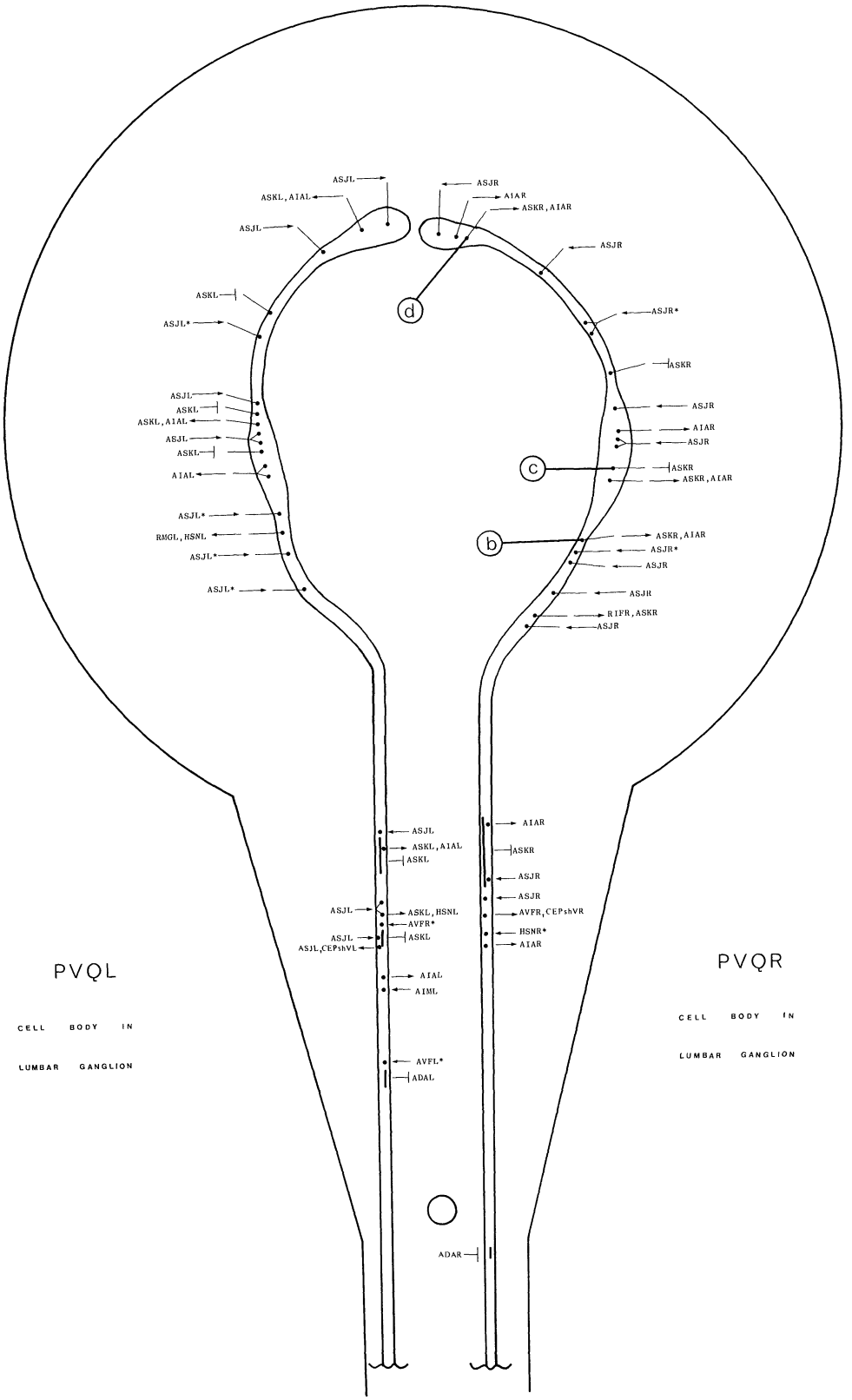
PVP is a pair of neurons with cell bodies situated in the pre-anal ganglion. Processes project anteriorly from the cell bodies, cross over (j), and then run up the ventral cord on either side of the hypodermal ridge. The processes of PVP then enter the nerve ring and run round either side of it, in the middle of the neuropile, until they meet and terminate with a gap junction and vesicle-filled swellings on the dorsal mid-line (g). The processes in the ring seem to be closely associated with AVB; they also vary considerably in diameter. In the nerve ring, the main synaptic output is to AVB (a, d), PVC (a), RIG (b), AVA (c), AVH (c) and there is some synaptic input from RIF (*c) and AVH. In the ventral cord, there are a few synapses onto the hypodermis (f) and AVL (e); there are many gap junctions to AQR and DVC (*d) and a few to PQR (*h), PHA (*d), AVK and VDn (h).

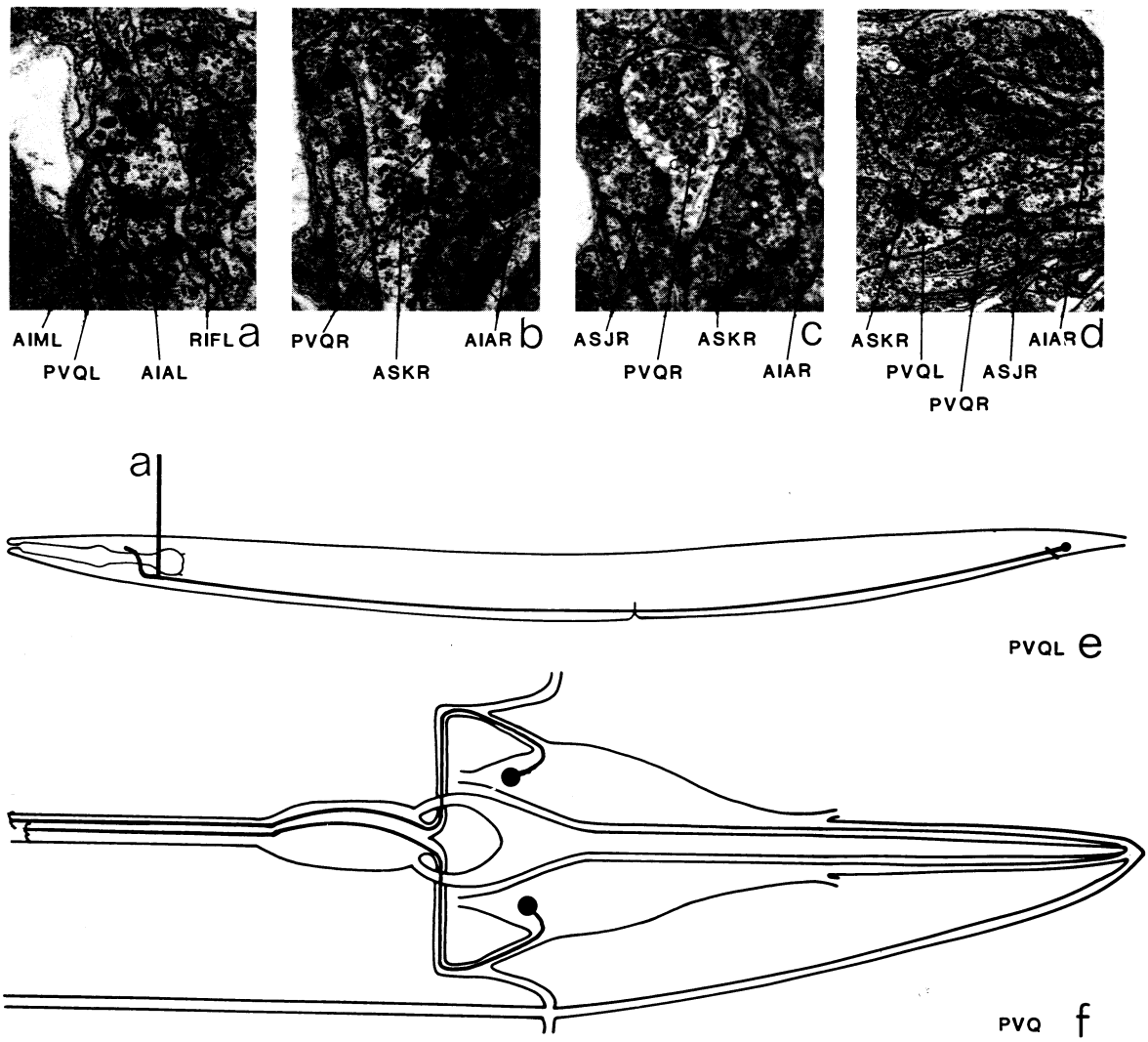
Magnifications: (a, b, d) ×25500, (c, e, f, h) ×17000, (g) ×12750.

PVP VENTRAL CORD SYNAPSES

partners	gap junctions	synapses from	synapses to and corecipients
AVL	—	—	1, PVQ, DVC, DD2
HDC	—	—	3
DVC	12	—	1, AVL
PVQ	—	—	AVL
PVC	—	—	AVH
AVH	—	—	PVC
DD2	—	—	AVL
DVB	—	1+1 m	—
VC3	—	1 m	—
AVG	—	1 m	—
VC1	—	1 m	—
AVK	5	—	—
PQR	4	—	—
PHA	3	—	—
AQR	3	—	—
VD13	2	—	—
PVT	1	—	—
PVP	1	—	—
VD3	1	—	—
VD4	1	—	—
VD5	1	—	—

PVQ


ASJL
ASKL, AIAL
ASJL
ASKL
ASJL*
ASJL
ASKL
ASKL, AIAL
ASJL
ASKL
AIAL
ASJL*
RMGL, HSNL
ASJL*
ASJL*
ASJR
AIAR
ASKR, AIAR
ASJR
ASJR*
ASKR
ASJR
AIAR
ASJR
ASKR
ASKR, AIAR
ASKR, AIAR
ASJR*
ASJR
ASJR
RIFR, ASKR
ASJR
d
c
b
ASJL
ASKL, AIAL
ASKL
ASJL
ASKL, HSNL
AVFR*
ASJL
ASKL
ASJL, CEPshVL
AIAL
AIML
AVFL*
ADAL
AIAR
ASKR
ASJR
ASJR
AVFR, CEPshVR
HSNR*
AIAR
ADAR
PVQL
CELL BODY IN LUMBAR GANGLION
PVQR
CELL BODY IN LUMBAR GANGLION



PVQ

Members: PVQL, PVQR.

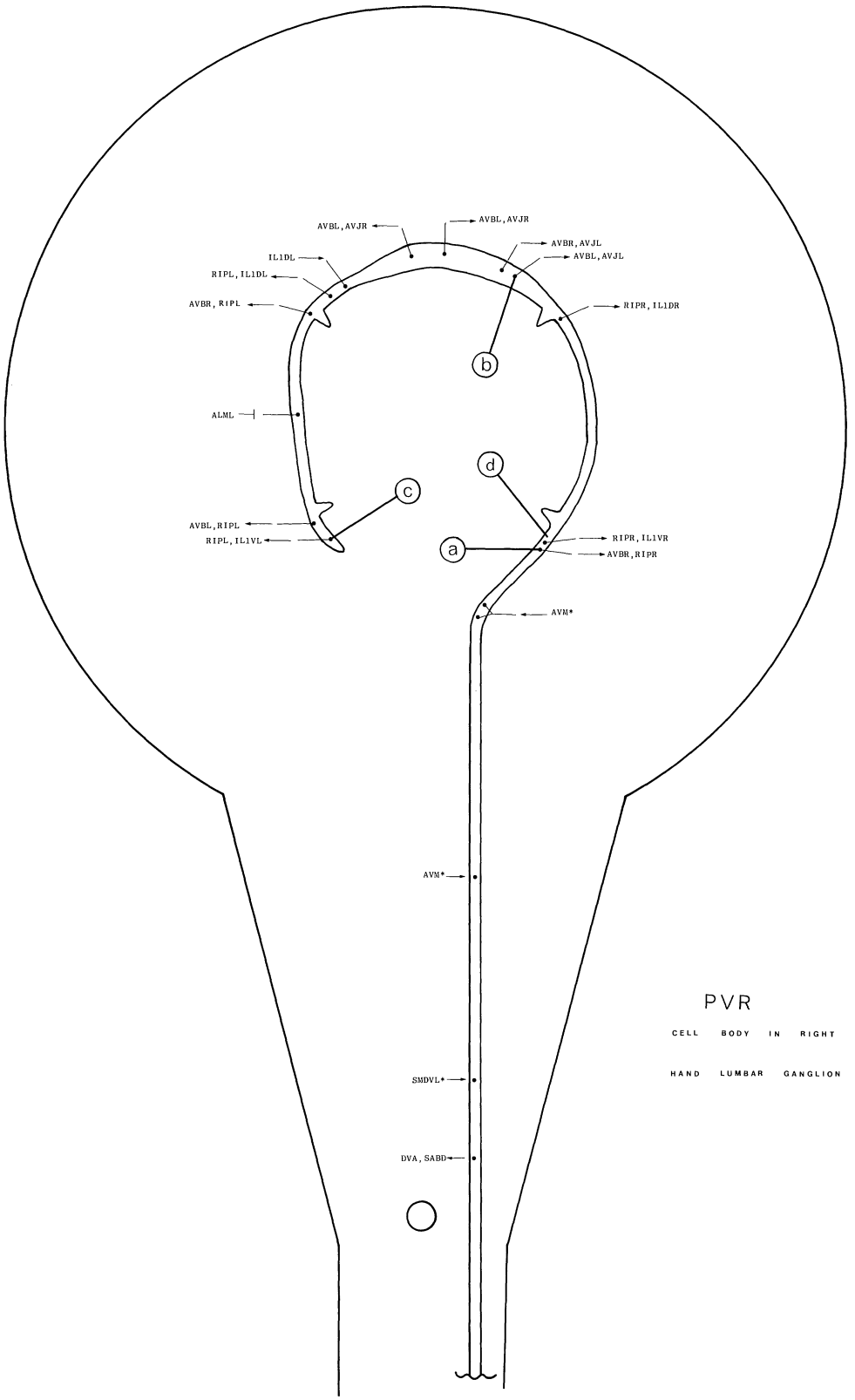
PVQ is a pair of interneurons with cell bodies in the lumbar ganglia. Processes enter the posterior extremity of the ventral cord via the lumbar commissures; initially, both run anteriorly on the right-hand side of the hypodermal ridge. When the end of the pre-anal ganglion is reached, PVQL crosses over to the left-hand side of the hypodermal ridge and runs all the way along the ventral cord up to the nerve ring in this position, whereas PVQR runs on the right-hand side along with most of the processes of the ventral cord (figure 15). As the ring is approached, the processes move up to the dorsal surface of the neuropile of the ventral ganglion. The processes then run round each side of the ring, near the posterior face, in close association with the processes of ASJ. They meet and terminate on the dorsal mid-line; there is a gap junction at the point of contact on the JSH series but the two processes do not quite touch on the N2U series. The processes of PVQ have prominent lateral (b, c) and dorsal (d) vesicle-filled varicosities. There are many dark vesicles present in these regions; the rest of the

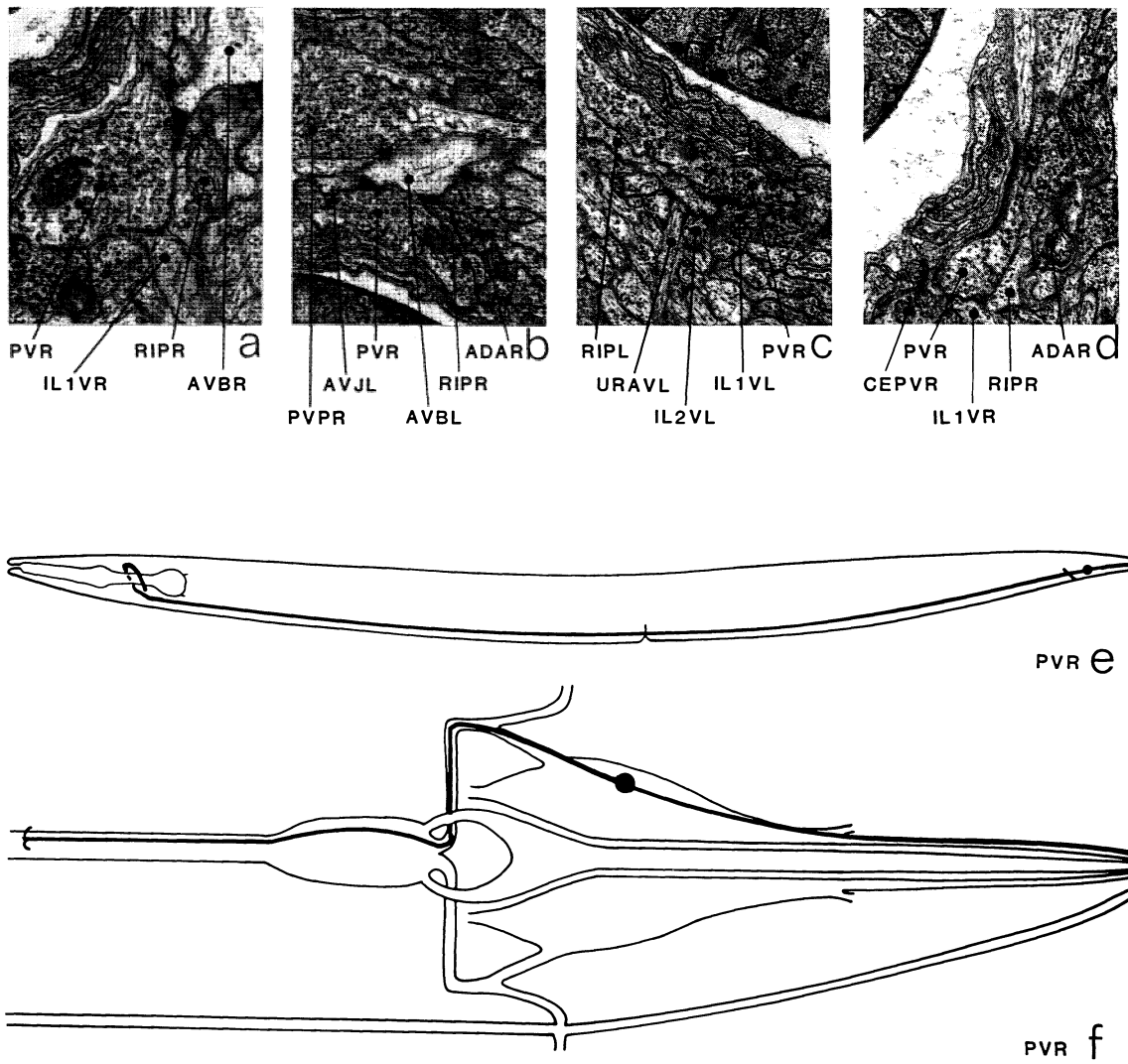
cytoplasm stains rather lightly, giving the processes of PVQ a characteristic appearance (BDU looks similar but has smaller processes with fewer vesicles). The main synaptic output is to AIA (a, b, c, d), sometimes in dyadic combination with ASK (b, c). There are also a few minor synapses to AVF and HSN. The synaptic input is almost exclusively from ASJ (*a), in the nerve ring. There are gap junctions to ASK (*a, b) and ADA. There are practically no synapses of any consequence in the ventral cord, except possibly for a few synapses from PHA (*b) in the tail.

Magnifications: (a) ×25500, (b–d) ×17000.

PVQ VENTRAL CORD SYNAPSES

partners	gap junctions	synapses from	synapses to and corecipients
HSN	—	—	1
AVL	—	—	1
DD1	—	—	VD1
VD1	—	—	DD1
DVB	—	—	DVC
DVC	—	—	DVB
PVQ	2	—	—
PHA	—	4 m	—
VC3	—	2+1 m	—
AVH	—	1+2 m	—
AVK	—	1	—
AVJ	—	1	—
AVF	1	1 m	—
AVG	—	1 m	—
ADA	1	—	—


AVBL, AVJR
AVBL, AVJR
AVBR, AVJL
AVBL, AVJL
IL1DL
RIPL, IL1DL
AVBR, RIPL
RIPR, IL1DR
b
ALML
d
c
AVBL, RIPL
RIPL, IL1VL
a
RIPR, IL1VR
AVBR, RIPR
AVM*
AVM*
SMDVL*
DVA, SABD
PVR
CELL BODY IN RIGHT
HAND LUMBAR GANGLION



PVR

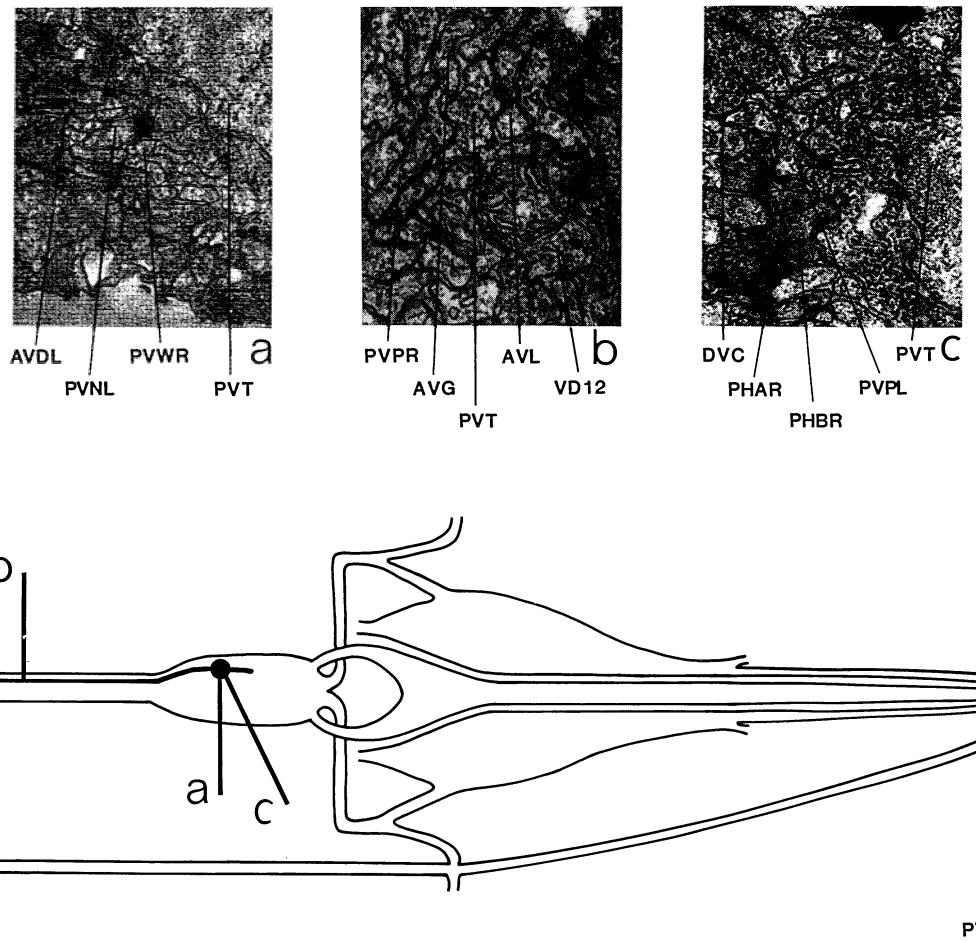
Member: PVR.

PVR has a cell body situated in the right lumbar ganglion. A posteriorly directed process runs to nearly the end of the tailspike (e); this observation suggests that it could be a sensory dendrite. An anteriorly directed process enters the pre-anal ganglion via the right lumbar commissure and has a gap junction with PLMR as it crosses its process. It runs anteriorly up the ventral cord near the ventral extremity of the process bundle. The process then enters the right-hand side of the nerve ring and runs right round it in an anticlockwise direction, adjacent to the inner surface of the neuropile, and ends in the left ventral region of the ring. Small branches project anteriorly from the process at each quadrant and run in the middle of the process bundles from the labial sensory receptors (IL1-b). No synapses are seen on these branches. Dark-staining regions are present in the basal lamina on the inner surface of the ring, adjacent to the process of PVR, in a few places (d). The main synaptic output is in the nerve ring and is directed to AVB (a), RIP (a, c) and AVJ (b). There is a gap junction to ALM (*d). In the ventral cord there is some synaptic input from AVM, DVA and PVM, and there are gap junctions to DVA and PLMR.

Magnifications: (a) ×25500, (b–d) ×17000.

PVR VENTRAL CORD SYNAPSES

partners	gap junctions	synapses from	synapses to and corecipients
PDE	—	1 m	PDE
PVC	—	1 m	1
AVK	—	—	1
DB2	—	—	1
DB3	—	—	1
DA9	—	—	1
DVA	2	1+2 m	—
PVM	—	2 m	—
LUA	2	1	—
PLM	2	—	—



PVT

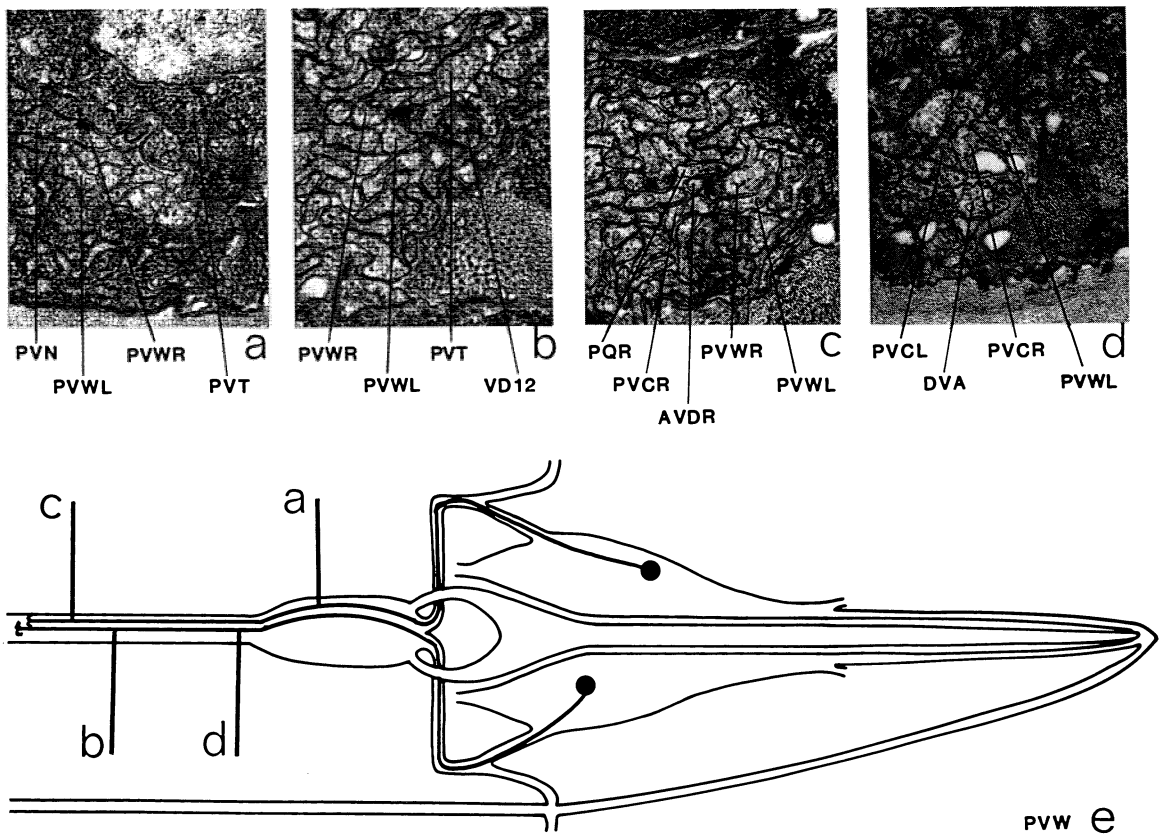
Member: PVT.

PVT has a large cell body, situated in the pre-anal ganglion, which sends out a fairly large, anteriorly directed process that runs near the middle of the ventral cord (b). This process presumably terminates somewhere in the posterior body, as it does not seem to be present in the anterior ventral cord. No synaptic outputs have been seen from this neuron. It receives some synaptic input from PVN (a) and PVW (*a); there is also a gap junction to PVP (c).

Magnifications: (a–c) ×25 500.

PVT VENTRAL CORD SYNAPSES

partners	gap junctions	synapses from	synapses to and corecipients
PVW	—	1+2 m	—
PVN	—	2	—
PVP	1	—	—



PVW

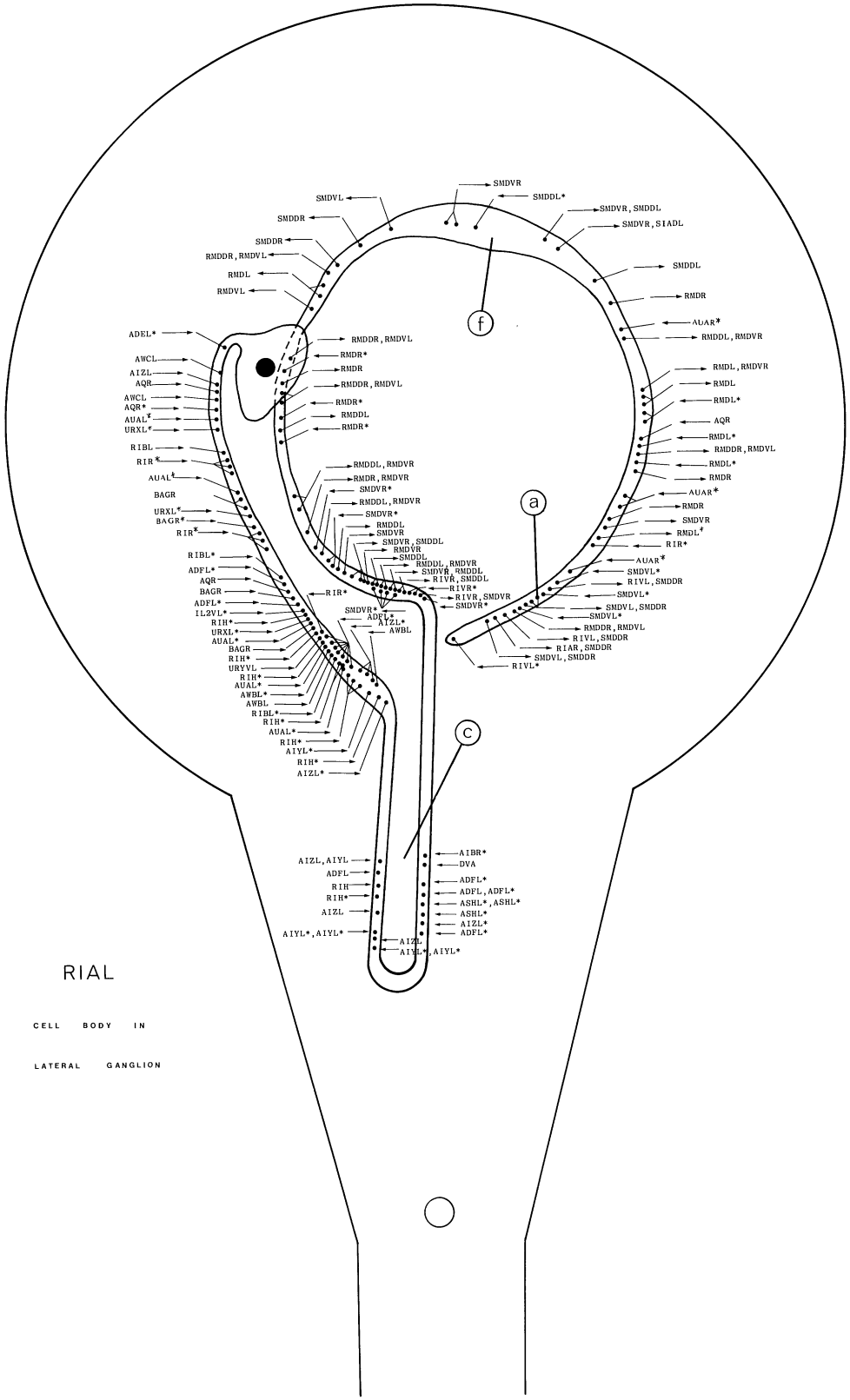
Members: PVWL, PVWR.

PVW is a set of two interneurons with cell bodies situated in the lumbar ganglia. Anteriorly directed processes enter the pre-anal ganglia via the lumbar commissures and then run alongside each other near the centre of the process bundle of the ventral cord, adjacent and ventral to the processes of PVN. The processes of PVW end somewhere in the posterior body regions, although the exact point has not been located. PVW makes a few rather small synapses in the cord, each having only a few synaptic vesicles. The main postsynaptic partners are PVT (a, b) and possibly AVD (c); there are gap junctions to PVC (d).

Magnifications: (a–d) ×25500.

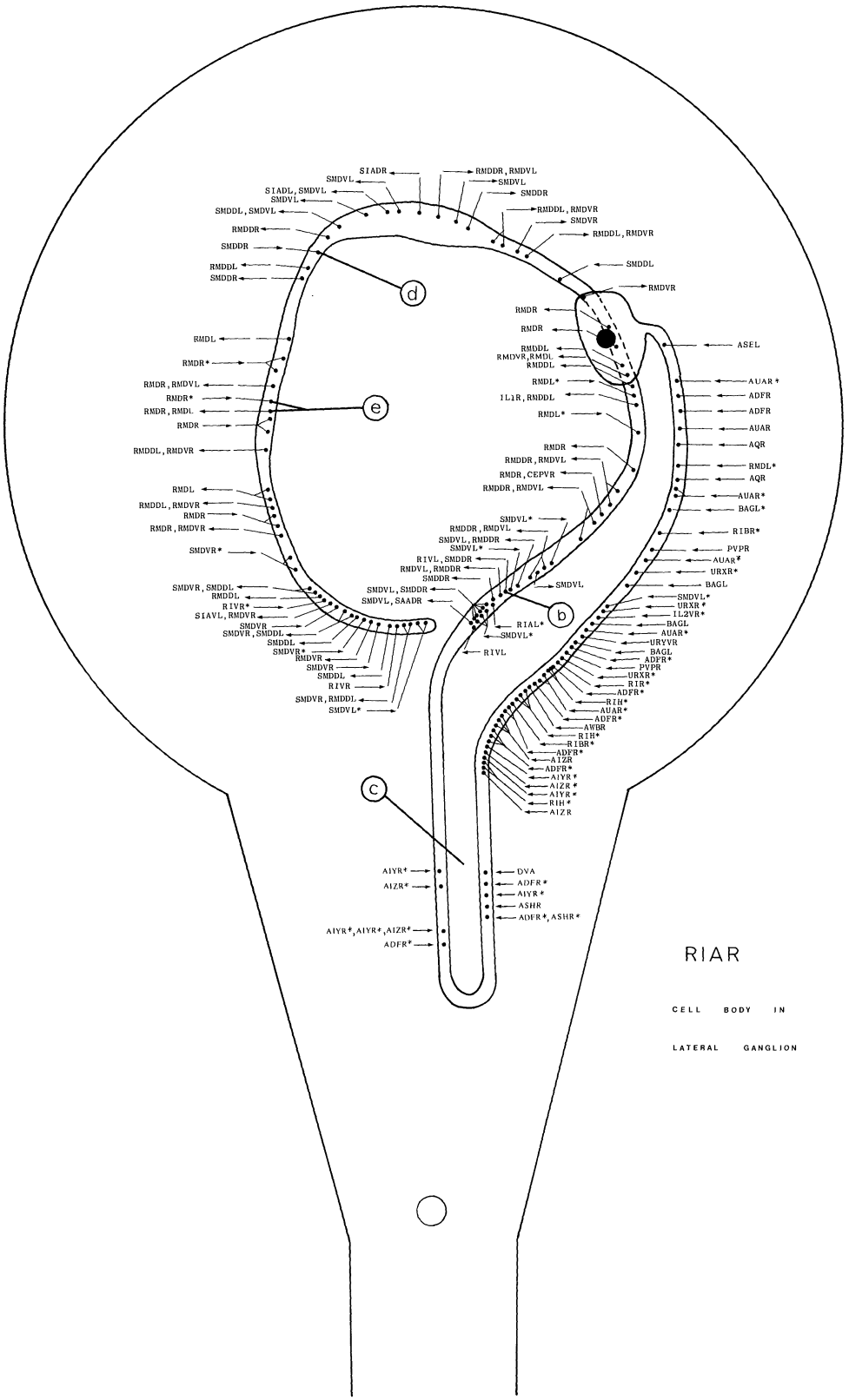
PVW VENTRAL CORD SYNAPSES

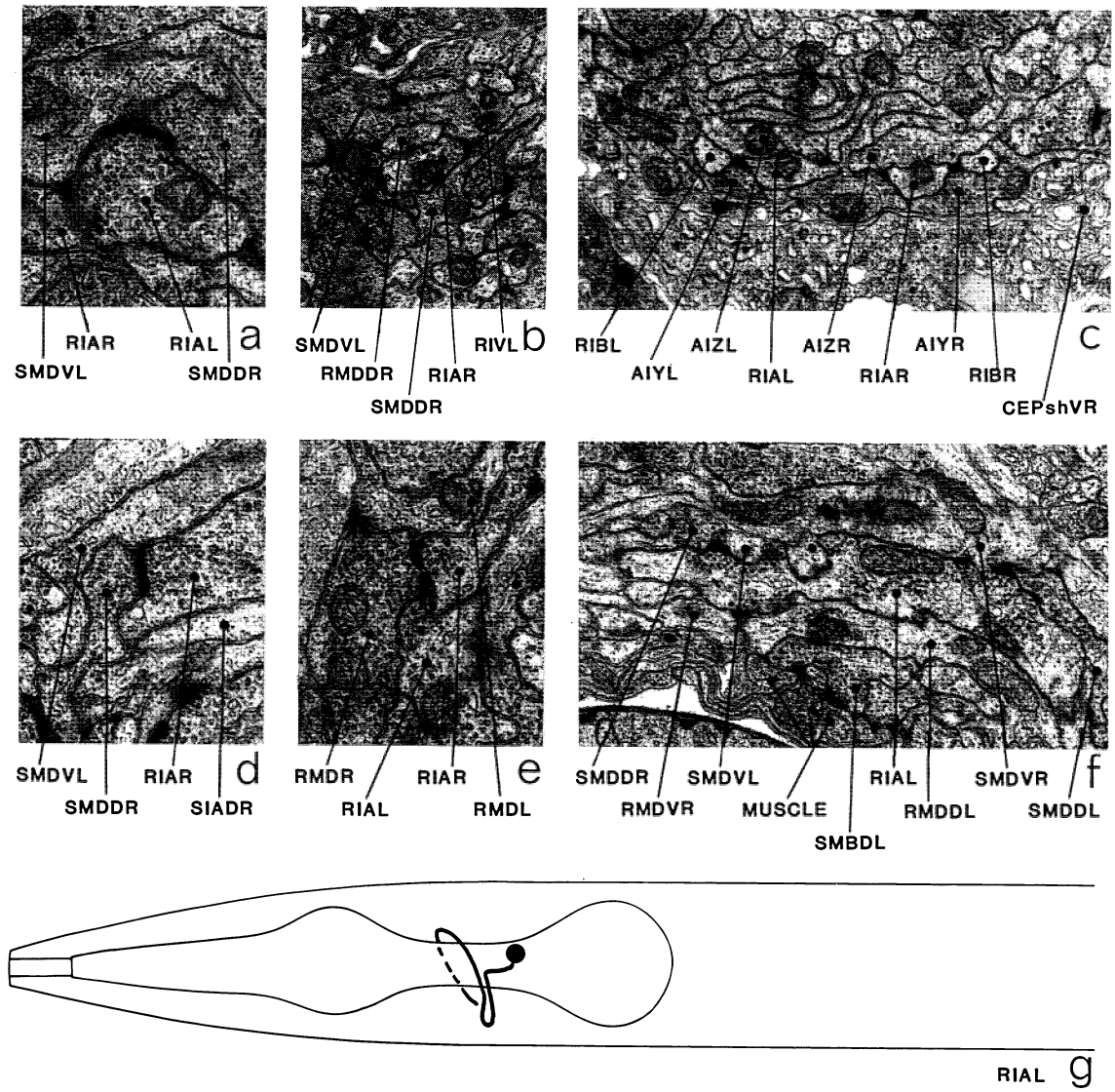
partners	gap junctions	synapses from	synapses to and corecipients
PVT	—	—	1, PVW, AVJ
PVC	3	1 m	AVD
PVW	—	1 m	PVT
AVJ	—	—	PVT
AVD	—	—	PVC
AVA	—	—	VA12
VA12	—	—	AVA
PVN	—	3 m	—
LUA	—	2 m	—
AVL	—	1 m	—



RIAL

CELL BODY IN LATERAL GANGLION


SIADR
SMDVL
SIADL, SMDVL
SMDVL
SMDDL, SMDVL
RMDDR
SMDDR
RMDDL
SMDDR
RMDDR, RMDVL
SMDVL
SMDDR
RMDDL, RMDVR
SMDVR
RMDDL, RMDVR
SMDDL
RMDVR
d
RMDR
RMDR
RMDDL
RMDVR, RMDL
RMDDL
RMDL*
IL1R, RMDDL
RMDL*
ASEL
AUAR*
ADFR
ADFR
AUAR
AQR
RMDL
RMDR*
RMDR, RMDVL
RMDR*
RMDR, RMDL
RMDR
RMDDL, RMDVR
e
RMDR
RMDDR, RMDVL
RMDR, CEPVR
RMDDR, RMDVL
RMDL*
AQR
AUAR*
BAGL*
RMDL
RMDDL, RMDVR
RMDR
RMDR, RMDVR
SMDVR*
SMDVL*
RMDDR, RMDVL
SMDVL, RMDDR
SMDVL*
RIVL, SMDDR
RMDVL, RMDDR
SMDDR
SMDVL
RIBR*
PVPR
AUAR*
URXR*
BAGL
SMDVR, SMDDL
RMDDL
RIVR*
SIAVL, RMDVR
SMDVR
SMDVR, SMDDL
SMDDL
SMDVR*
RMDVR
SMDVR
SMDDL
RIVR
SMDVR, RMDDL
SMDVL*
SMDVL, SMDDR
SMDVL, SAADR
b
RIAL*
SMDVL*
RIVL
SMDVL*
URXR*
BAGL
SMDVL*
URXR*
IL2VR*
BAGL
AUAR*
URYVR
BAGL
ADFR*
PVPR
URXR*
RIR*
ADFR*
RIH*
AUAR*
ADFR*
AWBR
RIH*
RIBR*
ADFR*
AIZR
ADFR*
AIYR*
AIZR*
AIYR*
RIH*
AIZR
c
AIYR*
AIZR*
AIYR*, AIYR*, AIZR*
ADFR*
DVA
ADFR*
AIYR*
ASHR
ADFR*, ASHR*
RIAR
CELL BODY IN LATERAL GANGLION

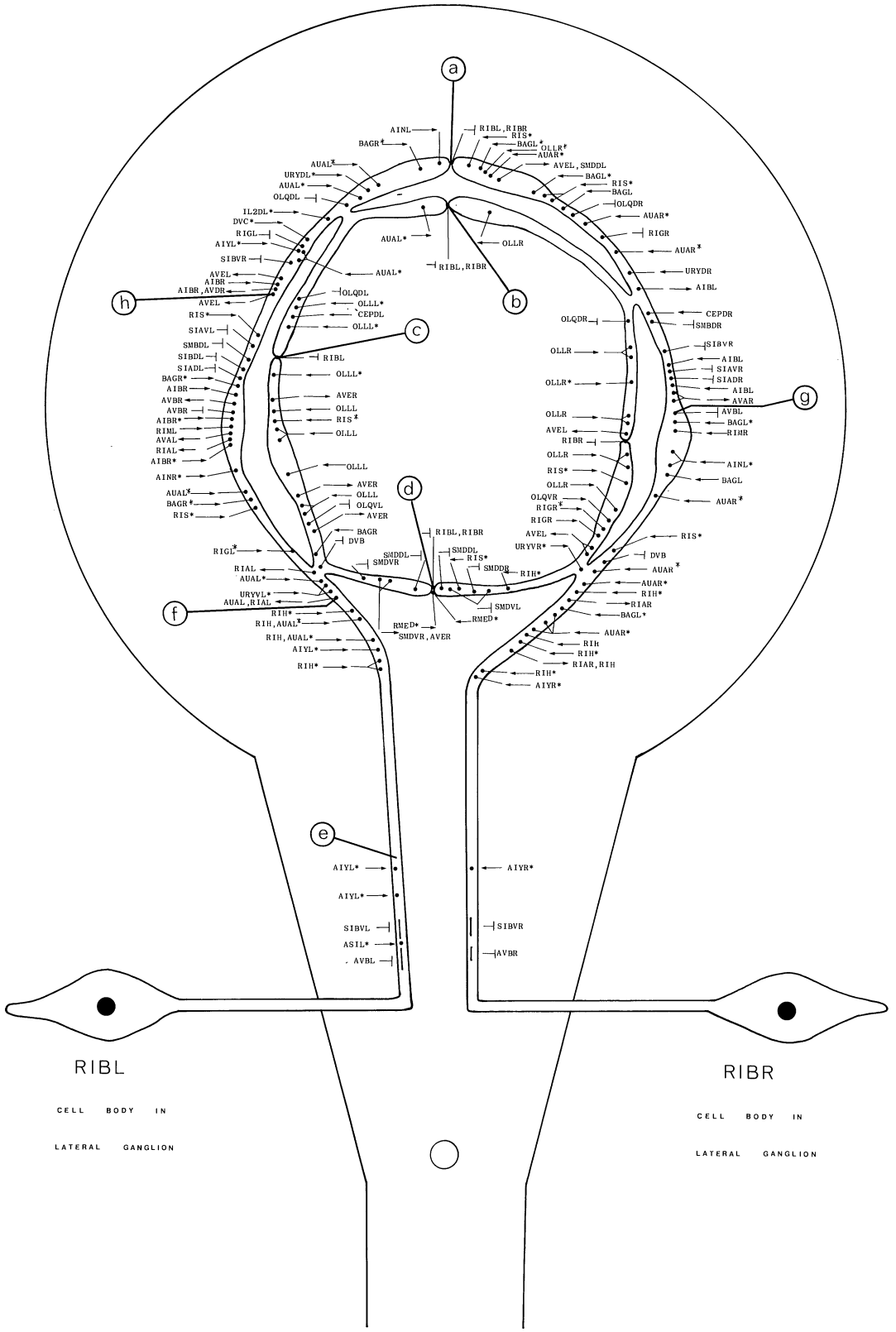


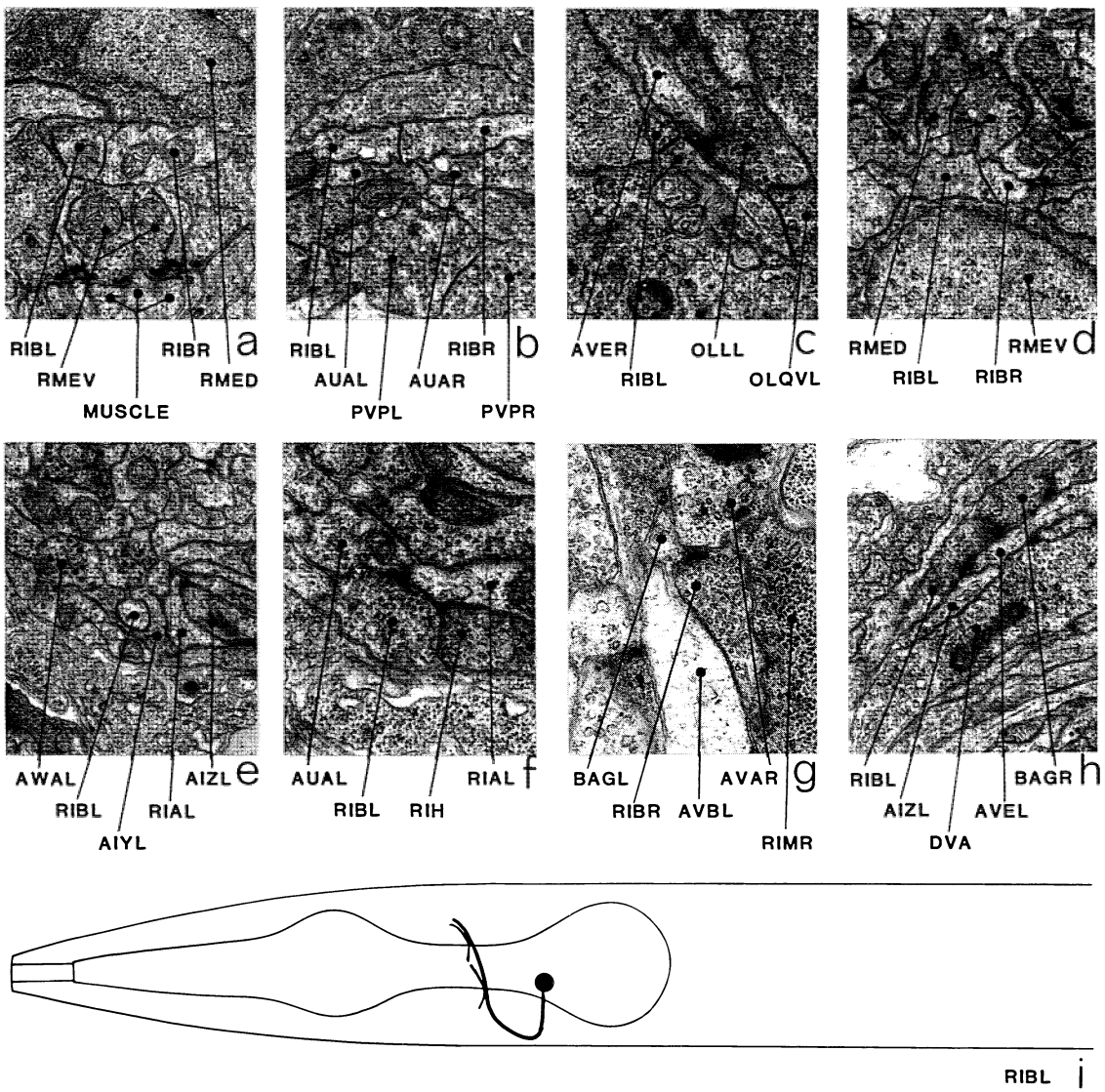
RIA

Members: RIAL, RIAR.

RIA is a set of two prominent interneurons with cell bodies situated in the lateral ganglia, adjacent to the neuropile of the nerve ring. Large processes enter the nerve ring directly sub-dorsally and run round the ring initially near the posterior face and enter the ventral cord. They loop round into the neuropile of the ventral ganglion and re-enter the ring on the ipsilateral side (g). They then run round the nerve ring near the anterior surface and in close association with the processes of their contralateral partners and the processes of RMD which often surround them (*d). RIA is presynaptic only on the distal regions of its processes in the nerve ring, which have many synapses (f). It synapses onto SMD (a) and RMD (e) at numerous sites in these regions. There are also a few synapses to RIV (b). SMD and RMDL/R (but not RMDD/V) synapse back onto RIA reciprocally. Often reciprocal pairs are adjacent (d, e). RIA is one of the major integrating neurons in the nerve ring; it receives synaptic input from ADF (*a), SMD (d), RMDL/R (e), AIZ (*a), RIH (*a), AIY (*e), AUA (*a), BAG (*a), AQR (*d), URX (*a), RIR (*a), RIB (*f), ASH (*d), AWB (*b) and RIV (*e). Characteristic structures are seen in the neuropile of the ventral ganglion, where RIA receives synapses from AIZ and AIY (c).

Magnifications: (a, d, e) ×25500, (b) ×17000, (c, f) ×12750.


a
b
c
d
e
f
g
h
AINL
BAGR*
AUAL*
URYDL*
AUAL*
OLQDL
IL2DL*
DVC*
RIGL
AIYL*
SIBVR
AVEL
AIBR
AIBR,AVDR
AVEL
RIS*
SIAVL
SMBDL
SIBDL
SIADL
BAGR*
AIBR
AVBR
AVBR
AIBR*
RIML
AVAL
RIAL
AIBR*
AINR*
AUAL*
BAGR*
RIS*
RIBL,RIBR
RIS*
BAGL*
OLLR*
AUAR*
AVEL,SMDDL
BAGL*
RIS*
BAGL
OLQDR
AUAR*
RIGR
AUAR*
URYDR
AIBL
CEPDR
SMBDR
SIBVR
AIBL
SIAVR
SIADR
AIBL
AVAR
AVBL
BAGL*
RIMR
AINL*
BAGL
AUAR*
RIS*
DVB
AUAR*
AUAR*
RIH*
RIAR
BAGL*
AUAR*
RIH
RIH*
RIAR,RIH
RIH*
AIYR*
AUAL*
OLLR
RIBL,RIBR
OLQDL
OLLL*
CEPDL
OLLL*
RIBL
OLLL*
AVER
OLLL
RIS*
OLLL
OLLL
AVER
OLLL
OLQVL
AVER
BAGR
DVB
RIBL,RIBR
SMDDL
SMDVR
SMDDL
RIS*
SMDDR
RIH*
SMDVL
RMED*
RMED*
SMDVR,AVER
OLLR
OLLR
OLLR
OLLR
OLLR
OLQVR
RIGR*
RIGR
AVEL
URYVR*
RIGL*
RIAL
AUAL*
URYVL*
AUAL,RIAL
RIH*
RIH,AUAL*
RIH,AUAL*
AIYL*
RIH*
AIYL*
AIYL*
SIBVL
ASIL*
AVBL
AIYR*
SIBVR
AVBR
RIBL
CELL BODY IN
LATERAL GANGLION
RIBR
CELL BODY IN
LATERAL GANGLION

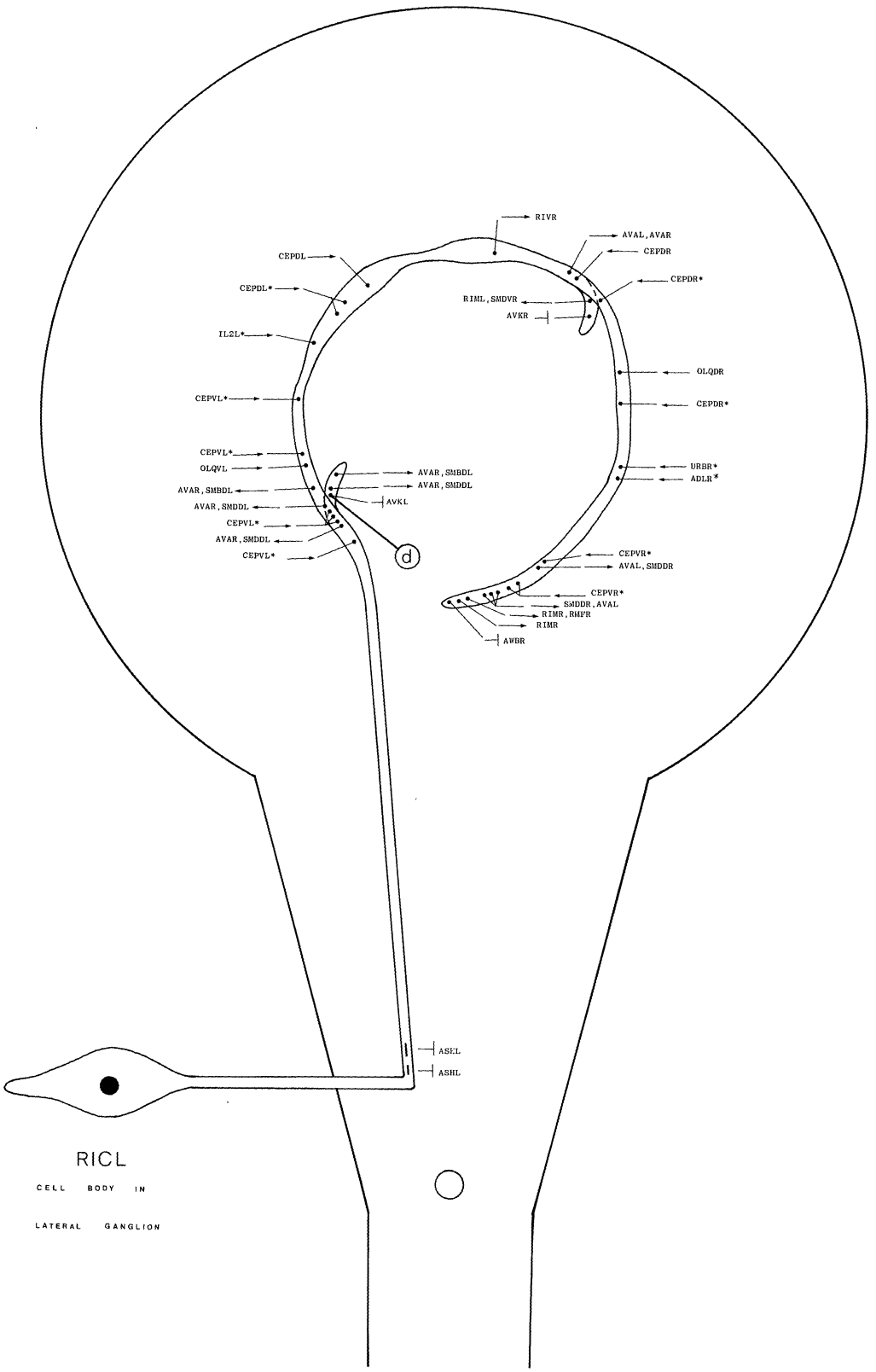


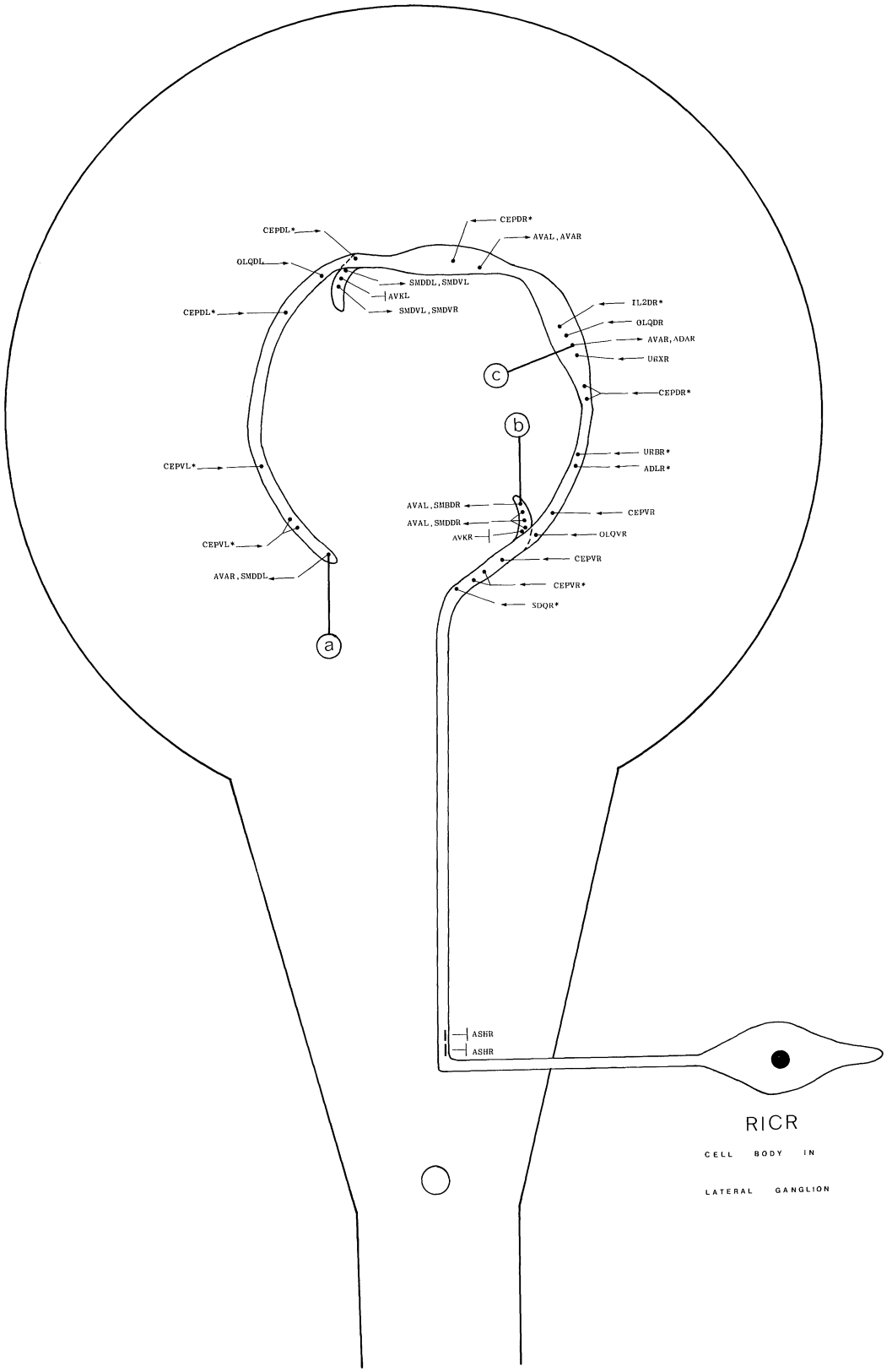
RIB

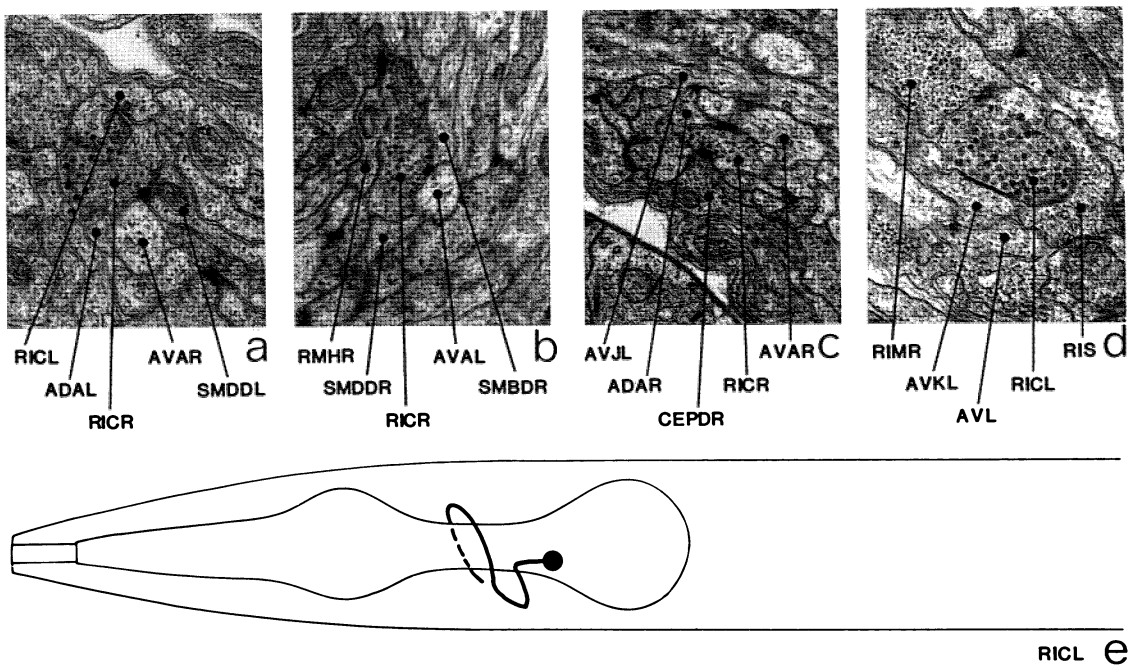
Members: RIBL, RIBR.

RIB is a set of two interneurons with cell bodies in the lateral ganglia. Processes enter the ventral cord via the amphidial commissures and project anteriorly, running in the ventral regions of the cord. AIY often wraps round the processes of RIB in the region of the ventral ganglion (e). Processes enter the ring and run round it near the outside surface and the posterior face, eventually meeting and stopping at the dorsal mid-line with a gap junction to their contralateral partners (a). There are two branch points situated near the sub-dorsal and the sub-ventral process bundles from the labial sensilla; dorsally and ventrally directed branches from these points run, closely associated with the processes of AVE, in the anterior regions of the nerve ring. These processes terminate with gap junctions to their contralateral partners on the dorsal (b) and ventral (d) mid-lines. There are also laterally situated gap junctions between processes of the same cell (c). The main synaptic outputs are to AVE (h), RIA (f), AIB, AIZ (h) and AVA (g) but the synapses are generally rather small. The main synaptic inputs are from: OLL (*a), AUA (*a), AIY (*e), BAG (*a), RIG (*d), AIN (*c), AIB (*a), RIS (*c), RIH (*b) and URY. RIB is unusual as it has gap junctions to many other classes of cell; these are OLQ (c), AVB (g), RIG (*g), SIB (*c), SIA (*a), SMB, DVB and SMD.

Magnifications: (a, b, d, e, h) ×12750, (c, f, g) ×25500.


RIVR
AVAL, AVAR
CEPDR
CEPDR*
CEPDL
CEPDL*
RIML, SMDVR
AVKR
IL2L*
OLQDR
CEPDR*
CEPVL*
CEPVL*
OLQVL
AVAR, SMBDL
AVAR, SMDDL
AVKL
URBR*
ADLR*
AVAR, SMBDL
AVAR, SMDDL
AVAR, SMDDL
CEPVL*
AVAR, SMDDL
CEPVL*
d
CEPVR*
AVAL, SMDDR
CEPVR*
SMDDR, AVAL
RIMR, RMFR
RIMR
AWBR
ASEL
ASHL
RICL
CELL BODY IN
LATERAL GANGLION


CEPDL*
CEPDR*
AVAL, AVAR
OLQDL
SMDDL, SMDVL
AVKL
CEPDL*
SMDVL, SMDVR
IL2DR*
OLQDR
AVAR, ADAR
URXR
c
CEPDR*
b
URBR*
ADLR*
CEPVL*
AVAL, SMBDR
CEPVR
AVAL, SMDDR
AVKR
OLQVR
CEPVL*
CEPVR
AVAR, SMDDL
CEPVR*
SDQR*
a
ASHR
ASHR
RICR
CELL BODY IN
LATERAL GANGLION

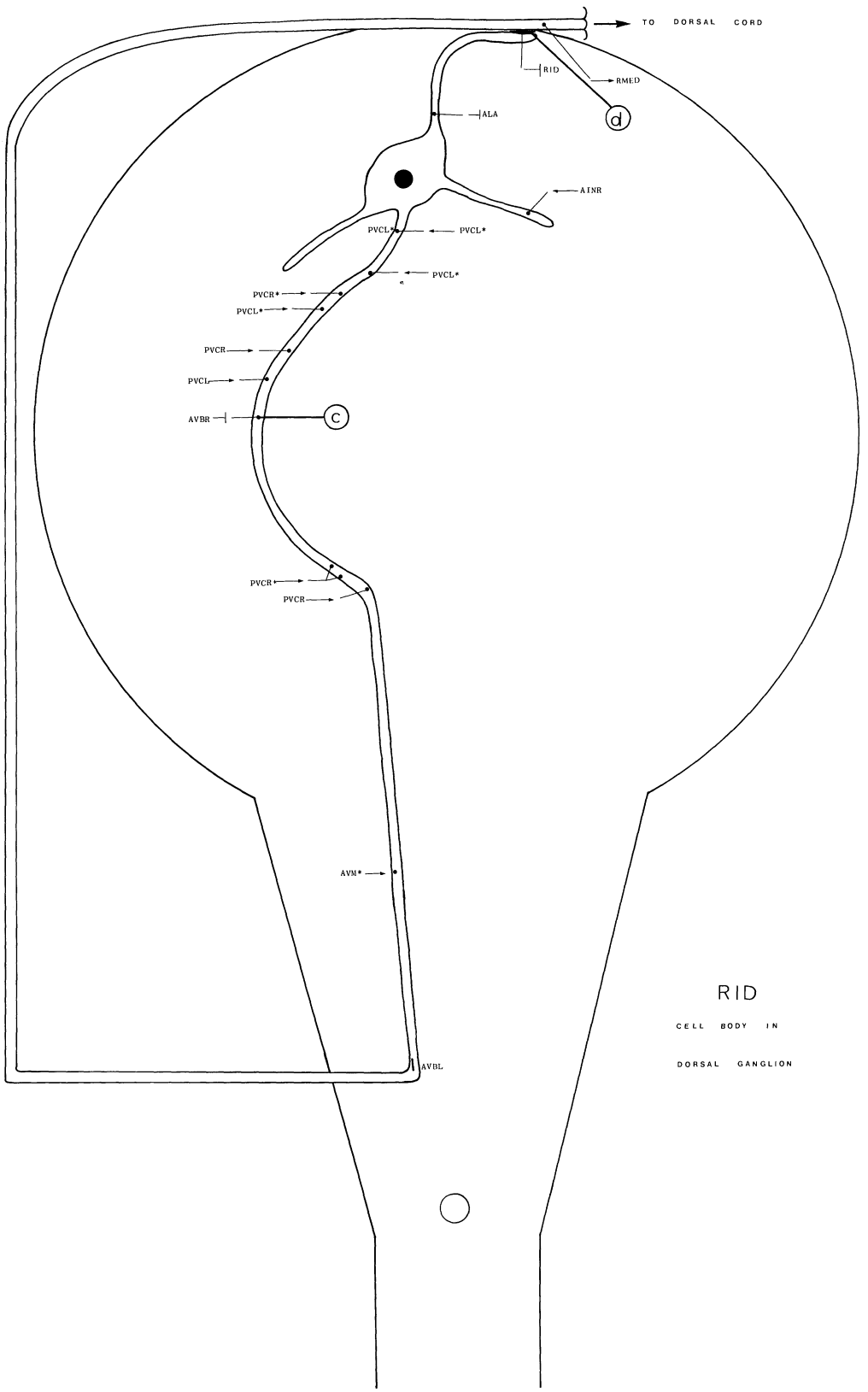


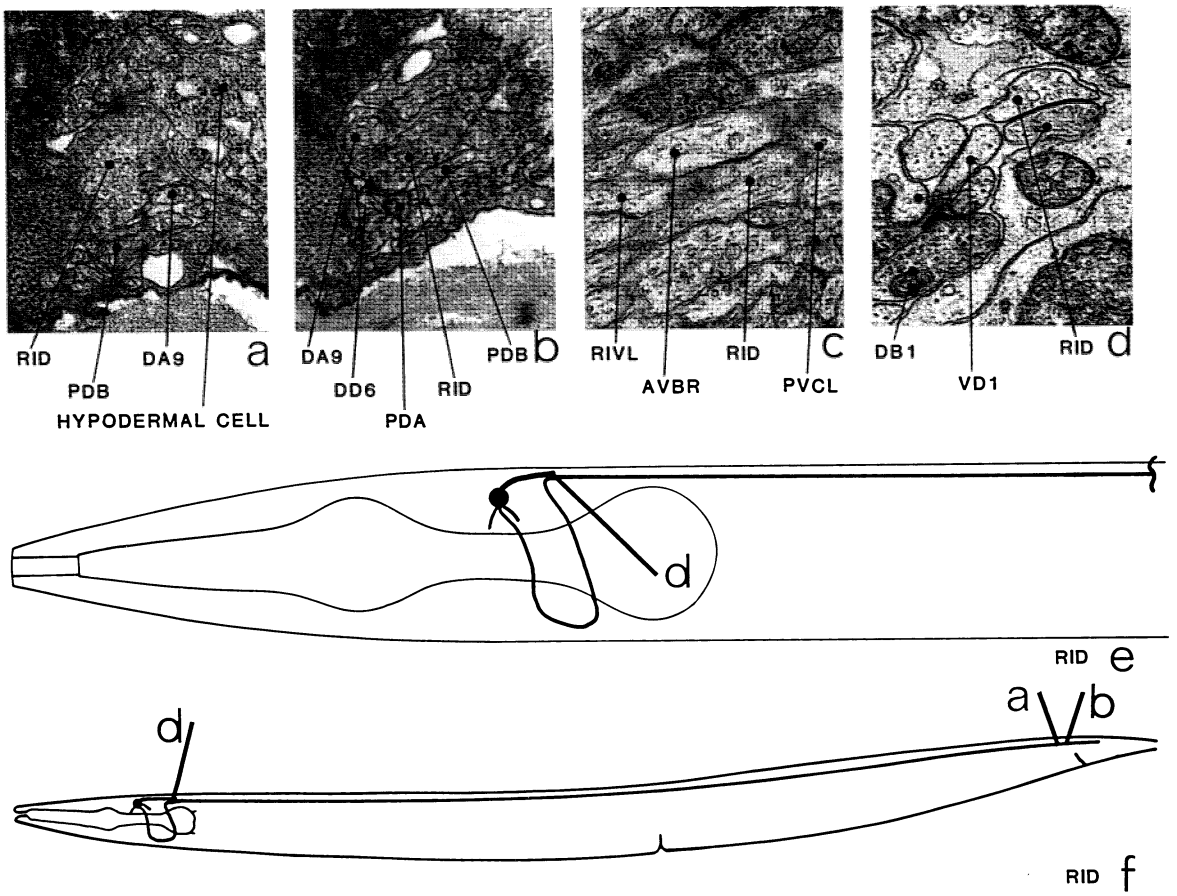
RIC

Members: RICL, RICR.

RIC is a pair of interneurons with cell bodies situated in the posterior regions of the lateral ganglia. Processes leave the cell body and enter the ventral cord via the amphidial commissures. Here they turn and run anteriorly into the nerve ring running on the dorsal surface of the neuropile. When they enter the nerve ring they move to the middle of the neuropile and run right round the nerve ring; the distal regions of each process running in close association with the proximal regions of the process of its contralateral partner. Short anteriorly directed branches come off each process sub-ventrally and sub-dorsally on the contralateral side. The main synaptic output is to AVA (a, b, c), SMD (a), and SMBD (b). There are some dark-cored vesicles present in the pre-synaptic terminals (a). The main synaptic input is from CEP (*a) and OLQ (*a); there are also some inputs from URB (*d) and URX. RIC has gap junctions to ASH and AVK (d).

Magnifications: (a, d) $\times 25500$, (b, c) $\times 17000$.


TO DORSAL CORD
RID
RMED
d
ALA
AINR
PVCL*
PVCL*
PVCL*
PVCR*
PVCL*
PVCR
PVCL
AVBR
c
PVCR
PVCR
AVM*
AVBL
RID
CELL BODY IN
DORSAL GANGLION



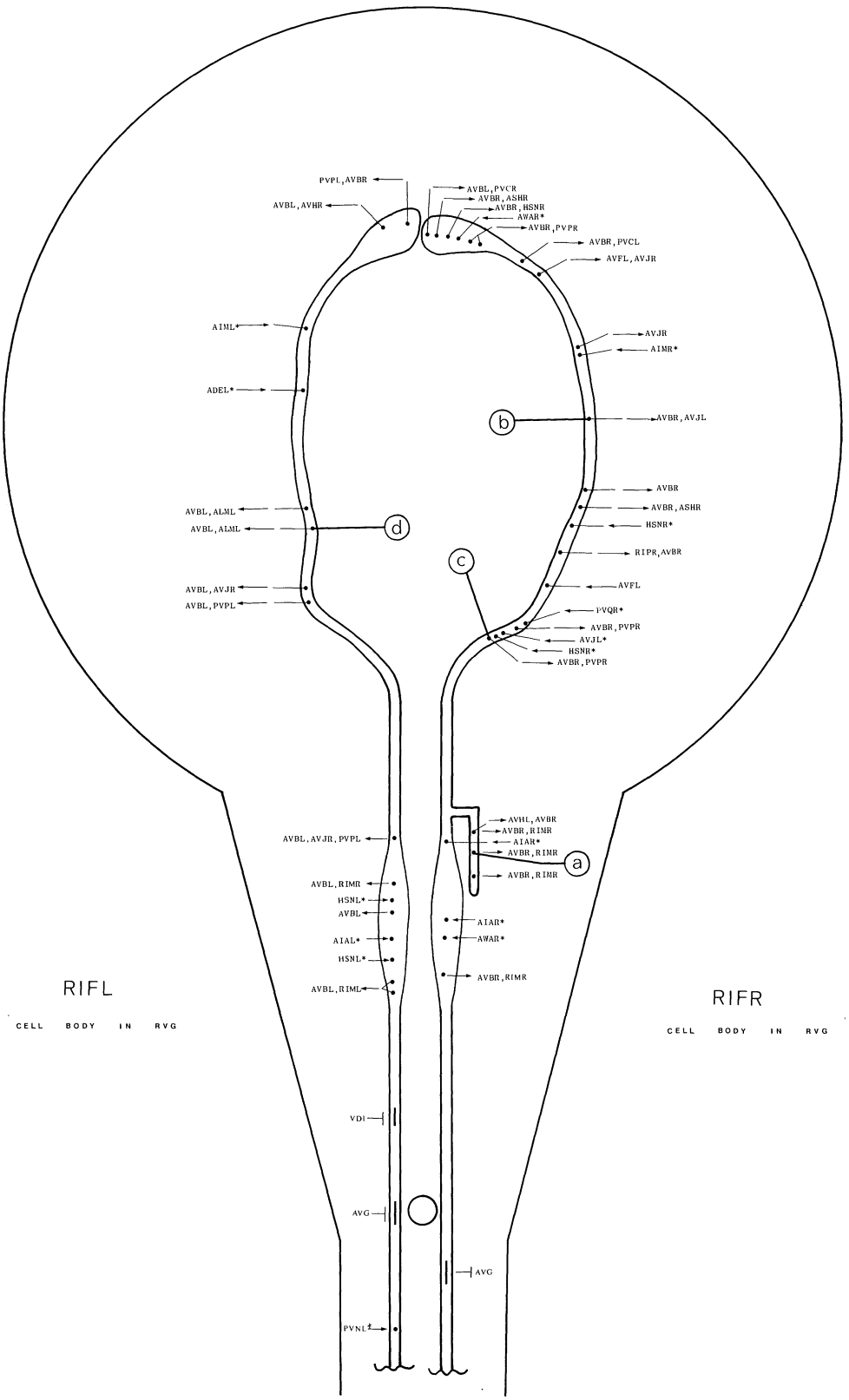
RID

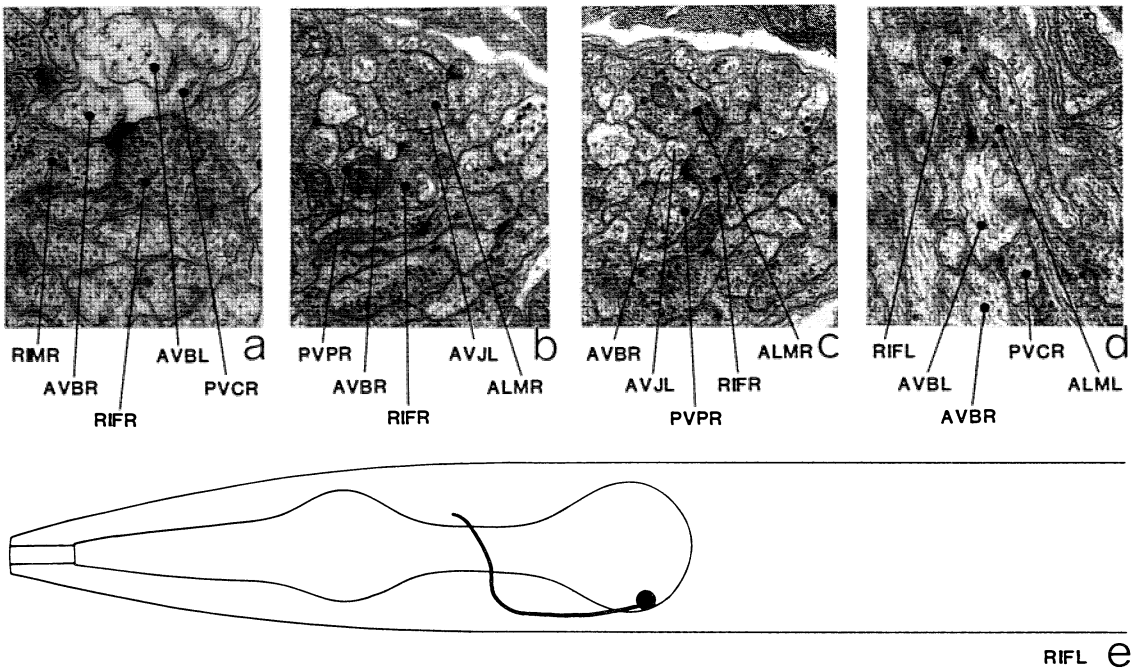
Member: RID.

RID is a single motoneuron that innervates dorsal body muscles. Its cell body is situated in the dorsal ganglion on the dorsal mid-line. A single process emanates from the ventral side of the cell body and runs down one side of the nerve ring and enters the neuropile of the ventral ganglion. In the N2U series, this process was on the left-hand side; in the JSH series, it ran to the right. The process then leaves the ventral cord via the amphidial commissure and runs round to the dorsal cord. Here it meets a short process that has come directly from the cell body and has a gap junction with it (d). RID probably runs along the length of the dorsal cord. It has not been followed for the whole length but its process has been identified in the posterior regions of the cord on the basis of the morphology of its synapses. RID has a few, rather small, synapses, which are all in the dorsal cord. These are mainly to hypodermal cells (a), DDn motor neurons (b) and dorsal muscles. The synaptic input is from PVC in the nerve ring. Gap junctions are made to AVB (c) and ALA (*c).

Magnifications: (a–d) ×25500.

RIF


PVPL, AVBR
AVBL, AVHR
AVBL, PVCR
AVBR, ASHR
AVBR, HSNR
AWAR*
AVBR, PVPR
AVBR, PVCL
AVFL, AVJR
AIML*
AVJR
AIMR*
ADEL*
b
AVBR, AVJL
AVBR
AVBR, ASHR
HSNR*
RIPR, AVBR
AVBL, ALML
AVBL, ALML
d
c
AVBL, AVJR
AVBL, PVPL
AVFL
PVQR*
AVBR, PVPR
AVJL*
HSNR*
AVBR, PVPR
AVHL, AVBR
AVBR, RIMR
AIAR*
AVBR, RIMR
a
AVBR, RIMR
AVBL, AVJR, PVPL
AVBL, RIMR
HSNL*
AVBL
AIAL*
HSNL*
AVBL, RIML
AIAR*
AWAR*
AVBR, RIMR
VD1
AVG
AVG
PVNL
RIFL
CELL BODY IN RVG
RIFR
CELL BODY IN RVG

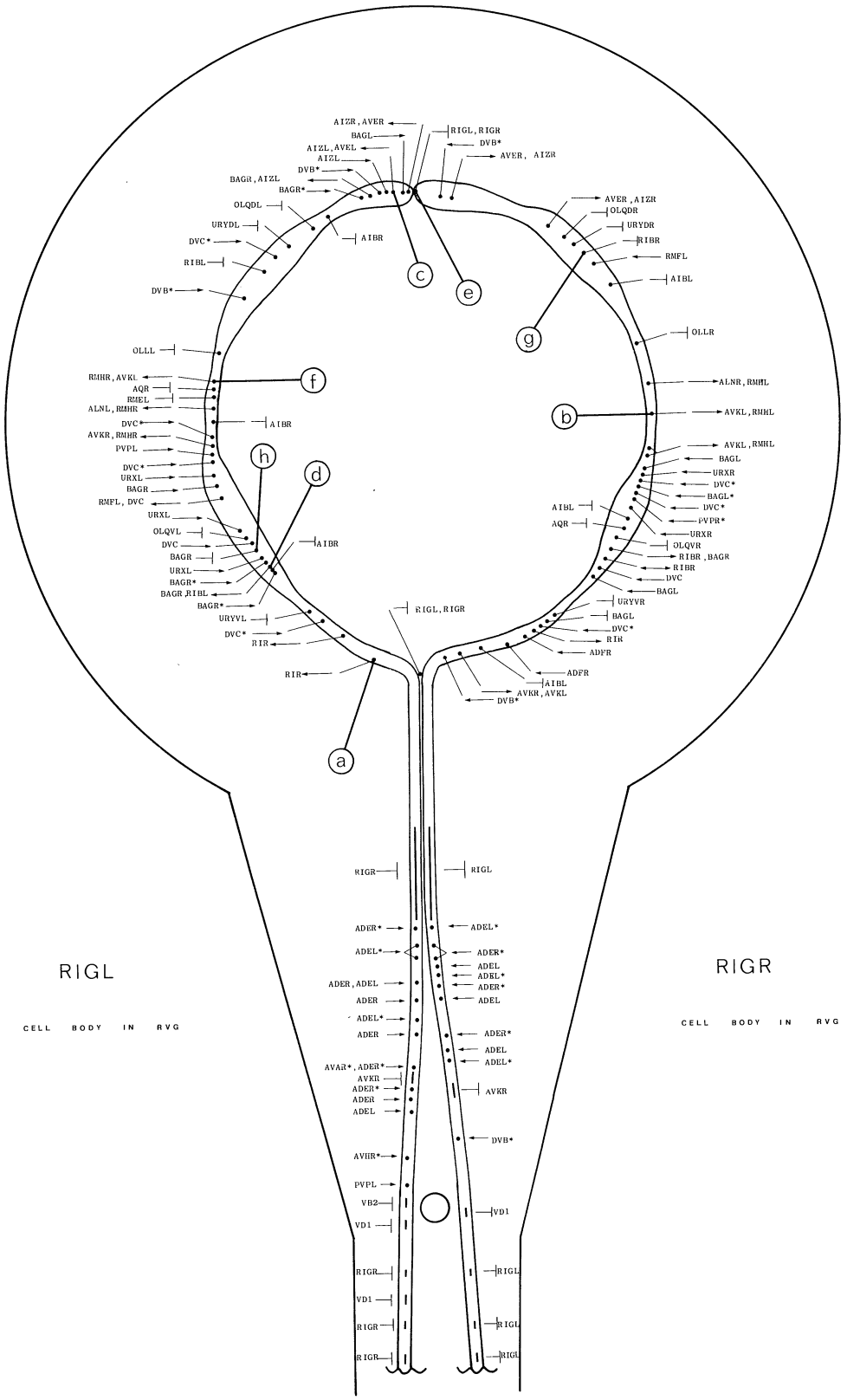


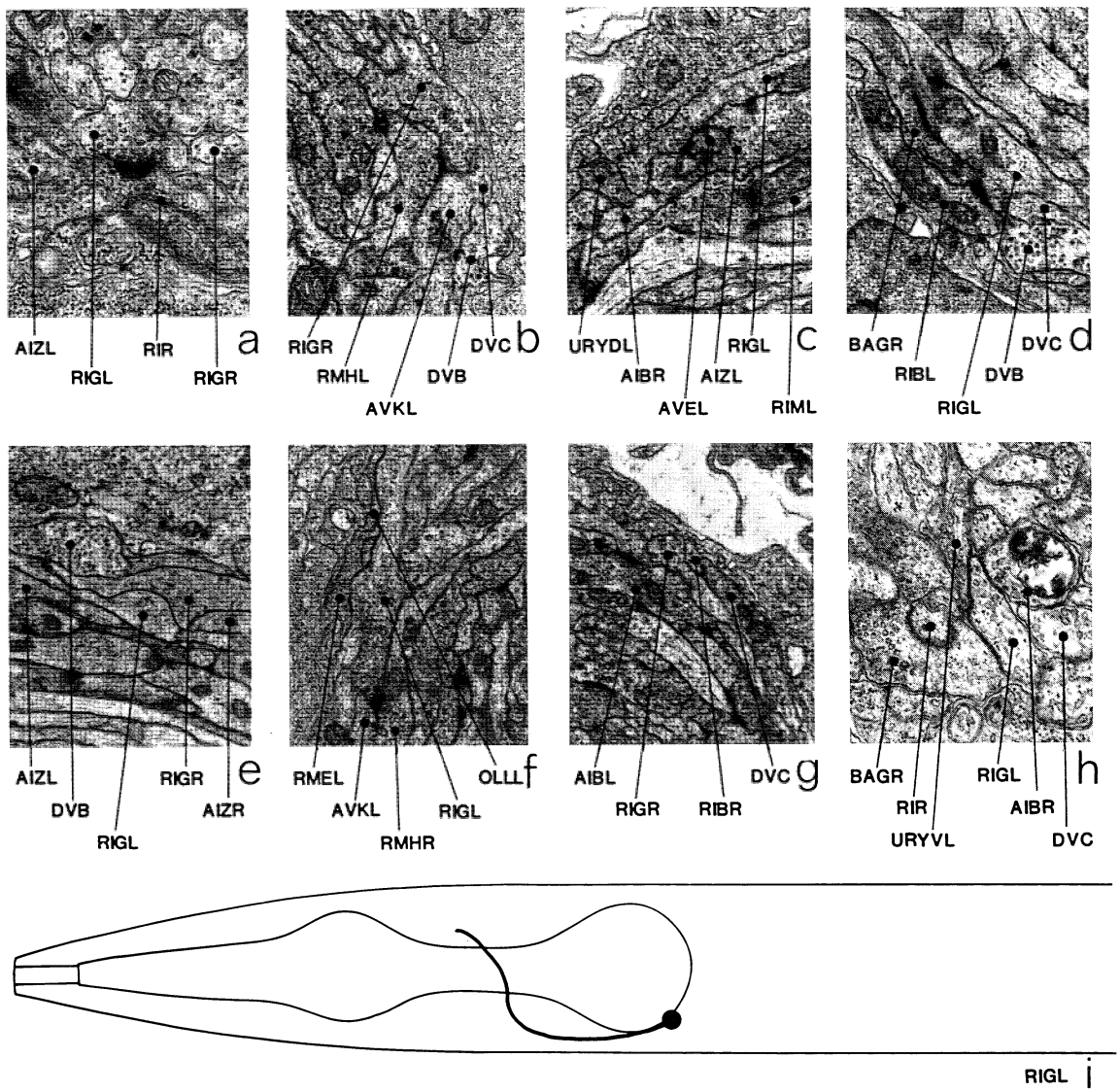
RIF

Members: RIFL, RIFR.

RIF is a set of two interneurons with cell bodies situated in the retro-vesicular ganglion. Processes run anteriorly from the cell bodies and run in the interior of the ventral nerve cord symmetrically disposed about the mid-line. They move to the dorsal surface of the cord as the ring is approached and then run round either side of the ring on the inside surface near the posterior face. The processes of RIF meet and terminate on the dorsal mid-line but do not have a gap junction. The main synaptic output is to AVB in dyadic combination with RIM (a), AVJ (b), PVP (c) or ALM (d). The main synaptic input is from AIA (*a) via large synapses in the neuropile of the ventral ganglion. There is also some synaptic input from HSN (*g). A short process from AVG (*b) often pokes into the cell body of one of the RIFs. AVG has gap junctions with both RIFs.

Magnifications: (a, d) $\times 25500$, (b, c) $\times 17000$.


AIZR, AVER
BAGL
AIZL, AVEL
AIZL
DVB*
BAGR, AIZL
BAGR*
OLQDL
URYDL
DVC*
RIBL
DVB*
OLLL
RMHR, AVKL
AQR
RMEL
ALNL, RMHR
DVC*
AVKR, RMHR
PVPL
DVC*
URXL
BAGR
RMFL, DVC
URXL
OLQVL
DVC
BAGR
URXL
BAGR*
BAGR, RIBL
BAGR*
URYVL
DVC*
RIR
RIR
AIBR
AIBR
RIGL, RIGR
DVB*
AVER, AIZR
AVER, AIZR
OLQDR
URYDR
RIBR
RMFL
AIBL
OLLR
ALNR, RMHL
AVKL, RMHL
AVKL, RMHL
BAGL
URXR
DVC*
BAGL*
DVC*
PVPR*
URXR
OLQVR
RIBR, BAGR
RIBR
DVC
BAGL
AIBL
AQR
URYVR
BAGL
DVC*
RIR
ADFR
ADFR
AIBL
AVKR, AVKL
DVB*
a
b
c
d
e
f
g
h
RIGR
RIGL
ADER*
ADEL*
ADEL*
ADER*
ADER, ADEL
ADEL
ADER
ADEL*
ADER*
ADER
ADEL
ADER*
AVAR*, ADER*
AVKR
ADER*
ADER
ADEL
AVKR
DVB*
AVHR*
PVPL
VB2
VD1
VD1
RIGR
VD1
RIGL
RIGR
RIGL
RIGR
RIGL
RIGL
CELL BODY IN RVG
CELL BODY IN RVG

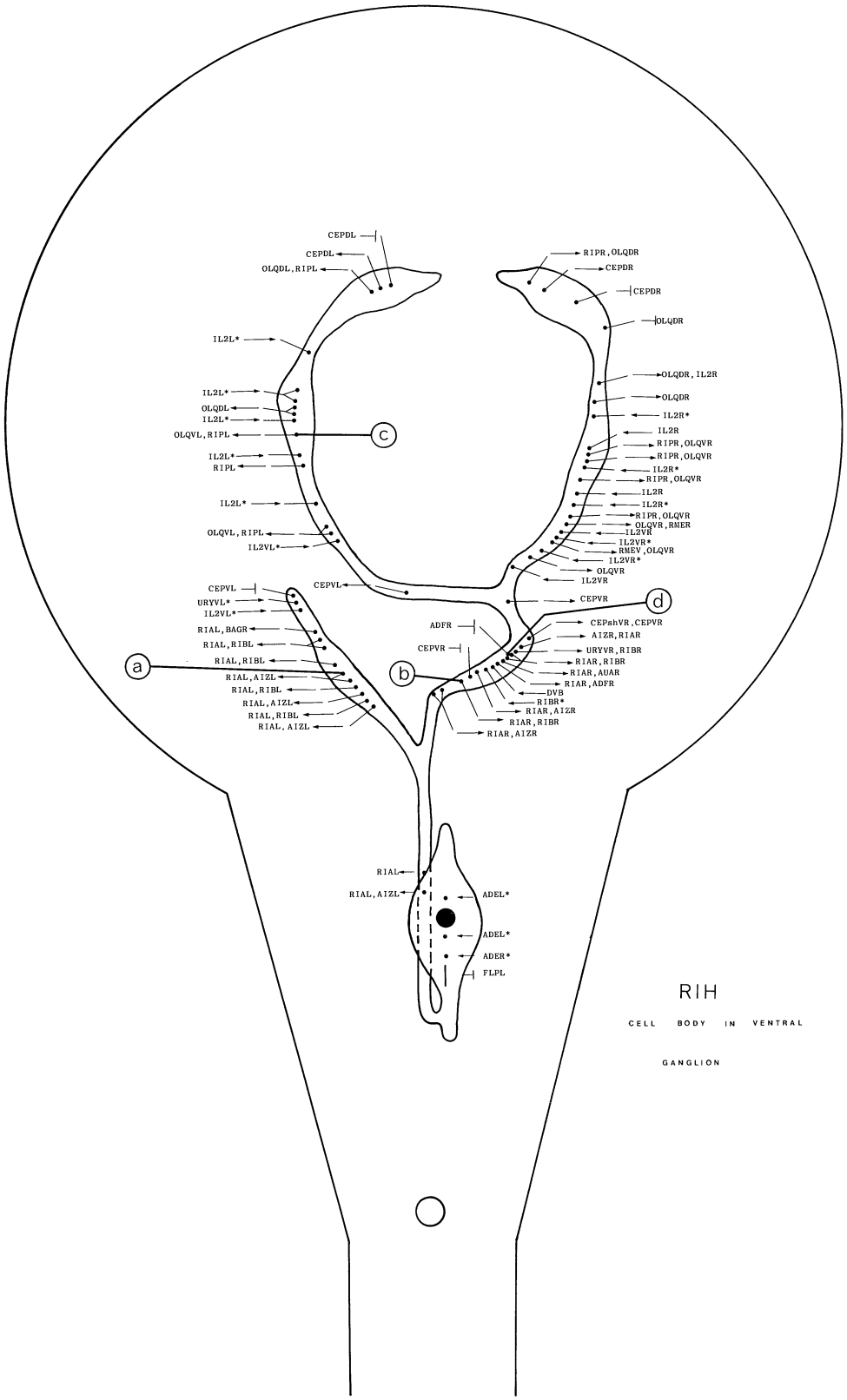


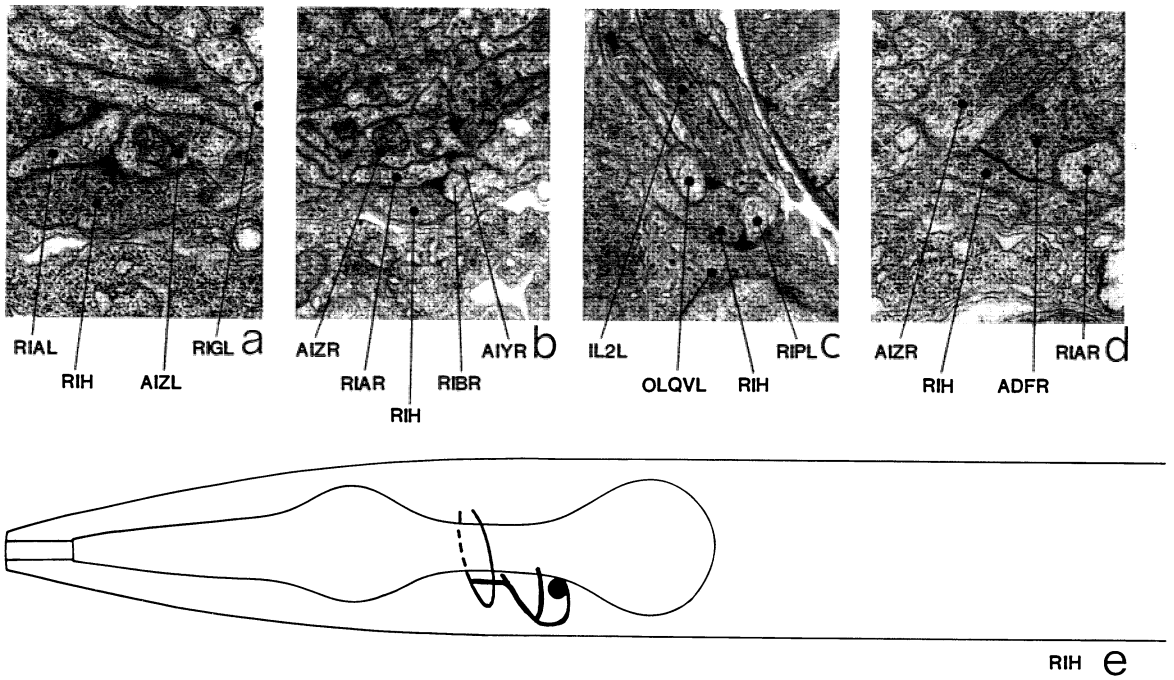
RIG

Members: RIGL, RIGR.

RIG is a set of two interneurons with cell bodies situated in the retro-vesicular ganglion. Processes from each cell body run anteriorly, closely apposed in the middle of the ventral cord. As they approach the nerve ring, the processes move down into the ventral region of the nerve cord. They then enter the nerve ring and run round each side of it, near the anterior face and outside surface of the neuropile, until they meet and terminate on the dorsal mid-line with a gap junction. The main synaptic output is to RIR (a), RMH (b), AVE (c), AIZ (c), AVK (b), RIB (d) and BAG (d). There are extensive synaptic inputs from ADE (*a) in the neuropile of the ventral ganglion and some synapses from DVC (*a), PVP (*b), URX (*d), BAG (*b) and DVB in the nerve ring. RIG is striking because of the quantity and diversity of its gap junctions. It has gap junctions with itself (e), URY (c, h), OLQ (*f), OLL (f), RIB (g), BAG (h), AQR and AVK.

Magnifications: (a, h) ×25500, (b–d, f) ×17000, (e, g) ×12750.


CEPDL
CEPDL
OLQDL,RIPL
IL2L*
IL2L*
OLQDL
IL2L*
OLQVL,RIPL
IL2L*
RIPL
IL2L*
OLQVL,RIPL
IL2VL*
CEPVL
URYVL*
IL2VL*
RIAL,BAGR
RIAL,RIBL
RIAL,RIBL
RIAL,AIZL
RIAL,RIBL
RIAL,AIZL
RIAL,RIBL
RIAL,AIZL
RIPR,OLQDR
CEPDR
CEPDR
OLQDR
OLQDR,IL2R
OLQDR
IL2R*
IL2R
RIPR,OLQVR
RIPR,OLQVR
IL2R*
RIPR,OLQVR
IL2R
IL2R*
RIPR,OLQVR
OLQVR,RMER
IL2VR
IL2VR*
RMEV,OLQVR
IL2VR*
OLQVR
IL2VR
CEPVL
CEPVR
ADFR
CEPVR
CEPshVR,CEPVR
AIZR,RIAR
URYVR,RIBR
RIAR,RIBR
RIAR,AUAR
RIAR,ADFR
DVB
RIBR*
RIAR,AIZR
RIAR,RIBR
RIAR,AIZR
RIAL
RIAL,AIZL
ADEL*
ADEL*
ADER*
FLPL
a
b
c
d
RIH
CELL BODY IN VENTRAL GANGLION



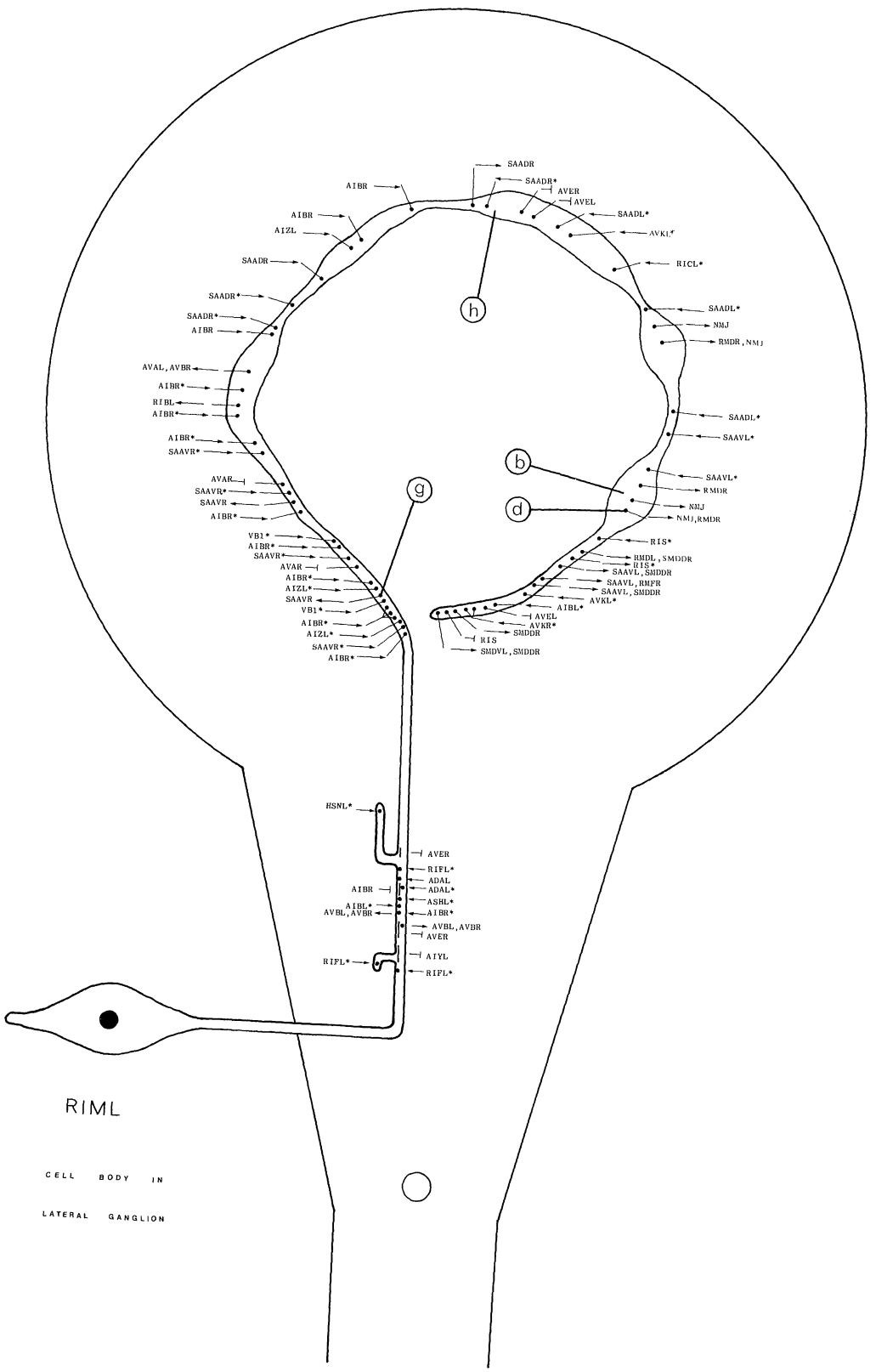
RIH

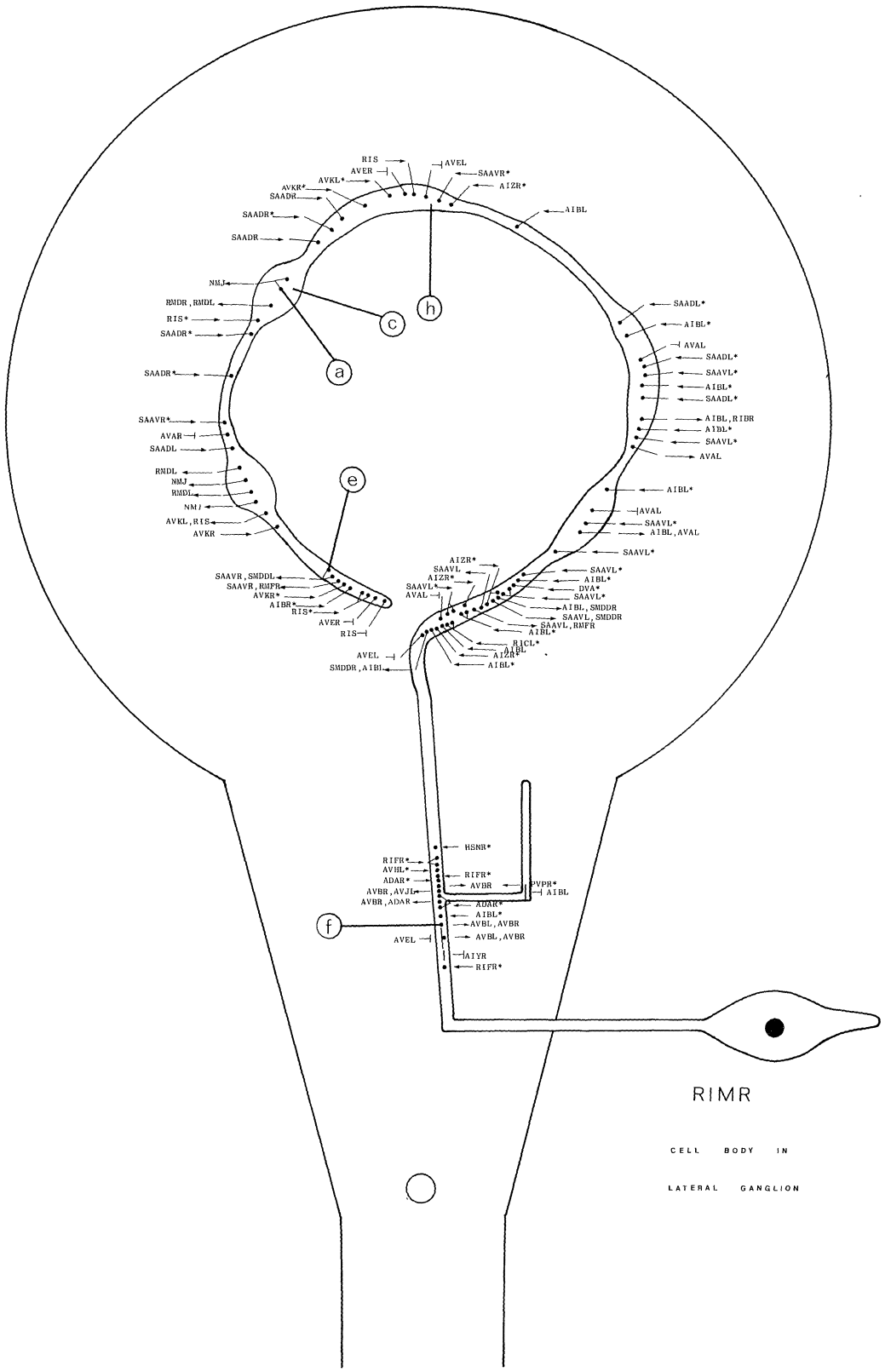
Member: RIH.

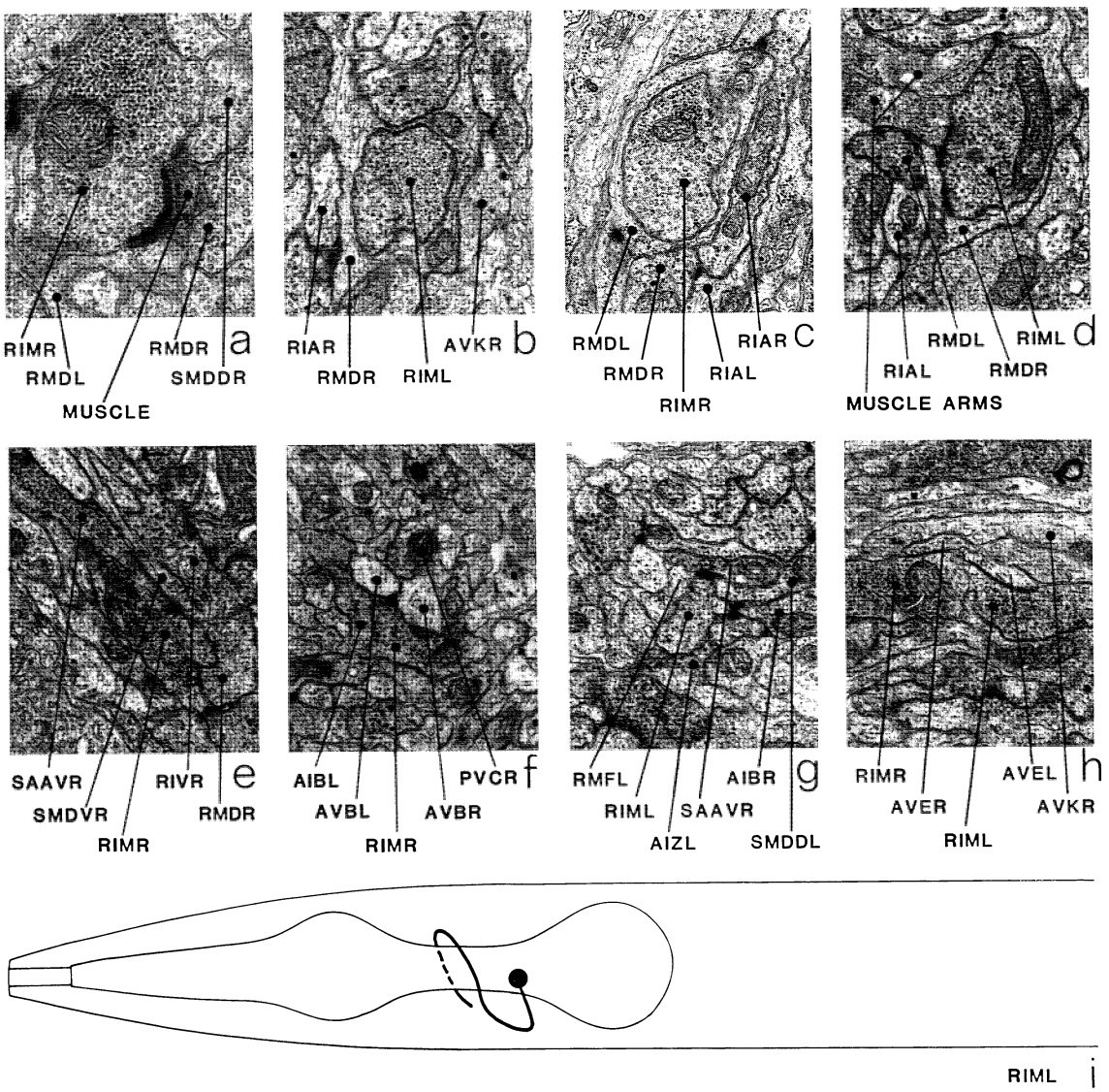
RIH is an interneuron with a single, large, cell body situated on the ventral mid-line at the anterior end of the ventral ganglion (figure 16). A process comes off the cell body posteriorly and then turns and runs ventrally to the ventral extremity of the neuropile. It then runs anteriorly in this position until it bifurcates with each process running round the outside surface of the nerve ring. These two processes appear symmetrical; however, the left-hand one ends after a short distance and the right-hand process changes direction and runs anteriorly through the neuropile of the nerve ring until it reaches the anterior surface. At this point the process bifurcates again and each branch runs round the ring and ends near the dorsal mid-line. The unusual architecture of this neuron results in its processes' inhabiting two quite separate neighbourhoods. The main synaptic outputs after the first bifurcation are to RIA (a), AIZ (a) and RIB (b) at dyadic synapses. After the second bifurcation, the main synaptic outputs are to RIP (c), OLQ (c), at dyadic synapses, and CEP. The main synaptic input is from IL2 (*c, *d). RIH has gap junctions with ADF (d), CEP, OLQ (*g) and FLP (*d).

Magnifications: (a) ×25500, (b–d) ×17000.

RIM


SAADR
SAADR*
AVER
AVEL
SAADL*
AVKL*
RICL*
AIBR
AIBR
AIZL
SAADR
SAADR*
SAADR*
AIBR
AVAL, AVBR
AIBR*
RIBL
AIBR*
AIBR*
SAAVR*
AVAR
SAAVR*
SAAVR
AIBR*
VB1*
AIBR*
SAAVR*
AVAR
AIBR*
AIZL*
SAAVR
VB1*
AIBR*
AIZL*
SAAVR*
AIBR*
h
g
b
d
SAADL*
NMJ
RMDR, NMJ
SAADL*
SAAVL*
SAAVL*
RMDR
NMJ
NMJ, RMDR
RIS*
RMDL, SMDDR
RIS*
SAAVL, SMDDR
SAAVL, RMFR
SAAVL, SMDDR
AVKL*
AIBL*
AVEL
AVKR*
SMDDR
RIS
SMDVL, SMDDR
HSNL*
AVER
RIFL*
ADAL
AIBR
ADAL*
ASHL*
AIBL*
AVBL, AVBR
AIBR*
AVBL, AVBR
AVER
AIYL
RIFL*
RIFL*
RIML
CELL BODY IN LATERAL GANGLION


RIS
AVER
AVEL
SAAVR*
AIZR*
AVKR*
AVKL*
SAADR
SAADR*
SAADR
AIBL
NMJ
RMDR, RMDL
RIS*
SAADR*
SAADR*
SAAVR*
AVAR
SAADL
RMDL
NMJ
RMDL
NMJ
AVKL, RIS
AVKR
SAAVR, SMDDL
SAAVR, RMFL
AVKR*
AIBR*
RIS*
AVER
RIS
AVEL
SMDDR, AIBL
a
c
h
e
f
SAADL*
AIBL*
AVAL
SAADL*
SAAVL*
AIBL*
SAADL*
AIBL, RIBR
AIBL*
SAAVL*
AVAL
AIBL*
AVAL
SAAVL*
AIBL, AVAL
SAAVL*
AIZR*
SAAVL
AIZR*
SAAVL
AVAL
SAAVL*
AIBL*
DVA*
SAAVL*
AIBL, SMDDR
SAAVL, SMDDR
SAAVL, RMFR
AIBL*
RICL*
AIBL
AIZR*
AIBL*
HSNR*
RIFR*
AVHL*
ADAR*
AVBR, AVJL
AVBR, ADAR
RIFR*
AVBR
PVPR*
AIBL
ADAR*
AIBL*
AVBL, AVBR
AVBL, AVBR
AVEL
AIYR
RIFR*
RIMR
CELL BODY IN
LATERAL GANGLION

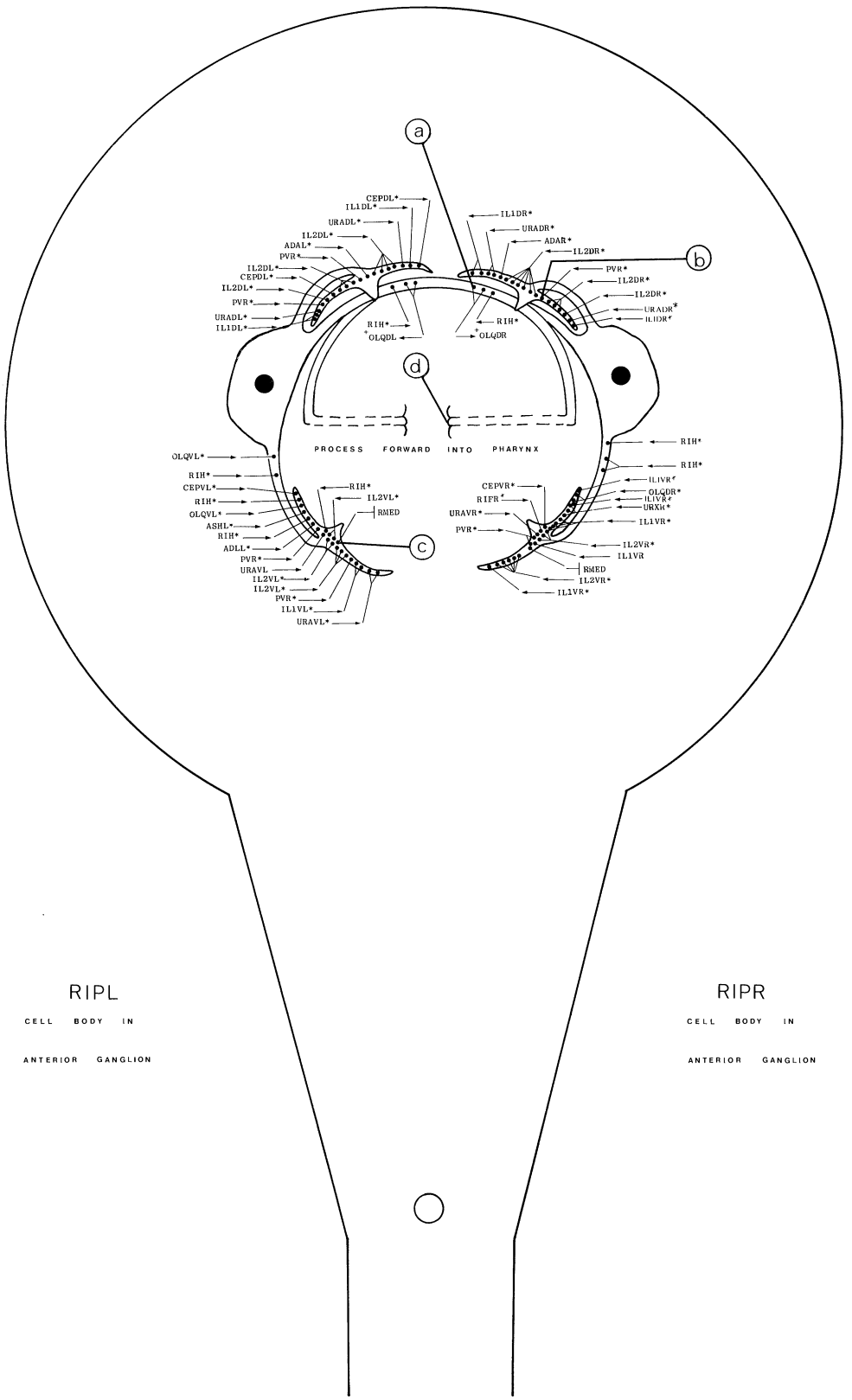


RIM

Members: RIML, RIMR.

RIM is a set of two motoneurons that innervate muscles in the head via NMJs in the nerve ring. The cell bodies are situated in the lateral ganglia and send processes into the ventral cord via the amphidial commissures. These run anteriorly through the neuropile of the ventral ganglion and then make one complete circuit round the anterior regions of the nerve ring near the outside surface. They are closely associated with the processes of AIB for most of the way round the ring. RIM is the only motoneuron class in the nerve ring that does not have axons situated on the inner surface of the nerve ring and so is only accessible to muscle arms where they penetrate the ring at the four muscle spurs (figure 14). Large NMJs are formed on the anterior side of each of the muscle spurs (a) and are usually intercepted by dendrites from RMD motoneurons (d). The processes of RIM and RMD form characteristic structures, which are seen just anterior to the NMJ region in each quadrant, where the RMD process flattens into a sheet and covers the anterior surface of a varicosity in the RIM process near the NMJ (b, c). The main neuron classes that are postsynaptic to RIM are: RMD (d), SAA (g), SMD (e) and AVB (f). The main synaptic inputs are from AIB (*a), AIZ (*g), SAA (*b) and RIS (*b). There are several gap junctions to AVE (h) and some to AVA, RIS and AIY (*d).

Magnifications: (a) ×25500, (b, c, g, h) ×12750, (d–f) ×17000.



RIPL

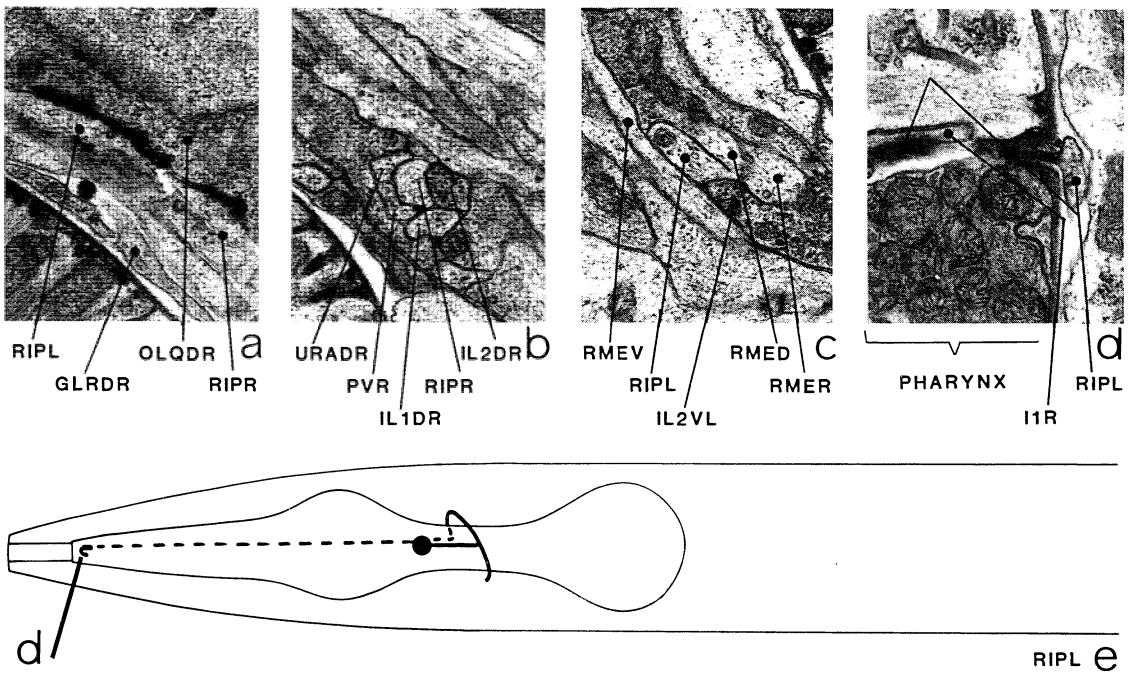
CELL BODY IN

ANTERIOR GANGLION

RIPR

CELL BODY IN

ANTERIOR GANGLION

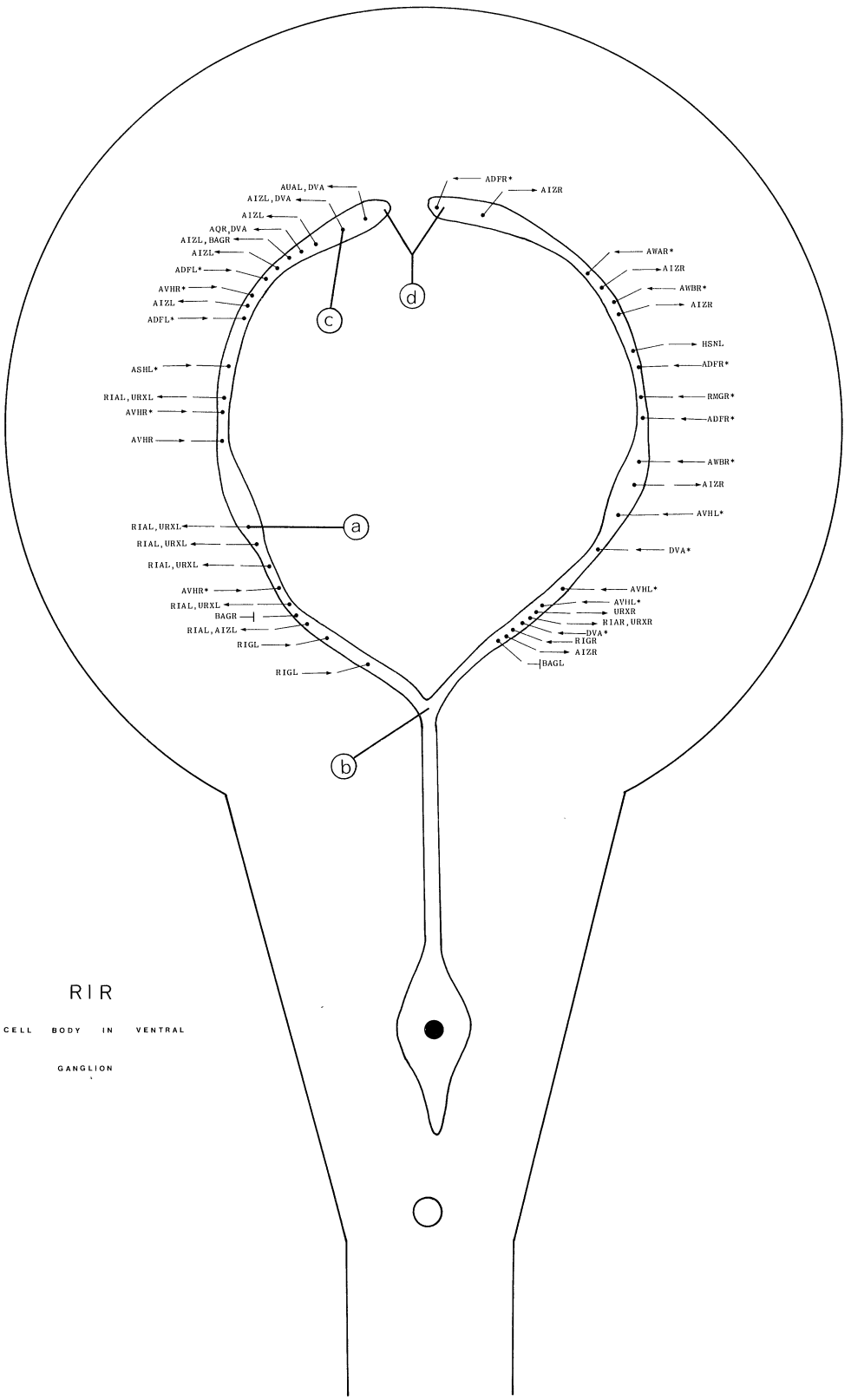


RIP

Members: RIPL, RIPR.

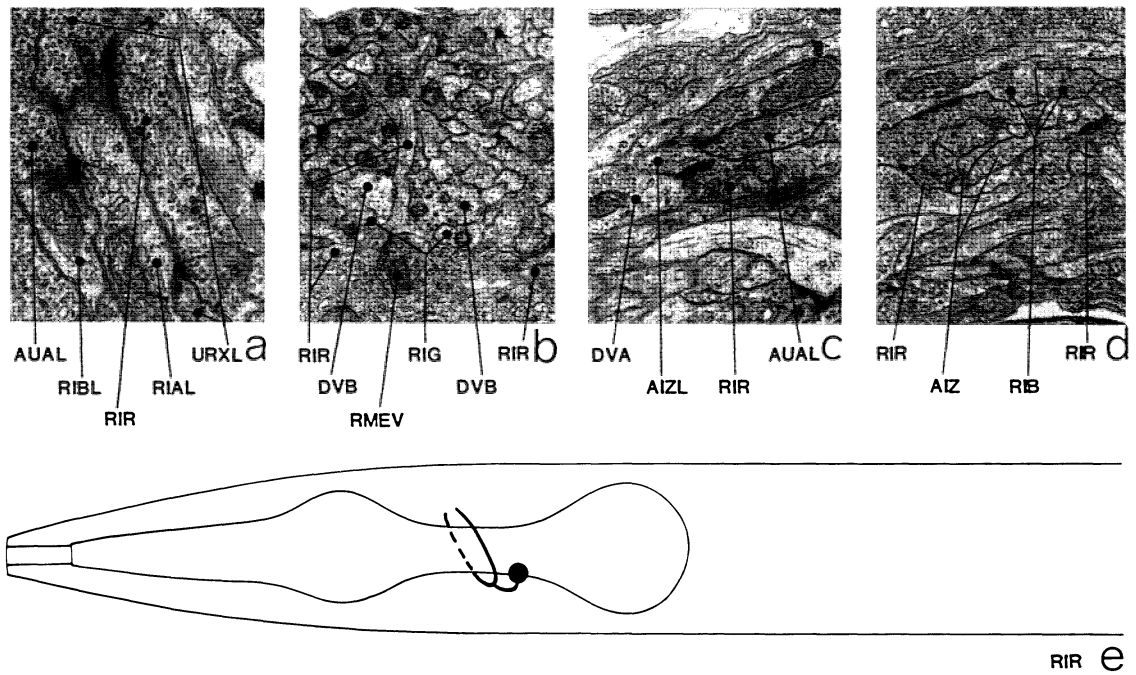
The RIP interneurons mediate the only direct interconnections between the pharyngeal and the central nervous systems. They have two laterally situated cell bodies immediately anterior to the nerve ring. A dorsally directed process emanates from each cell body and runs round the anterior surface of the ring neuropile to the contralateral side. These processes then turn and run anteriorly, in the lateral labial process bundles, finally entering the pharynx near its anterior extremity (d). The processes from RIP end soon after entering the pharynx with a gap junction to the I1 interneurons of the pharyngeal nervous system (Albertson & Thomson 1976). A dorsal and a ventrally directed process leave each cell body, run round the anterior surface of the ring and then enter the ring neuropile sub-dorsally and sub-ventrally. Here, the processes fan out into dendrites, which intercept NMJs from URA (*a) and IL1 (*e). The central part of each process carries on running posteriorly in the centre of the bundle of processes from the labial sensory neurons (b) and eventually peters out. No obvious chemical synapses are made by RIP, although what appear to be presynaptic specializations with no synaptic vesicles are present adjacent to OLQ neurons on the dorsal side of the ring (+ and a). The main synaptic inputs are from IL1 (*e), URA (*a), IL2 (*a), RIH (*c) and PVR (*c). There are gap junctions to RMED (c) ventrally.

Magnifications: (a–d) ×25500.



RIR

CELL BODY IN VENTRAL GANGLION

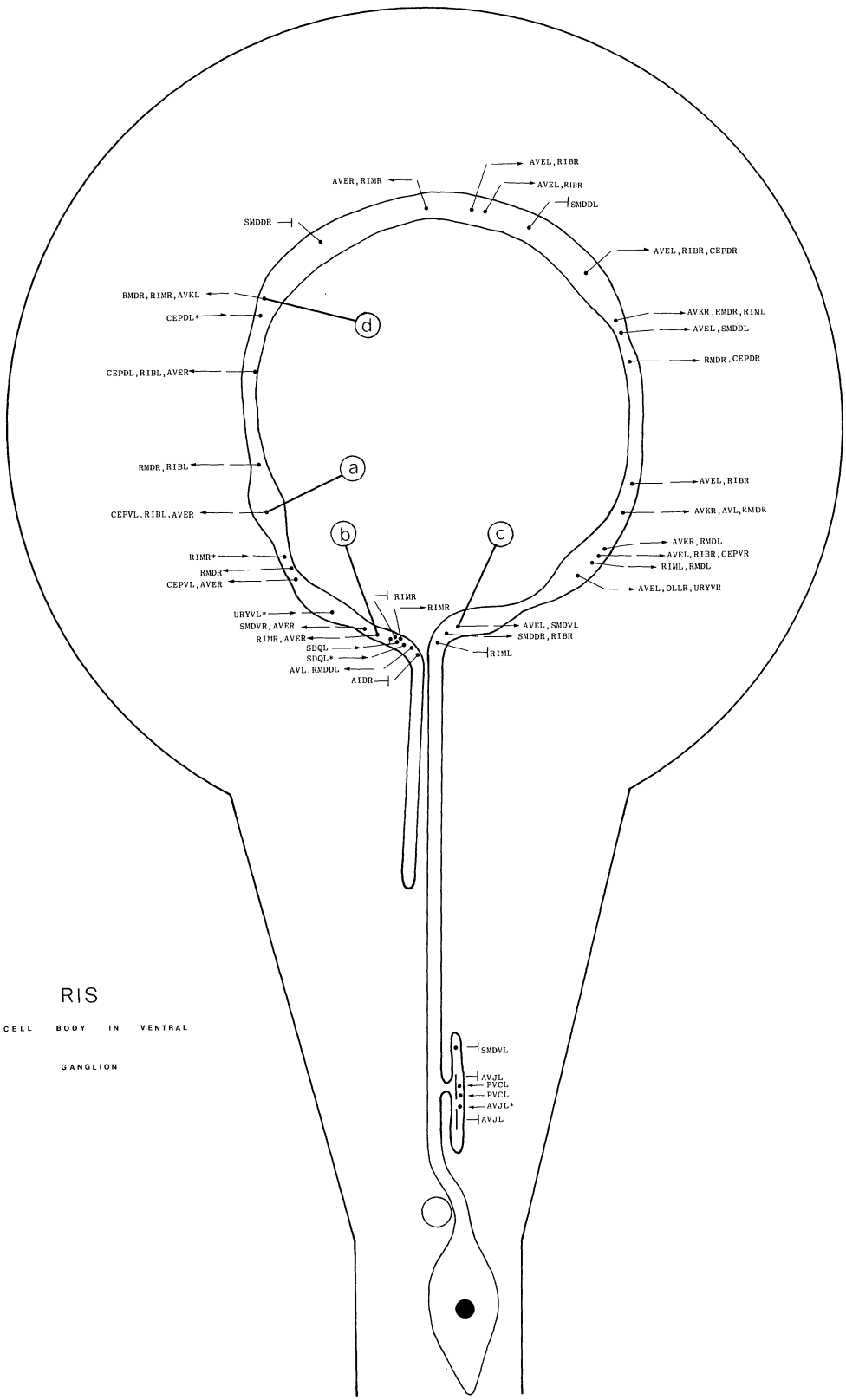


RIR

Member: RIR.

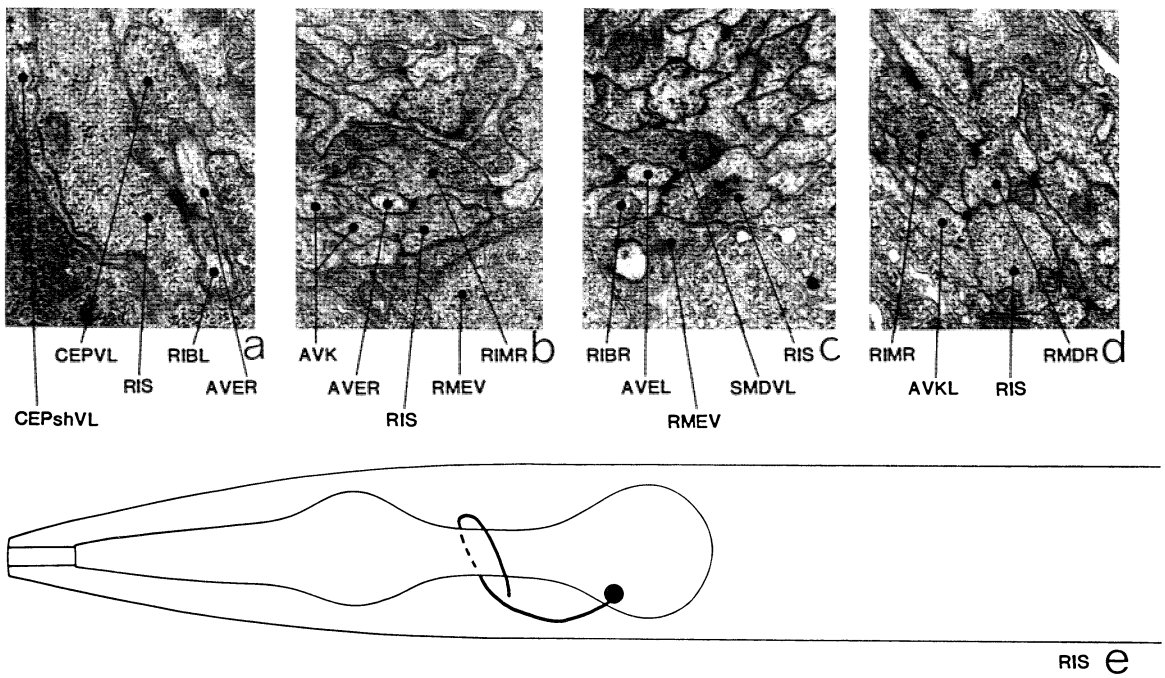
RIR is an interneuron with a single cell body in the ventral ganglion. An anteriorly directed process leaves the cell body and runs on the dorsal surface of the nerve cord on the mid-line. As the nerve ring is approached this process abruptly turns and moves down to the ventral surface of the nerve cord. At this point, it divides into two processes (b), which run round the nerve ring near the middle of the neuropile and terminate near the dorsal mid-line (d). The main synaptic outputs of RIR are to RIA (a), AIZ (c) and URX (a). The main synaptic inputs are from AVH (*a), RIG (*a), ADF and DVA (*e). There are gap junctions to BAG (*d).

Magnifications: (a) ×25500, (b, d) ×12750, (c) ×17000.



RIS

CELL BODY IN VENTRAL GANGLION

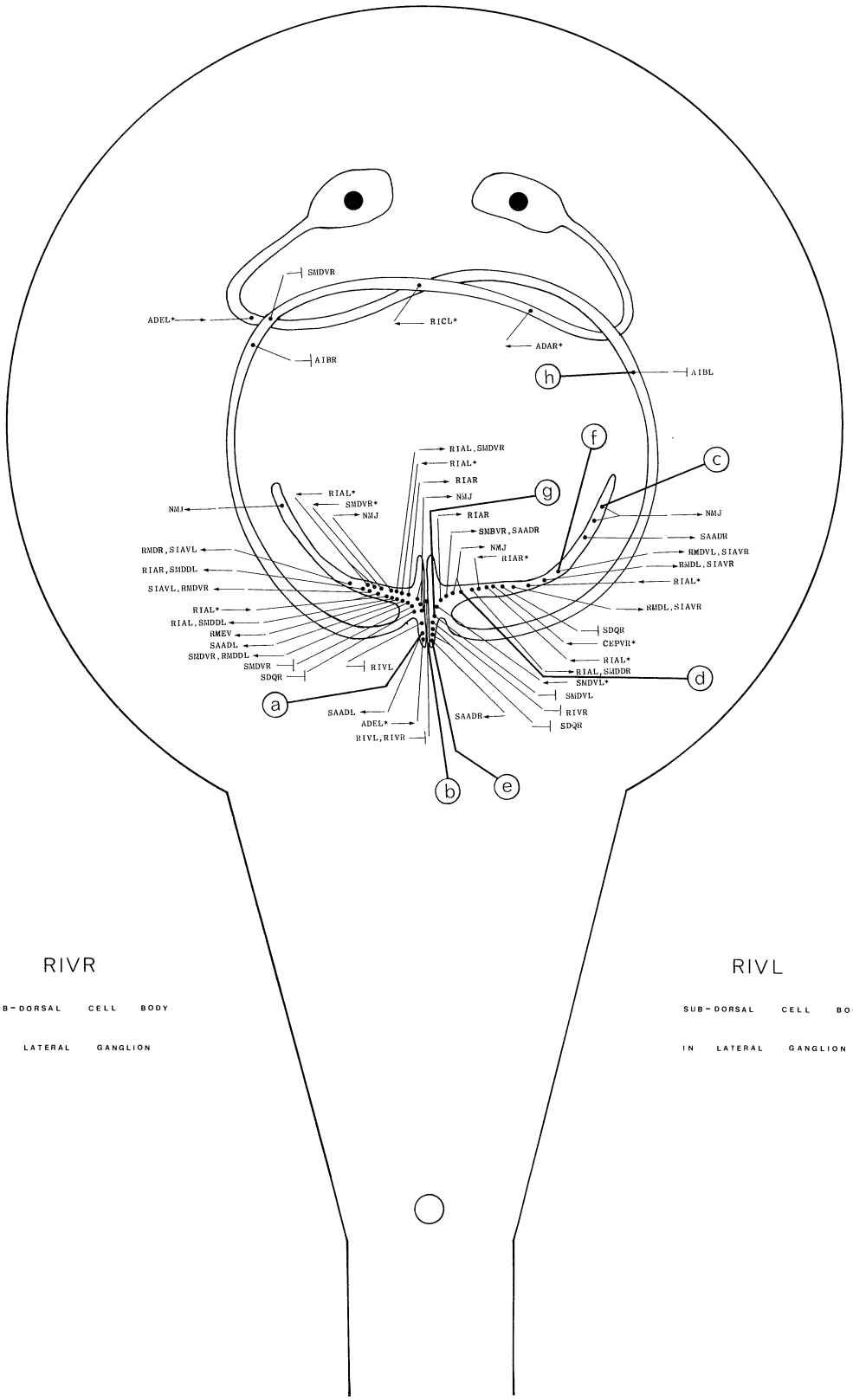


RIS

Member: RIS.

RIS is an interneuron with a single cell body situated on the right-hand side of the ventral ganglion behind the excretory duct. A single, fairly large process leaves the cell body and runs anteriorly on the dorsal surface of the nerve cord. A short branch dips down into the body of the nerve cord and makes a very characteristic gap junction to AVJ (*c). The main process runs in the middle of the dorsal surface of the nerve cord until the nerve ring is reached. It then runs round the nerve ring in an anticlockwise direction, running near the anterior face and outside surface. The right- and left-hand regions of the process appear symmetrical, although they are running in opposite directions with respect to the cell body. The main synaptic outputs are to AVE (a), RIM (b), RMD (d), RIB (c), CEP (a) and AVK, usually in various dyadic and triadic combinations. There is not much synaptic input; what there is comes mainly from SDQ and PVC. Gap junctions are made to AVJ (*c), SMD, RIM and AIB.

Magnifications: (a) 25500, (b–d) 17000.



RIVR

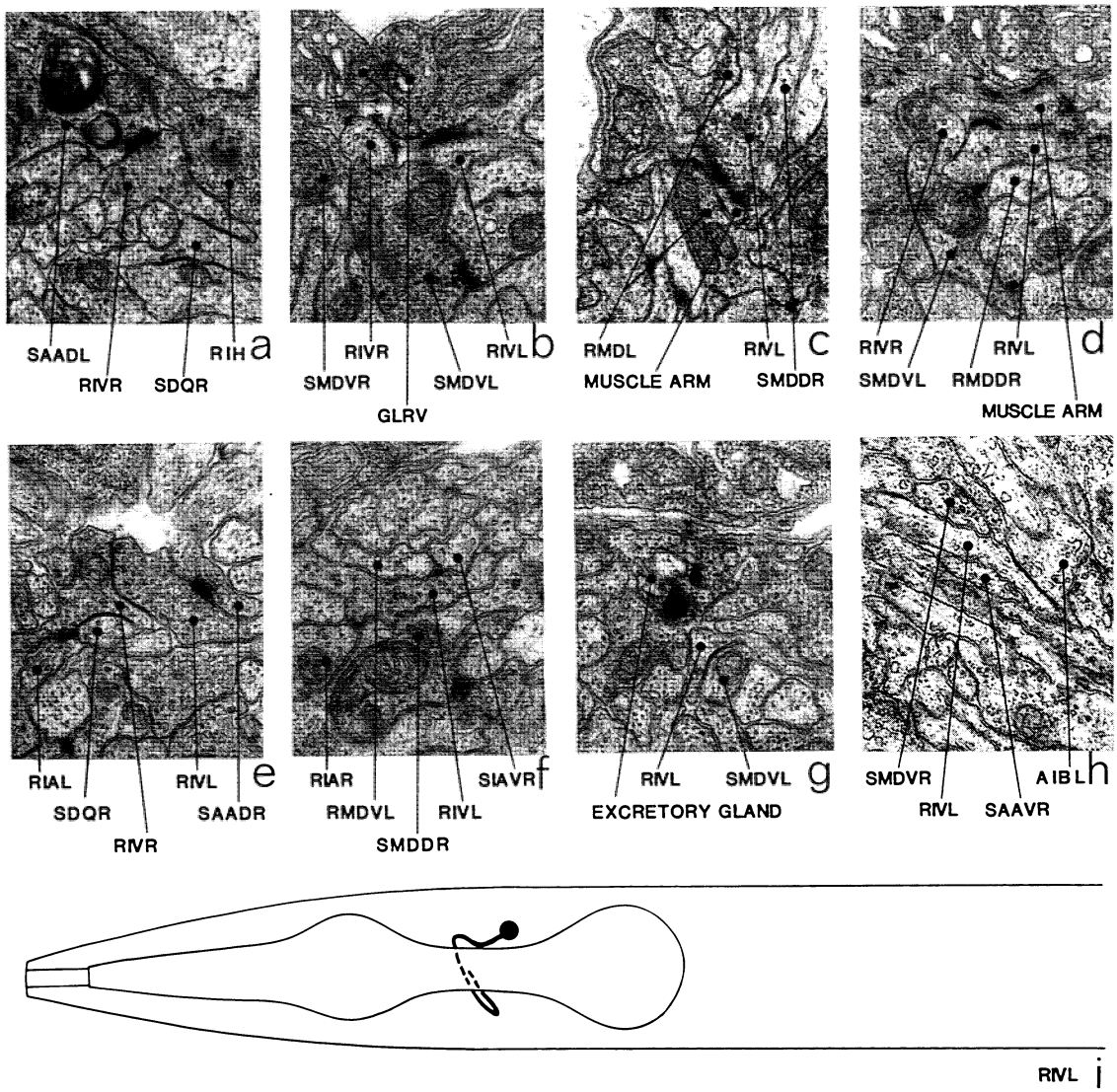
SUB-DORSAL CELL BODY

IN LATERAL GANGLION

RIVL

SUB-DORSAL CELL BODY

IN LATERAL GANGLION

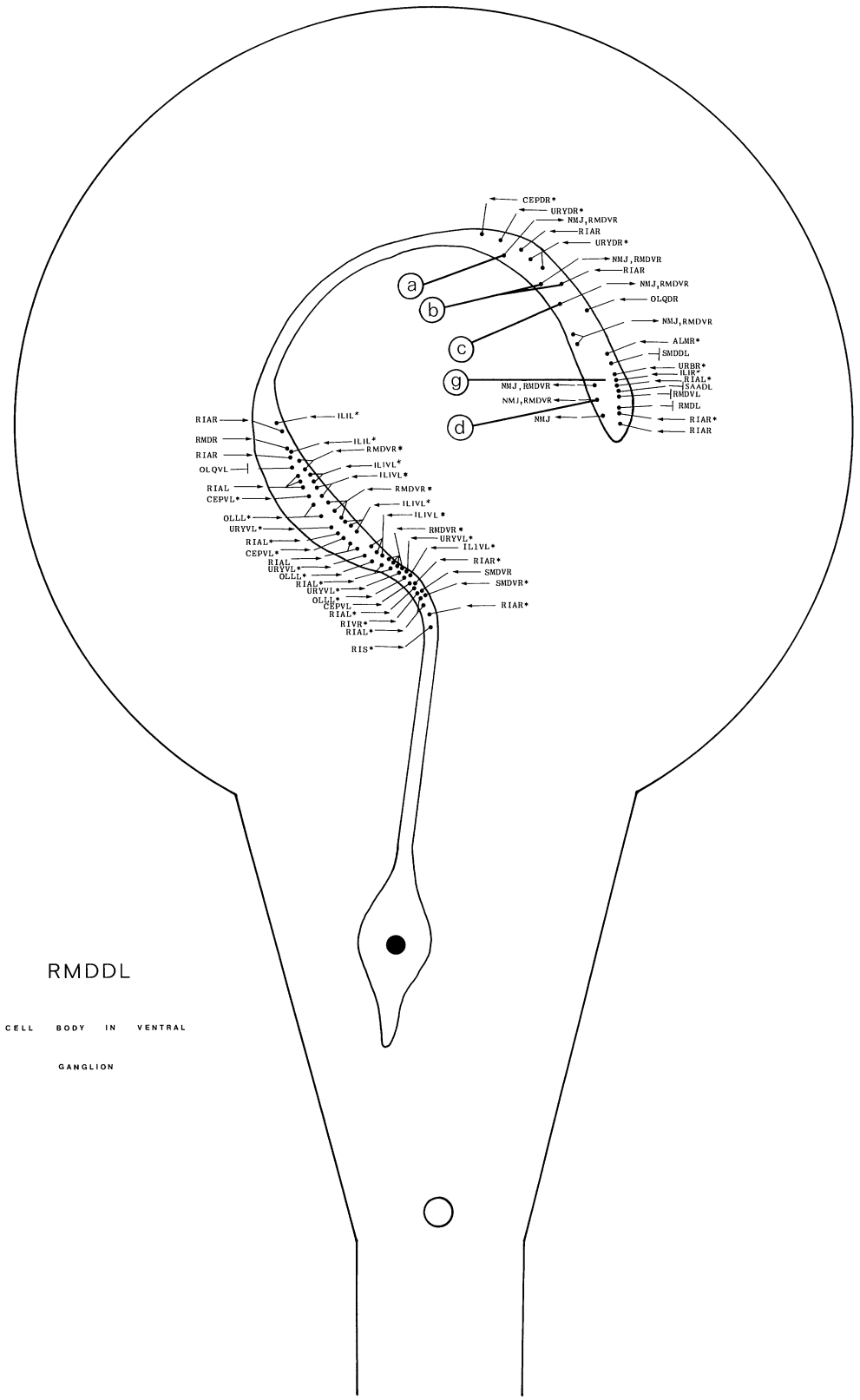


RIV

Members: RIVL, RIVR.

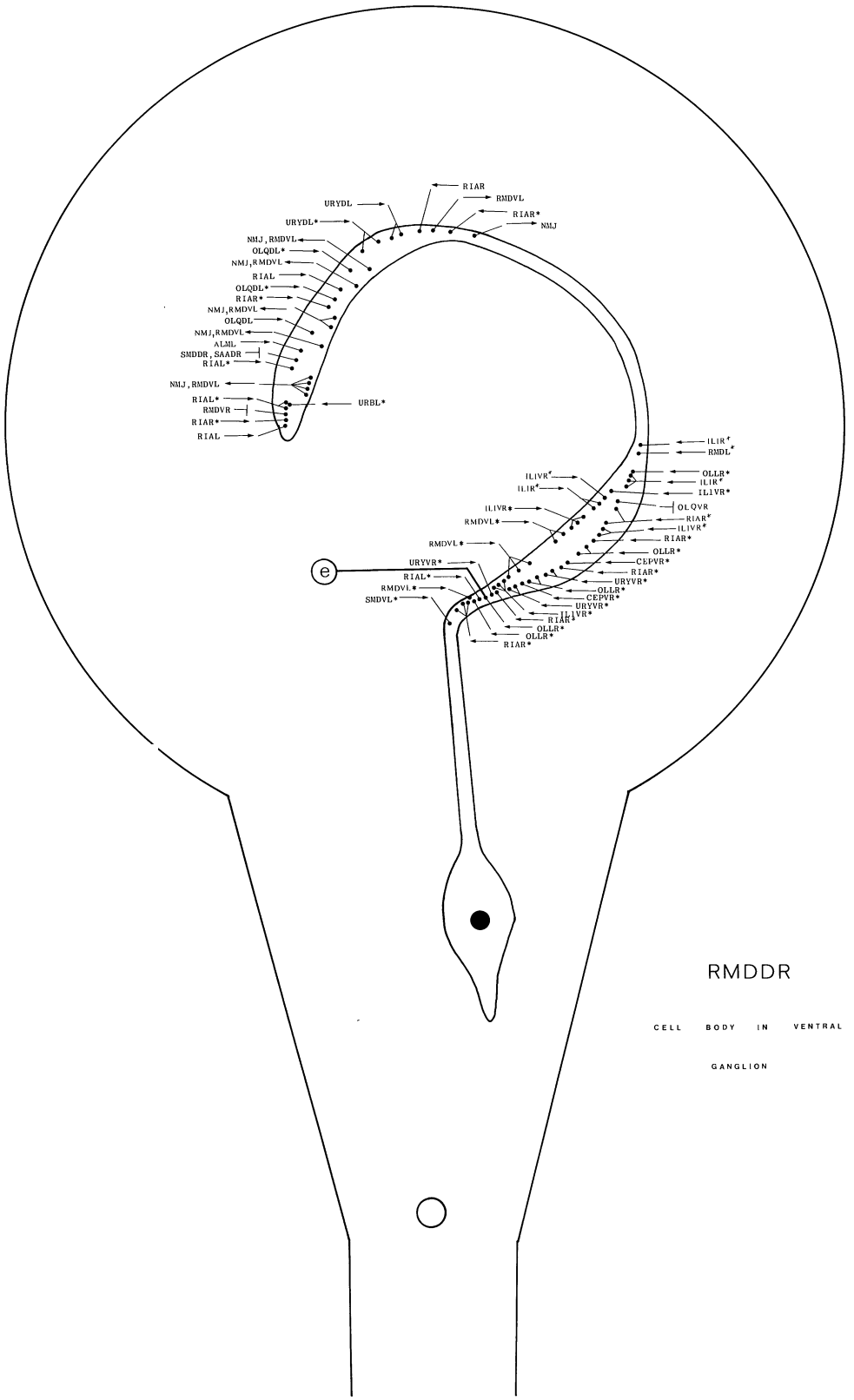
RIV is a pair of interneurons/motoneurons with cell bodies situated sub-dorsally in the lateral ganglia. Processes from each cell body enter the ring sub-dorsally, cross over to the contralateral side of the ring, and then run round it in the middle of the neuropile until they meet at the ventral mid-line in the anterior region of the neuropile of the ventral ganglion. At this point the processes turn round and run dorsally along the inside surface of the nerve ring, eventually ending laterally. Small projections at the region of contact run anteriorly and posteriorly from each process adjacent to the basal lamina on the inside of the ring. Darkly staining regions adjacent to the lamina are seen near the ends of these projections (b). The main synaptic outputs are to SAAD via fairly prominent monadic synapses (a, e) and NMJs (c, d). There are also smaller synapses to RMD (d), SMD (d), SIA (f) and RIA (e). All the synaptic outputs are in the ventral region of the nerve ring. The main synaptic inputs are from RIA (*b). Gap junctions are made to SDQ (a, e), SMD (g), AIB (h) and to itself (e).

Magnifications: (a, b, d–h) ×25500, (c) ×17000.



RMDDL

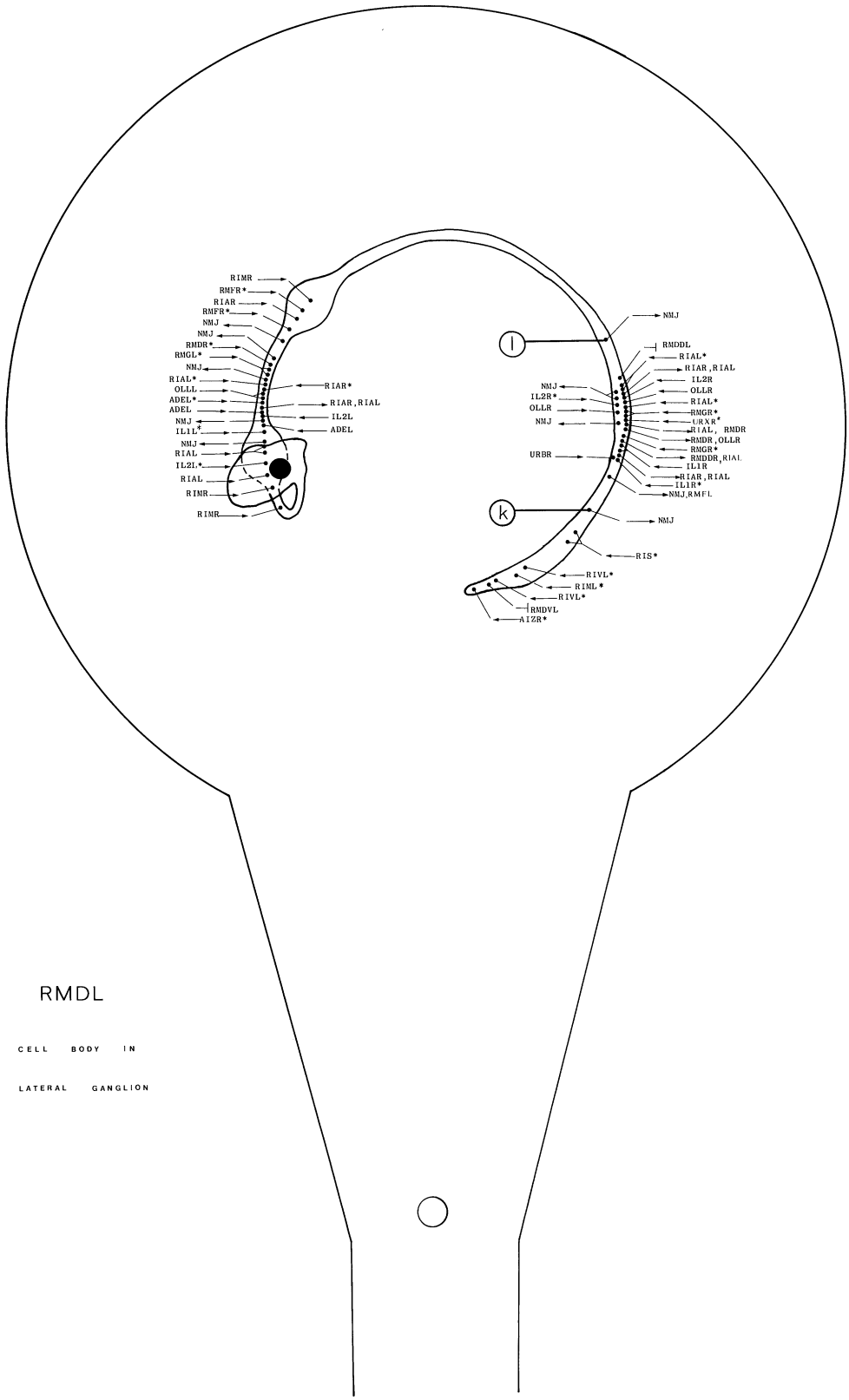
CELL BODY IN VENTRAL GANGLION



RMDDR

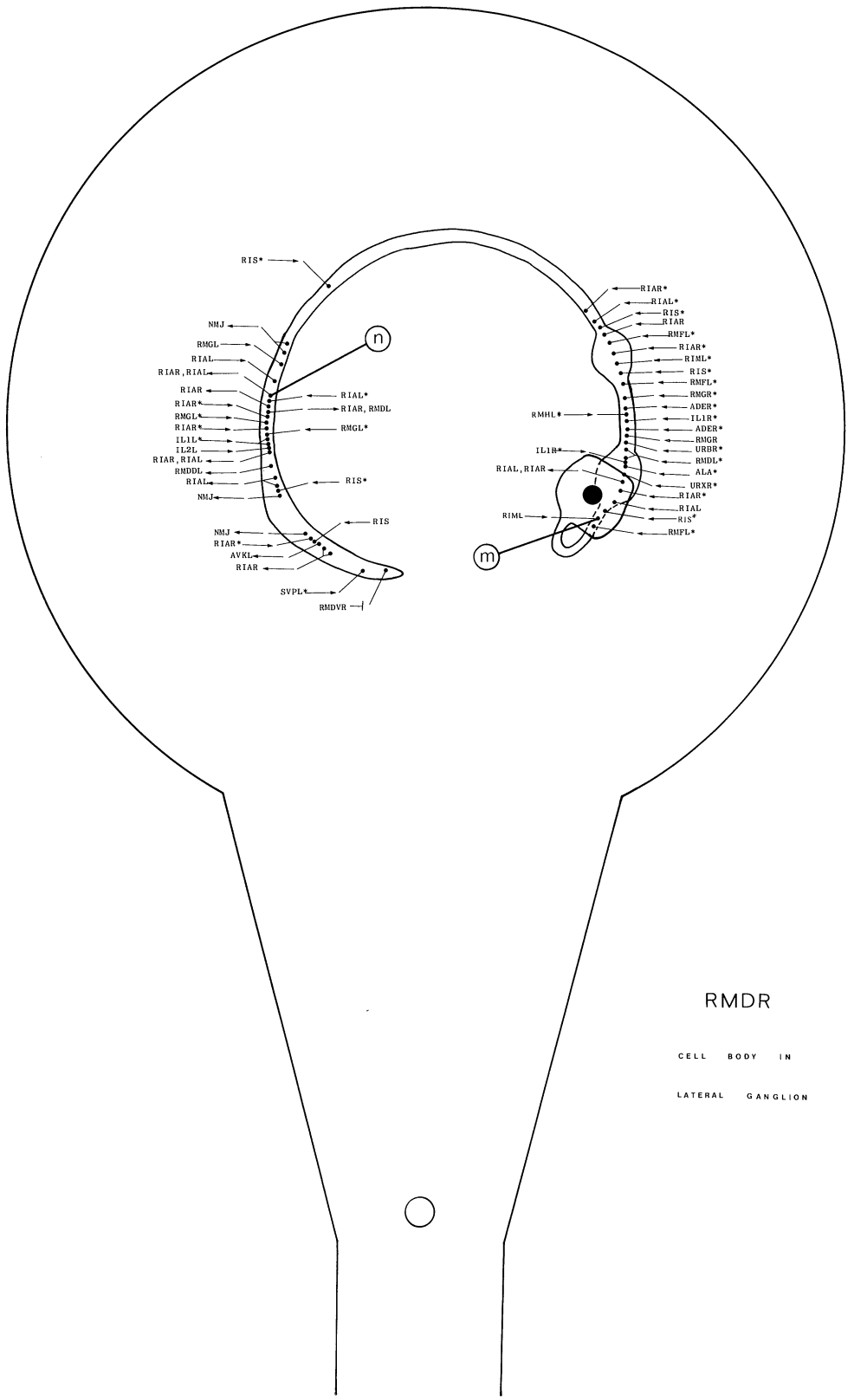
CELL BODY IN VENTRAL GANGLION

RMD



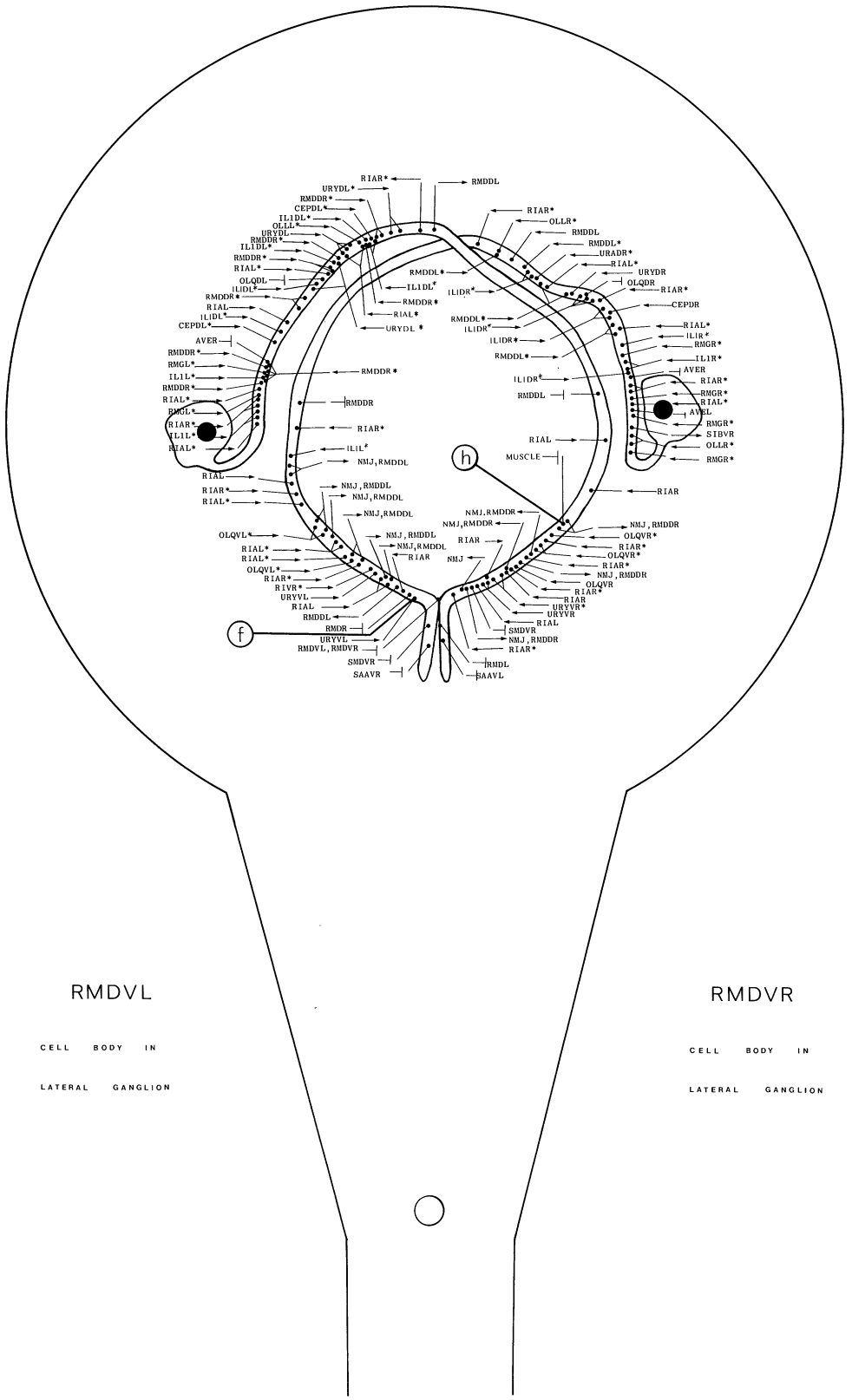
RMDL

CELL BODY IN LATERAL GANGLION



RMDR

CELL BODY IN LATERAL GANGLION

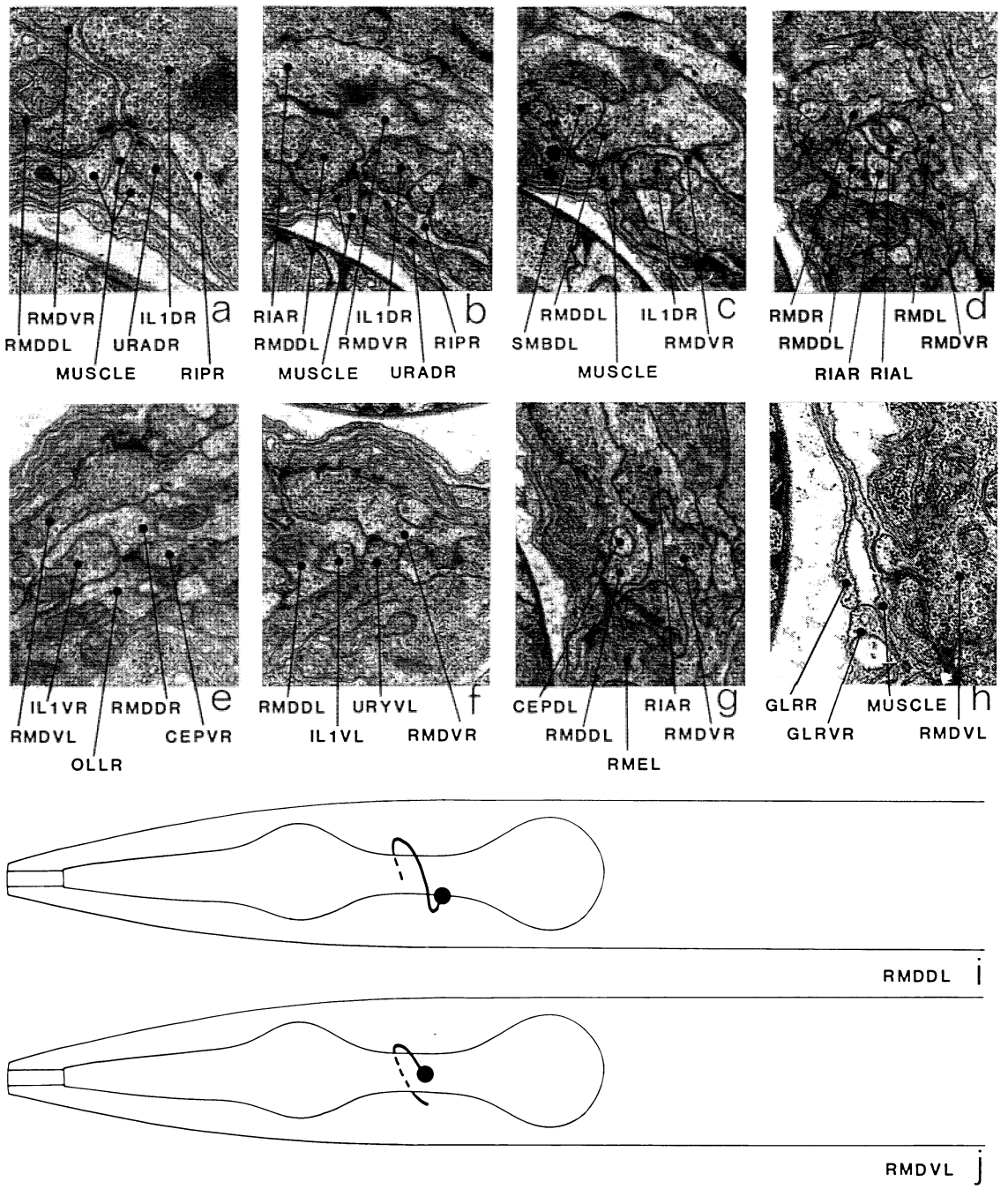


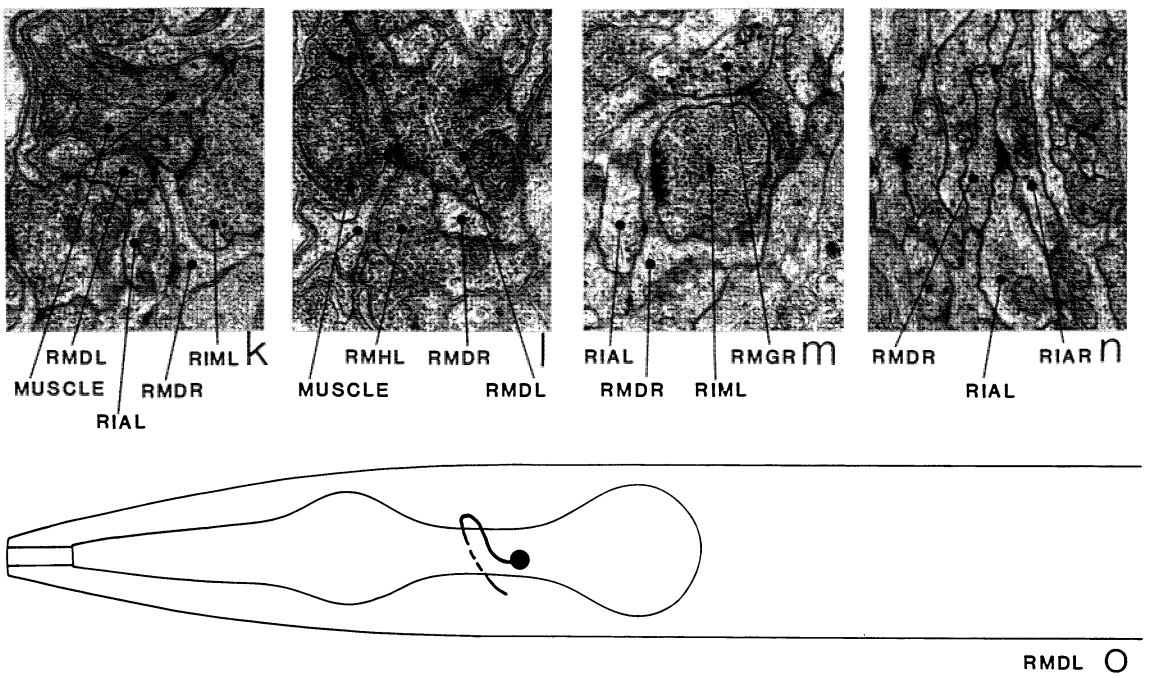
RMDVL

CELL BODY IN LATERAL GANGLION

RMDVR

CELL BODY IN LATERAL GANGLION


RMDVR
RMDDL
IL1DR
URADR
MUSCLE
RIPR
a
RIAR
RMDDL
IL1DR
RMDVR
MUSCLE
URADR
RIPR
b
RMDDL
IL1DR
SMBDL
RMDVR
MUSCLE
c
RMDR
RMDDL
RMDL
RMDVR
RIAR
RIAL
d
IL1VR
RMDDR
RMDVL
CEPVR
OLLR
e
RMDDL
URYVL
IL1VL
RMDVR
f
CEPDL
RIAR
RMDDL
RMDVR
RMEL
g
GLRR
MUSCLE
GLRVR
RMDVL
h
RMDDL
i
RMDVL
j



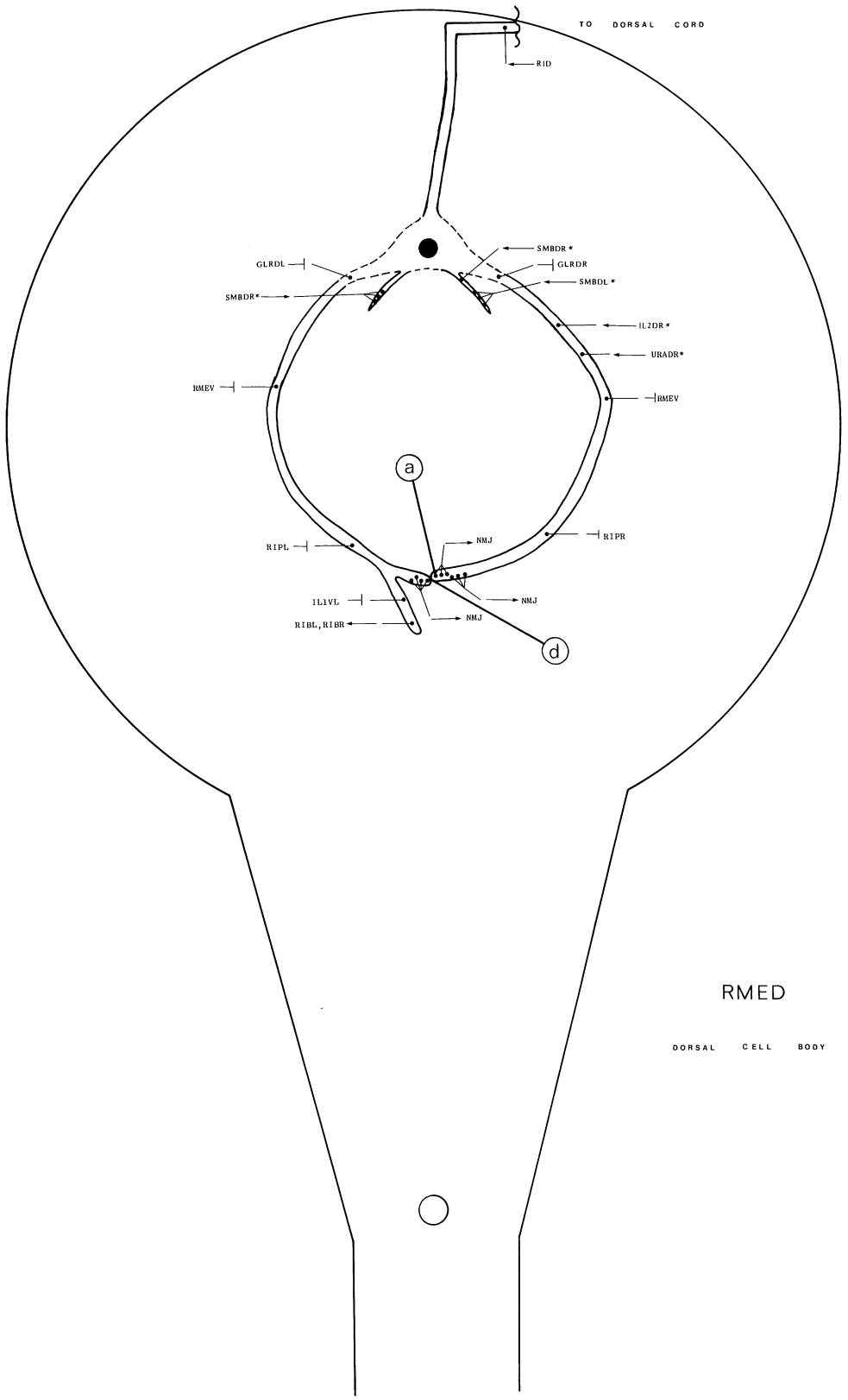
RMD

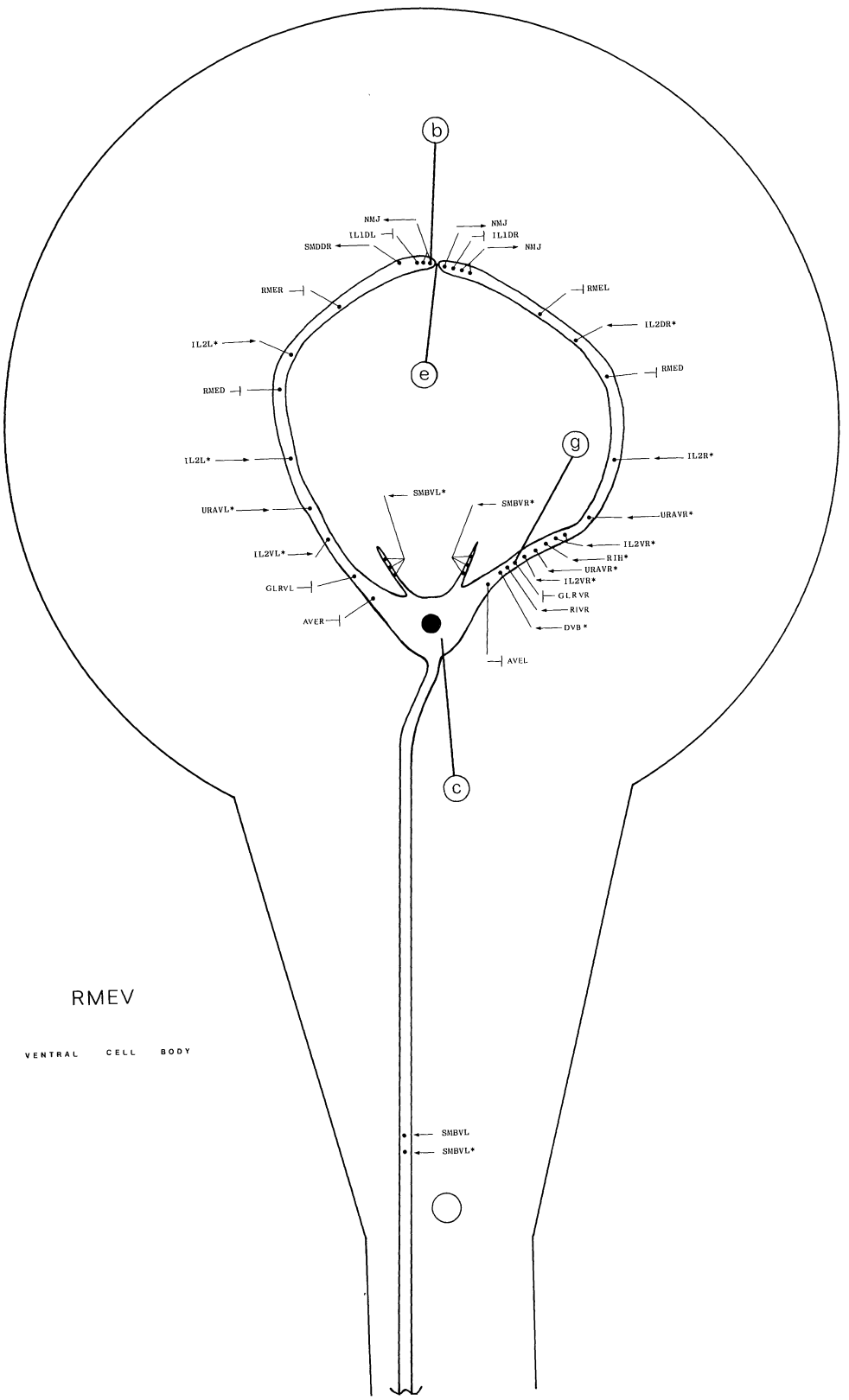
Members: RMDDL, RMDDR, RMDL, RMDR, RMDVL, RMDVR.

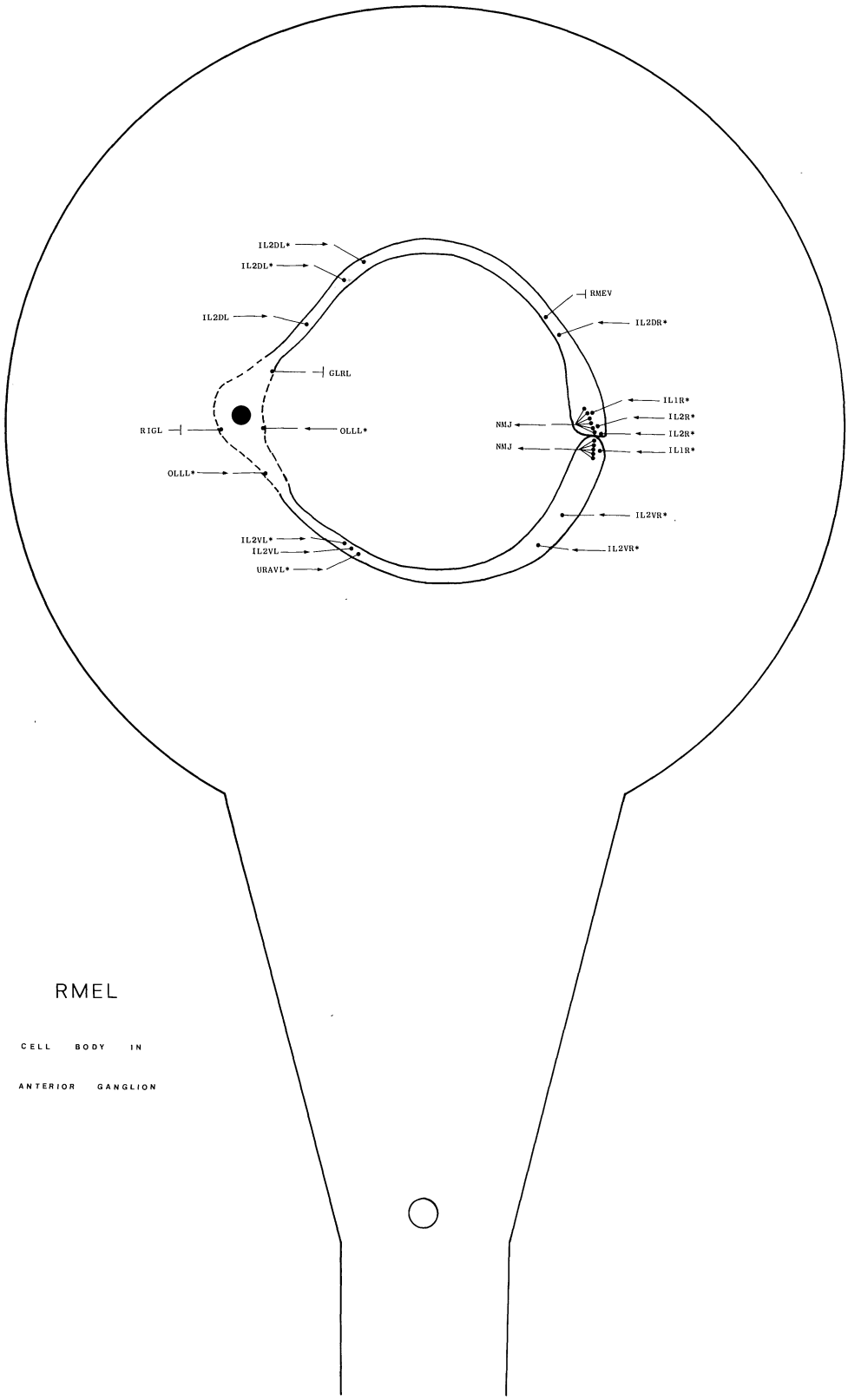
RMD is a set of six major motoneurons, which innervate muscles in the head via NMJs in the nerve ring. The cell bodies of RMDV and RMD are situated in the lateral ganglia adjacent to the ring neuropile; those of RMDD are in the ventral ganglion (figure 16). Processes enter the nerve ring laterally in the case of RMDV (j) and RMDL/R (o), and via the ventral cord in the case of RMDD (i), and run round the ring for three quadrants. The proximal regions of these processes run closely associated together and are also closely associated with, and often surround, the processes of RIA (d). The processes of this group run in the middle of the anterior regions of the neuropile of the ring. The distal regions of each of the RMD processes move towards the inside surface of the ring, where they have their NMJs. RMDD wraps round the process of CEPD in a characteristic manner (g). The main regions of synaptic input are diametrically opposite the regions of NMJs (the NMJs present on the left-hand side of RMDL are atypical and have not been seen on the other reconstructed series). The NMJs of RMDD/V are usually in a complex that consists of NMJs from RMD, IL1 and URA and dendrites from RMD and RIP (a, b). Sometimes the complex is seen without the RIP and URA processes (c). RMDL/R behave somewhat differently and could, possibly, be considered as a separate class. Most of the NMJs of RMDL/R are part of a complex, present on each of the four muscle arm spurs (figure 14), in which an RMDL/R dendrite is sandwiched between an RMDL/R NMJ and an RIM NMJ (k). There are also a few RMDL/R NMJs laterally that are not part of any complex (l). The processes of RMDL/R flatten out and form caps over the anterior surfaces of the NMJ regions of RIM, which are situated directly anterior to the muscle arm spurs (m, RIM-*b, RIM-*c). The main synaptic outputs of RMDL/R are onto contralateral RMDL/Rs (as corecipients at NMJs) and RIA (n); the main synaptic inputs are: RIA (*e), RIM (m), RMG (*a), IL1, ADE (*c), RMF (*e), contralateral RMDL/Rs, RIS (*d), RMH

(*a) and OLL (d). There are also gap junctions to RMDD/V, but not to each other. The only synaptic output of RMDD/V, apart from NMJs, is to contralateral RMDD/Vs at the NMJ complexes; the main synaptic inputs are from RIA (*f), URY (f), contralateral RMDD/Vs (a, b), IL1 (a, b), OLL (*d), CEP (*h), RIV (*d) and OLQ (*b). There are gap junctions to SAA, RMDD/V, SMD, RMDL/R, AVE and OLQ. OLQ has an interesting complementary synaptic relation to RMDD/V; OLQD synapses onto RMDD and has gap junctions to RMDV, whereas OLQV synapses onto RMDV and has gap junctions with RMDD. Occasionally the processes of RMDD/V appear to penetrate the basal lamina separating nervous tissue from muscle arms, and have gap junctions directly onto muscle arms (h).

Magnifications: (a, h, l) ×25500, (b, c, e–g, k, m, n) ×12750, (d) ×17000.

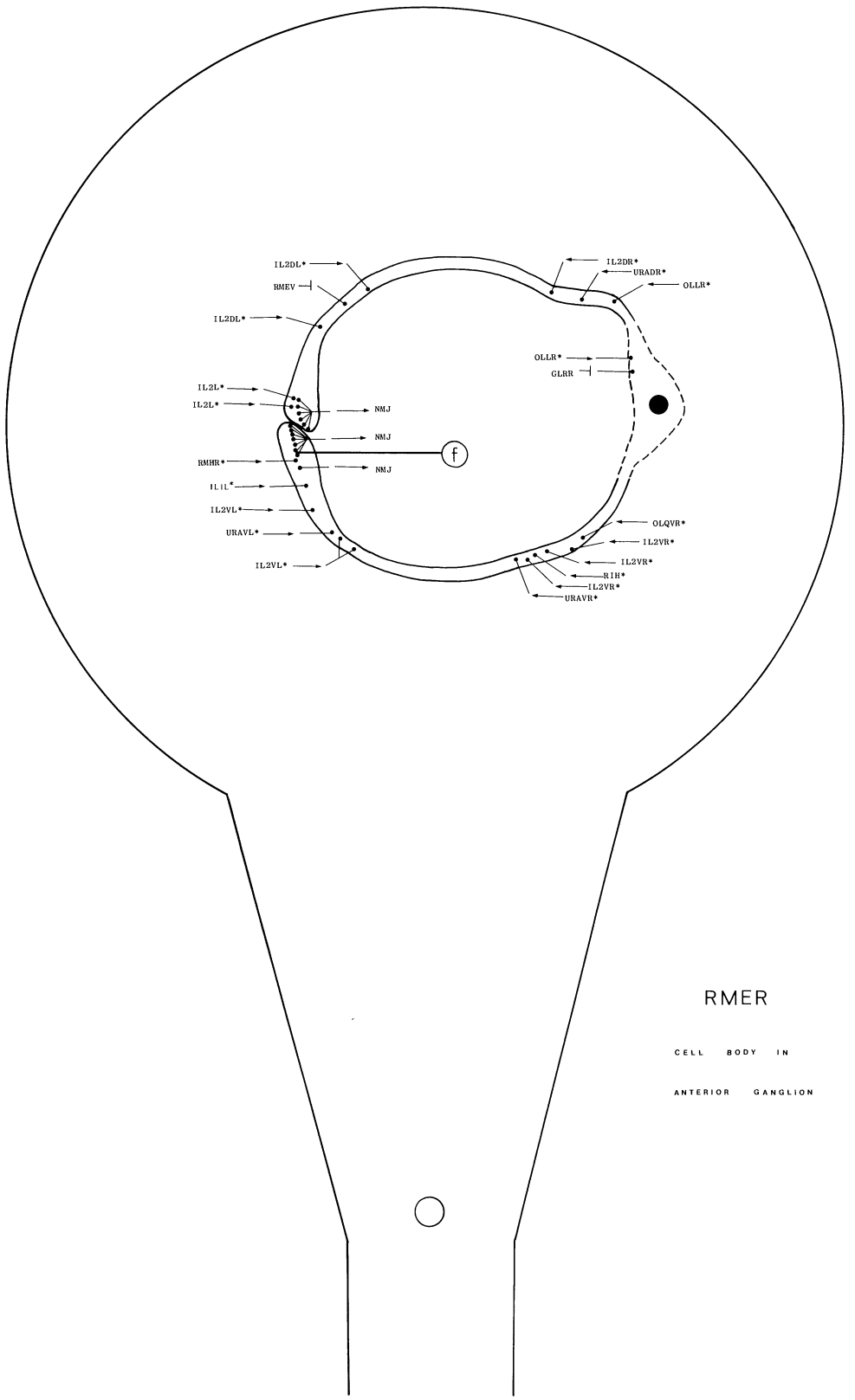

TO DORSAL CORD
RID
SMBDR*
GLRDL
GLRDR
SMBDR*
SMBDL*
IL2DR*
URADR*
RMEV
RMEV
a
RIPL
NMJ
RIPR
IL1VL
NMJ
NMJ
RIBL, RIBR
d
RMED
DORSAL CELL BODY

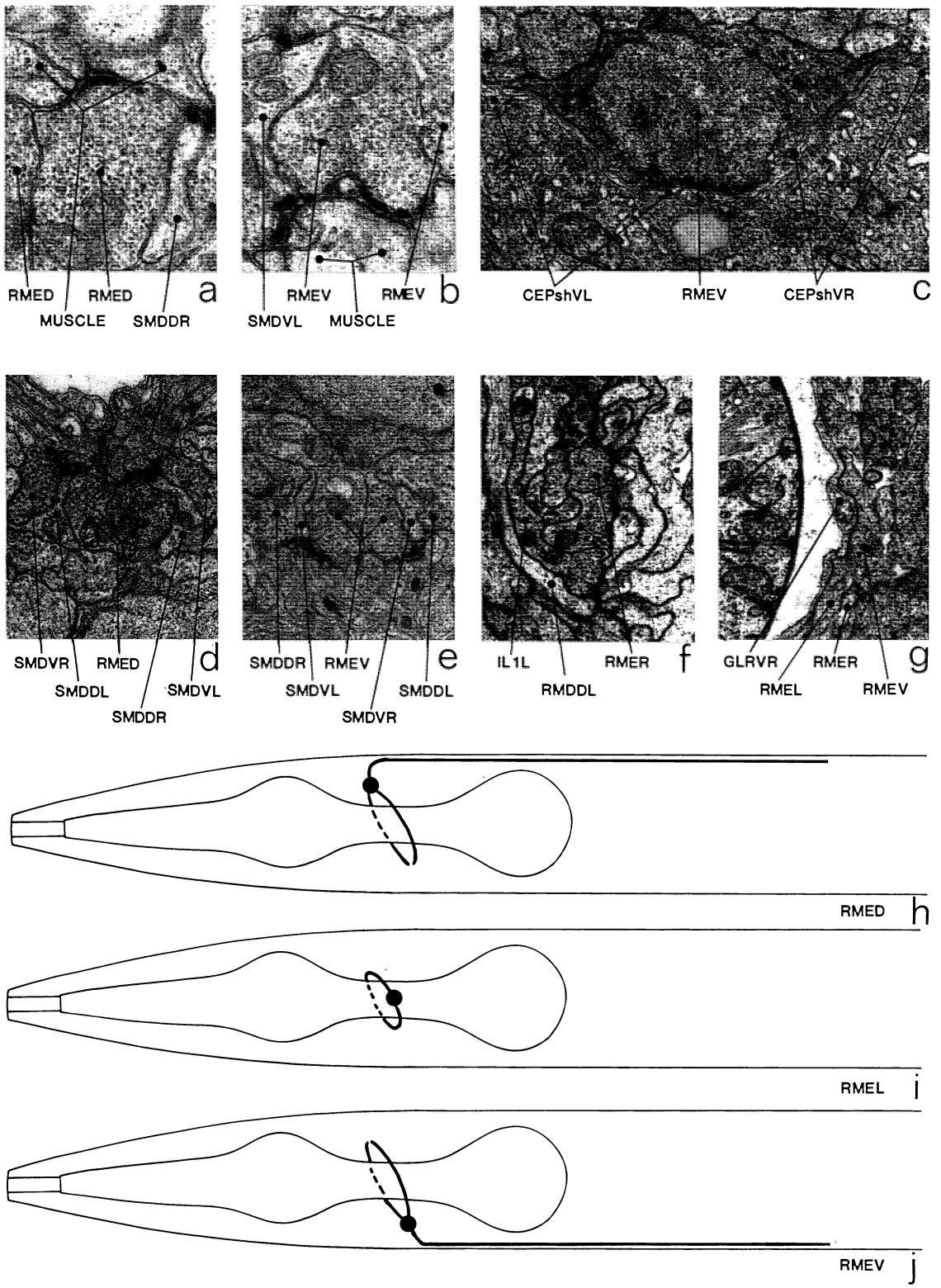

b
NMJ
IL1DL
SMDDR
NMJ
IL1DR
NMJ
RMER
RMEL
IL2DR*
IL2L*
e
RMED
RMED
g
IL2L*
IL2R*
SMBVL*
SMBVR*
URAVL*
URAVR*
IL2VR*
IL2VL*
RIH*
URAVR*
IL2VR*
GLRVL
GLRVR
RIVR
AVER
DVB*
AVEL
c
SMBVL
SMBVL*
RMEV
VENTRAL CELL BODY



RMEL

CELL BODY IN ANTERIOR GANGLION


IL2DL*
RMEV
IL2DL*
IL2L*
IL2L*
RMHR*
IL1L*
IL2VL*
URAVL*
IL2VL*
NMJ
NMJ
NMJ
f
IL2DR*
URADR*
OLLR*
OLLR*
GLRR
OLQVR*
IL2VR*
IL2VR*
RIH*
IL2VR*
URAVR*
RMER
CELL BODY IN
ANTERIOR GANGLION

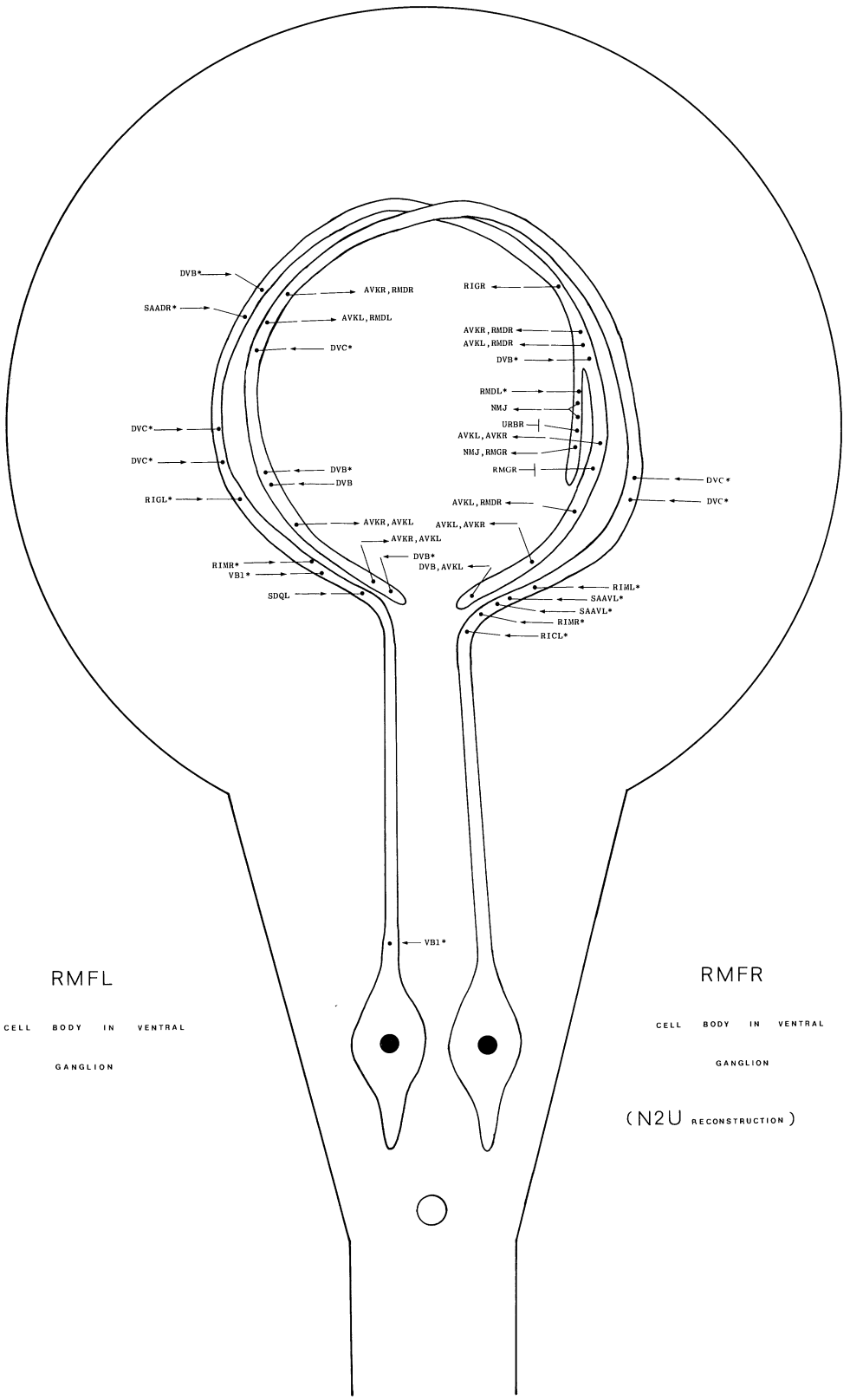

RMED
RMED
MUSCLE
SMDDR
a
RMEV
RMEV
SMDVL
MUSCLE
b
CEPshVL
RMEV
CEPshVR
c
SMDVR
RMED
SMDDL
SMDVL
SMDDR
d
SMDDR
RMEV
SMDVL
SMDDL
SMDVR
e
IL1L
RMER
RMDDL
f
GLRVR
RMER
RMEL
RMEV
g
RMED
h
RMEL
i
RMEV
j

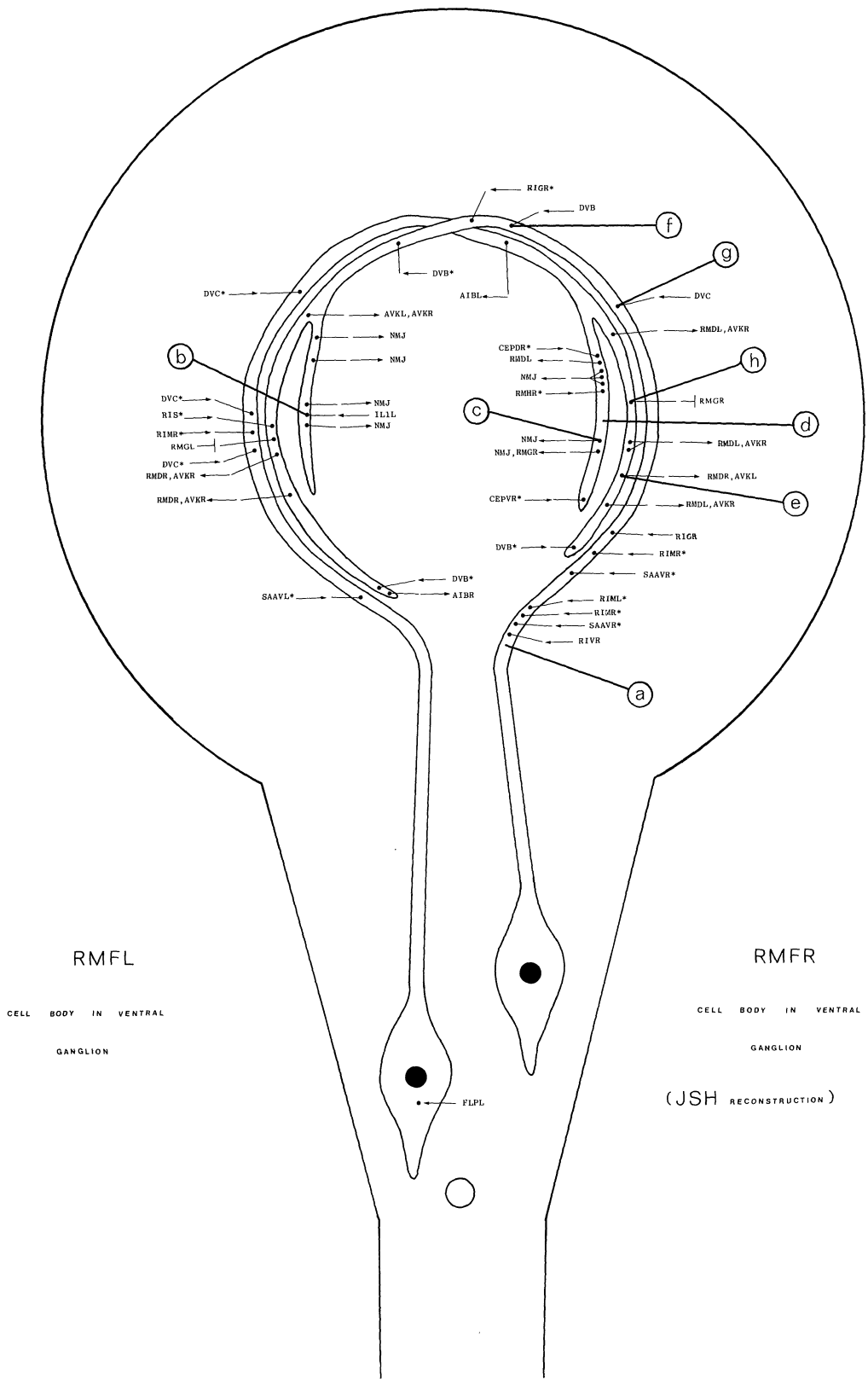
RME

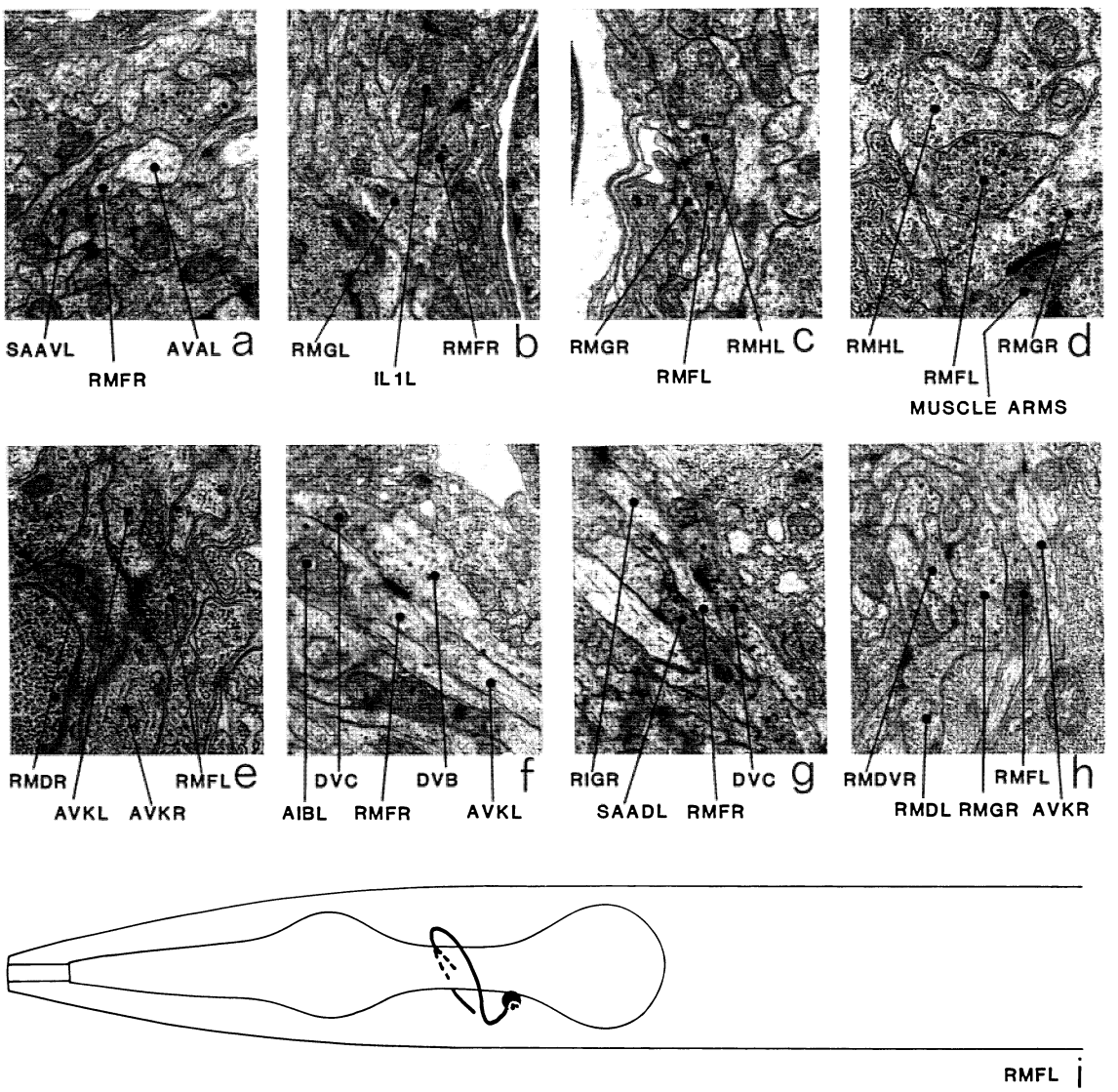
Members: RMED, RMEV, RMEL, RMER.

RME is a set of four motoneurons, with NMJs in the nerve ring, which innervate head muscles. The members of this class have an unusual fourfold symmetry; cell bodies are situated mid-dorsally (RMED), mid-ventrally (RMEV), left laterally (RMEL) and right laterally (RMER). Each cell has a twofold symmetry and sends out two processes, which run in opposite directions round the nerve ring near the anterior surface. These processes run alongside processes of adjacent RMEs and meet at the distal side of the nerve ring, forming NMJs at this point (d, e, f and figure 14). This meeting point is always located on the mid-line opposite to that on which the cell body is located. RMED/V each send out an extra process; these run down the ventral and dorsal cords respectively, for about 150 μm, and then peter out without making any significant synaptic connections along their length. RMED/V also have two small dendrites, emanating from their cell bodies, which intercept the NMJs of SMB (*e). The cell bodies of all the RME neurons are closely apposed to the nerve ring and are ensheathed by the thin sheet-like processes of the CEPsh cells that surround the neuropile of the nerve ring (c). RMEL/R synapse exclusively onto muscle; RMED/V synapse onto muscle (a, b) but probably also synapse onto adjacent SMD processes (d, e). RME receives synaptic input from IL2 (*c), SMB (*e) (RMED/V only), OLL (RMEL/R only) and possibly URA (*c). There are gap junctions to itself, AVE, RIP and IL1D/V (*g), and prominent gap junctions to the glial cells, GLR (g); RME is the only neuron class that makes contact with these cells (figure 15).

Magnifications: (a, b) × 25500, (c–g) × 12750.


DVB*
SAADR*
AVKR,RMDR
AVKL,RMDL
DVC*
DVC*
DVC*
DVB*
DVB
RIGL*
AVKR,AVKL
AVKR,AVKL
DVB*
RIMR*
VB1*
SDQL
DVB,AVKL
RIGR
AVKR,RMDR
AVKL,RMDR
DVB*
RMDL*
NMJ
URBR
AVKL,AVKR
NMJ,RMGR
RMGR
AVKL,RMDR
AVKL,AVKR
DVC*
DVC*
RIML*
SAAVL*
SAAVL*
RIMR*
RICL*
VB1*
RMFL
CELL BODY IN VENTRAL GANGLION
RMFR
CELL BODY IN VENTRAL GANGLION
(N2U RECONSTRUCTION)


RIGR*
DVB
f
g
DVB*
AIBL
DVC*
DVC
AVKL, AVKR
RMDL, AVKR
NMJ
NMJ
CEPDR*
RMDL
b
h
NMJ
RMHR*
DVC*
RIS*
NMJ
IL1L
NMJ
RMGR
c
d
RIMR*
RMGL
NMJ
RMDL, AVKR
DVC*
NMJ, RMGR
RMDR, AVKR
RMDR, AVKL
RMDR, AVKR
CEPVR*
e
RMDL, AVKR
RIGR
DVB*
RIMR*
SAAVR*
DVB*
SAAVL*
AIBR
RIML*
RIGR*
SAAVR*
RIVR
a
FLPL
RMFL
CELL BODY IN VENTRAL GANGLION
RMFR
CELL BODY IN VENTRAL GANGLION
(JSH RECONSTRUCTION)

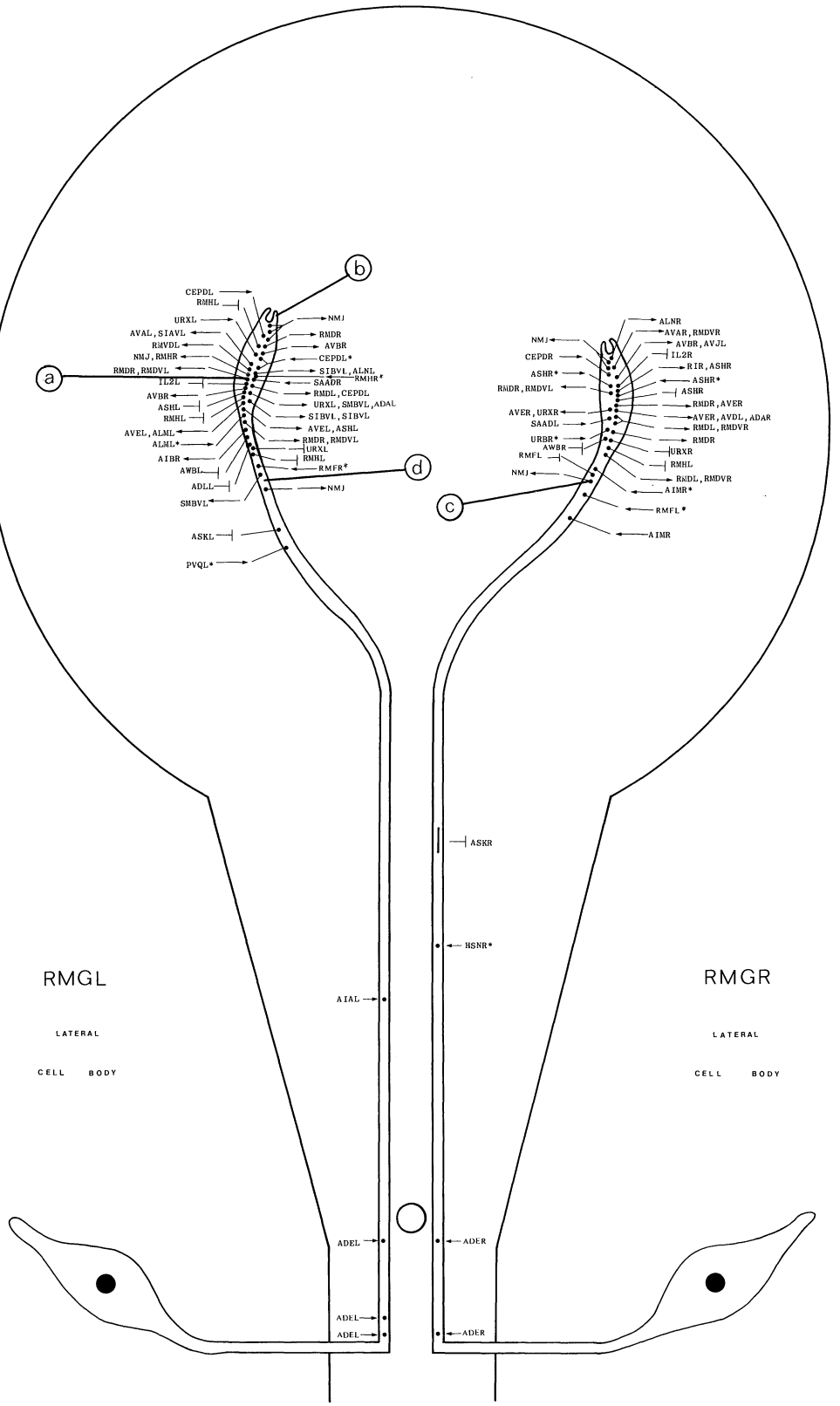


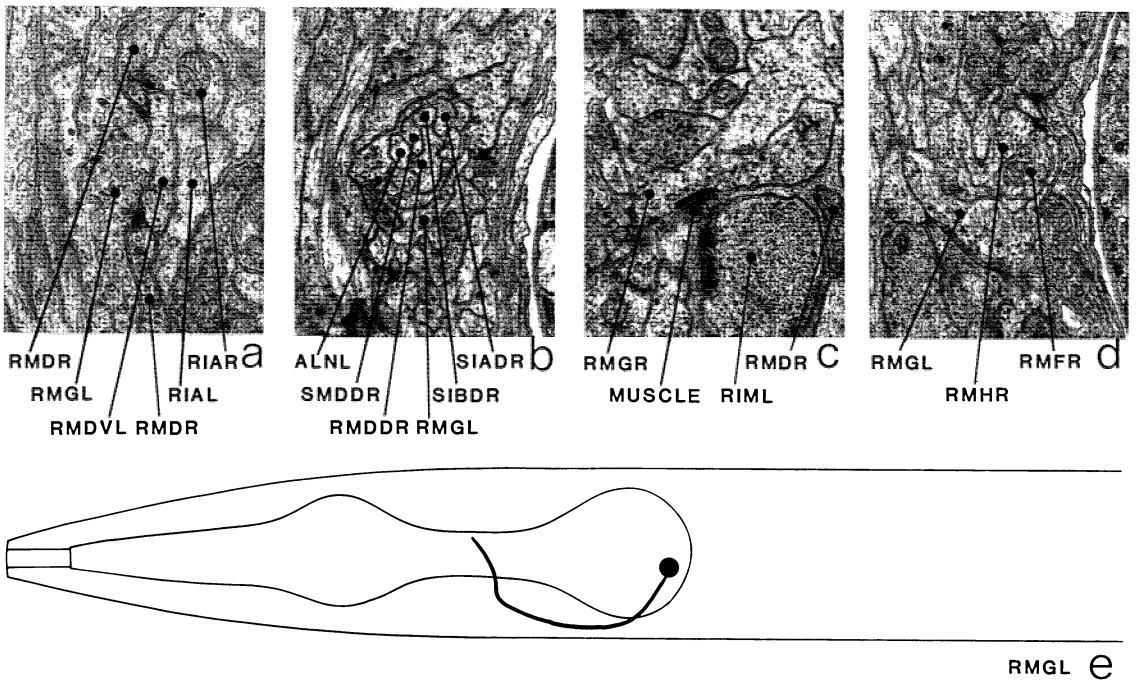
RMF

Members: RMFL, RMFR.

RMF is a set of two motoneurons, which innervate head muscles via NMJs in the nerve ring. The cell bodies of RMF are situated in the ventral ganglion and send anteriorly directed processes into the nerve ring. These processes are initially closely associated with those of AVA (a) but then move away from AVA in the nerve ring and run right round it near the outside surface and anterior face. A branch comes off each process at a distal sub-dorsal position. (Only one was present in the N2U reconstruction, but two were seen in other reconstructions, so a diagram of RMF from the JSH animal has been included). This branch moves to the inside surface of the nerve ring and has NMJs. The main synaptic outputs are: NMJs, which are often dyadic or triadic with RMG as a corecipient (c); AVK (e); and RMD (e). Some of the synaptic vesicles of RMF have dark-looking cores (d). The main synaptic input comes from DVB (f) and DVC (g). There are gap junctions to RMG (h).

Magnifications: (a–c, f–h) ×12750, (d, e) ×25500.


a
b
c
d
CEPDL
RMHL
URXL
AVAL, SIAVL
RMVDL
NMJ, RMHR
RMDR, RMDVL
IL2L
AVBR
ASHL
RMHL
AVEL, ALML
ALML*
AIBR
AWBL
ADLL
SMBVL
ASKL
PVQL*
NMJ
RMDR
AVBR
CEPDL*
SIBVL, ALNL
RMHR*
SAADR
RMDL, CEPDL
URXL, SMBVL, ADAL
SIBVL, SIBVL
AVEL, ASHL
RMDR, RMDVL
URXL
RMHL
RMFR*
NMJ
NMJ
CEPDR
ASHR*
RMDR, RMDVL
AVER, URXR
SAADL
URBR*
AWBR
RMFL
NMJ
ALNR
AVAR, RMDVR
AVBR, AVJL
IL2R
RIR, ASHR
ASHR*
ASHR
RMDR, AVER
AVER, AVDL, ADAR
RMDL, RMDVR
RMDR
URXR
RMHL
RMDL, RMDVR
AIMR*
RMFL*
AIMR
ASKR
HSNR*
AIAL
RMGL
LATERAL
CELL BODY
RMGR
LATERAL
CELL BODY
ADEL
ADEL
ADEL
ADER
ADER

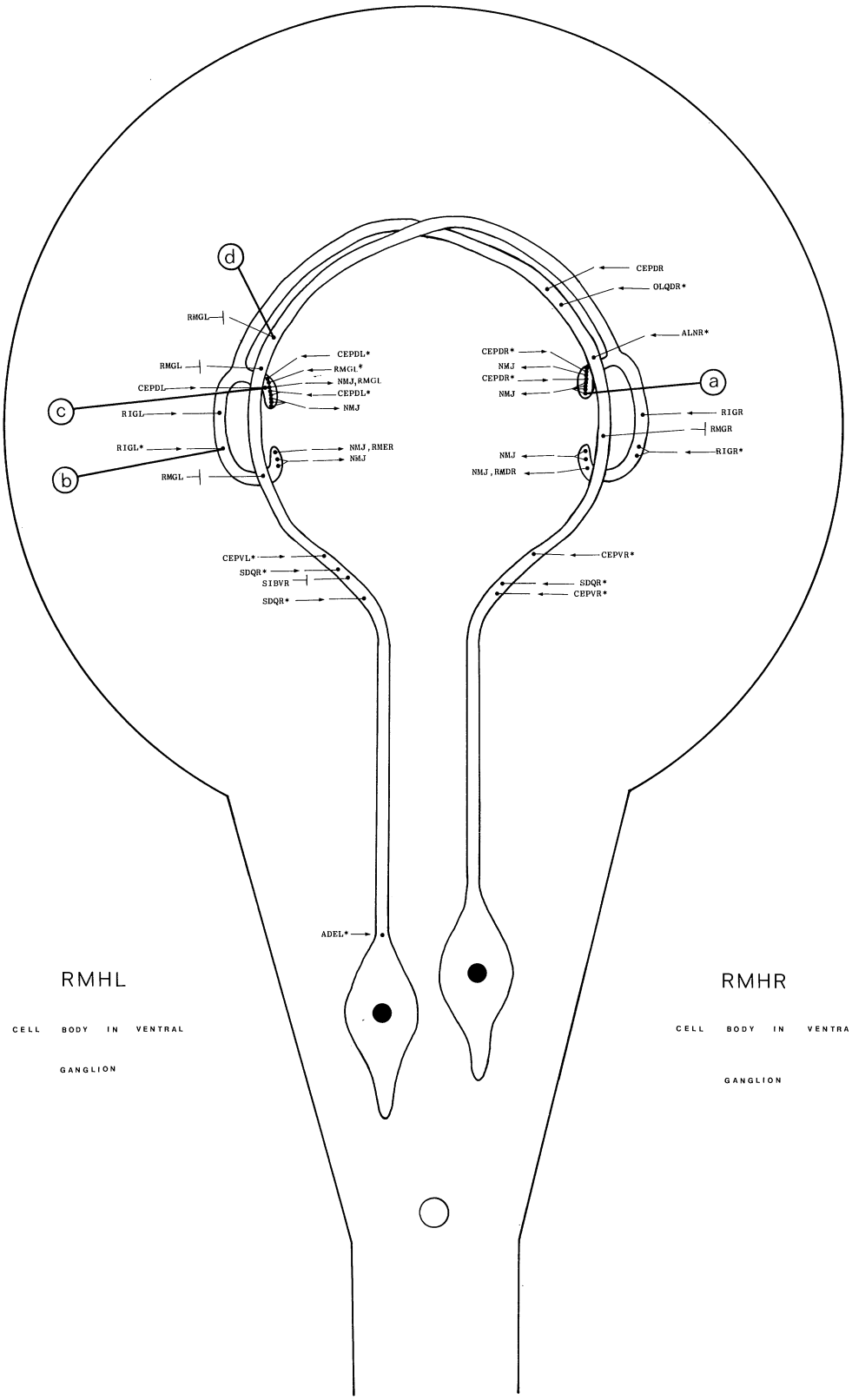


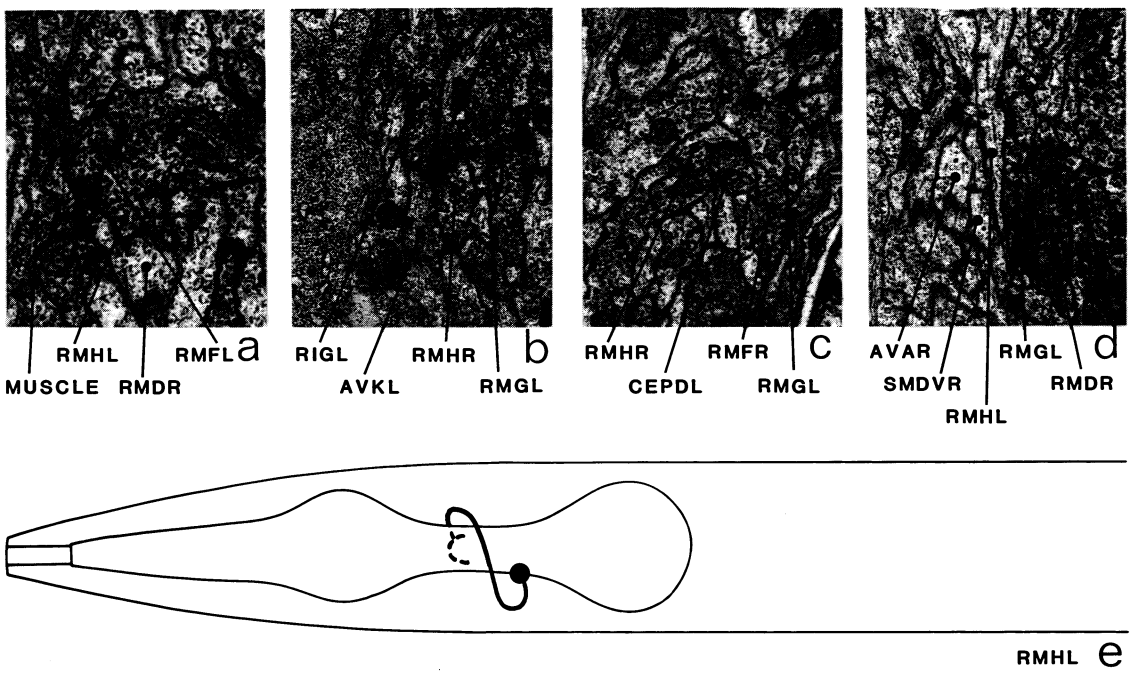
RMG

Members: RMGL, RMGR.

RMG is a set of two motoneurons, which innervate muscles in the head via NMJs in the nerve ring. The cell bodies of RMG are situated laterally, just behind the pharynx, and enter the ventral cord via the deirid commissures. The processes run near the dorsal surface of the ventral cord and enter the nerve ring, which they run partly round, near the inner surface, terminating sub-dorsally at characteristic structures, where they wrap round a bundle of processes (b). RMG has NMJs on the lateral side of each of the four muscle spurs (c and figure 14). The synaptic vesicles are large; some are dark-cored (a). It also has synaptic output to RMD (a) and AVE. The main synaptic input is from ADE, CEP and also, possibly, RMF via processes that intercept NMJs (d). RMG has gap junctions with many classes of cell, namely AWB (*d), RMH (*d), RMF (*h), ASK, IL2L/R, ASH, ADL and URX.

Magnifications: (a) ×25500, (b–d) ×12750.


d
RMGL
RMGL
CEPDL
RIGL
c
RIGL*
b
RMGL
CEPDL*
RMGL*
NMJ, RMGL
CEPDL*
NMJ
NMJ, RMER
NMJ
CEPVL*
SDQR*
SIBVR
SDQR*
ADEL*
CEPDR
OLQDR*
ALNR*
CEPDR*
NMJ
CEPDR*
NMJ
a
RIGR
RMGR
RIGR*
NMJ
NMJ, RMDR
CEPVR*
SDQR*
CEPVR*
RMHL
CELL BODY IN VENTRAL GANGLION
RMHR
CELL BODY IN VENTRAL GANGLION

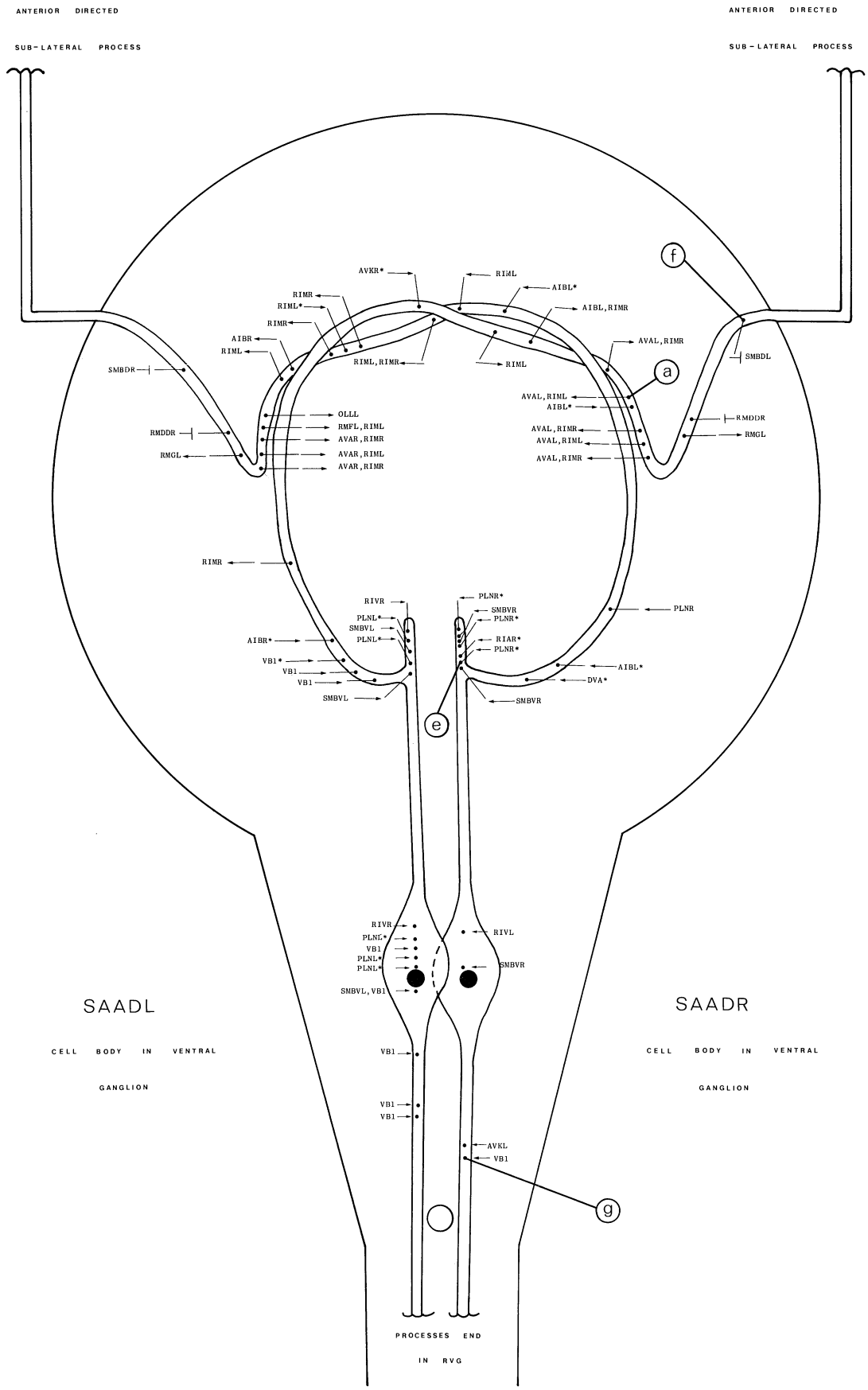


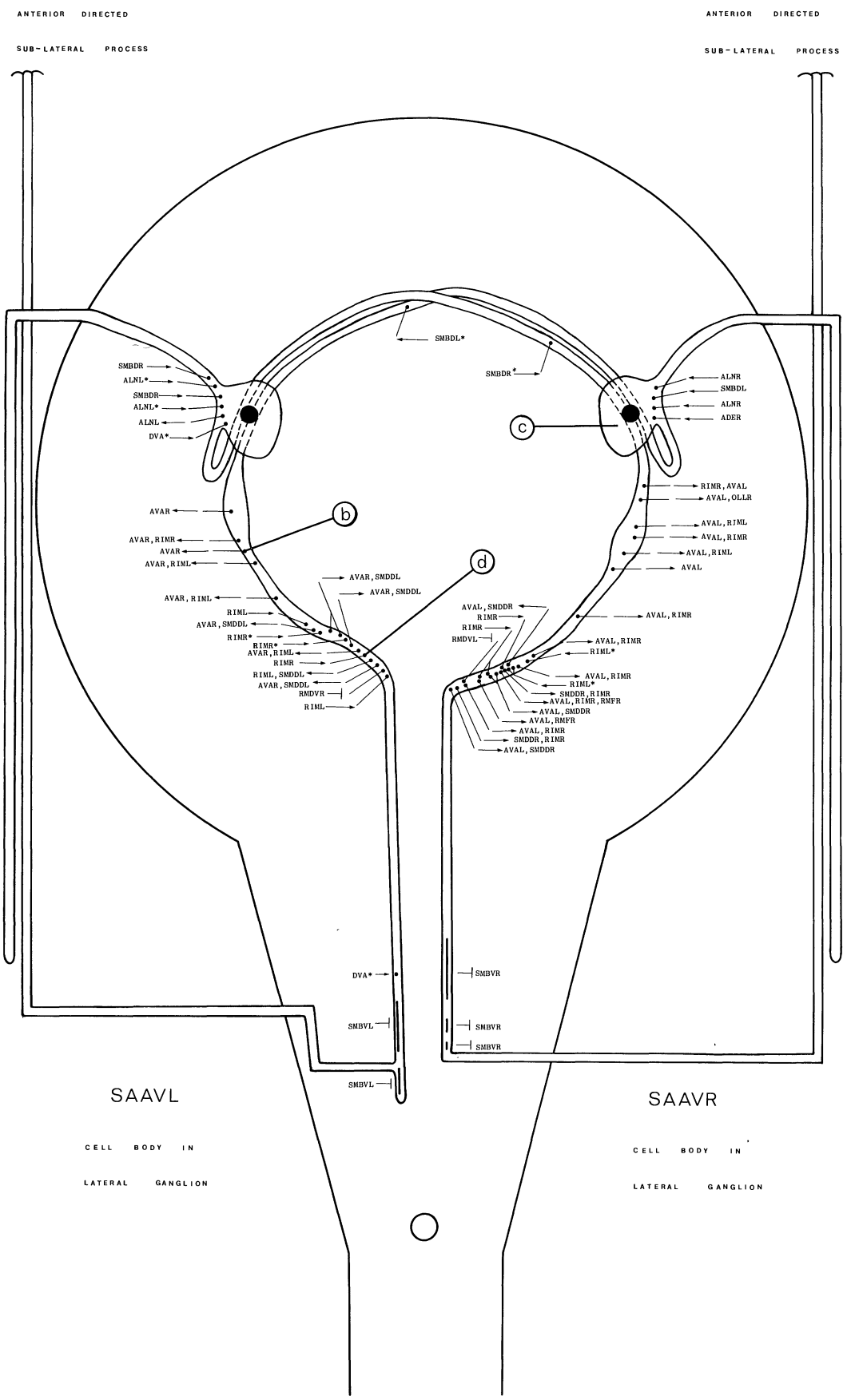
RMH

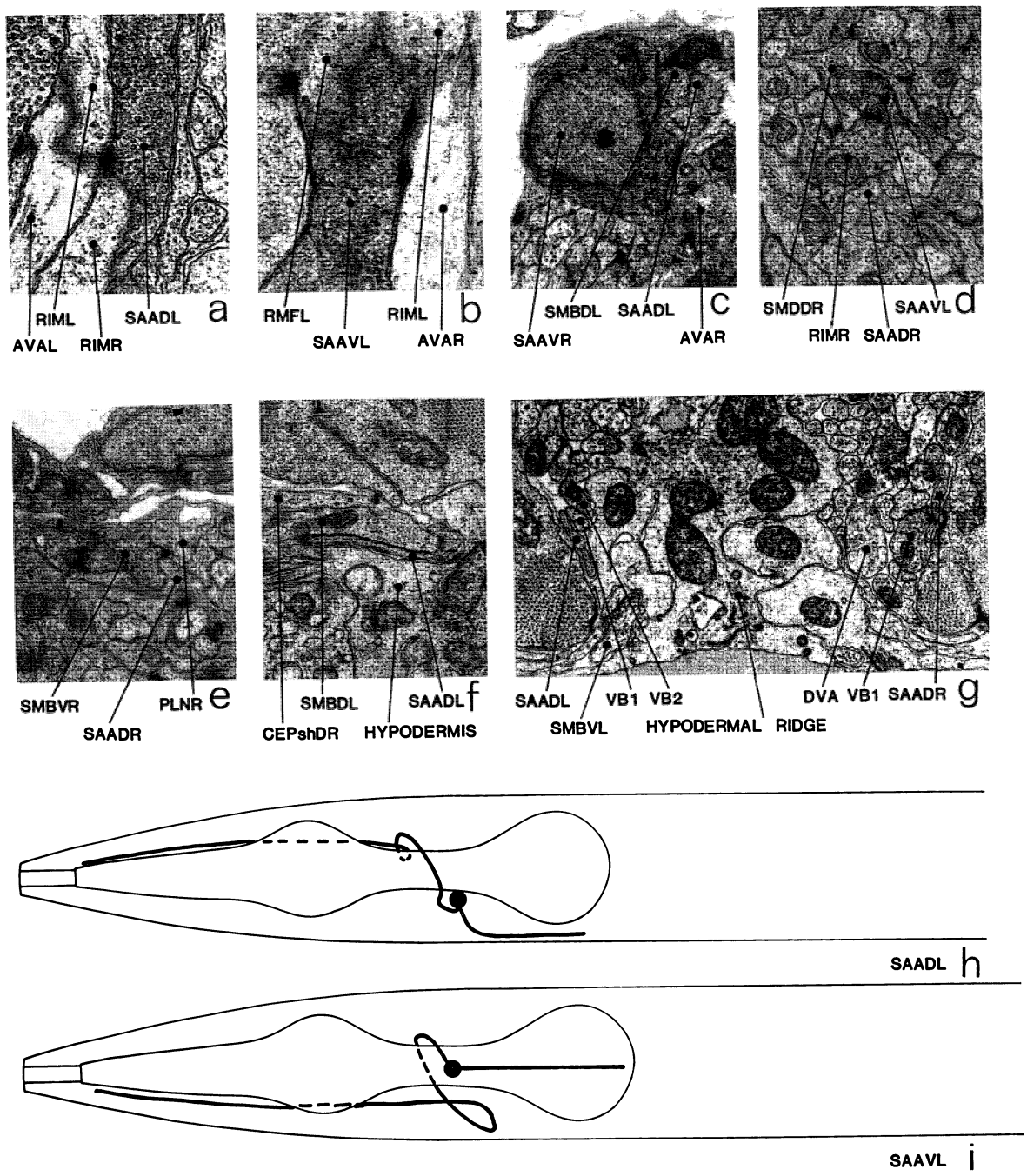
Members: RMHL, RMHR.

RMH is a set of two motoneurons which innervate muscles in the head via NMJs in the nerve ring. The cell bodies of RMH are situated in the ventral ganglion and send out anteriorly directed processes, which enter the nerve ring and run round it near the inside surface to the contralateral side. Here they form two looped structures which have regions of NMJs symmetrically disposed about the lateral line. Some of the NMJs are intercepted by dendrites from RMD (a). The main source of synaptic input is from RIG (b) and CEP (c). There are gap junctions to RMG (d).

Magnifications: (a) ×25500, (b–d) ×12750.


ANTERIOR DIRECTED SUB-LATERAL PROCESS
ANTERIOR DIRECTED SUB-LATERAL PROCESS
AVKR*
RIML
AIBL*
RIMR
RIML*
AIBL,RIMR
RIMR
AIBR
RIML
RIML,RIMR
RIML
AVAL,RIMR
SMBDR
SMBDL
a
AVAL,RIML
AIBL*
RMDDR
AVAL,RIMR
AVAL,RIML
RMGL
AVAL,RIMR
OLLL
RMFL,RIML
AVAR,RIMR
AVAR,RIML
AVAR,RIMR
RMDDR
RMGL
RIMR
RIVR
PLNR*
SMBVR
PLNL*
PLNR*
SMBVL
PLNL*
RIAR*
PLNR*
AIBR*
VB1*
VB1
VB1
SMBVL
PLNR
AIBL*
DVA*
SMBVR
e
RIVR
RIVL
PLNL*
VB1
PLNL*
PLNL*
SMBVR
SMBVL,VB1
SAADL
CELL BODY IN VENTRAL GANGLION
SAADR
CELL BODY IN VENTRAL GANGLION
VB1
VB1
VB1
AVKL
VB1
g
PROCESSES END IN RVG


ANTERIOR DIRECTED
SUB-LATERAL PROCESS
ANTERIOR DIRECTED
SUB-LATERAL PROCESS
SMBDL*
SMBDR*
SMBDR
ALNL*
SMBDR
ALNL*
ALNL
DVA*
ALNR
SMBDL
ALNR
ADER
c
RIMR, AVAL
AVAL, OLLR
AVAL, RIML
AVAL, RIMR
AVAL, RIML
AVAL
b
AVAR
AVAR, RIMR
AVAR
AVAR, RIML
d
AVAR, SMDDL
AVAR, SMDDL
AVAR, RIML
RIML
AVAR, SMDDL
RIMR*
RIMR*
AVAR, RIML
RIMR
RIML, SMDDL
AVAR, SMDDL
RMDVR
RIML
AVAL, SMDDR
RIMR
RIMR
RMDVL
AVAL, RIMR
RIML*
AVAL, RIMR
RIML*
SMDDR, RIMR
AVAL, RIMR, RMFR
AVAL, SMDDR
AVAL, RMFR
AVAL, RIMR
SMDDR, RIMR
AVAL, SMDDR
DVA*
SMBVL
SMBVL
SMBVR
SMBVR
SMBVR
SAAVL
CELL BODY IN LATERAL GANGLION
SAAVR
CELL BODY IN LATERAL GANGLION



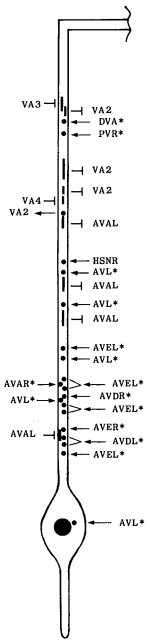
SAA

Members: SAADL, SAADR, SAAVL, SAAVR.

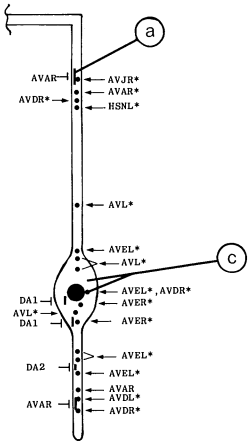
SAA is a set of four interneurons that send processes anteriorly up the sub-lateral cords in the head. The cell bodies of SAAD are situated in the ventral ganglion (figure 16). Those of SAAV are situated slightly dorsal of the lateral lines, closely apposed to, and posterior to, the neuropile of the nerve ring (h, i). The SAAV pair sends additional processes down the lateral lines (i). These processes run laterally alongside those of FLP for about 20 μm and then end.

The main processes from the cell bodies of SAAV enter the ring sub-dorsally and run round it; they then leave ventrally, on the contralateral side, and enter the ventral cord. They run posteriorly for a short distance in the cord and leave via the amphidial commissures to take up their positions along with the processes of SABV in the anterior ventral sub-lateral cords. The SAAD pair sends anteriorly directed processes into the ring, which run round it until they reach a contralateral, sub-dorsal position where they turn and run posteriorly through the ring neuropile, and then turn again to enter the dorsal sub-lateral cords along with the processes of SABD. Processes from SMBD poke into the cell bodies of SAAV, where they form chemical synapses (SMB-d). SMD cells wrap round the processes of SAA neurons ventrally (SMD-c, d). All the SAA neurons run in close association with the processes of AVA and RIM in the nerve ring; their major synaptic outputs are to these processes (a, b) and also to those of SMD. RIM synapses back onto the SAA neurons reciprocally (d). SAA has gap junctions to RMD. There are several dorsal–ventral asymmetries exhibited by these cells: PLN synapses onto SAAD (e) and ALN onto SAAV; SMBV synapses onto SAAD and makes gap junctions with SAAV, whereas SMBD synapses onto SAAV but makes a gap junction with SAAD (f). RIV (*a) synapses only onto SAAD, as does VB1, which synapses onto two posteriorly directed processes, which emanate from the cell bodies of SAAD (g); these processes end in the retro-vesicular ganglion (h).

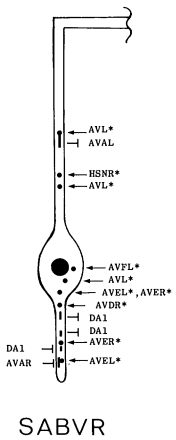
Magnifications: (a, b) $\times 25500$, (c) $\times 8500$, (d–g) $\times 12750$.



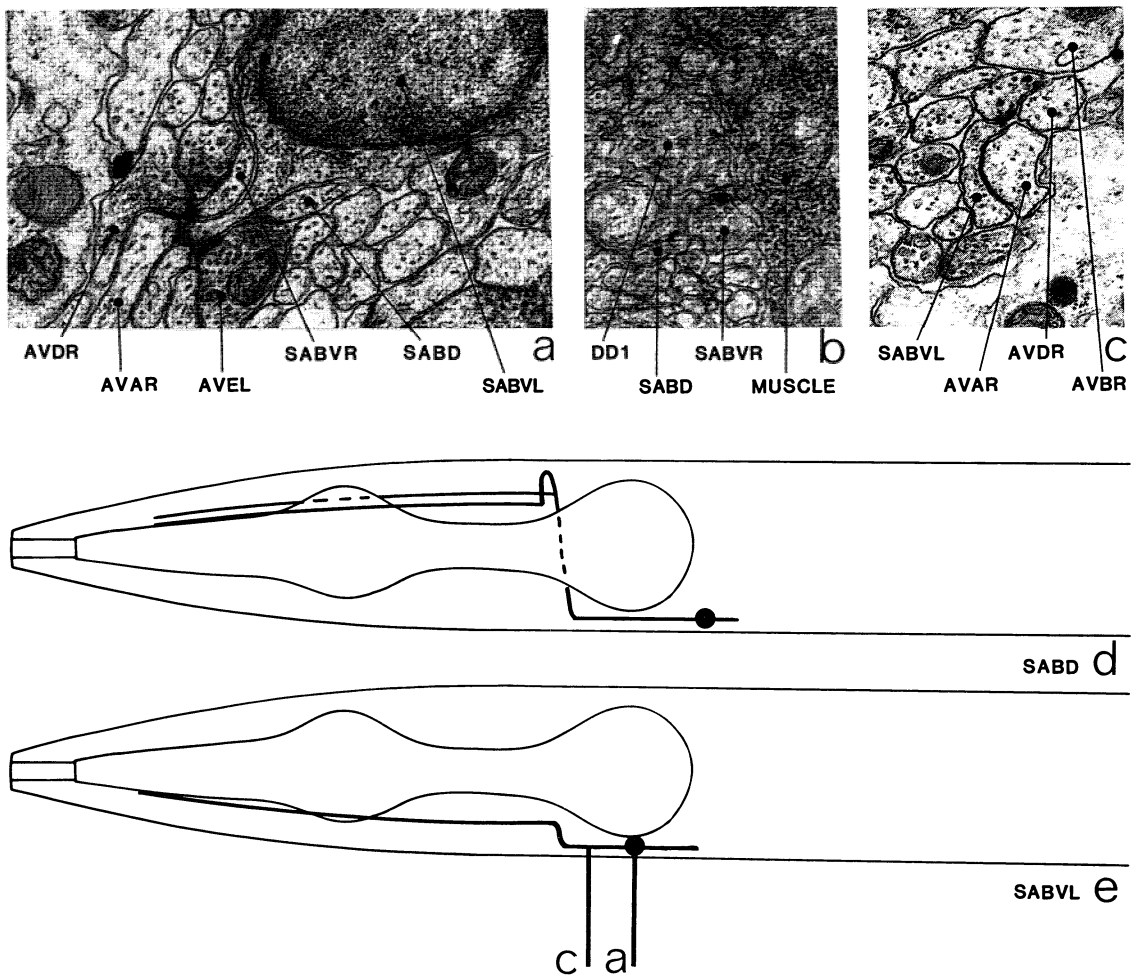
SABD



SABVL



SABVR

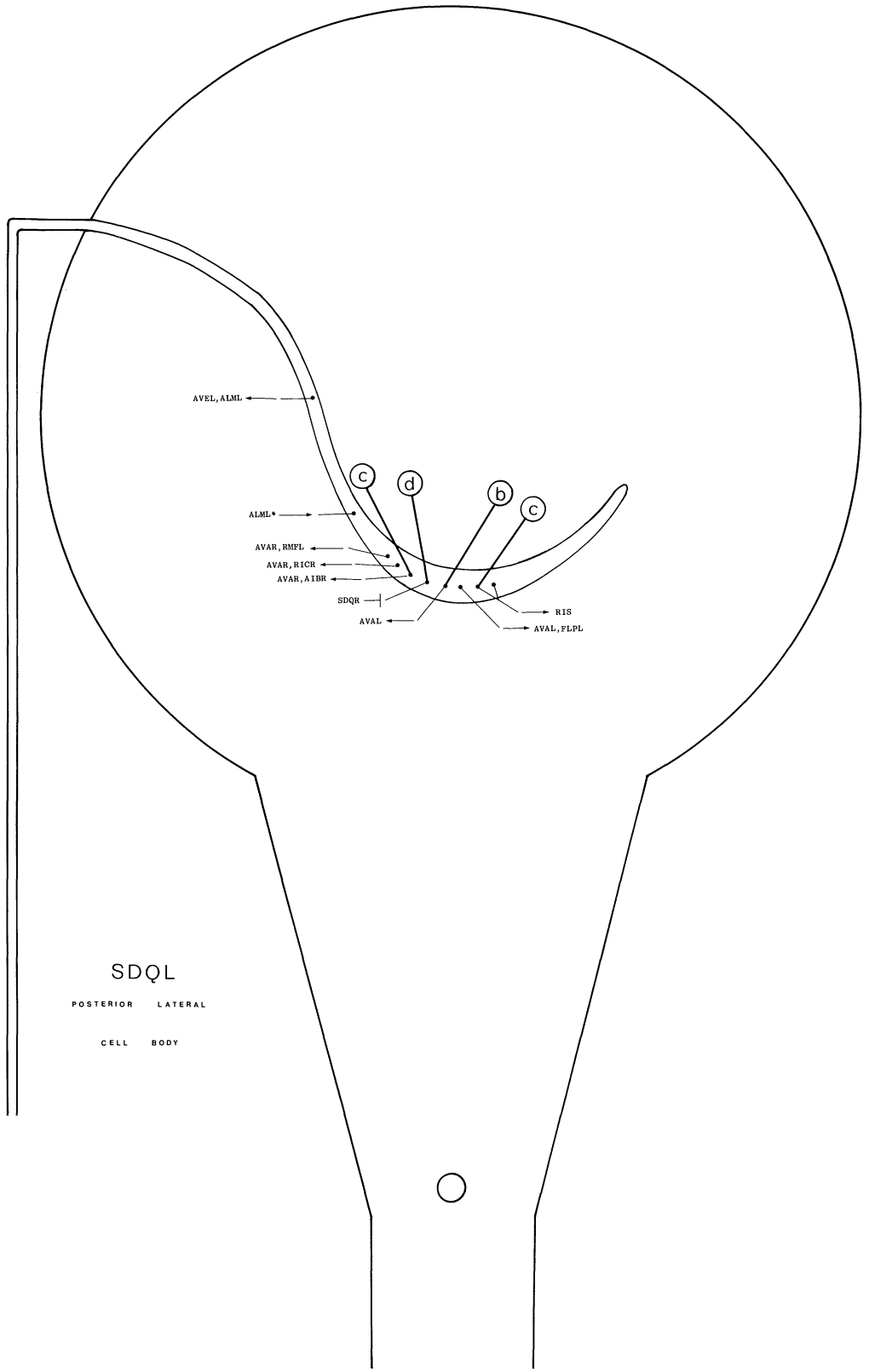


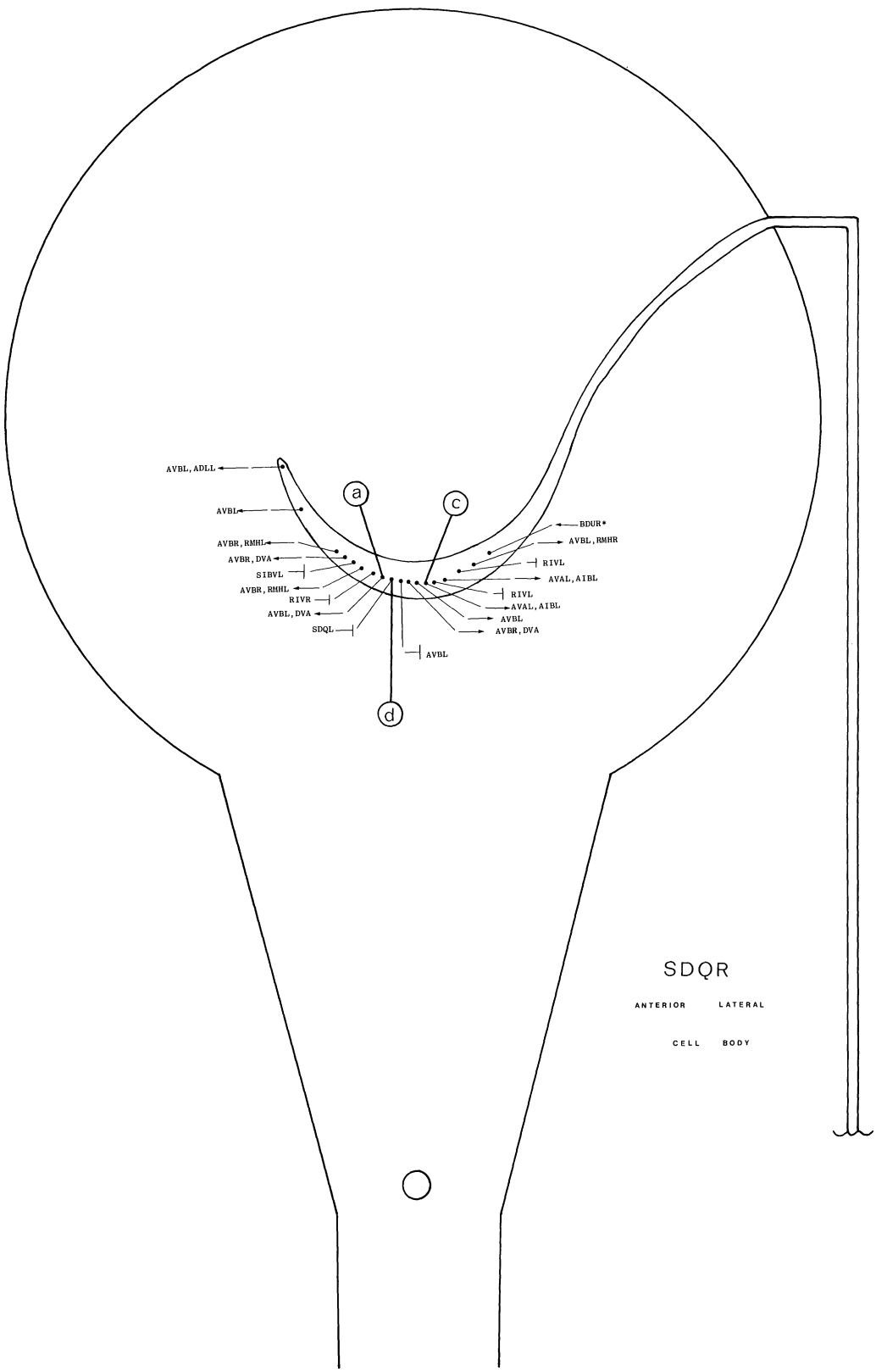
SAB

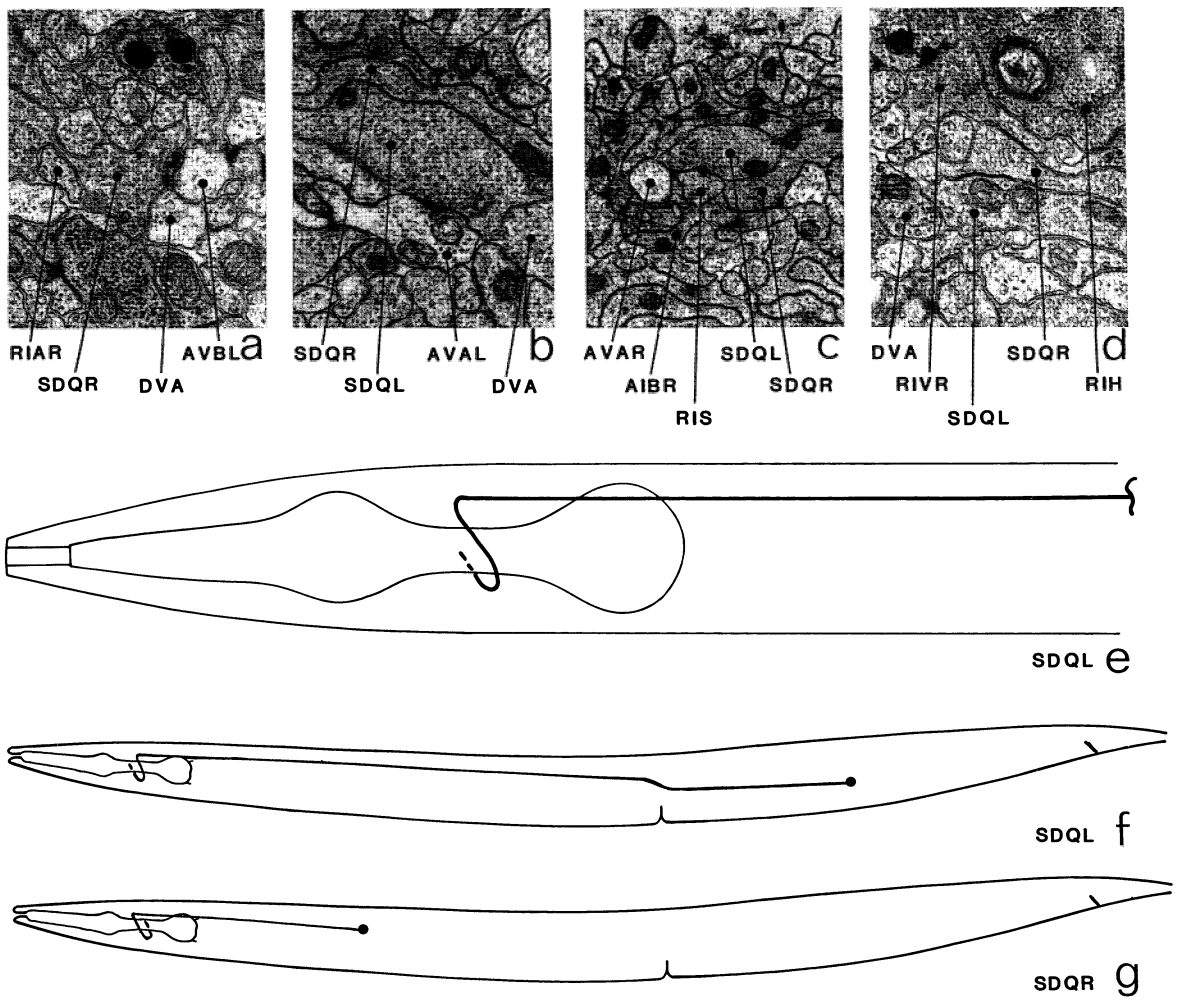
Members: SABD, SABVL, SABVR.

SAB is a set of three interneurons, which send processes anteriorly up the sub-lateral cords in the head. All the cell bodies, which are situated in the retro-vesicular ganglion, send out anteriorly directed processes which leave the ventral cord via the amphidial commissures. The processes of SABV join the anterior sub-ventral cords along with the processes of SAAV (e); the process of SABD runs round the right-hand side of the animal and sends a process into each anterior sub-dorsal cord along with one from SAAD (d). No synaptic output has been seen from SAB in adults; however, in the L1 larval stage, SABs have several NMJs in the anterior ventral cord (b). The synaptic input onto SABs is much the same as that onto VAn and DAn motoneurons; it comes from AVD (a), AVE (a) and AVA (a). These synapses are often clustered together (a), making synaptic complexes that are a characteristic feature of the neuropile of the retro-vesicular ganglion. SAB has gap junctions to AVA (c), DAn and VAn.

Magnifications: (a, c) $\times 25500$, (b) $\times 34000$.


AVEL, ALML
c
d
b
c
ALML
AVAR, RMFL
AVAR, RICR
AVAR, AIBR
SDQR
AVAL
RIS
AVAL, FLPL
SDQL
POSTERIOR LATERAL
CELL BODY


AVBL, ADLL
AVBL
AVBR, RMHL
AVBR, DVA
SIBVL
AVBR, RMHL
RIVR
AVBL, DVA
SDQL
AVBL
BDUR*
AVBL, RMHR
RIVL
AVAL, AIBL
RIVL
AVAL, AIBL
AVBL
AVBR, DVA
a
c
d
SDQR
ANTERIOR
LATERAL
CELL
BODY

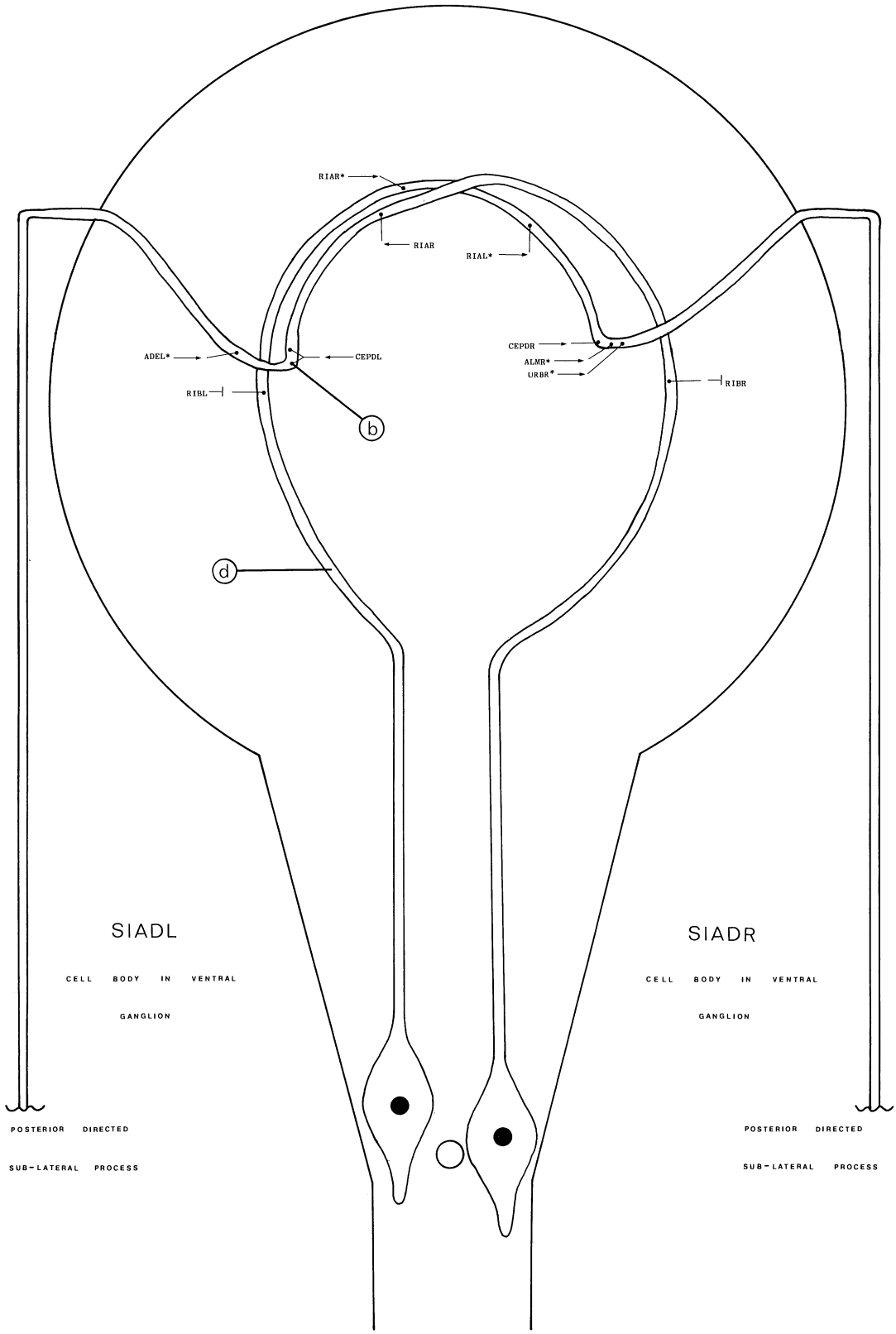


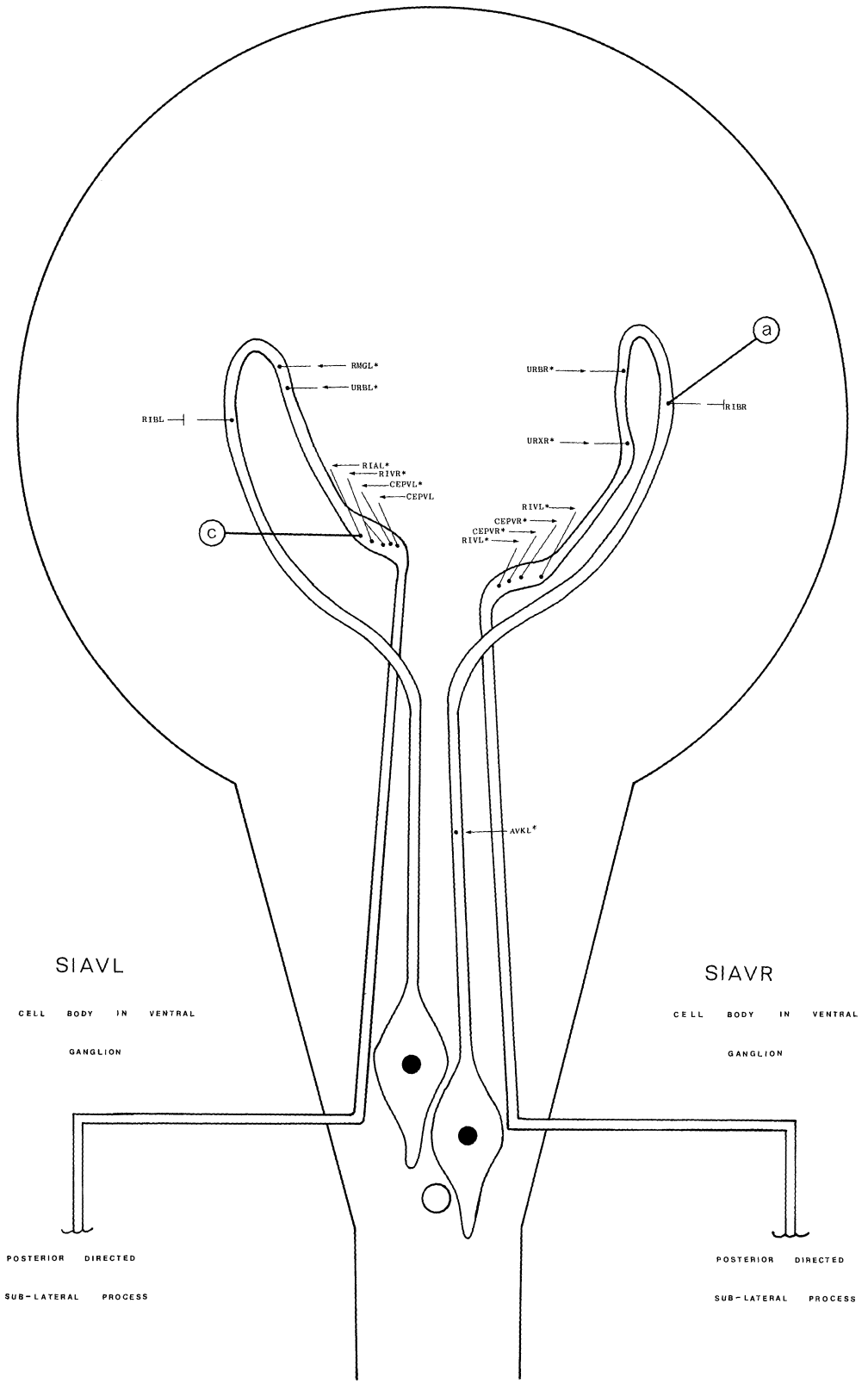
SDQ

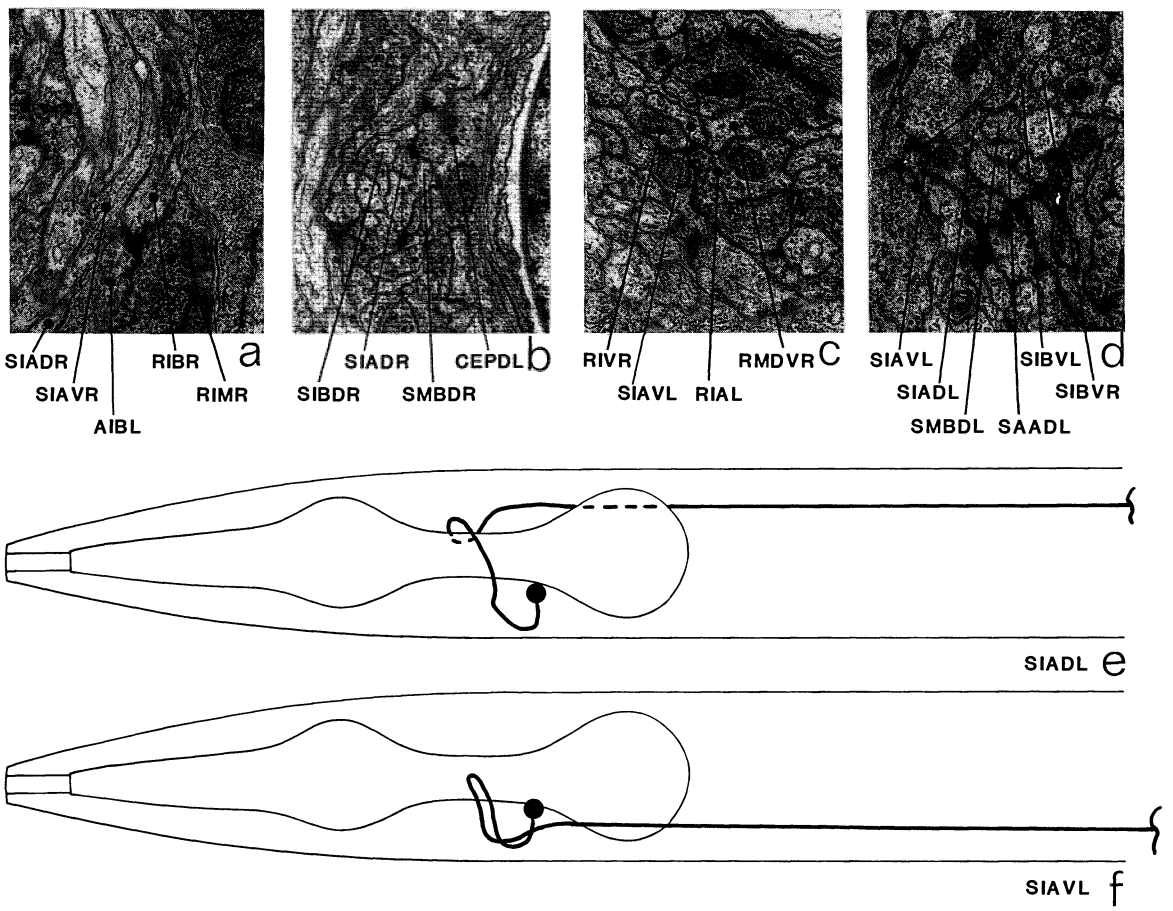
Members: SDQL, SDQR.

SDQ is a set of two interneurons with laterally located cell bodies. The cell body of SDQL is situated in the anterior body; that of SDQR, in the posterior body. Both send out single, anteriorly directed processes, which initially run laterally but later run in the dorsal sub-lateral cords, and then, along with the other processes from these cords, enter the nerve ring sub-dorsally. The processes run ventrally round the inner surface of the ring and end sub-ventrally on the contralateral side. Most of the synapses are situated mid-ventrally, where the processes enlarge somewhat. There is significantly more synaptic output from SDQR than SDQL and this may reflect the fact that the process of SDQR is shorter than that of SDQL. The main synaptic outputs are to AVB (a), AVA (b, c), DVA (a), AIB (c) and RIS (c). There are gap junctions to itself (d), AVB and RIV (d).

Magnifications: (a, b, d) ×25000, (c) ×17000.


RIAR*
RIAR
RIAL*
ADEL*
CEPDL
RIBL
CEPDR
ALMR*
URBR*
RIBR
b
d
SIADL
CELL BODY IN VENTRAL GANGLION
POSTERIOR DIRECTED SUB-LATERAL PROCESS
SIADR
CELL BODY IN VENTRAL GANGLION
POSTERIOR DIRECTED SUB-LATERAL PROCESS


RMGL*
RVBL*
RIBL
RIAL*
RIVR*
CEPVL*
CEPVL
C
URBR*
a
RIBR
URXR*
RIVL*
CEPVR*
CEPVR*
RIVL*
AVKL*
SIAVL
CELL BODY IN VENTRAL GANGLION
SIAVR
CELL BODY IN VENTRAL GANGLION
POSTERIOR DIRECTED SUB-LATERAL PROCESS
POSTERIOR DIRECTED SUB-LATERAL PROCESS

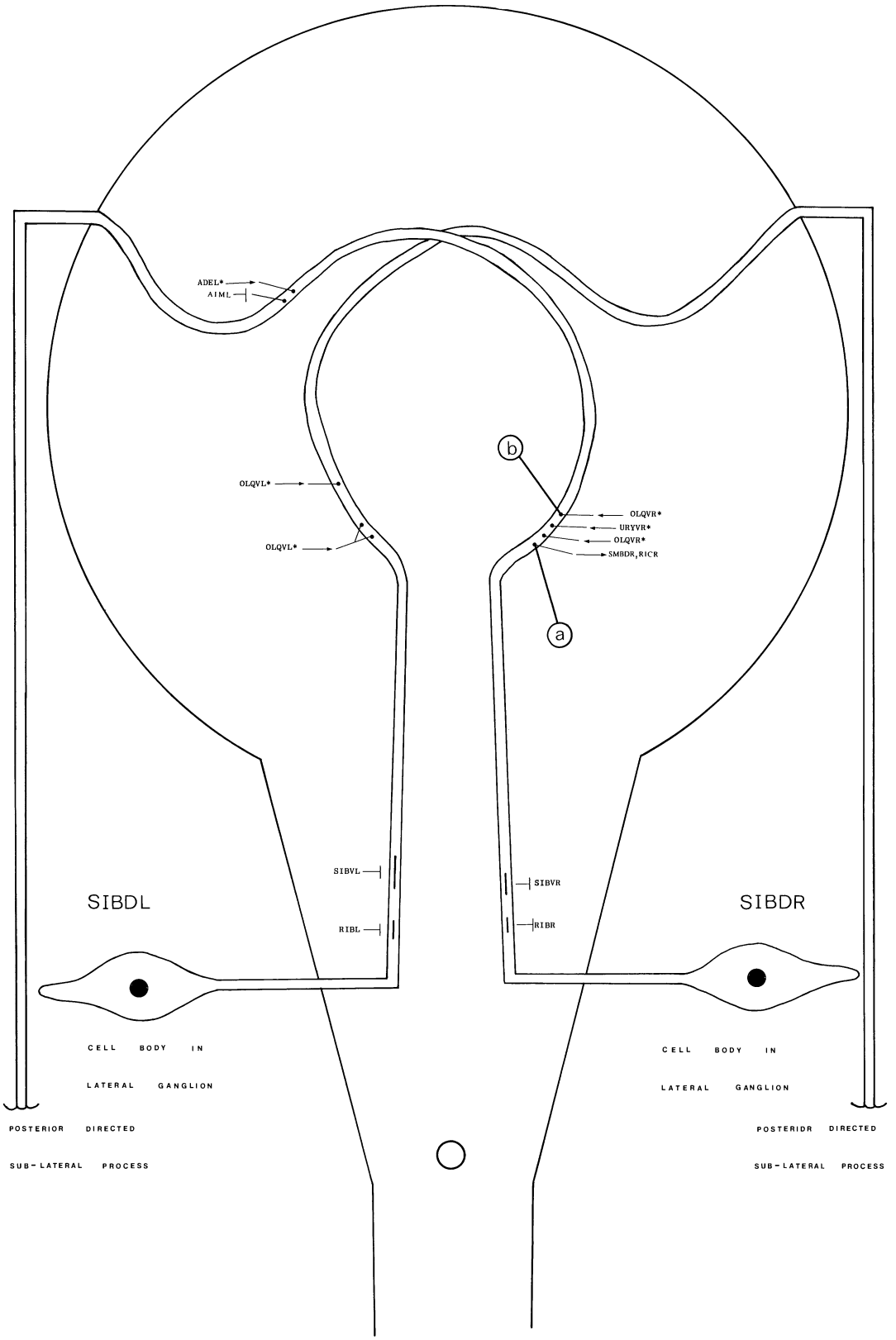


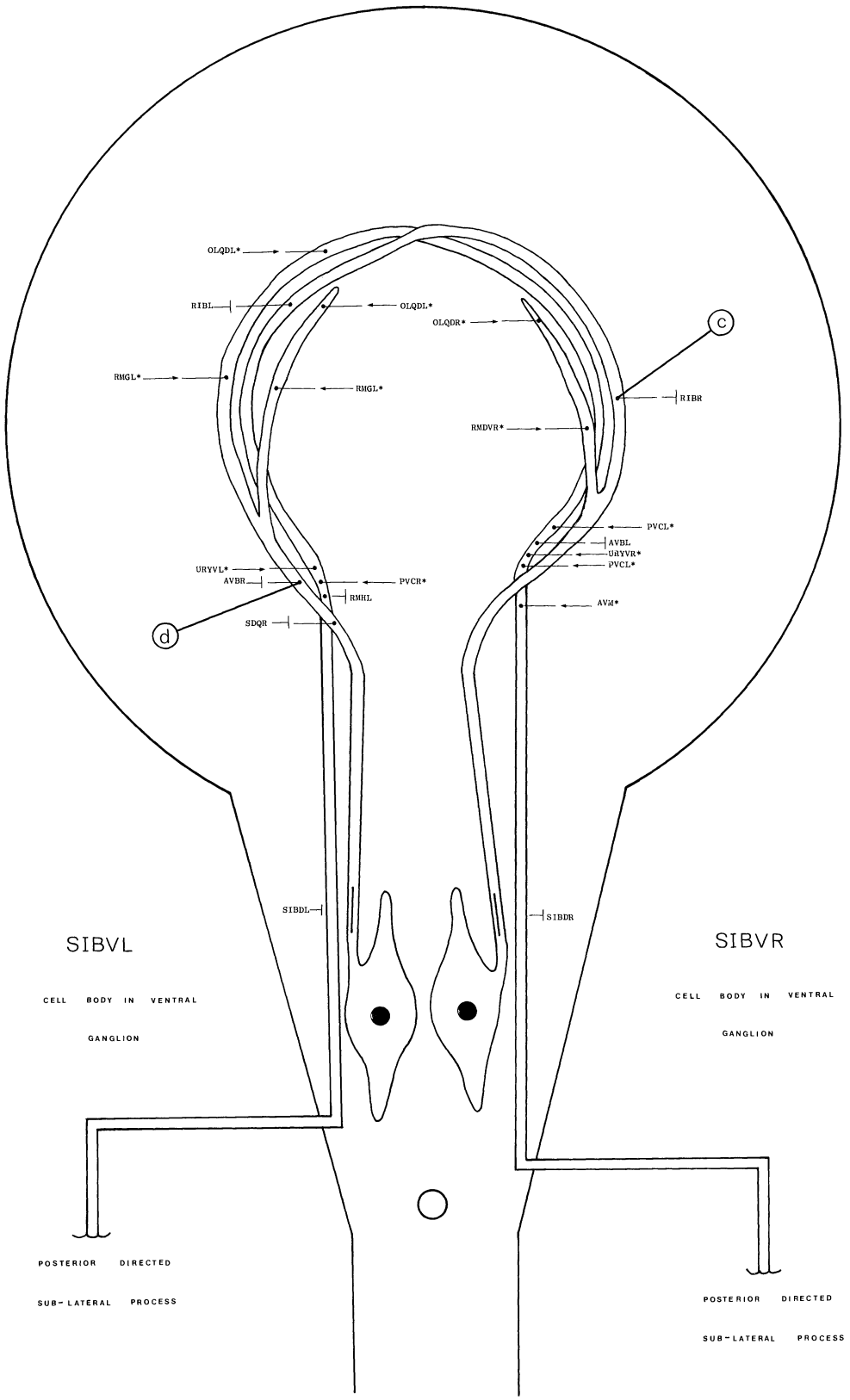
SIA

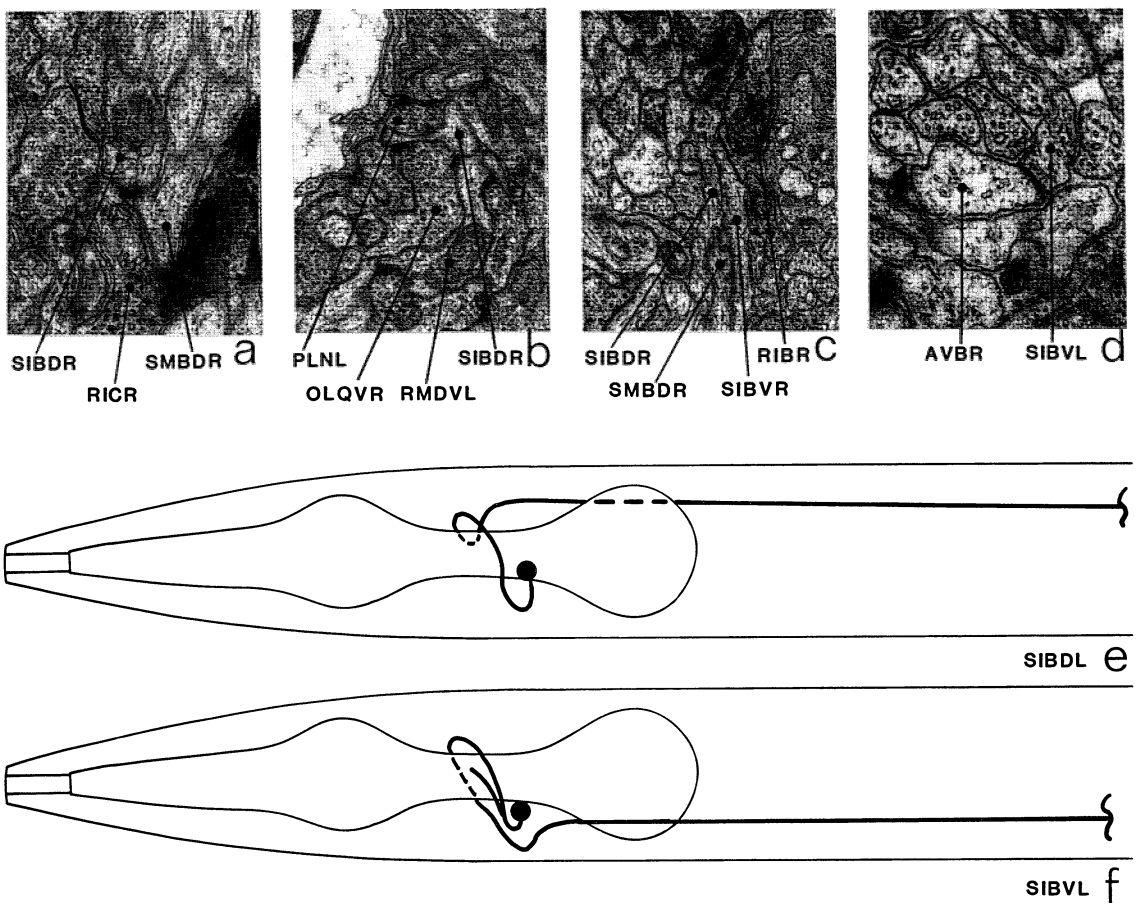
Members: SIADL, SIADR, SIAVL, SIAVR.

SIA is a set of four interneurons, which send processes posteriorly down the sub-lateral cords. All four cell bodies are in the ventral ganglion. The SIAD pair sends processes that enter and run round the nerve ring, leaving it on the contralateral side along with the four other processes that make up the sub-lateral cords (e). The SIAV pair sends processes into the ring, which loop back on the ipsilateral side, reentering the neuropile of the ventral ganglion; these processes then leave the ventral cord at the amphidial commissures and enter the sub-lateral cords along with four other processes (f). SIA is unusual in that it appears to have no synaptic outputs except, perhaps, via gap junctions to RIB (a). Synaptic input is sparse and comes mainly from CEP (b) and RIA (c). SIA is similar in some respects to SIB; the two sets of processes run together in the nerve ring near the centre of the neuropile (d).

Magnifications: (a–d) ×12750.


ADEL*
AIML
OLQVL*
OLQVL*
b
OLQVR*
URYVR*
OLQVR*
SMBDR,RICR
a
SIBVL
RIBL
SIBVR
RIBR
SIBDL
SIBDR
CELL BODY IN LATERAL GANGLION
POSTERIOR DIRECTED SUB-LATERAL PROCESS
CELL BODY IN LATERAL GANGLION
POSTERIDR DIRECTED SUB-LATERAL PROCESS


OLQDL*
RIBL
OLQDL*
OLQDR*
C
RMGL*
RMGL*
RIBR
RMDVR*
PVCL*
AVBL
URYVR*
PVCL*
URYVL*
AVBR
PVCR*
RMHL
AVM*
d
SDQR
SIBDL
SIBDR
SIBVL
CELL BODY IN VENTRAL GANGLION
SIBVR
CELL BODY IN VENTRAL GANGLION
POSTERIOR DIRECTED SUB-LATERAL PROCESS
POSTERIOR DIRECTED SUB-LATERAL PROCESS

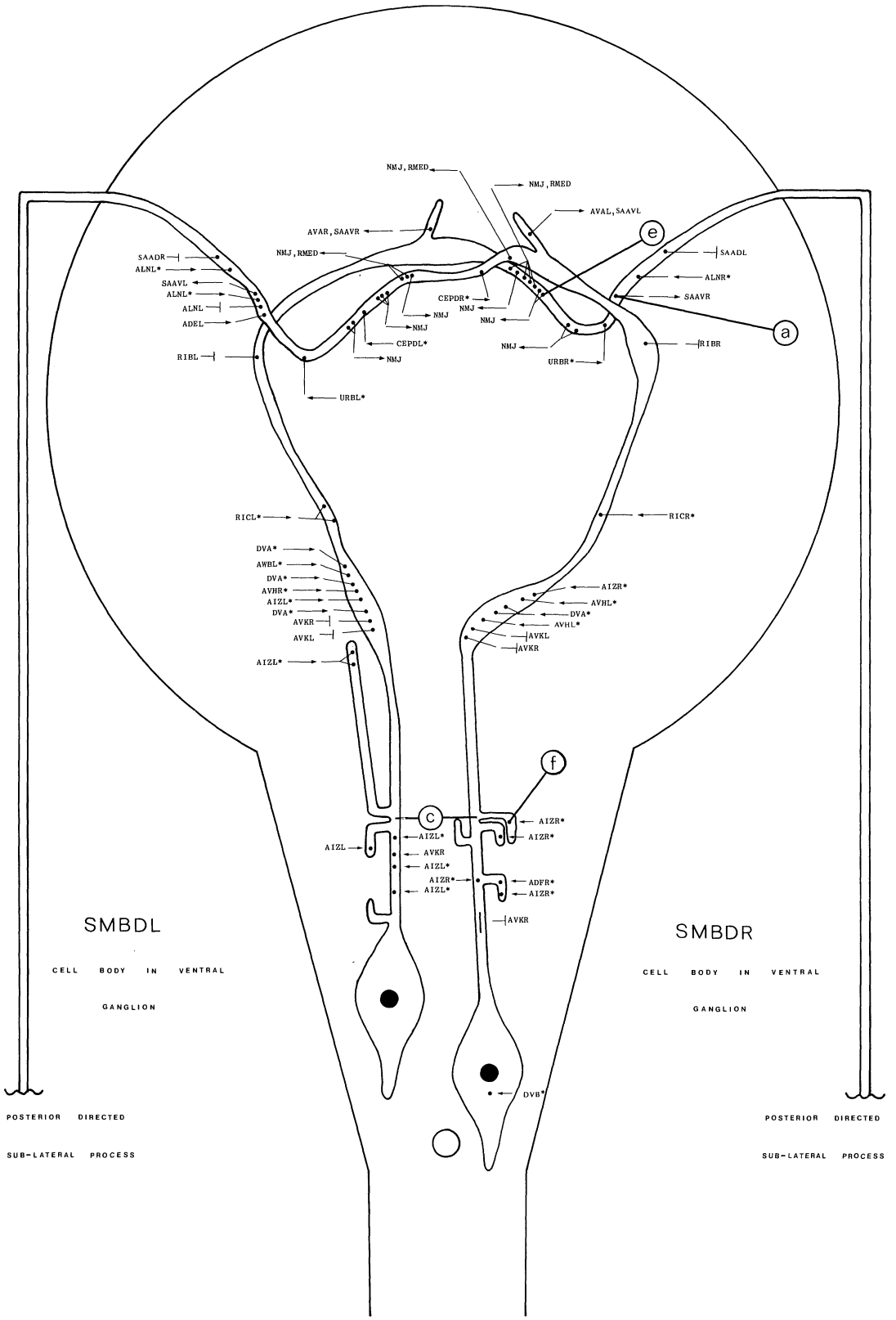


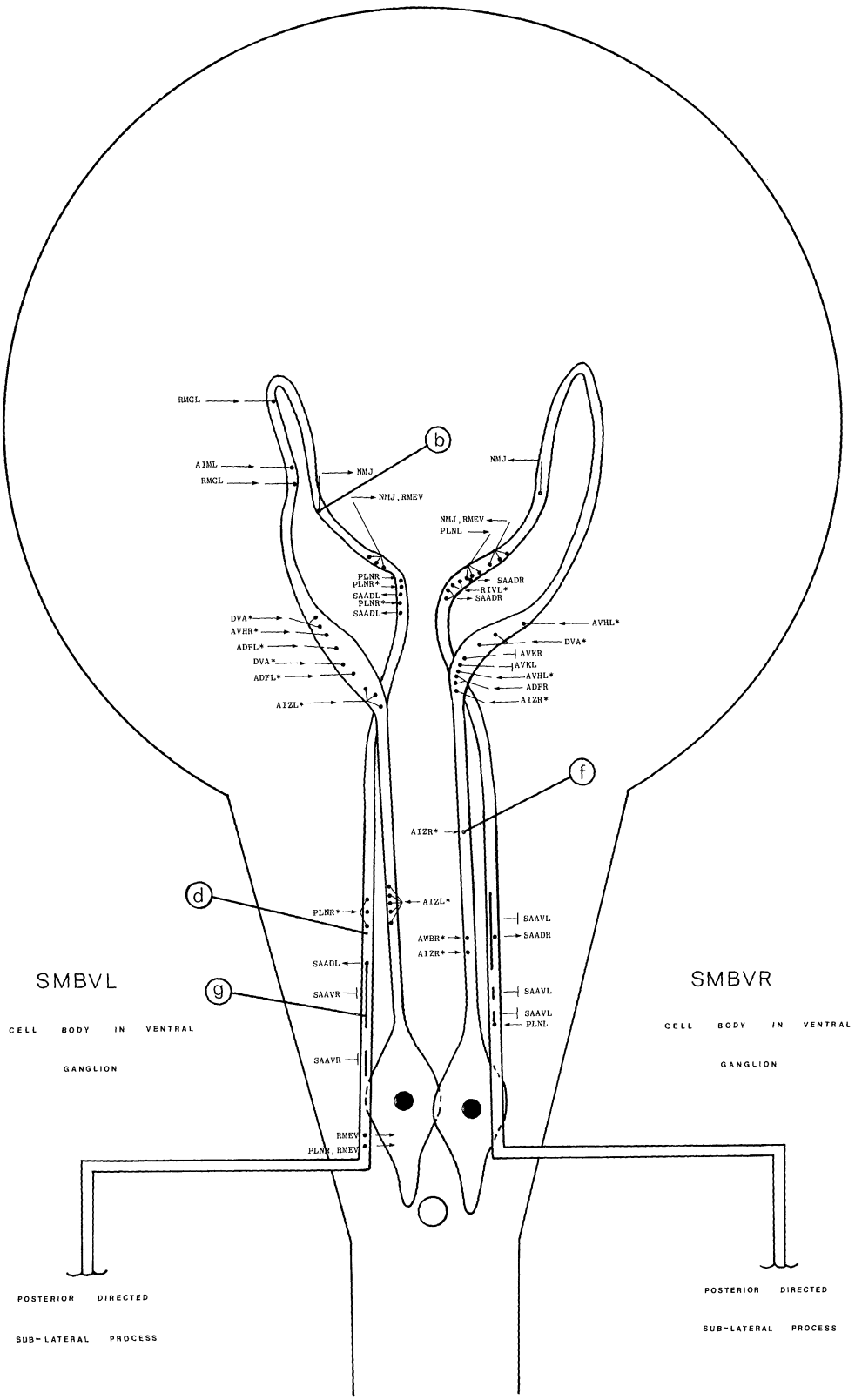
SIB

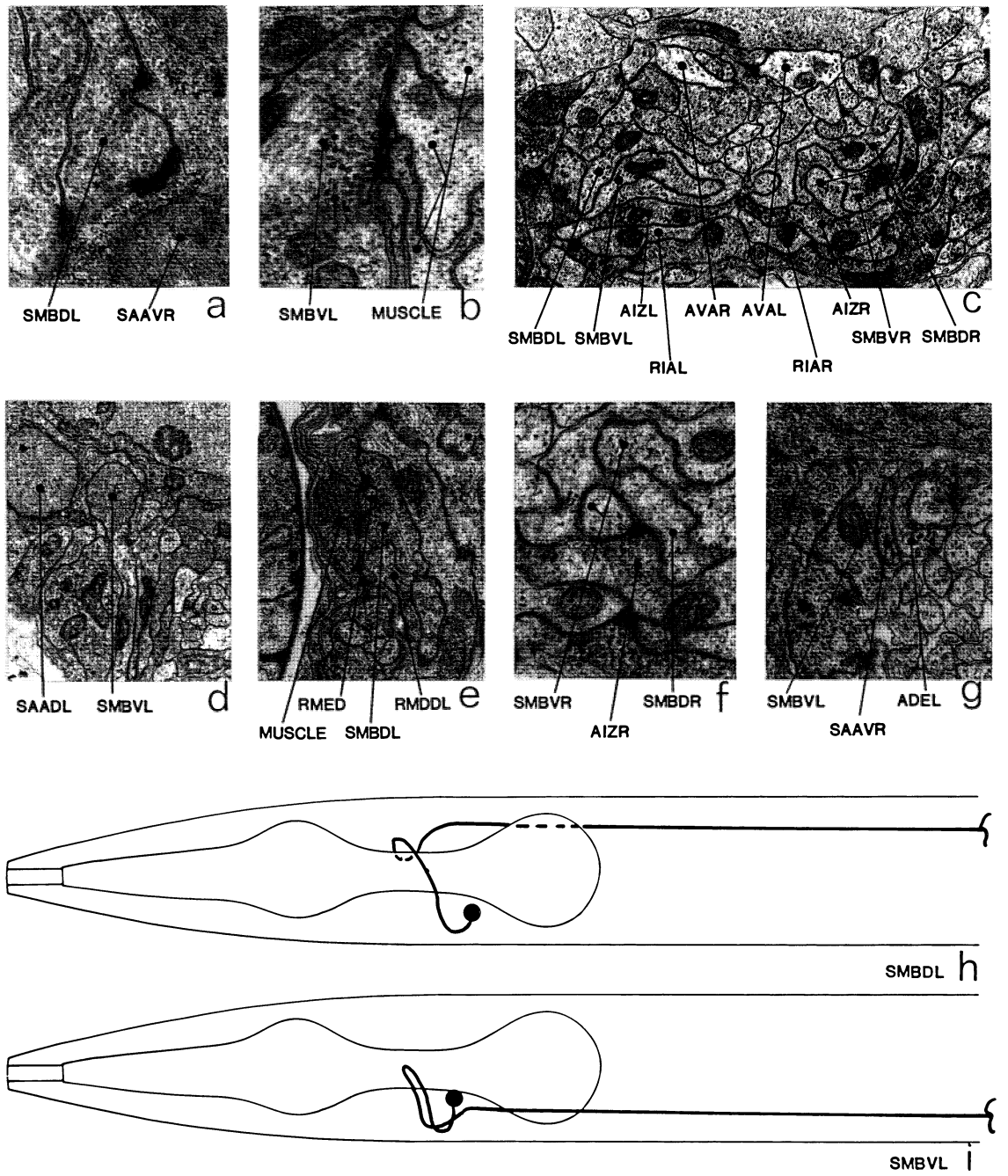
Members: SIBDL, SIBDR, SIBVL, SIBVR.

SIB is a set of four interneurons, which send processes posteriorly down the sub-lateral cords. SIBV has cell bodies, in the ventral ganglion, which send processes that run right round the nerve ring and return to the neuropile of the ventral ganglion (f). They then enter the ventral sub-lateral cords via the amphidial commissures along with four other processes. The SIBD pair have cell bodies situated in the lateral ganglia. They send processes into the ventral cord via the amphidial commissures and then run round the nerve ring, leaving it sub-dorsally on the contralateral side along with the four other processes that make up the dorsal sub-lateral cords (e). No presynaptic contacts have been seen on these cells except for occasional regions that show typical presynaptic specializations but have no vesicles (a). In one place the process of an SIBD cell was seen in the motor endplate region of the nerve ring (b) but again no vesicles were seen. SIB has synaptic input from OLQ (*b) and has gap junctions to RIB (c), itself (SIBD to SIBV), AVB (d) (SIBV only) and AIM (*d) (SIBD only). SIB is similar in some respects to SIA and their two sets of processes run together in the nerve ring near the centre of the neuropile (SIA-d).

Magnifications: (a, d) $\times 25500$, (b, c) $\times 12750$.


NMJ, RMED
NMJ, RMED
AVAL, SAAVL
AVAR, SAAVR
NMJ, RMED
SAADR
ALNL*
SAAVL
ALNL*
ALNL
ADEL
RIBL
URBL*
CEPDR*
NMJ
NMJ
NMJ
CEPDL*
NMJ
NMJ
URBR*
SAADL
ALNR*
SAAVR
RIBR
e
a
RICL*
RICR*
DVA*
AWBL*
DVA*
AVHR*
AIZL*
DVA*
AVKR
AVKL
AIZL*
AIZR*
AVHL*
DVA*
AVHL*
AVKL
AVKR
f
c
AIZL
AIZL*
AVKR
AIZL*
AIZR*
AIZL*
AIZR*
AIZR*
ADFR*
AIZR*
AVKR
DVB*
SMBDL
CELL BODY IN VENTRAL GANGLION
SMBDR
CELL BODY IN VENTRAL GANGLION
POSTERIOR DIRECTED SUB-LATERAL PROCESS
POSTERIOR DIRECTED SUB-LATERAL PROCESS


RMGL
AIML
RMGL
NMJ
NMJ , RMEV
b
NMJ
NMJ , RMEV
PLNL
PLNR
PLNR*
SAADL
PLNR*
SAADL
SAADR
RIVL*
SAADR
DVA*
AVHR*
ADFL*
DVA*
ADFL*
AIZL*
AVHL*
DVA*
AVKR
AVKL
AVHL*
ADFR
AIZR*
f
AIZR*
d
PLNR*
AIZL*
SAAVL
SAADR
AWBR*
AIZR*
SAADL
g
SAAVR
SAAVL
SAAVL
PLNL
SAAVR
RMEV
PLNR , RMEV
SMBVL
CELL BODY IN VENTRAL GANGLION
SMBVR
CELL BODY IN VENTRAL GANGLION
POSTERIOR DIRECTED SUB-LATERAL PROCESS
POSTERIOR DIRECTED SUB-LATERAL PROCESS



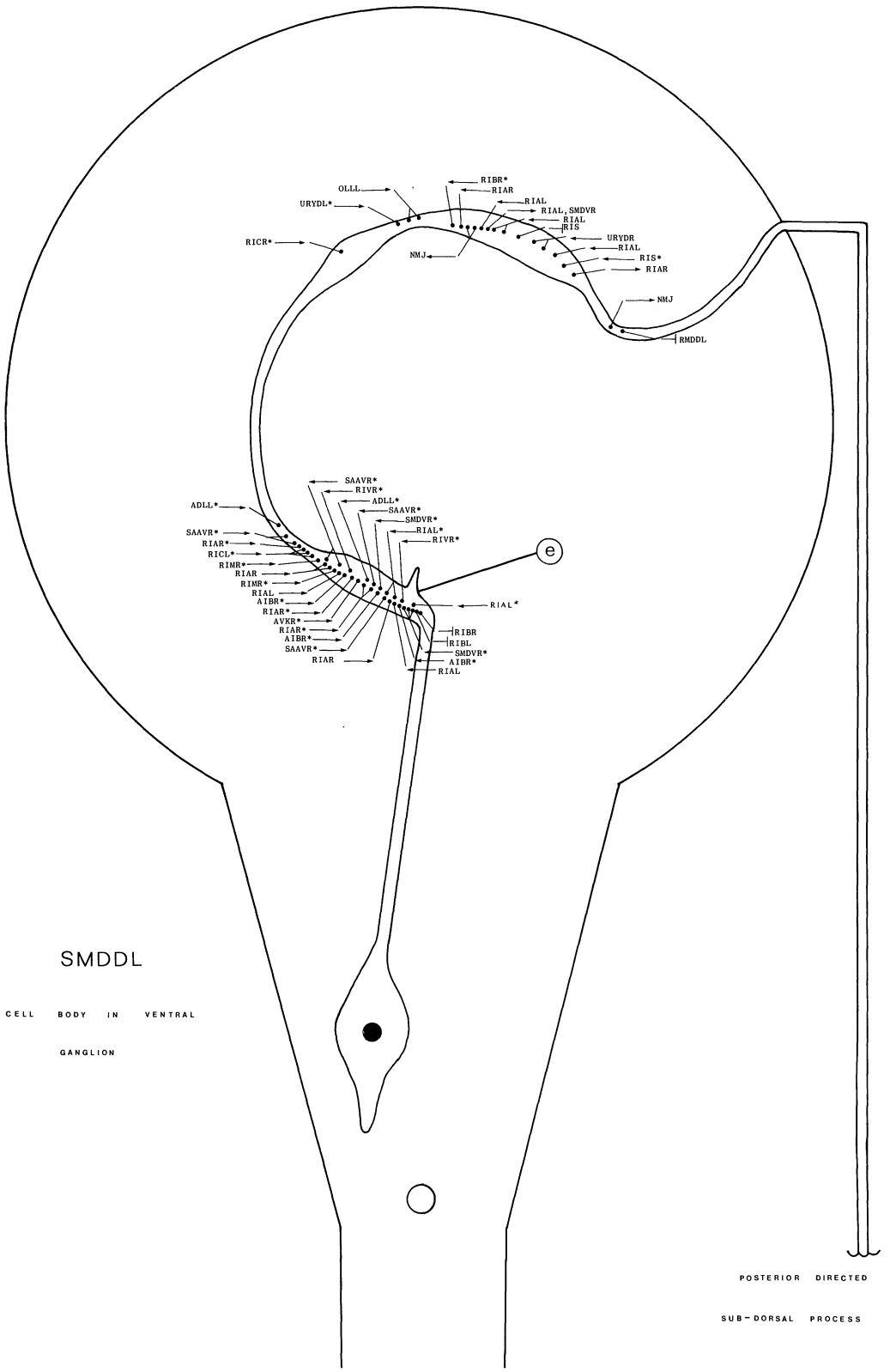
SMB

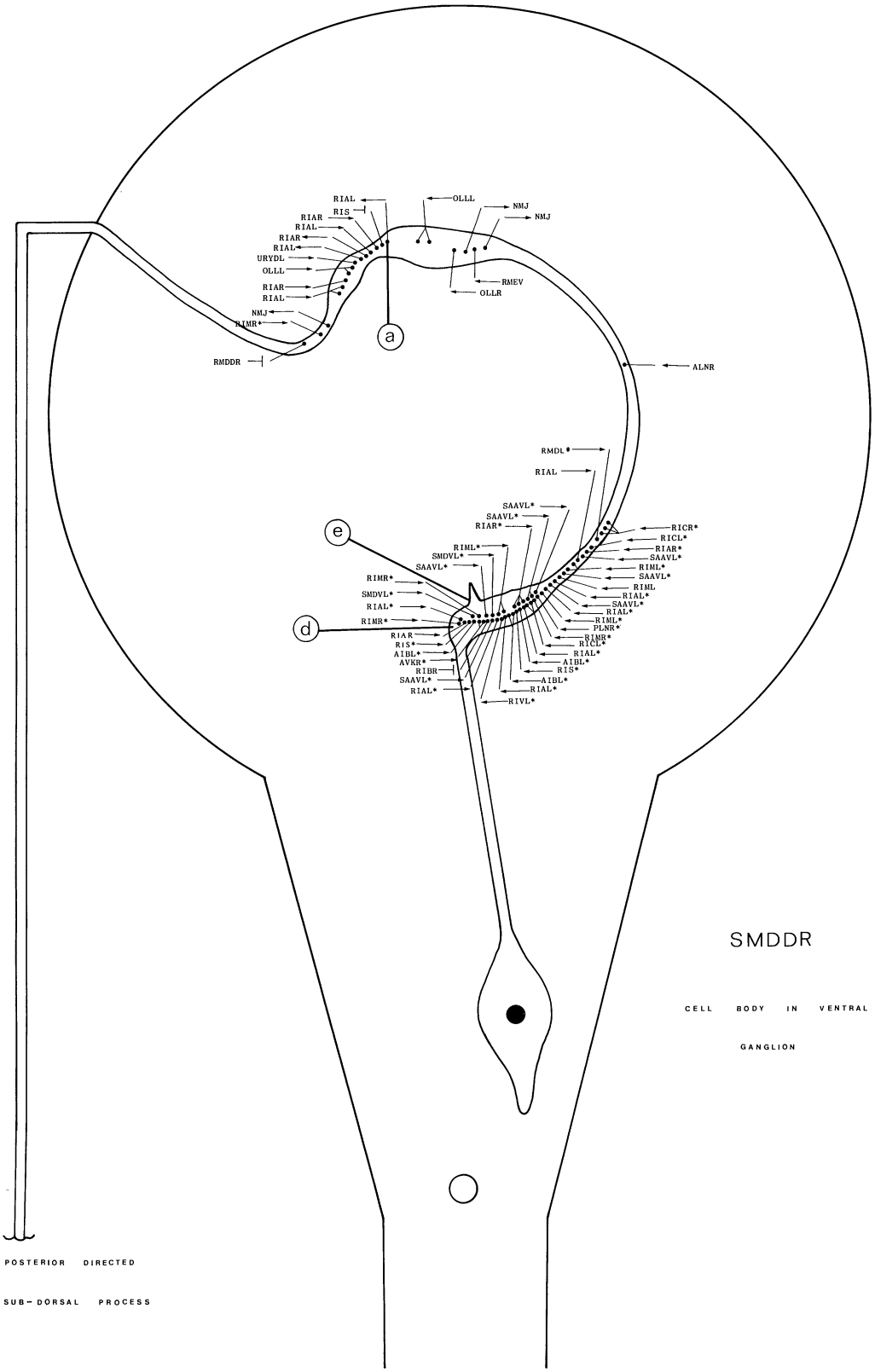
Members: SMBDL, SMBDR, SMBVL, SMBVR.

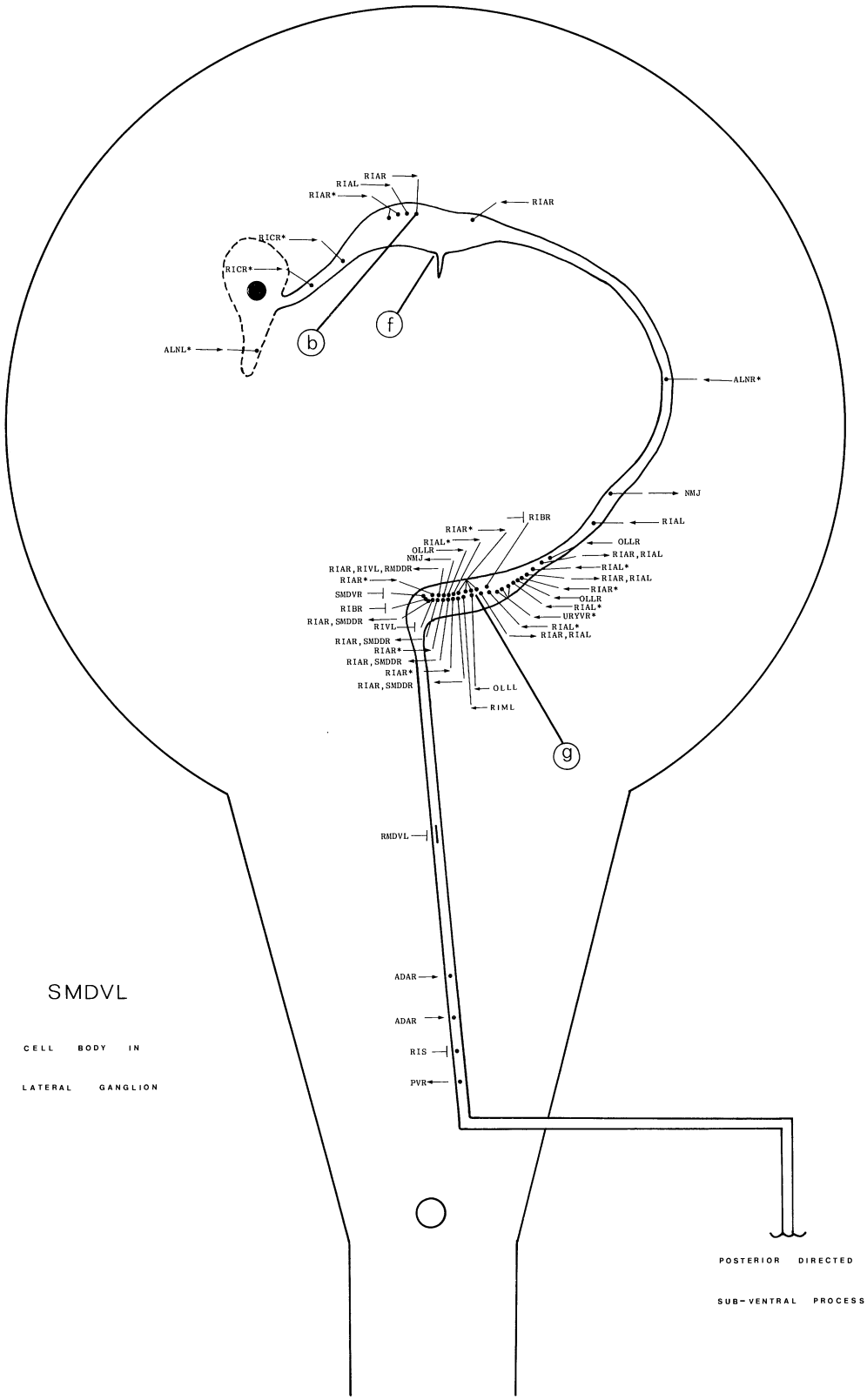
SMB is a set of four motoneurons, which innervate muscles in the head via NMJs in the nerve ring and also send processes posteriorly down the sub-lateral cords. The cell bodies of SMB are situated in the ventral ganglion and send anteriorly directed processes into the nerve ring (h, i) which initially run near the centre of the ring neuropile. When the processes of SMBV reach a sub-dorsal position they loop round and run back on the inside surface of the ring, where they have NMJs before reentering the neuropile of the ventral ganglion. They then leave

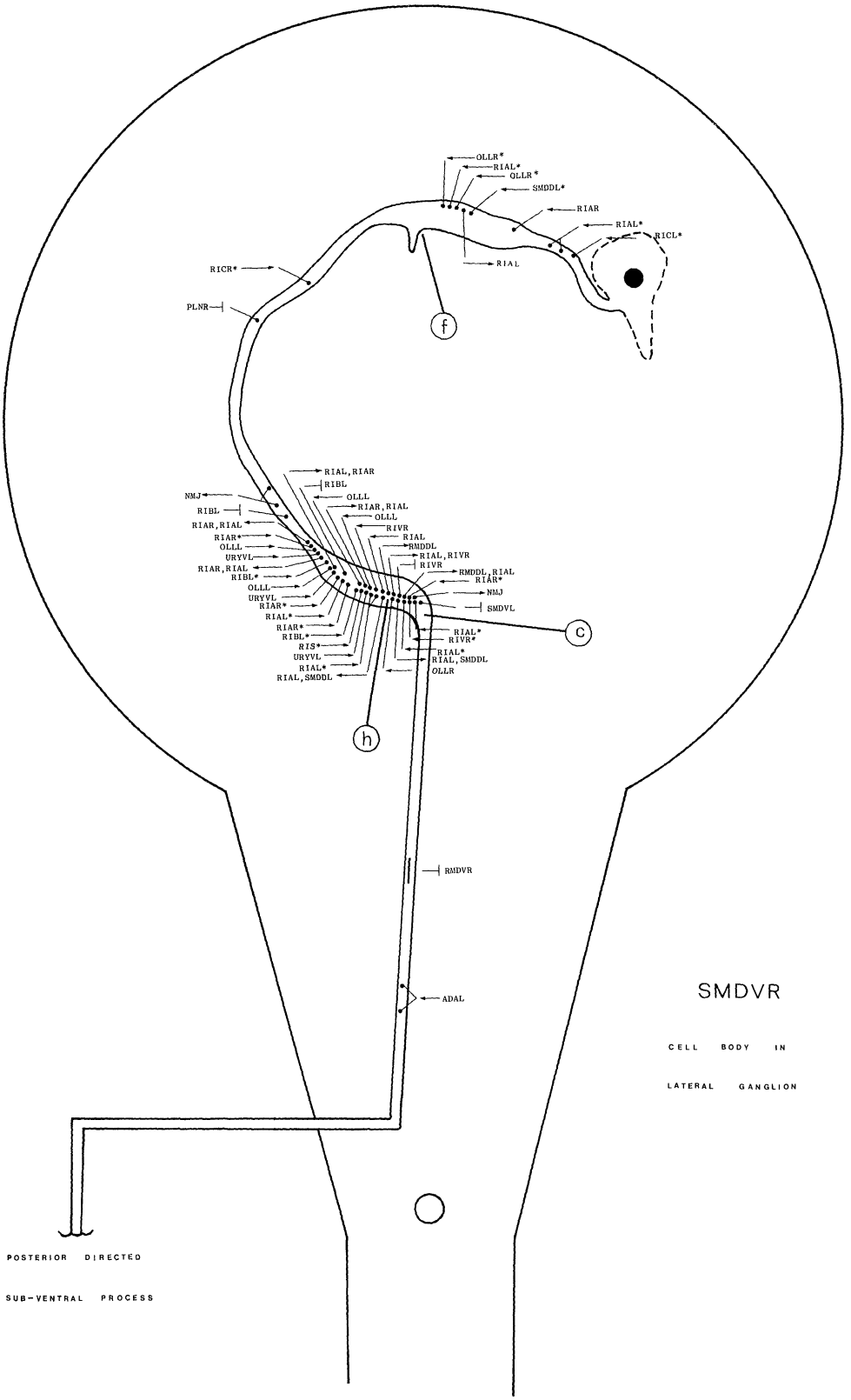
the ventral cord via the amphidial commissures and take up their positions, along with four other processes, in the ventral sub-lateral cords. The SMBD pair run round to the contralateral side of the nerve ring and there move down to the inside surface of the ring, where they have their NMJs. They leave the ring sub-dorsally and enter the dorsal sub-lateral cords along with four other processes. The processes of SMB form striking structures in the neuropile of the ventral ganglion, where they enlarge, flatten and wrap round each other (c). Another striking feature in the same region is formed by the synapses of SMBD onto SAAD; vesicle-filled processes from SMBD poke into the cell bodies of SAAD, where they synapse onto them (d). The NMJs of SMB are situated sub-ventrally and sub-dorsally and are intercepted by dendrites from RME (e). There are marked differences in the synaptic contacts made by SMBD and SMBV. Both have NMJs (b, e), receive their main synaptic input from AIZ (f), and a little from AVH (*b) and DVA, and have gap junctions to AVK (*e). In addition, SMBD alone synapses onto RMED (at dyadic NMJs (e)) and SAAV (a); it receives synaptic input from ALN (*b) and RIC (*b), and has gap junctions to SAAD and RIB. SMBV alone synapses onto RMEV (at dyadic NMJs) and SAAD; it receives synaptic input from PLN (*a) and ADF (*c) and has gap junctions to SAAV (g).

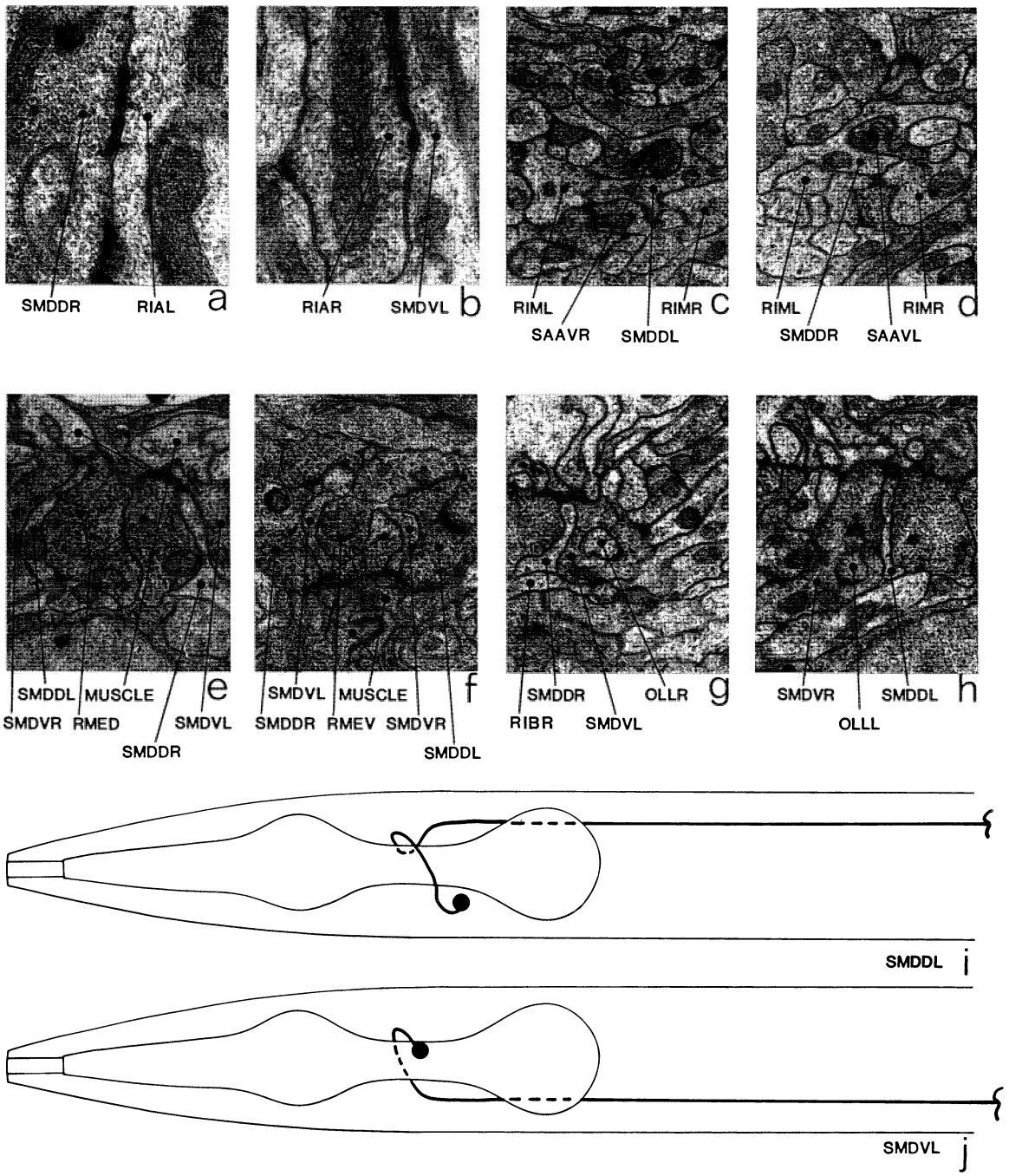
Magnifications: (a, b, f) $\times 25500$, (c, e, g) $\times 12750$, (d) $\times 8500$.


OLLL
URYDL*
RICR*
NMJ
RIBR*
RIAR
RIAL
RIAL, SMDVR
RIAL
RIS
URYDR
RIAL
RIS*
RIAR
NMJ
RMDDL
ADLL*
SAAVR*
RIVR*
ADLL*
SAAVR*
SMDVR*
RIAL*
RIVR*
SAAVR*
RIAR*
RICL*
RIMR*
RIAR
RIMR*
RIAL
AIBR*
RIAR*
AVKR*
RIAR*
AIBR*
SAAVR*
RIAR
e
RIAL*
RIBR
RIBL
SMDVR*
AIBR*
RIAL
SMDDL
CELL BODY IN VENTRAL GANGLION
POSTERIOR DIRECTED SUB-DORSAL PROCESS


RIAL
RIS
RIAR
RIAL
RIAR
RIAL
URYDL
OLLL
RIAR
RIAL
NMJ
RIMR*
RMDDR
OLLL
NMJ
NMJ
RMEV
OLLR
a
ALNR
RMDL*
RIAL
SAAVL*
SAAVL*
RIAR*
e
RIML*
SMDVL*
SAAVL*
RIMR*
SMDVL*
RIAL*
RIMR*
d
RIAR
RIS*
AIBL*
AVKR*
RIBR
SAAVL*
RIAL*
RICR*
RICL*
RIAR*
SAAVL*
RIML*
SAAVL*
RIML
RIAL*
SAAVL*
RIAL*
RIML*
PLNR*
RIMR*
RICL*
RIAL*
AIBL*
RIS*
AIBL*
RIAL*
RIVL*
SMDDR
CELL BODY IN VENTRAL GANGLION
POSTERIOR DIRECTED SUB-DORSAL PROCESS


RIAR
RIAL
RIAR*
RIAR
RICR*
RICR*
b
f
ALNL*
ALNR*
NMJ
RIBR
RIAR*
RIAL
RIAL*
OLLR
OLLR
NMJ
RIAR,RIAL
RIAR,RIVL,RMDDR
RIAL*
RIAR*
RIAR,RIAL
SMDVR
RIAR*
RIBR
OLLR
RIAL*
RIAR,SMDDR
URYVR*
RIVL
RIAL*
RIAR,SMDDR
RIAR,RIAL
RIAR*
RIAR,SMDDR
RIAR*
RIAR,SMDDR
OLLL
RIML
g
RMDVL
ADAR
ADAR
RIS
PVR
SMDVL
CELL BODY IN
LATERAL GANGLION
POSTERIOR DIRECTED
SUB-VENTRAL PROCESS


OLLR*
RIAL*
OLLR*
SMDDL*
RIAR
RIAL*
RICL*
RIAL
RICR*
PLNR
f
RIAL,RIAR
RIBL
NMJ
OLLL
RIBL
RIAR,RIAL
OLLL
RIAR,RIAL
RIVR
RIAR*
RIAL
OLLL
RMDDL
URVVL
RIAL,RIVR
RIAR,RIAL
RIVR
RIBL*
RMDDL,RIAL
OLLL
RIAR*
URYVL
NMJ
RIAR*
SMDVL
RIAL*
RIAR*
RIAL*
RIBL*
RIVR*
RIS*
RIAL*
URVVL
RIAL,SMDDL
RIAL*
OLLR
RIAL,SMDDL
c
h
RMDVR
ADAL
SMDVR
CELL BODY IN LATERAL GANGLION
POSTERIOR DIRECTED SUB-VENTRAL PROCESS



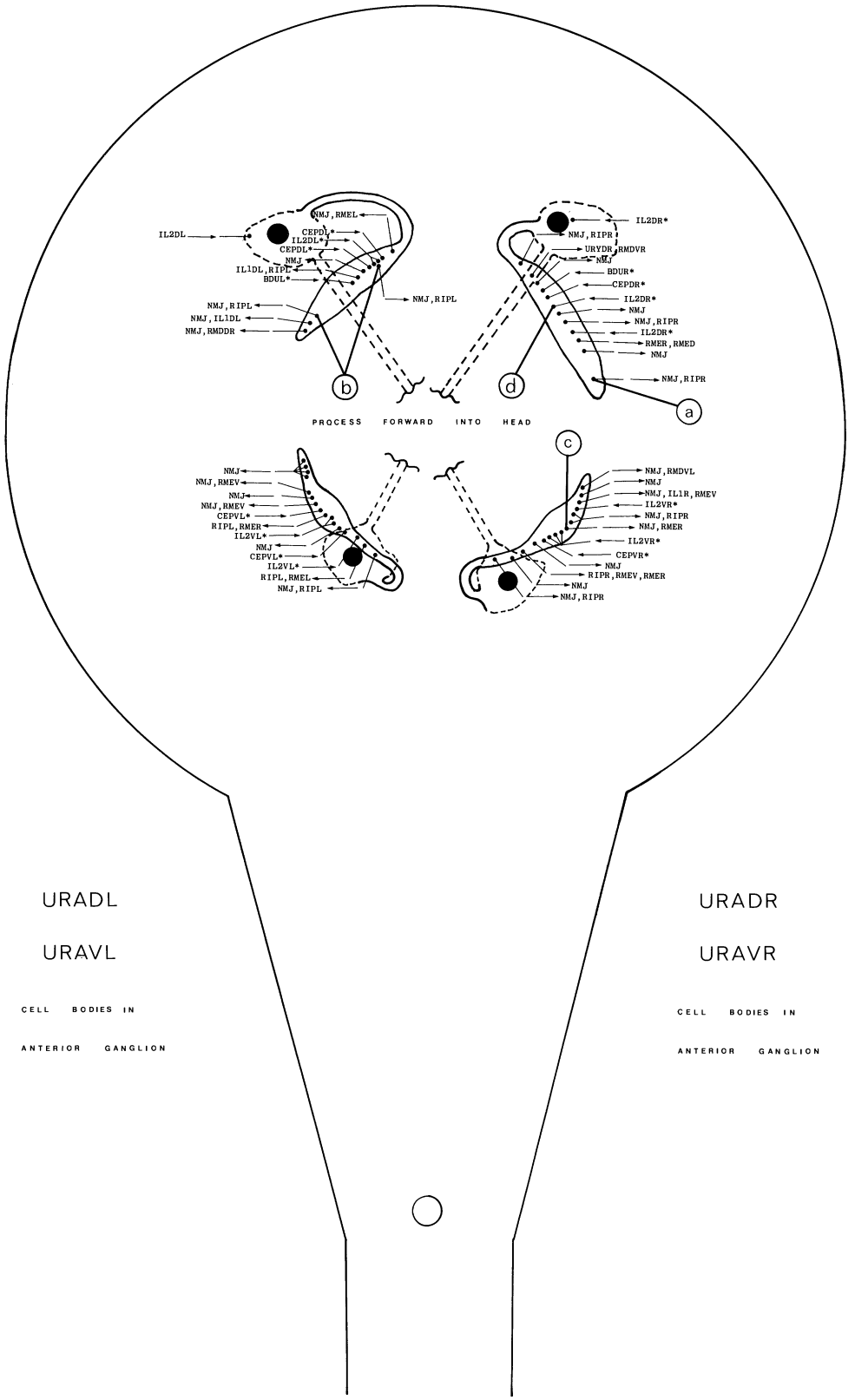
SMD

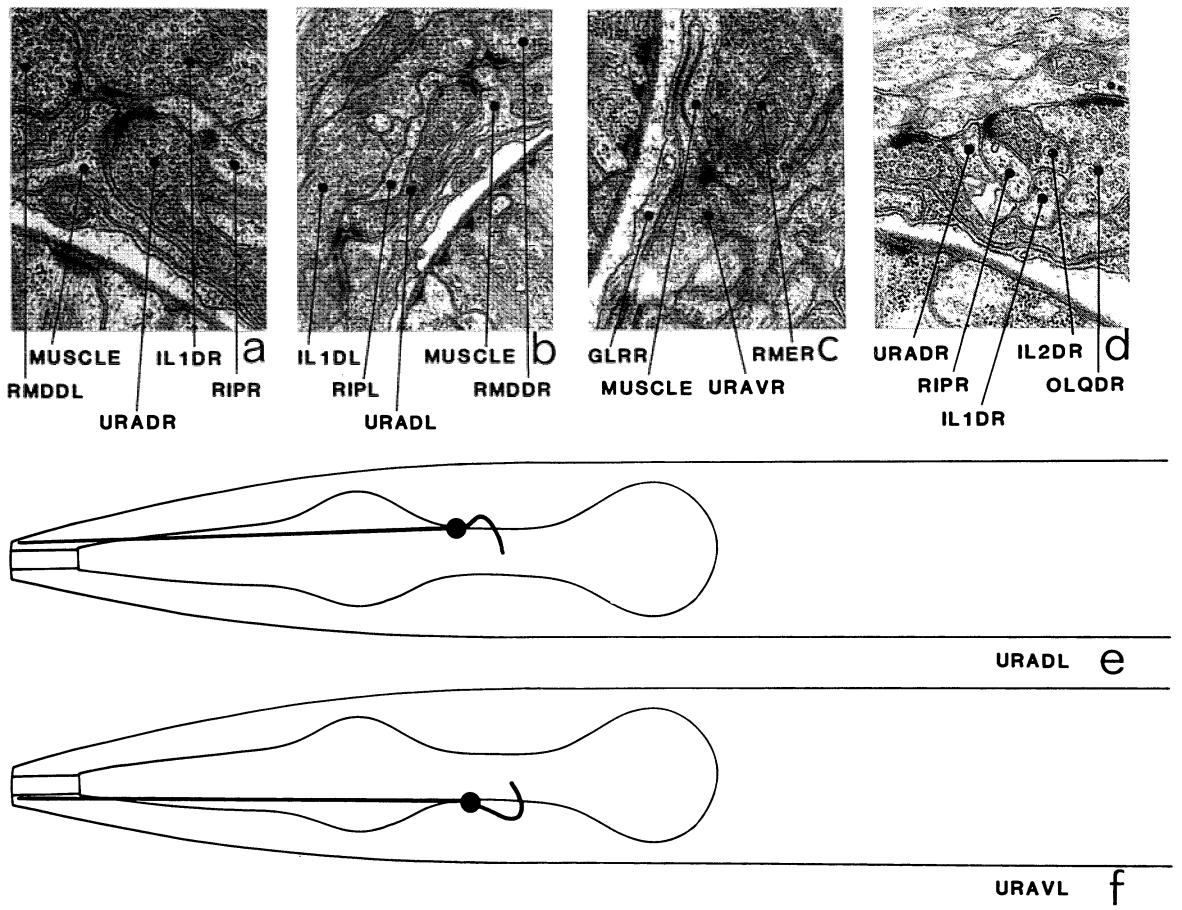
Members: SMDDL, SMDDR, SMDVL, SMDVR.

SMD is a set of four motoneurons, which innervate muscles in the head via NMJs in the nerve ring and also send processes posteriorly down the sub-lateral cords. The cell bodies of SMDV are situated sub-dorsally, close to the neuropile of the nerve ring (j). Processes enter the ring sub-dorsally from the cell bodies and move over to the contralateral side, running near the centre of the neuropile; they then enter the ventral cord. They leave the cord via the

amphidial commissures and take up their sub-ventral positions along with the other processes of the sub-cords. The cell bodies of SMDD are situated in the ventral ganglion and send anteriorly directed processes into the nerve ring (i). These processes run round the ring, near the centre of the neuropile, and leave at contralateral sub-dorsal positions to enter the sub-cords along with the other processes of the dorsal sub-cords. The dorsal processes of SMDV and the ventral processes of SMDD are large and have an irregular shape, often wrapping around the processes of SAA (c, d), with which they are closely associated. The NMJs of SMD are situated near the ventral (SMDV) and dorsal (SMDD) mid-lines at the anterior regions of the inner surface of the nerve ring and, together with RME NMJs, form distinctive structures in these regions (e, f and figure 14). SMD neurons send unusual small processes into the regions of the NMJs of their dorso-ventral symmetric partners (e–h), which have terminal electron-dense regions that look similar to presynaptic specializations. No synaptic vesicles are seen in these regions, however, so it seems unlikely that these processes are presynaptic. Their disposition suggests that they could be dendrites receiving synaptic input from RME and the symmetrically opposite members of their own class. The main synaptic outputs of SMD are to muscles (e, f, g, h) and RIA (a). The main synaptic inputs are from RIA (b), OLL (g, h), URY (*a), RIM (*e) and RIC (*b); there is probably also some synaptic input from RIV (*d) and RME (*d). There are gap junctions to RMD, RIS, RIB, RIV (SMDV only) and itself.

Magnifications: (a, b) $\times 25500$, (c–h) $\times 12750$.


NMJ,RMEL
IL2DL
CEPDL*
IL2DL*
CEPDL*
NMJ
IL1DL,RIPL
BDUL*
NMJ,RIPL
NMJ,RIPL
NMJ,IL1DL
NMJ,RMDDR
b
IL2DR*
NMJ,RIPR
URYDR,RMDVR
NMJ
BDUR*
CEPDR*
IL2DR*
NMJ
NMJ,RIPR
IL2DR*
RMER,RMED
NMJ
NMJ,RIPR
d
a
PROCESS FORWARD INTO HEAD
c
NMJ
NMJ,RMEV
NMJ
NMJ,RMEV
CEPVL*
RIPL,RMER
IL2VL*
NMJ
CEPVL*
IL2VL*
RIPL,RMEL
NMJ,RIPL
NMJ,RMDVL
NMJ
NMJ,IL1R,RMEV
IL2VR*
NMJ,RIPR
NMJ,RMER
IL2VR*
CEPVR*
NMJ
RIPR,RMEV,RMER
NMJ
NMJ,RIPR
URADL
URAVL
CELL BODIES IN
ANTERIOR GANGLION
URADR
URAVR
CELL BODIES IN
ANTERIOR GANGLION

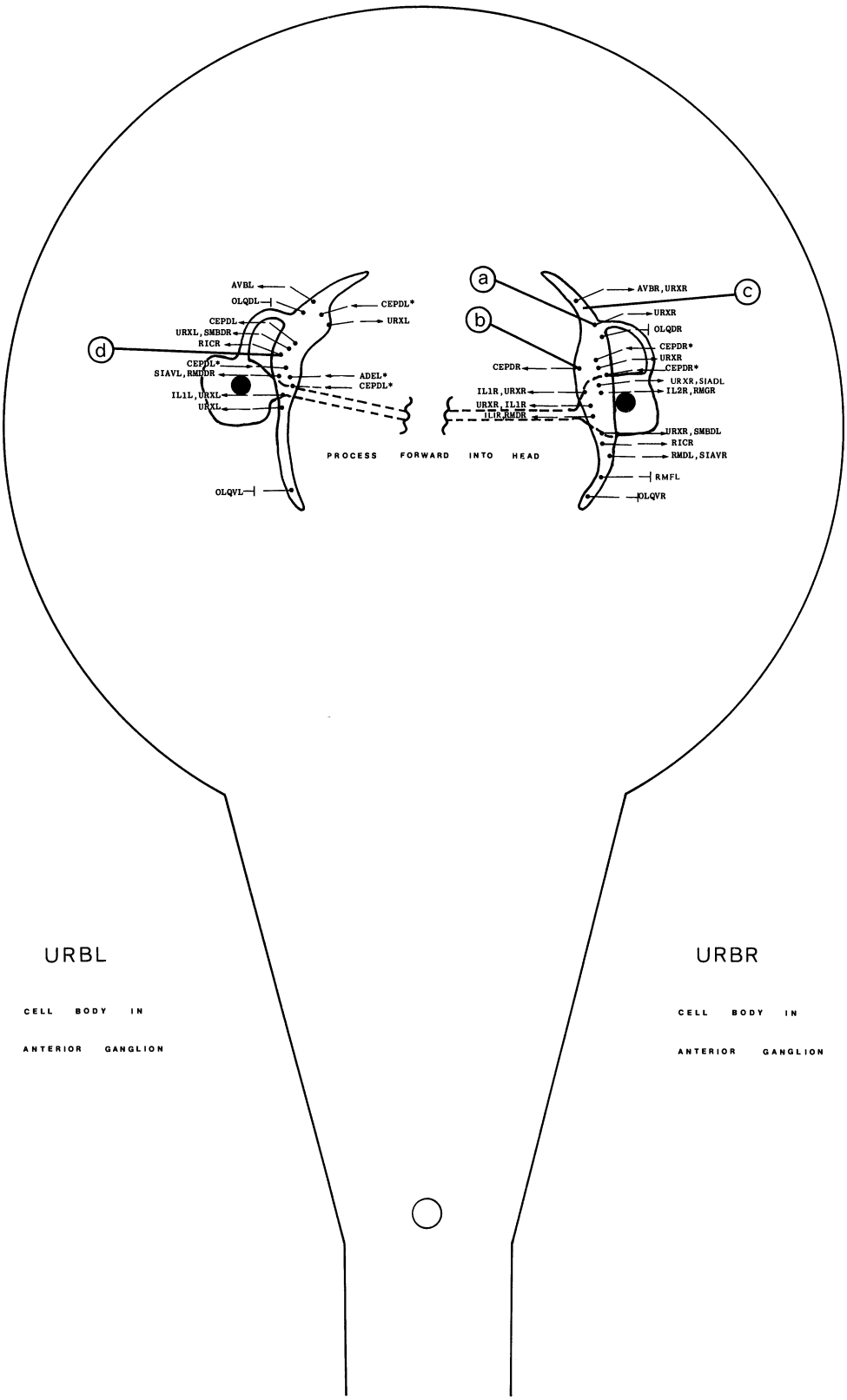


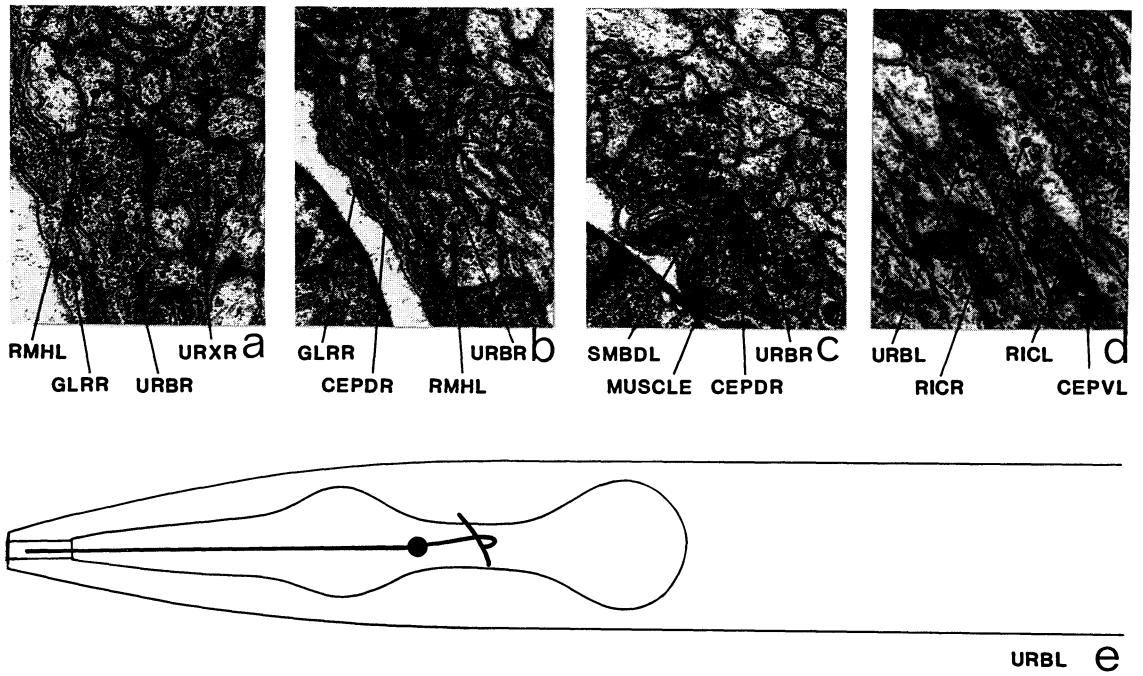
URA

Members: URADL, URADR, URAVL, URAVR.

URA is a set of four motoneurons, which innervate muscles in the head via NMJs in the nerve ring. The cell bodies are situated anteriorly to the neuropile of the nerve ring. Anteriorly directed processes emanate from the cell bodies and run in four of the six labial process bundles. These processes do not have a ciliated ending; they peter out at about the level of the junction of the pharynx and the buccal cavity. Posteriorly directed processes from the cell bodies rejoin the process bundles and run along the outside of the ring. The bundles then turn and run anteriorly, near the inside surface of the ring, until the fibres disperse in the anterior regions of the ring. Processes from URA run along the inner surface and anterior regions of the ring neuropile and terminate laterally. URA forms distinctive NMJs in the anterior regions of the ring and, together with RIP, IL1 and RMD, makes up characteristic synaptic complexes in these regions (a, b). NMJs are nearly always adjacent to the process of an RIP cell (a, b). This represents the sole synaptic output except for a few possible synapses to RME at an NMJ region (c). The main synaptic input is from IL2 (d) and CEP.

Magnifications: (a, c, d) ×25500, (b) ×12750.


a
b
c
d
AVBL
OLQDL
CEPDL*
URXL
CEPDL
URXL,SMBDR
RICR
CEPDL*
SIAVL,RMDDR
ADEL*
CEPDL*
IL1L,URXL
URXL
OLQVL
PROCESS FORWARD INTO HEAD
AVBR,URXR
URXR
OLQDR
CEPDR*
URXR
CEPDR*
CEPDR
URXR,SIADL
IL1R,URXR
IL2R,RMGR
URXR,IL1R
IL1R,RMDR
URXR,SMBDL
RICR
RMDL,SIAVR
RMFL
OLQVR
URBL
CELL BODY IN ANTERIOR GANGLION
URBR
CELL BODY IN ANTERIOR GANGLION

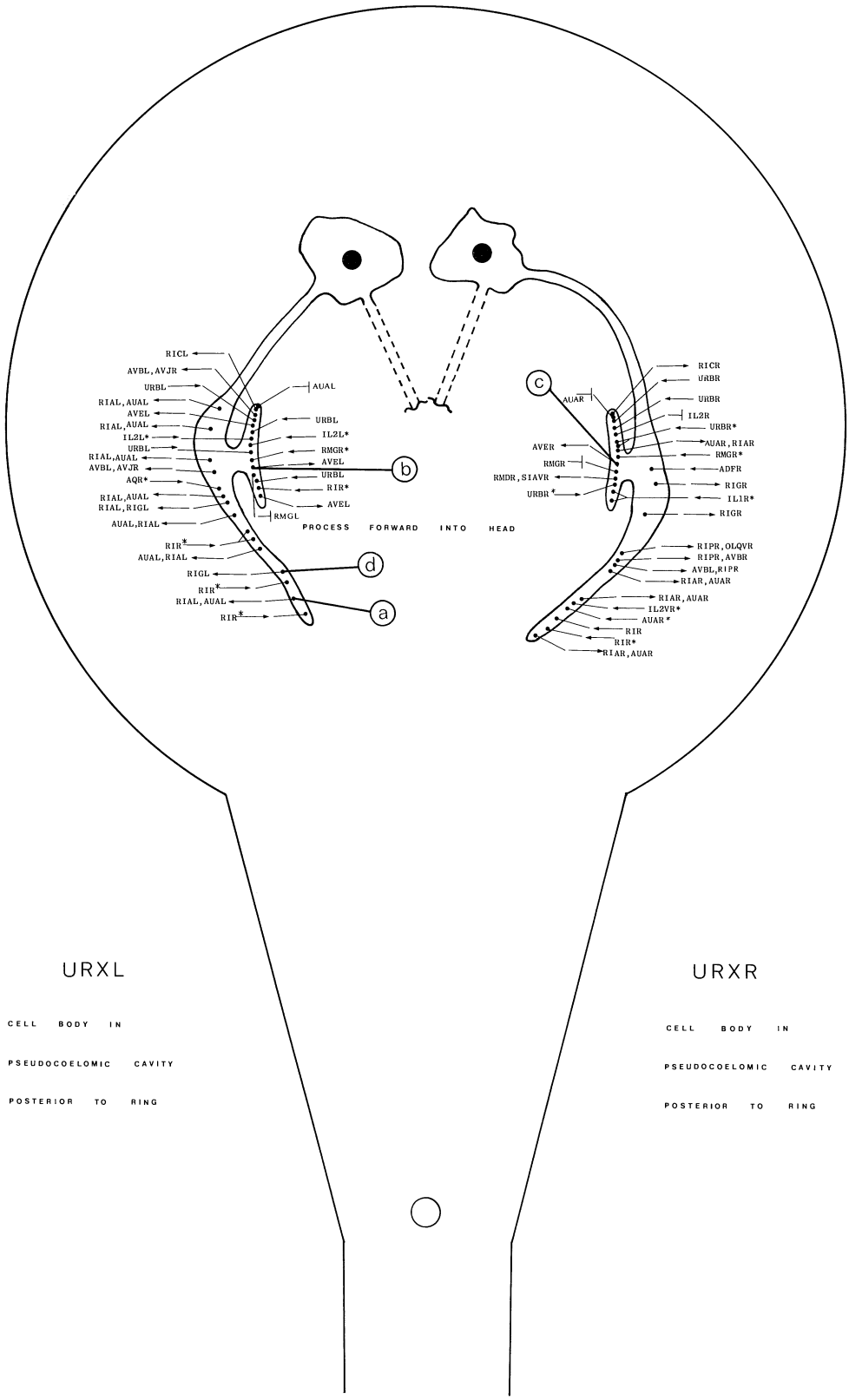


URB

Members: URBL, URBR.

URB is a set of two interneurons with cell bodies situated laterally, anteriorly to the nerve ring. Processes directed anteriorly from the cell bodies run up in the lateral process bundles. These processes peter out, with no terminal specializations, at about the level of the junction of the buccal cavity and the pharynx. The posterior branches from the cell bodies run along the outside of the nerve ring and then turn and run anteriorly and ventrally, near the inner surface of the nerve ring, eventually ending sub-ventrally. URB processes partly wrap round those of SMB (c) sub-dorsally in a characteristic manner. The main synaptic output is to URX (a), CEP (b), RIC (d) and IL1; there is some reciprocal synaptic input from CEP. There are gap junctions to OLQ (*e) at the distal ends of the processes in the ring.

Magnifications: (a, d) ×25500, (b, c) ×12750.

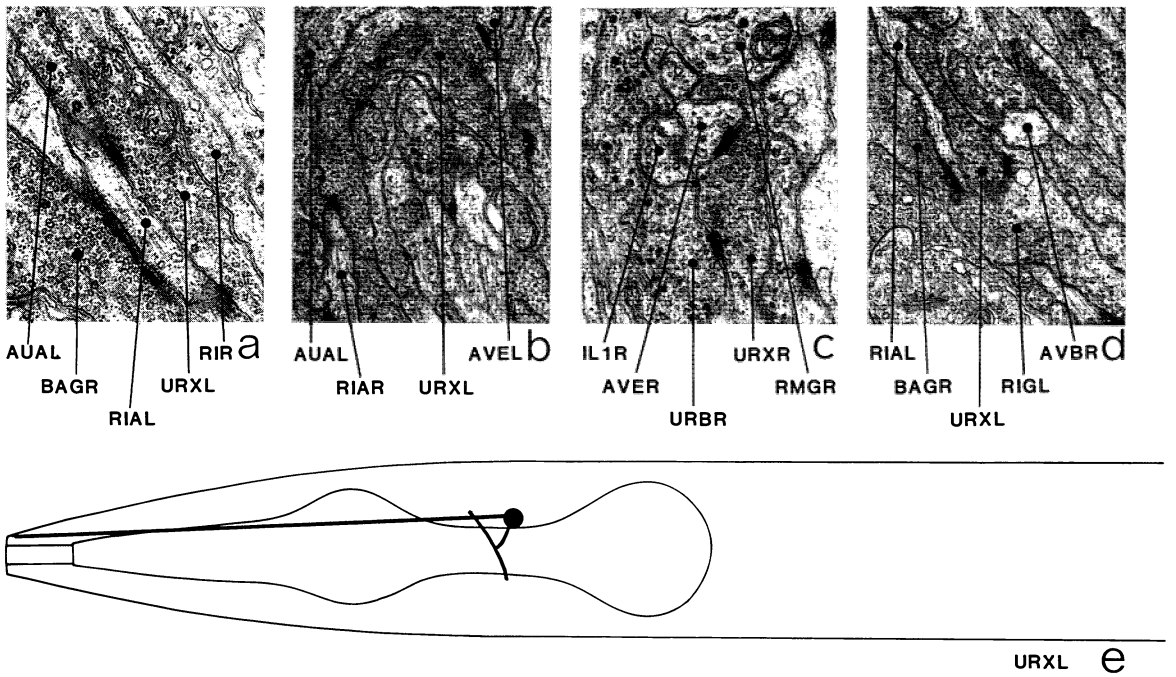


URXL

CELL BODY IN PSEUDOCOELOMIC CAVITY POSTERIOR TO RING

URXR

CELL BODY IN PSEUDOCOELOMIC CAVITY POSTERIOR TO RING

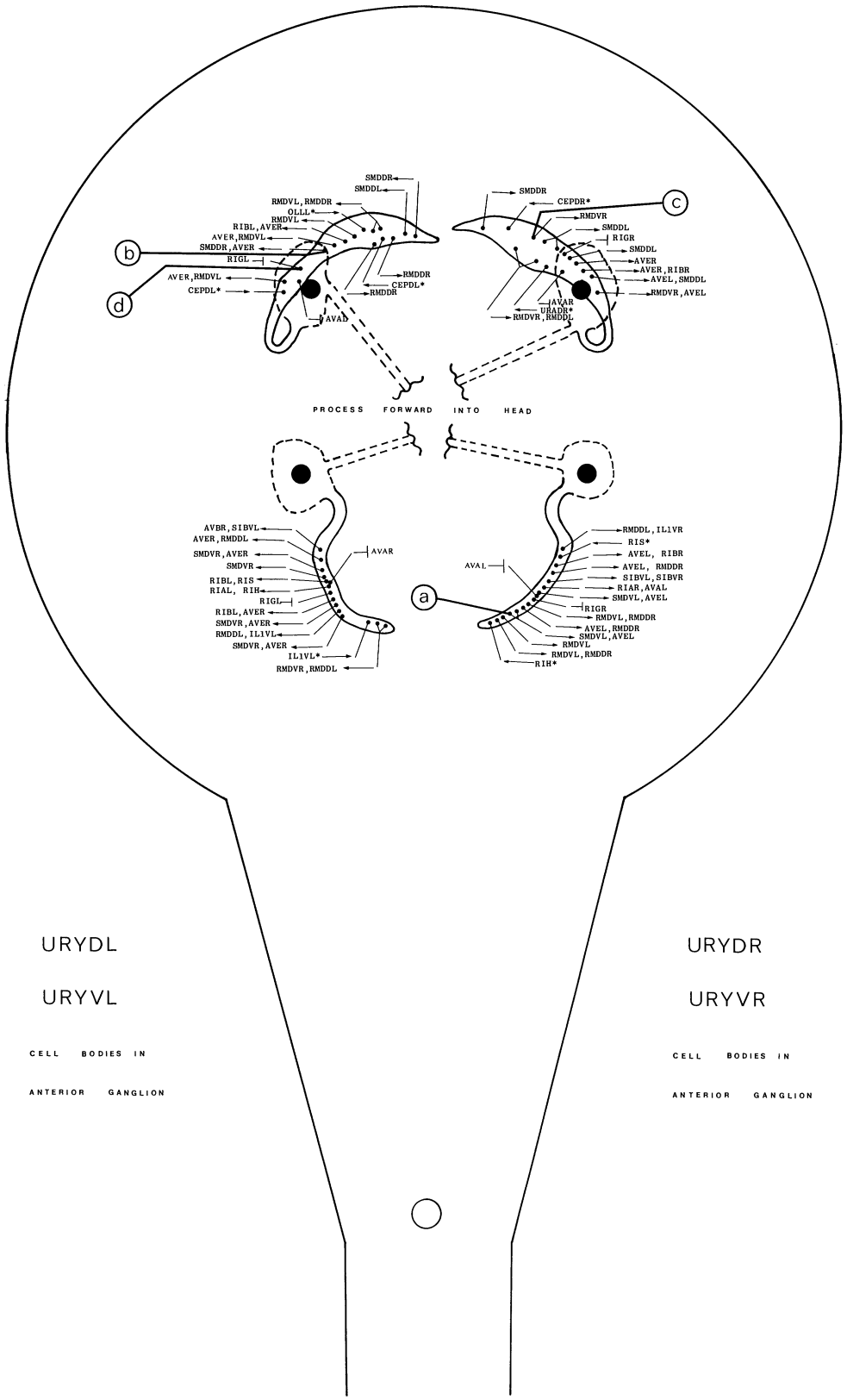


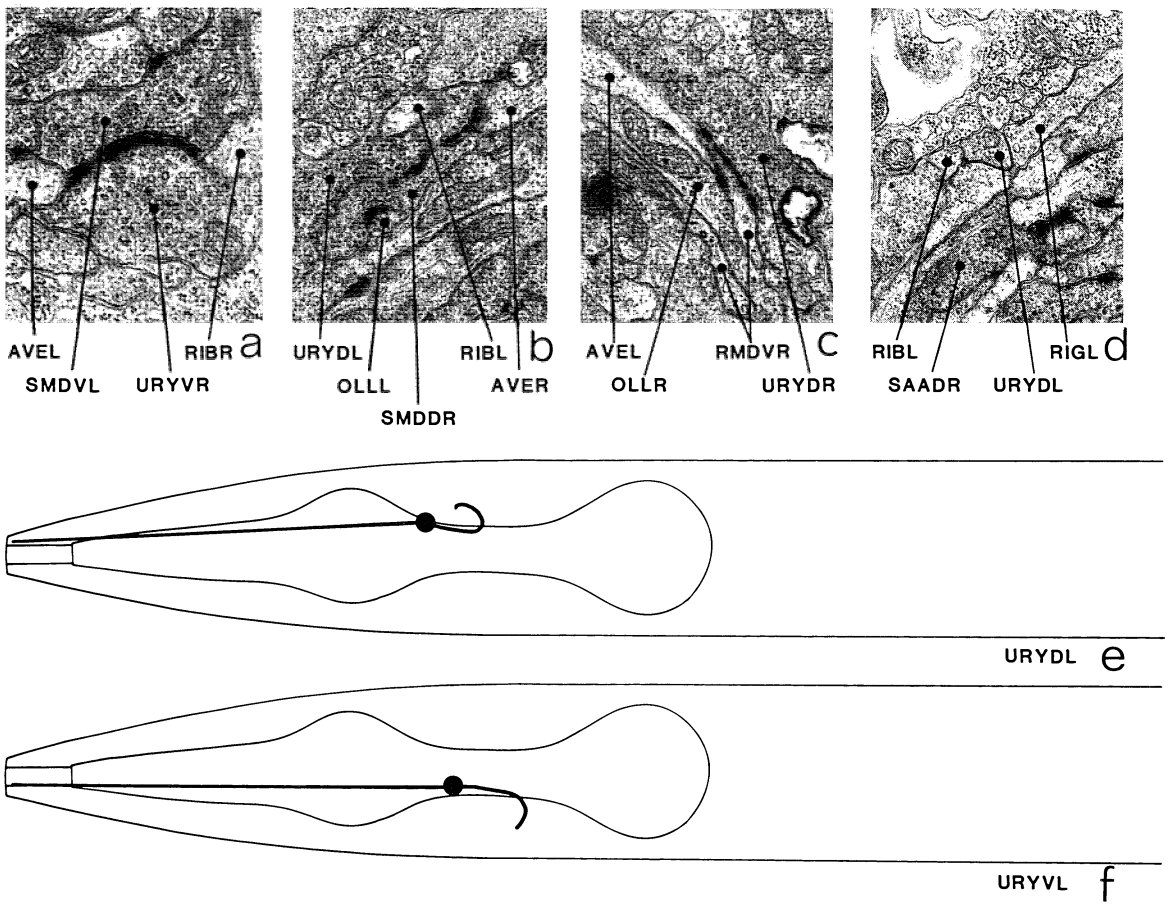
URX

Members: URXL, URXR.

URX is a set of two neurons with cell bodies that are situated sub-dorsally in the pseudocoelomic cavity just posterior to the ring neuropile. Processes project anteriorly from the cell bodies into the sub-dorsal labial process bundles and have specialized, flattened but non-ciliated endings associated with the dorsal inner labial sensilla (figure 1). A posteriorly directed process from the cell bodies loops round the ring, enters it sub-dorsally and then runs ventrally round the ring near the outside surface, ending sub-ventrally. Short branches project laterally into the regions of neuropile near the inner surface (b). The main synaptic output is to RIA and AUA (a) via exclusively dyadic synapses, to AVE on the lateral branches (b, c), to RIG (d), AVB and RIC. The main synaptic input is from URB (c) and RIR (*a). There are gap junctions to AUA, RMG and IL2.

Magnifications: (a, c) $\times 25500$, (b, d) $\times 12750$.


SMDDR
SMDDL
RMDVL,RMDDR
OLLL*
RMDVL
RIBL,AVER
AVER,RMDVL
SMDDR,AVER
RIGL
AVER,RMDVL
CEPDL*
RMDDR
CEPDL*
RMDDR
AVAD
b
d
SMDDR
CEPDR*
RMDVR
SMDDL
RIGR
SMDDL
AVER
AVER,RIBR
AVEL,SMDDL
RMDVR,AVEL
AVAR
URADR*
RMDVR,RMDDL
c
PROCESS FORWARD INTO HEAD
AVBR,SIBVL
AVER,RMDDL
SMDVR,AVER
SMDVR
RIBL,RIS
RIAL, RIH
RIGL
RIBL,AVER
SMDVR,AVER
RMDDL,IL1VL
SMDVR,AVER
IL1VL*
RMDVR,RMDDL
AVAR
AVAL
a
RMDDL,IL1VR
RIS*
AVEL, RIBR
AVEL, RMDDR
SIBVL,SIBVR
RIAR,AVAL
SMDVL,AVEL
RIGR
RMDVL,RMDDR
AVEL,RMDDR
SMDVL,AVEL
RMDVL
RMDVL,RMDDR
RIH*
URYDL
URYVL
CELL BODIES IN
ANTERIOR GANGLION
URYDR
URYVR
CELL BODIES IN
ANTERIOR GANGLION

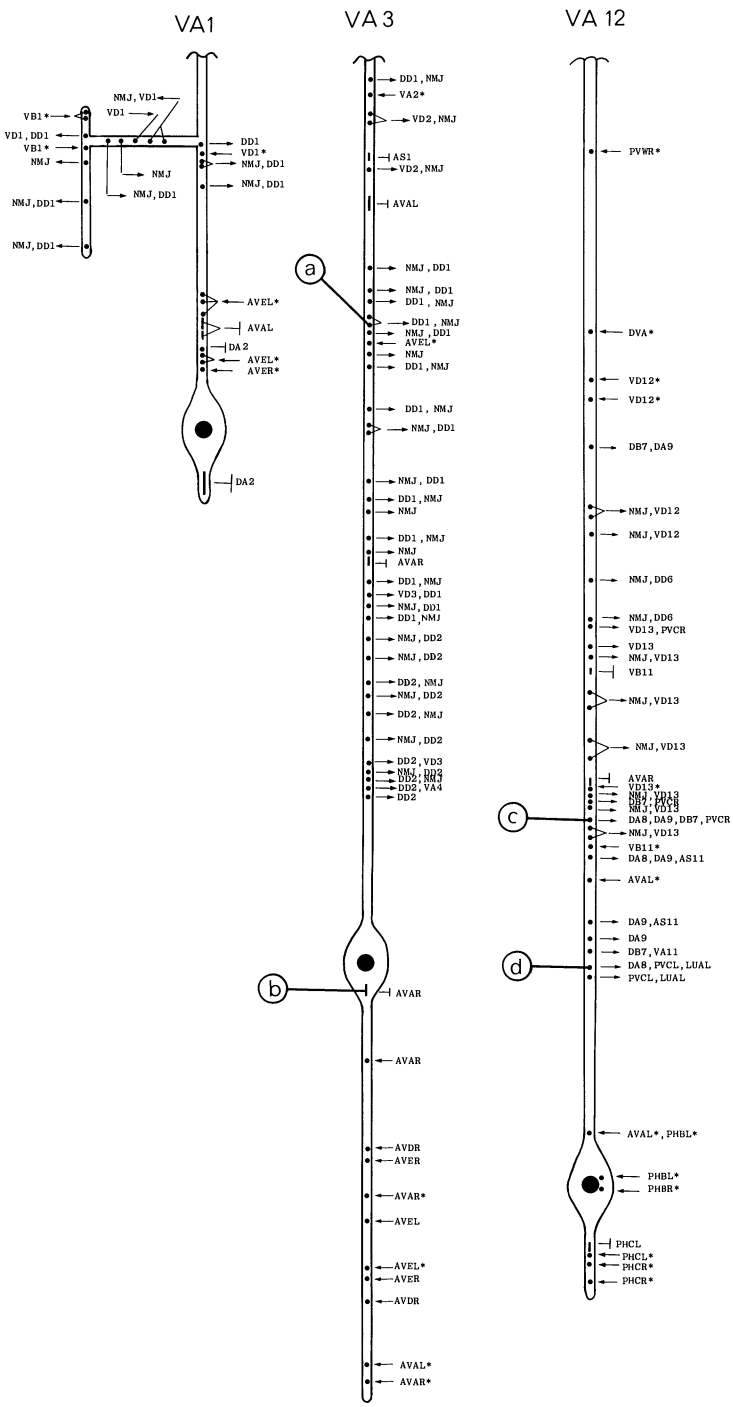


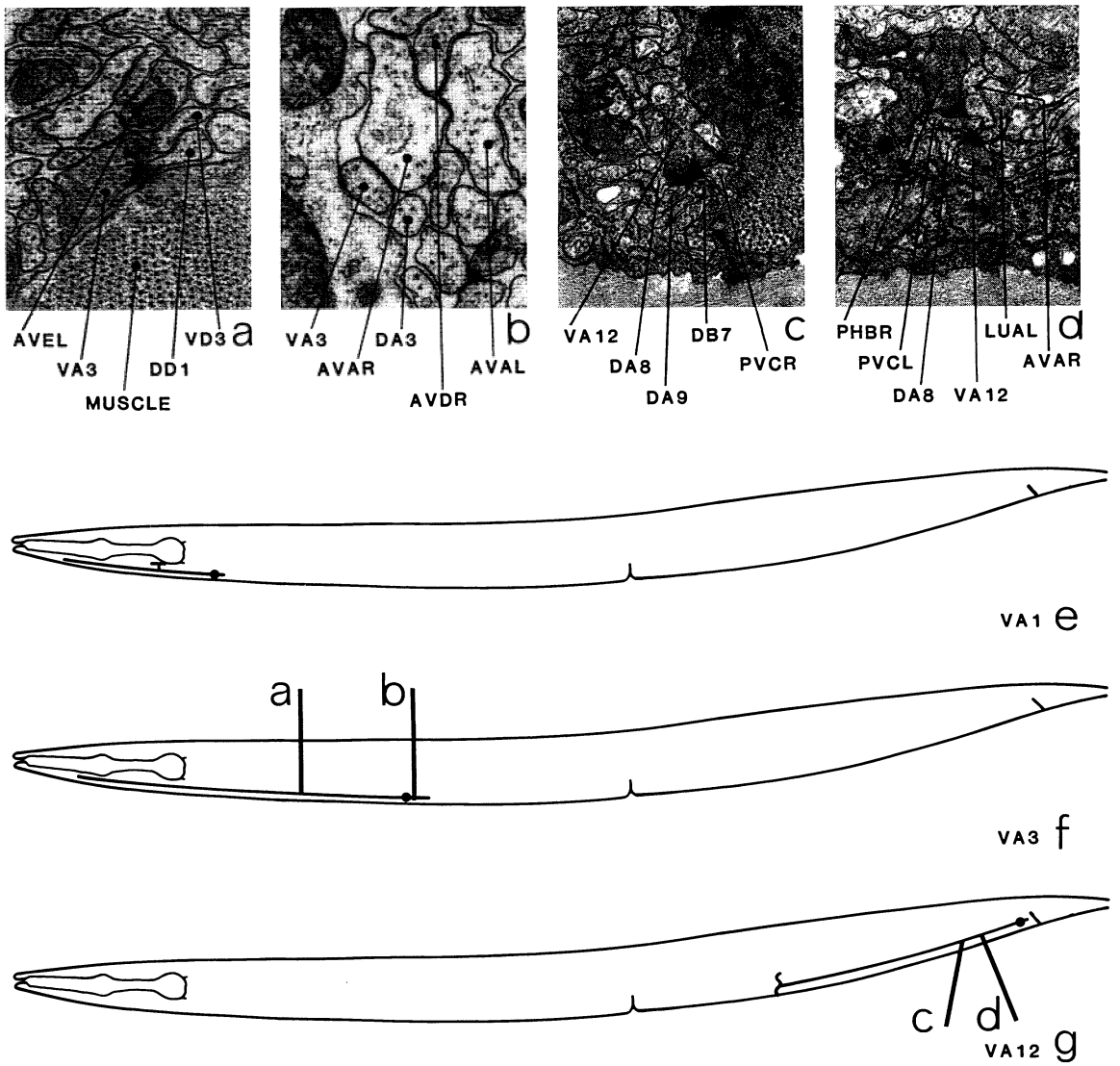
URY

Members: URYDL, URYDR, URYVL, URYVR.

URY is a set of four neurons with cell bodies situated anterior to the nerve ring. Processes project anteriorly from the cell bodies into the two sub-dorsal and the two sub-ventral labial process bundles. These processes enlarge and flatten at their endings (which are not ciliated), at which point they are closely apposed to the inner labial and the outer labial sheath cells (figure 1). A posteriorly directed branch from the sub-dorsal cell bodies forms a complete loop round the underside of the ring and then across to a point where it meets up with itself; it then runs dorsally round the ring near the outside surface. The sub-ventral cells are similar except that they do not loop round the ring but briefly enter the middle of the ring neuropile before returning to the outside regions of the neuropile and running ventrally. When the processes of the URY neurons run round the ring, they are in close association with the processes of RIB (b). The main synaptic output is to SMD via large monadic synapses (a), RMD, usually in association with AVE at dyadic synapses (b, c) and possibly also RIB. There are gap junctions to RIG (d) and AVA.

Magnifications: (a) ×25500, (b–d) ×12750.


VA1
VA 3
VA 12
NMJ, VD1
VB1*
VD1
VD1, DD1
VB1*
NMJ
NMJ, DD1
NMJ, DD1
NMJ
NMJ, DD1
DD1
VD1*
NMJ, DD1
NMJ, DD1
AVEL*
AVAL
DA 2
AVEL*
AVER*
DA2
a
b
DD1, NMJ
VA2*
VD2, NMJ
AS1
VD2, NMJ
AVAL
NMJ, DD1
NMJ, DD1
DD1, NMJ
DD1, NMJ
NMJ, DD1
AVEL*
NMJ
DD1, NMJ
DD1, NMJ
NMJ, DD1
NMJ, DD1
DD1, NMJ
NMJ
DD1, NMJ
NMJ
AVAR
DD1, NMJ
VD3, DD1
NMJ, DD1
DD1, NMJ
NMJ, DD2
NMJ, DD2
DD2, NMJ
NMJ, DD2
DD2, NMJ
NMJ, DD2
DD2, VD3
NMJ, DD2
DD2, NMJ
DD2, VA4
DD2
AVAR
AVAR
AVDR
AVER
AVAR*
AVEL
AVEL*
AVER
AVDR
AVAL*
AVAR*
PVWR*
DVA*
VD12*
VD12*
DB7, DA9
NMJ, VD12
NMJ, VD12
NMJ, DD6
NMJ, DD6
VD13, PVCR
VD13
NMJ, VD13
VB11
NMJ, VD13
NMJ, VD13
c
d
AVAR
VD13*
NMJ, VD13
DB7, PVCR
NMJ, VD13
DA8, DA9, DB7, PVCR
NMJ, VD13
VB11*
DA8, DA9, AS11
AVAL*
DA9, AS11
DA9
DB7, VA11
DA8, PVCL, LUAL
PVCL, LUAL
AVAL*, PHBL*
PHBL*
PHBR*
PHCL
PHCL*
PHCR*
PHCR*



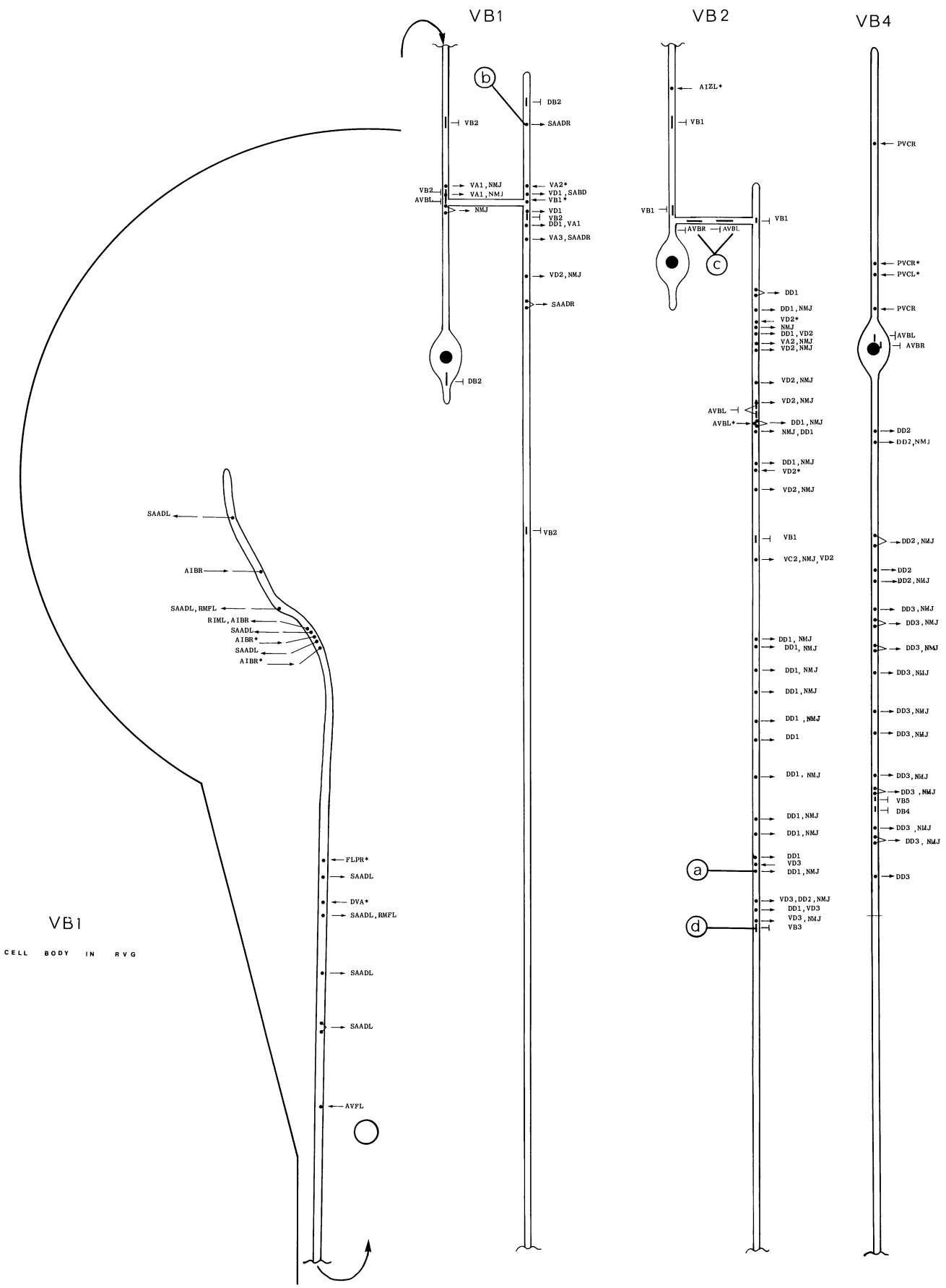
VAn

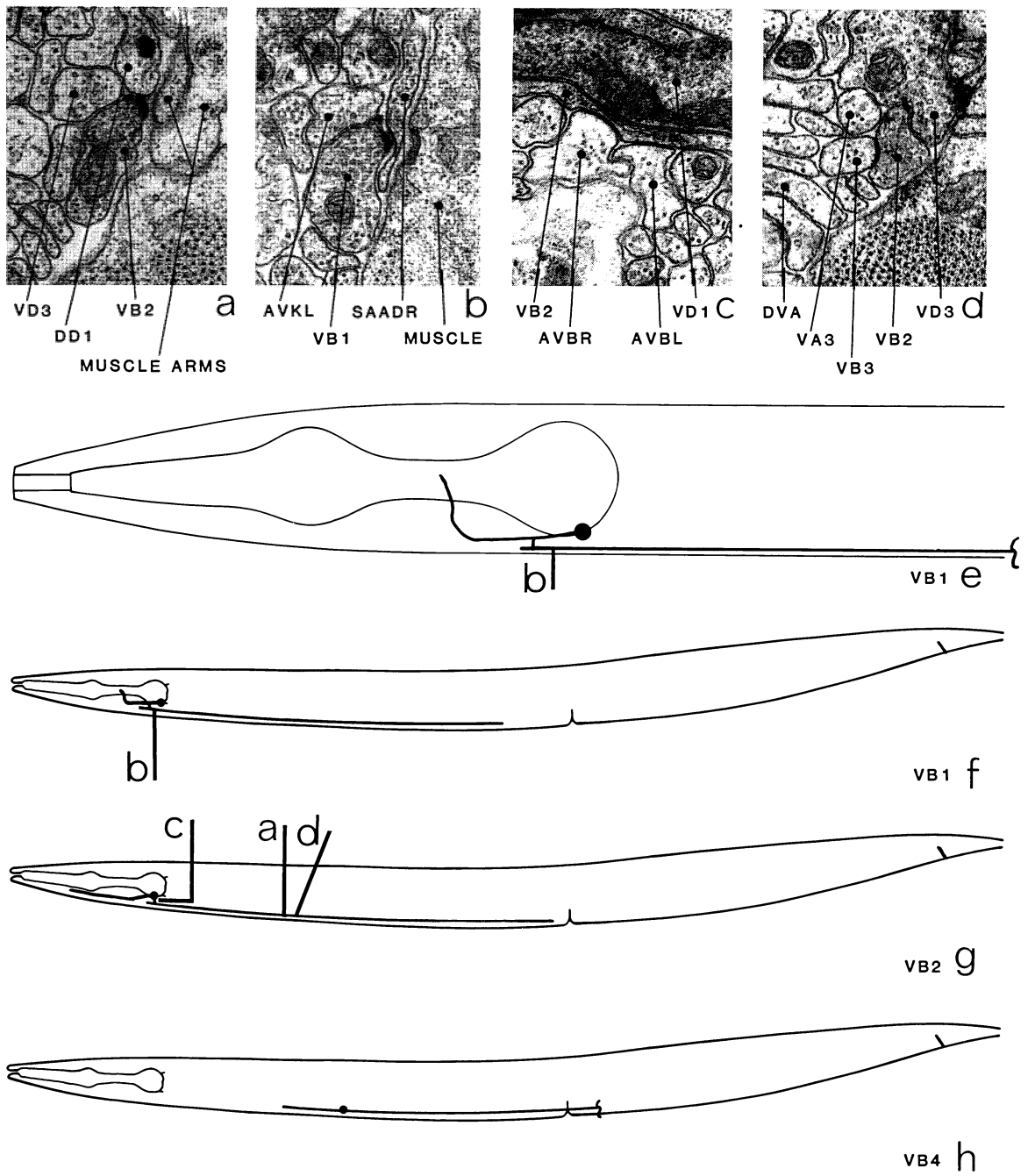
Members: VA1 to VA12.

VAn is a set of twelve motoneurons, distributed along the ventral cord, which innervate ventral body muscles. A typical VAn neuron (e.g. VA3 (f)) has a short, posteriorly directed process that runs in the ventral part of the process bundle. This process is always postsynaptic and receives synaptic input from AVA (*c) and AVD (*a); in addition, VA1 to VA3 receive synaptic input from AVE (*c). There are also gap junctions to AVA (b), ASn (*d) and other VAn neurons, but these may be situated on the anterior as well as the posterior processes. A long, anteriorly directed process leaves the cell body and moves to a position adjacent to the bounding basal lamina on the right-hand side of the cord, in between an adjacent ventral VBn process and a dorsal VDn process (figure 18). VAn processes have NMJs when they are in this position; the NMJs are nearly all dyadic synapses with DDn neurons as the other postsynaptic partner (a). The anterior process of a VAn eventually moves away from the NMJ region, its place being taken by the process of the adjacent anterior VAn. The anterior distal regions of

the VAn processes then run for some distance in the ventral region of the cord before ending with little or no synaptic contacts with other cells. The VAn neurons at either end of the cord (i.e. VA1 and VA12) are somewhat different from the rest. VA1 (e), in common with VB1 and VD1 which are all in the region immediately posterior to the excretory duct, branches and has its NMJs arranged transversely along a confined region along the dorsal surface of the nerve cord. VA12 (g) has a similar morphology to VA2–VA11 but has some additional types of synaptic contact. It receives synaptic input from PHC, PHB, AVA and possibly VD12 and VD13. It has dyadic NMJs with VD12, VD13 and DD6 as the other postsynaptic partners. In addition VA12 also synapses onto DA8 (c), DA9 (c), DB7 (c), AS11, and PVC (d) in various combinations at multiple synapses. There are gap junctions to AVA, PHC and VB11.

Magnifications: (a, c, d) $\times 25500$, (b) $\times 17000$.


VB1
VB2
VB4
b
c
a
d
DB2
SAADR
VB2
VA1, NMJ
VA1, NMJ
NMJ
VA2*
VD1, SABD
VB1*
VD1
VB2
DD1, VA1
VA3, SAADR
VD2, NMJ
SAADR
DB2
VB2
AIZL*
VB1
VB1
AVBR
AVBL
VB1
DD1
DD1, NMJ
VD2*
NMJ
DD1, VD2
VA2, NMJ
VD2, NMJ
VD2, NMJ
VD2, NMJ
AVBL
AVBL*
DD1, NMJ
NMJ, DD1
DD1, NMJ
VD2*
VD2, NMJ
VB1
VC2, NMJ, VD2
DD1, NMJ
DD1, NMJ
DD1, NMJ
DD1, NMJ
DD1, NMJ
DD1
DD1, NMJ
DD1, NMJ
DD1, NMJ
DD1
VD3
DD1, NMJ
VD3, DD2, NMJ
DD1, VD3
VD3, NMJ
VB3
PVCR
PVCR*
PVCL*
PVCR
AVBL
AVBR
DD2
DD2, NMJ
DD2, NMJ
DD2
DD2, NMJ
DD3, NMJ
DD3, NMJ
DD3, NMJ
DD3, NMJ
DD3, NMJ
DD3, NMJ
DD3, NMJ
DD3, NMJ
DD3, NMJ
VB5
DB4
DD3, NMJ
DD3, NMJ
DD3
SAADL
AIBR
SAADL, RMFL
RIML, AIBR
SAADL
AIBR*
SAADL
AIBR*
FLPR*
SAADL
DVA*
SAADL, RMFL
SAADL
SAADL
AVFL
VB1
CELL BODY IN RVG



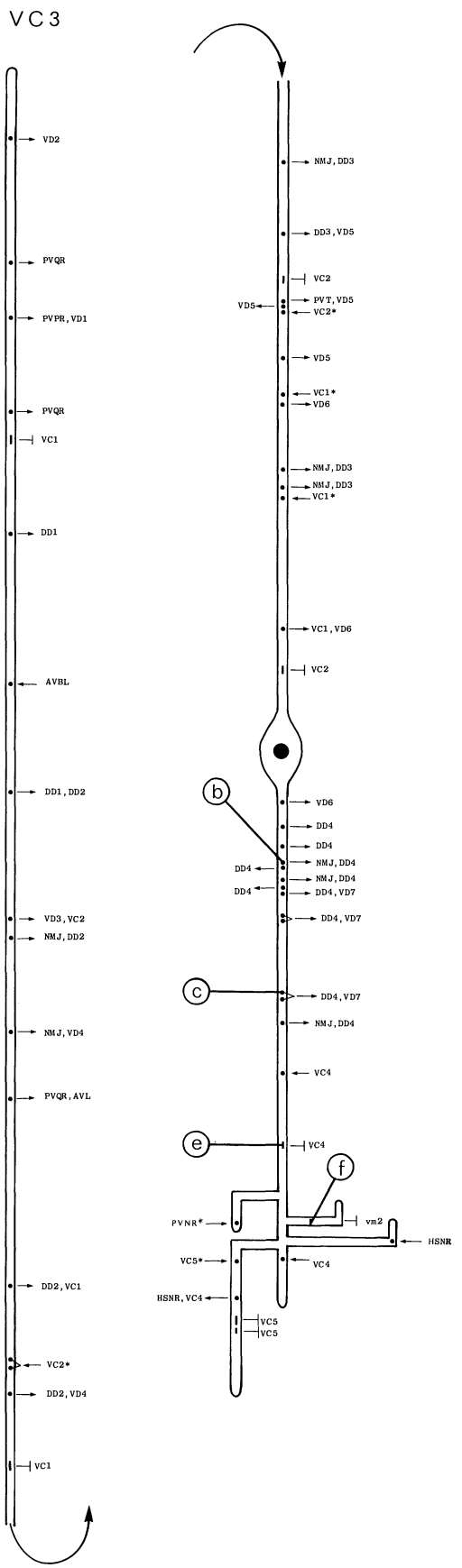
VBn

Members: VB1 to VB11.

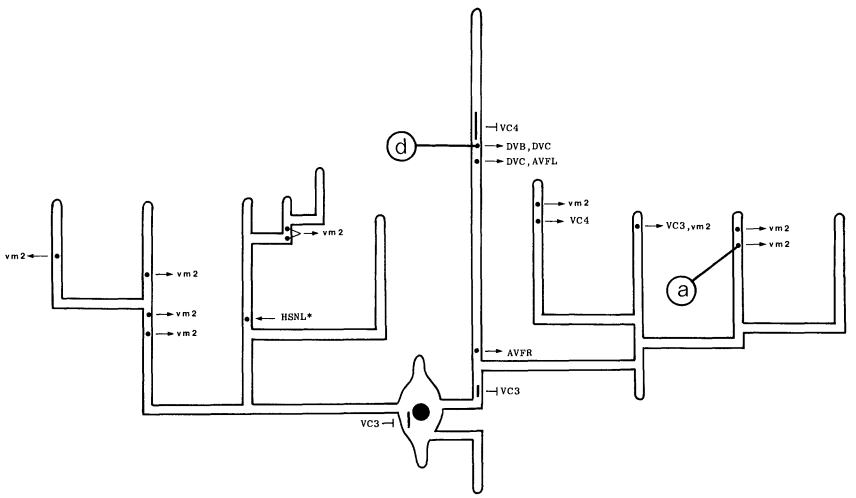
VBn is a set of eleven motoneurons, distributed along the ventral cord, which innervate ventral body muscles. A typical VBn (e.g. VB4 (h)) has a short, anteriorly directed process that runs in the ventral part of the cord. This process is always postsynaptic and receives synaptic input from PVC (except in VB1 and VB2) and occasionally DVA (*d). There are prominent gap junctions to AVB, which are usually (although not exclusively (c)) situated near the cell body. VBn also has gap junctions with other VBns (d) and DBns; these can be situated

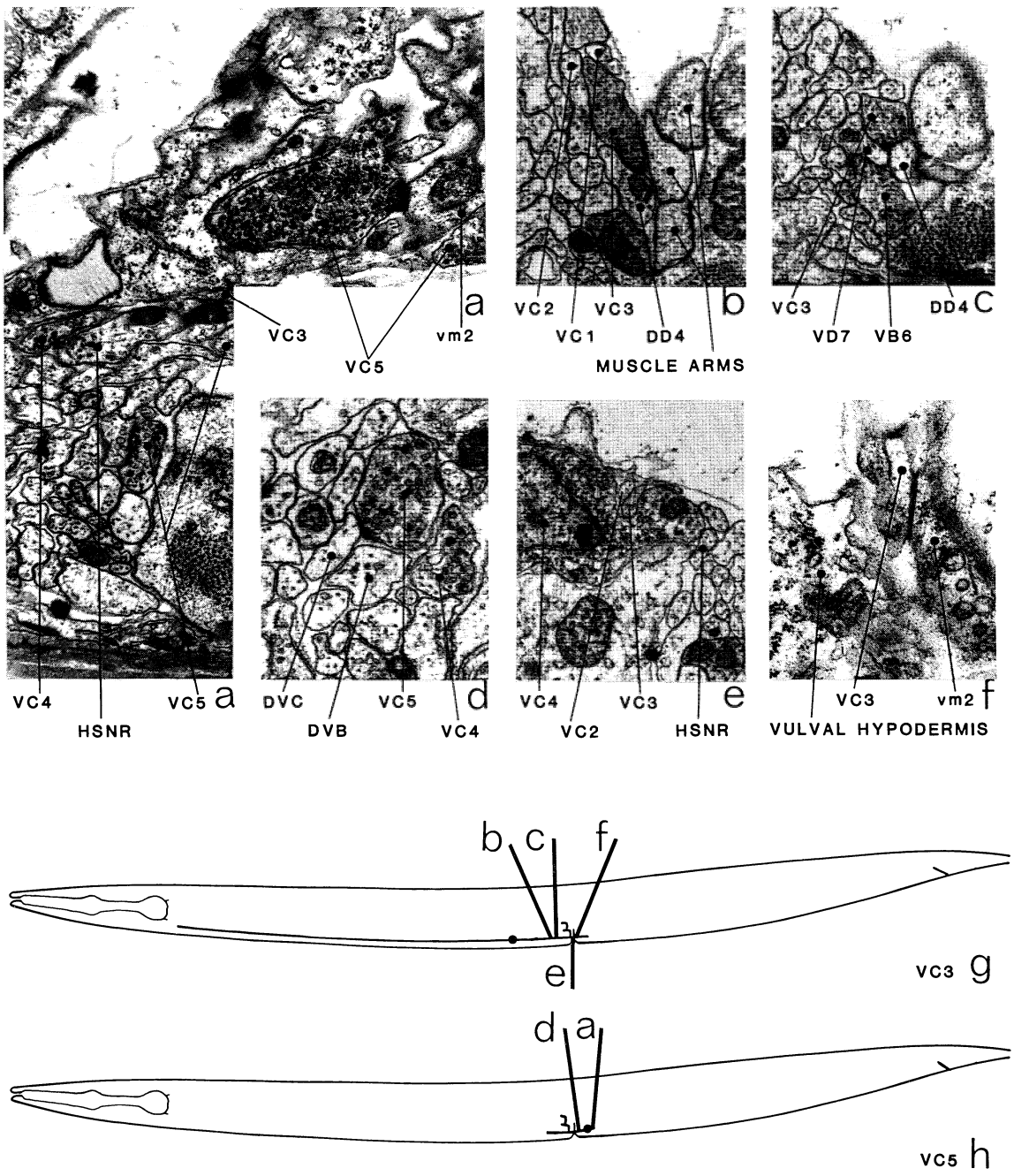
anywhere along the processes. A long, posteriorly directed process leaves the cell body and moves to a position adjacent to the bounding basal lamina on the right-hand side of the cord, next to a dorsal VAn process (figure 18). VBn processes have NMJs when they are in this position; the NMJs are nearly always dyadic synapses with DDn neurons as the other postsynaptic partner (a). The posterior process of VBn eventually moves away from the NMJ region, its place being taken by the process of the adjacent posterior VBn. The posterior distal regions of the VBn processes then run for some considerable distance in the ventral region of the cord, with little or no synaptic contact with other cells, before terminating. VB1 (e, f) and VB2 (g) differ in their morphology and in synaptic contacts from the other VBns. Both have branches that run transversely across the dorsal surface of the cord just posterior of the excretory duct, although only VB1 has NMJs in this region. VB1 also has a process that enters the left-hand side of the nerve ring, which synapses onto SAA (b) and receives some synaptic input from AIB.

Magnifications: (a–d) ×25500.


VC3
VD2
PVQR
PVPR,VD1
PVQR
VC1
DD1
AVBL
DD1,DD2
VD3,VC2
NMJ,DD2
NMJ,VD4
PVQR,AVL
DD2,VC1
VC2*
DD2,VD4
VC1
NMJ,DD3
DD3,VD5
VC2
VD5
PVT,VD5
VC2*
VD5
VC1*
VD6
NMJ,DD3
NMJ,DD3
VC1*
VC1,VD6
VC2
b
VD6
DD4
DD4
DD4
NMJ,DD4
NMJ,DD4
DD4,VD7
DD4
DD4,VD7
c
DD4,VD7
NMJ,DD4
VC4
e
VC4
f
PVNR*
vm2
HSNR
VC5*
VC4
HSNR,VC4
VC5
VC5

VC5


d
VC4
DVB, DVC
DVC, AVFL
vm2
VC4
VC3, vm2
vm2
vm2
a
vm2
vm2
vm2
vm2
vm2
HSNL*
AVFR
VC3
VC3



VCn

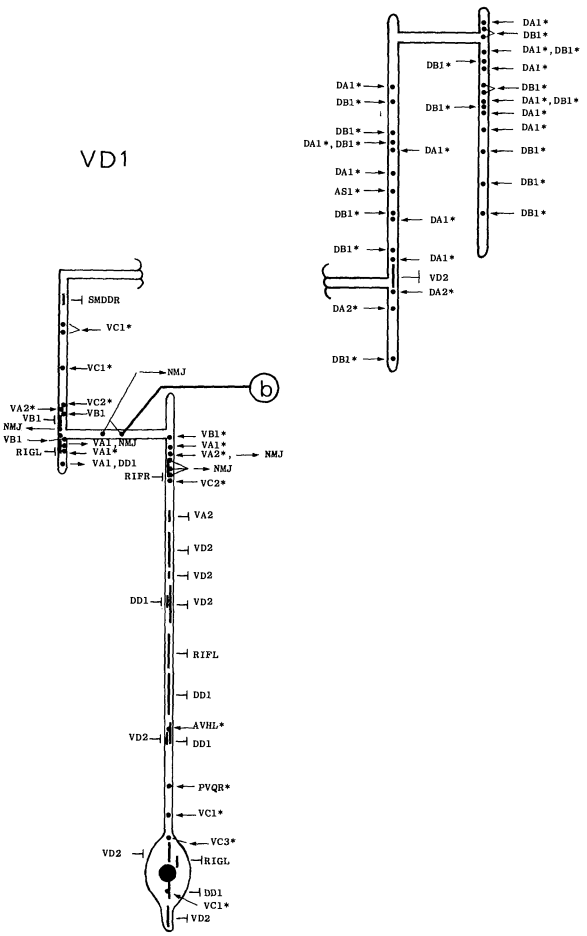
Members: VC1 to VC6.

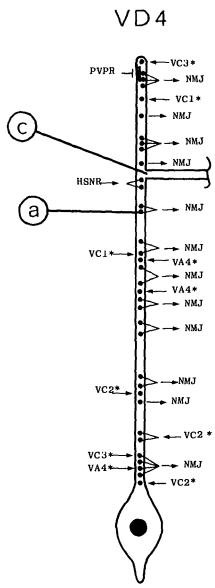
VCn is a set of six motoneurons in the ventral cord, which innervate ventral body muscles and the vm2 muscles of the vulva. VC4 and VC5 (h), which are situated nearest the vulva, have short processes in the ventral cord but send several processes dorsally along the vulval hyperdermis on each side of the vulval opening, where they have large, vesicle-filled varicosities and innervate vm2 vulval muscles (a). They also synapse onto other VC neurons and receive some synaptic input from HSN in these regions. VC1, VC2, VC3 and VC6 send

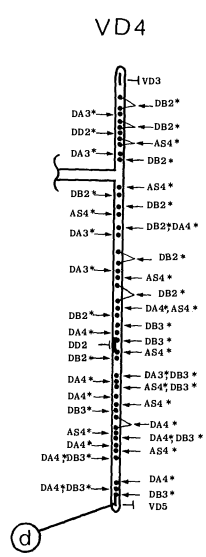
less extensive processes, which have similar synaptic contacts, into these vulval regions, but they have much longer processes in the ventral cord (h). These processes run near or adjacent to the bounding basal lamina in the dorsal region of the cord (figure 18). There they synapse onto DDn and VDn neurons (c) and have NMJs that are dyadic, with DDn and VDn as the second postsynaptic element (b). VCn neurons have gap junctions with each other (e) and also have some chemical synapses with each other. There are some features that seem to be unique for particular VCns that may be significant: VC5 synapses onto DVB and DVC (d) and VC3 has a gap junction directly to the process from a vm2 muscle (f).

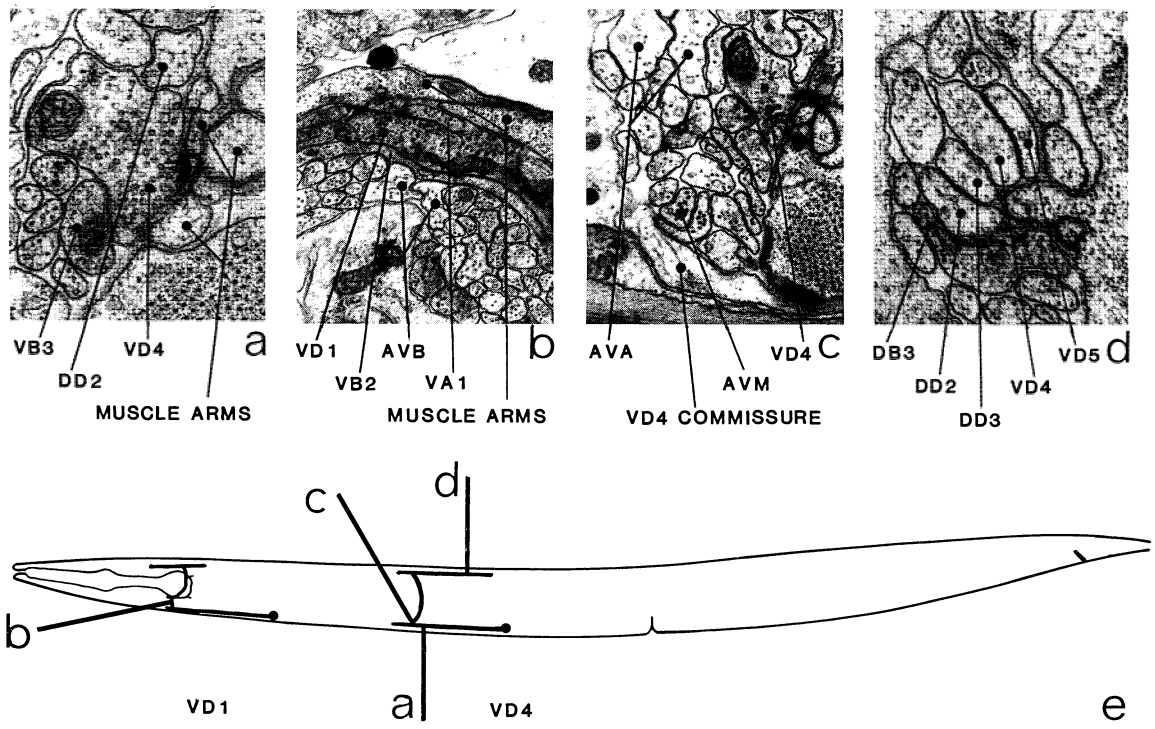
Magnifications: (a–c, e) ×17000, (d, f) ×25500.

VD1


VD1
SMDDR
VC1*
VC1*
NMJ
VC2*
VB1
VA2*
VB1
NMJ
VB1
RIGL
VA1, NMJ
VA1*
VA1, DD1
VB1*
VA1*
VA2*, NMJ
NMJ
RIPR
VC2*
VA2
VD2
VD2
DD1
VD2
RIFL
DD1
AVHL*
VD2
DD1
PVQR*
VC1*
VD2
VC3*
RIGL
DD1
VC1*
VD2
b
DA1*
DB1*
DA1*, DB1*
DB1*
DA1*
DB1*
DA1*, DB1*
DA1*
DA1*
DB1*
DB1*
DB1*
DB1*
DA1*
DB1*
DA1*, DB1*
DA1*
DA1*
AS1*
DB1*
DA1*
DB1*
DA1*
VD2
DA2*
DA2*
DB1*


VD4
PVPR
VC3*
NMJ
VC1*
NMJ
NMJ
NMJ
HSNR
NMJ
VC1*
NMJ
VA4*
NMJ
VA4*
NMJ
NMJ
VC2*
NMJ
NMJ
VC2*
VC3*
VA4*
NMJ
VC2*
c
a


VD4
VD3
DB2*
DA3*
DB2*
DD2*
AS4*
DA3*
DB2*
AS4*
DB2*
DB2*
AS4*
DB2*DA4*
DA3*
DB2*
DA3*
AS4*
DB2*
DB2*
DA4*, AS4*
DB2*
DA4*
DB3*
DD2
DB3*
DB2
AS4*
DA4*
DA3*DB3*
AS4*, DB3*
DA4*
AS4*
DB3*
DA4*
AS4*
DA4*
DA4*, DB3*
DA4*
AS4*
DA4*DB3*
DA4*
DB3*
VD5
d



VDn

Members: VD1 to VD13.

VDn is a set of thirteen motoneurons, with cell bodies in the ventral cord, which innervate ventral muscles. Each cell has an anteriorly directed process emanating from its cell body. This process has a branch, which leaves the ventral cord on the right as a commissure (c) and runs round to the dorsal cord. (VD2 is exceptional; it has a left-hand commissure.) The commissure splits, as it enters the dorsal cord, into an anteriorly and a posteriorly directed process, which span approximately the same region of the body as their ventral counterparts (e). (VD1 is exceptional in that its dorsal process is anterior to its ventral counterpart.) Both the dorsal and the ventral processes run adjacent to the basal lamina bounding the cord, in close association with the processes of DDn neurons. The ventral process lies between the processes of VCn dorsally and the other motoneuron classes ventrally (figure 18). The dorsal process runs ventrally to the other motoneuron axons (figure 19). The VDn processes in the dorsal cord are exclusively postsynaptic, receiving synaptic input from DAn (*a), DBn (*a) and ASn (*a) motoneurons at points where they have NMJs. The processes in the ventral cord are predominantly presynaptic and have many NMJs (a, b), most of which have only muscle as the postsynaptic partner. The processes of VDn and DDn do not have extended, apparently undifferentiated distal regions, as do the other motoneuron classes; instead, they end abruptly in close proximity to the end of a neighbouring process of the same class, often with a gap junction between them (d). VDn also has gap junctions to DDn and a few with PVP. VD1 has several additional 'odd' gap junctions.

Magnifications: (a, d) ×25500, (b) ×12750, (c) ×17000.

APPENDIX 2. REMAINING AMBIGUITIES

The reconstructions that we have described were done piecemeal, using data obtained from several animals. This was because of the difficulty of serial sectioning a complete individual. Inevitably there were some consequential problems in the identification of equivalent processes in different animals. These problems could, for the most part, be resolved, because of the reproducibility of relative process positions within bundles and the consistent synaptic behaviour of a given process. There are, however, a few remaining ambiguities, notably concerning process identification in the posterior ventral cord. This region was covered by the N2Y series, which was derived from an adult male. The male has significantly more processes running in its ventral cord than the hermaphrodite. These extra processes arise from male-specific neurons in the tail ganglia (Sulston *et al.* 1980). Their presence made it difficult to identify some of the processes from neurons common to both sexes, particularly those that were rather featureless, with few characteristic synapses. We have listed the cases for which these problems exist.

DVB AND DVC

The processes from these two neurons are always closely associated. They sometimes twist round each other and so cannot be distinguished by their relative positions. We cannot, therefore, be sure whether the cell bodies labelled DVB and DVC connect to the processes labelled DVB and DVC in the nerve ring or whether they have been crossed over. We have chosen the interpretation that is shown on the basis of synaptic criteria, but these are not particularly compelling.

ALA, CAN AND PVD

These neuron classes have processes that run together alongside the two lateral arms of the excretory canal. They have not been followed along the length of the animal, although they have been sampled at intervals along their length. The three processes make virtually no synaptic connections along the canal and look rather similar. Two of the processes end at about the level of the anus; the third enters the lumbar ganglion on each side, where it makes a few synapses onto PVC. This process has been tentatively assigned to ALA, but it could equally well belong to either of the other classes.

PVW, PQR AND PVT

These classes have cell bodies in the lumbar ganglia and the pre-anal ganglion; they send out processes, which project anteriorly up the ventral cord. Processes from these neurons have not been positively identified in the N2Y series and are not present in the anterior ventral cord (i.e. they could not be accounted for in the N2U series). It therefore seems likely that they terminate somewhere in the posterior ventral cord. The process of PQR appeared to be petering out at the end of the JSE series and was almost certainly about to end. The same cannot be said of PVT, however. The single neuron of this class had a large cell body in the pre-anal ganglion with a single, substantial, anteriorly directed process. This process had few synaptic contacts and was still going at the anterior extent of the JSE series. It seems rather surprising that such a process should end, presumably without making any significant synaptic contacts. An alternative interpretation is that this process divides somewhere in the posterior cord and becomes the two processes currently assigned to PVNL/R in the anterior cord. The location of the process of PVT in the cord is consistent with this interpretation. It would mean, however, that in this case PVNL/R would have to terminate in the posterior cord.

RID, PDA AND PDB

These three classes have processes in the dorsal cord, which have not been completely followed. RID sends a process into the anterior end of the cord; a process that looks similar has been identified in the posterior dorsal cord. It therefore seems likely that the dorsal process of RID spans the length of the cord. The process of PDA and PDB enter the dorsal cord near its posterior extremity. They project anteriorly but have not been identified in the anterior cord.

APPENDIX 3. NAME EQUIVALENCES

In some previous publications on *C. elegans* neuroanatomy, different systems of nomenclature have been used. We have included a list of equivalences to facilitate cross-referencing between these papers.

Ware *et al.* (1975):

LSM (lateral sub-medial)	— CEP.	DM	— RMED.
MSM (medial sub-medial)	— OLQ.	VM	— RMEL.
VL (ventro-lateral)	— OLL.	Oe	— RIP.
ILR (inner labial)	— IL1.		
ILN (inner labial)	— IL2.	60	— GLR.
Cap cell	— Socket cell.		
Pocket cell	— Sheath cell.		

Ward *et al.* (1975):

C	— CEP.		
O (sub-dorsal and sub-ventral)	— OLQ.		
O (lateral)	— OLL.		
I1	— IL1.		
I2	— IL2.		
e	— ASE.	a	— AWA.
f	— ADF.	b	— AWB.
g	— ASG.	c	— AWC.
h	— ASH.		
i	— ASI.	x	— URX.
j	— ASJ.	y	— URY.
k	— ASK.		
l	— ADL.	n	— BAG.
		m	— FLP.

White *et al.* (1976):

α	— AVA.	Ventral A	— VAn.
β	— AVB.	Dorsal A	— DAn.
δ	— AVD & AVE.	Ventral B	— VBn.
γ	— PVC.	Dorsal B	— DBn.
		Ventral D	— VDn.
		Dorsal D	— DDn.
		Ventral C	— VCn.
		Dorsal AS	— ASn.

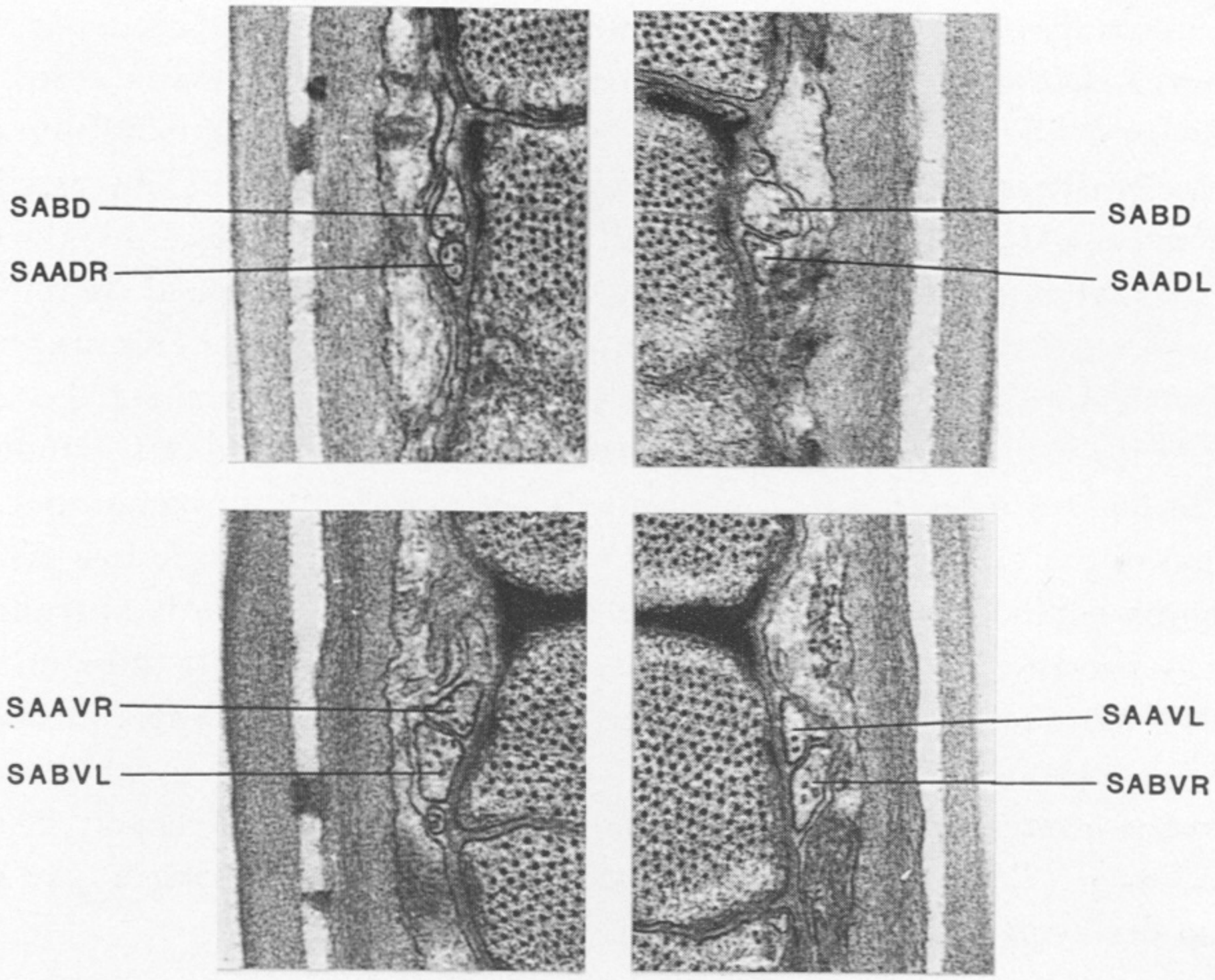


FIGURE 8. Most of the sub-lateral processes originate from the nerve ring and run longitudinally underneath the muscle quadrants close to the line of apposition of the two muscle rows. Apart from a single NMJ, no synapses have been seen on these processes. There are two processes in each of the sub-lateral cords anterior to the ring (a) and five in each of the cords posterior to the ring (b). The individual processes run in fixed positions within the cords. The posterior cords include processes from PLN and SDQ, which must have grown in the opposite direction to the others, as their cell bodies are situated laterally in the body (figure 7). Apart from the processes of these cells, the sublateral processes eventually peter out (figures 6 and 7).

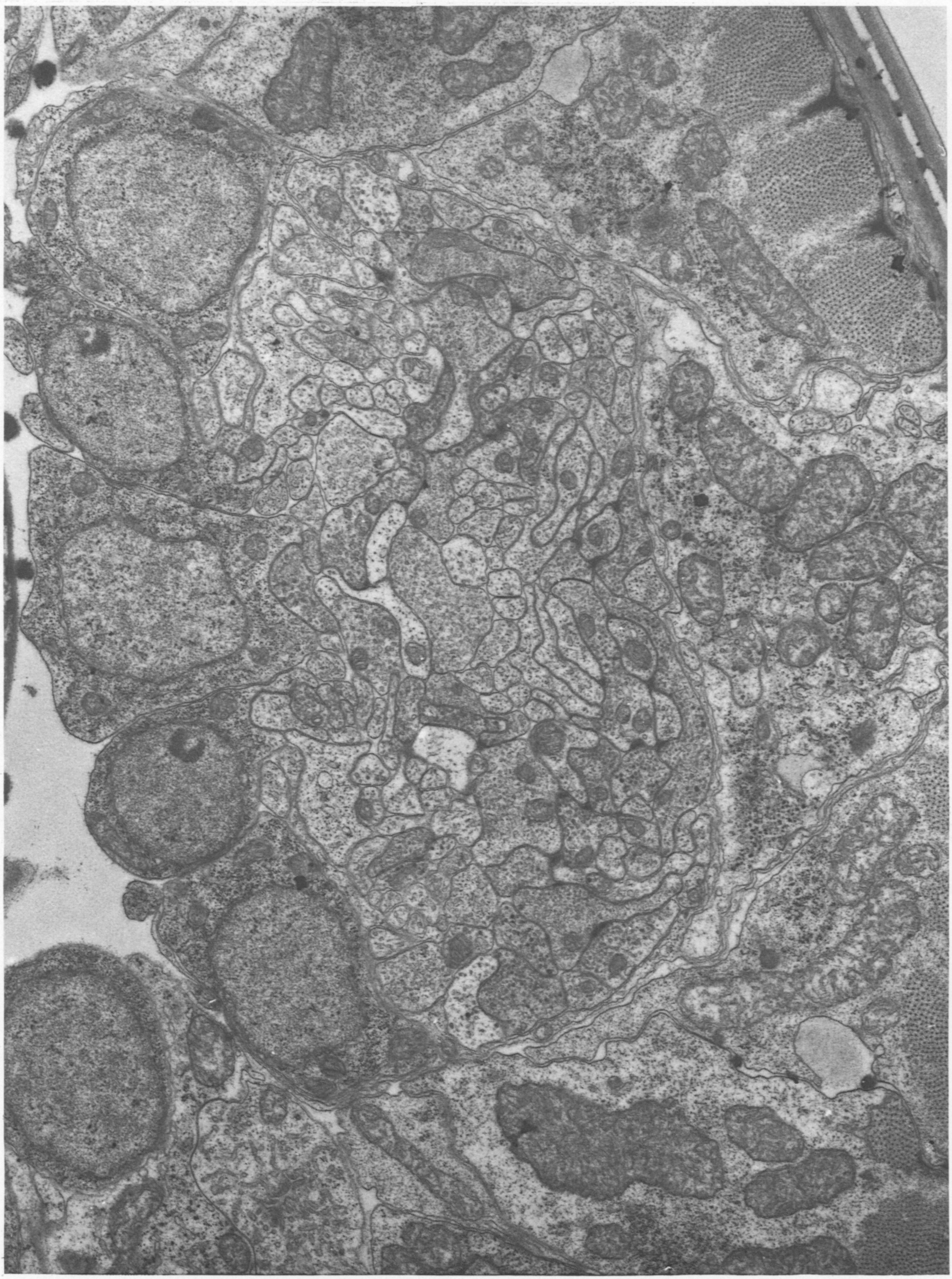
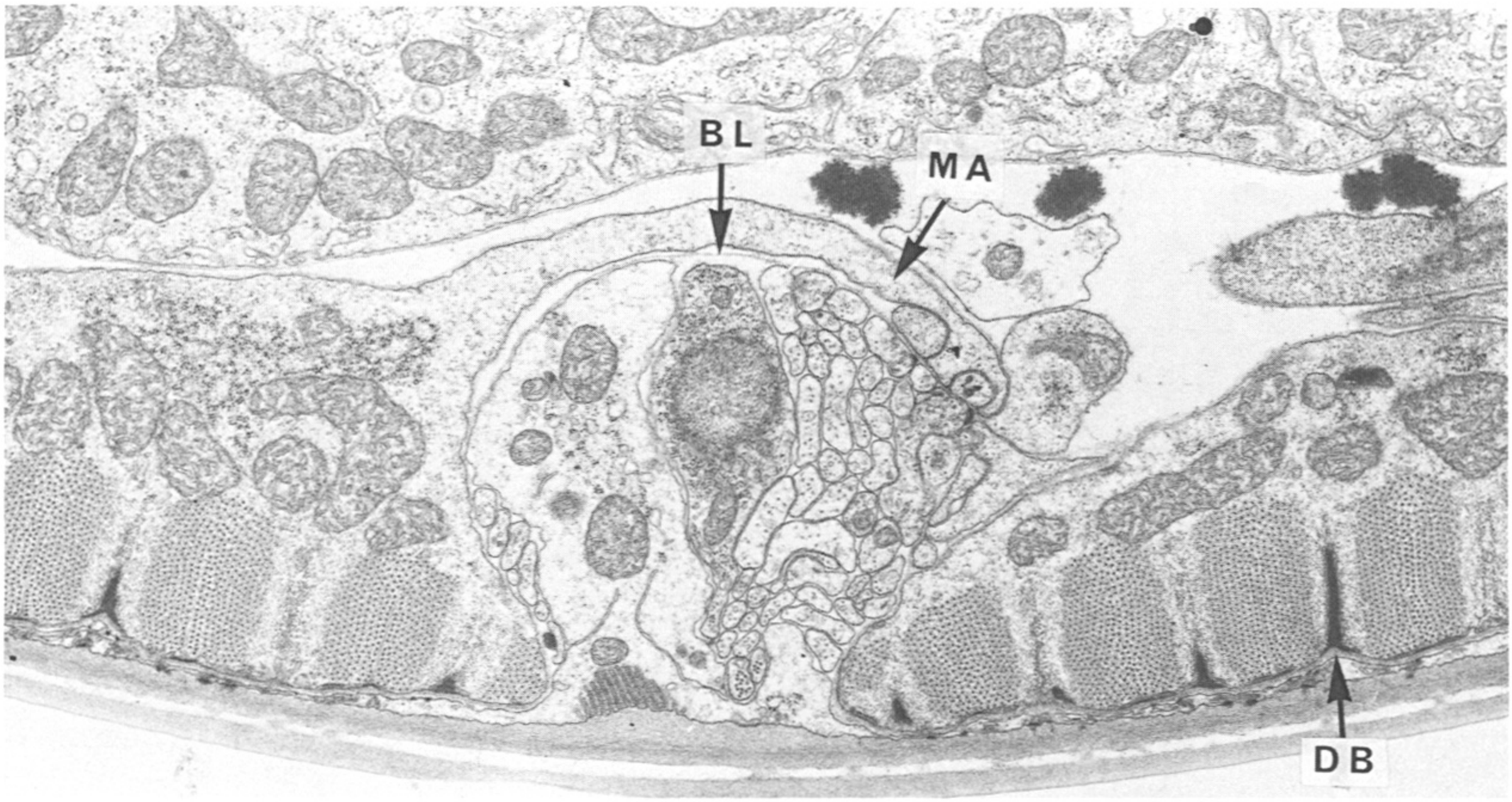


FIGURE 16 (a).



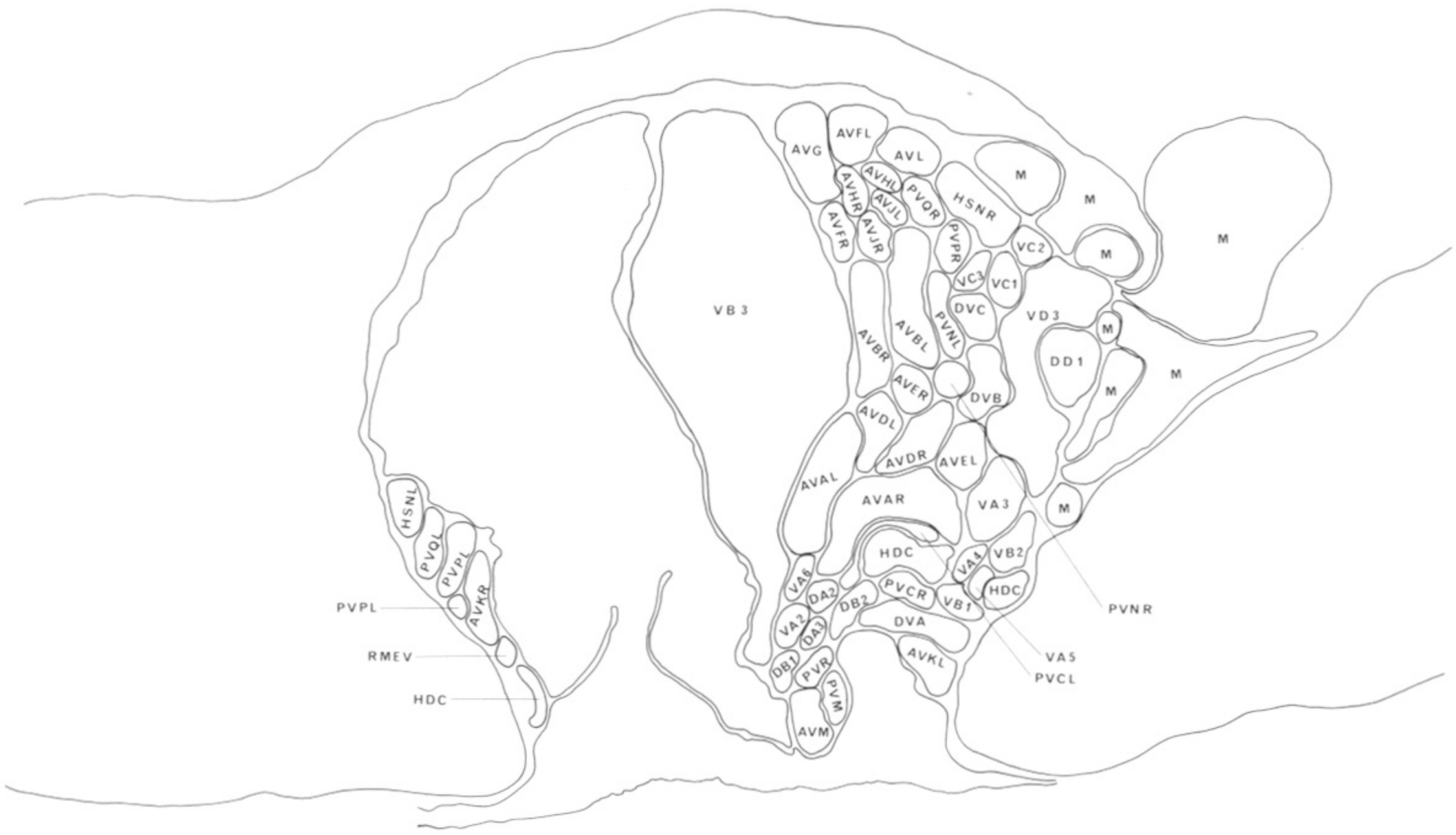


FIGURE 18. Transverse section through the ventral cord (above) and process identifications (below). The ventral cord consists of a process bundle that runs alongside a longitudinal ridge of hypodermis; the whole structure is bounded by a thin basal lamina (BL). Axons of motoneurons arrange themselves next to the basal lamina on the right-hand side of the cord in a fixed arrangement. The usual sequence of motoneuron classes from dorsal to ventral is VCn, VDn, DDn, VAn, and VBn. NMJs are made in this region (one from a VD3 is seen in this section); the motoneurons synapse through the basal lamina onto muscle arms (MA) from both left and right ventral muscle quadrants. The NMJs of a motoneuron are in a well-defined region along its process; outside this region, the process moves away from the basal lamina to the ventral regions of the process bundle. The VDn and DDn neurons are an exception in that their processes terminate abruptly outside the NMJ regions. The cell bodies of the motoneurons that innervate body muscles are arranged in a linear sequence in the ventral cord (figure 4). The ventral cord also contains the interneurons that synapse onto these motoneurons and other interneurons with little or no synaptic activity in the cord. The arrangement of processes in the cord is fairly consistent along the length of the cord, although there may be local distortions. Fingers of hypodermis (HDC) often project from hypodermal cells and run along the cord for short distances. Muscle cells have darkly staining, conical, dense bodies (DB) in the Z bands.

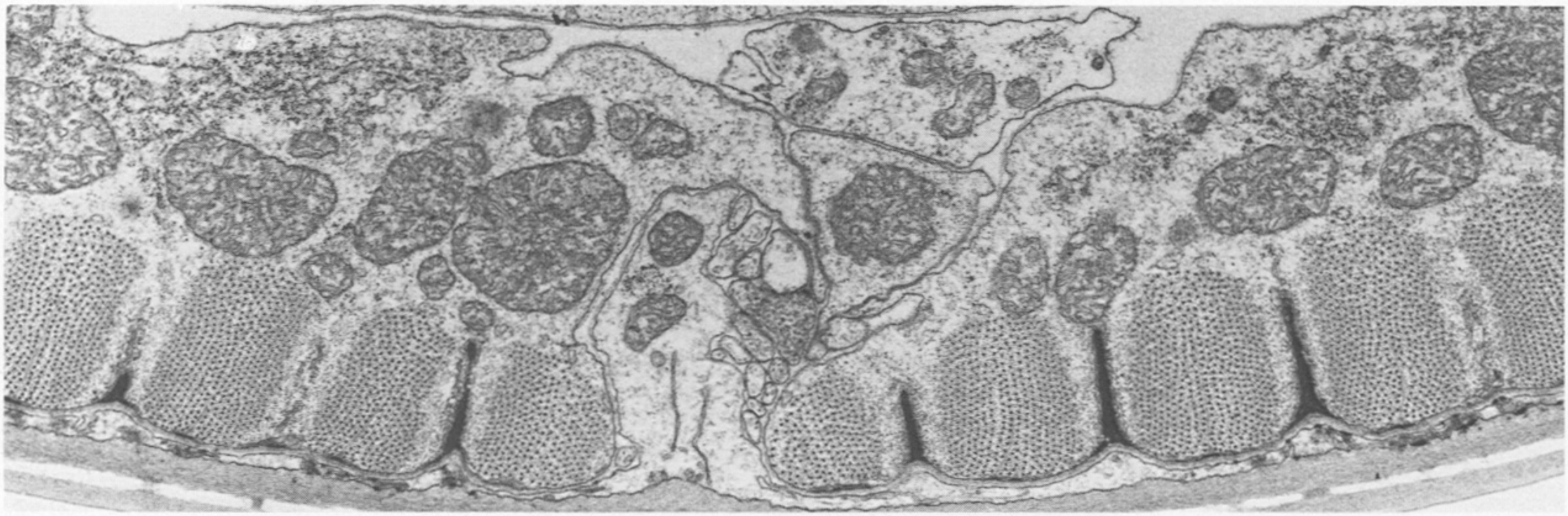
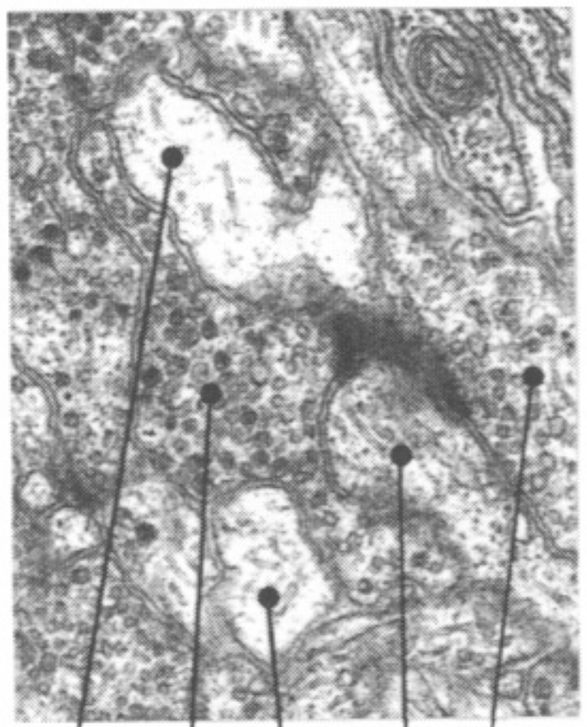
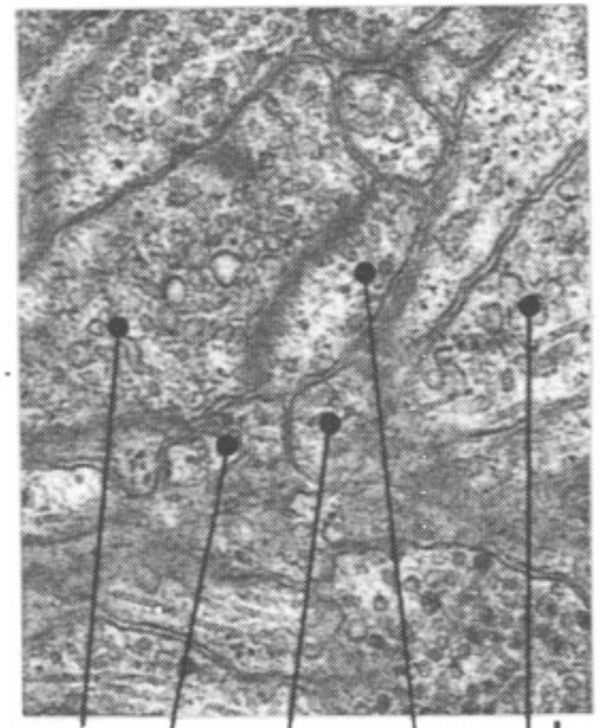
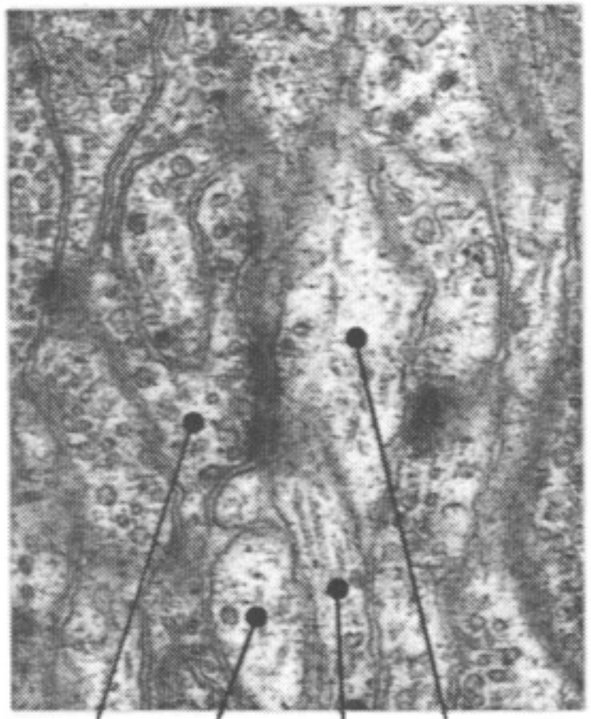
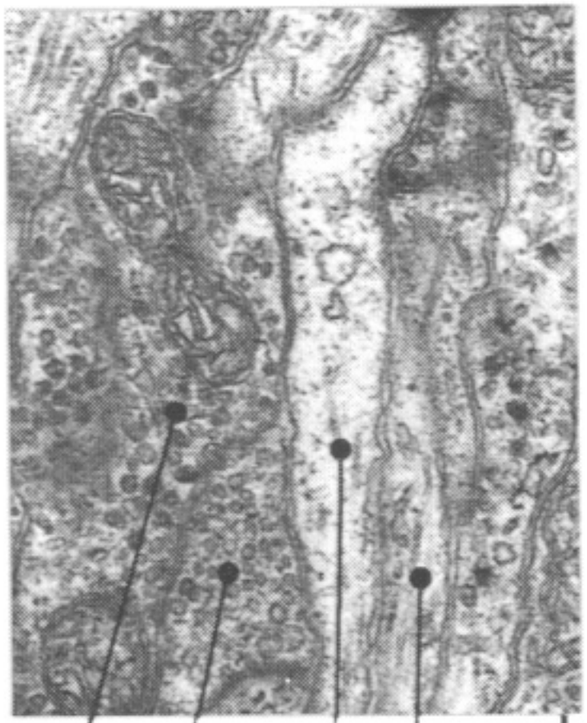


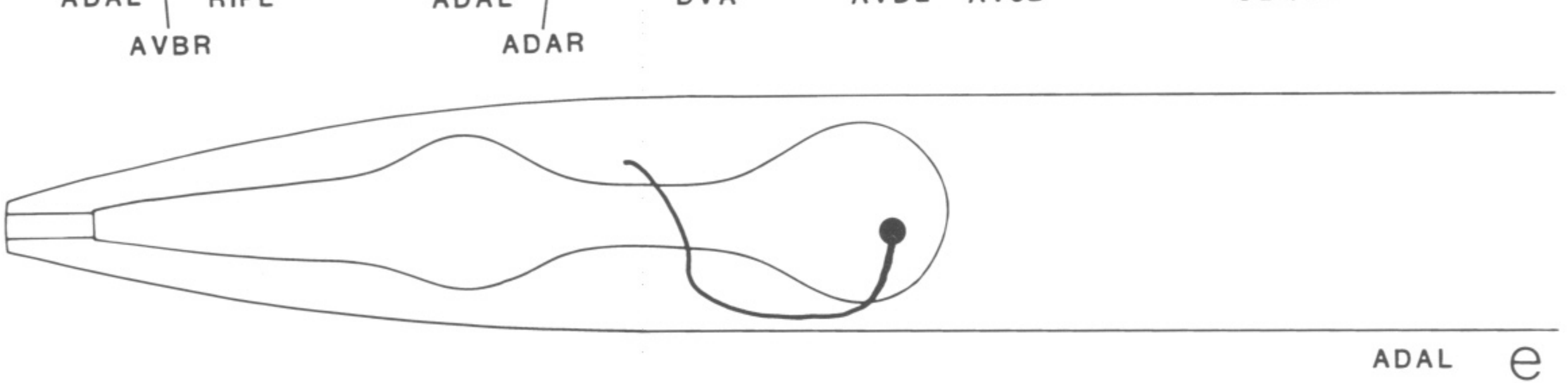
FIGURE 19. Transverse section through the dorsal cord (above) and process identifications (below). The dorsal cord is similar in overall structure to the ventral cord but is much simpler, as it has fewer processes and no cell bodies. The processes in the dorsal cord are all motoneuron axones except for the processes of VDn and RMED. DAn, DBn, ASn, DDn and VDn all have processes in the dorsal cord that originate from cell bodies in the ventral cord via circumferential commissures (figure 7). RID sends a process along the length of dorsal cord from its cell body, which is situated in the dorsal ganglion.


AVBL
ADAL
RIPL
PVR
a

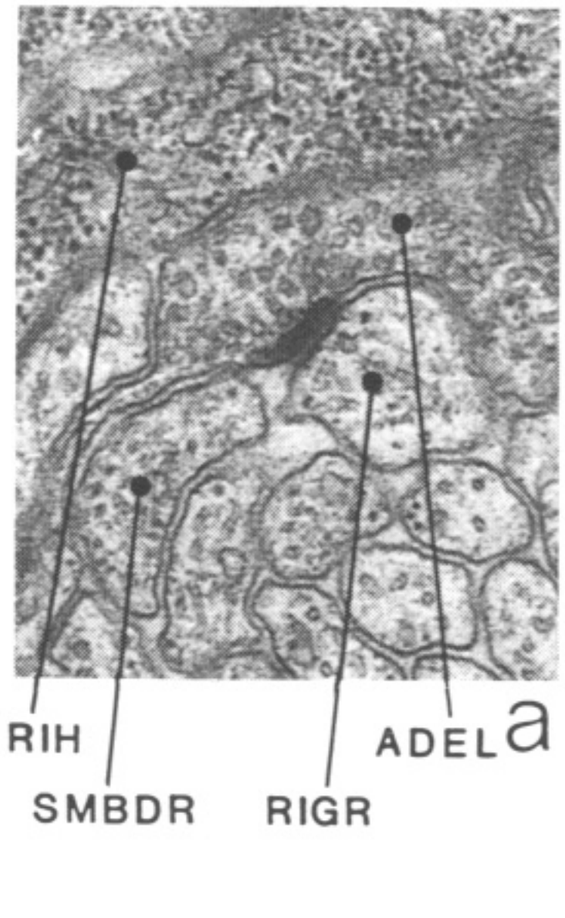

AIZL
ADAL
AIZR
DVA
b

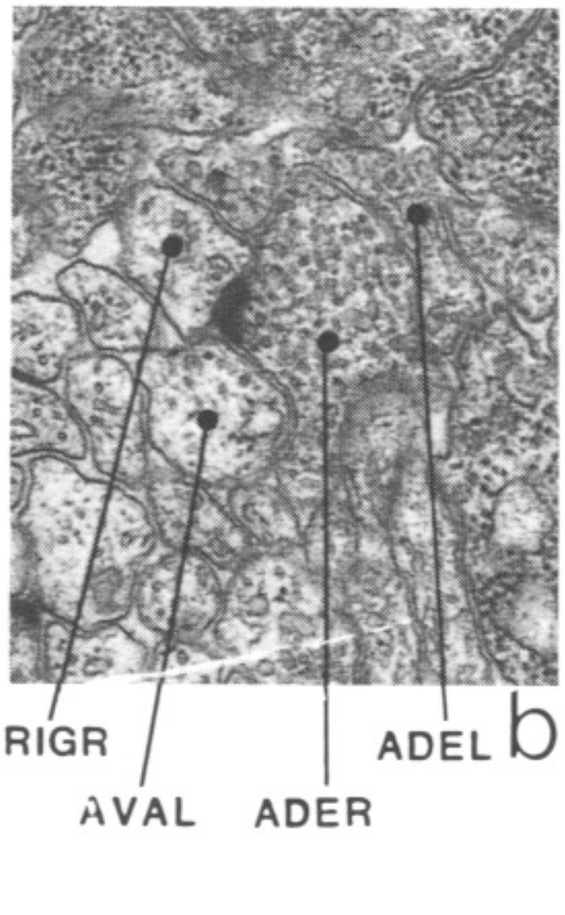

ADAR
AVDL
AVJL
AVBR
C

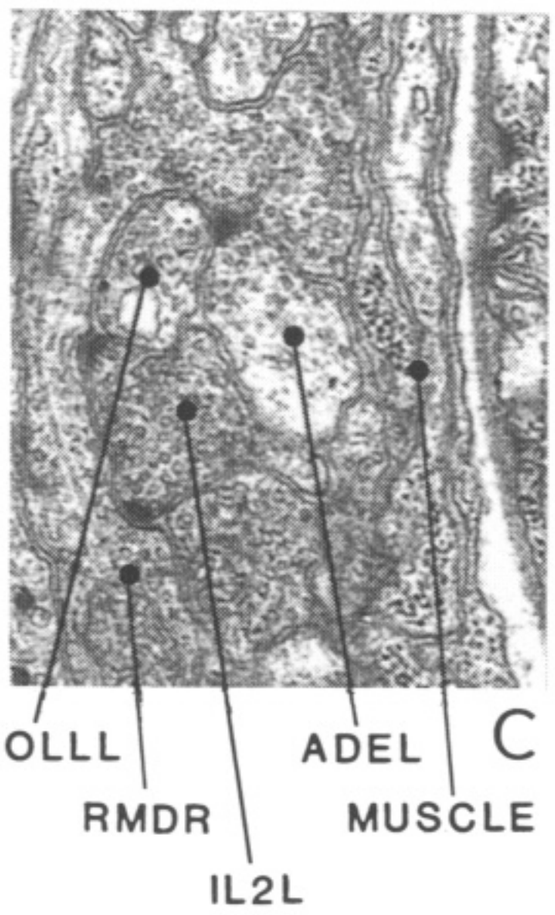

ADAR
OLQVR
AVDL
AVJL
d

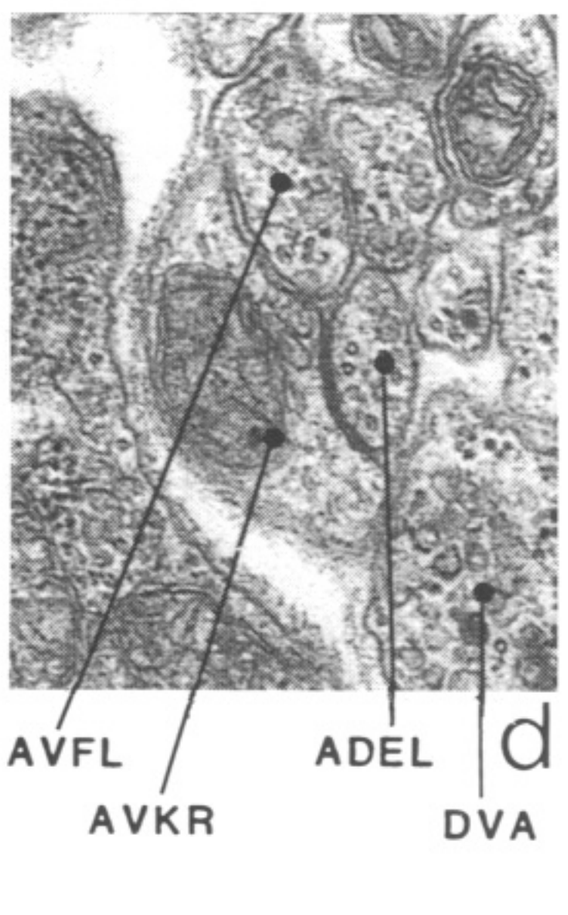

AVBR
ADAR
ADAL
e

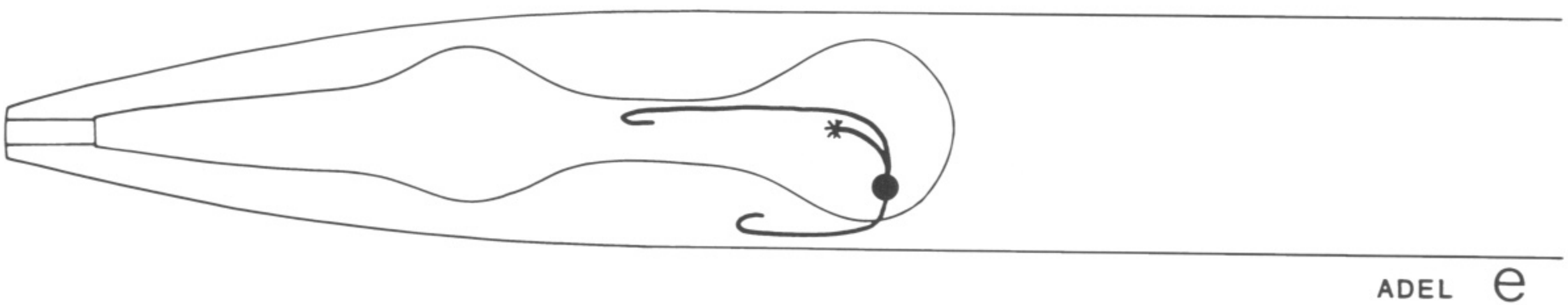
ADA


RIH
SMBDR
RIGR
ADEL
a

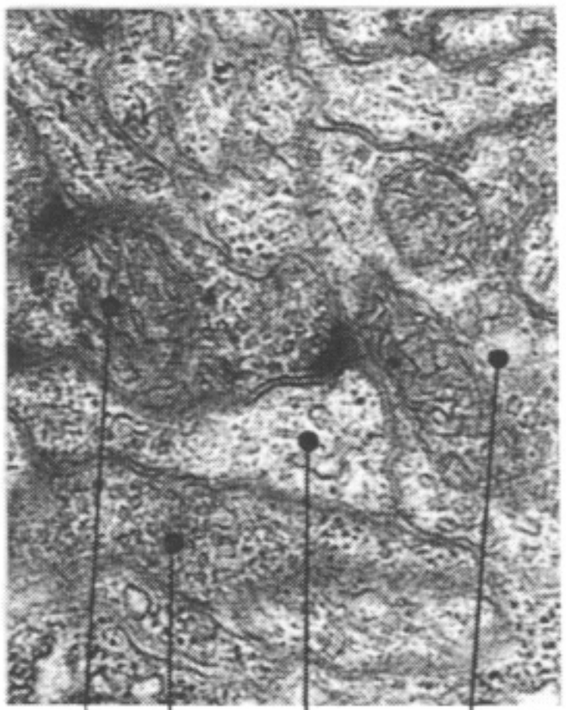

RIGR
AVAL
ADER
ADEL
b

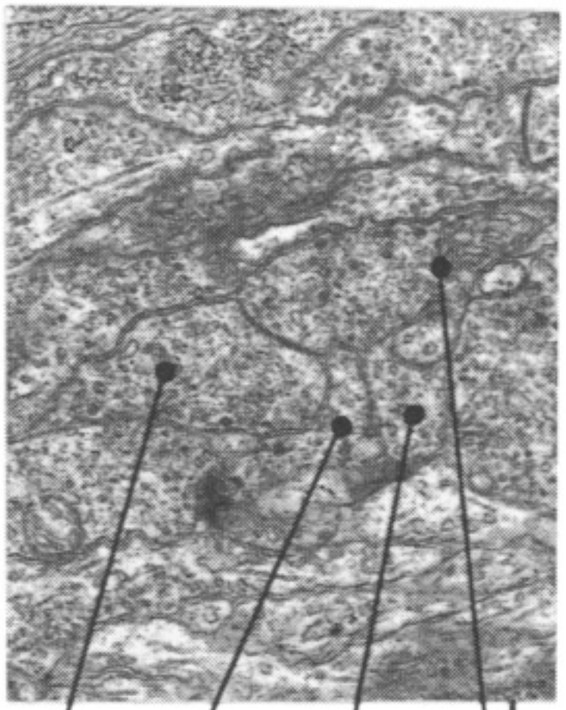

OLLL
RMDR
IL2L
ADEL
MUSCLE
c

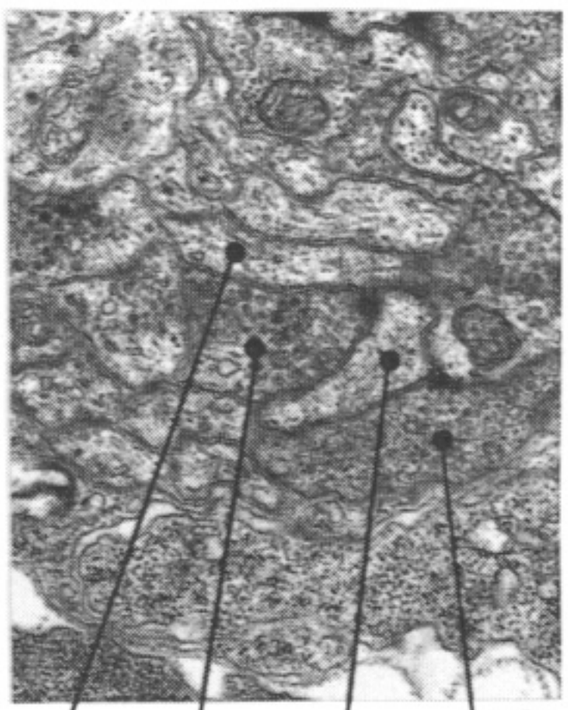

AVFL
AVKR
ADEL
DVA
d

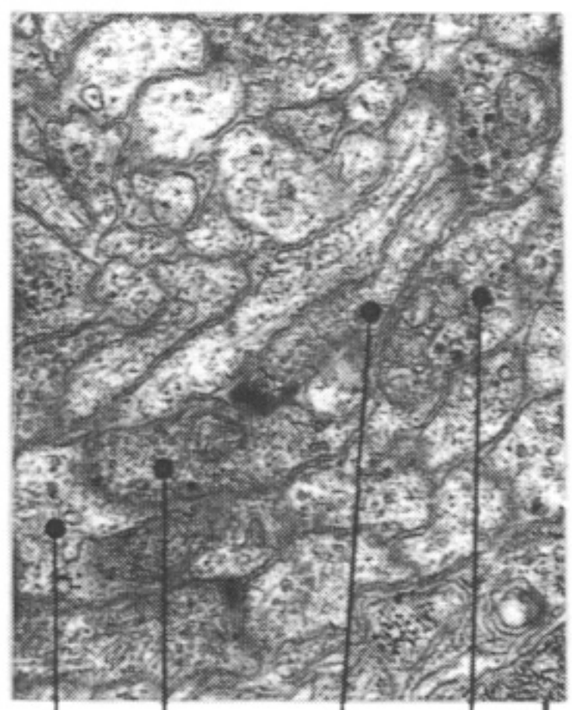

ADEL
e

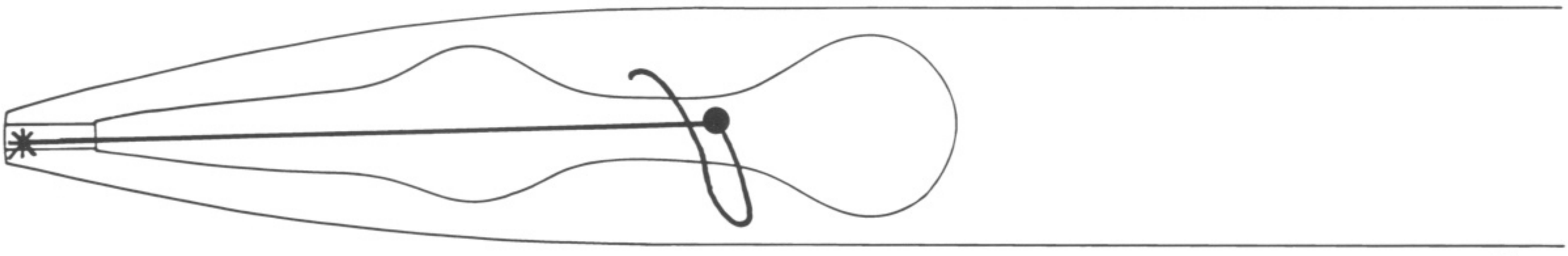
ADE


ADFL
RIAR
RIH
AIZL
a

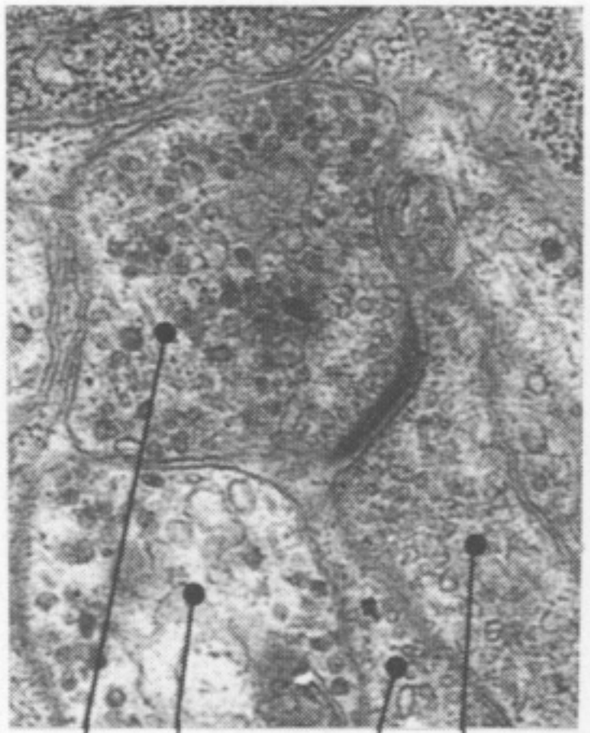

ADFL
ASHR
ASHL
ADFR
b

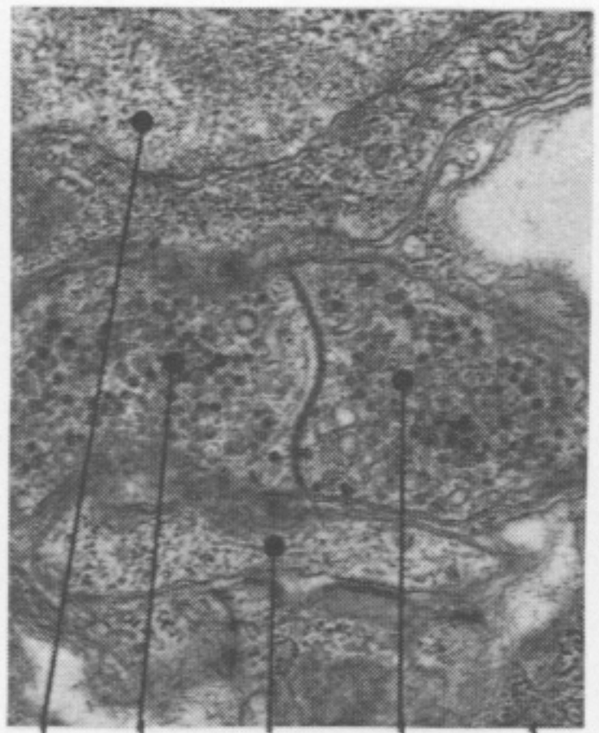

SMBVL
RIAL
ADFL
RIH
c

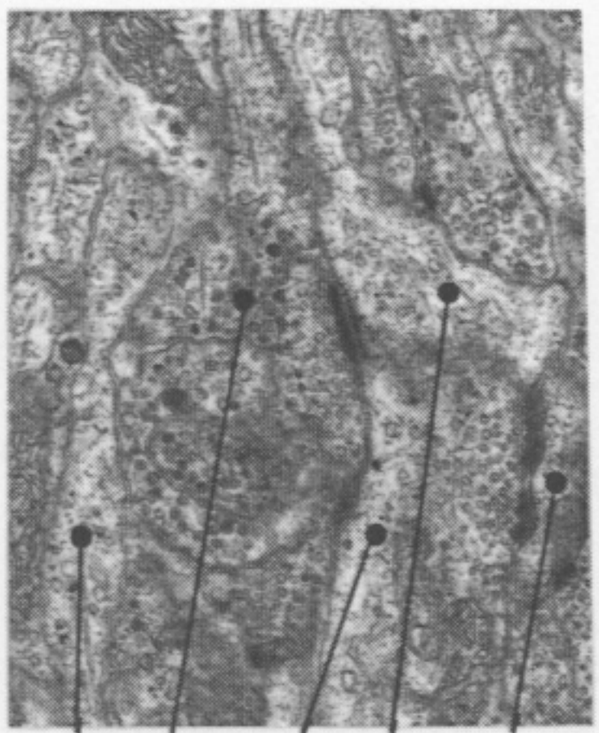

RIAR
AWBR
ADFR
AWAR
d

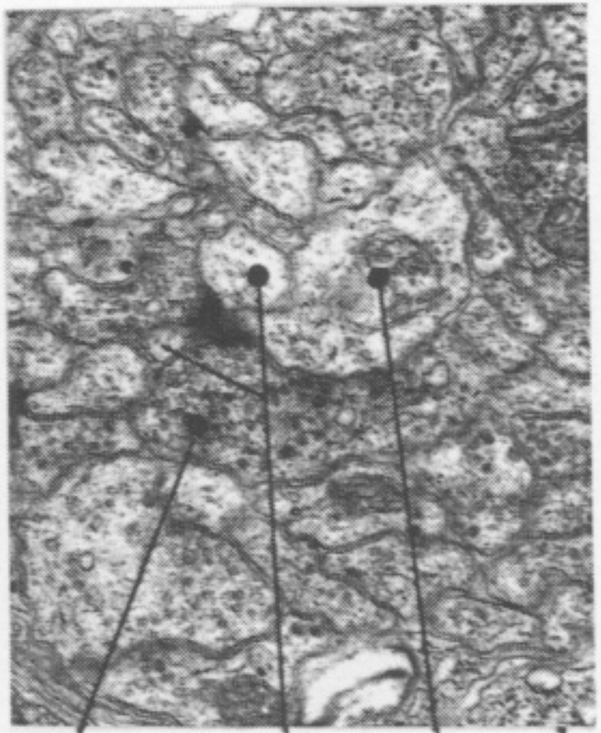

ADFL
e

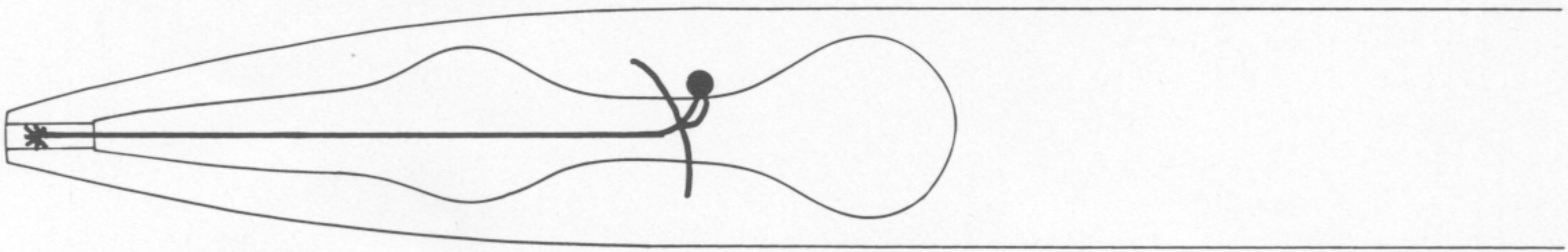
ADF

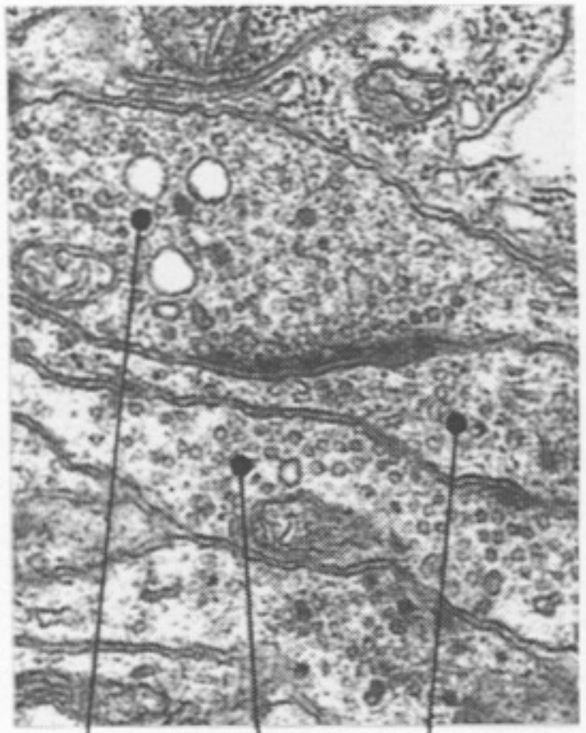

ADLR
AIAR
a
PVQR
ASKR


RID
ALA
b
ADLL
ADLR

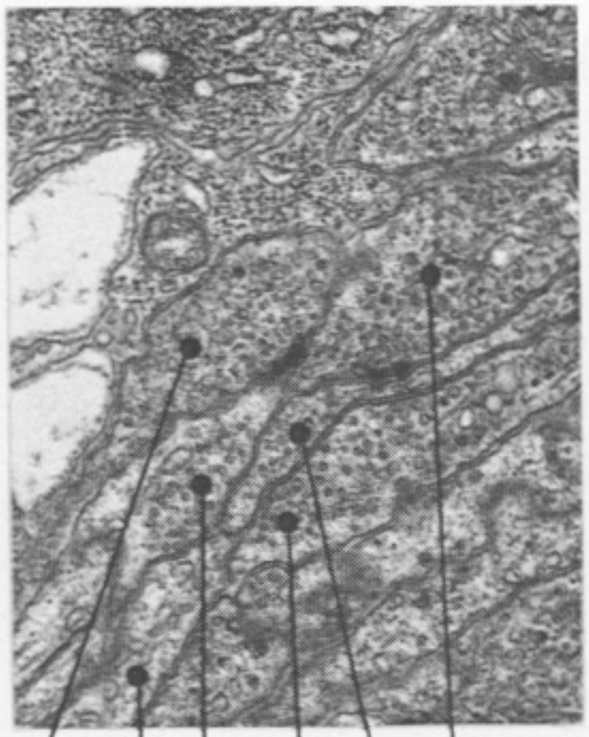

AVFR
AIYR
C
ADLR
ASER
AIBR

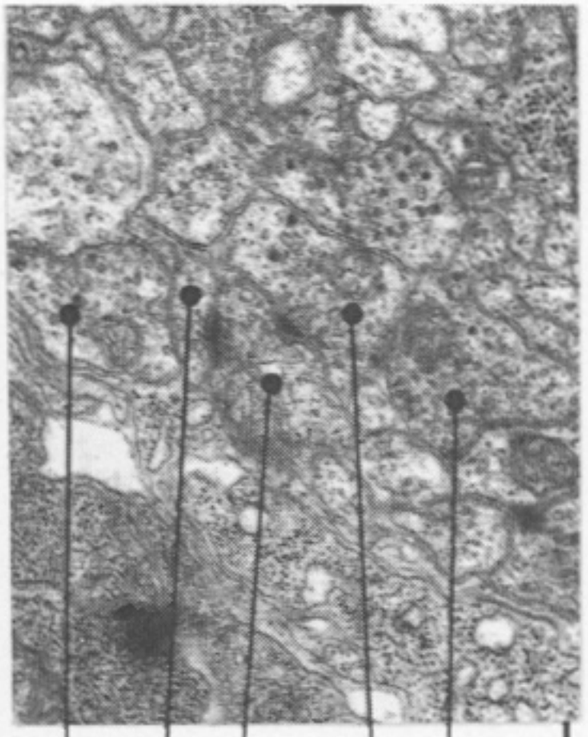

ADLL
AVAR
d
AVDR

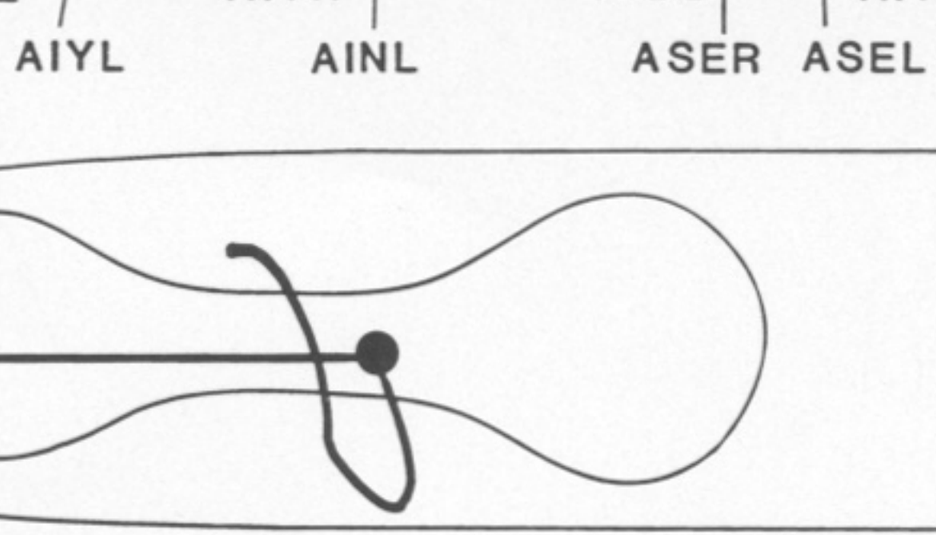

ADLL
e


AFDR
ASER
AIYR
a

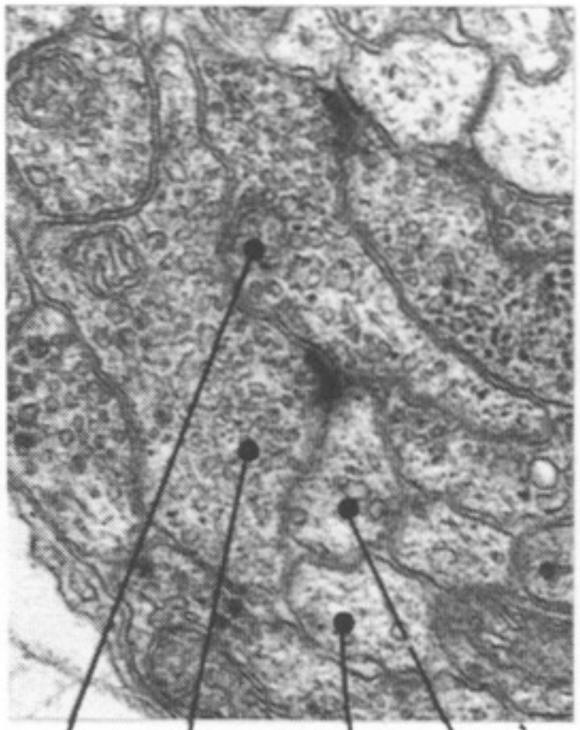

AFDL
AFDR
ASEL
AIYR
b

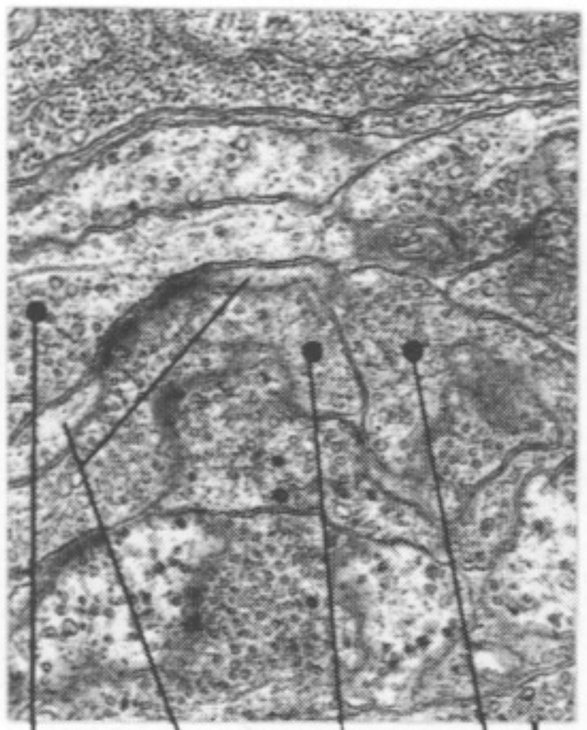

AINR
AFDL
C
AIBL
AIYL

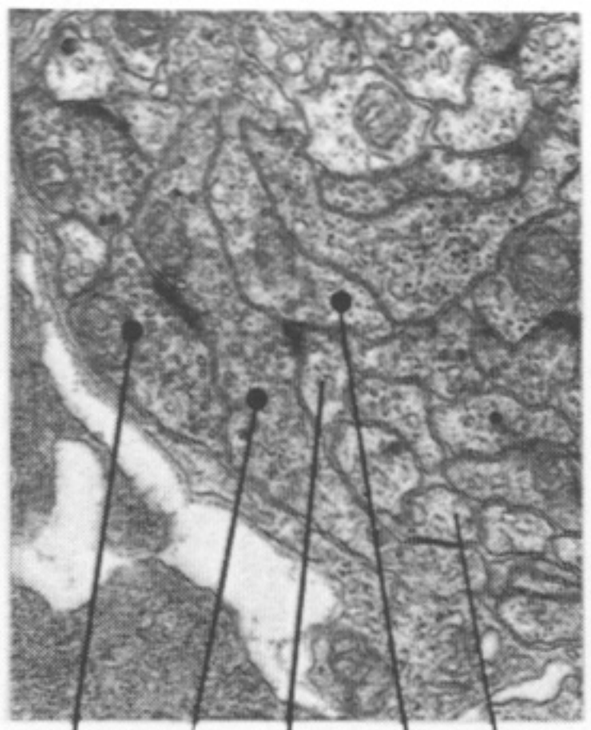

AWCL
ADFL
d
AIYL
AWAL

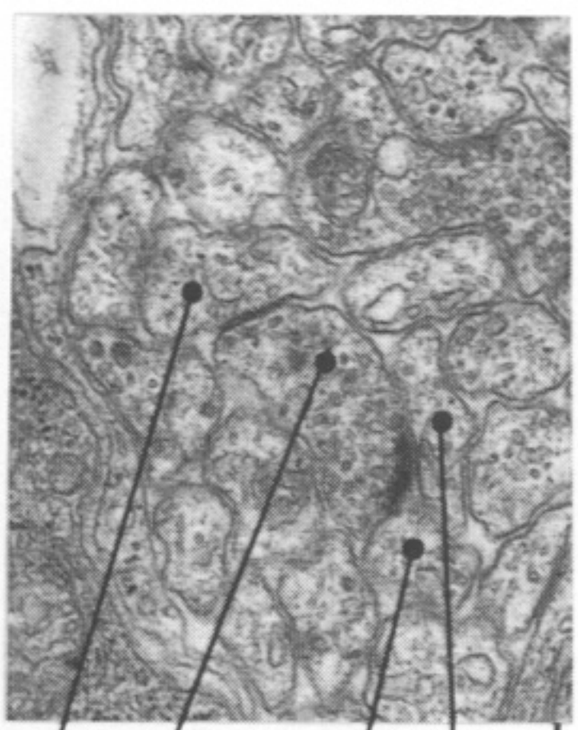

AIYL
AINL
ASER
ASEL
AFDL
AFDL
e

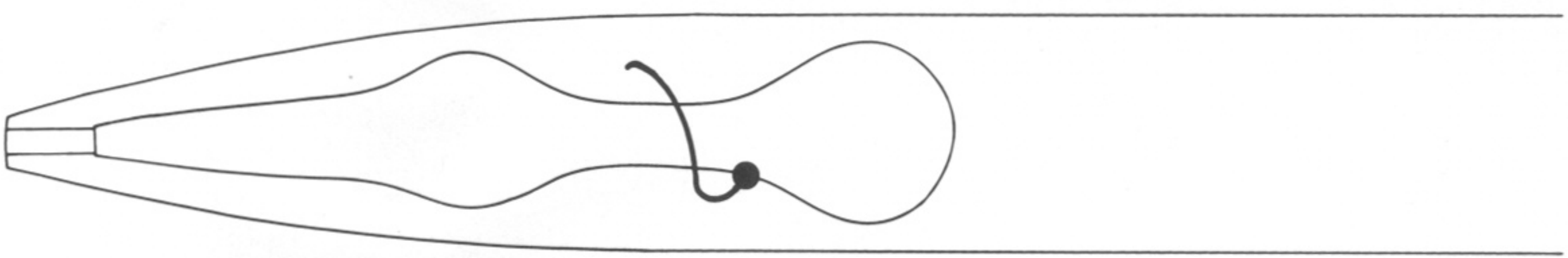
AFD


RIFL
AIAL
AWCL
AIBL
a

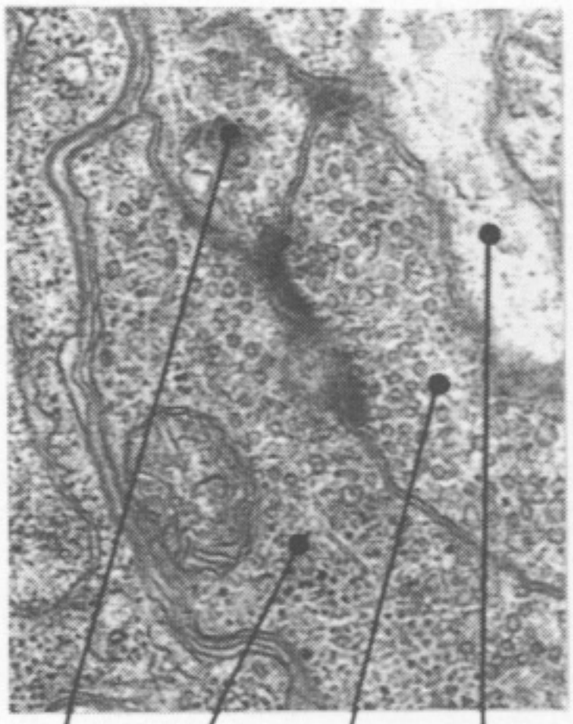

AWCR
AIBL
AIAL
AIAR
b

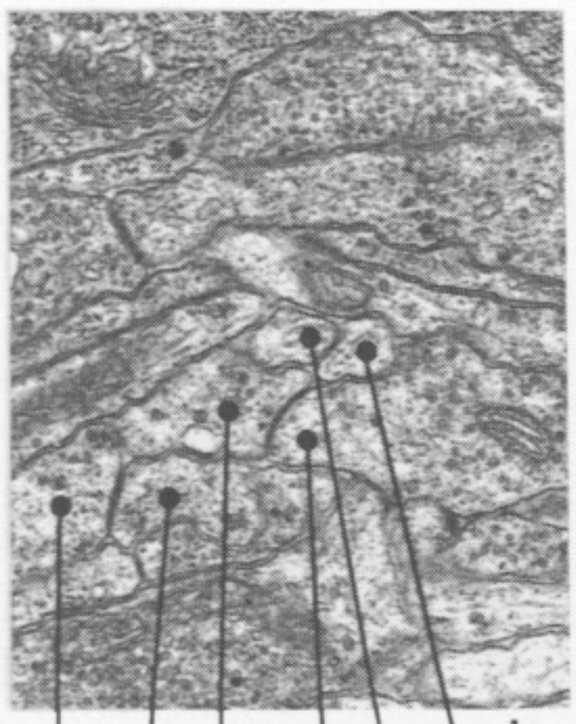

ASGL
AIAL
AIBL
RIFL
ASIL
c

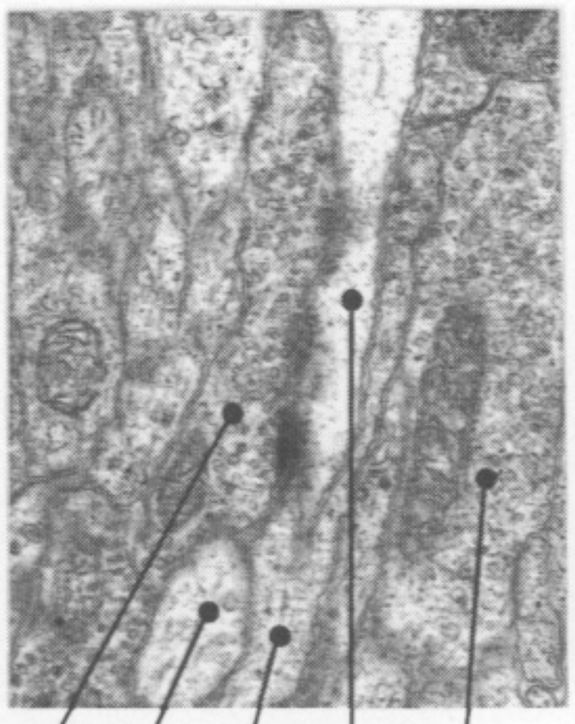

AIAL
AWAL
AWBL
ADFL
d

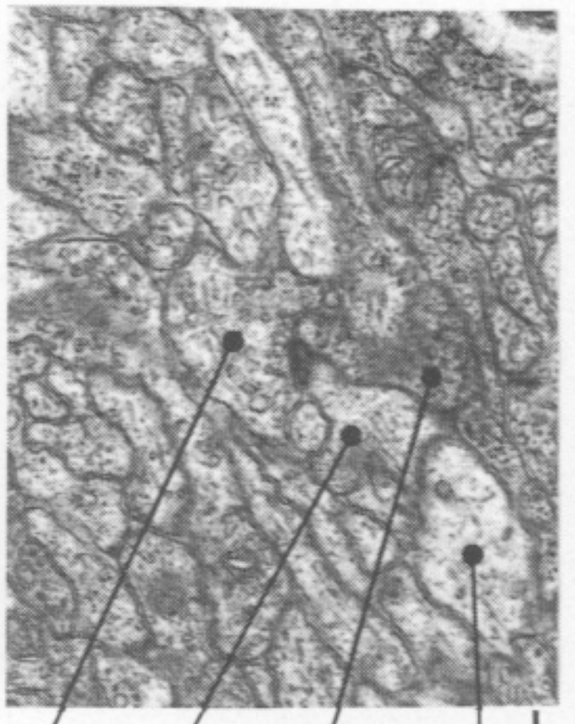

AIAL
e

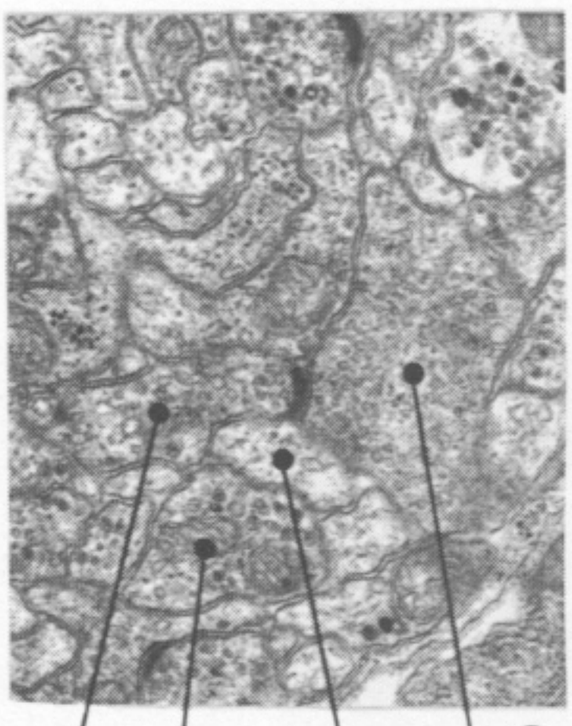
AIA

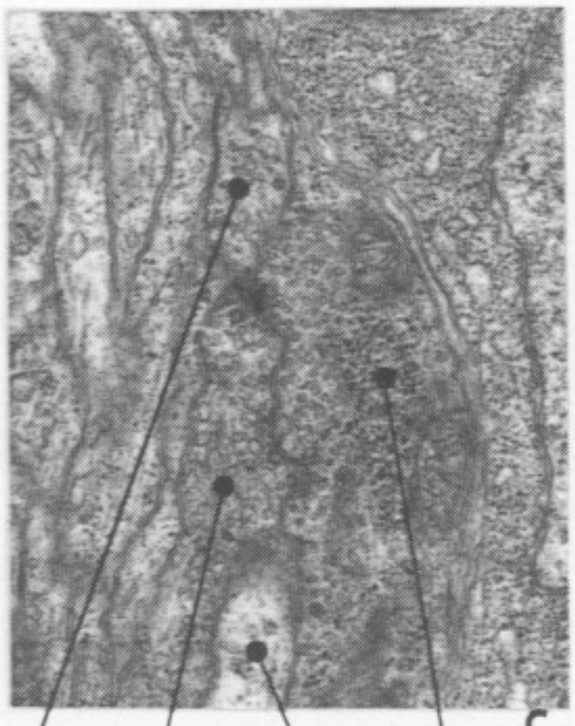

RIBL
RIML
AIBR
AVBR
a

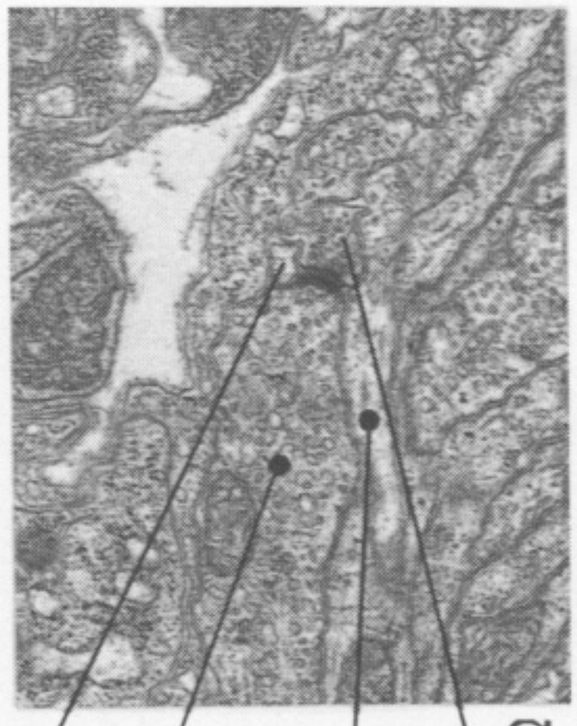

AWAL
AWAR
AWBL AWBR
AIBL
AIBR
b

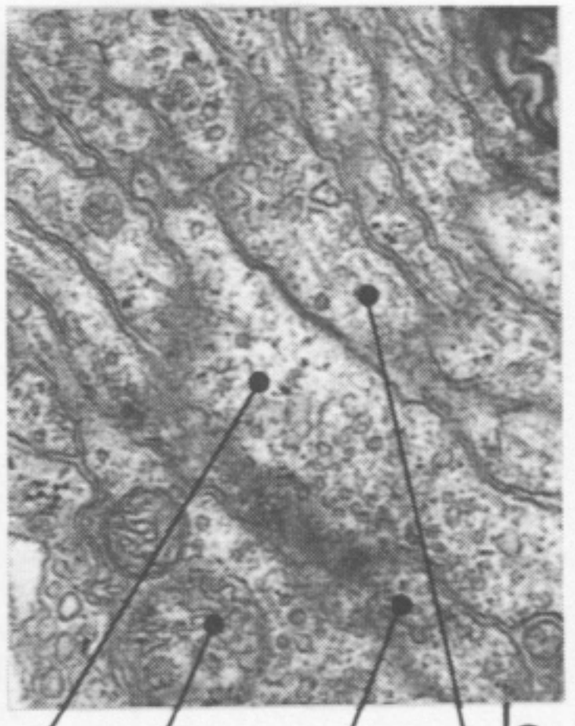

AIBL
AVAL
AVBL
RIGR
RIMR
c

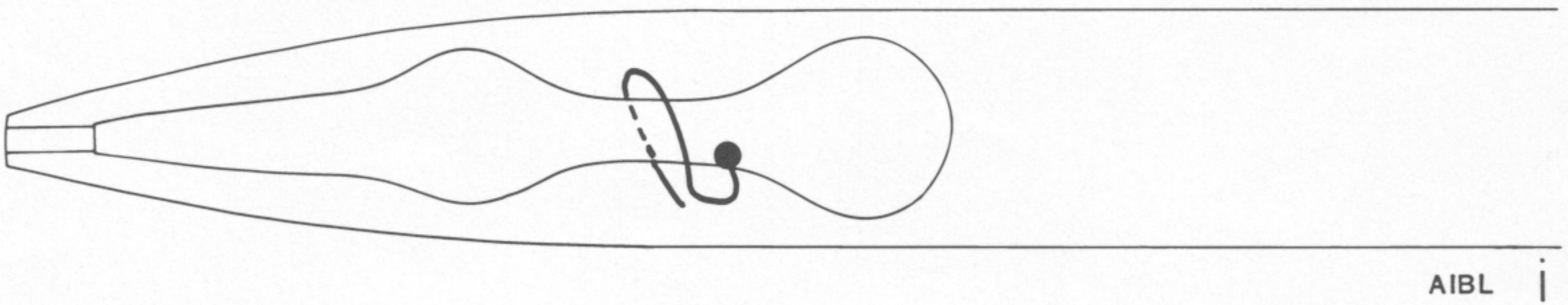

AIBL
RIMR
SAADL
AVAL
d


ASHR
ASER
AIBR
AIAR
e

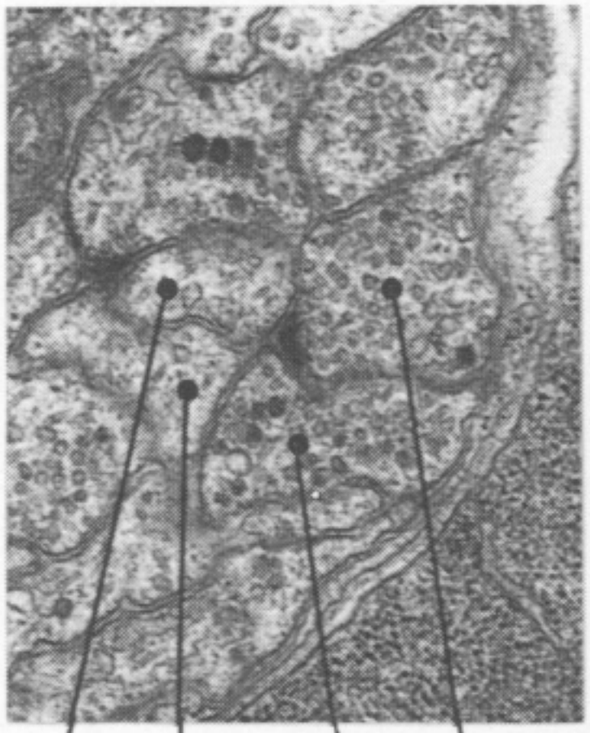

RIBL
AIBL
AVAL
RIML
f

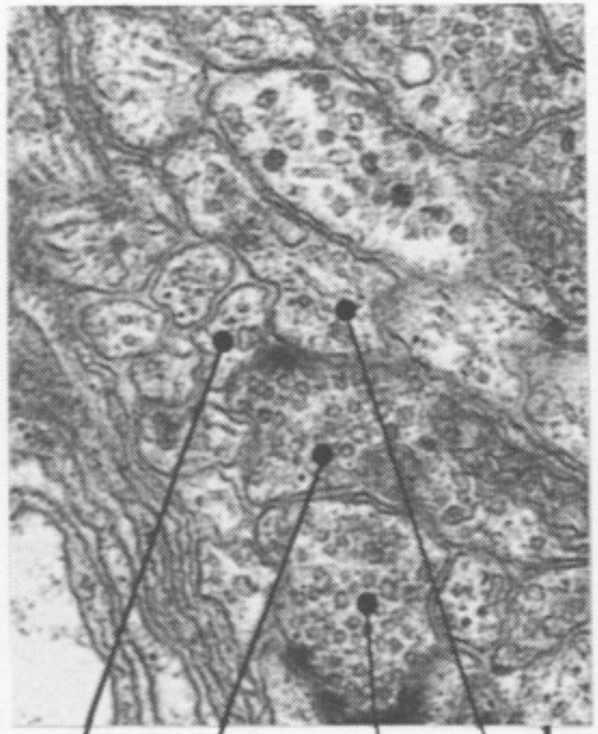

DVC
AIBR
AVDR
RIBL
g

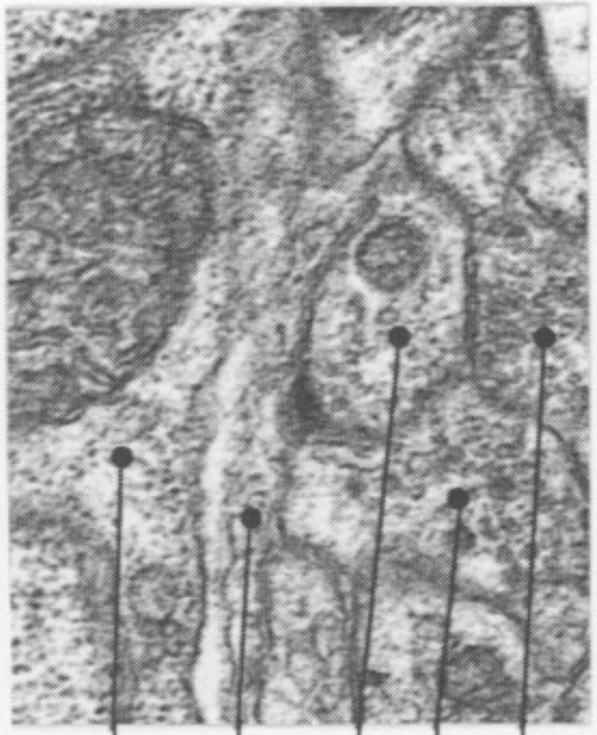

RIGL
RIBL
AIBR
BAGL
h

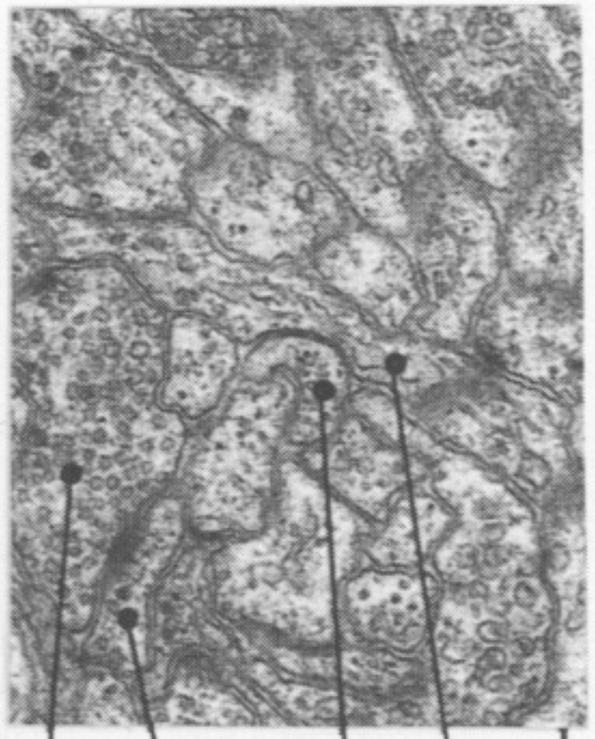

AIBL
i

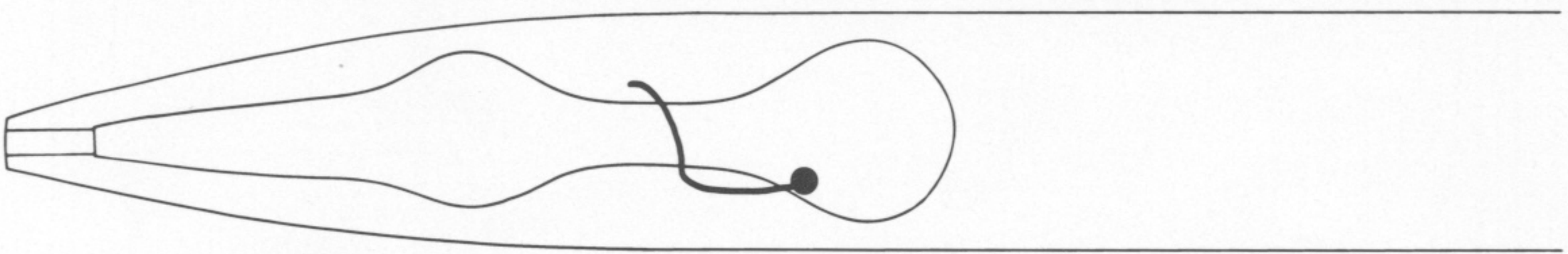
AIB


AIAR
AIBR
ASGR
AIMR
a

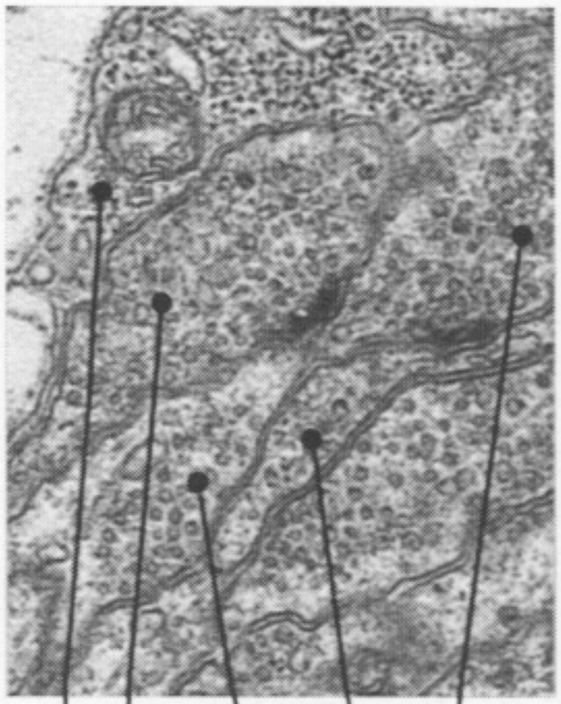

AVDR
AIMR
ALMR
ASJR
b

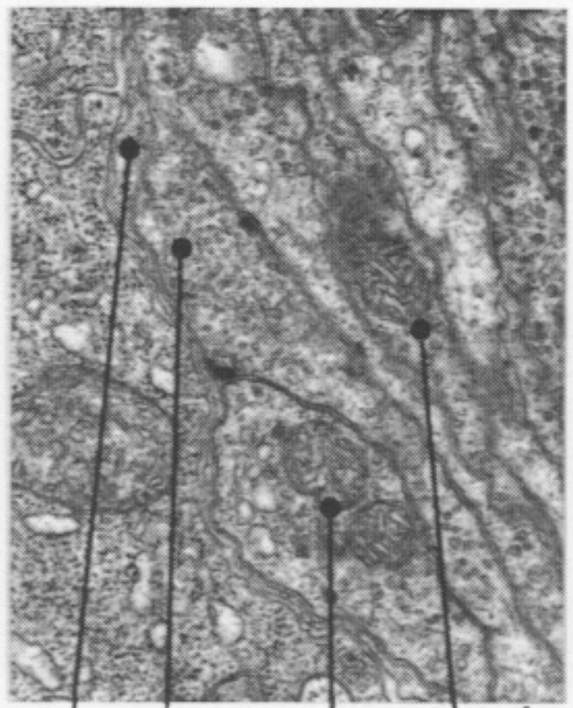

MUSCLE
CEPshVL
AIML
ASGL
AIAL
c

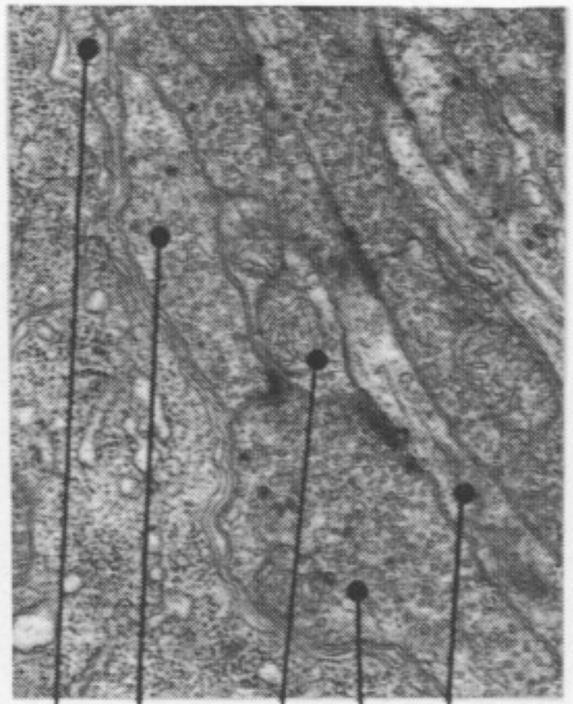

ALMR
CEPDR
SIBDL
AIMR
d

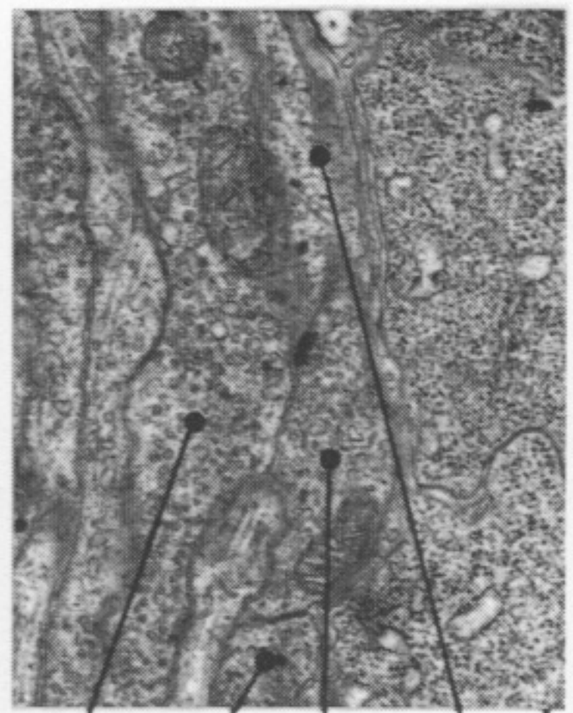

AIML
e

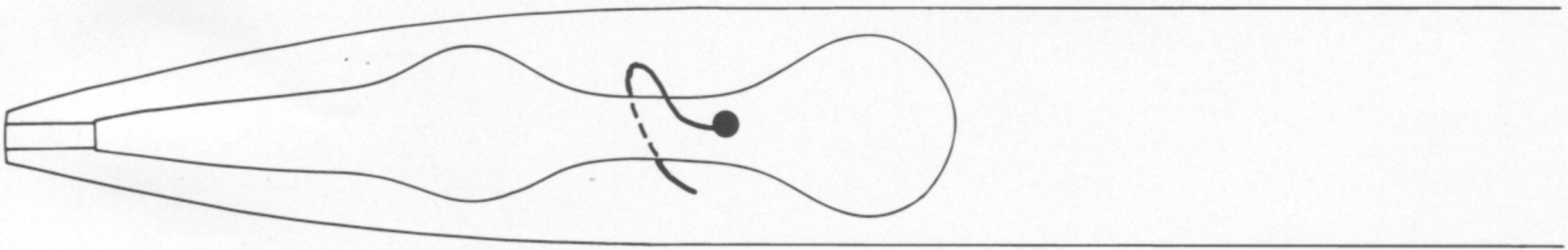
AIM


AINR
AFDL
a
CEPshDL
AIYL
ASER

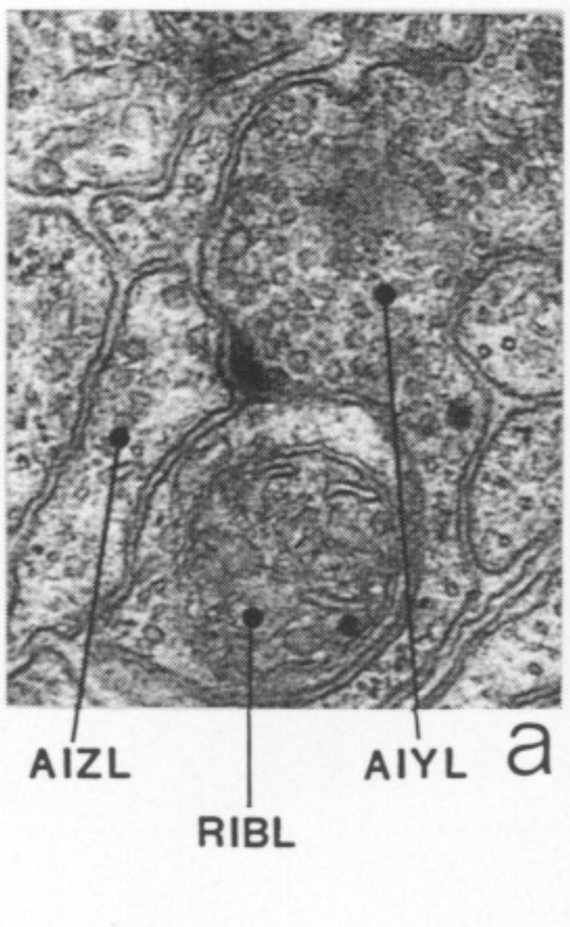

AINR
AUAL
b
CEPshVL
BAGR

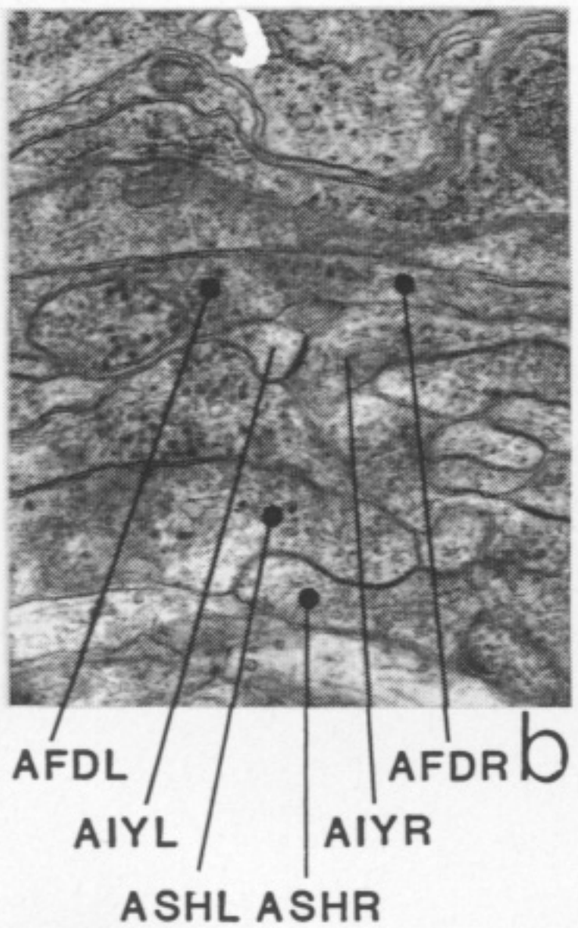

AINR
RIAL
C
CEPshVL
BAGR
RIBL

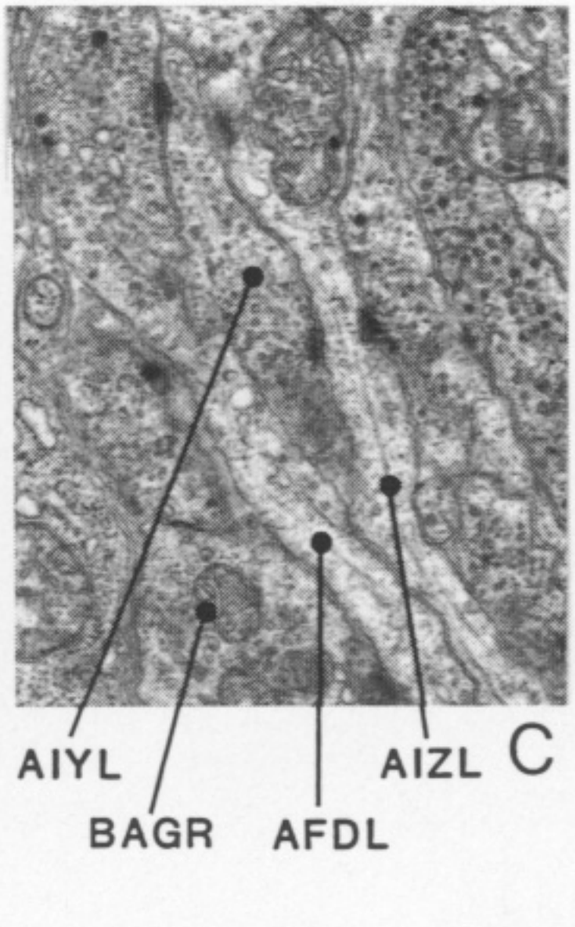

AUAR
AFDR
d
BAGL
AINL

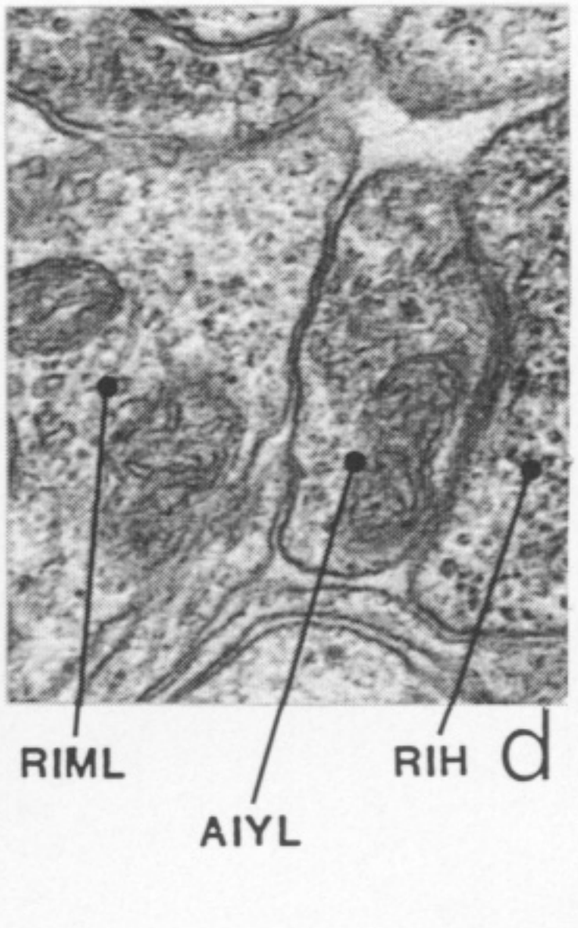

AINL
e

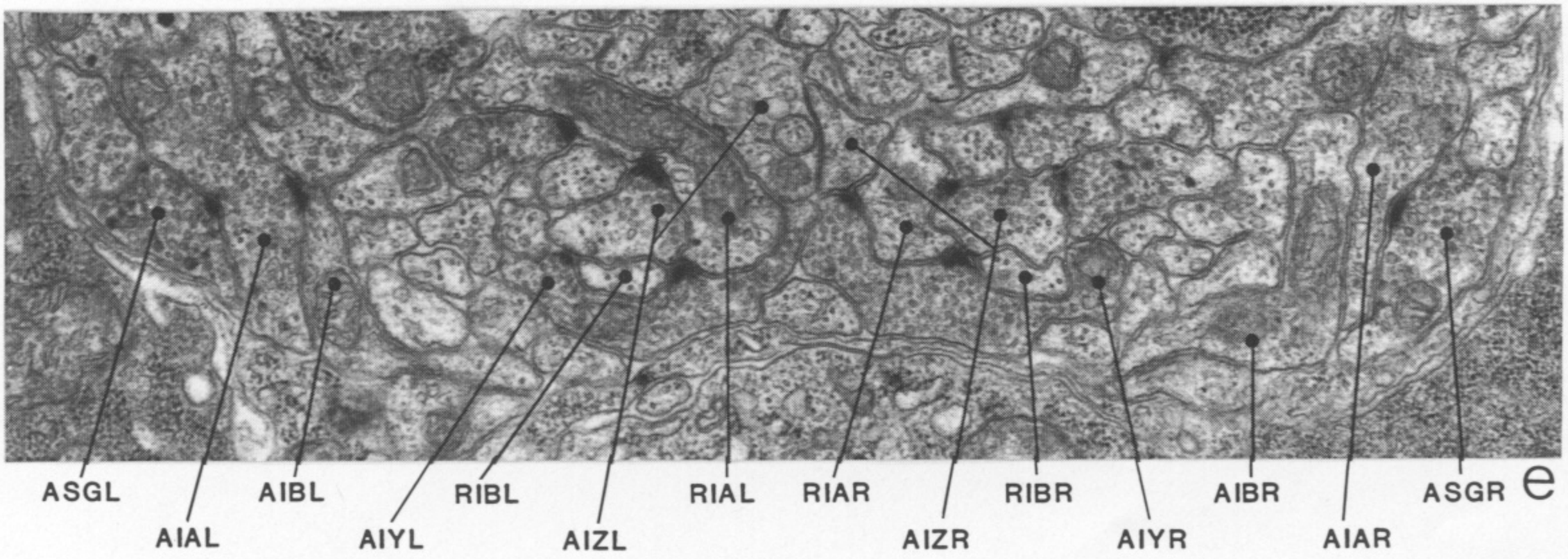
AIN

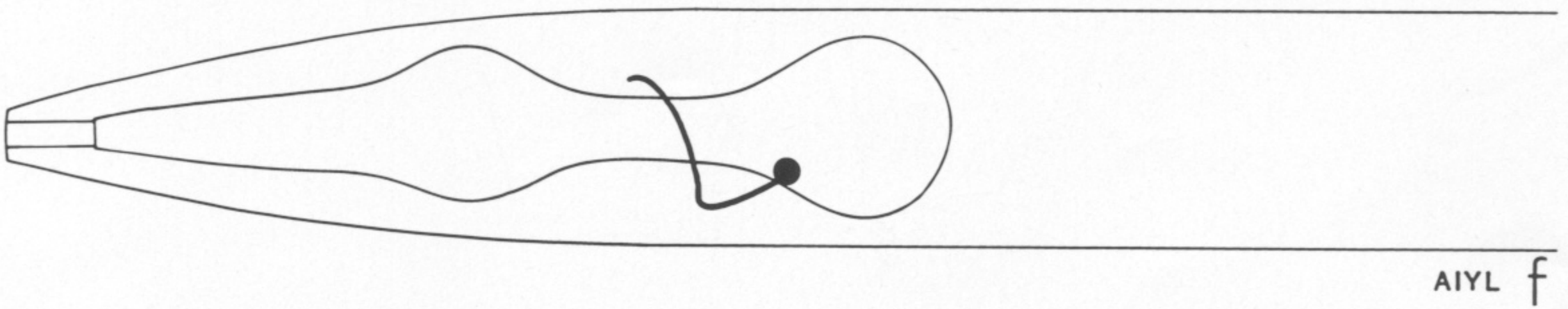

AIZL
RIBL
AIYL
a


AFDL
AIYL
AIYR
AFDR
b
ASHL ASHR

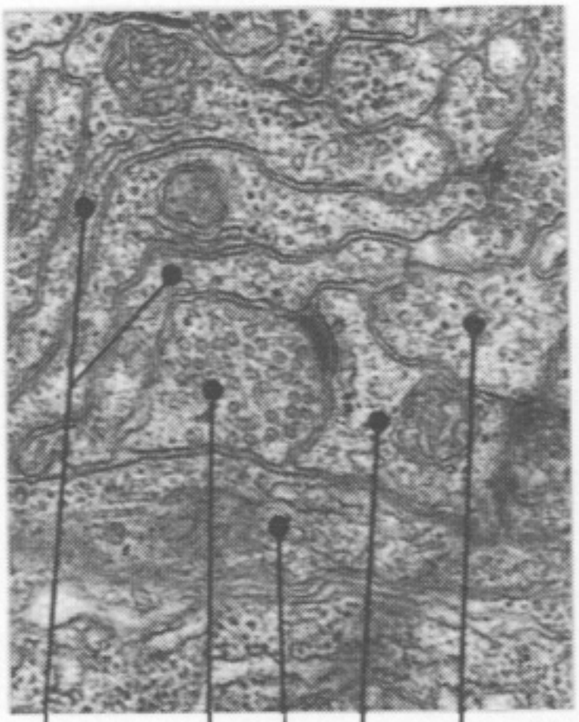

AIYL
BAGR
AFDL
AIZL
c

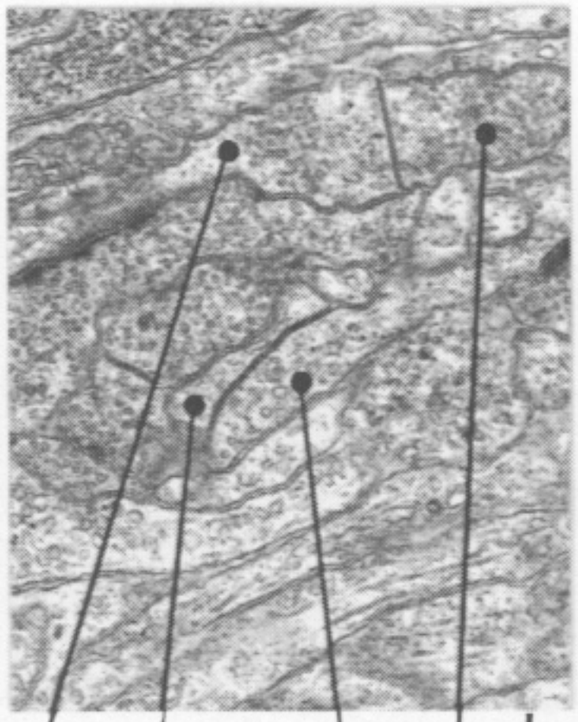

RIML
AIYL
RIH
d

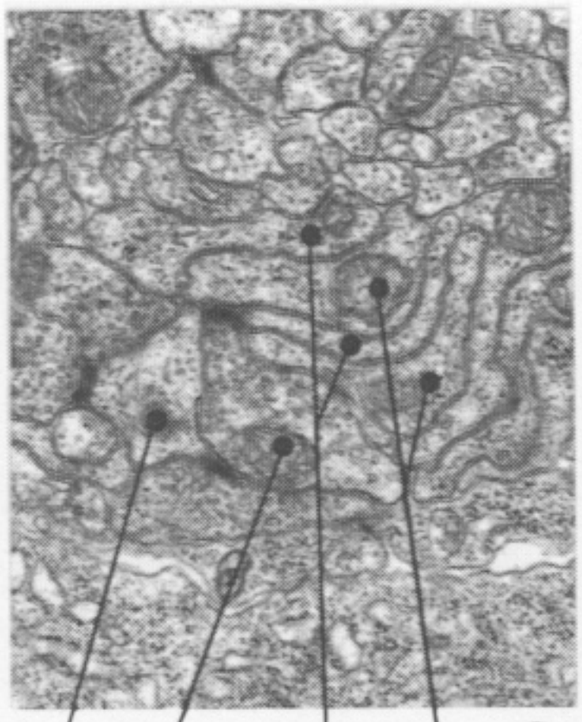

ASGL
AIBL
RIBL
RIAL
RIAR
RIBR
AIBR
ASGR
e
AIAL
AIYL
AIZL
AIZR
AIYR
AIAR

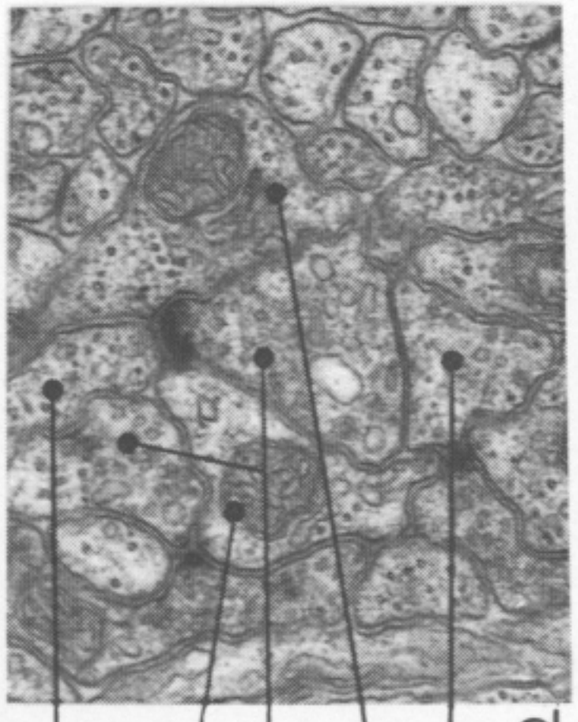

AIYL
f

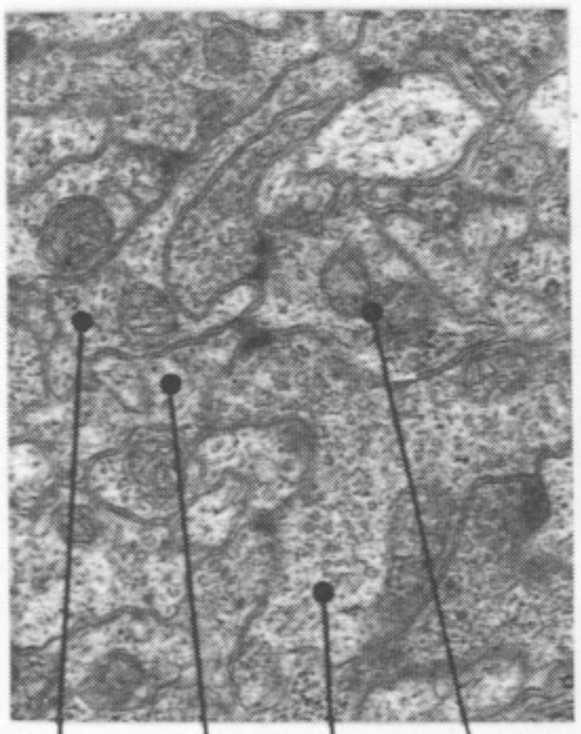
AIY

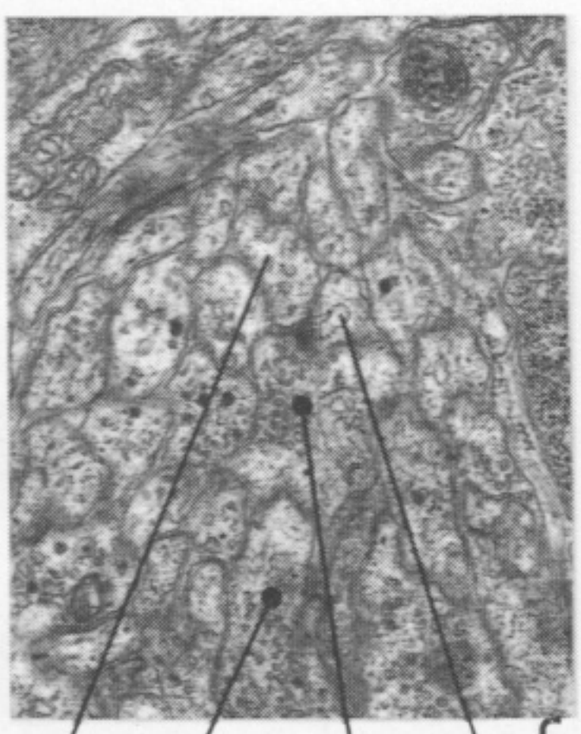

SMBDR
AIZR
RIAR
RIH
AIZR
a

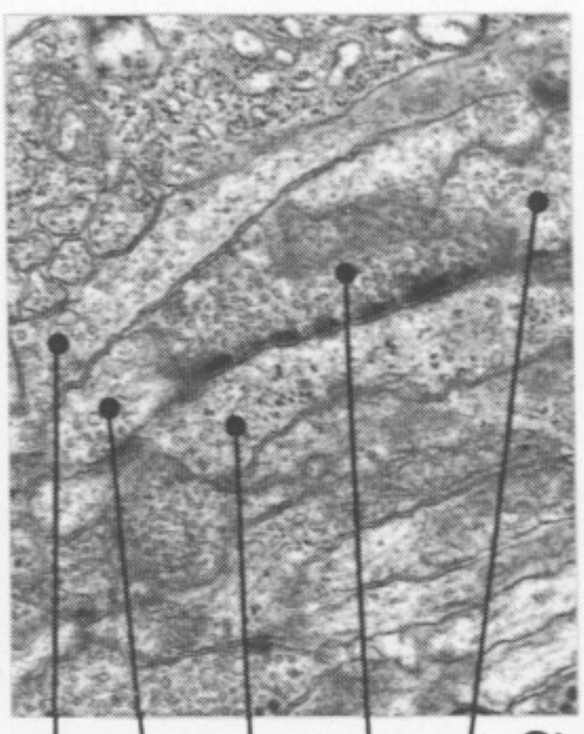

RIBL
AIZL
AIZR
RIBR
b

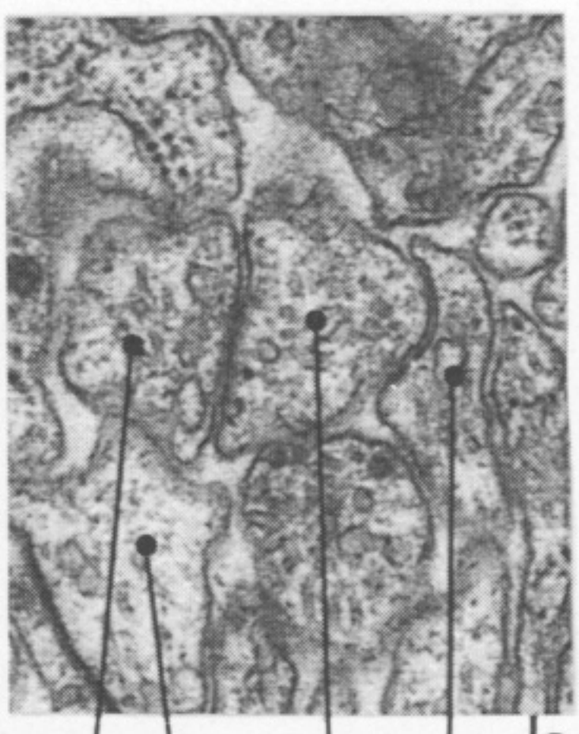

RIAL
AIZL
SMBDL
SMBVL
c


SMBVL
RIAL
SMBDL
AIZL
AIZR
d


SMDDR
AIBL
AIZR
RIMR
e

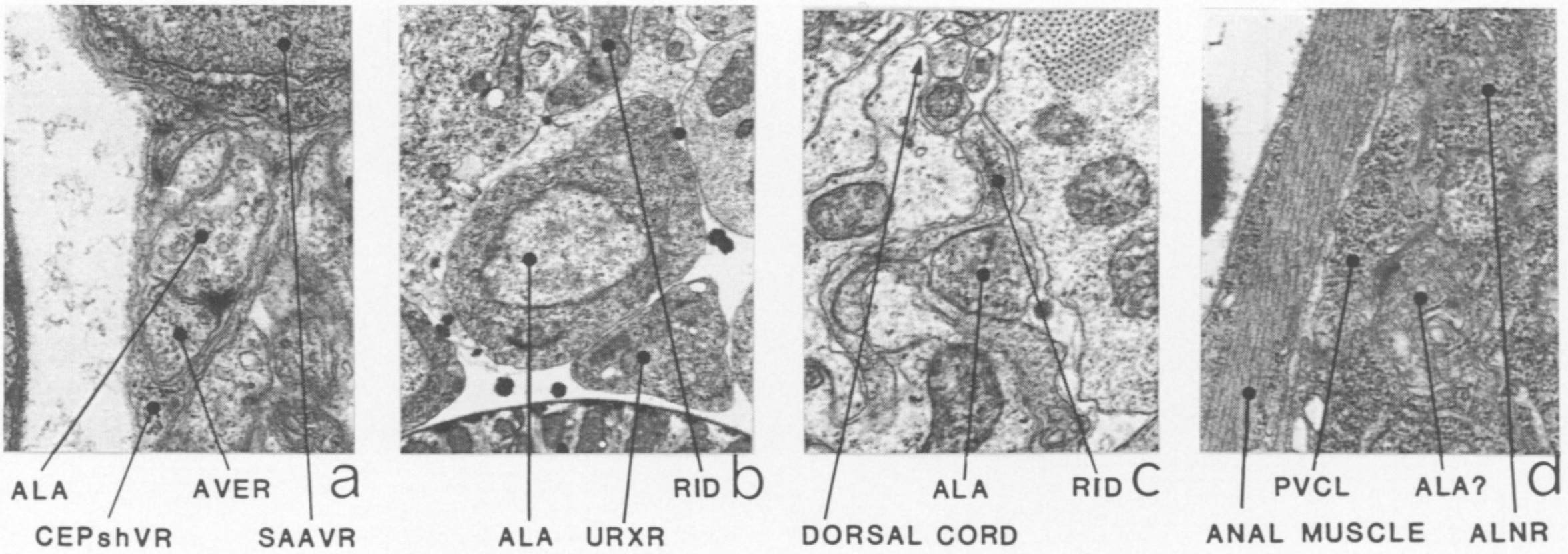

AIBR
ADFR
AIZR
AIAR
f


RIGL
AIBR
RIML
AIZL
AIBR
g

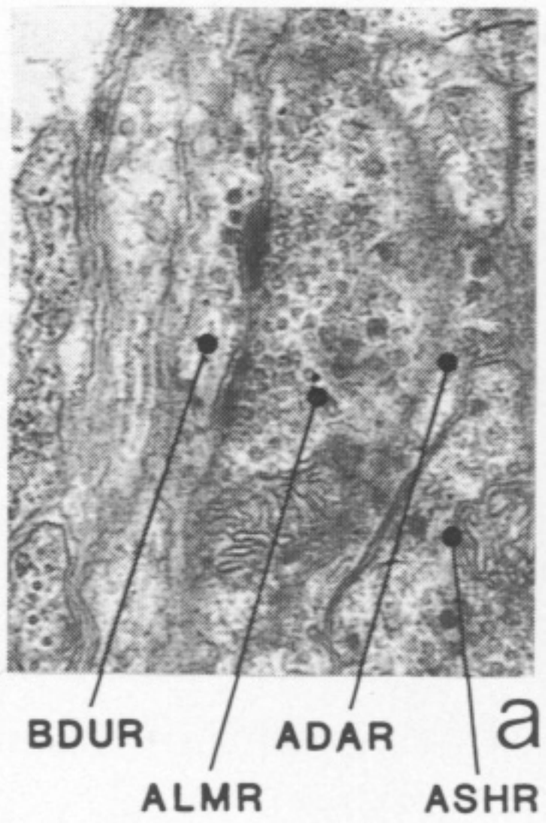

ASHR
AVBR
AIZR
ASGR
h

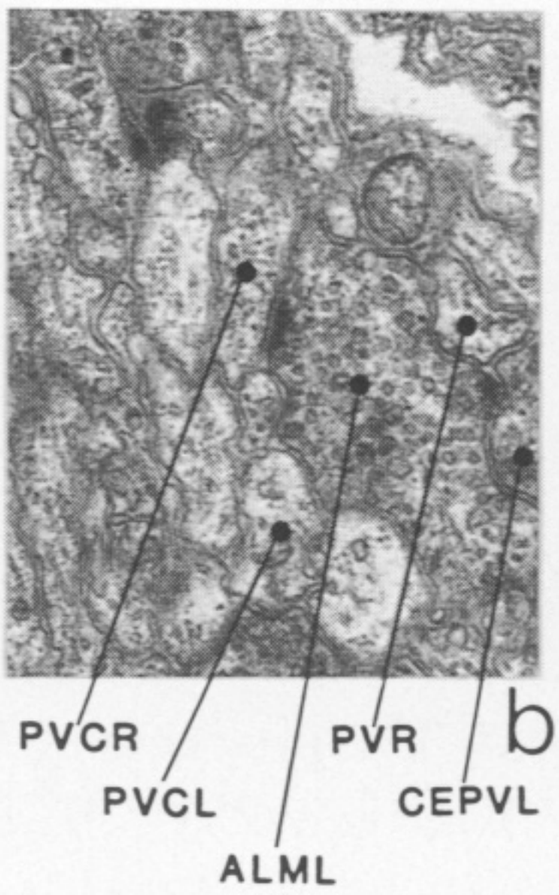
AIZL
i

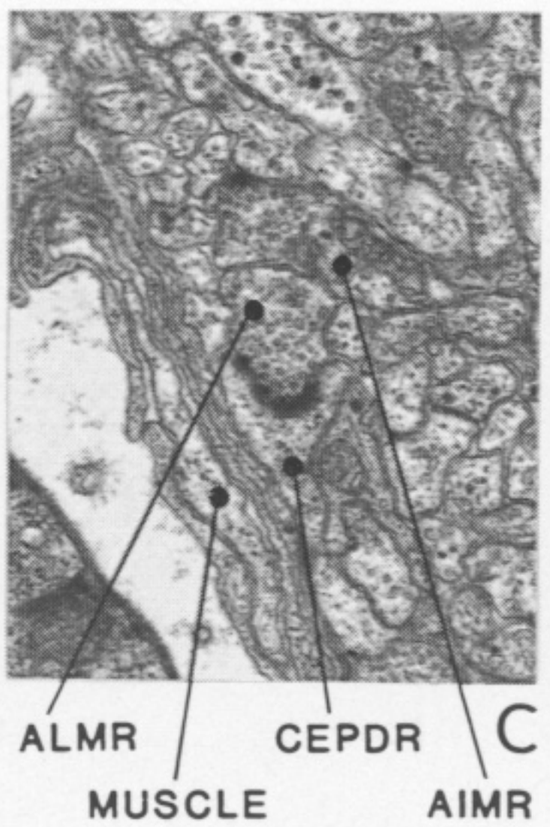
AIZ

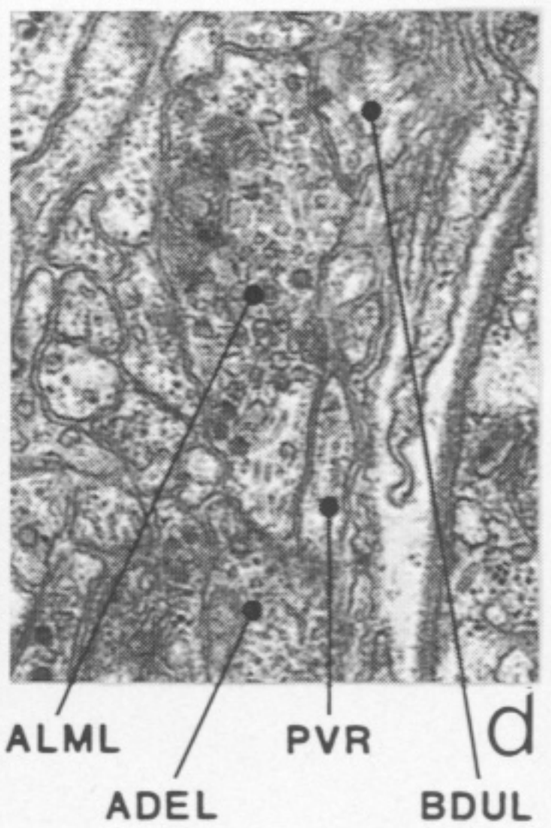

ALA
AVER
a
CEPshVR
SAAVR
RID
b
ALA
URXR
ALA
RID
C
DORSAL CORD
PVCL
ALA?
d
ANAL MUSCLE
ALNR
ALA
e
d
ALA
f

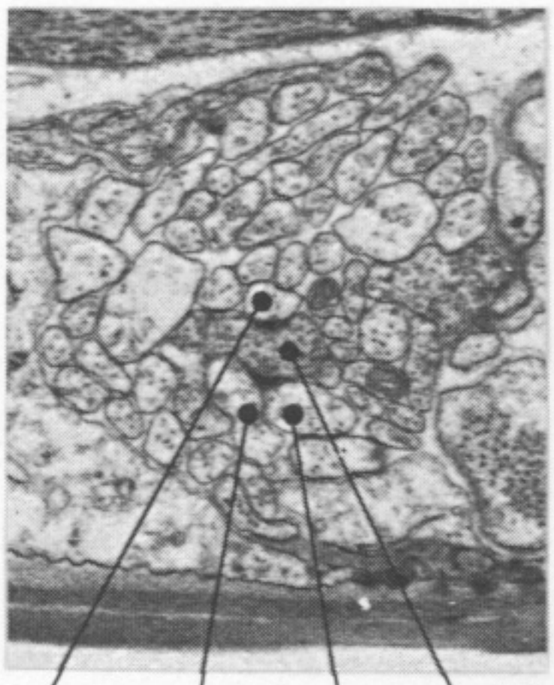
ALA

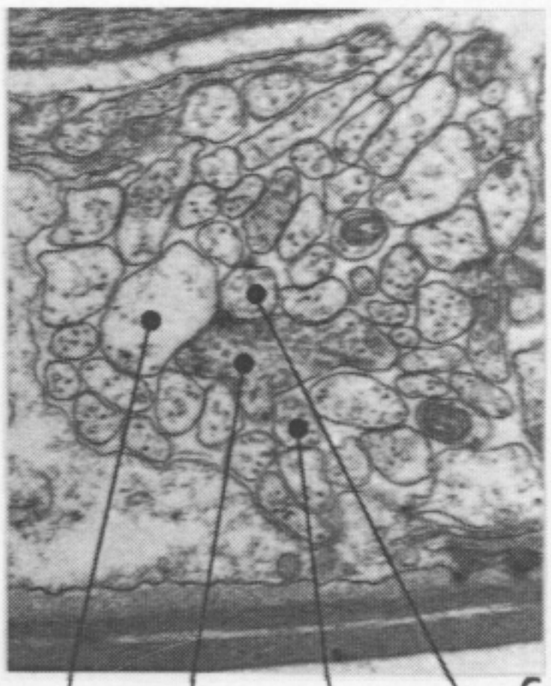

BDUR
ADAR
a
ALMR
ASHR

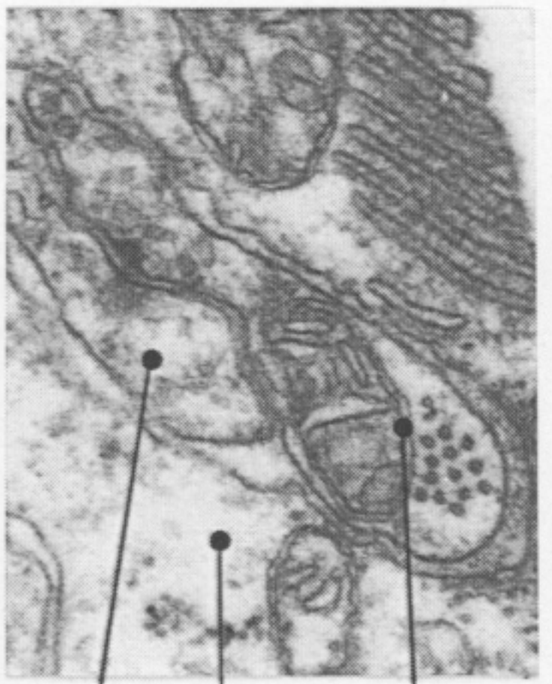

PVCR
PVR
b
PVCL
CEPVL
ALML

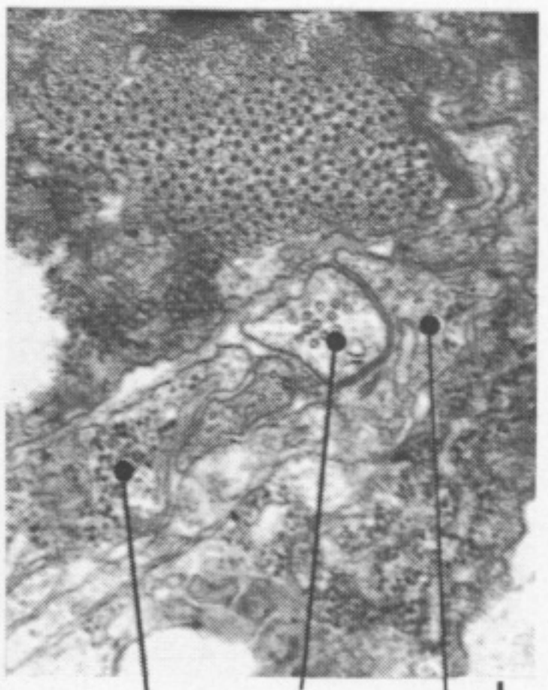

ALMR
CEPDR
c
MUSCLE
AIMR

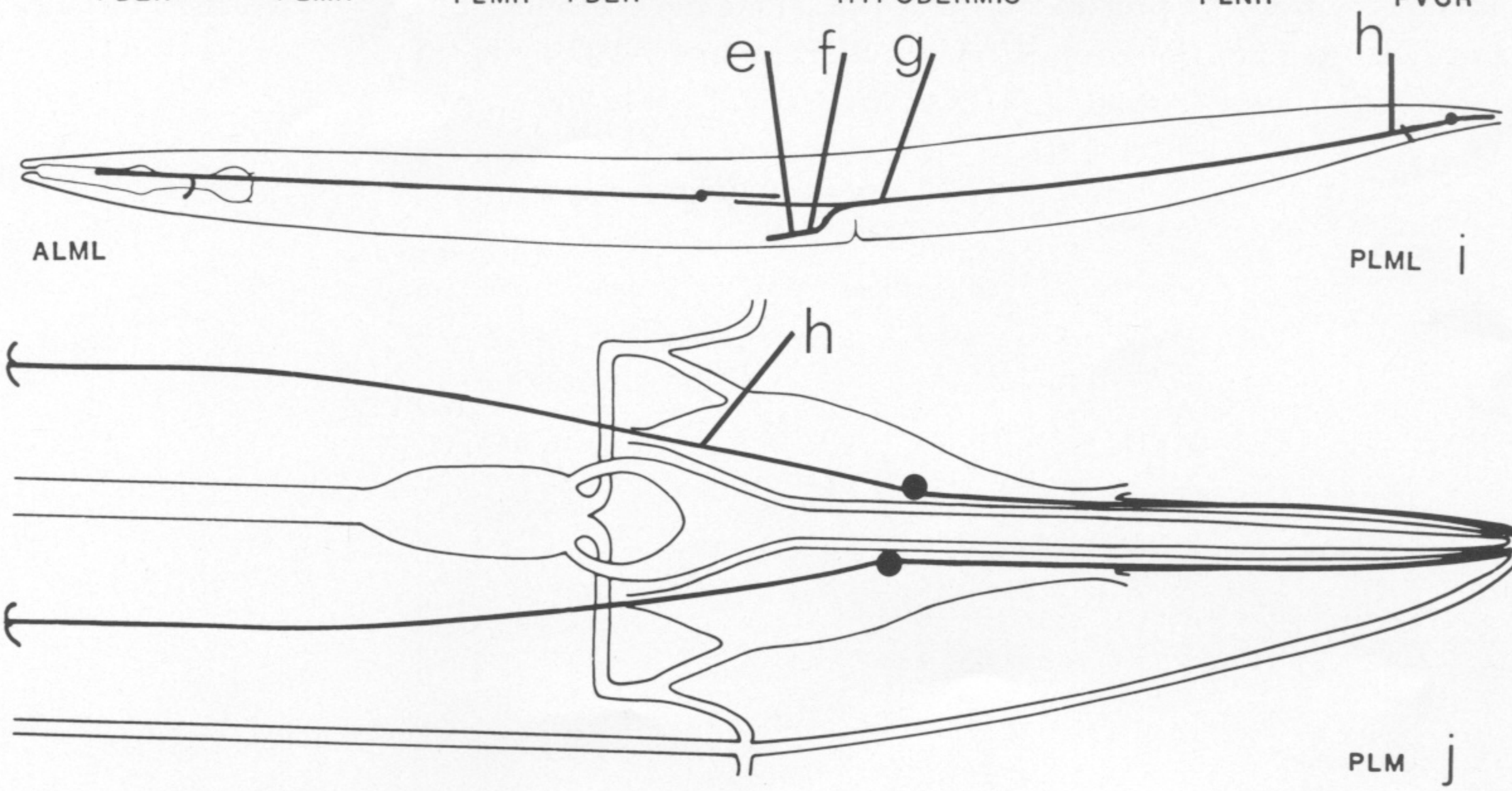

ALML
PVR
d
ADEL
BDUL


AVDL
DVA
e
PDER
PLMR

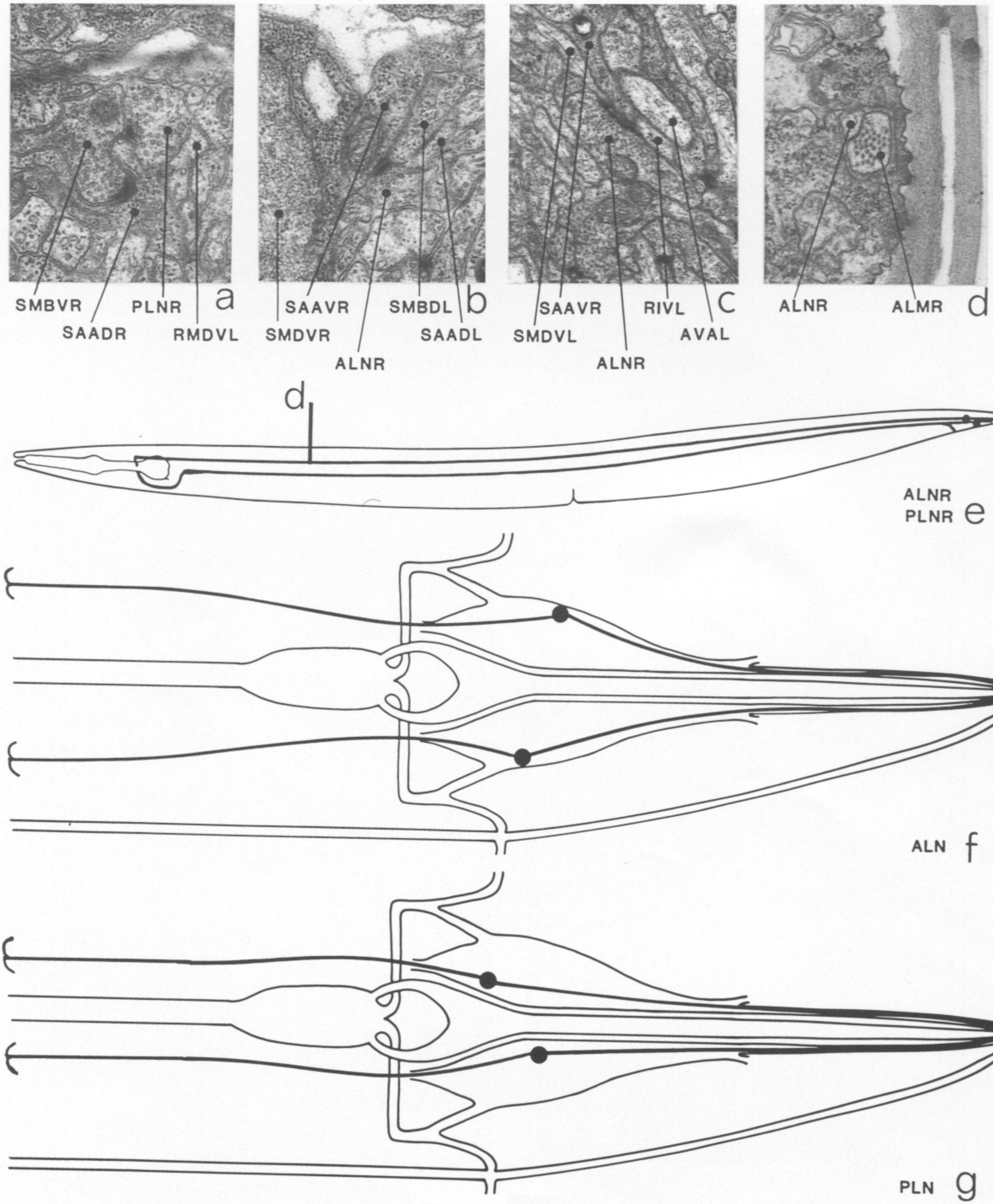

AVAL
AVDR
f
PLMR
PDER


HSNR
PLMR
g
HYPODERMIS

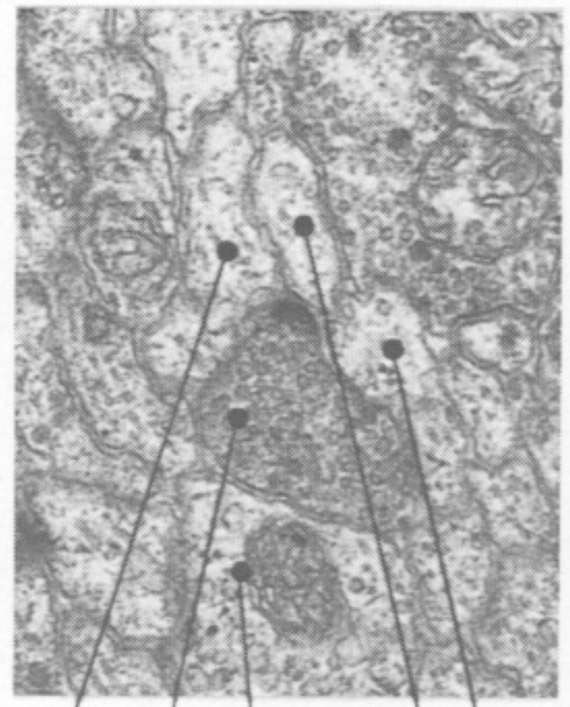

PLMR
h
PLNR
PVCR

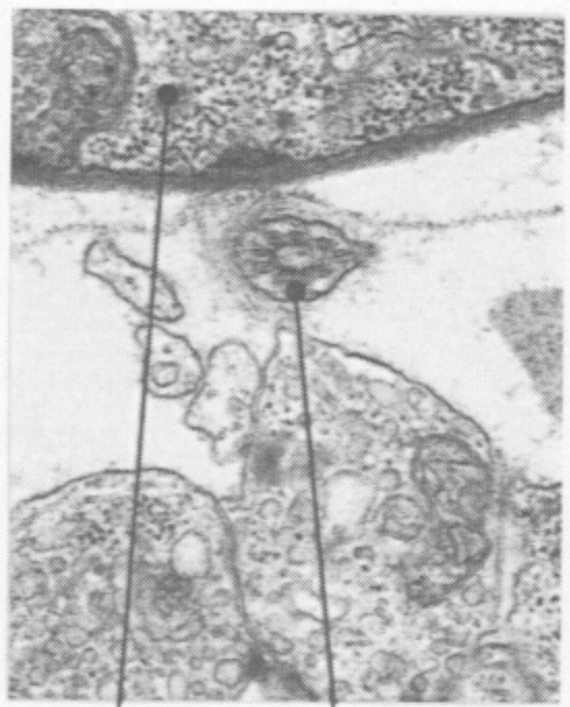

e
f
g
h
ALML
PLML
i
h
PLM
j

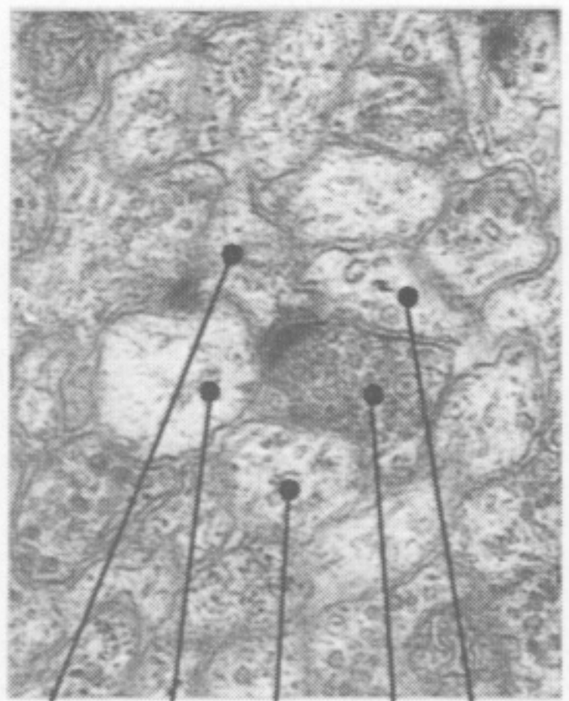
ALM AND PLM

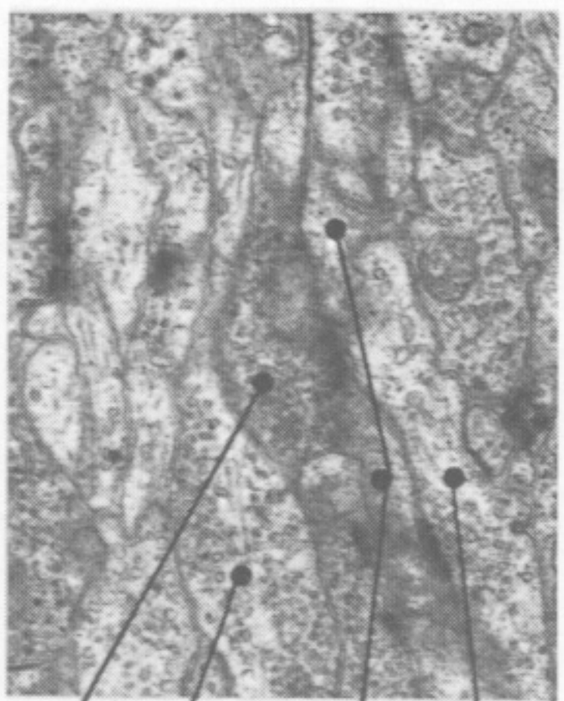

SMBVR
SAADR
PLNR
RMDVL
a
SAAVR
SMDVR
ALNR
SMBDL
SAADL
b
SAAVR
SMDVL
ALNR
RIVL
AVAL
c
ALNR
ALMR
d
d
ALNR
PLNR
e
ALN
f
PLN
g

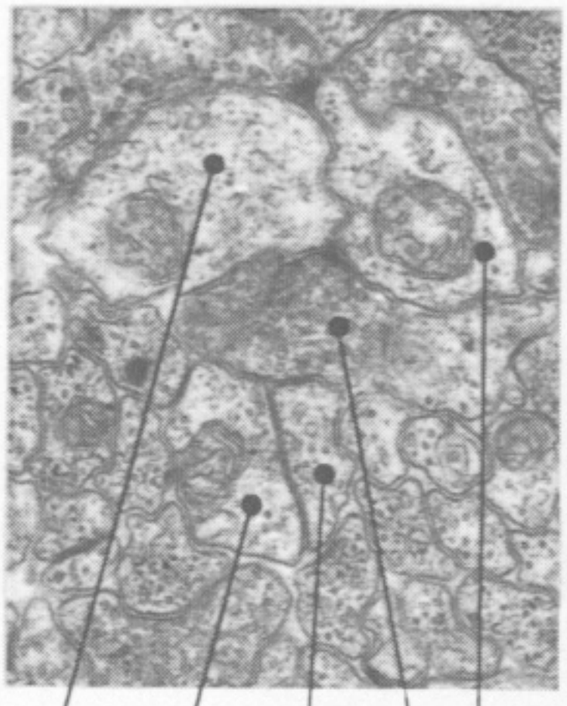
ALN AND PLN

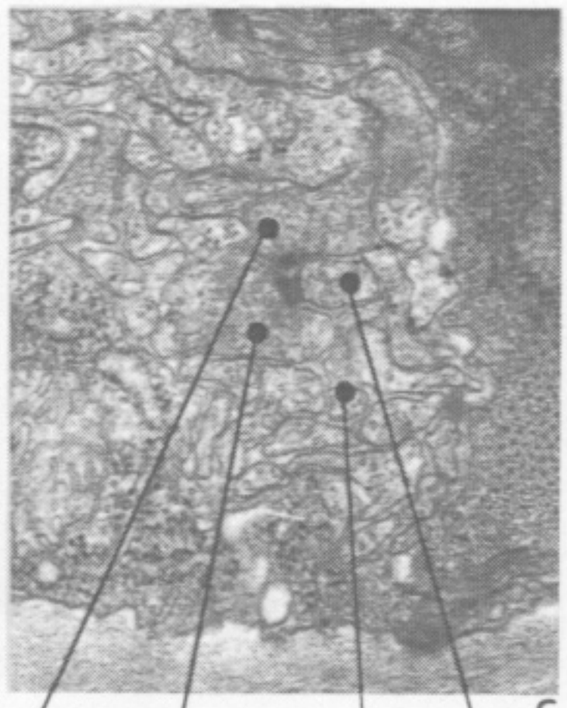

AVBR
PVCL
a
AQR
AVDR
DVA

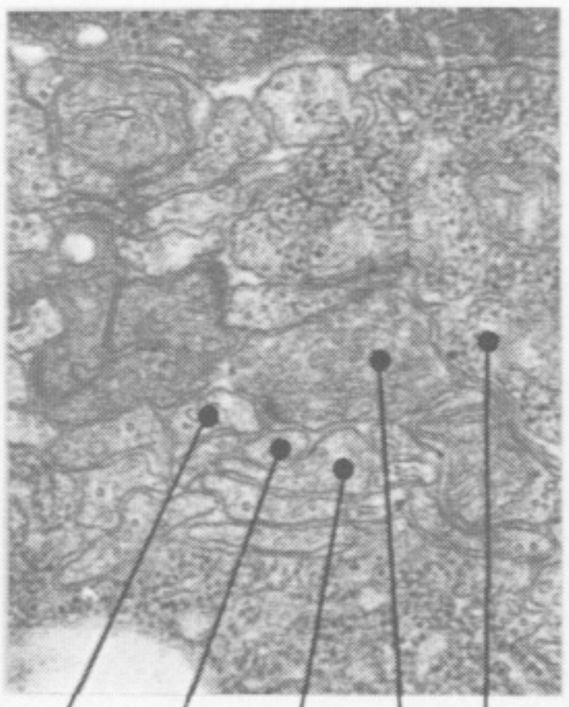

PHARYNX
b
AQR
BASAL BODY

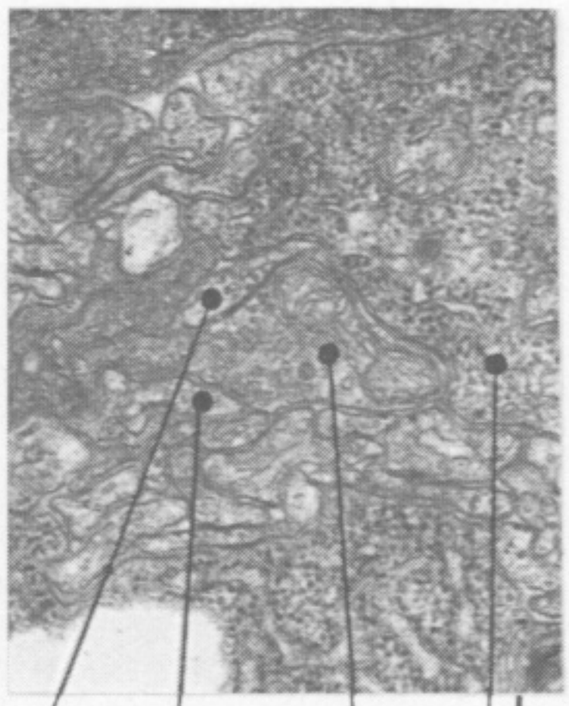

AVAL
AQR
c
AVBL
PVCR
DVA

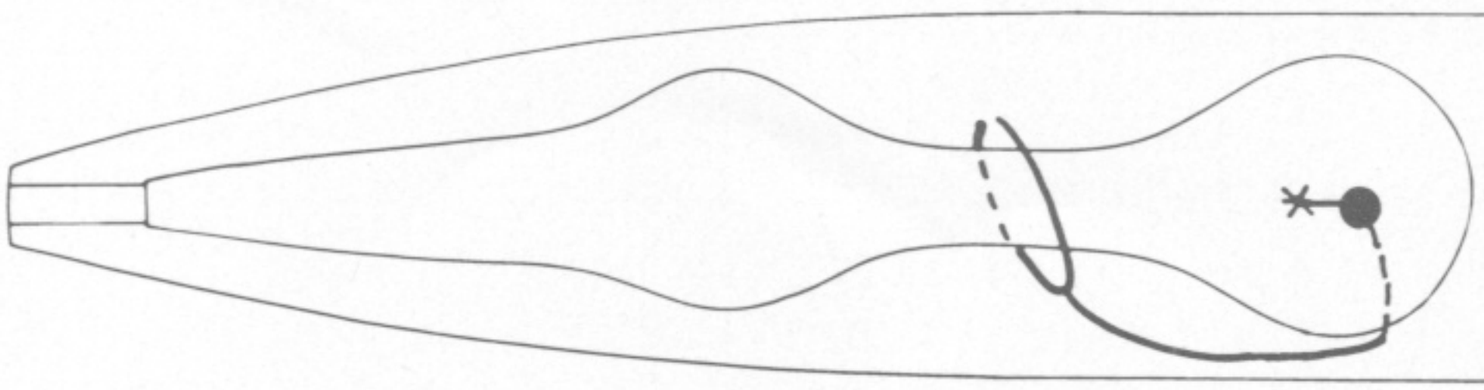

AQR
RIAR
d
PVPR
BAGL

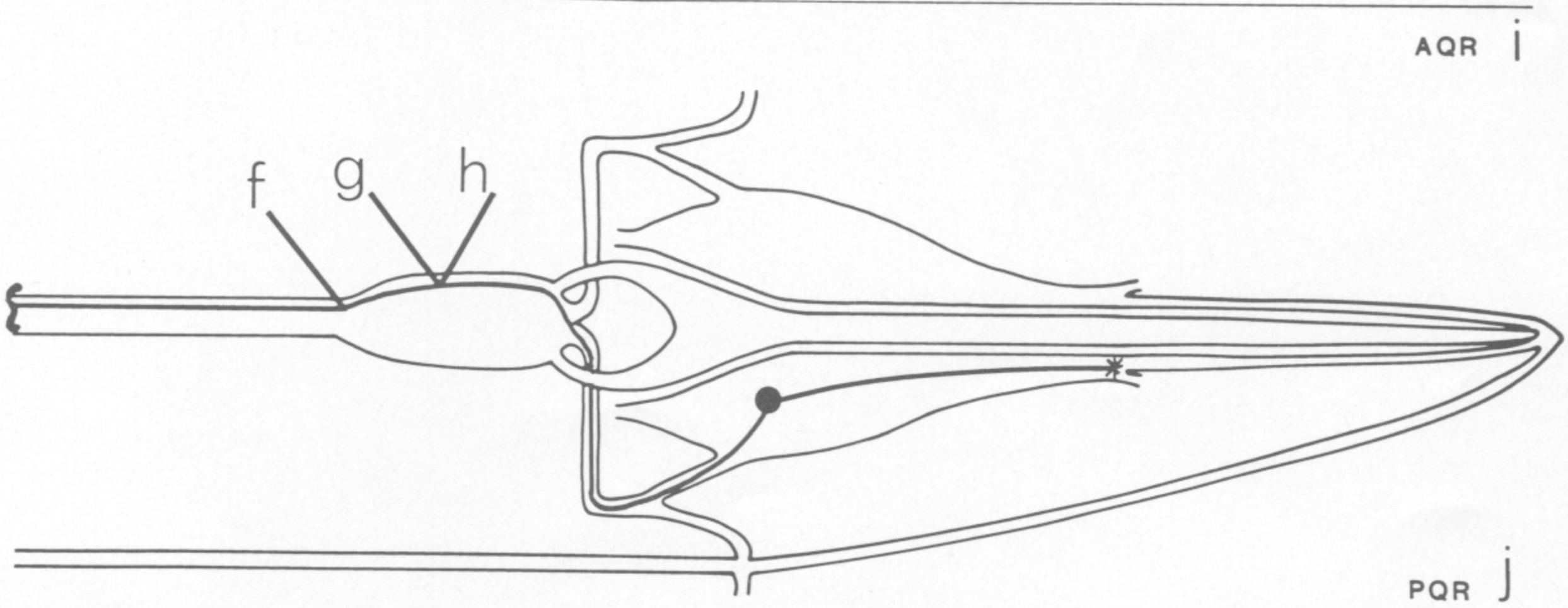

AVAR
AQR
e
RIGL
AVAL
RIGR

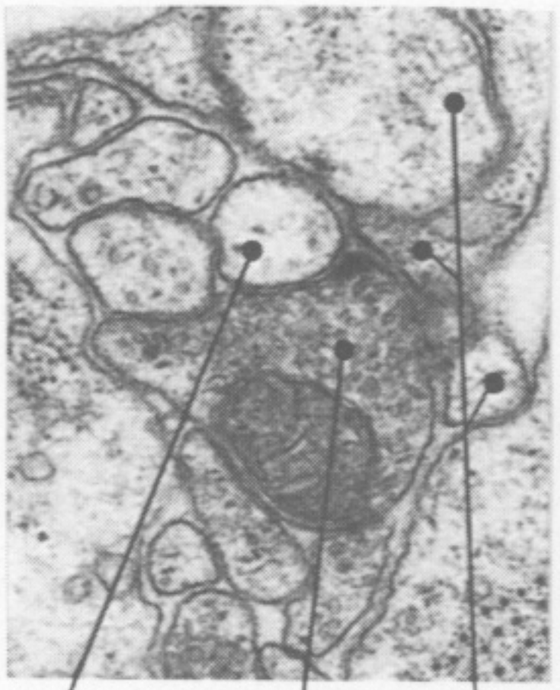

LUAR
DB7
f
PQR
AVAL

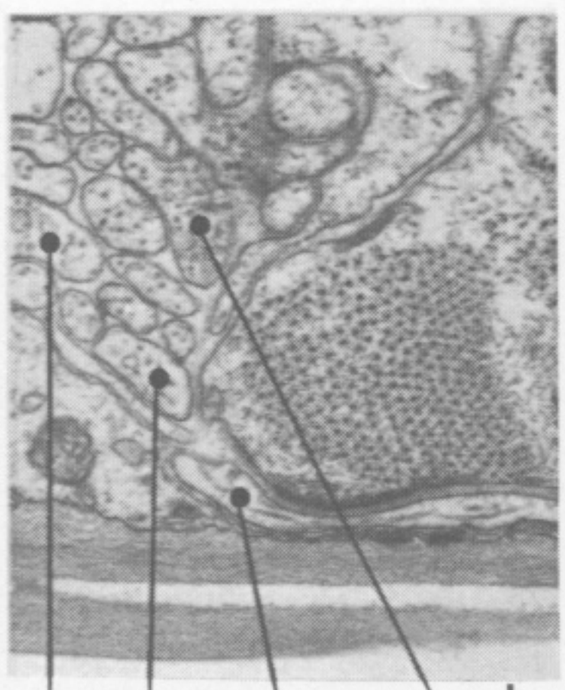

AVAR
PQR
g
AVDR
PVT
LUAL

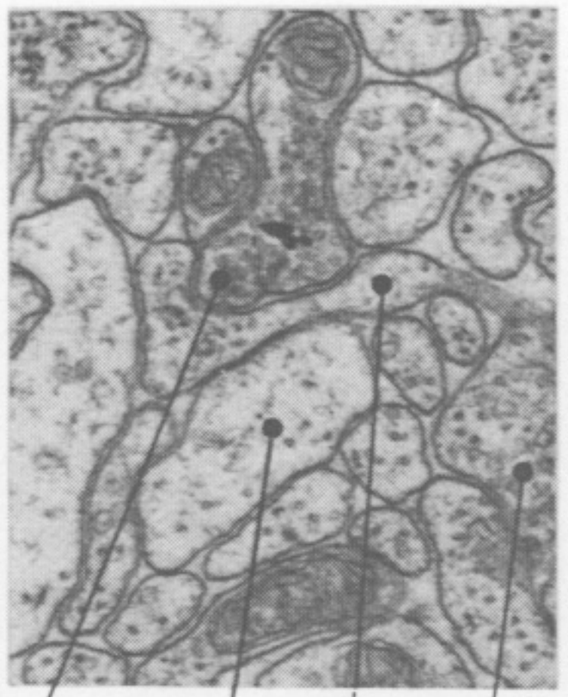

PVPL
PQR
h
AVAR
PVT

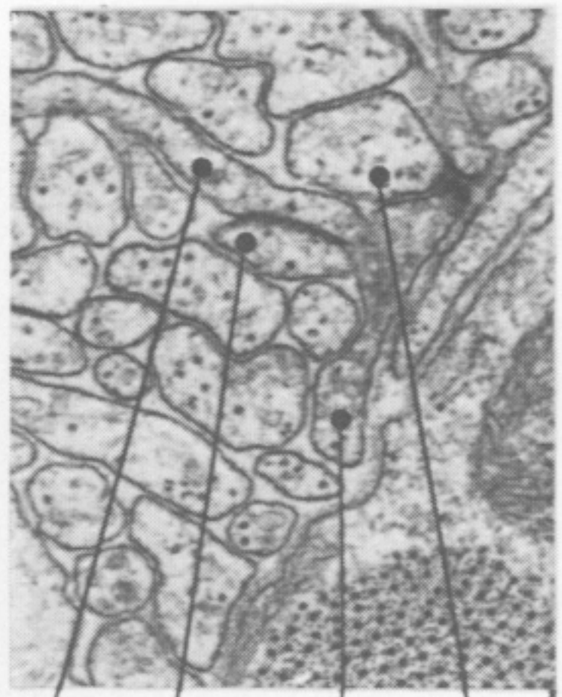

AQR
i

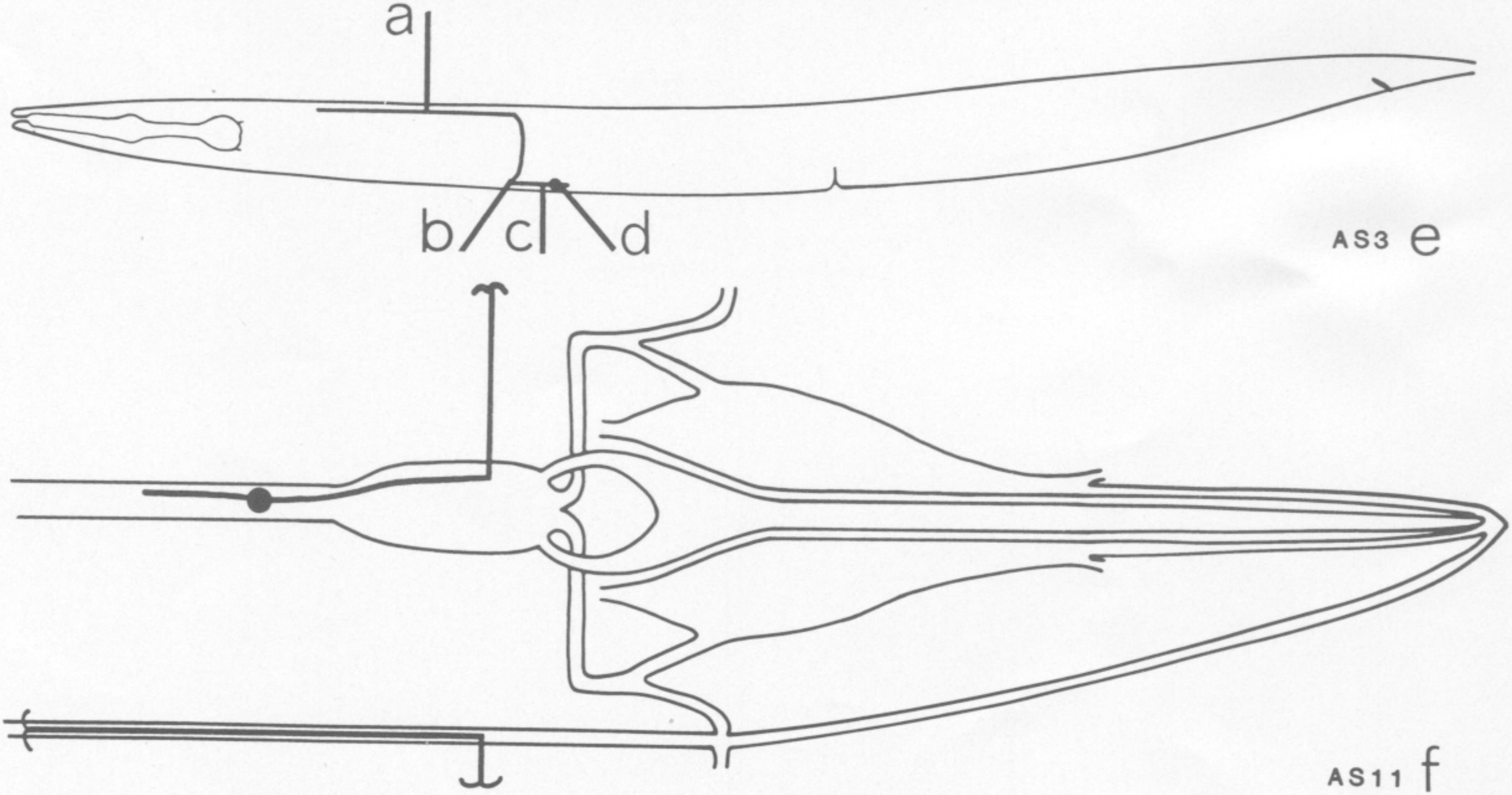

f
g
h
PQR
j


VD3
AS3
a
MUSCLE ARMS

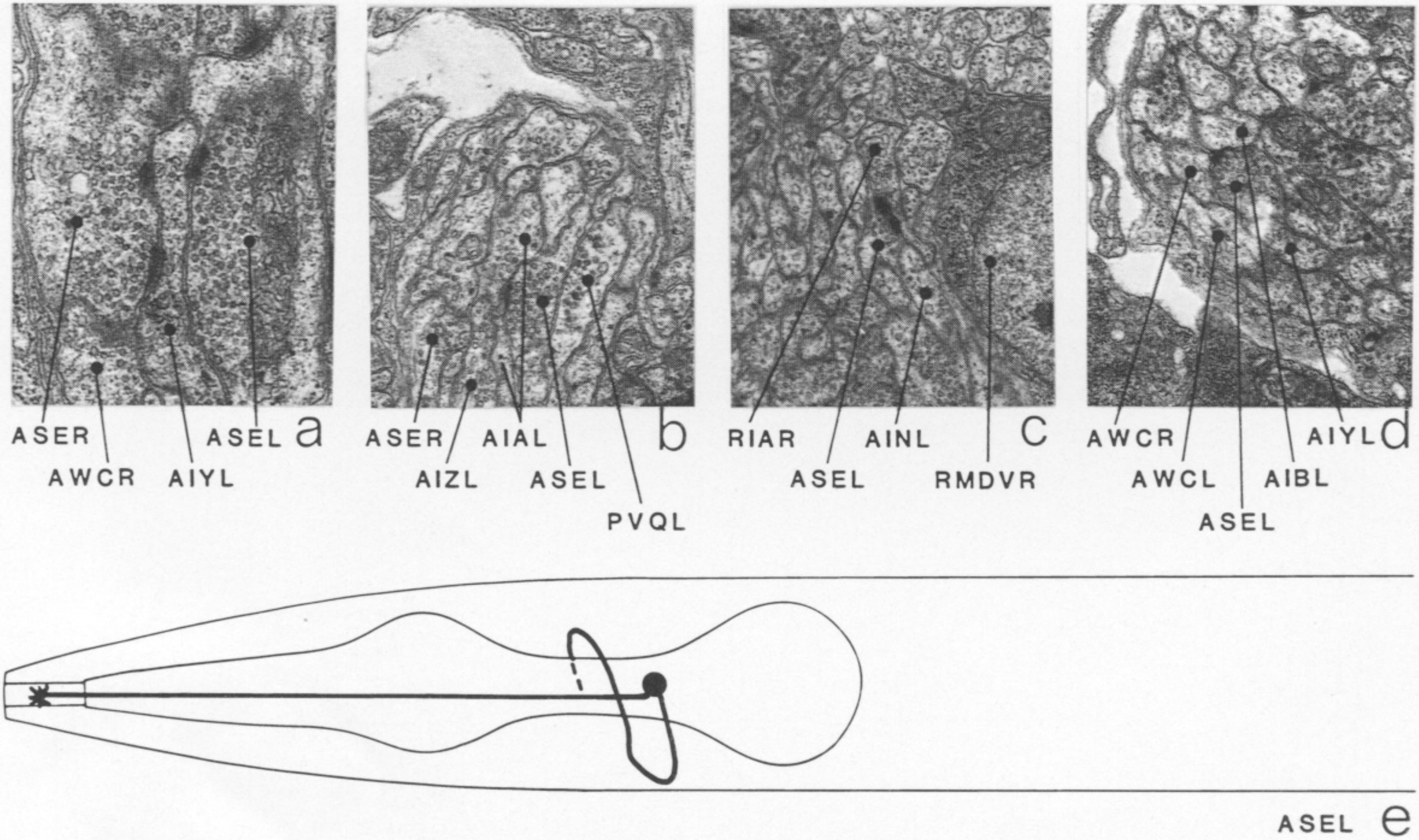

DVA
VB3
b
AVKL
AS3 COMMISSURE


AVER
AS3
c
AVAR
VA4

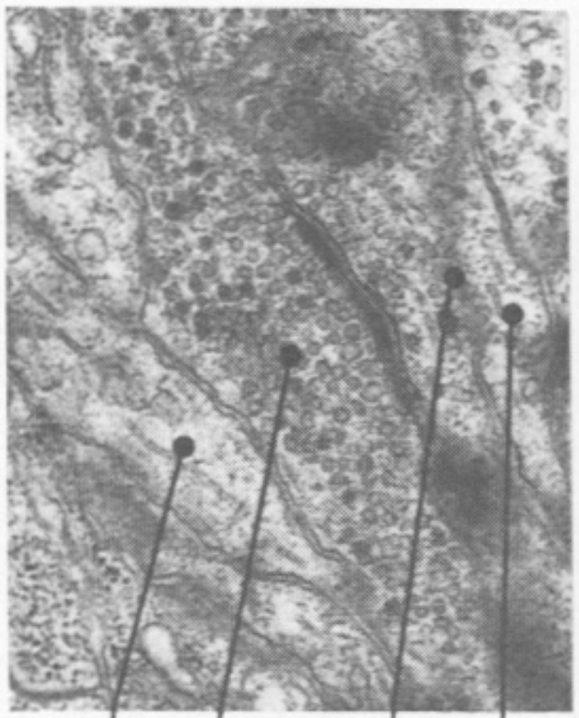

AS3
VB3
d
VA6
VD4

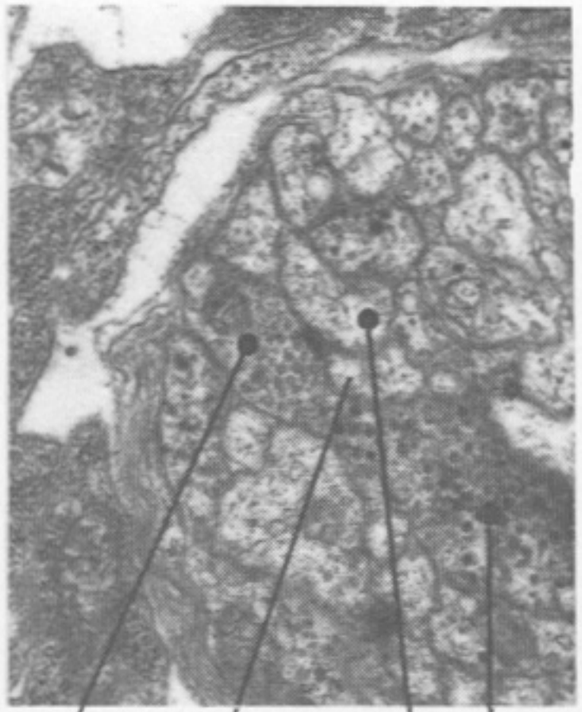

a
b
c
d
AS3 e
AS11 f

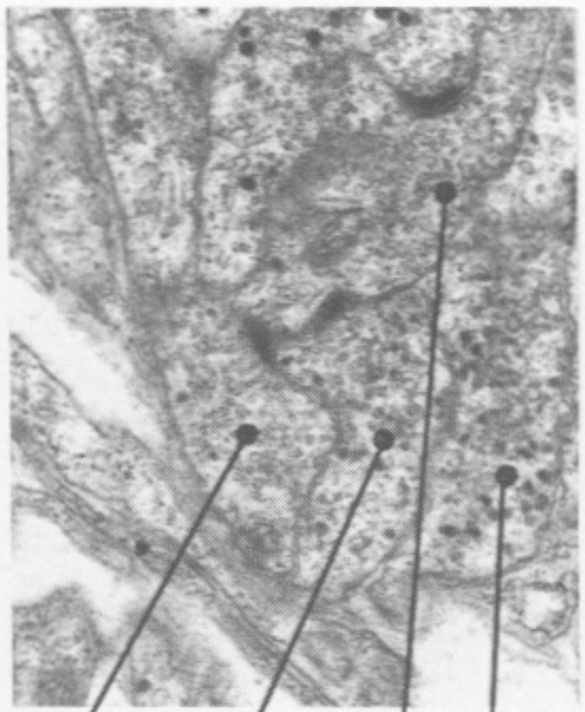
ASn

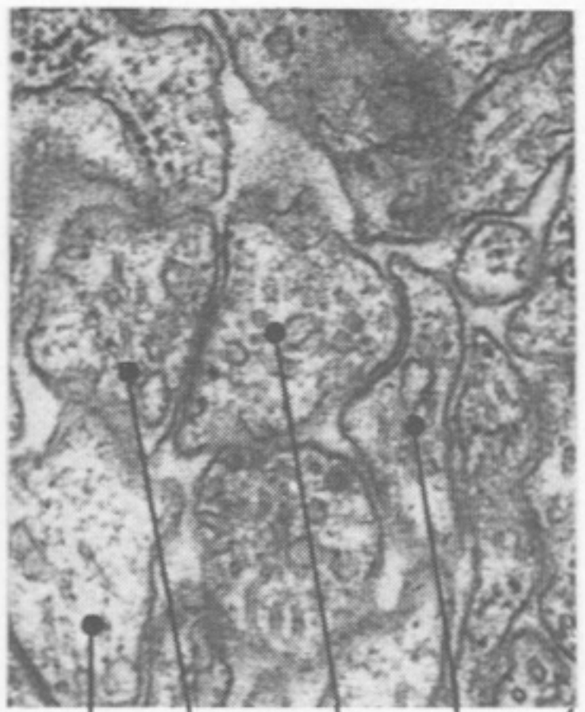

ASER
AWCR
AIYL
ASEL
a
ASER
AIZL
AIAL
ASEL
PVQL
b
RIAR
ASEL
AINL
RMDVR
c
AWCR
AWCL
AIBL
AIYL
d
ASEL
ASEL
e

ASE

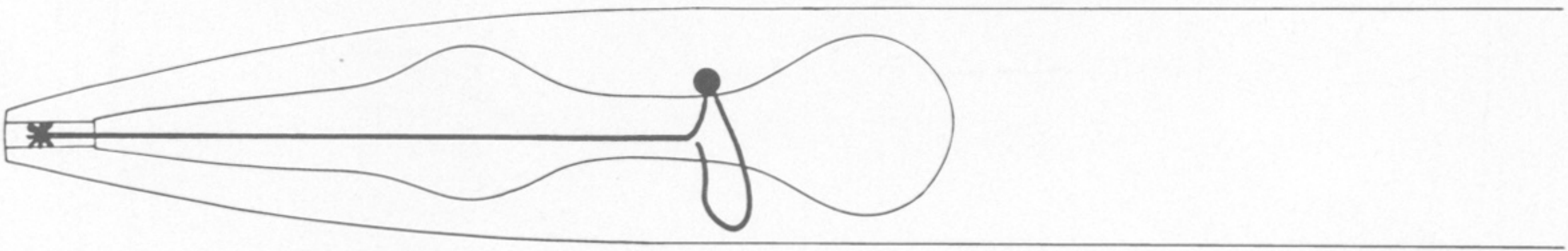




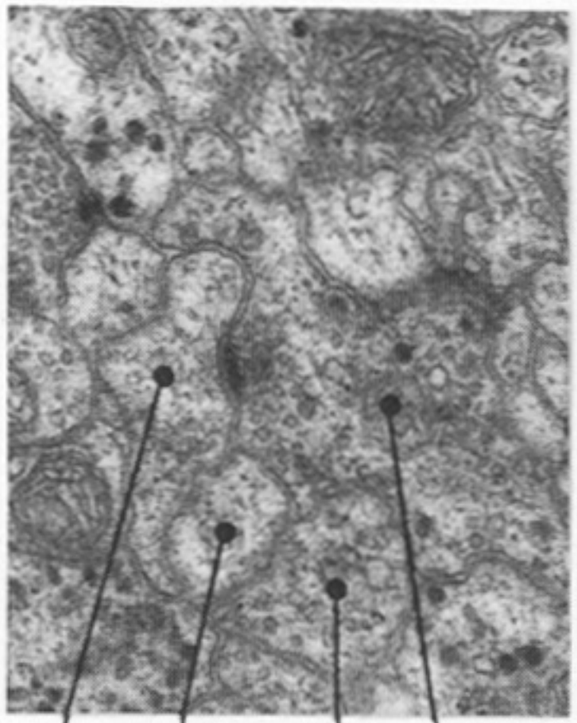


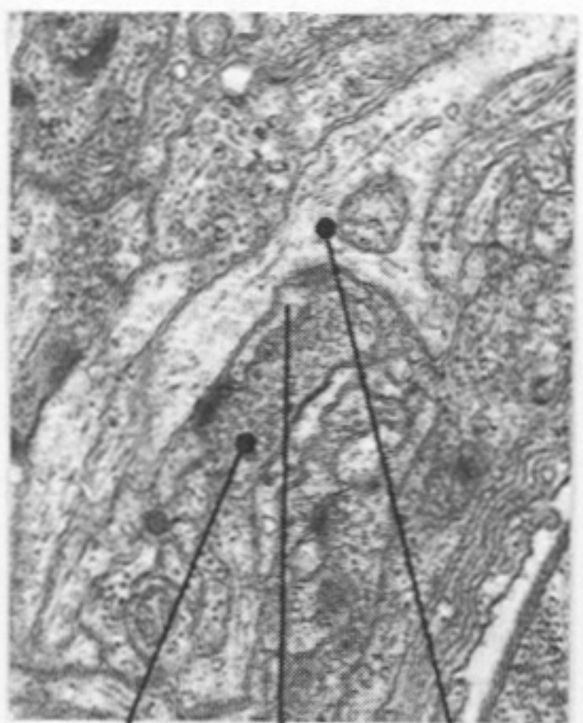


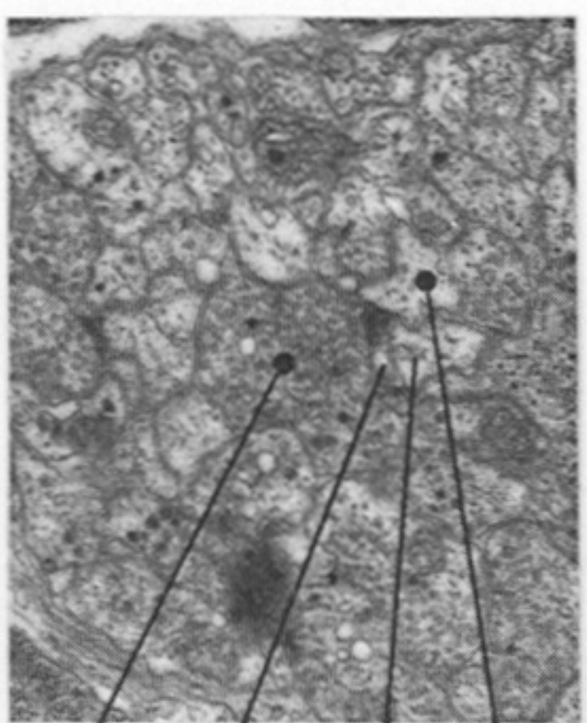
ASGL ASKL AIBL ADLL ASGR ASIR ASHR ASGR

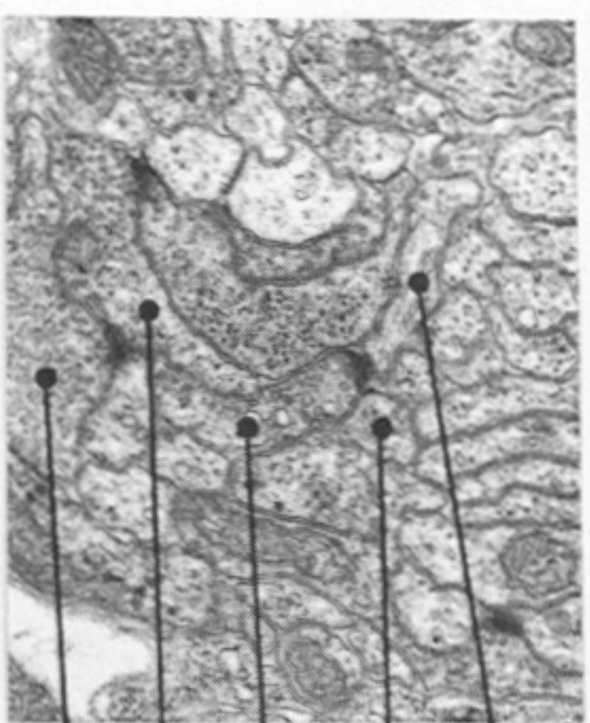


ASG

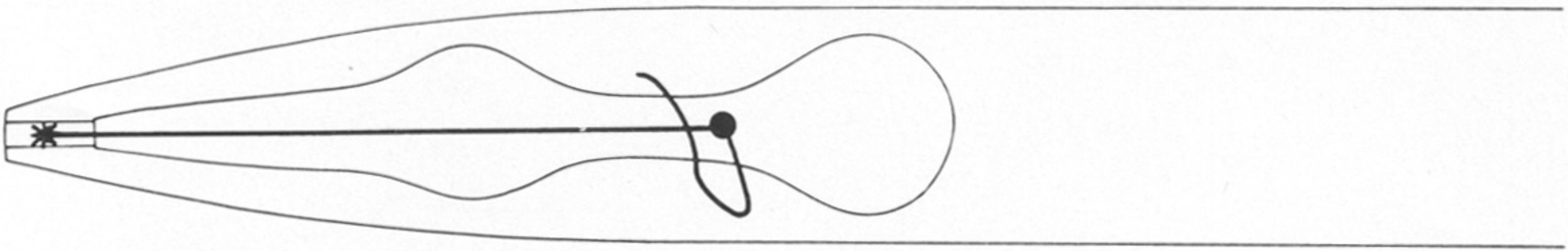








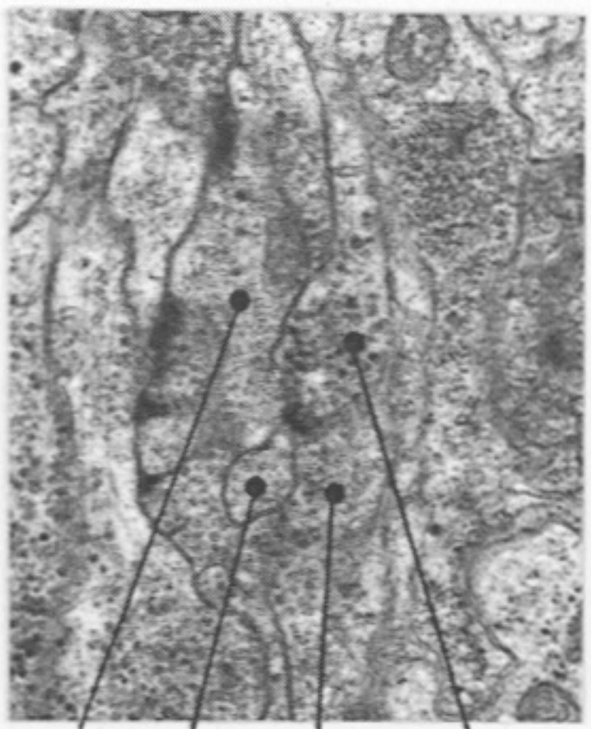
AIBL ASEL AVAL AVAR AVBR AIAL ASHL RIAL

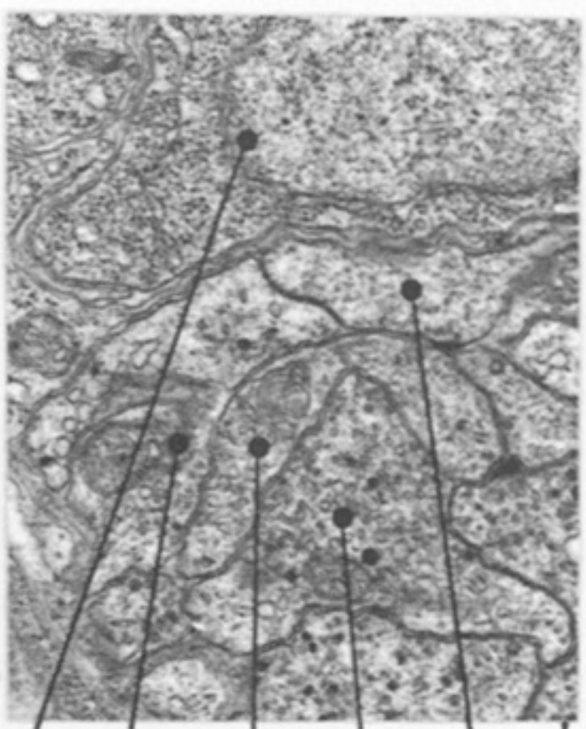


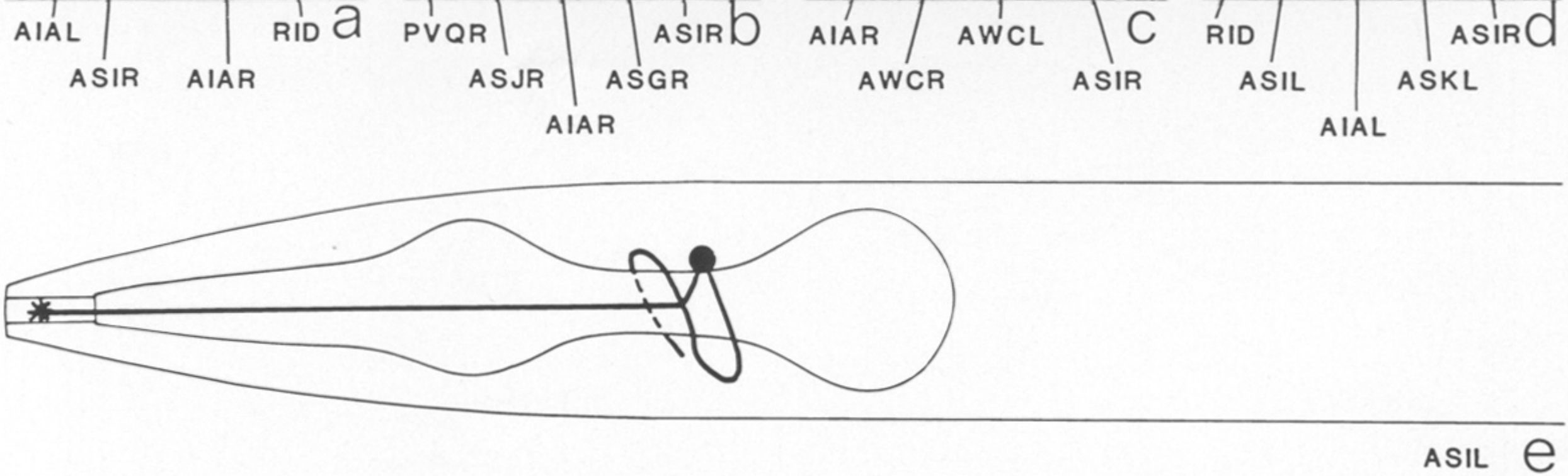
ASH


AIAL
ASIR
AIAR
RID
a

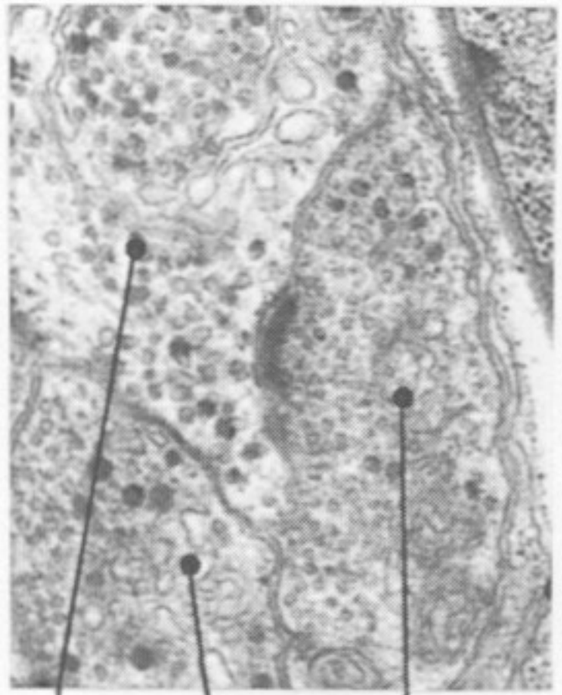

PVQR
ASJR
ASGR
ASIR
b

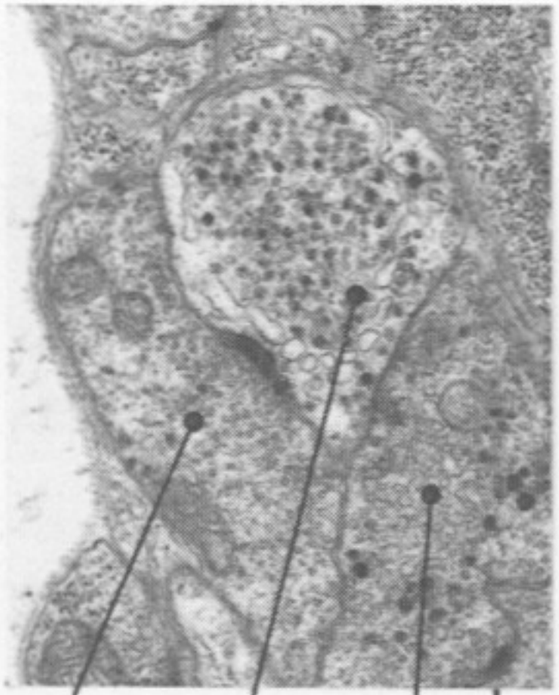

AIAR
AWCR
AWCL
ASIR
c

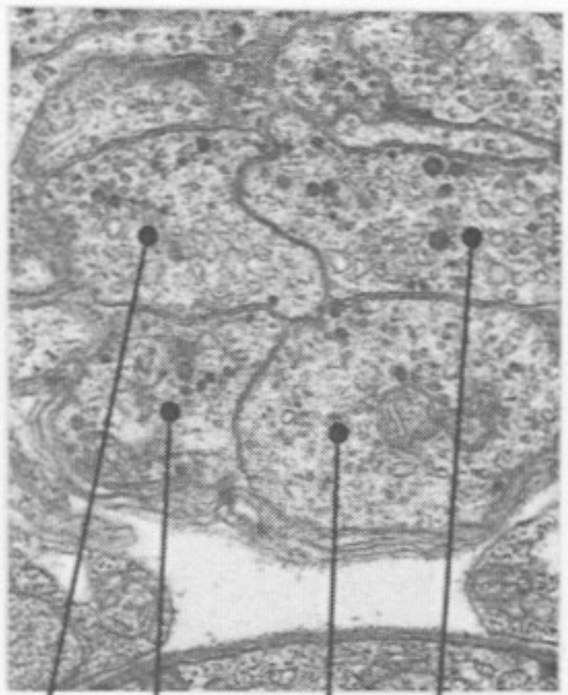

RID
ASIL
ASKL
ASIR
d

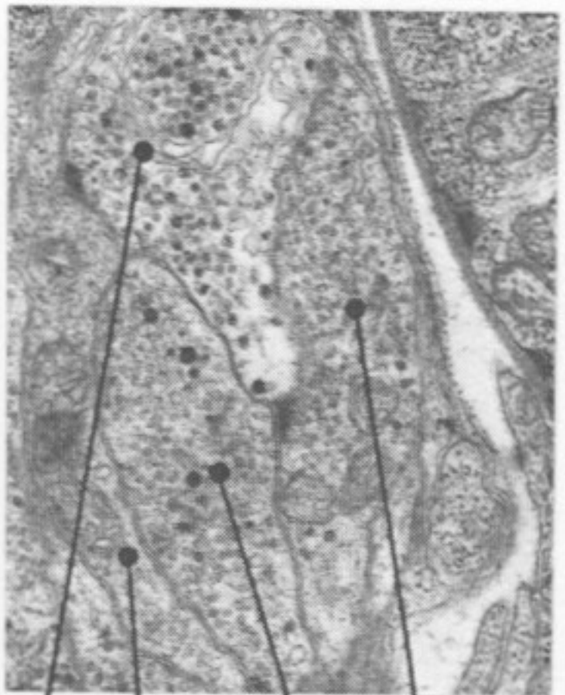

AIAR
AIAL
ASIL
e

ASI

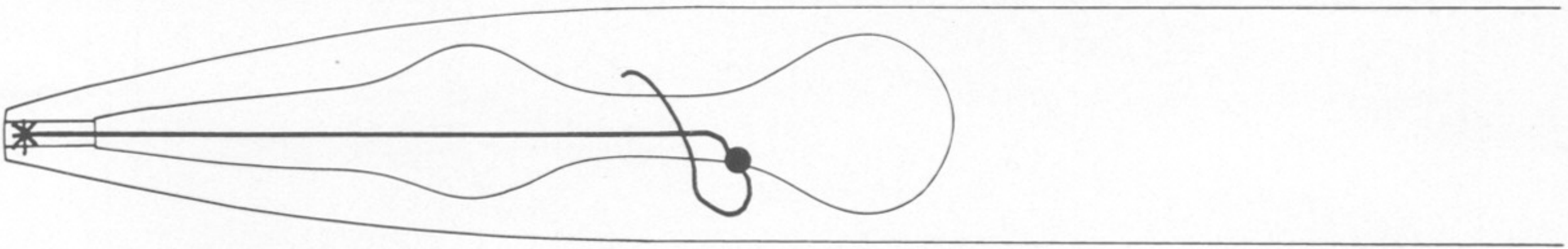




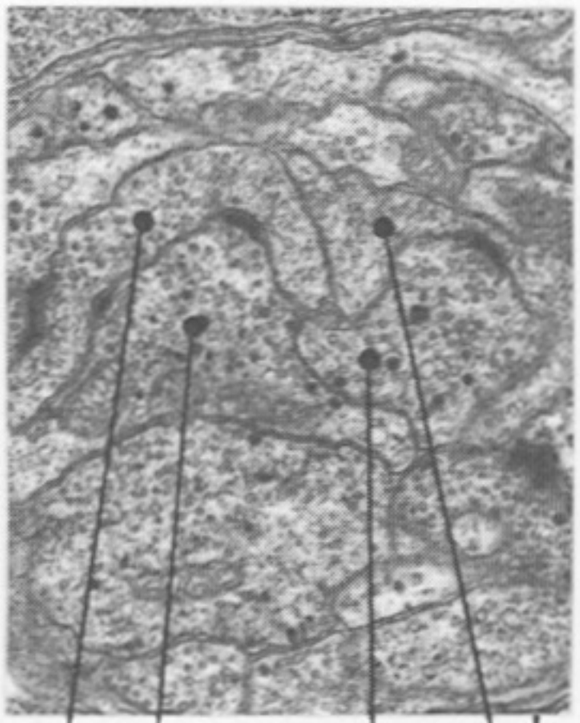


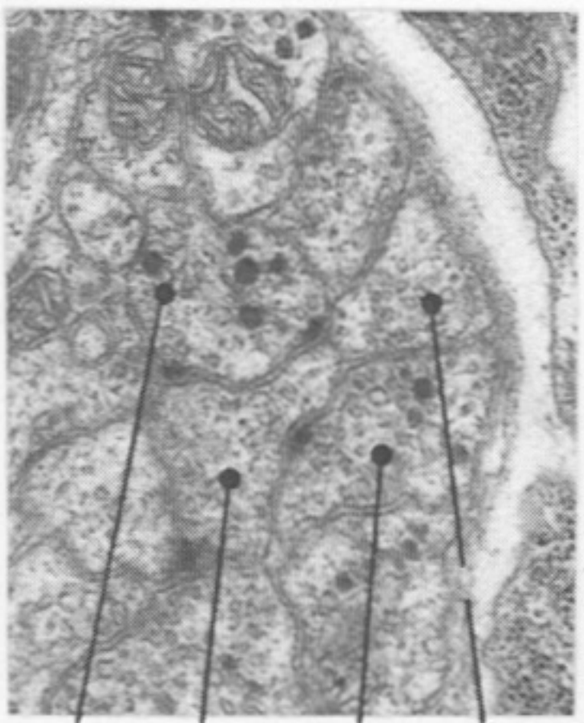


ASKL PVQR ASJL ASJR AIAL ASKL

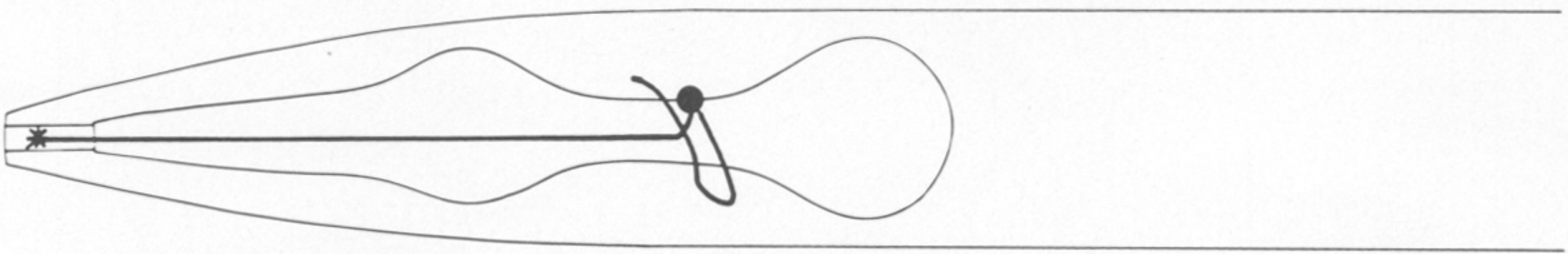


ASJ

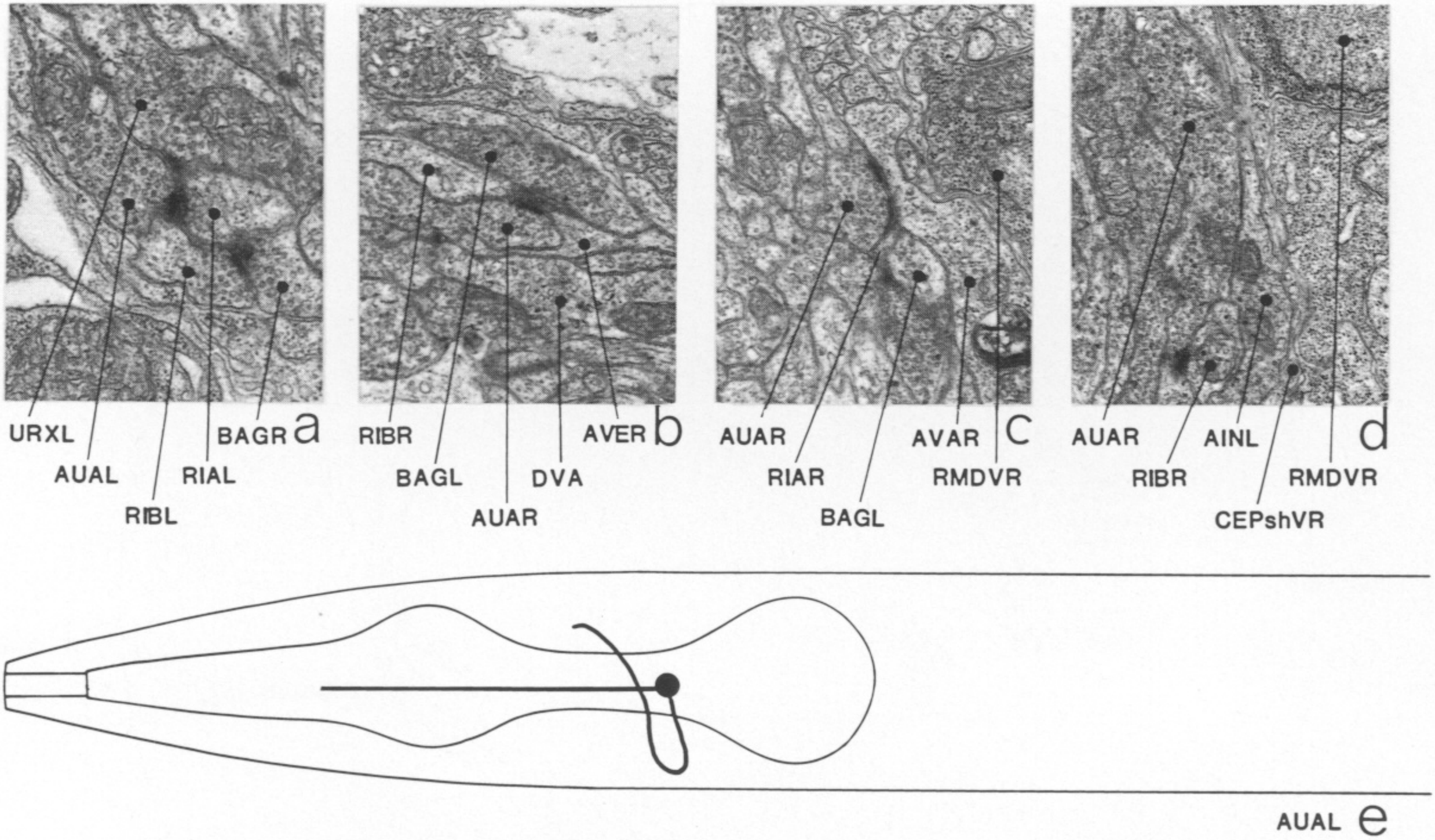




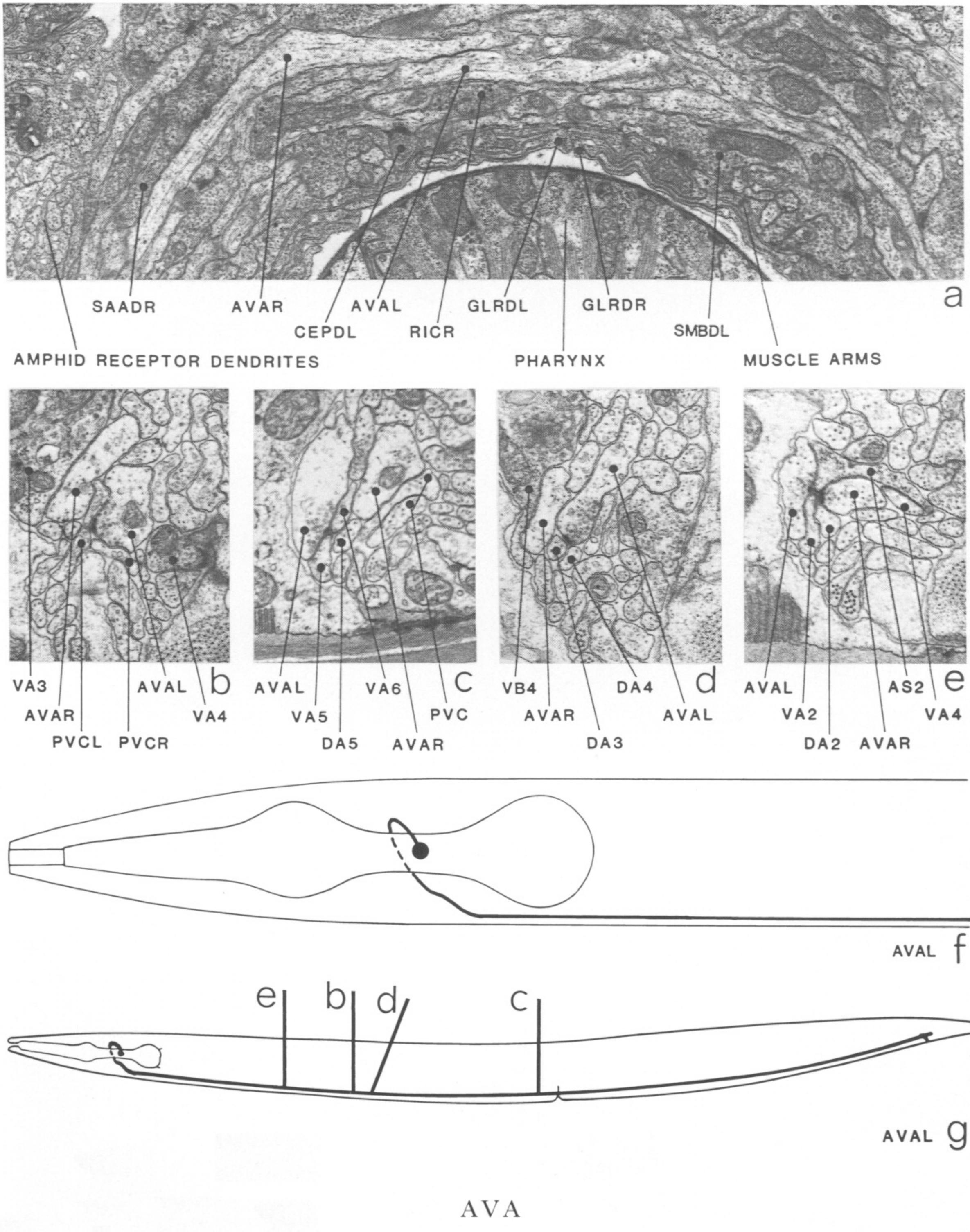
PVQR AIAR ASKL ASKR AIAR AIMR PVQR AIBR



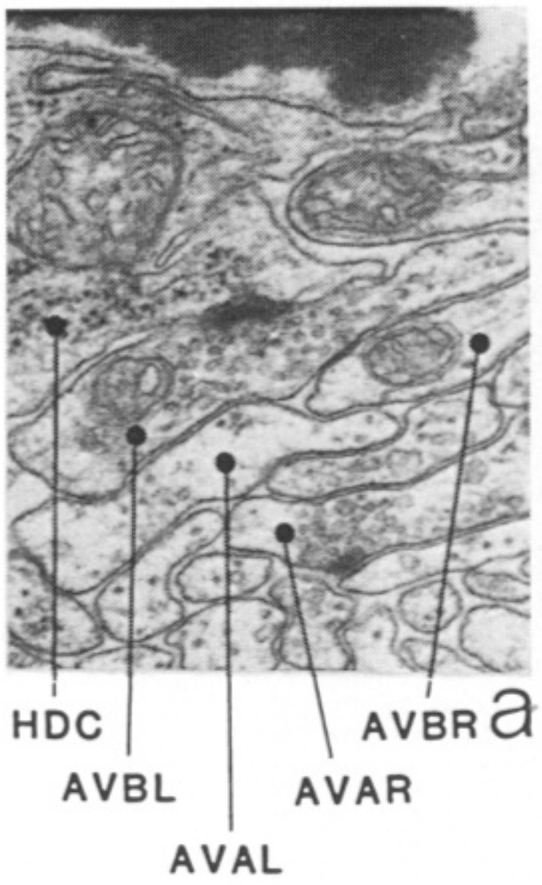
ASK

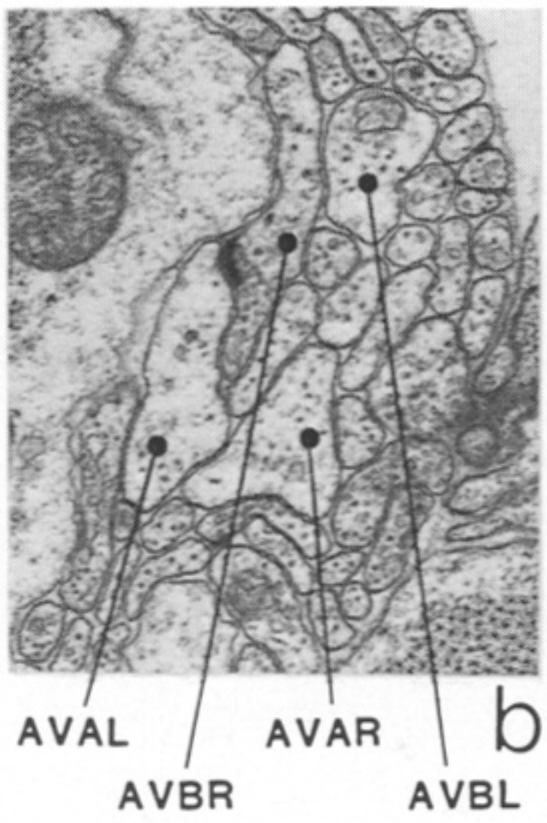

URXL
AUAL
RIBL
RIAL
BAGR
a
RIBR
BAGL
AUAR
DVA
AVER
b
AUAR
RIAR
AVAR
RMDVR
c
AUAR
RIBR
AINL
CEPshVR
RMDVR
d
AUAL
e

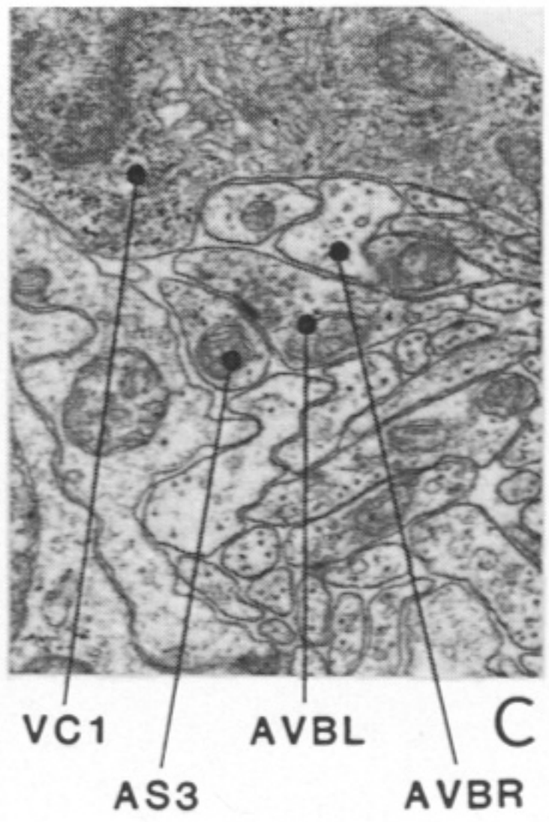
AUA

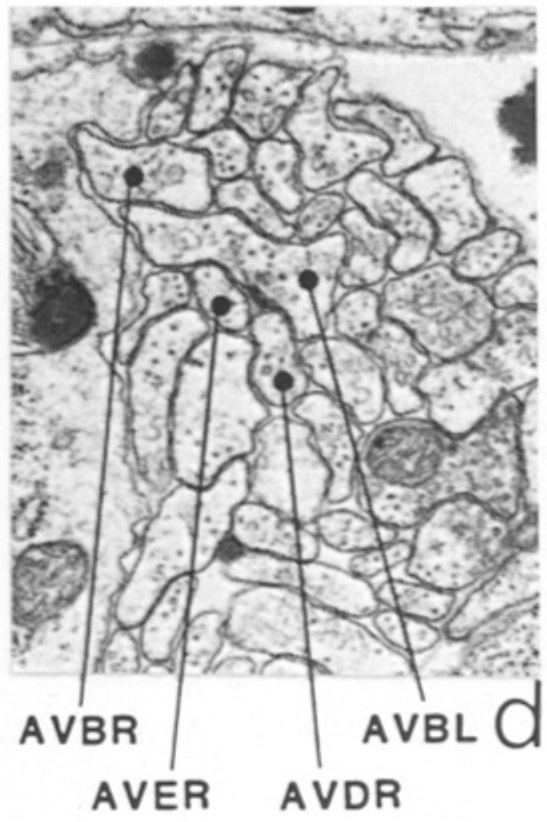

SAADR
AVAR
CEPDL
AVAL
RICR
GLRDL
GLRDR
SMBDL
AMPHID RECEPTOR DENDRITES
PHARYNX
MUSCLE ARMS
a
VA3
AVAR
PVCL
PVCR
AVAL
VA4
b
AVAL
VA5
DA5
VA6
AVAR
PVC
c
VB4
AVAR
DA3
DA4
AVAL
d
AVAL
VA2
DA2
AS2
AVAR
VA4
e
AVAL
f
e
b
d
c
AVAL
g

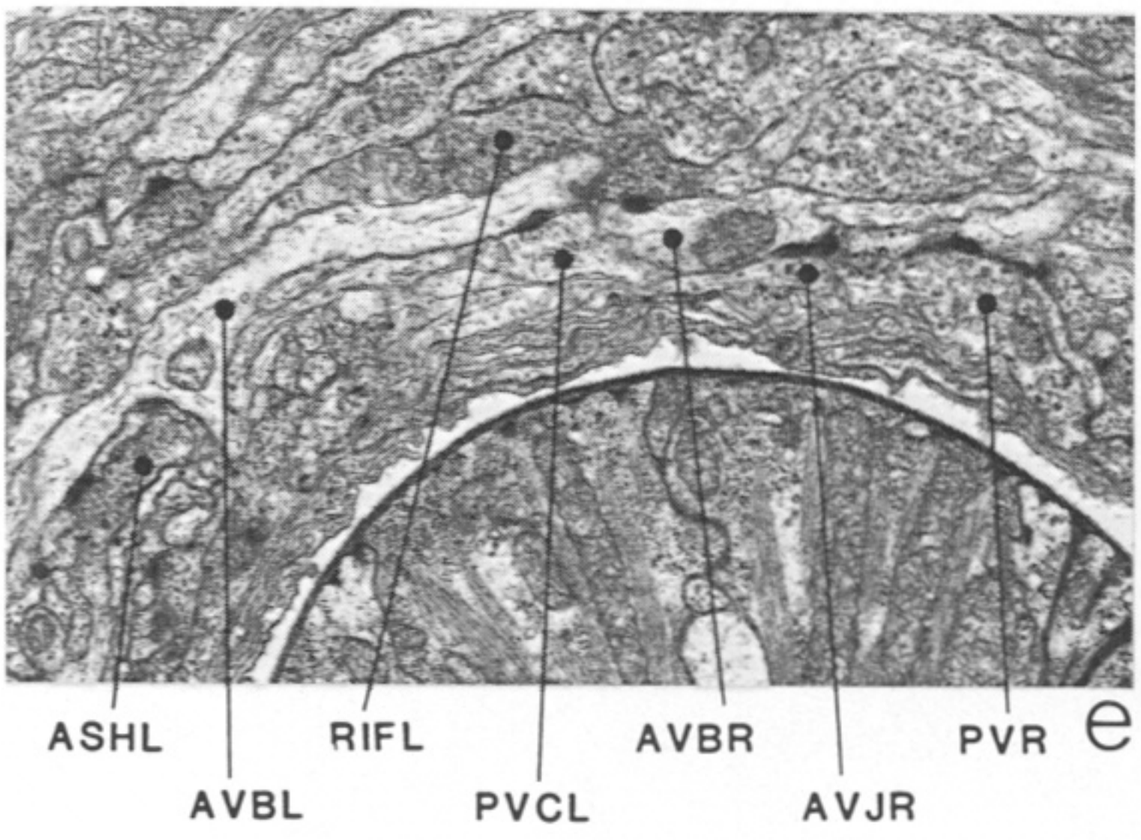
AVA

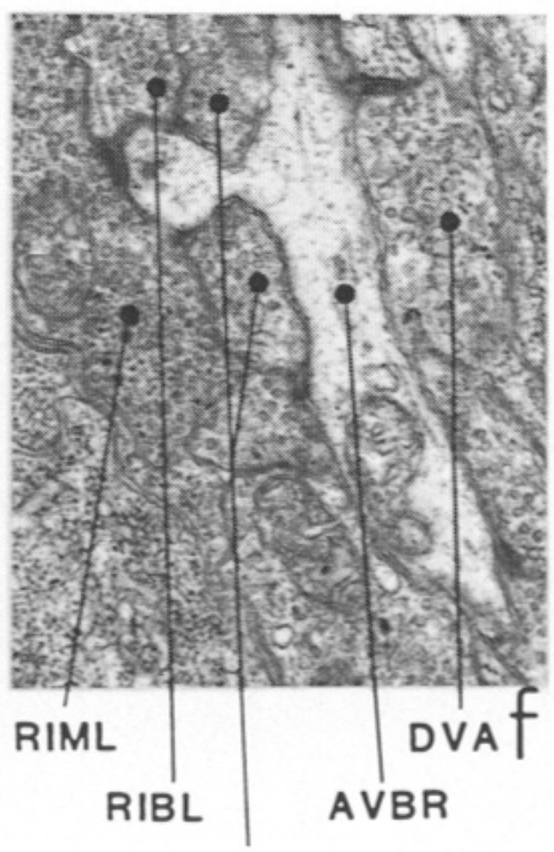

HDC
AVBL
AVAL
AVAR
AVBR
a


AVAL
AVBR
AVAR
AVBL
b

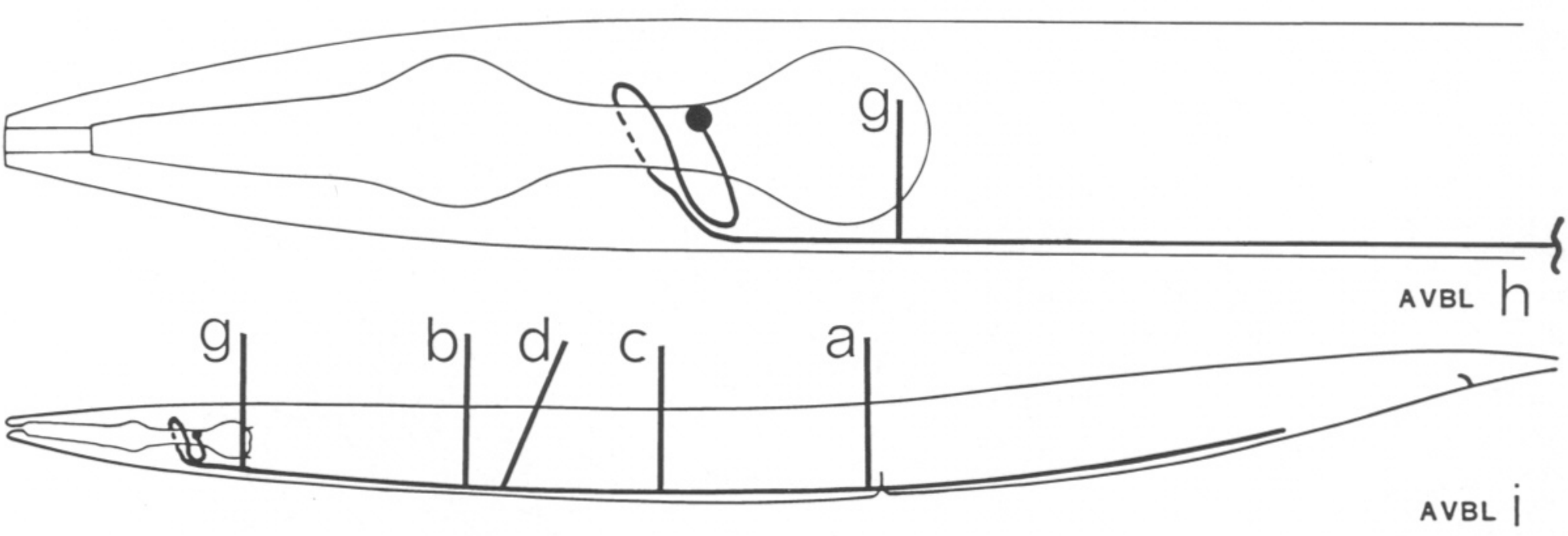

VC1
AS3
AVBL
AVBR
c


AVBR
AVER
AVDR
AVBL
d

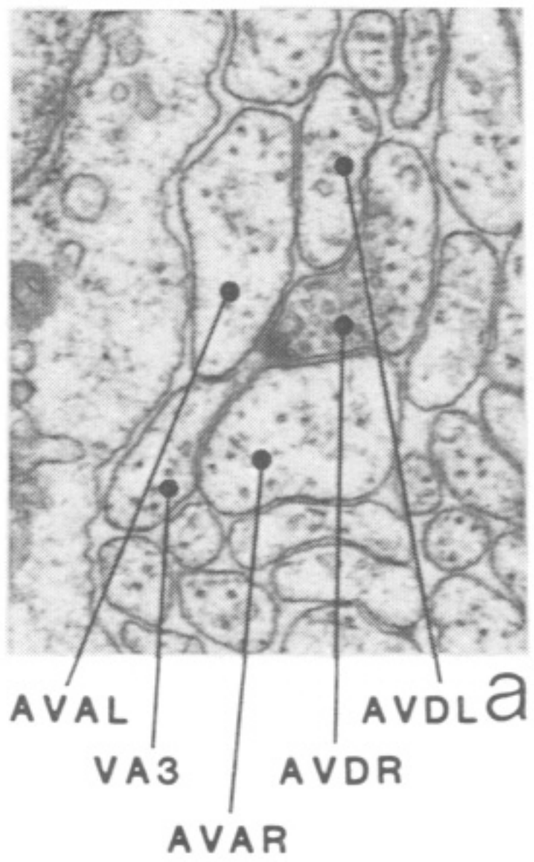

ASHL
AVBL
RIFL
PVCL
AVBR
AVJR
PVR
e

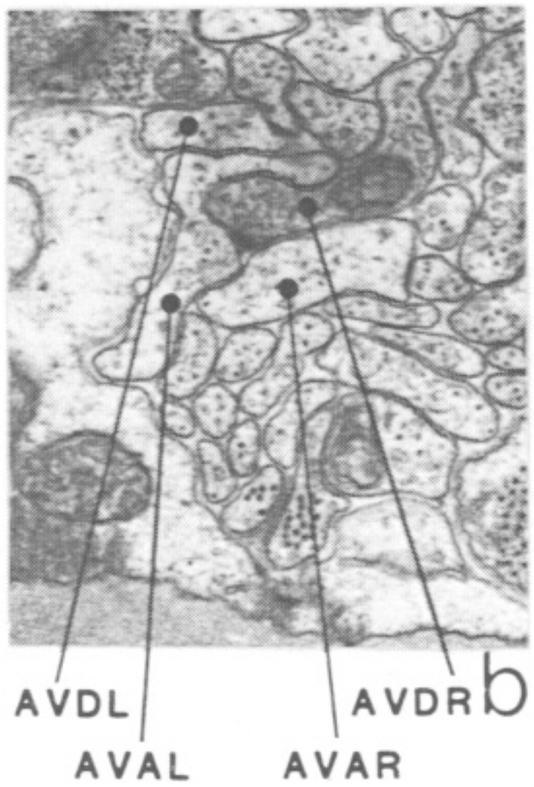

RIML
RIBL
AIBR
AVBR
DVA
f

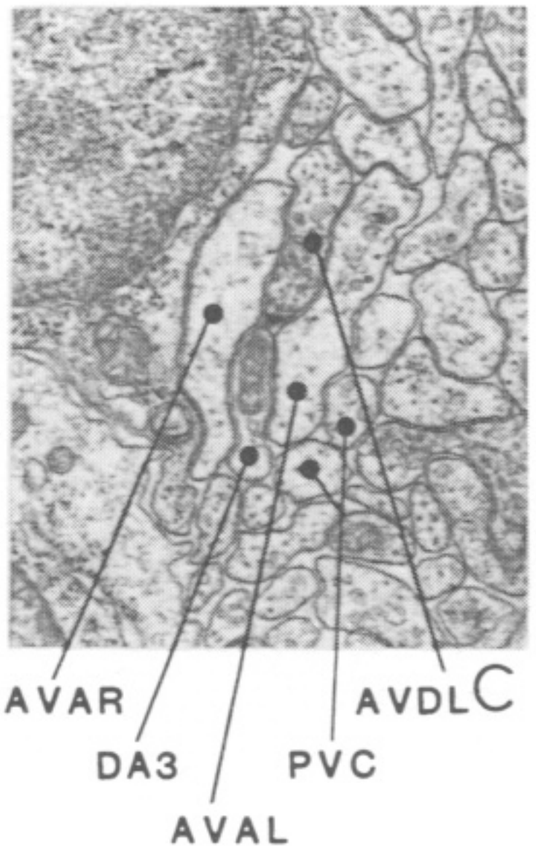

AVBL
AVBR
RIMR
PVCR
PVPR
g

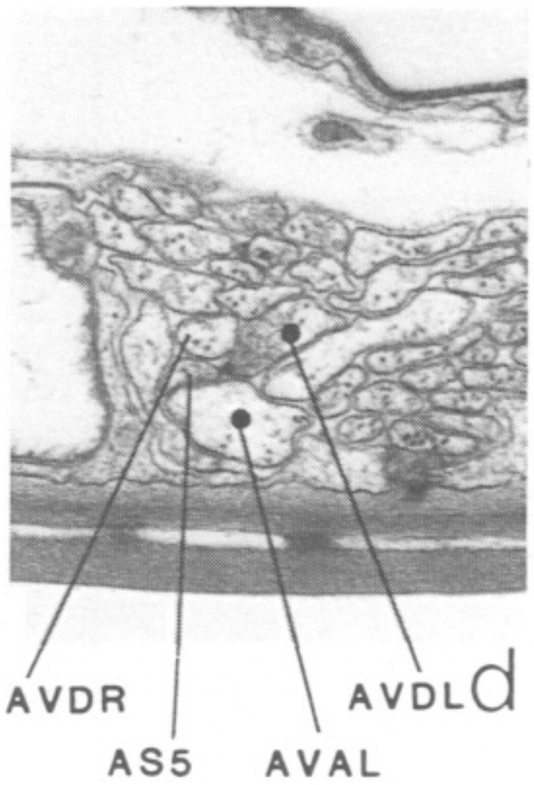

g
AVBL
h
g
b
d
c
a
AVBL
i

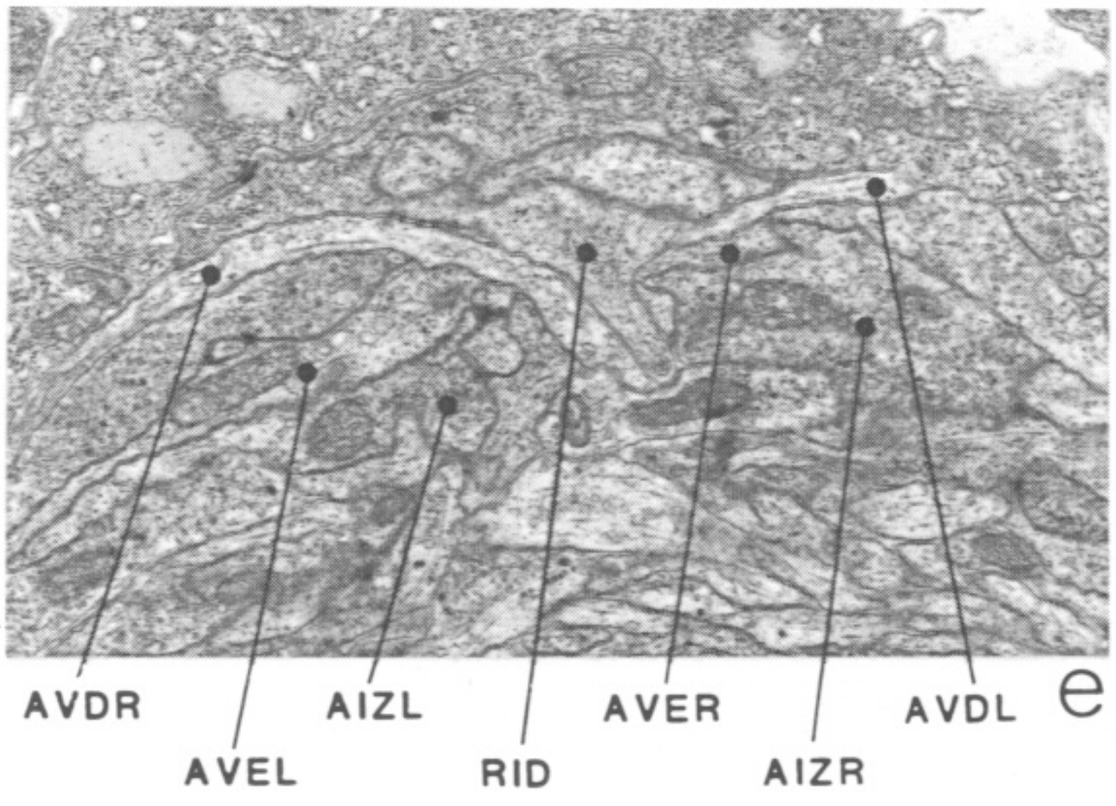
AVB

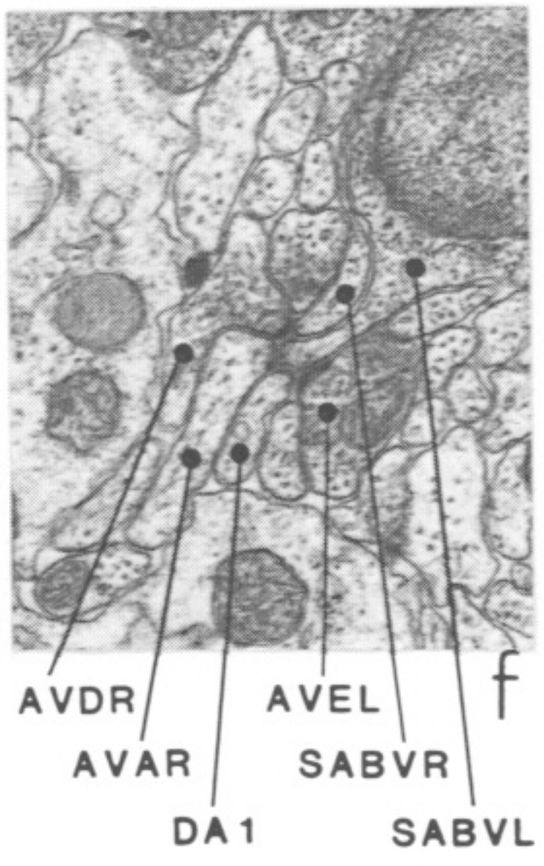

AVAL
VA3
AVAR
AVDR
AVDL
a

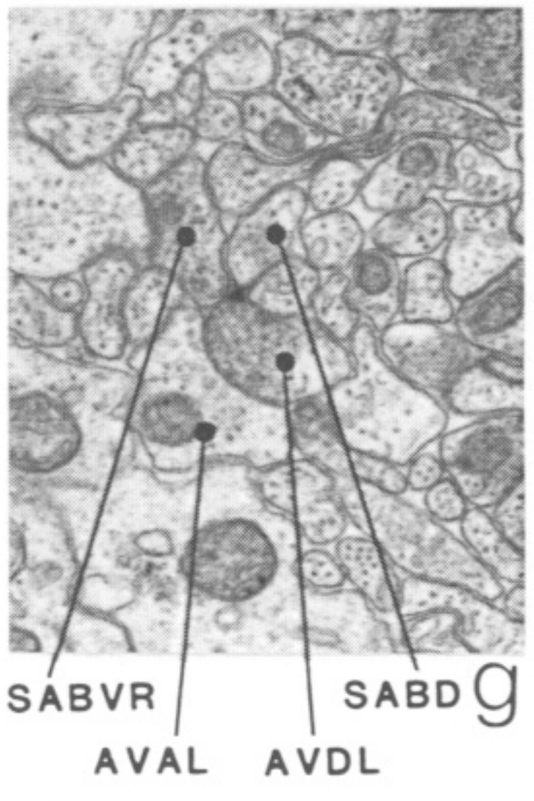

AVDL
AVAL
AVAR
AVDR
b

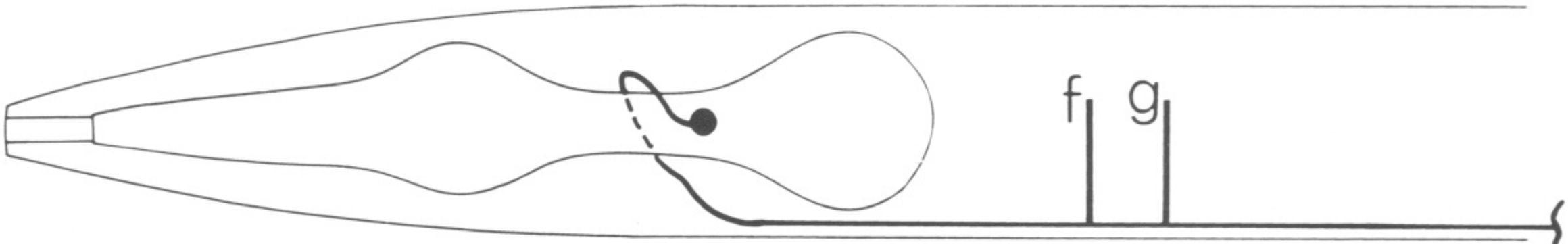

AVAR
DA3
AVAL
PVC
AVDL
c

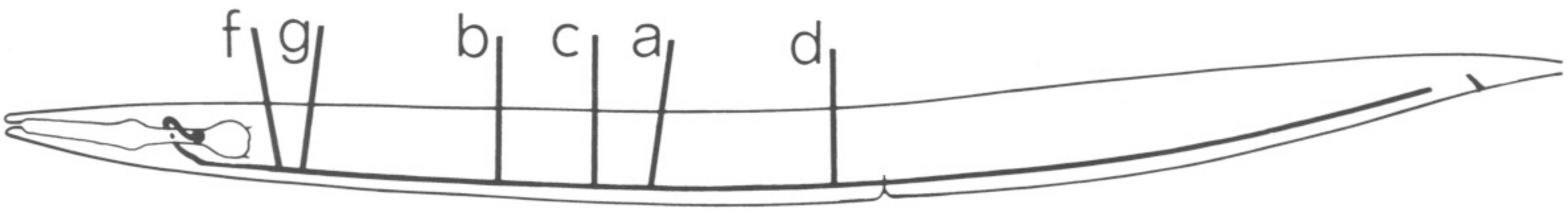

AVDR
AS5
AVAL
AVDL
d


AVDR
AVEL
AIZL
RID
AVER
AIZR
AVDL
e


AVDR
AVAR
DA1
AVEL
SABVR
SABVL
f

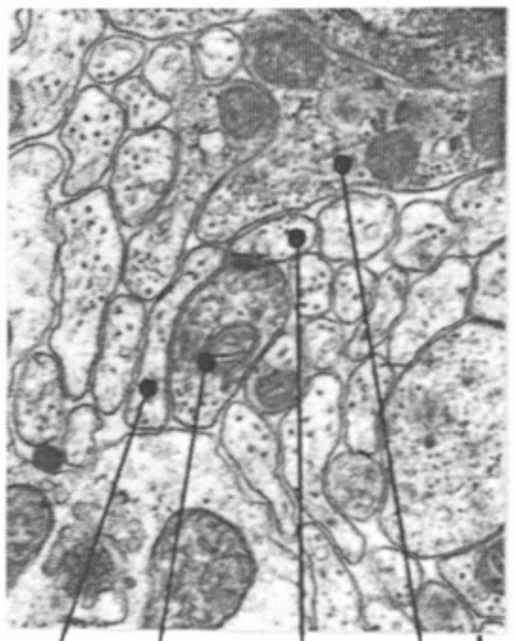

SABVR
AVAL
AVDL
SABD
g

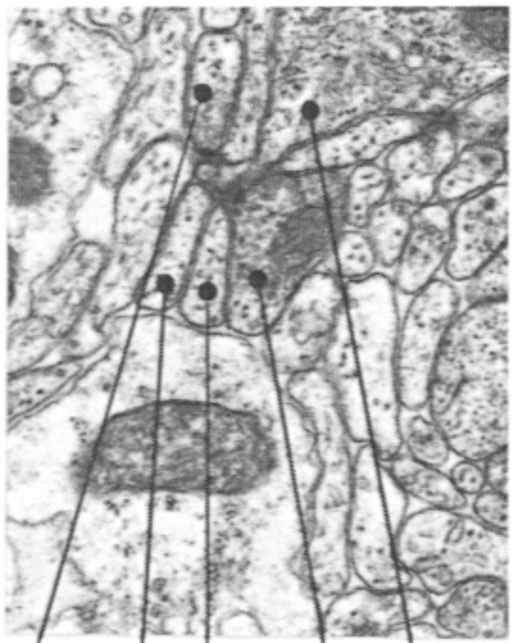

f
g
AVDL
h

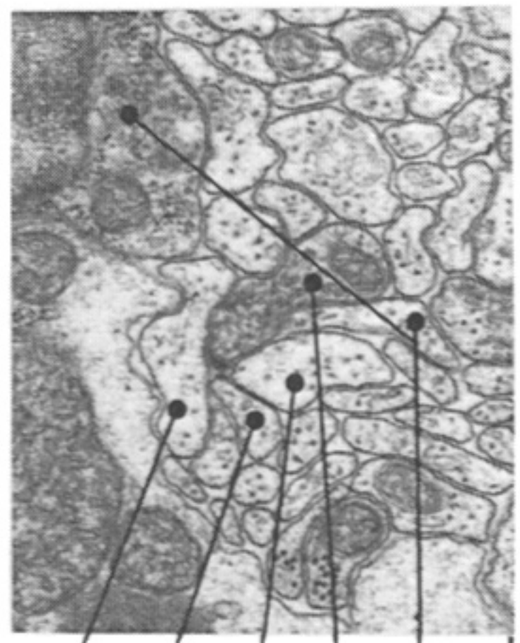

f
g
b
c
a
d
AVD
j

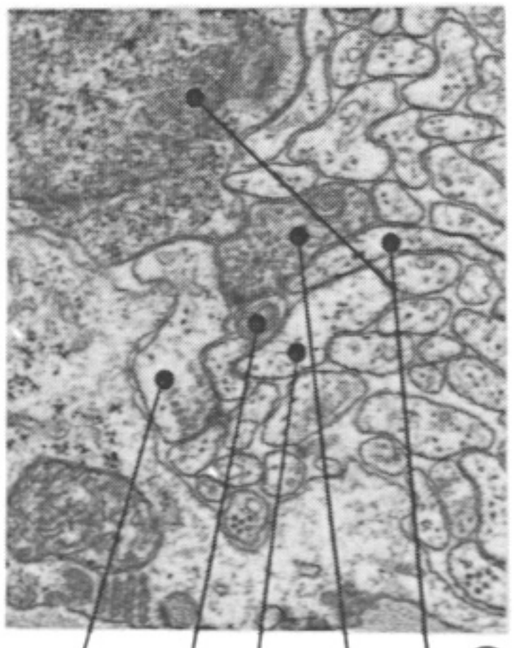
AVD

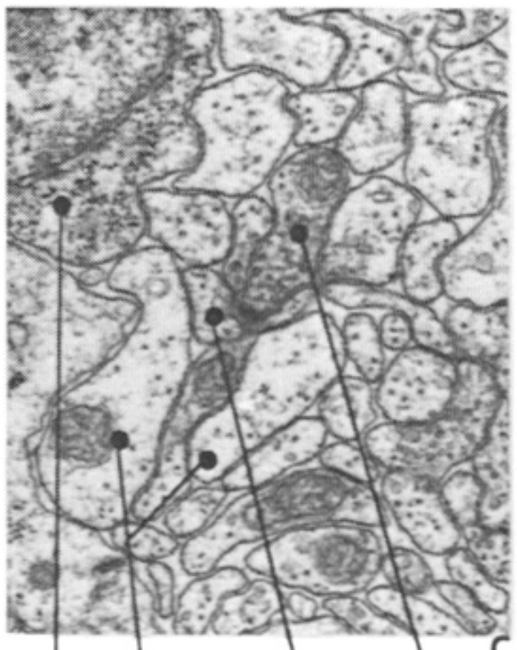

VB4
AVAR
AVDL
AVEL
AVDR
a

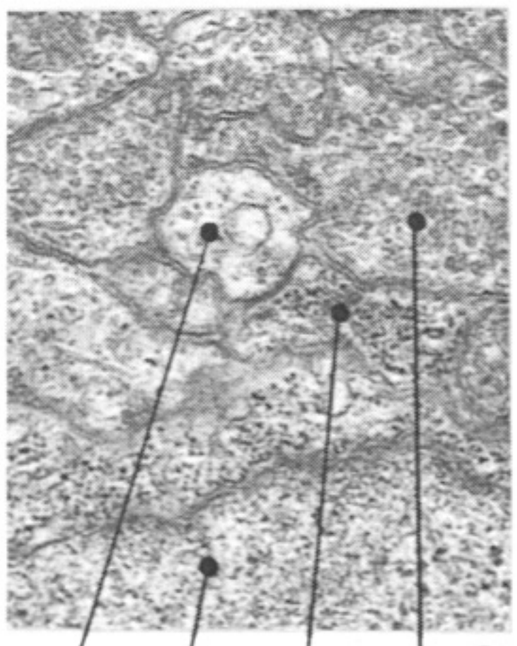

VA1
AVEL
SABD
SABVL
b


AVER
DA1
VA1
AVEL
SABVL
c

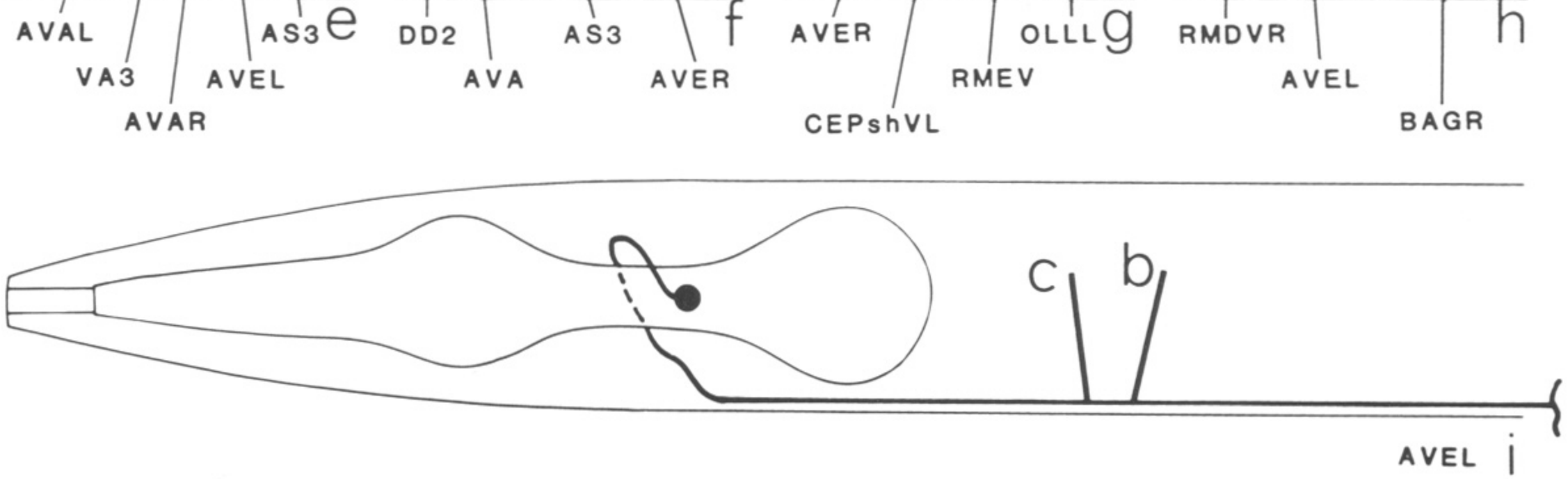

AVAL
DA2
AVAR
AVER
AS2
d

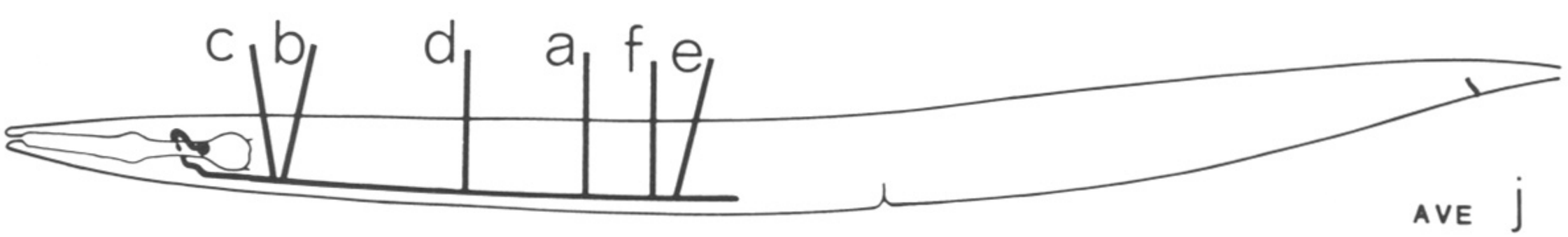

AVAL
VA3
AVAR
AVEL
AS3
e


DD2
AVA
AS3
AVER
f

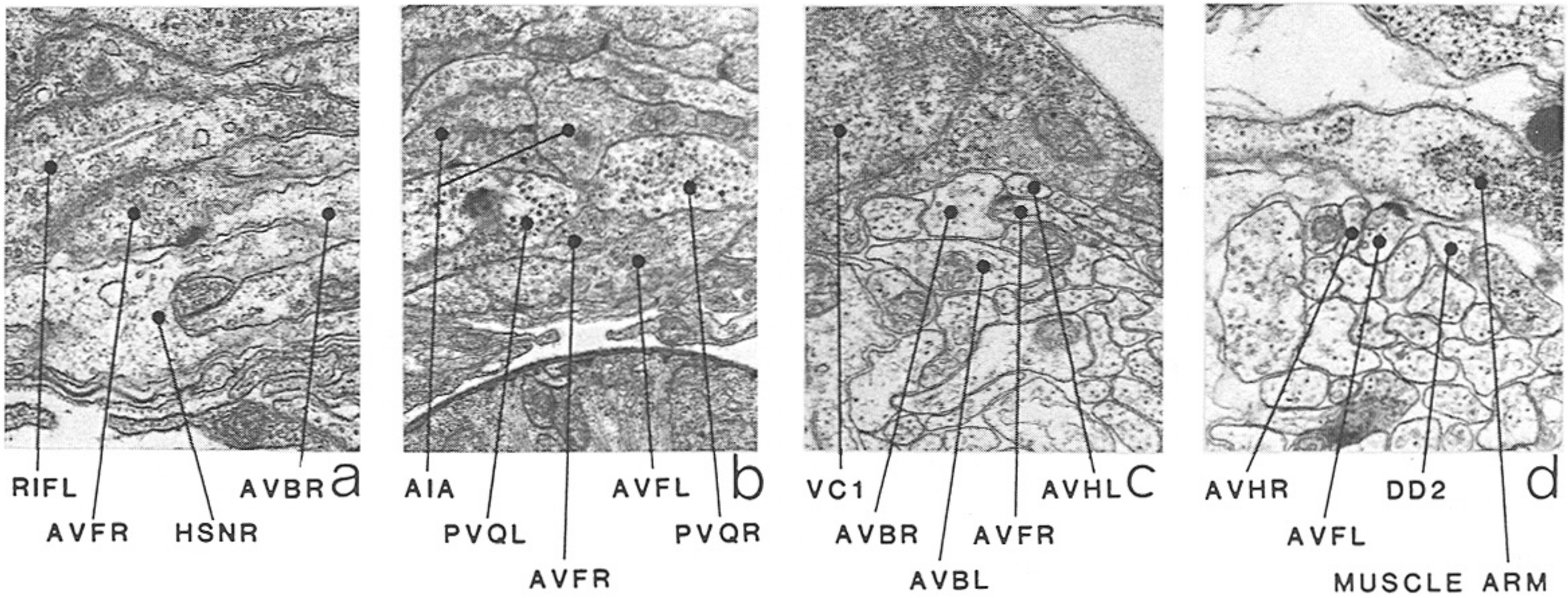

AVER
CEPshVL
RMEV
OLLL
g


RMDVR
AVEL
BAGR
h

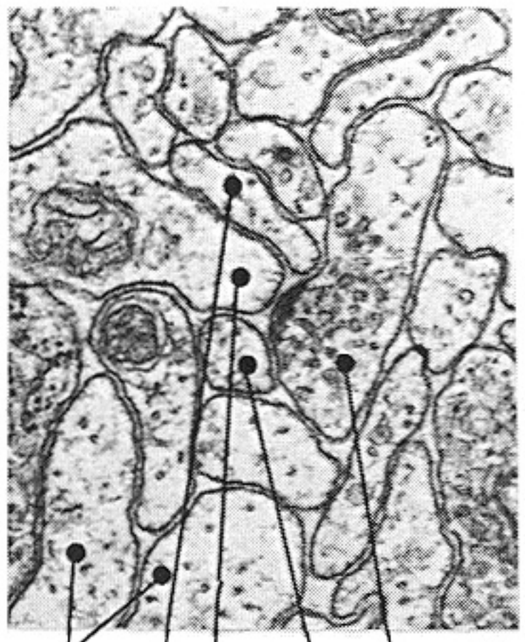

c
b
AVEL
j

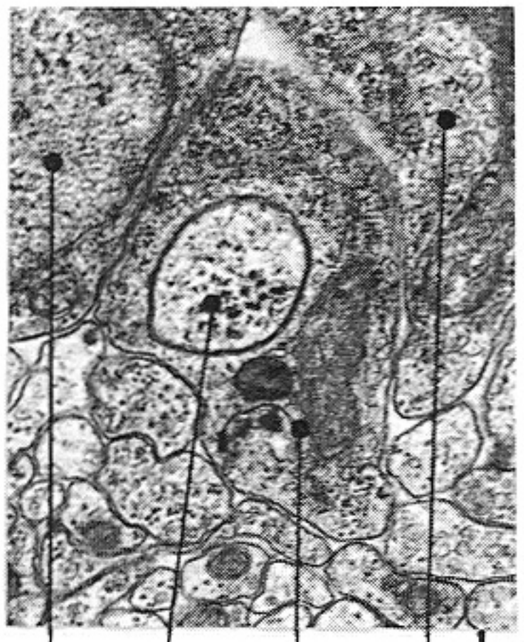

c
b
d
a
f
e
AVE
j

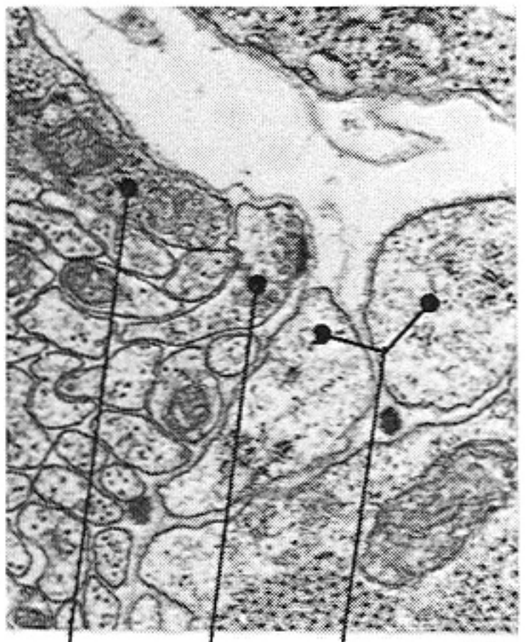
AVE

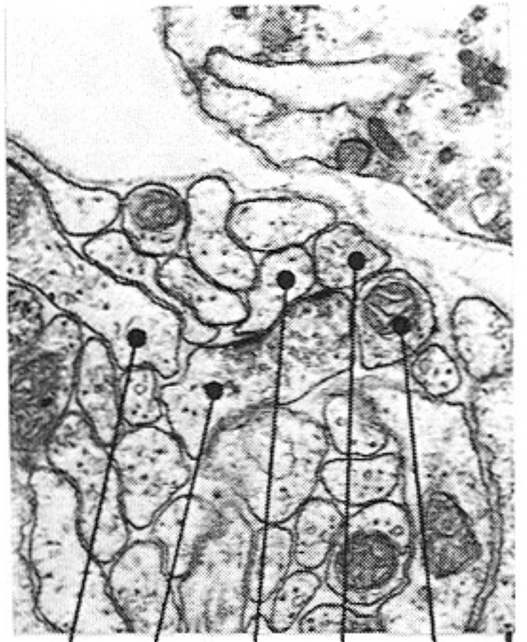

RIFL
AVFR
HSNR
AVBR
a
AIA
PVQL
AVFR
AVFL
PVQR
b
VC1
AVBR
AVBL
AVFR
AVHL
c
AVHR
AVFL
DD2
MUSCLE ARM
d
AVFL
e
c
d
AVF
f

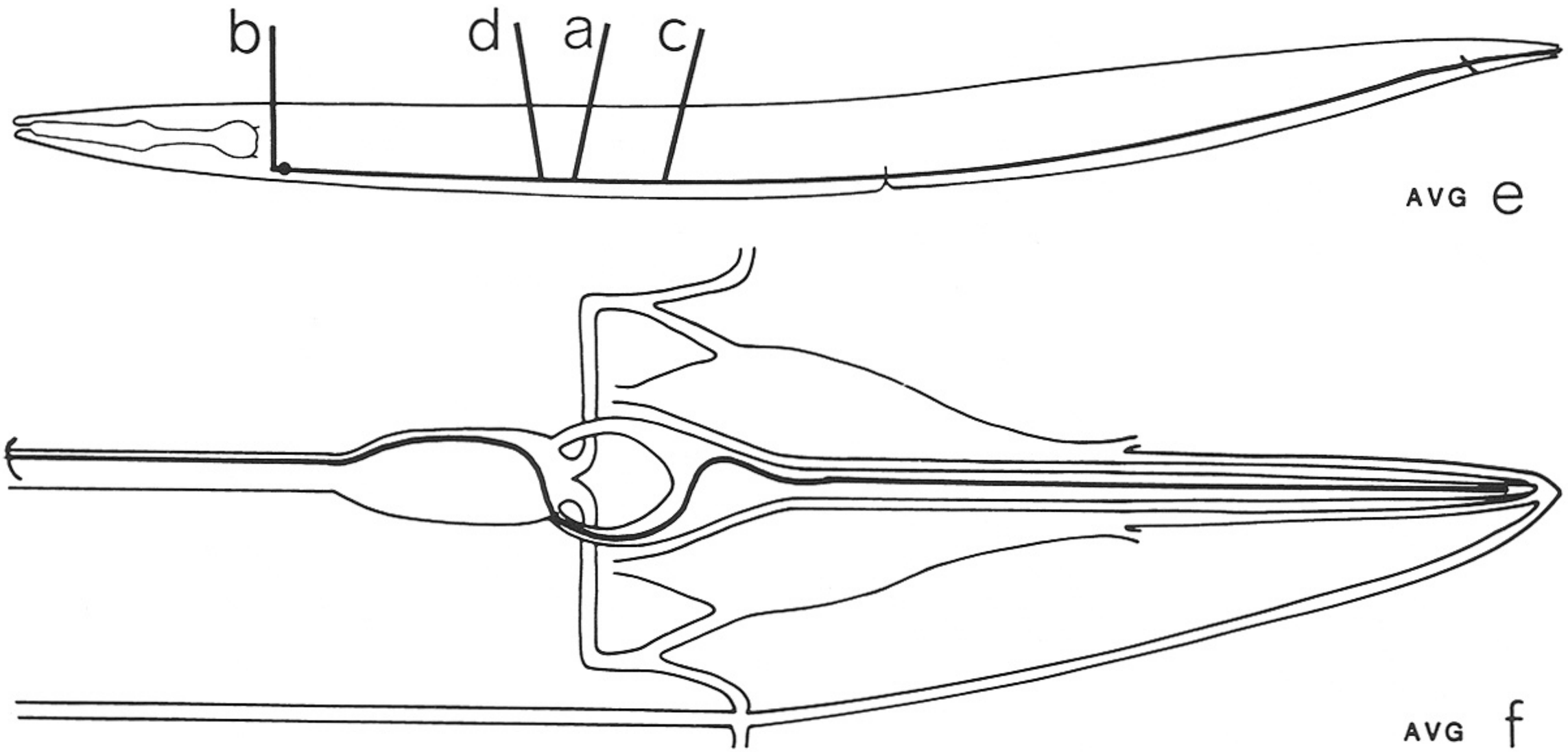
AVF


AVA
AVG
a
AVJR
AVER
AVBL

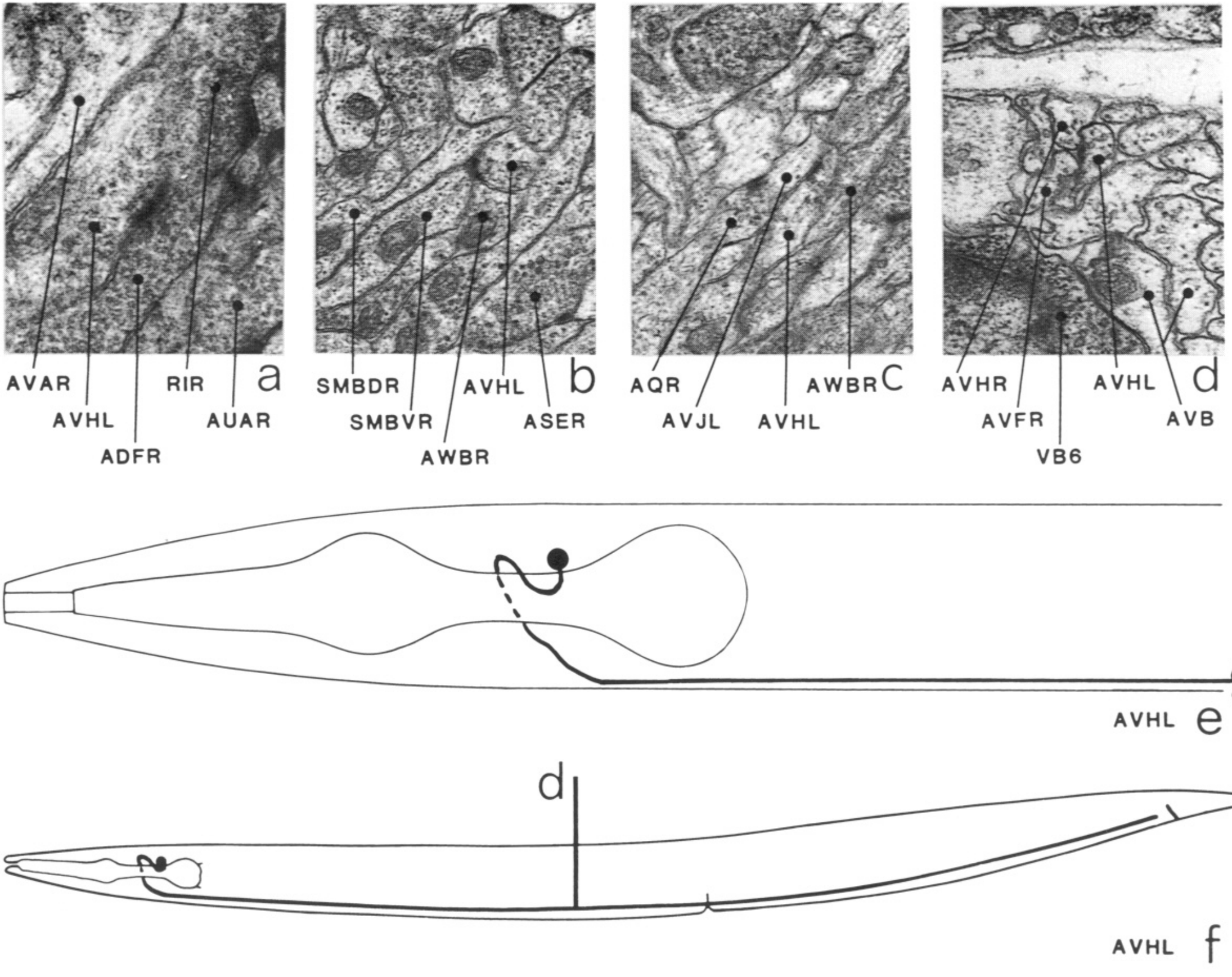

VB1
RIFR
b
AVG
RIGR


VC1
AVG
C
MUSCLE ARMS

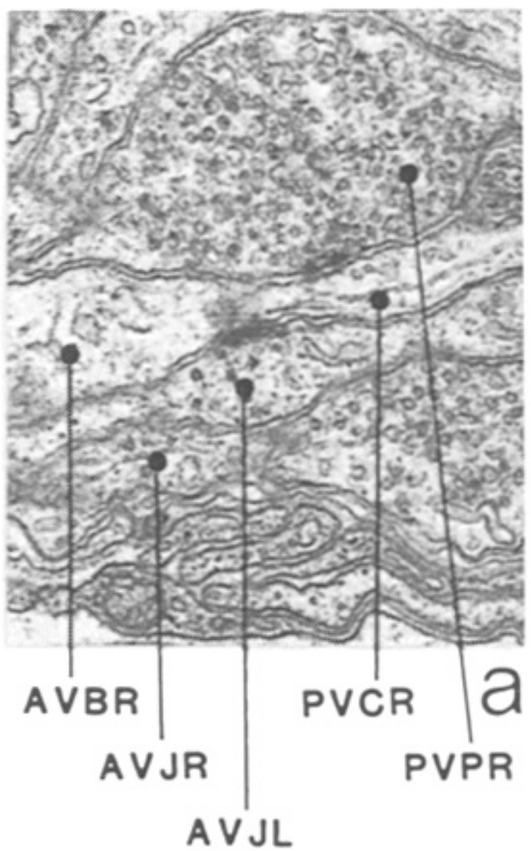

AVBL
VC1
d
AVG
VC2
AVFL

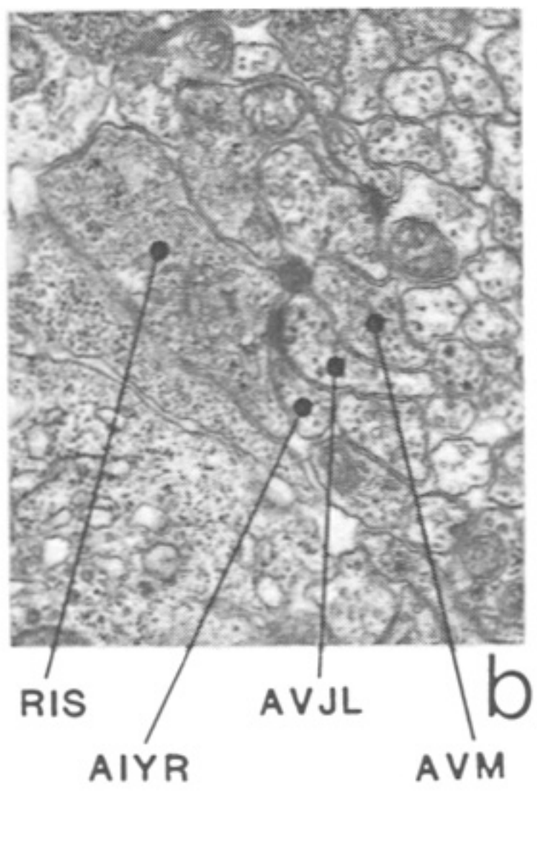

b
d
a
c
AVG
e
AVG
f

AVG

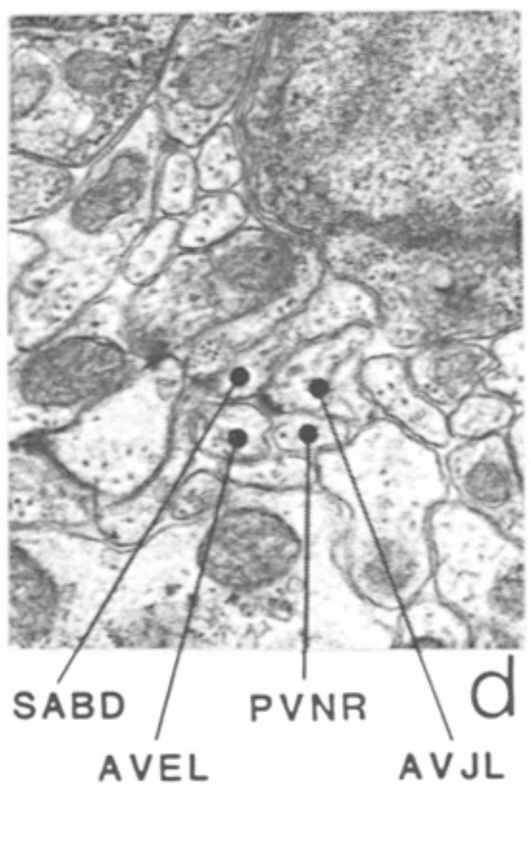

AVAR
AVHL
ADFR
RIR
AUAR
a
SMBDR
SMBVR
AWBR
AVHL
ASER
b
AQR
AVJL
AVHL
AWBR
c
AVHR
AVFR
VB6
AVHL
AVB
d
AVHL
e
d
AVHL
f

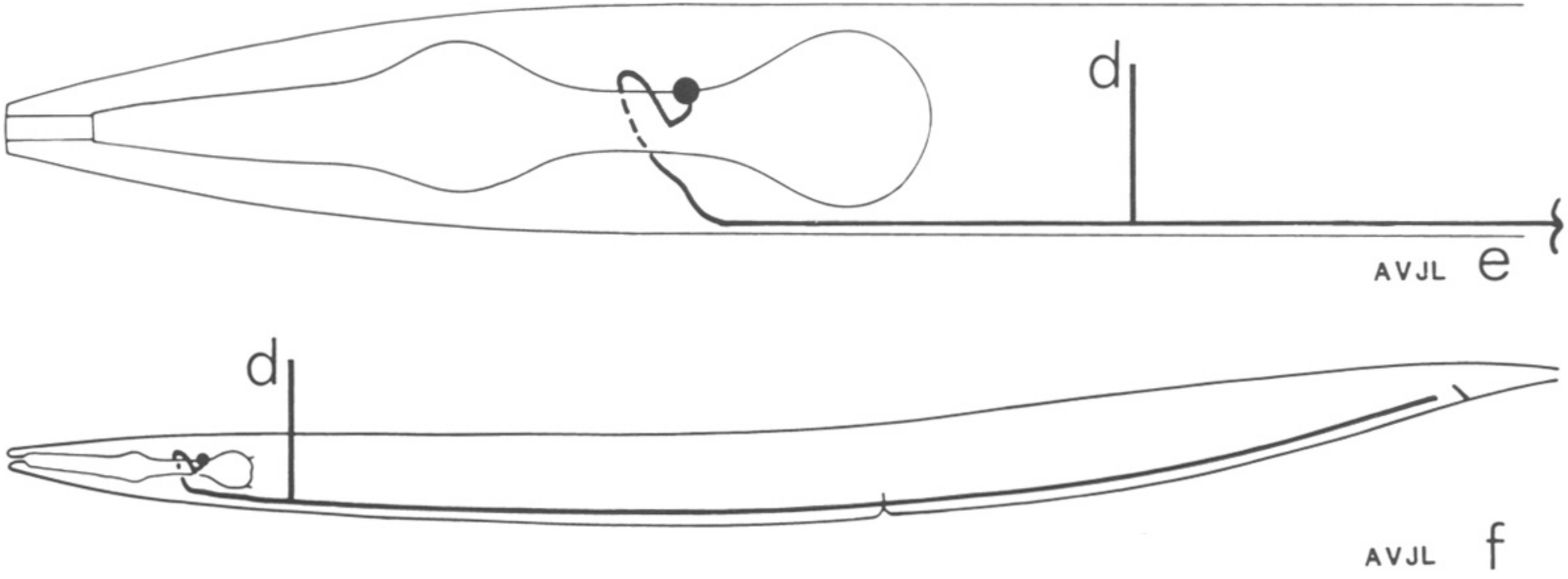
AVH


AVBR
AVJR
AVJL
PVCR
PVPR
a

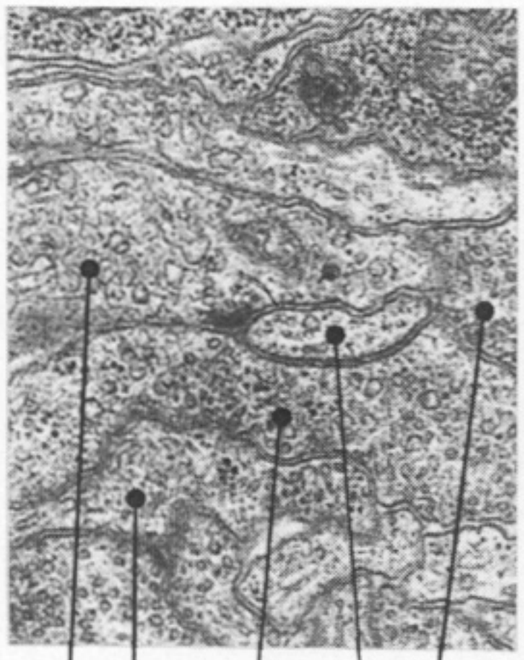

RIS
AIYR
AVJL
AVM
b

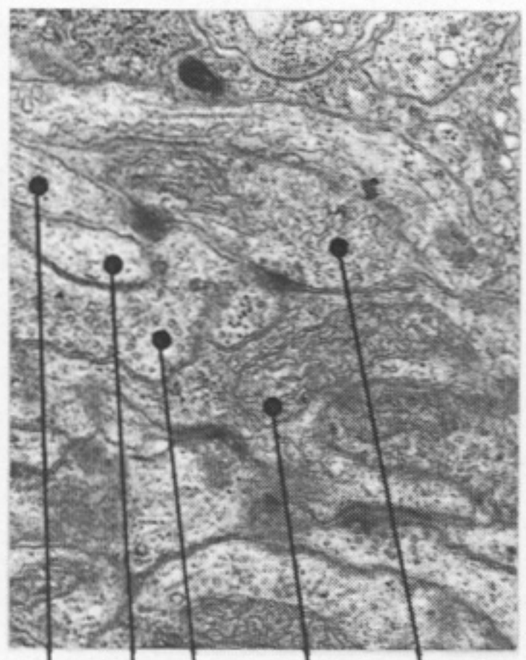

RIS
RIFR
AVJL
PVNR
BDUR
c

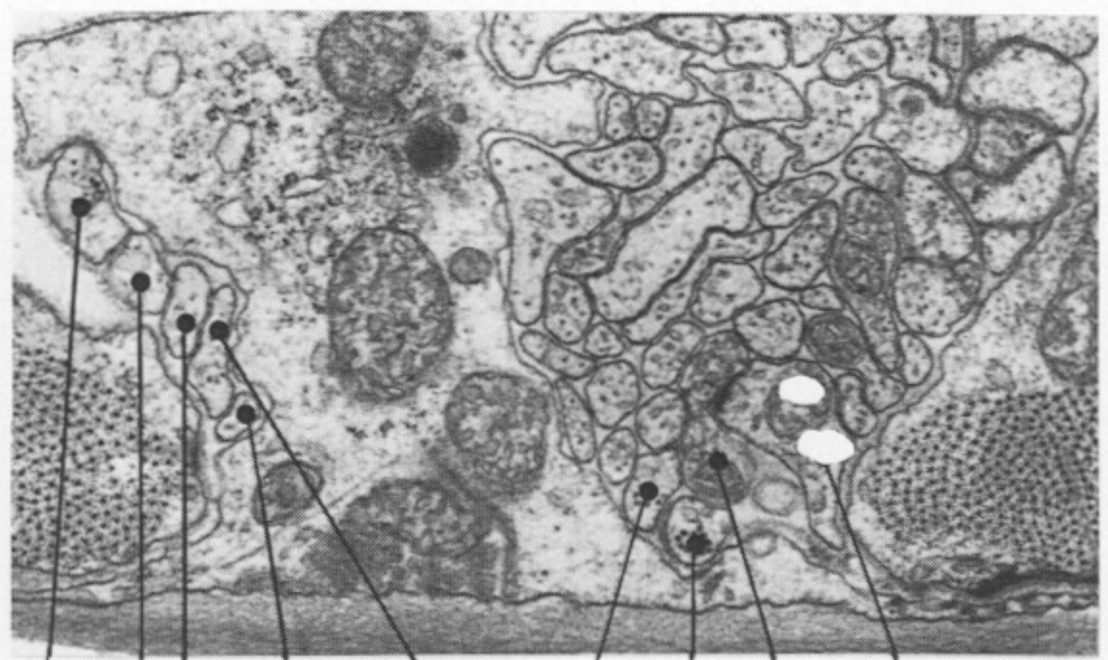

SABD
AVEL
PVNR
AVJL
d

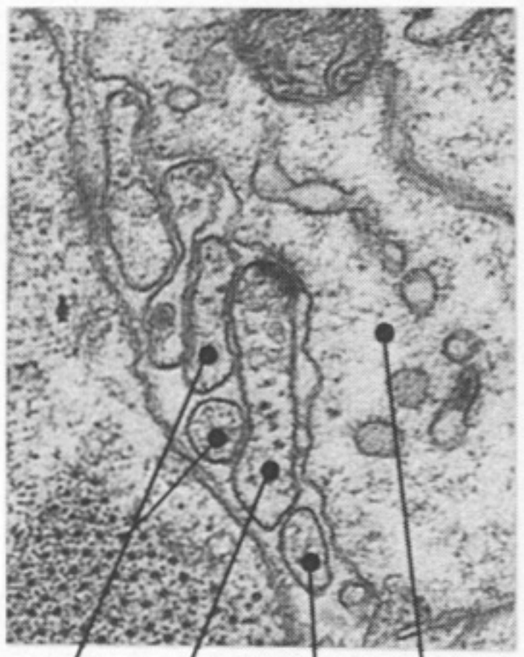

d
AVJL
e
d
AVJL
f

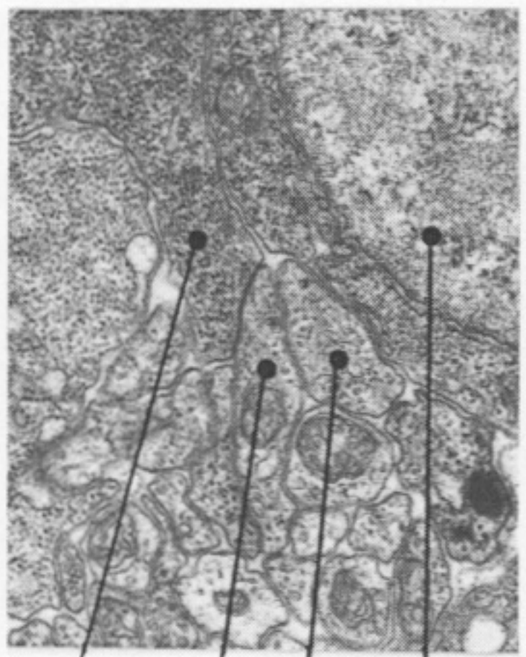
AVJ

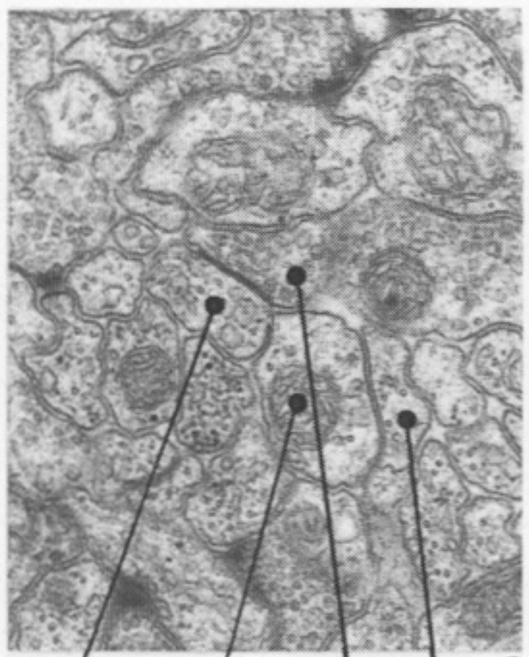

AVKL
SMDVL
RIMR
AVER
RIS
a

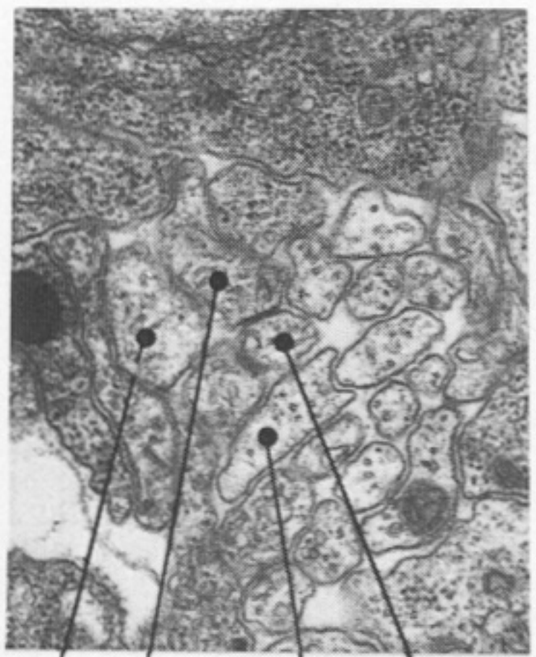

AVKL
AVEL
RIML
SMDVR
AVKR
b

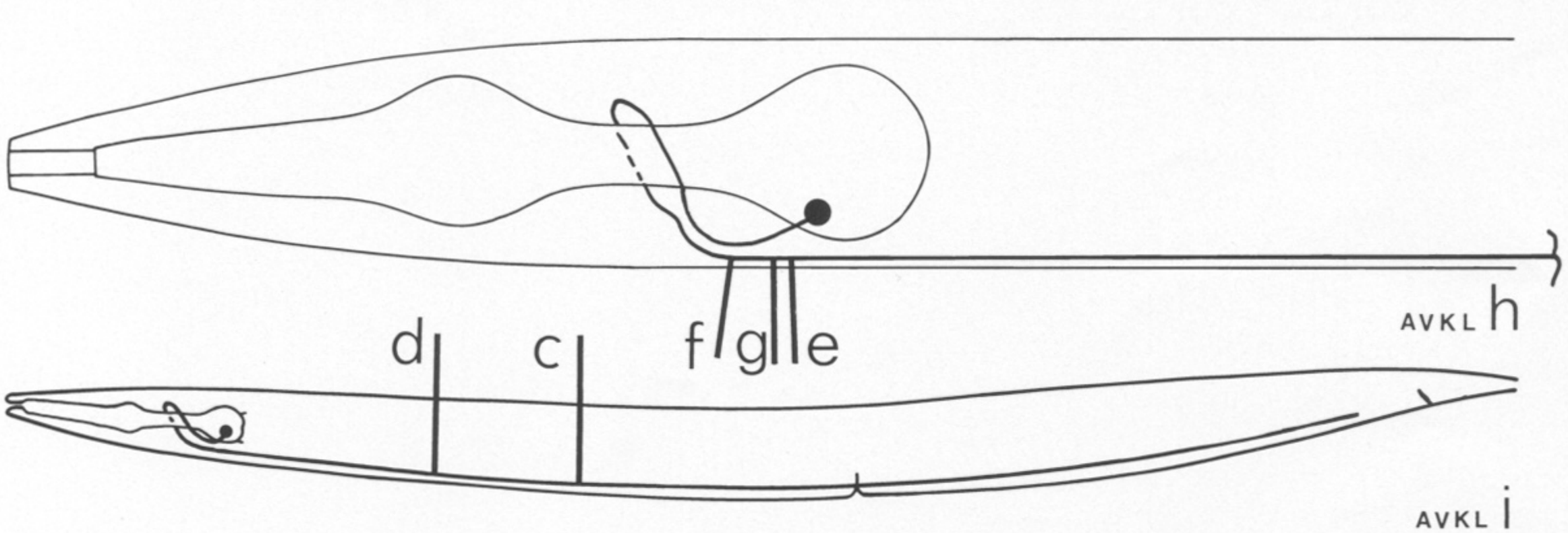

HSNL
PVQL
PVPL
RMEV
AVKR
PVM
AVM
PDEL
AVKL
c


PVPL
AVKR
RMEV
HDC
d

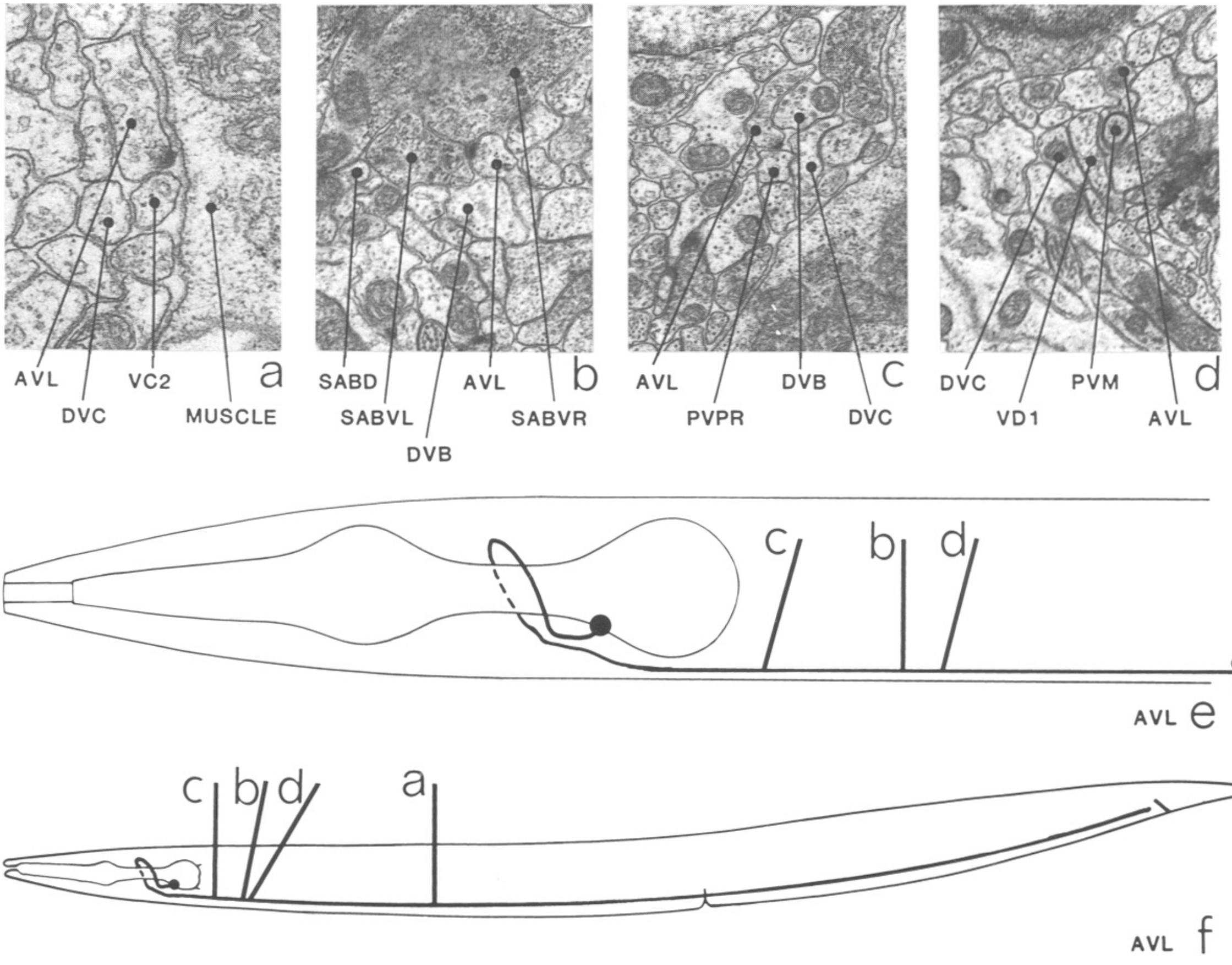

SMBVR
AVKR
RIS
SMBDR
e


AVKL
RIGL
AQR
RIGR
f

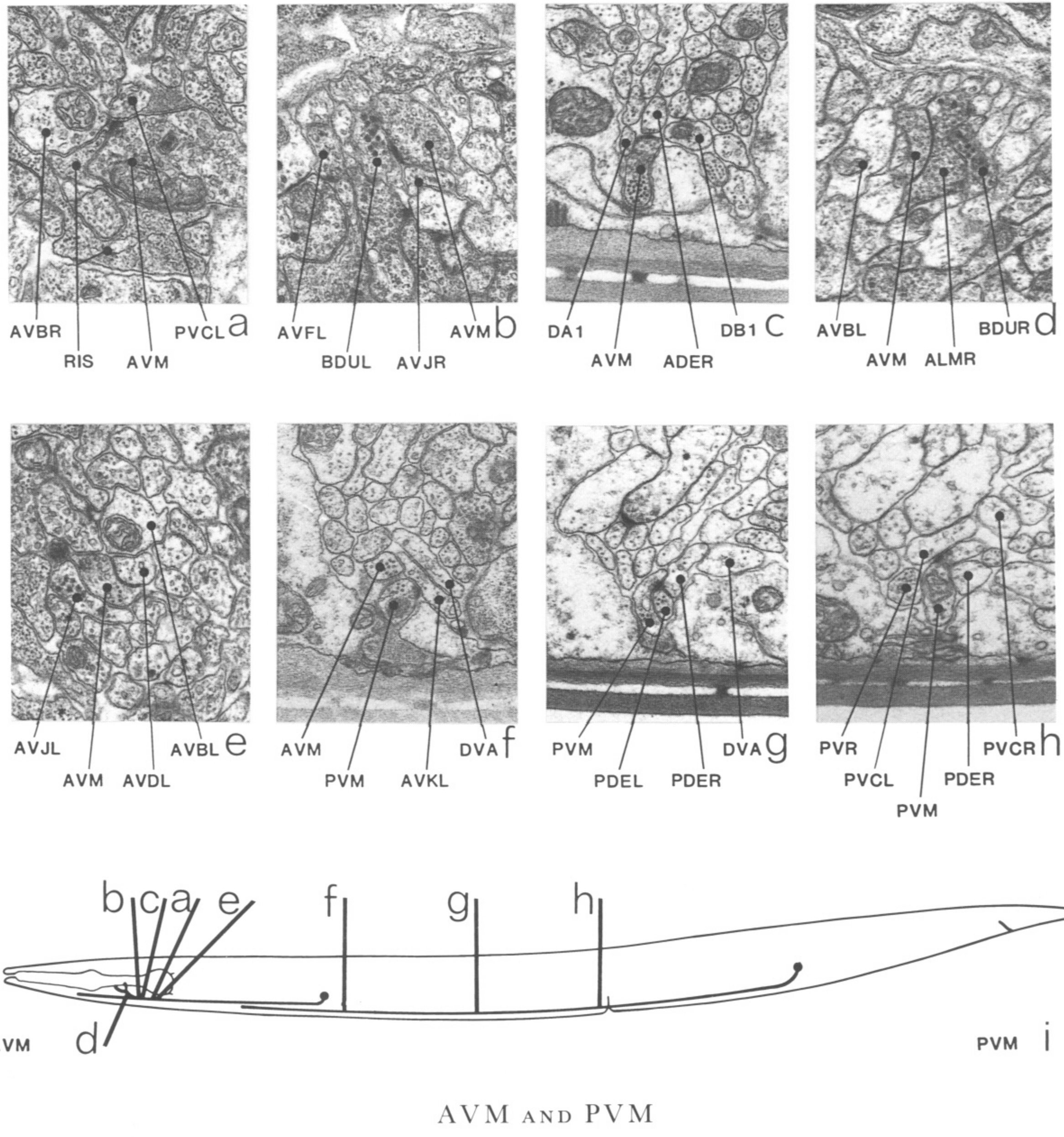

RIGL
AVKL
AVAR
PVPL
g


d
c
f
g
e
AVKL h
AVKL i

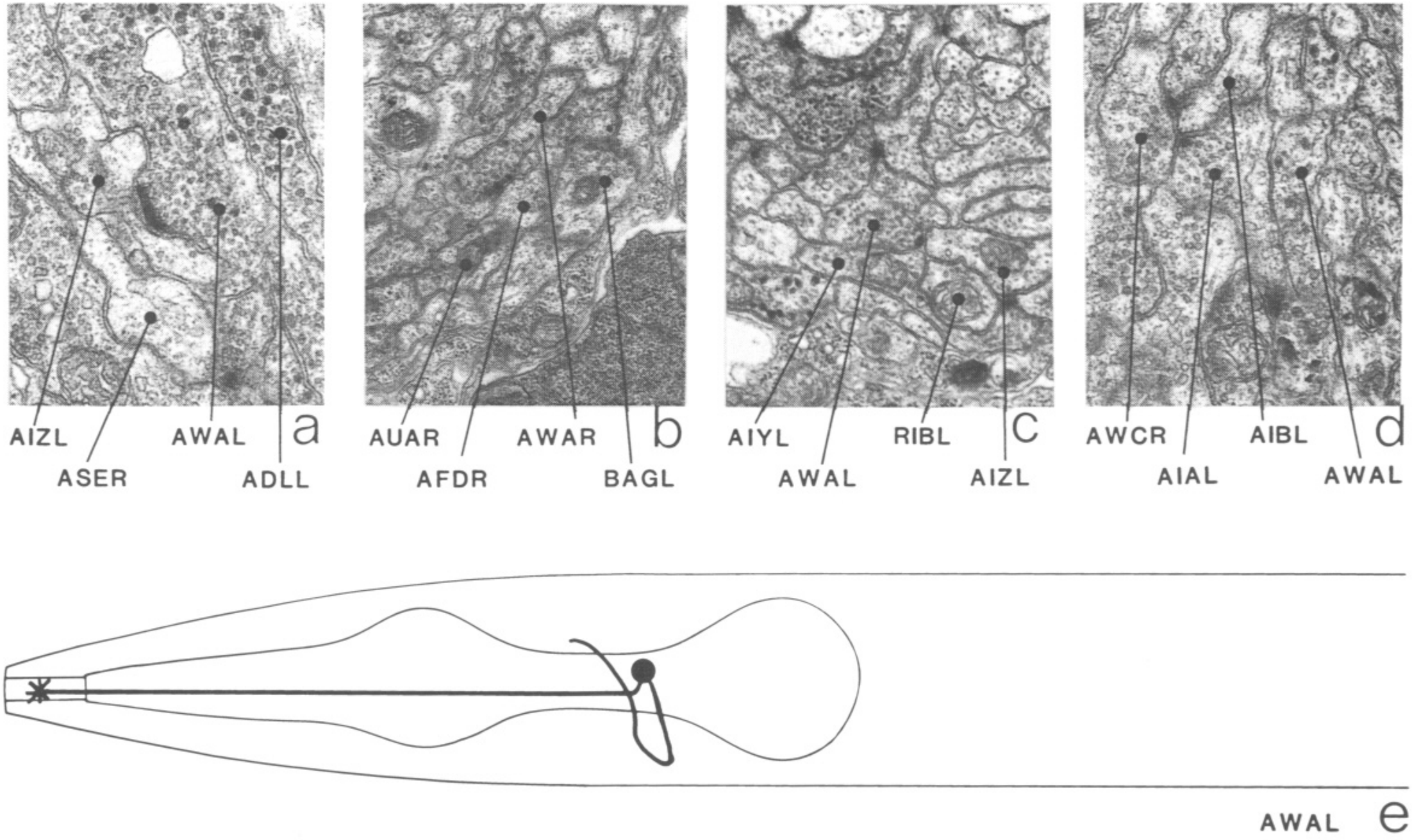
AVK


AVL
VC2
a
DVC
MUSCLE
SABD
AVL
b
SABVL
SABVR
DVB
AVL
DVB
c
PVPR
DVC
DVC
PVM
d
VD1
AVL
c
b
d
AVL e
c
b
d
a
AVL f

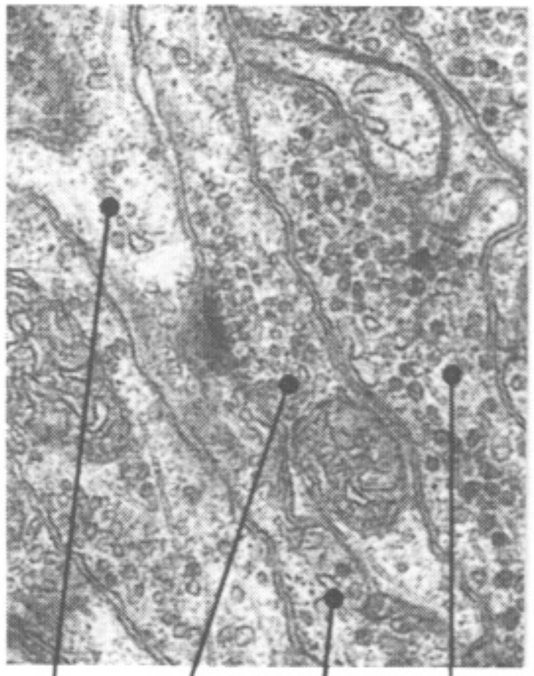
AVL


AVBR
RIS
AVM
PVCL
a
AVFL
BDUL
AVJR
AVM
b
DA1
AVM
ADER
DB1
C
AVBL
AVM
ALMR
BDUR
d
AVJL
AVM
AVDL
AVBL
e
AVM
PVM
AVKL
DVA
f
PVM
PDEL
PDER
DVA
g
PVR
PVCL
PVM
PDER
PVCR
h
b
c
a
e
f
g
h
AVM
d
PVM
i

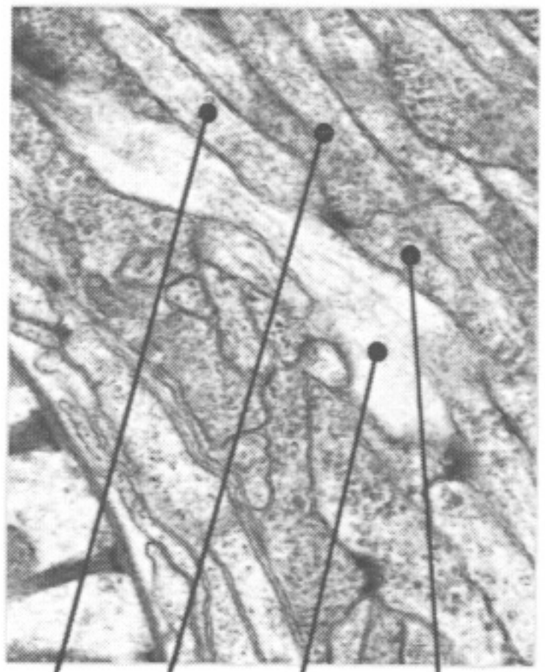
AVM AND PVM


AIZL
AWAL
a
AUAR
AWAR
b
AIYL
RIBL
c
AWCR
AIBL
d
ASER
ADLL
AFDR
BAGL
AWAL
AIZL
AIAL
AWAL
AWAL
e

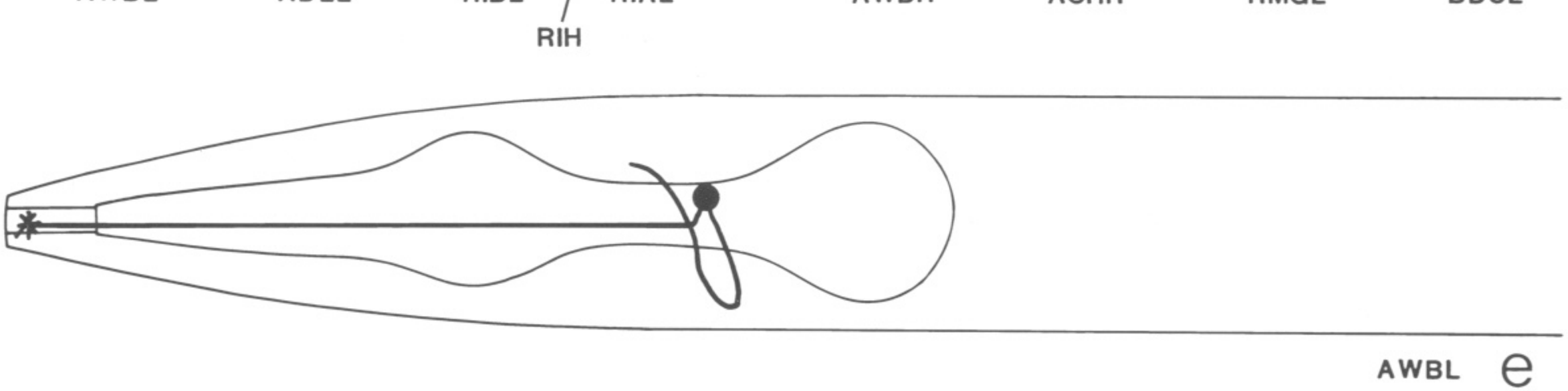
AWA


AIZL
AWBL
ADFL
ADLL
a

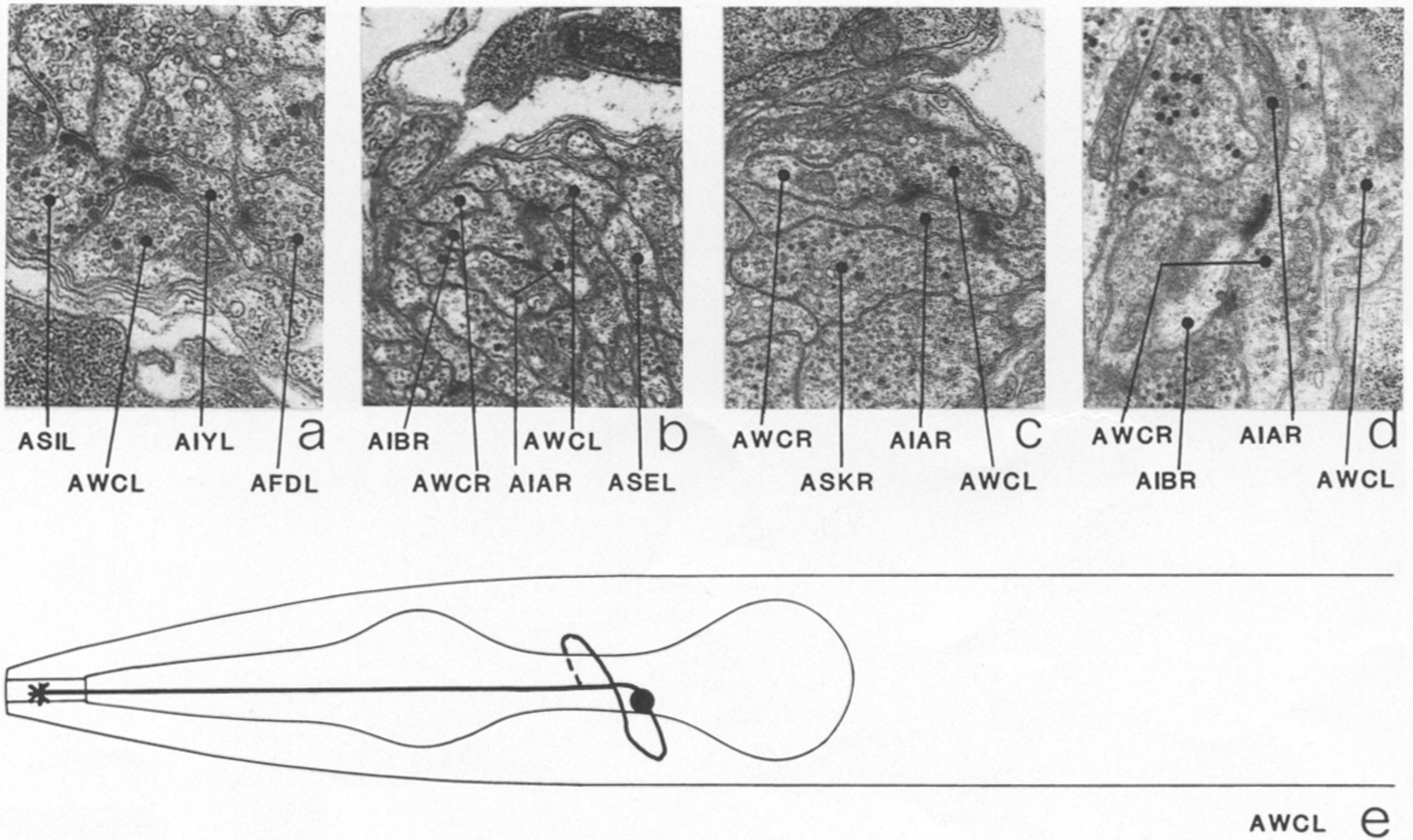

AWBL
RIBL
RIAL
AIZL
b


HSNR
AWBR
AVBR
ASHR
c

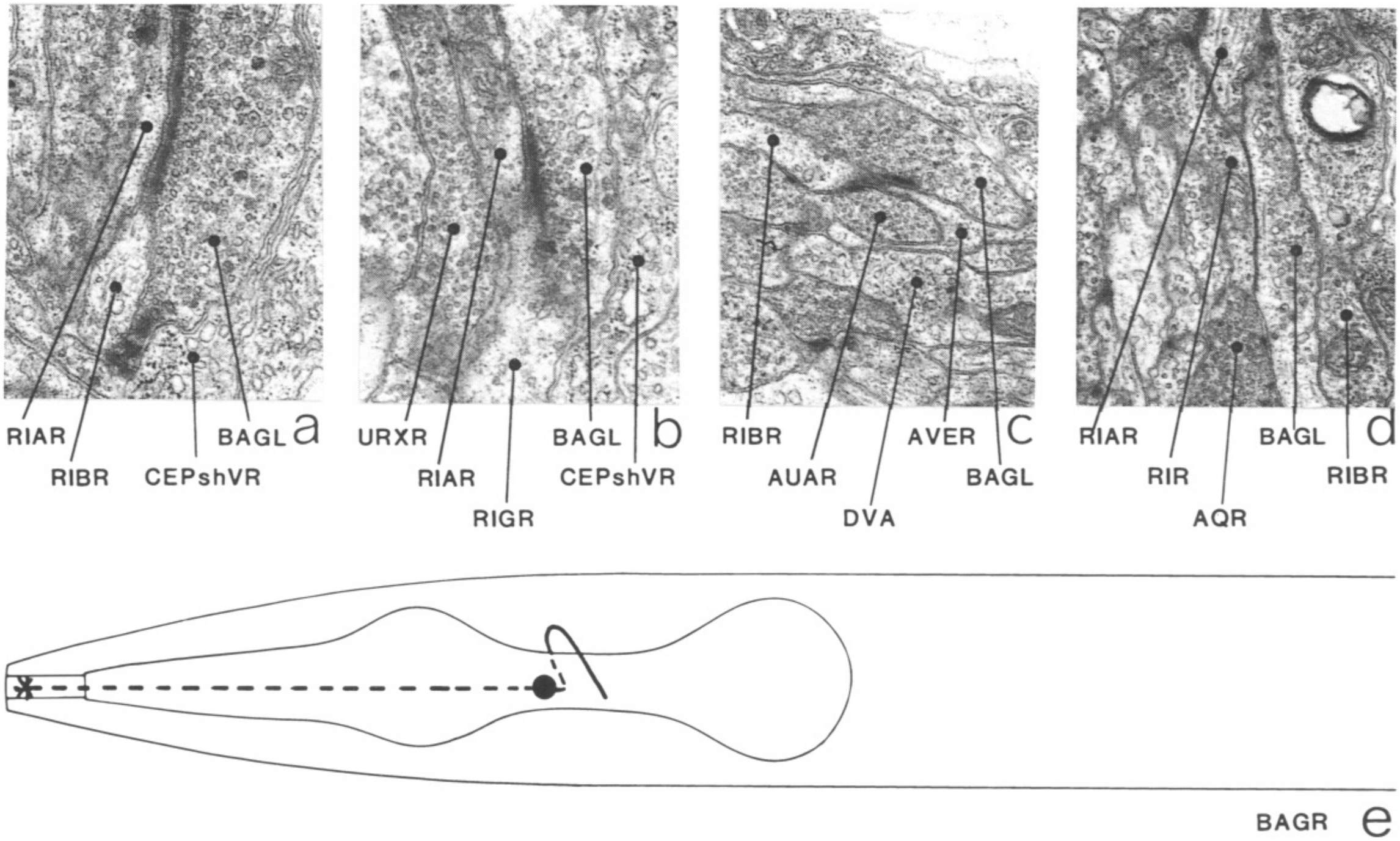

AWBL
RMGL
ALML
BDUL
d


RIH
AWBL
e

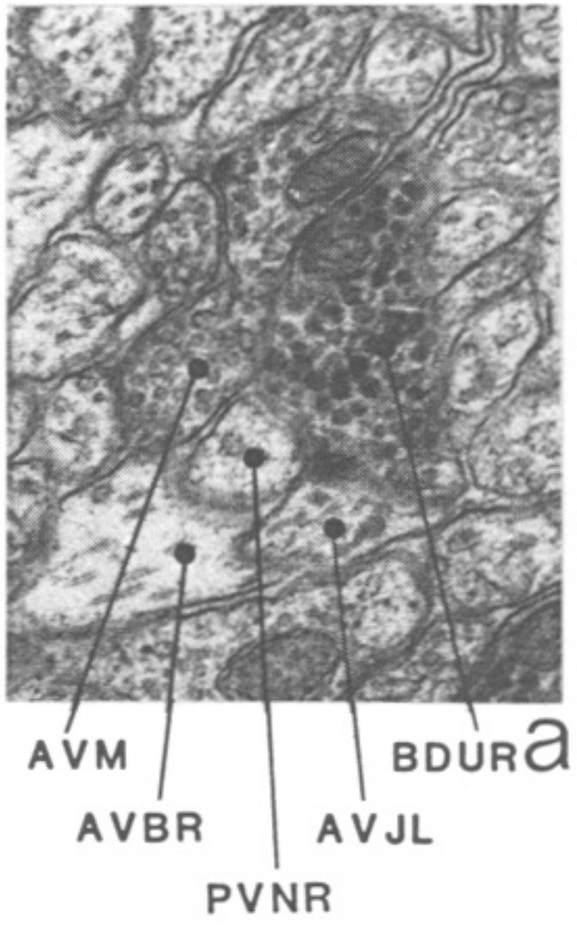
AWB

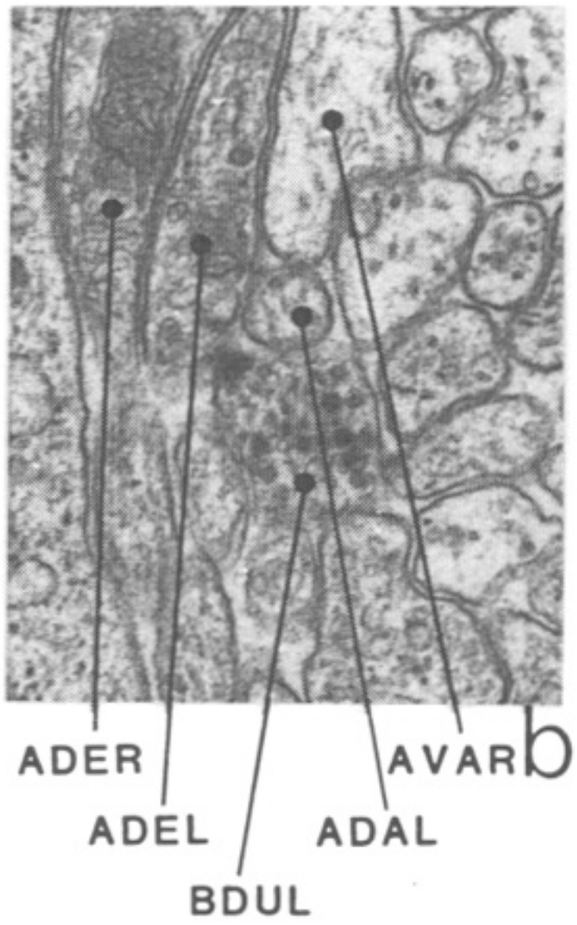

ASIL
AWCL
AIYL
AFDL
a
AIBR
AWCR
AIAR
AWCL
ASEL
b
AWCR
ASKR
AIAR
AWCL
c
AWCR
AIBR
AIAR
AWCL
d
AWCL
e

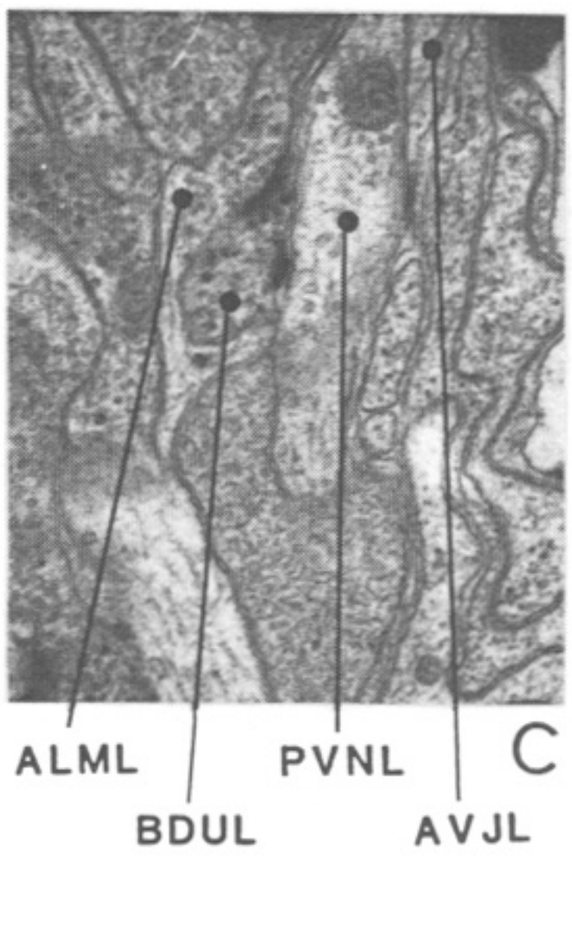
AWC

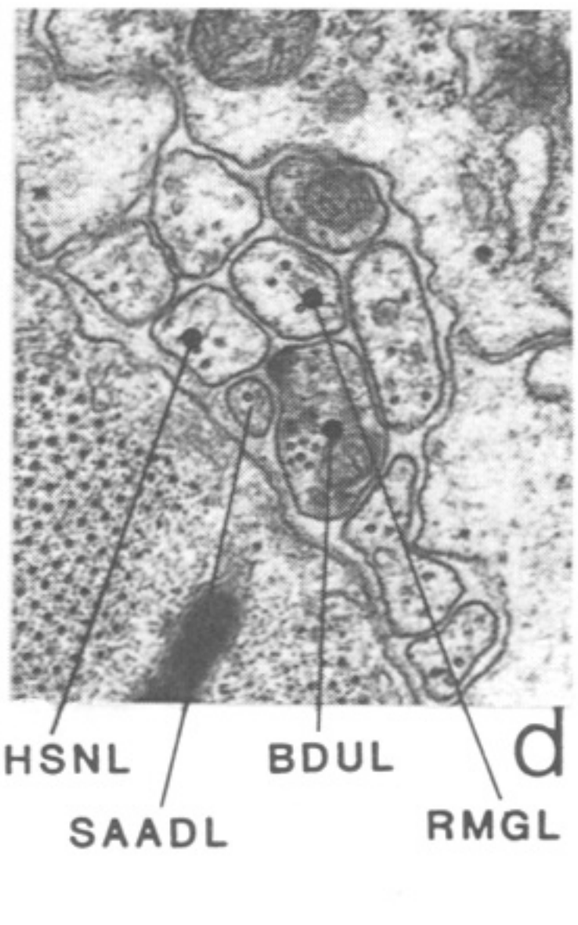

RIAR
RIBR
CEPshVR
BAGL
a
URXR
RIAR
RIGR
BAGL
CEPshVR
b
RIBR
AUAR
DVA
AVER
BAGL
c
RIAR
RIR
AQR
BAGL
RIBR
d
BAGR
e

BAG


AVM
AVBR
PVNR
AVJL
BDUR
a

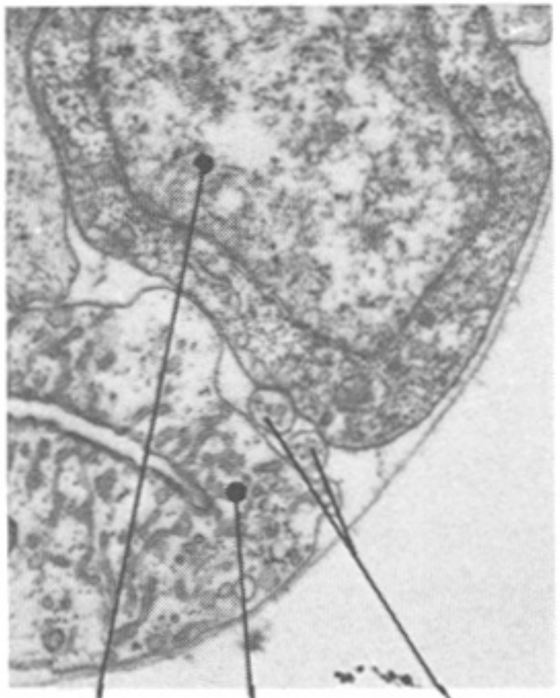

ADER
ADEL
BDUL
ADAL
AVAR
b

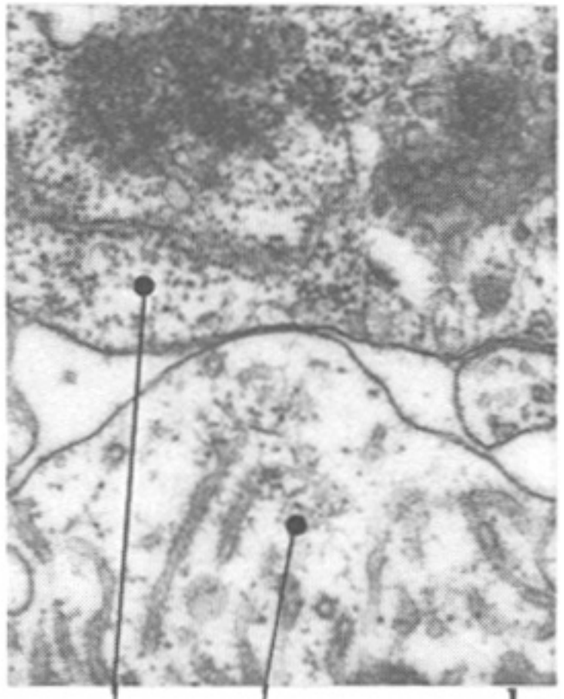

ALML
BDUL
PVNL
AVJL
c

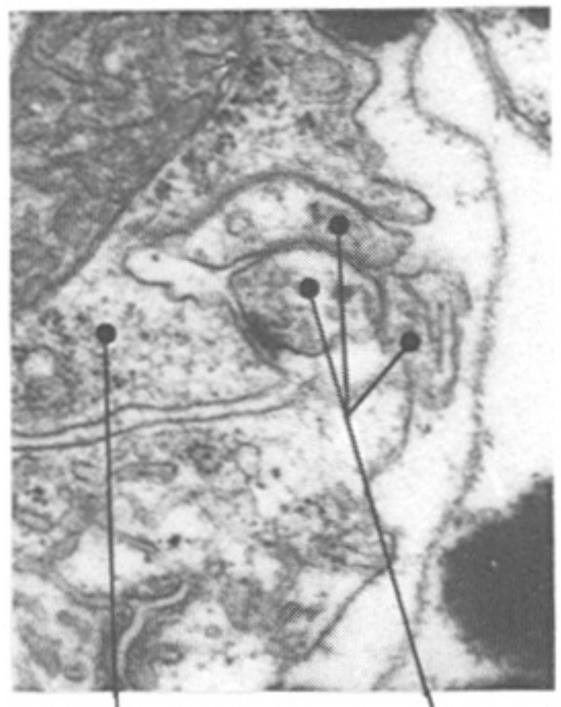

HSNL
SAADL
BDUL
RMGL
d

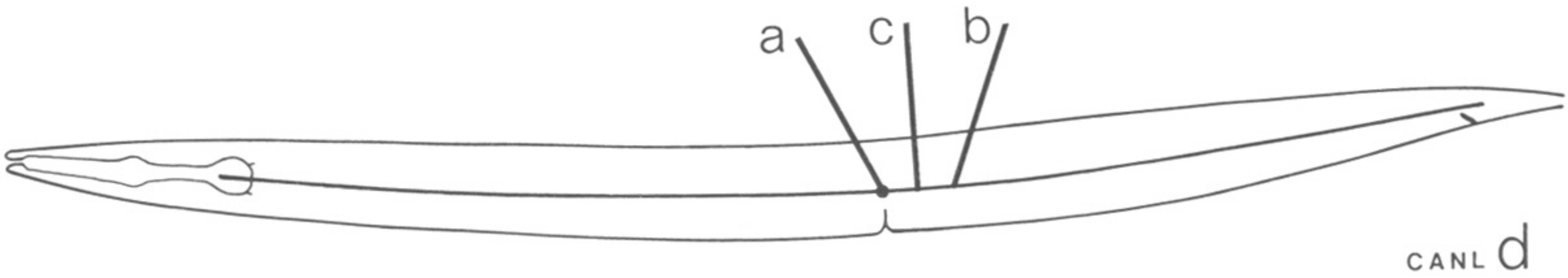
a
b
d
BDUL e
BDUL f

BDU

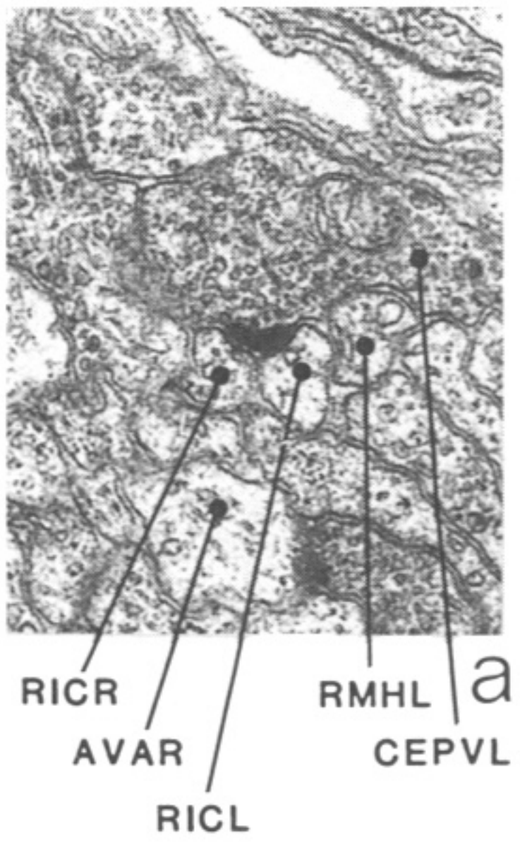

CANL
EXCRETORY CANAL
CANAL ASSOCIATED PROCESSES
a

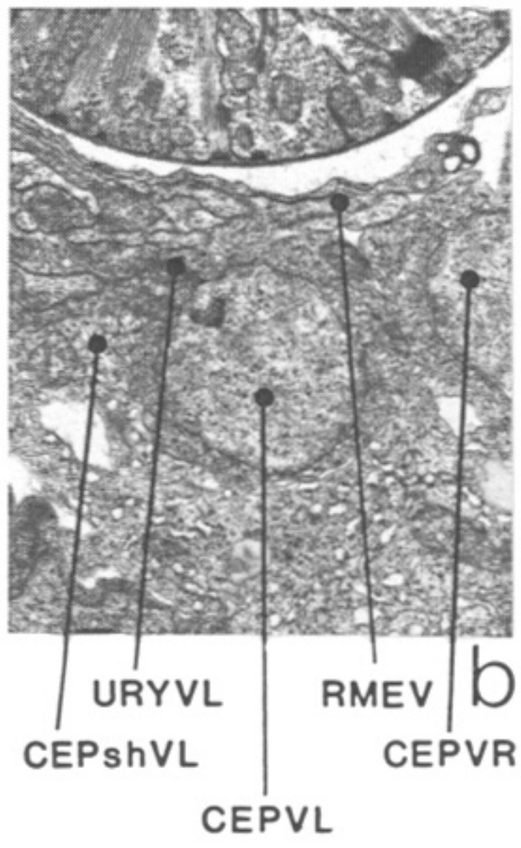

CANL
EXCRETORY CANAL
b

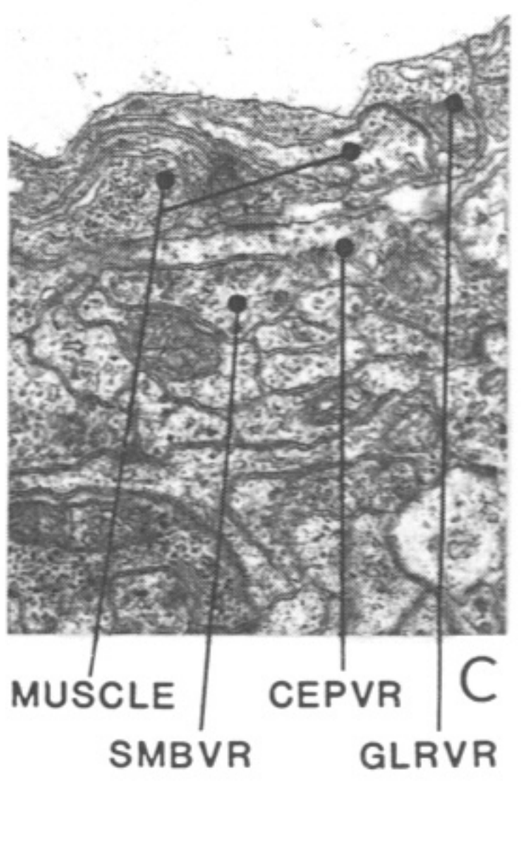

HYPODERMIS
CANAL ASSOCIATED PROCESSES
c

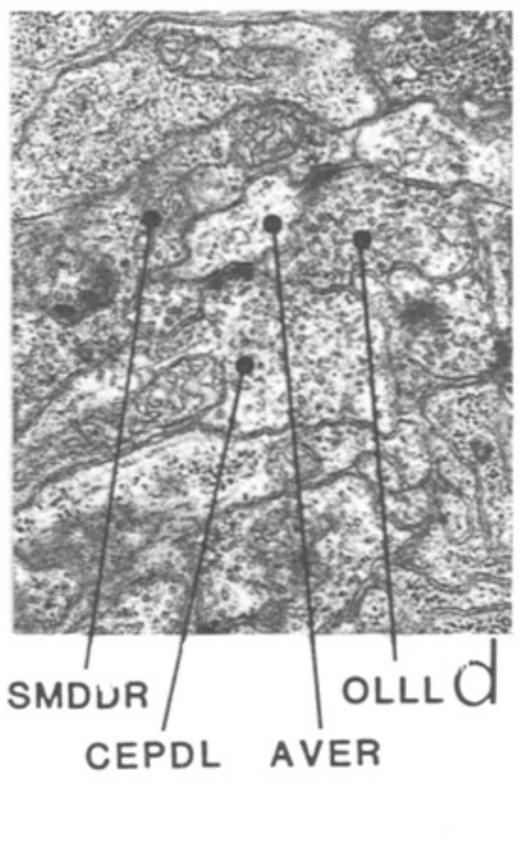

a
c
b
CANL d

CAN

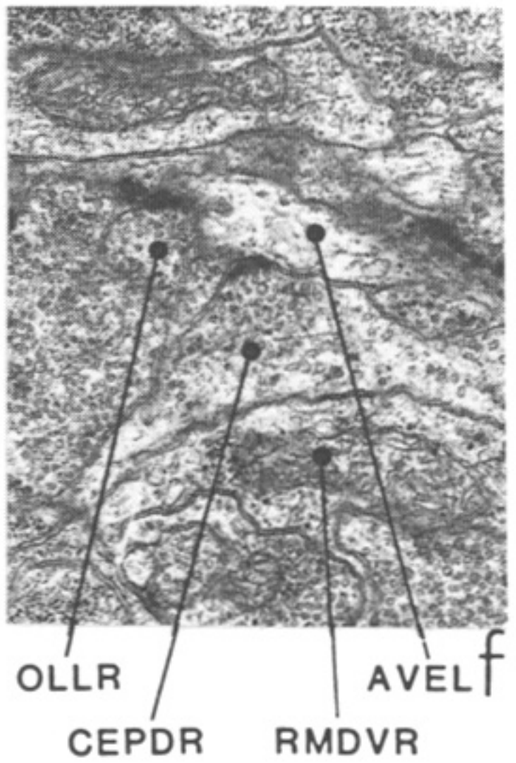

RICR
AVAR
RICL
RMHL
CEPVL
a

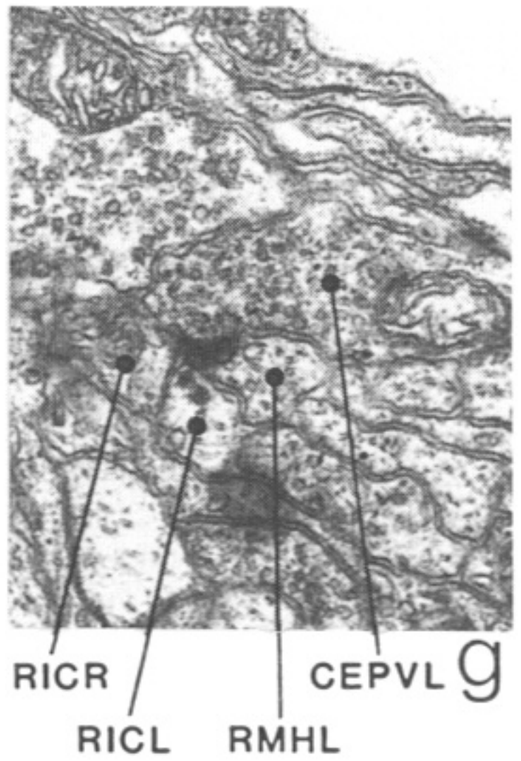

URYVL
CEPshVL
CEPVL
RMEV
CEPVR
b

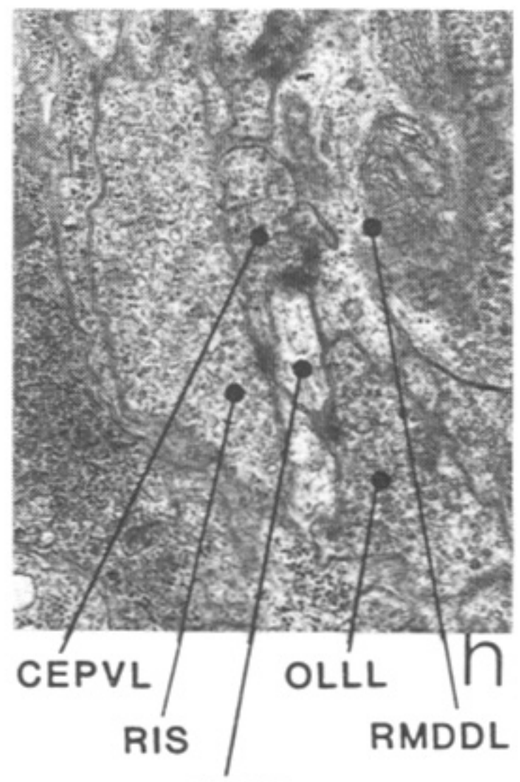

MUSCLE
SMBVR
CEPVR
GLRVR
c

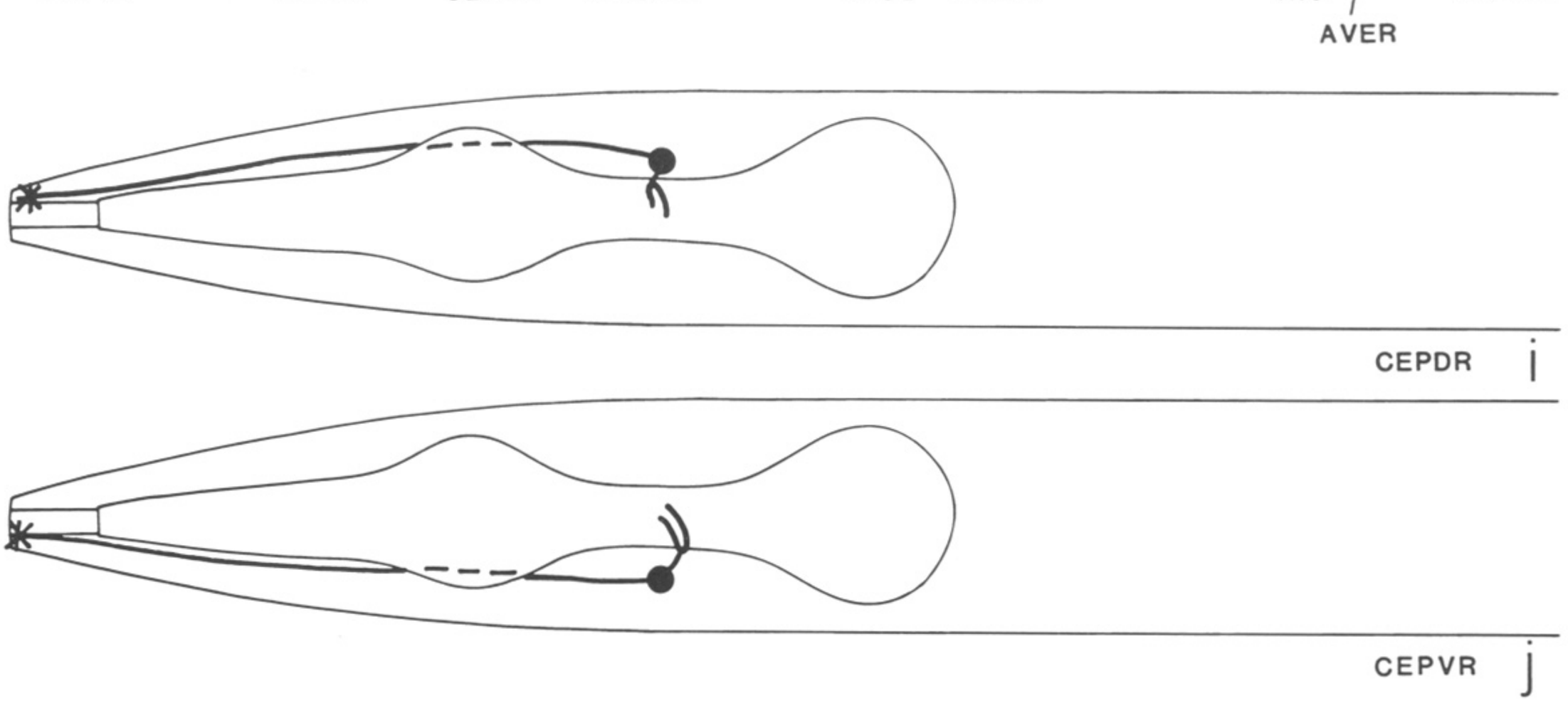

SMDDR
CEPDL
AVER
OLLL
d


PVR
CEPVR
OLQVR
IL1VR
e

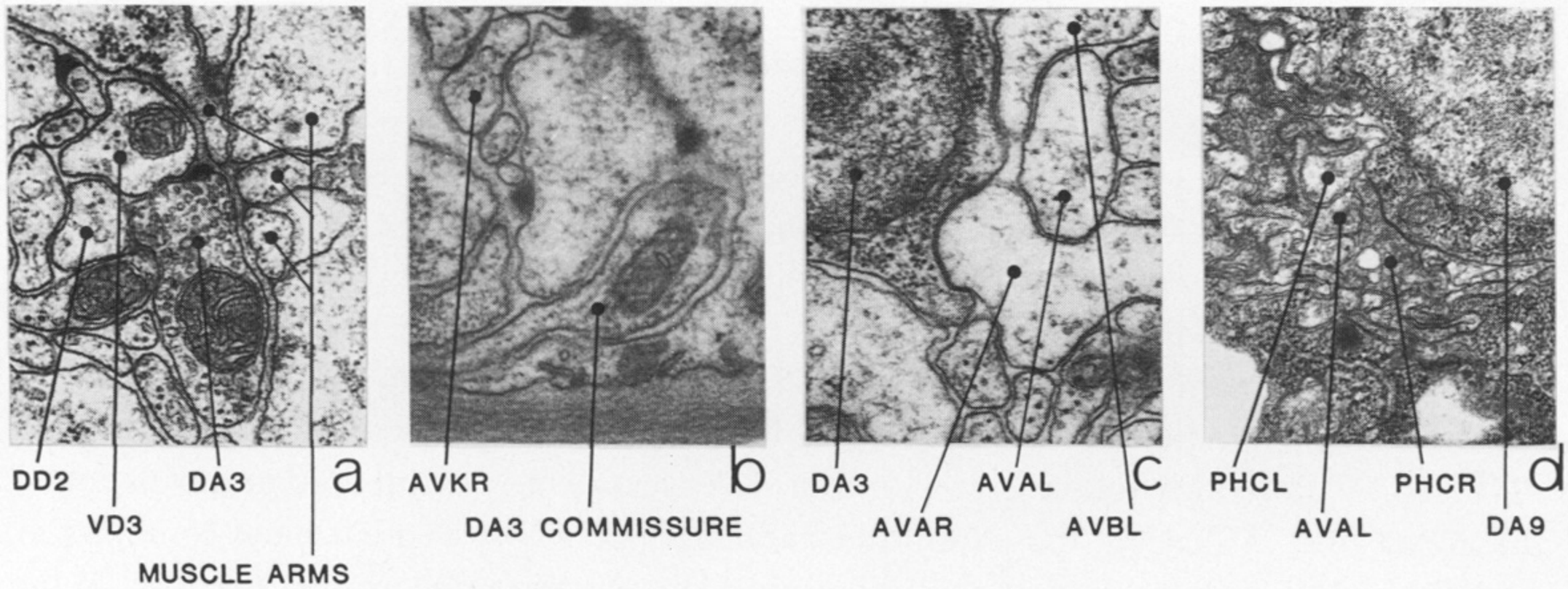

OLLR
CEPDR
RMDVR
AVEL
f

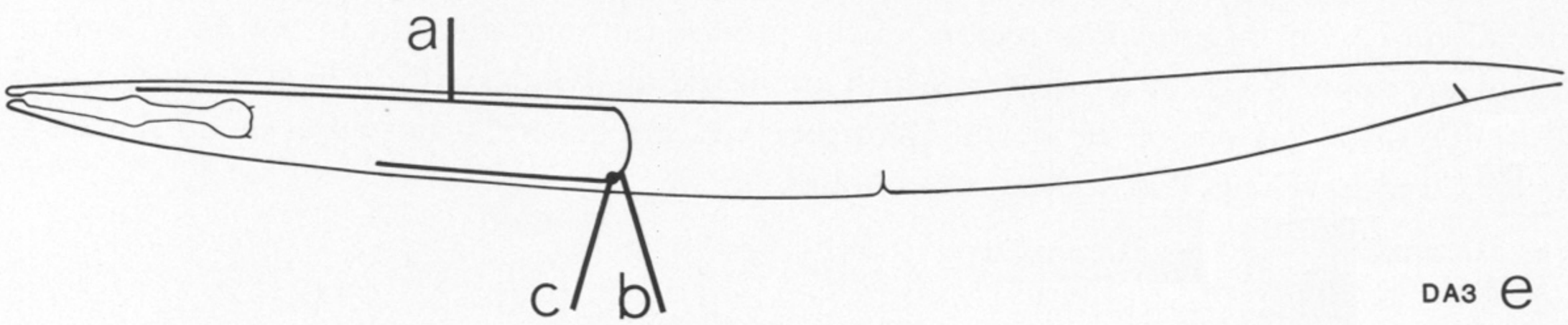

RICR
RICL
RMHL
CEPVL
g


CEPVL
RIS
AVER
OLLL
RMDDL
h

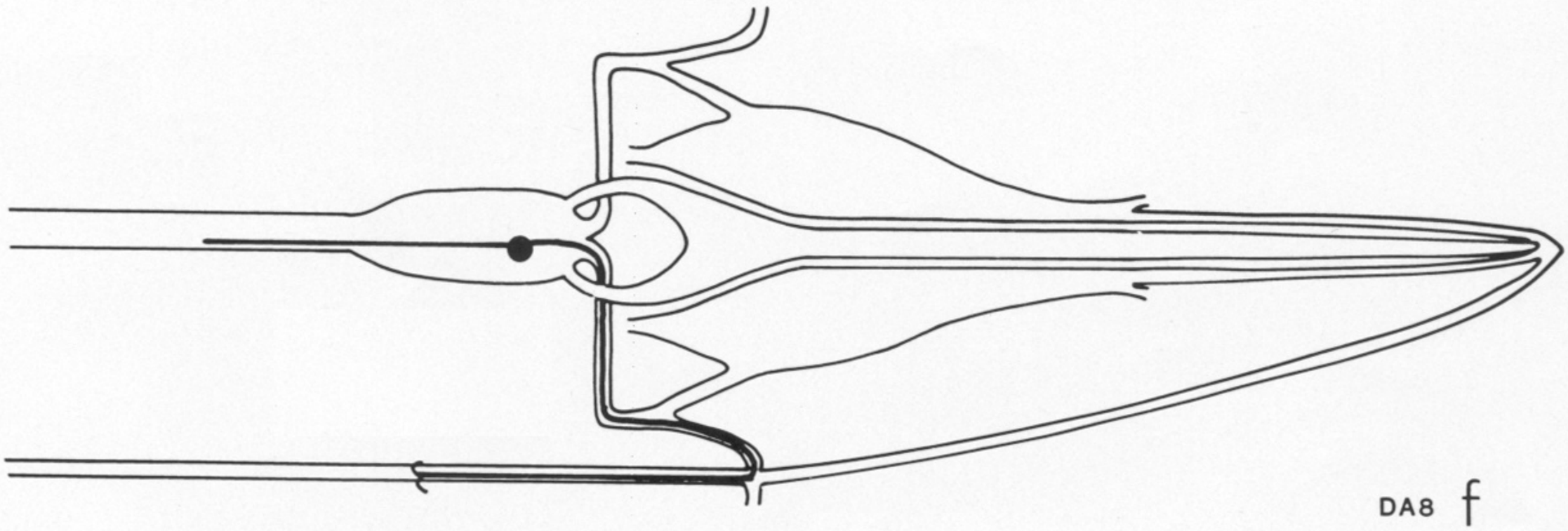

CEPDR
i
CEPVR
j

CEP

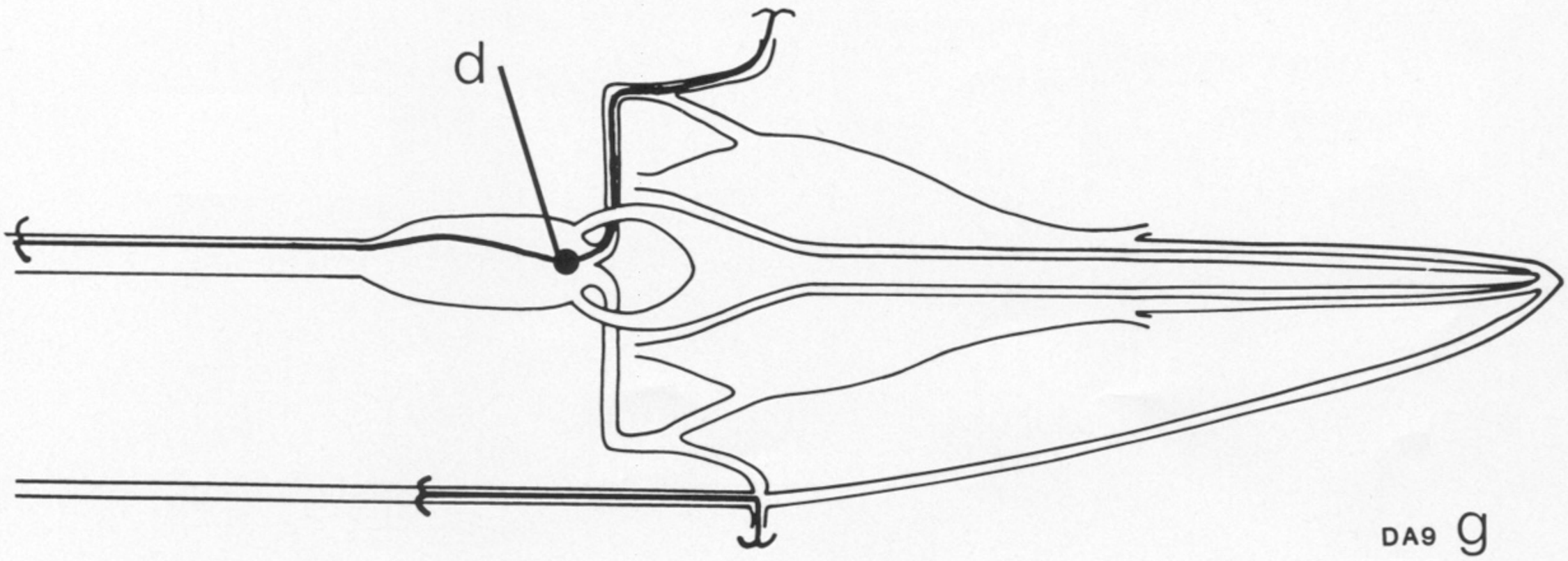




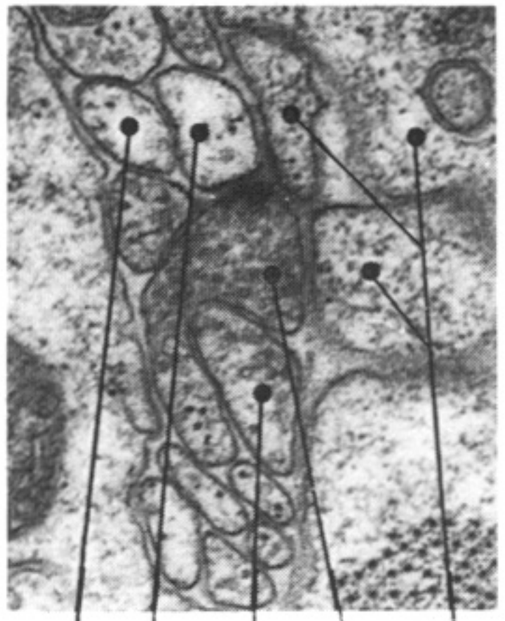
DA3 e



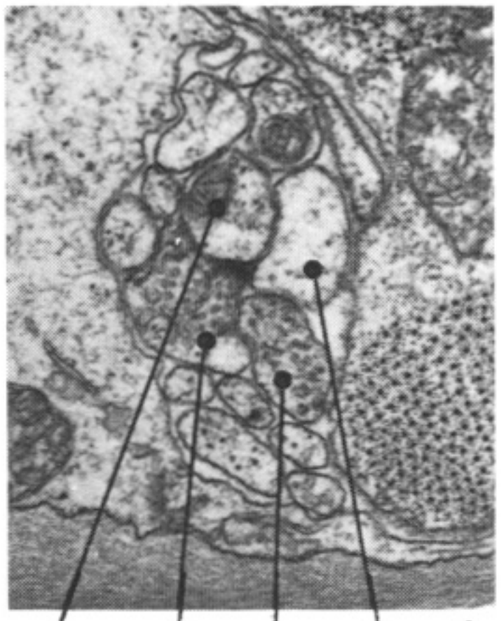
DA8 f



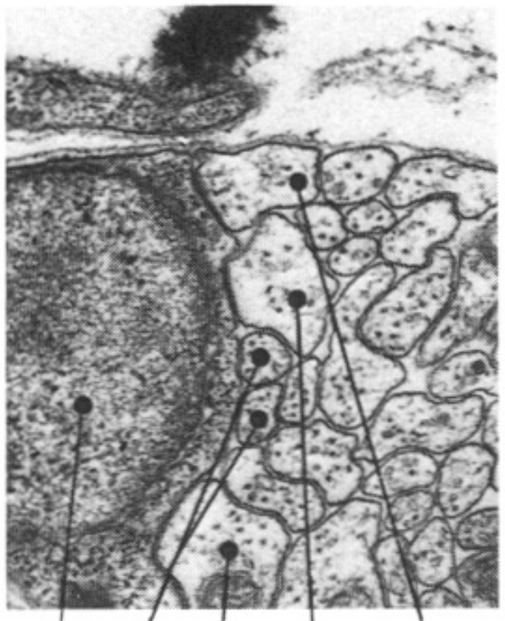
DA9 g



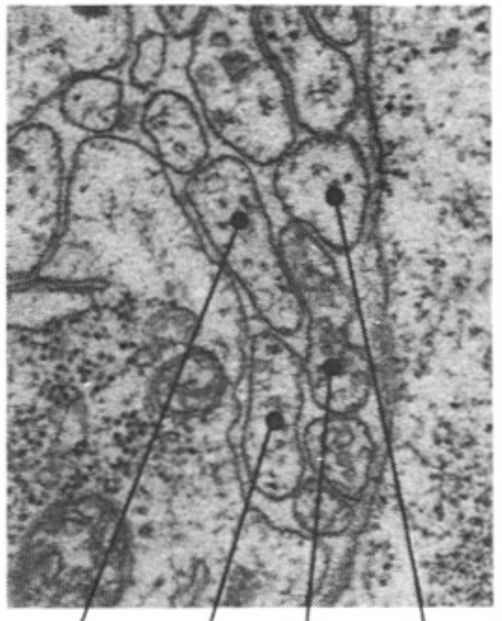
a



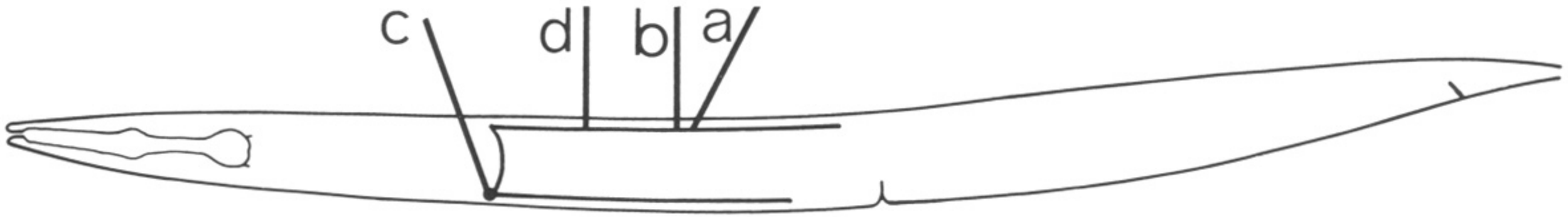
b



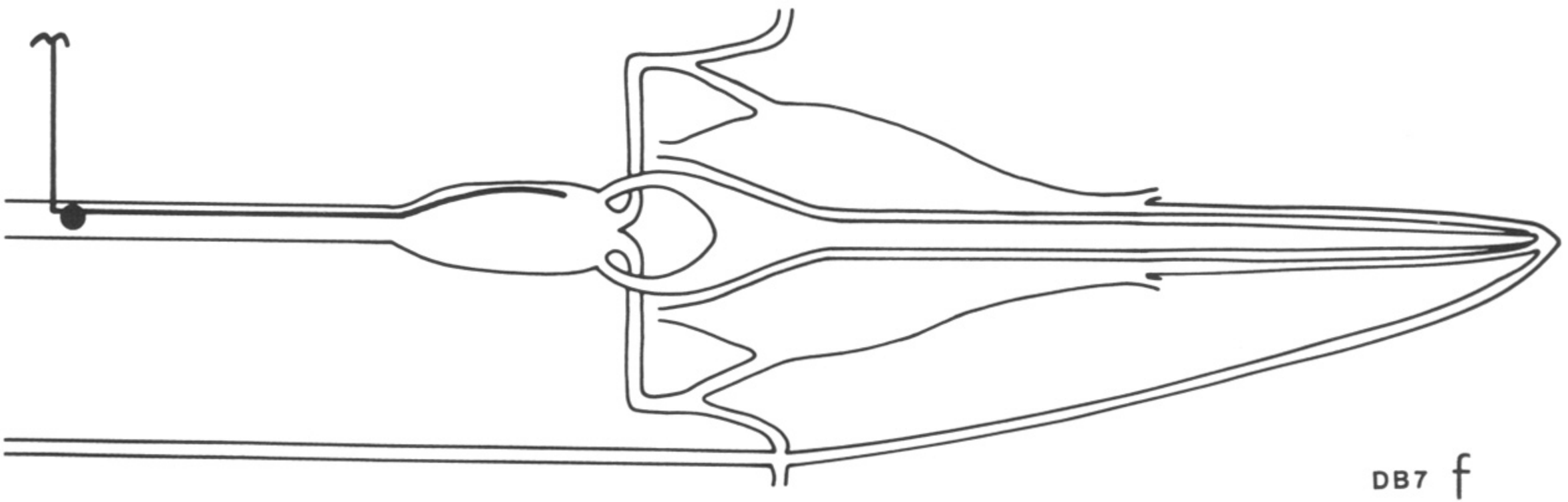
c



d

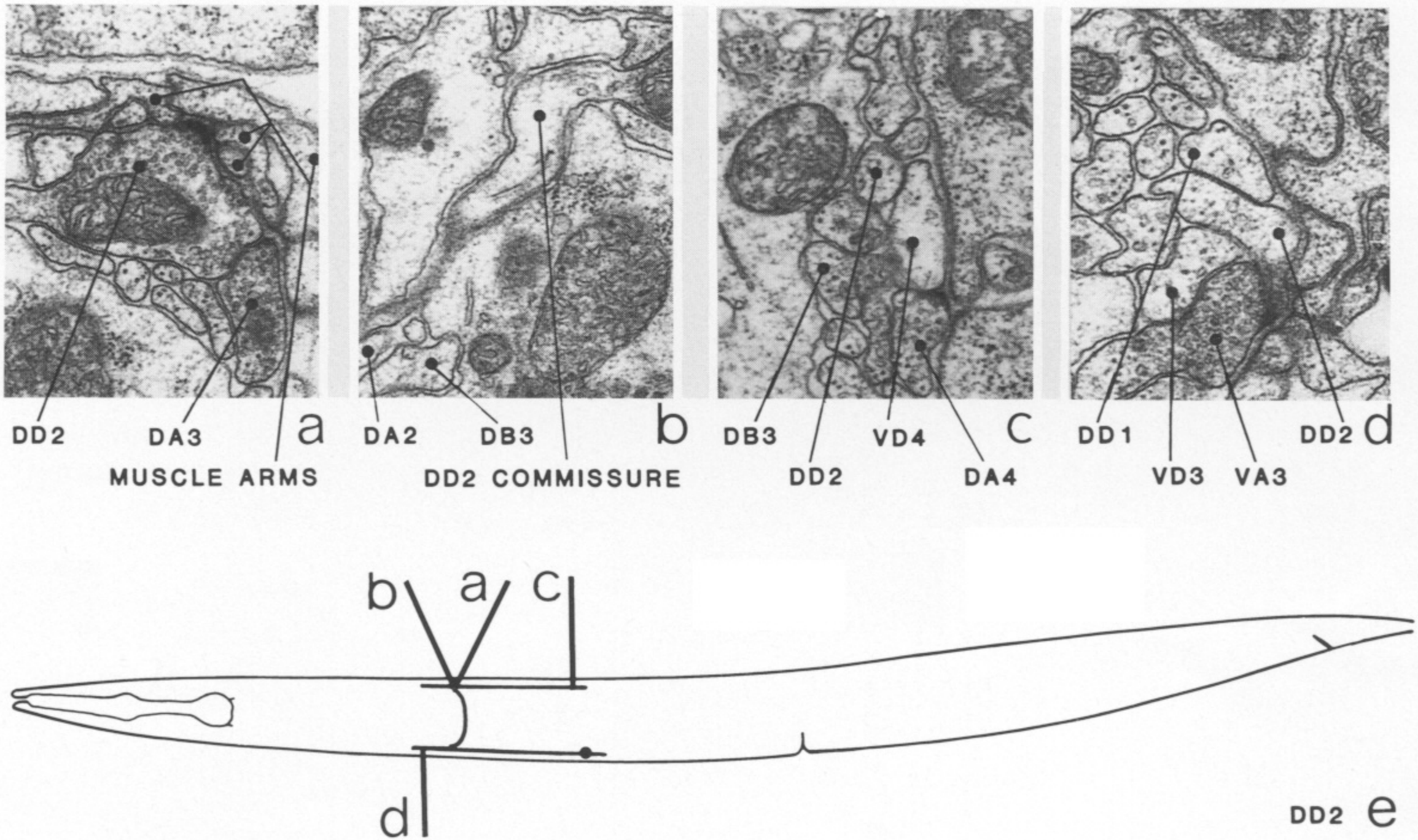


DB3 e

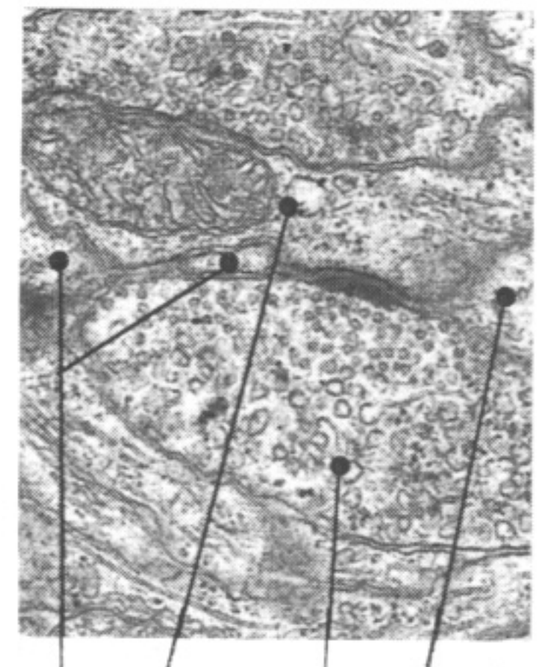


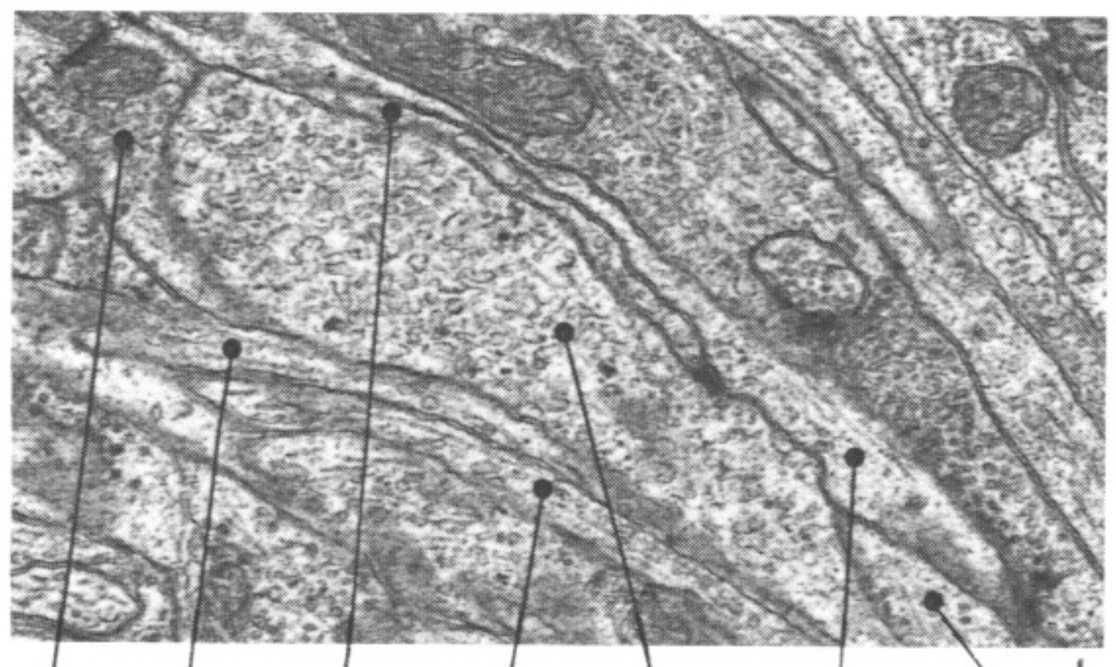
DB7 f

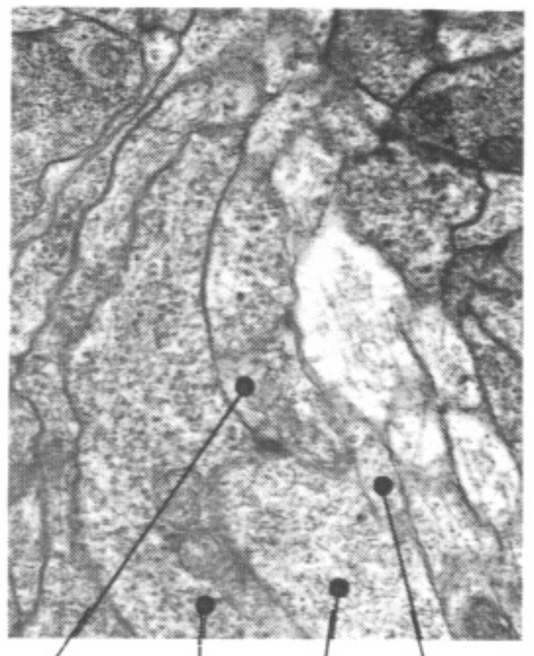
DBn

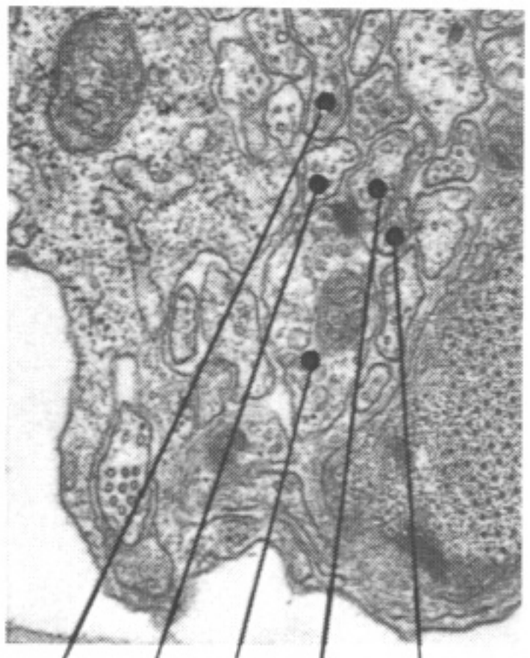

DD2
DA3
a
DA2
DB3
b
DB3
VD4
c
DD1
DD2
d
MUSCLE ARMS
DD2 COMMISSURE
DD2
DA4
VD3
VA3
b
a
c
d
DD2
e

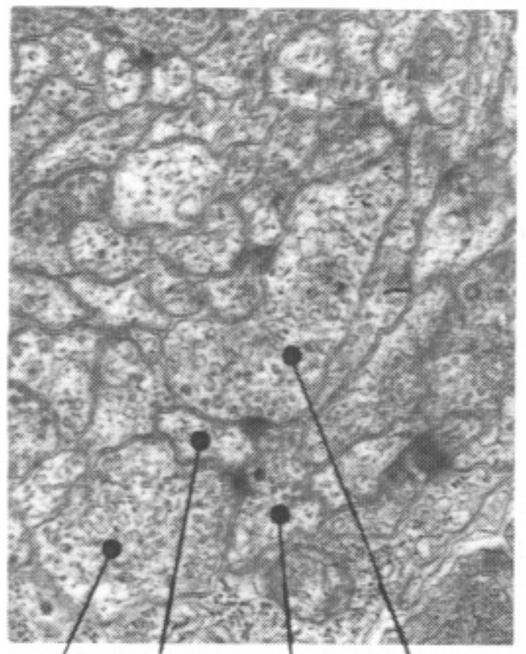
DDn

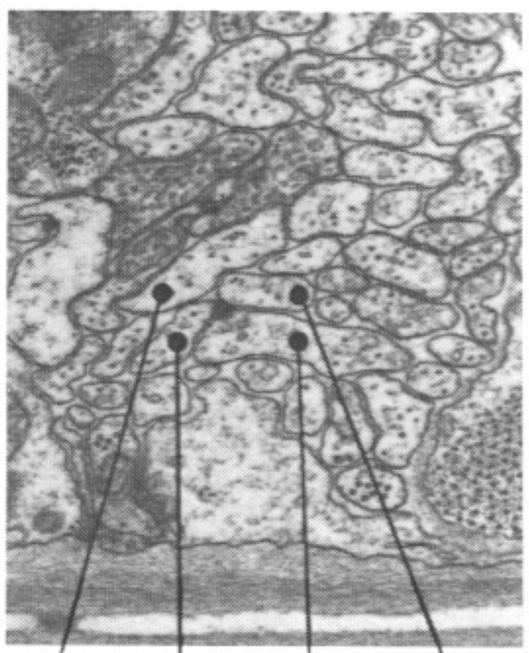

AIZR
AVER
DVA
AIZR
a

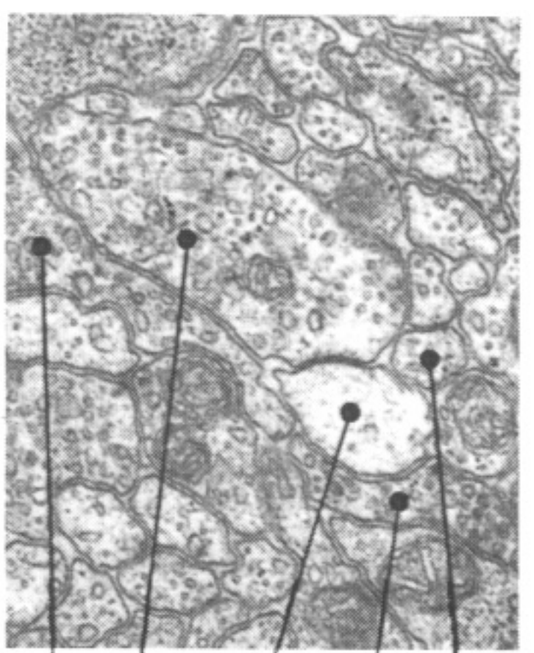

AIZR
SIBDL
AUAR
SIBVR
DVA
AVER
AIZR
b

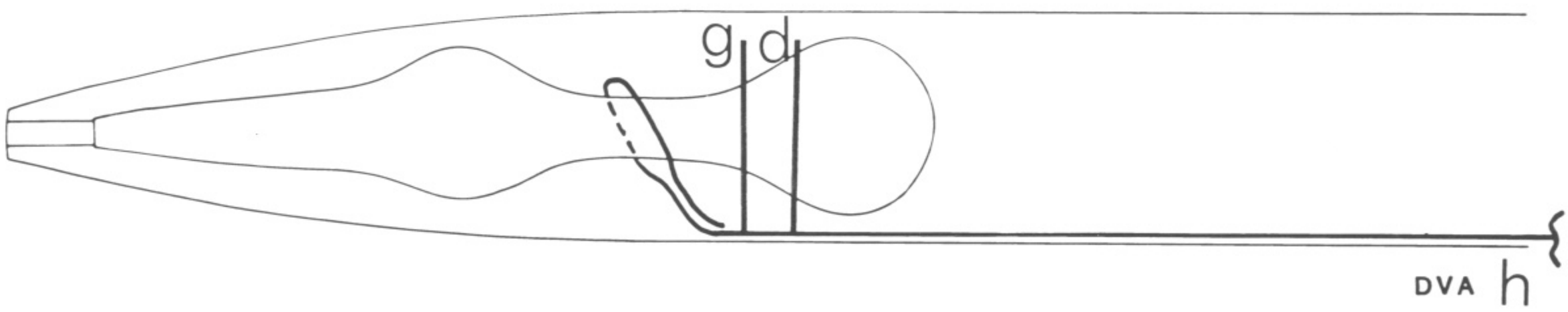

AVAL
AQR
DVA
PVCL
c

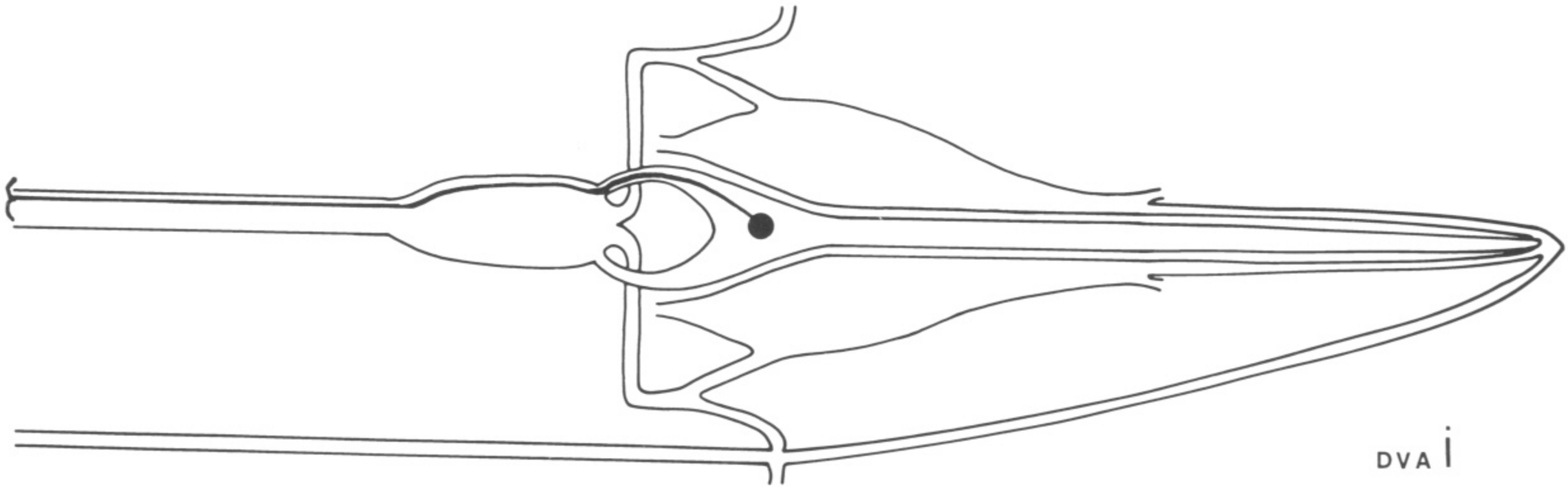

FLPL
PVR
DVA
VB1
SABD
d

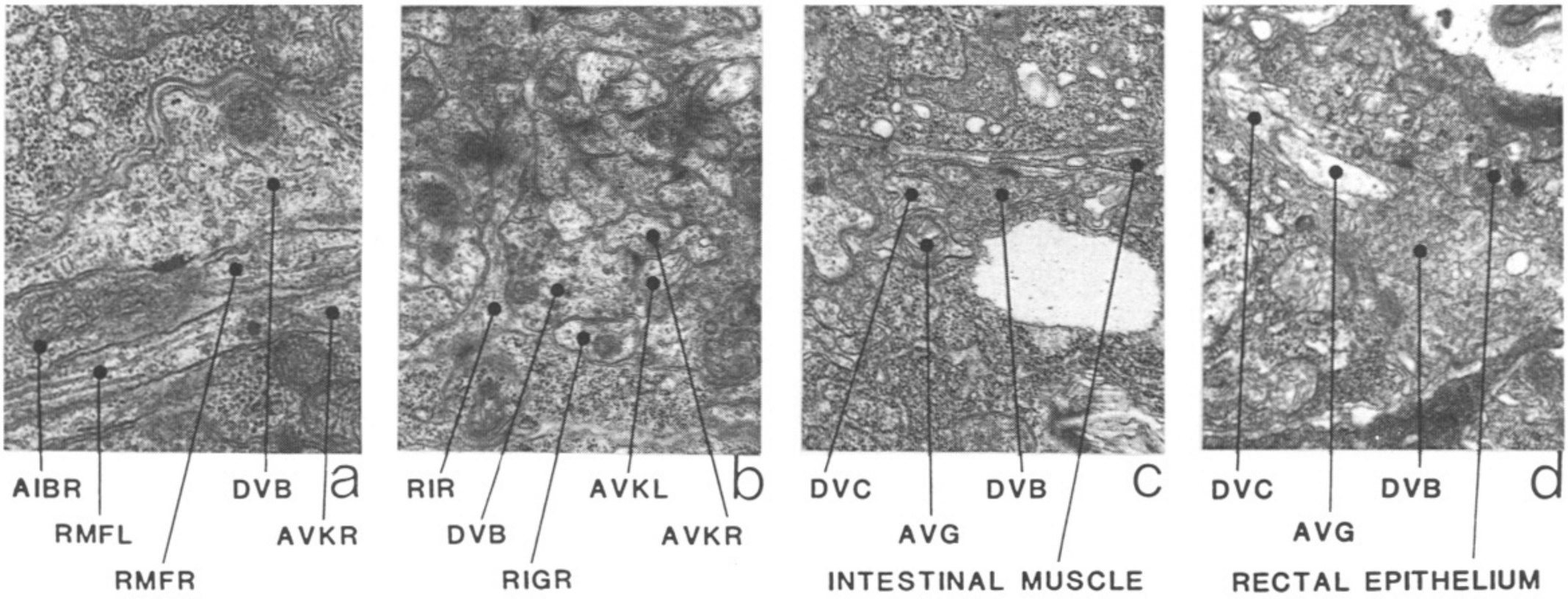

RIGR
AVEL
RIR
DVA
e

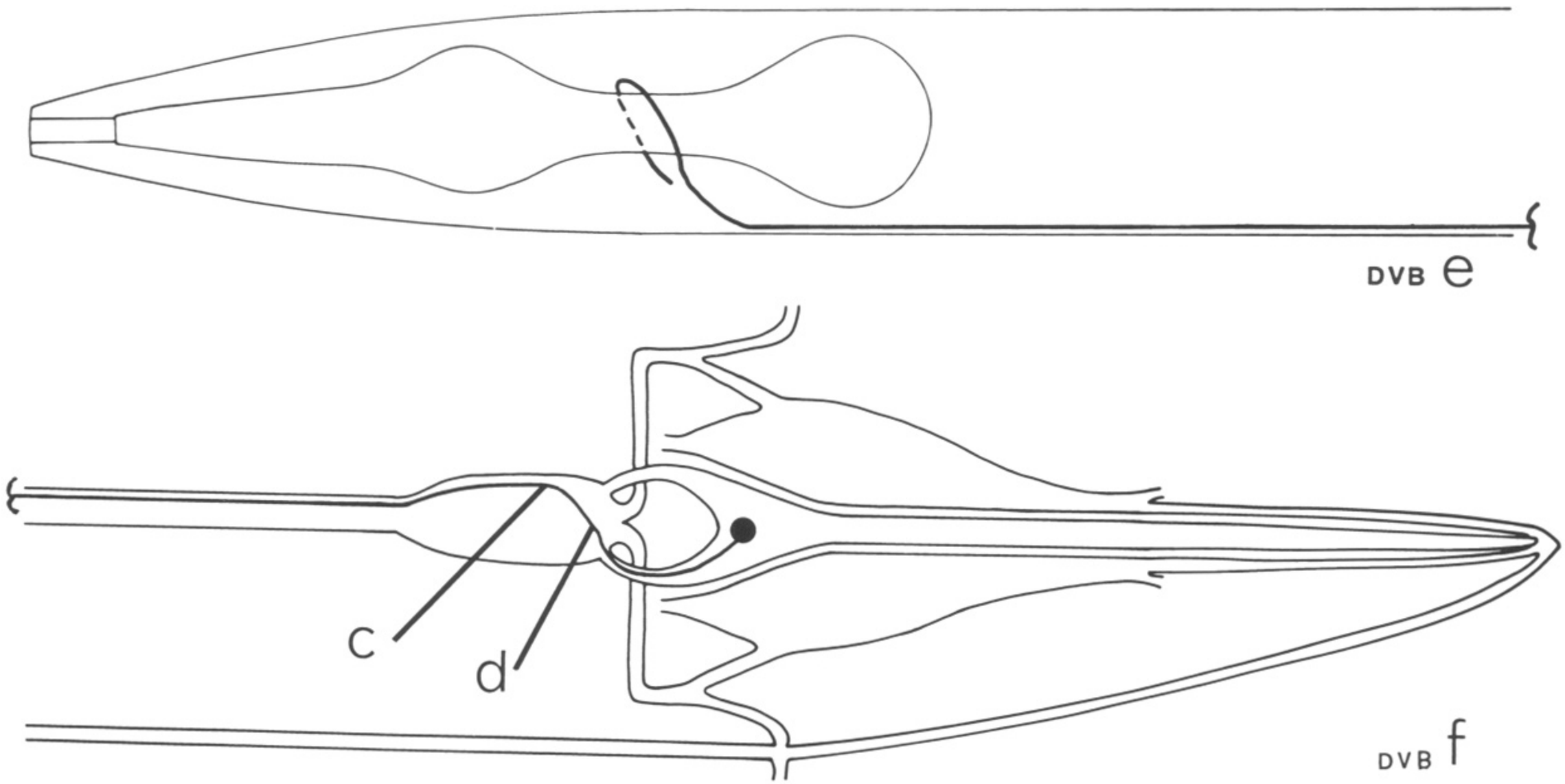

AVAR
DB3
DVA
PVCL
f


FLPL
DVA
AVBL
ADAR
PVPR
g

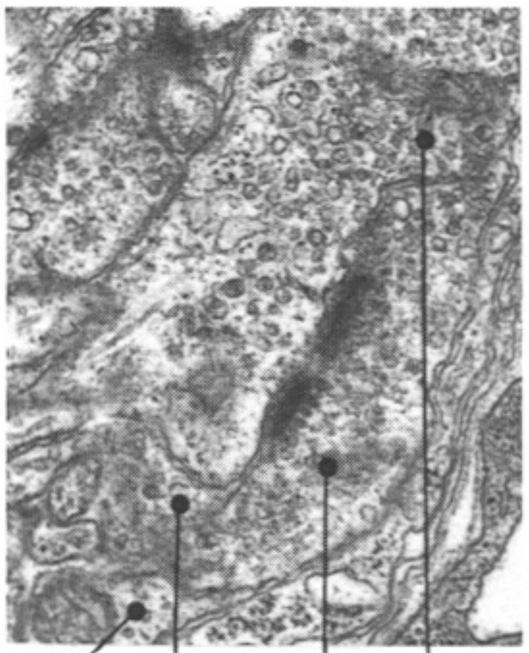

g
d
DVA
h

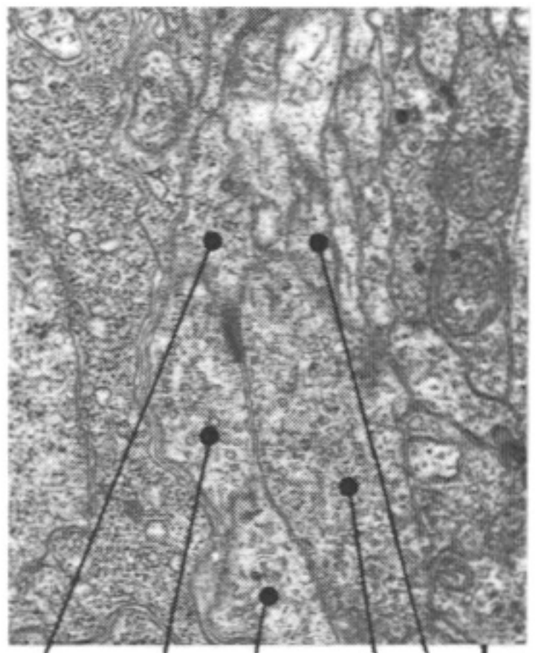

DVA
i

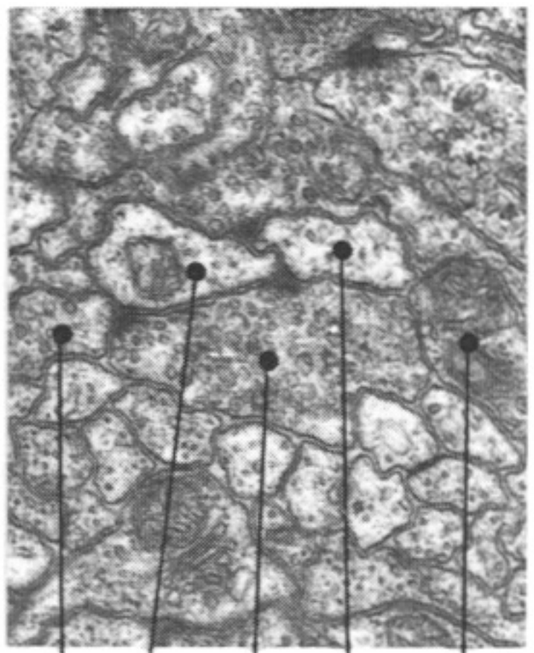

AIBR
RMFL
RMFR
DVB
AVKR
a
RIR
DVB
RIGR
AVKL
AVKR
b
DVC
AVG
DVB
INTESTINAL MUSCLE
c
DVC
AVG
DVB
RECTAL EPITHELIUM
d

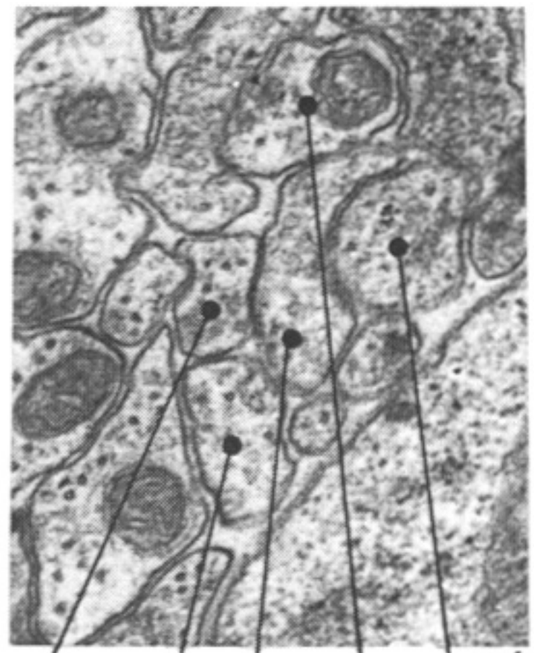

DVB
e
c
d
DVB
f

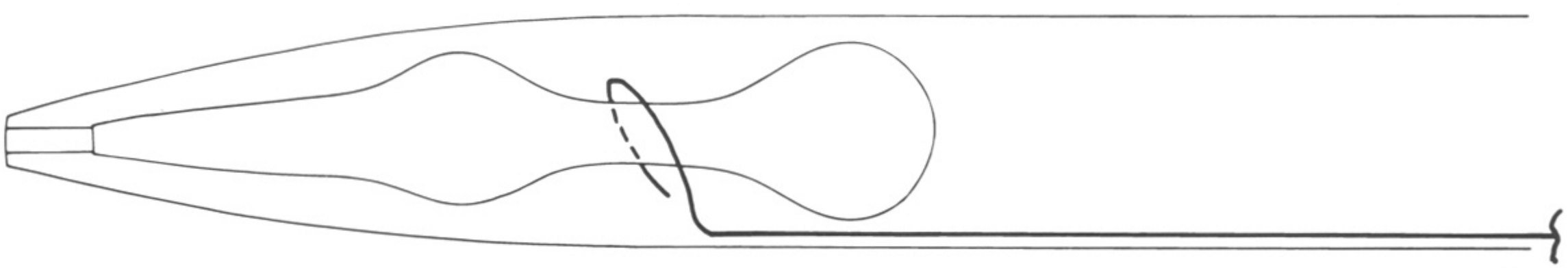
DVB

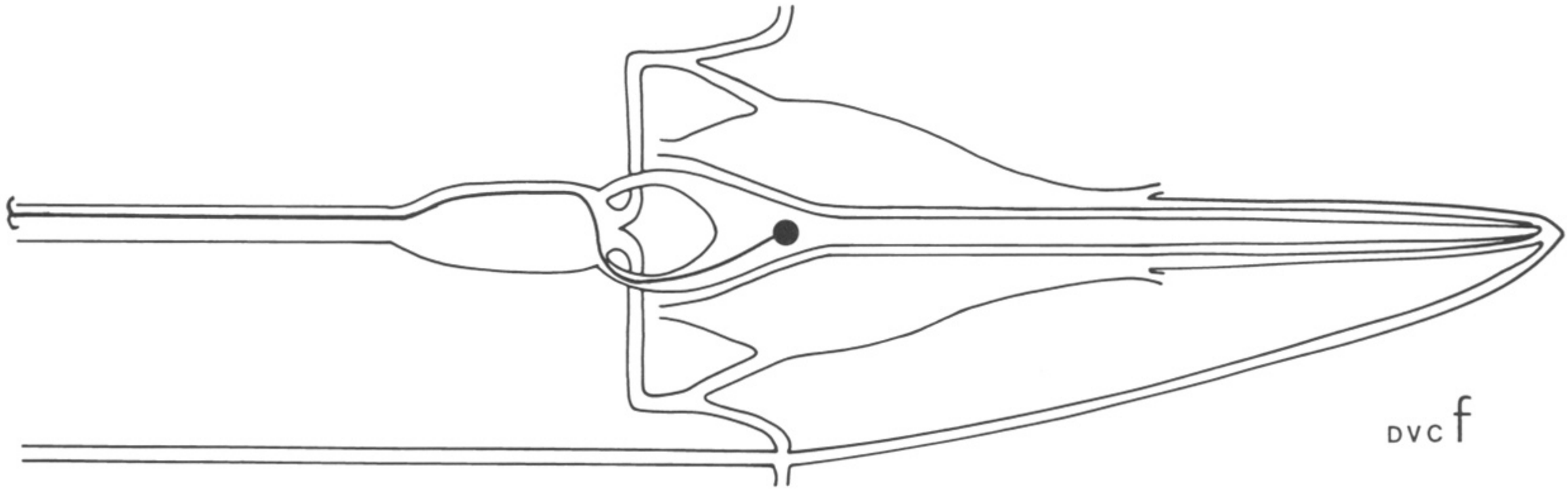

RIBR
BAGL
DVC
RIGR
a


RMFL
DVC
DVB
RIGL
SAADL
b

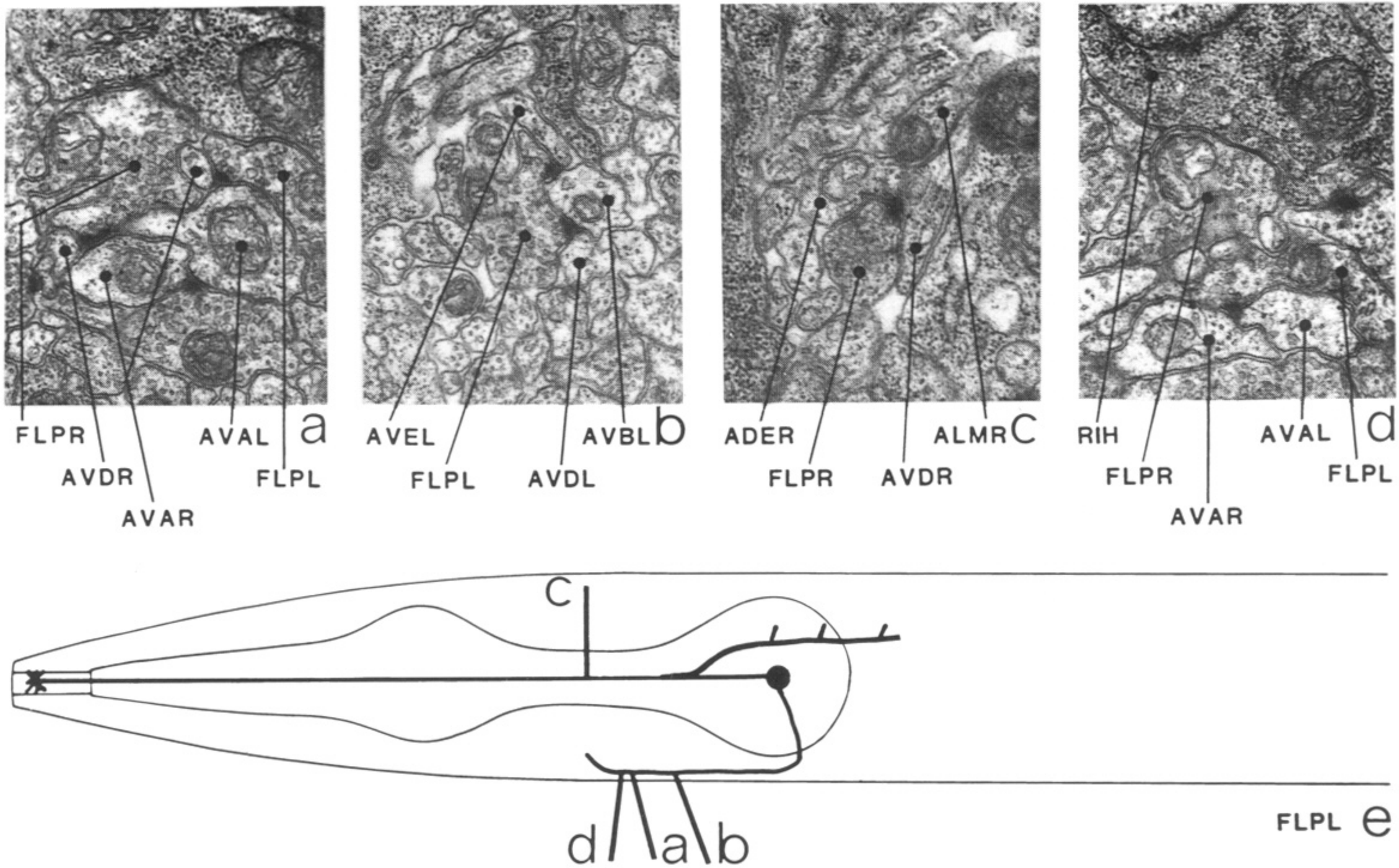

AIBR
AVAR
DVC
AVAL
AIBL
c


PVPR
AQR
DVC
DVB
VD1
d

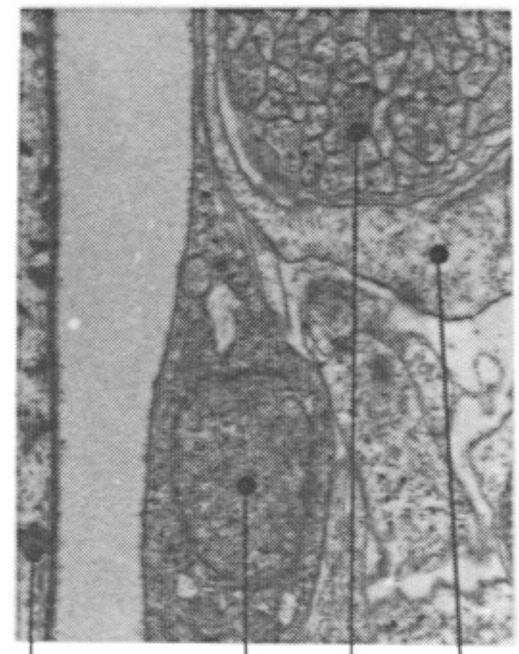

DVC e

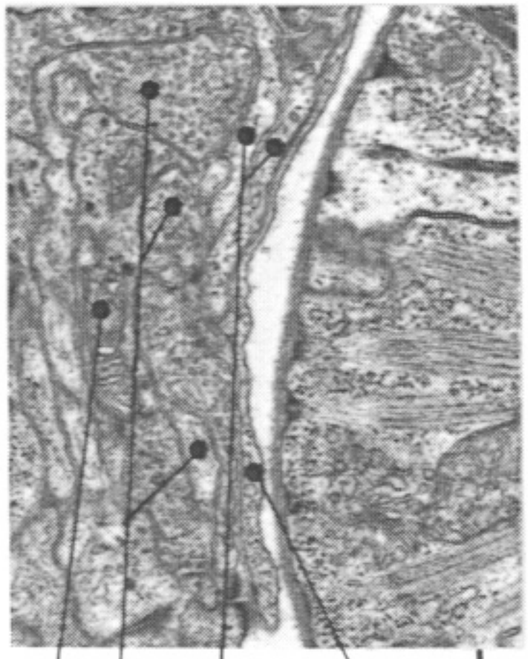

DVC f

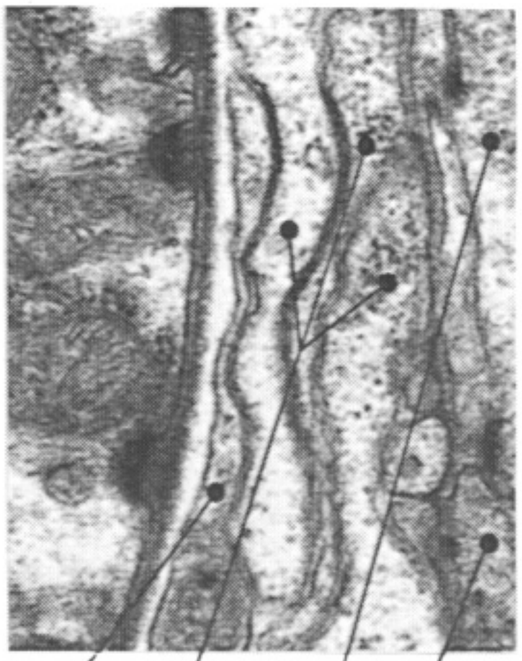
DVC

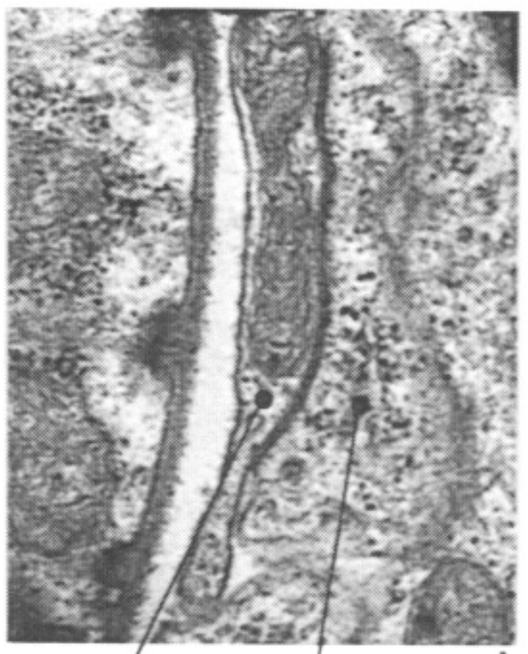

FLPR
AVDR
AVAR
AVAL
FLPL
a
AVEL
FLPL
AVDL
AVBL
b
ADER
FLPR
AVDR
ALMR
c
RIH
FLPR
AVAR
AVAL
FLPL
d
C
d
a
b
FLPL
e

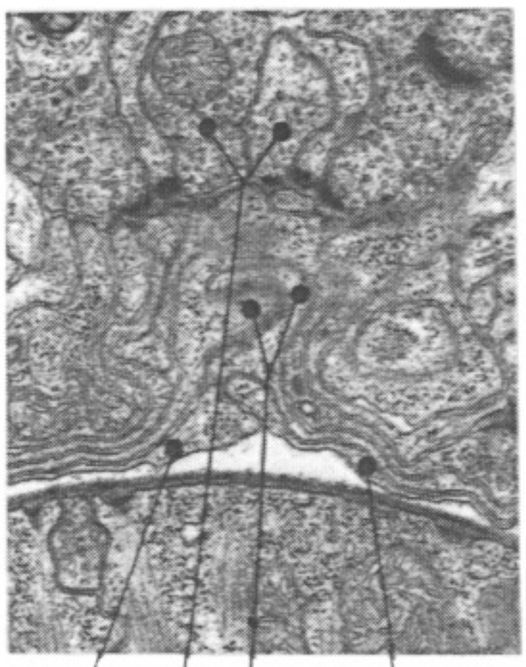
FLP

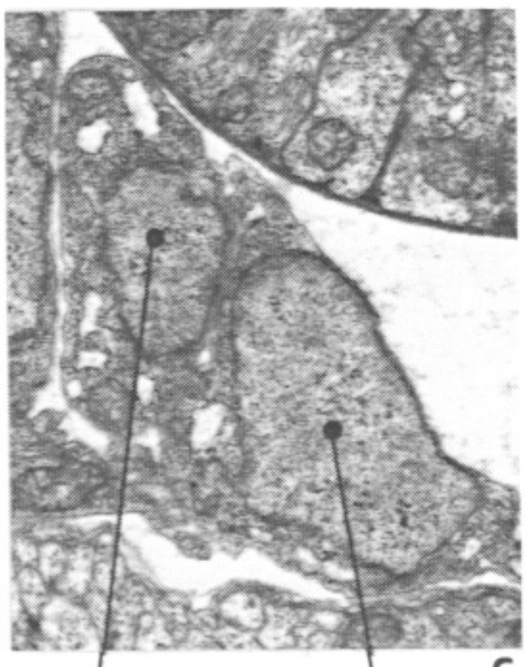

GLRVL
RING NEUROPILE
PHARYNX MUSCLE ARM
a

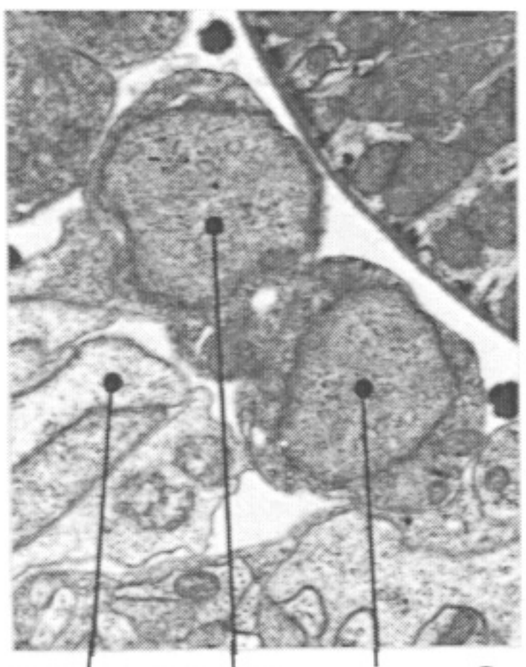

IL2L
RMEL
MUSCLE
GLRL
b


GLRR
MUSCLE
ADER
RMDDL
c

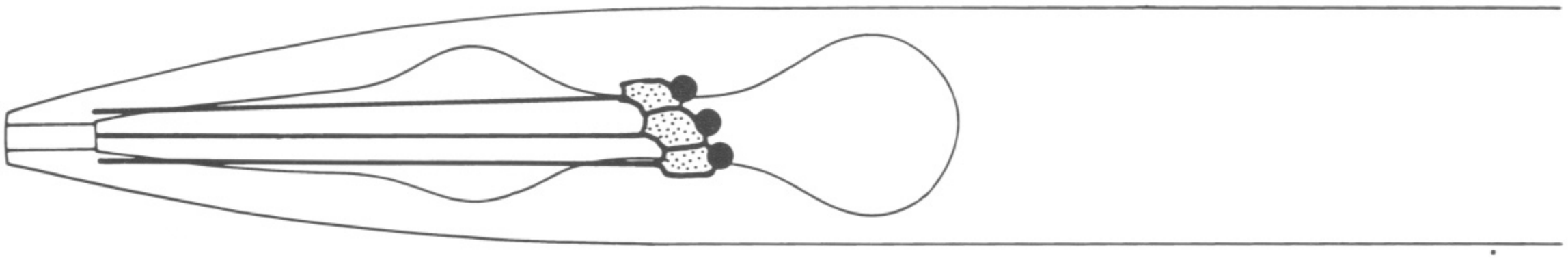

GLRR
RMER
d


GLRDL
GLRDR
e
RMEV
MUSCLE

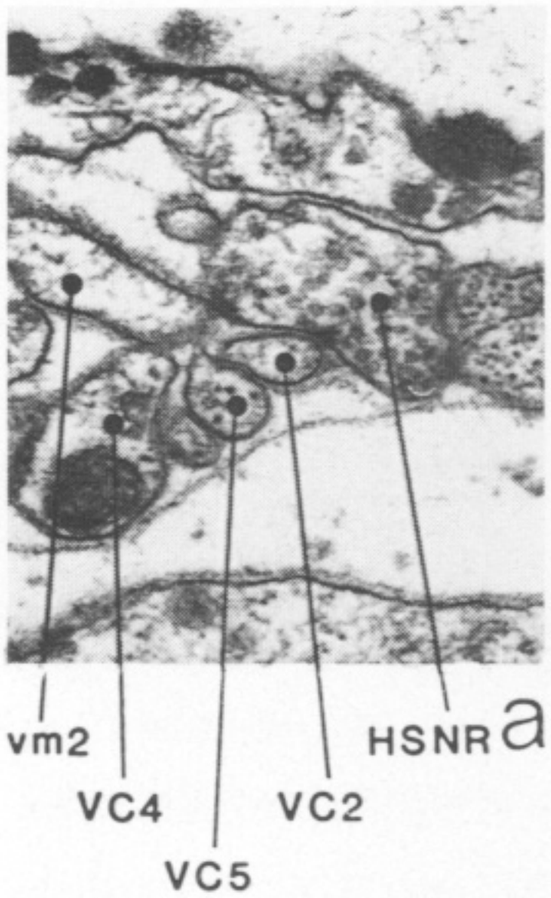

GLRL
GLRVL
f


MUSCLE
GLRVL
g
GLRL

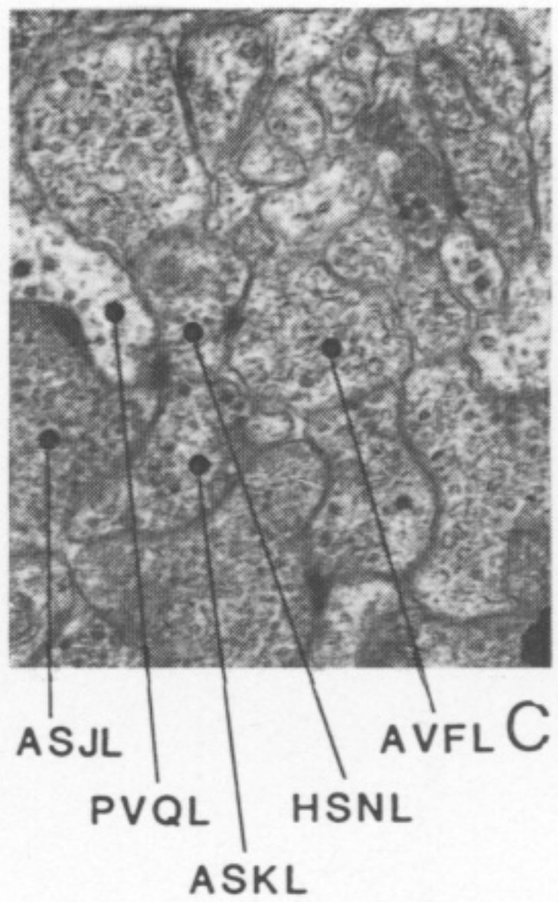

IL1VR
GLRVR
h
URAVR
CEPshVR
CEPVR

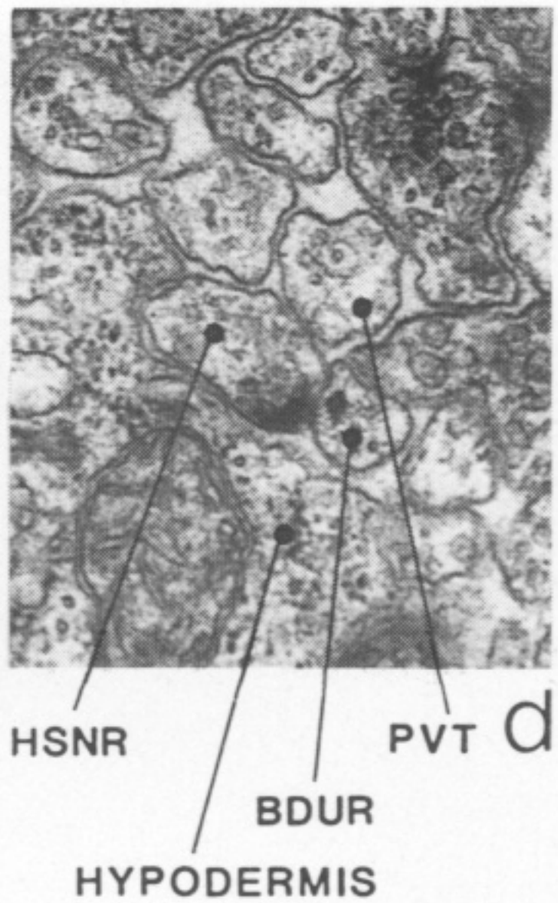

GLRDL
i
GLRL
GLRVL

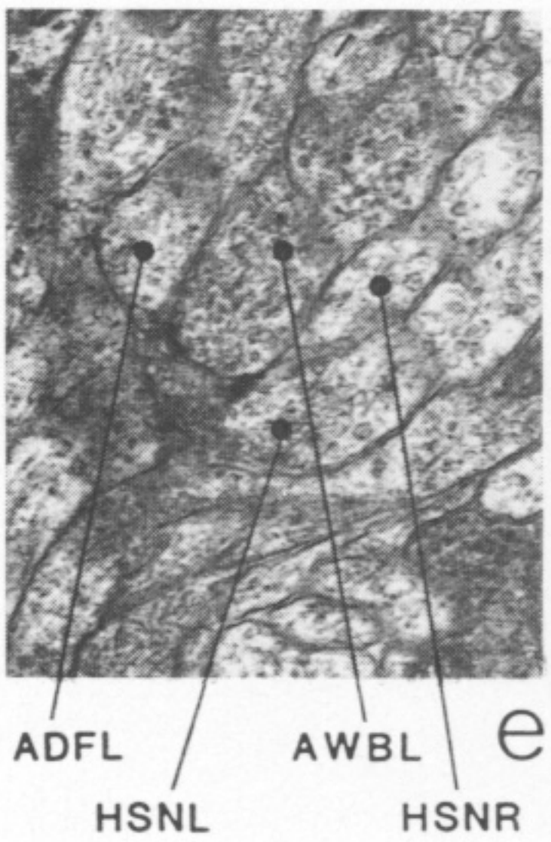
GLR

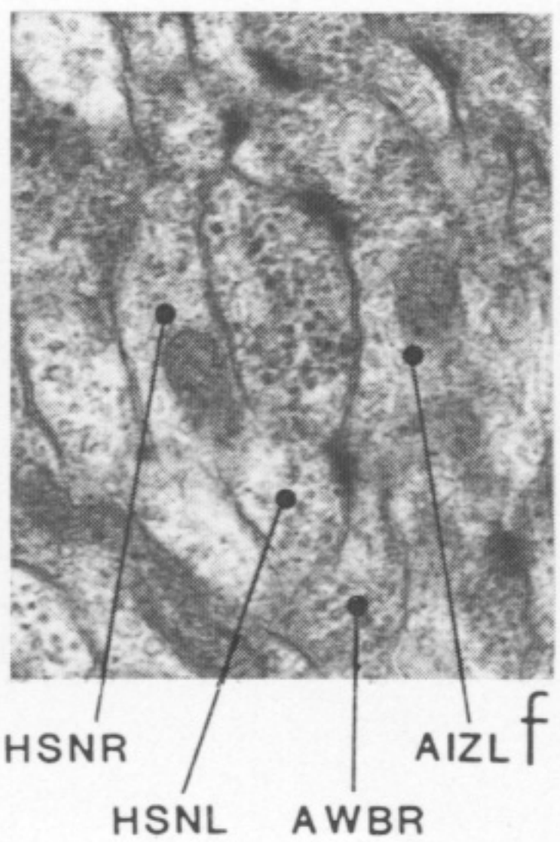

vm2
VC4
VC5
VC2
HSNR
a

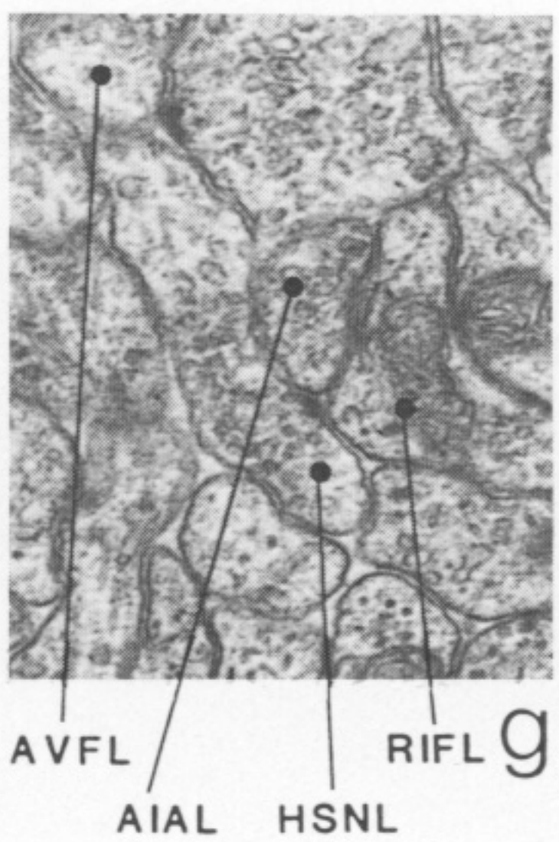

VC3
VC5
vm2
VC2
HSNR
b

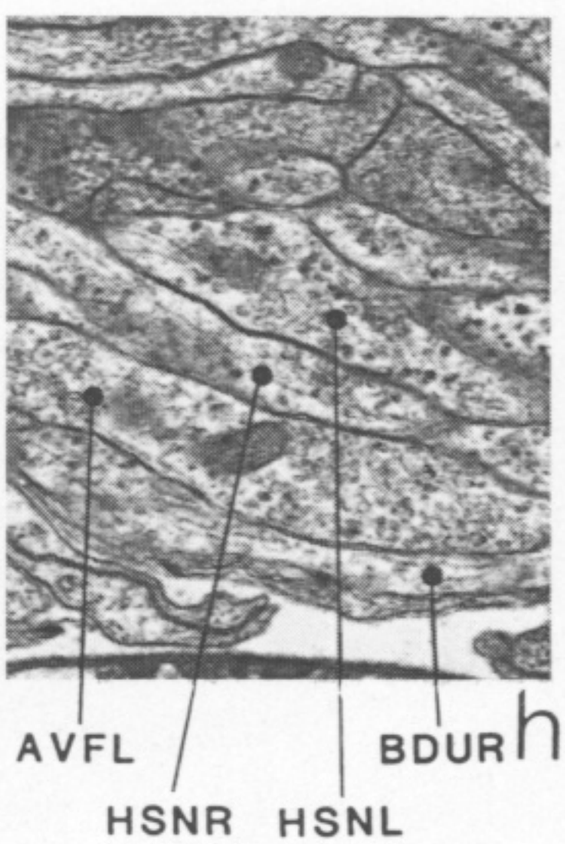

ASJL
PVQL
ASKL
HSNL
AVFL
C

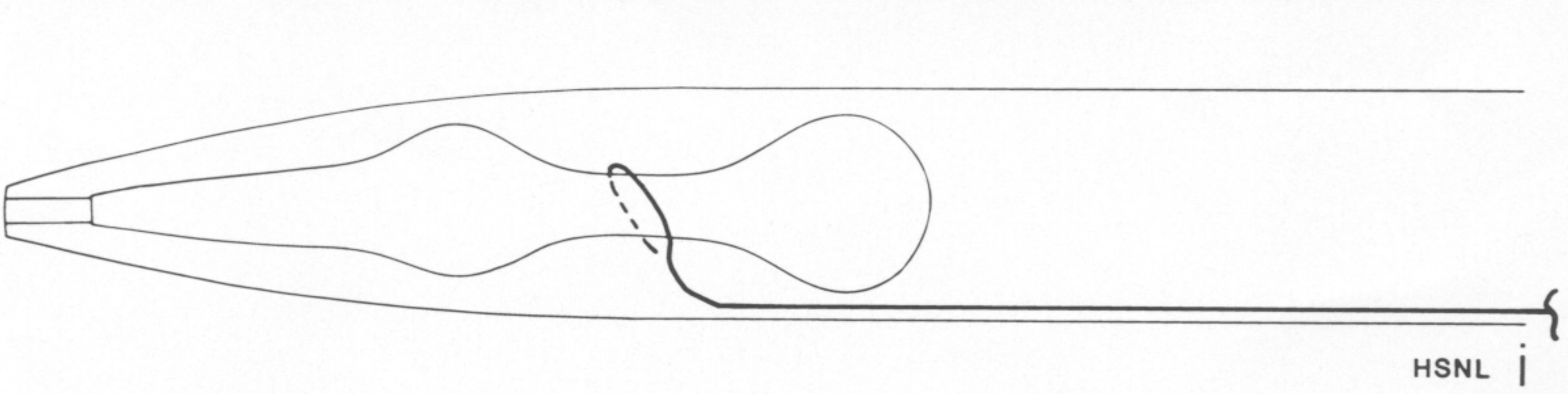

HSNR
HYPODERMIS
BDUR
PVT
d

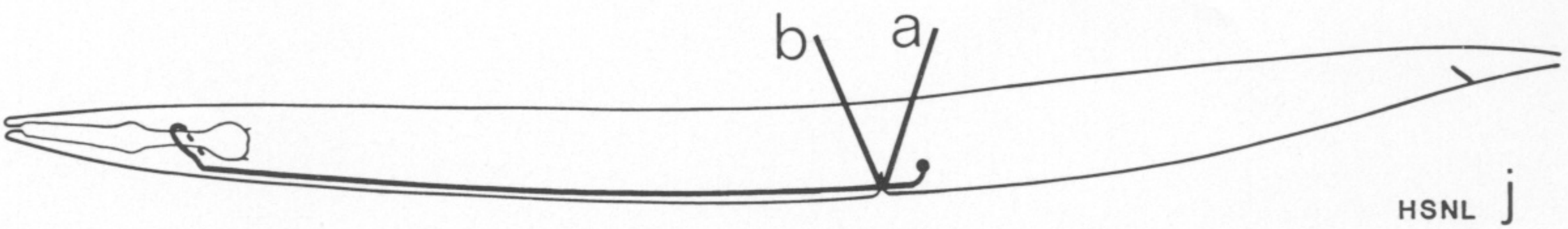

ADFL
HSNL
AWBL
HSNR
e

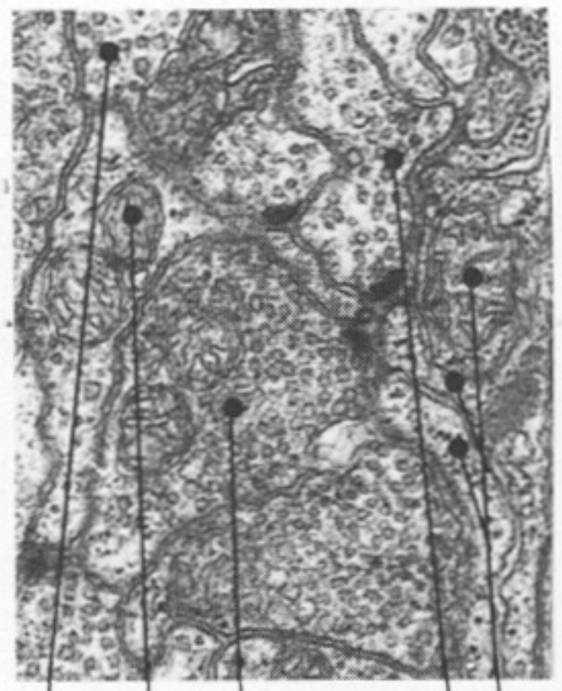

HSNR
HSNL
AWBR
AIZL
f

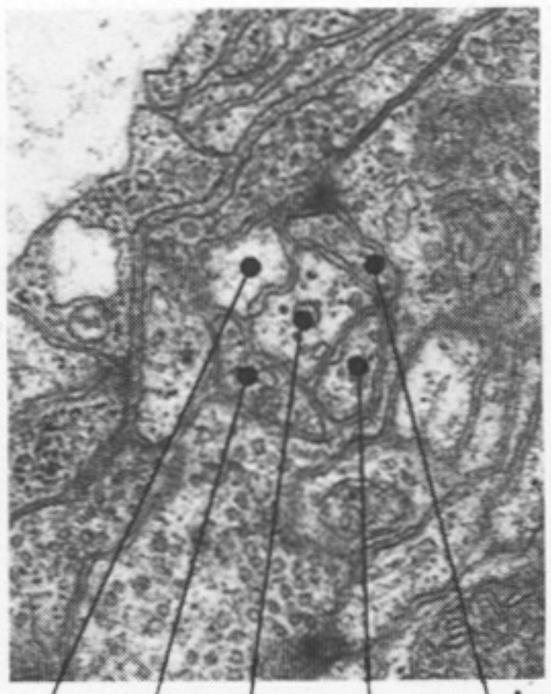

AVFL
AIAL
HSNL
RIFL
g

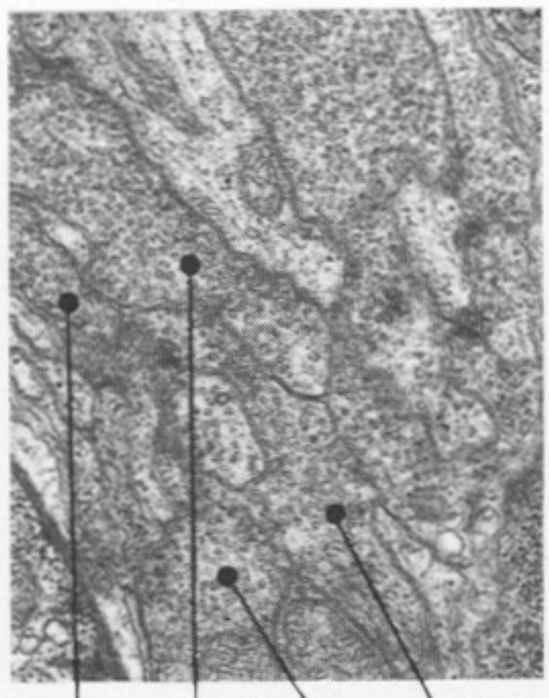

AVFL
HSNR
HSNL
BDUR
h

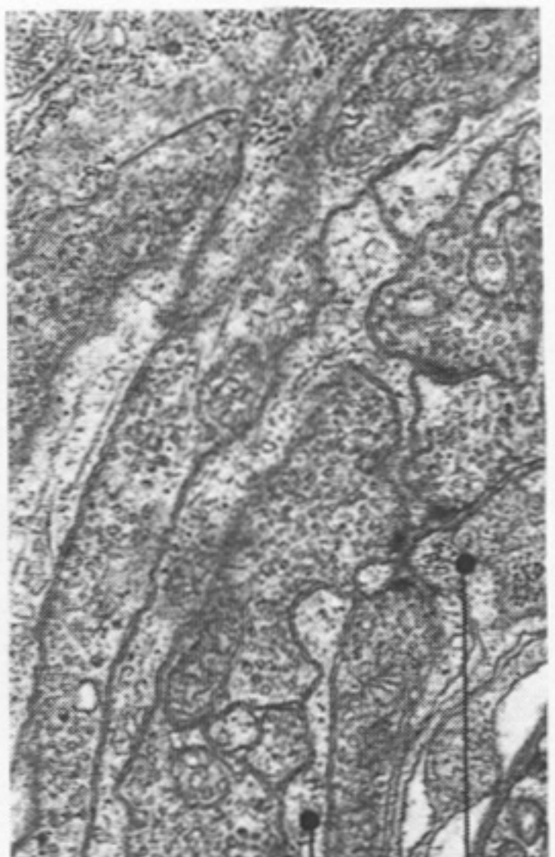

HSNL
i

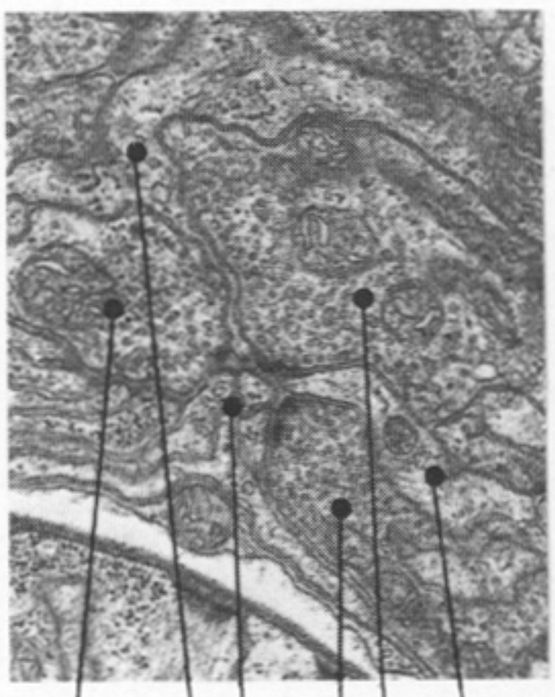

b
a
HSNL
j

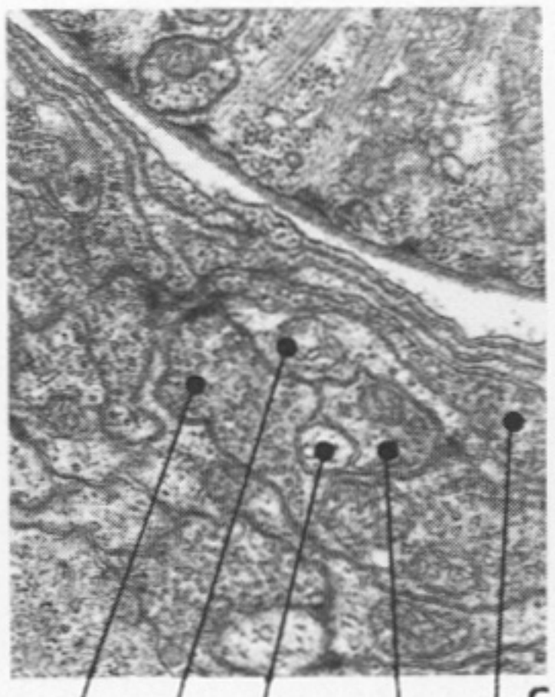

RIAL
RMDVL
IL1L
RMDDR
MUSCLE
a

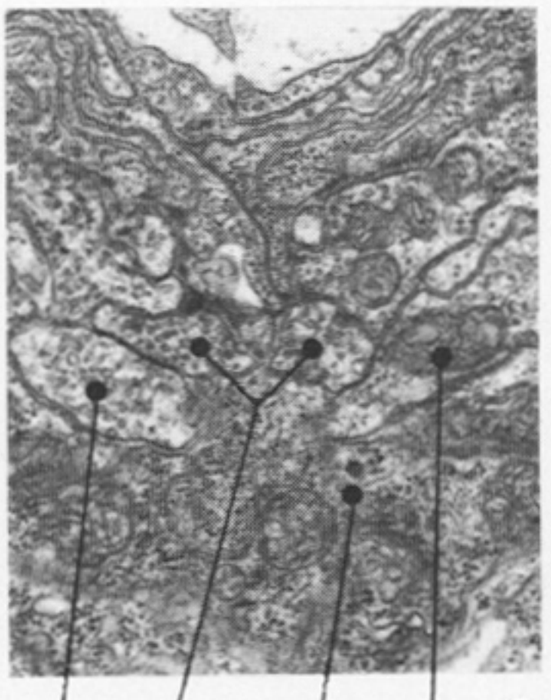

PVR
IL1VR
RIPR
IL2VR
URAVR
b

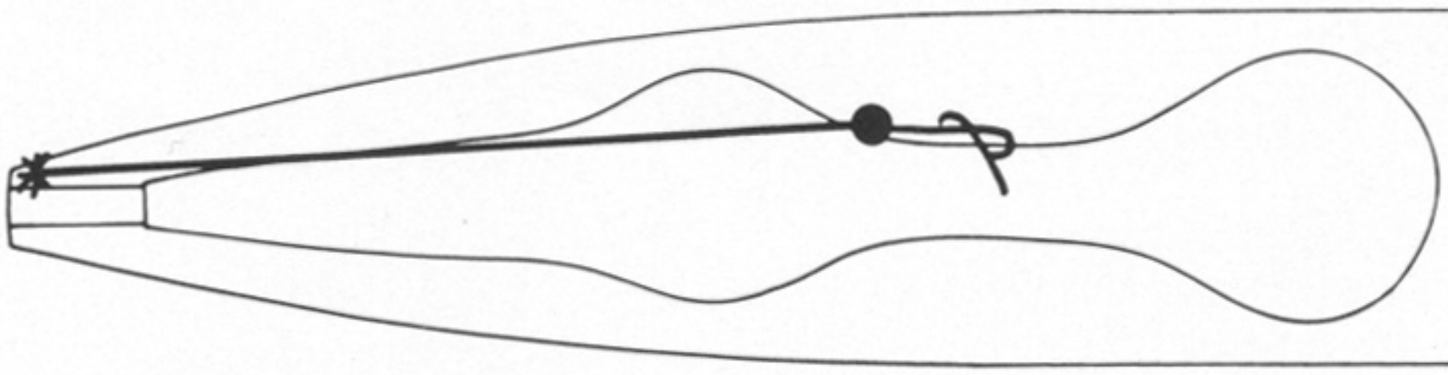

URADR
IL1DR
RMEL
IL1R
C

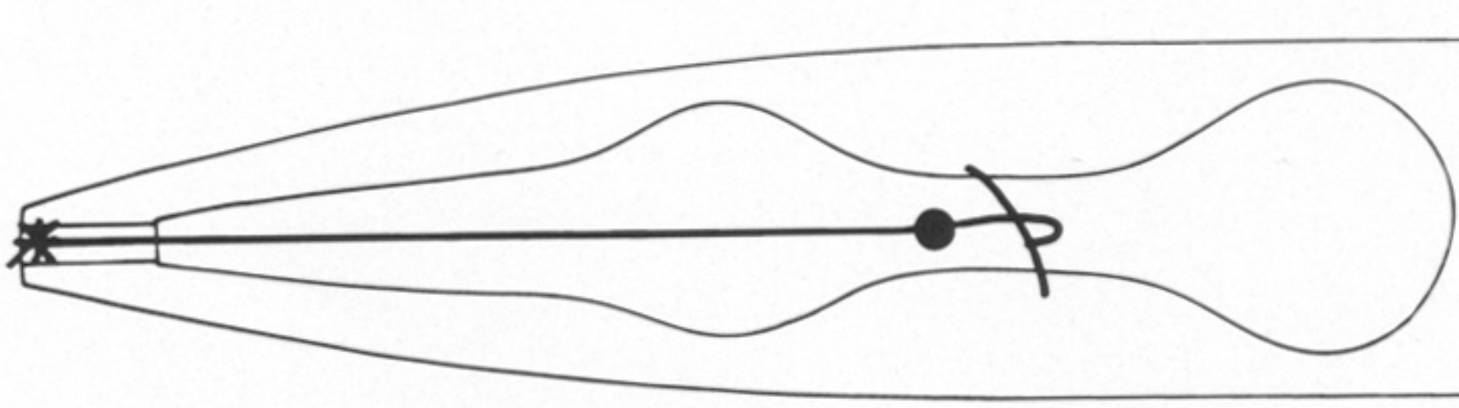

IL1DL
IL1L
RIPL
URADL
MUSCLE
d

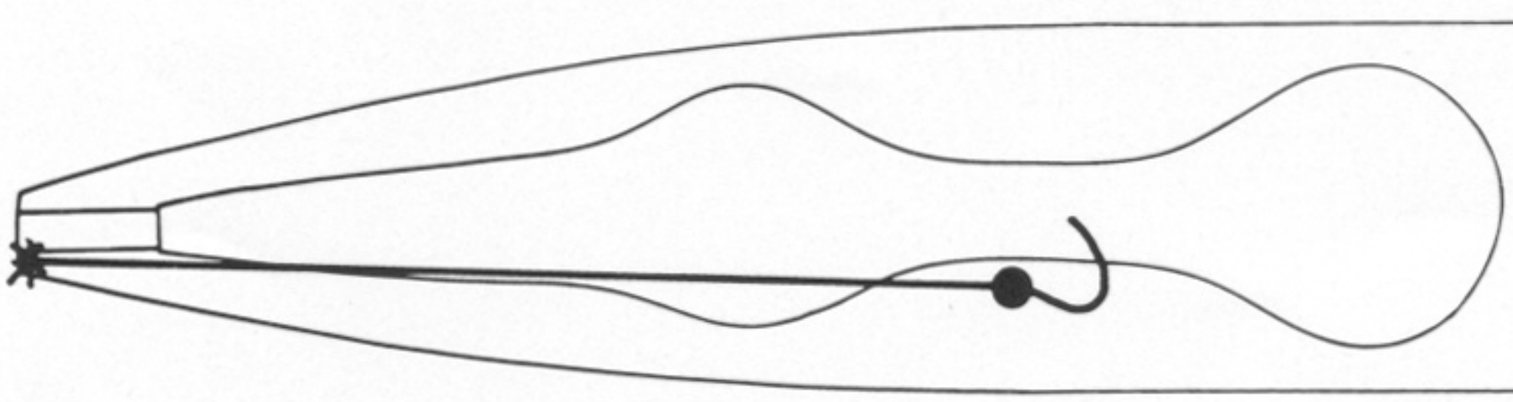

RMDDL
RMDVR
MUSCLE
IL1DR
URADR
RIPR
e


IL1VL
RIPL
OLQVL
IL2VL
URAVL
f

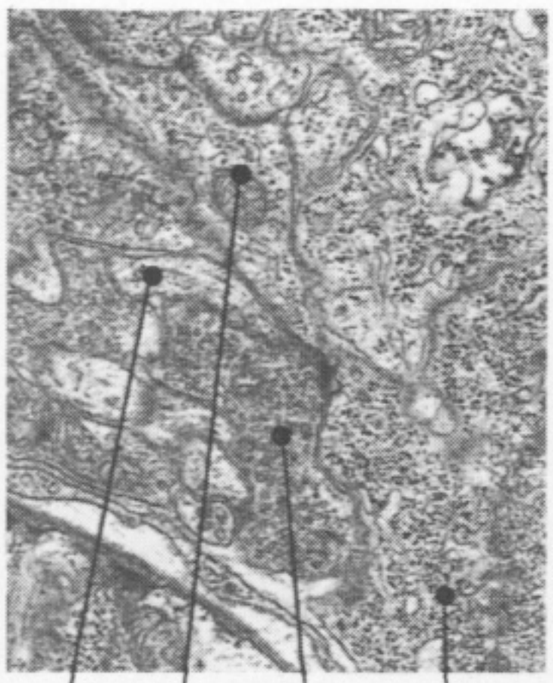

IL1VL
RMED
RMEV
IL1VR
g


IL1DL
h


IL1L
i

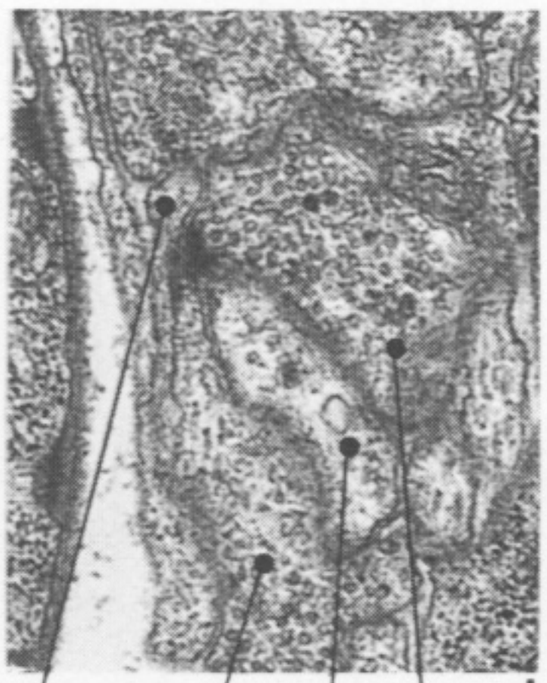

IL1VL
j

a

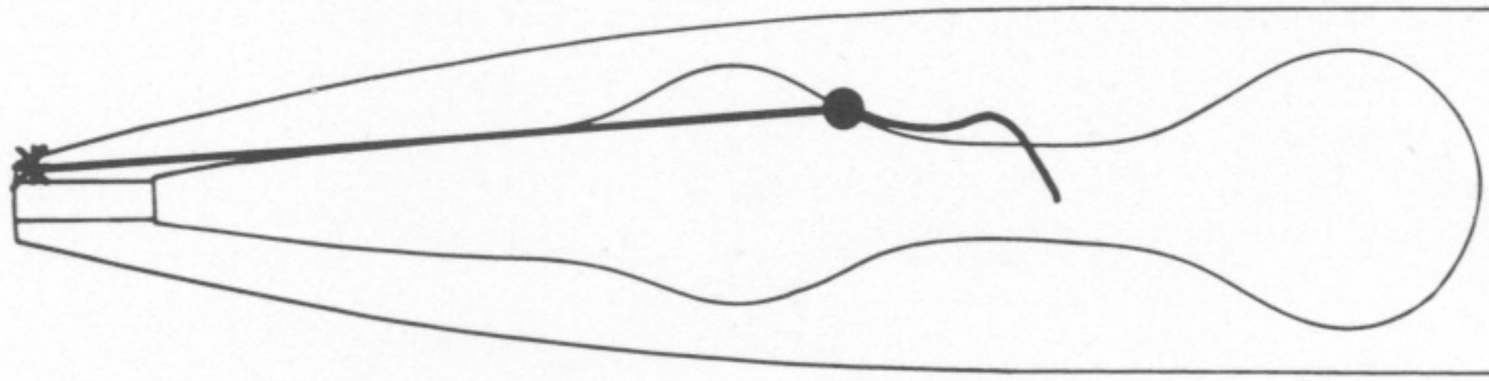


b

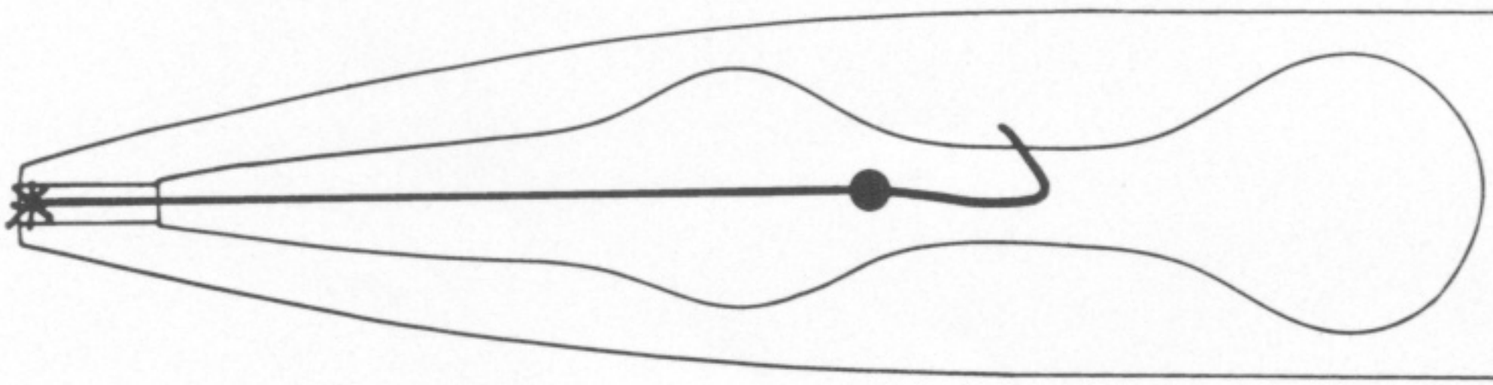
c



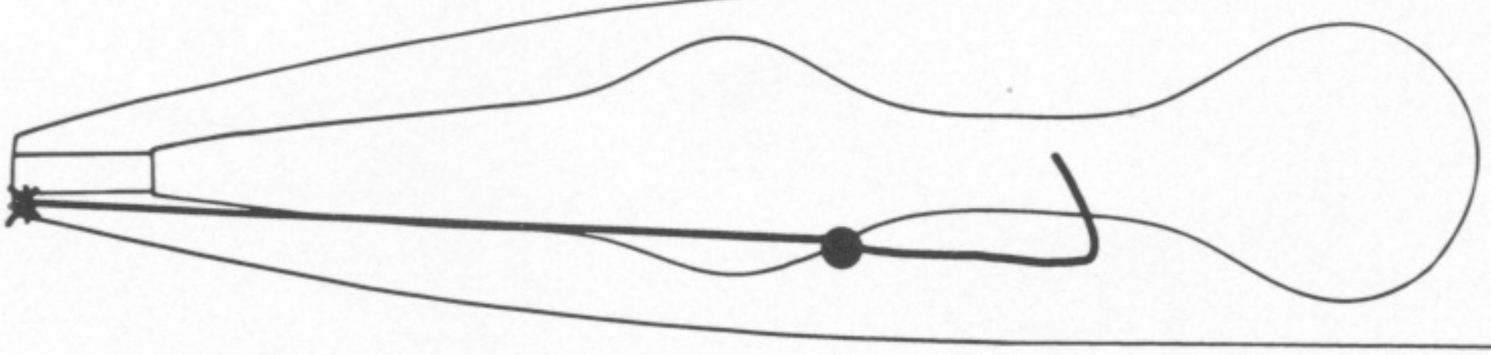
d



IL2DL e

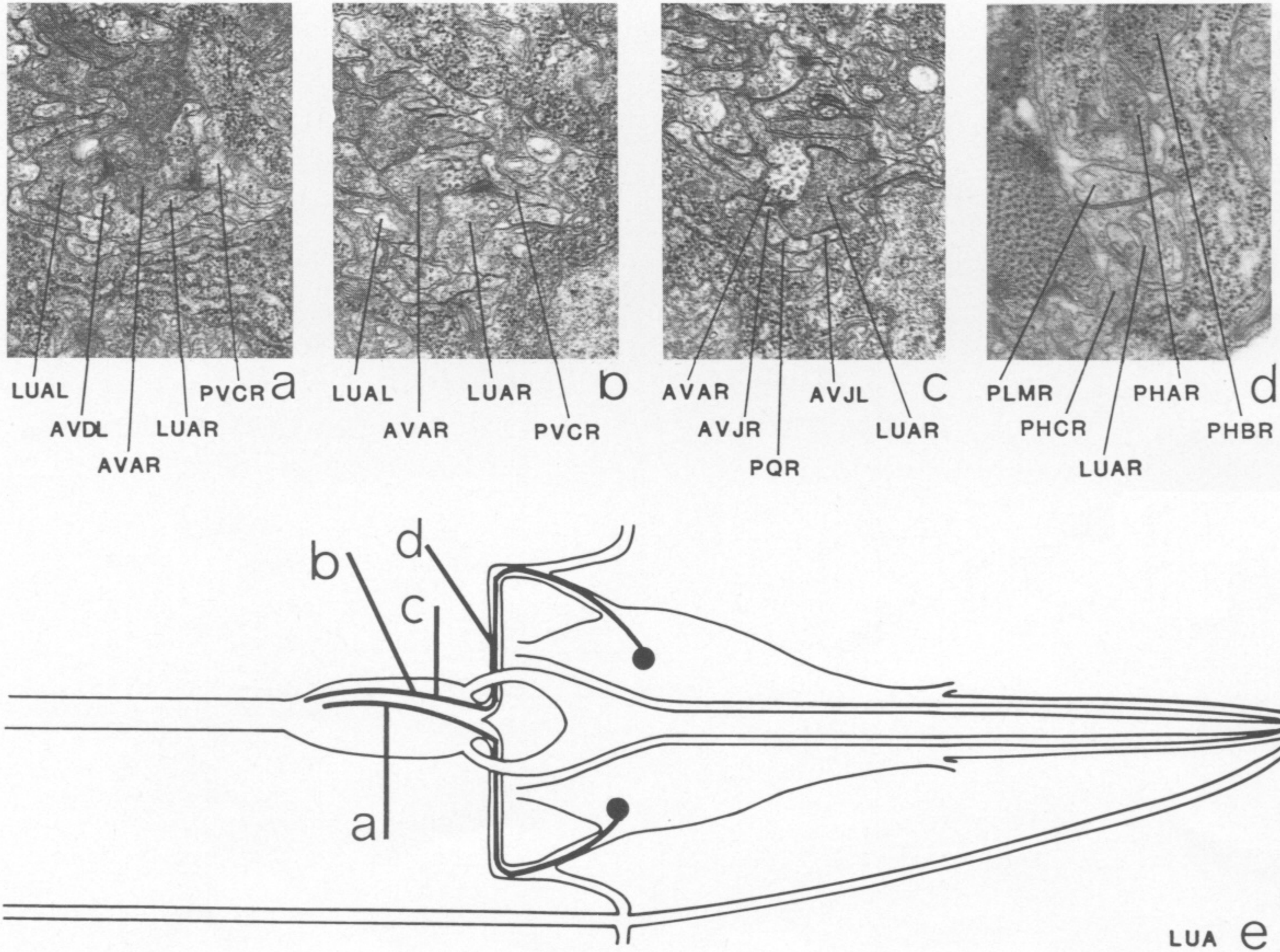


IL2L f

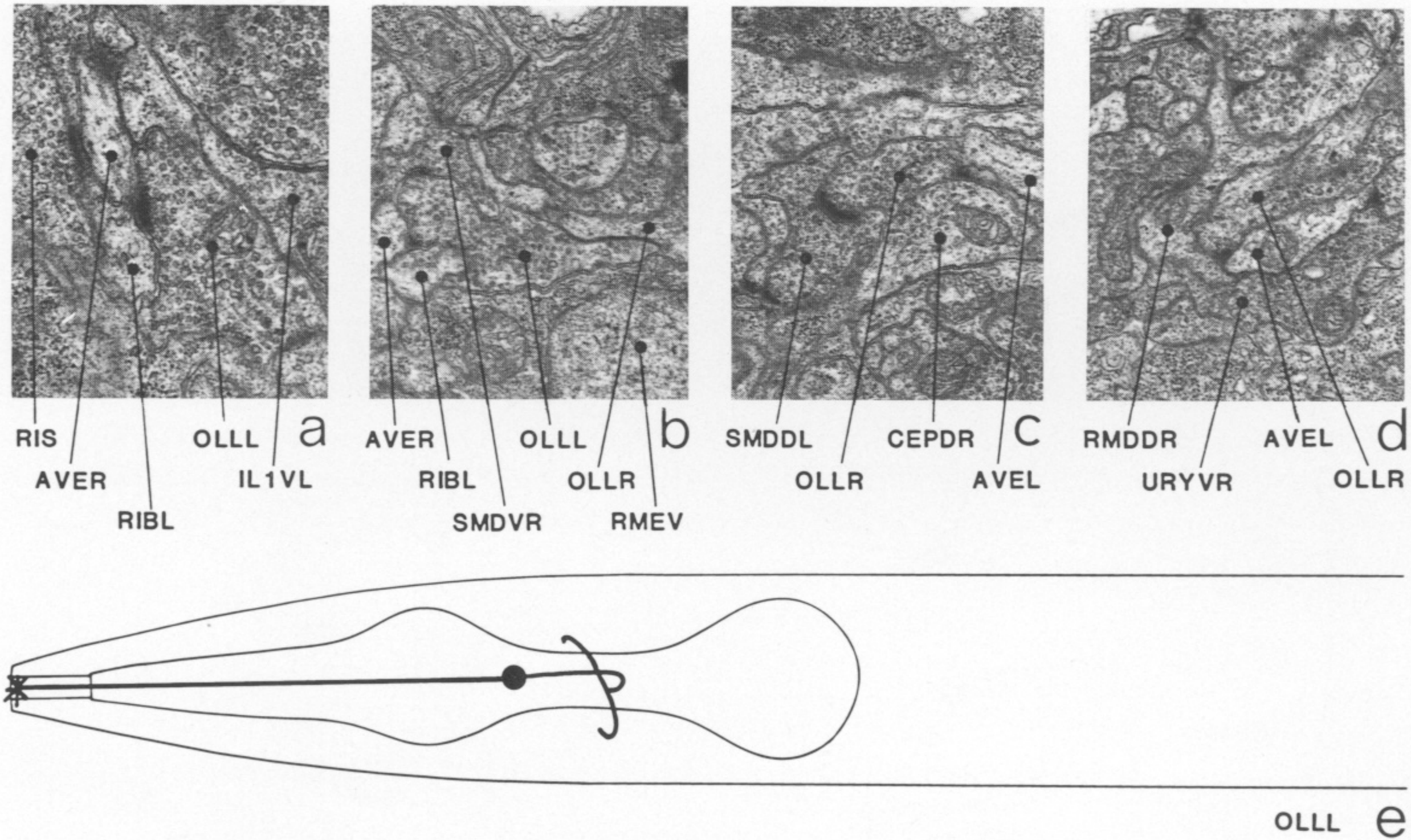


IL2VL g

IL2

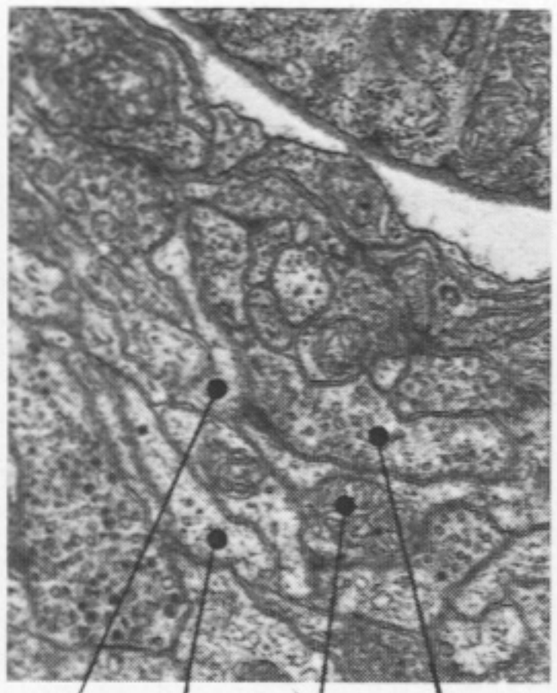

LUAL
AVDL
AVAR
LUAR
PVCR
a
LUAL
AVAR
LUAR
PVCR
b
AVAR
AVJR
PQR
AVJL
LUAR
C
PLMR
PHCR
LUAR
PHAR
PHBR
d
b
d
c
a
LUA
e

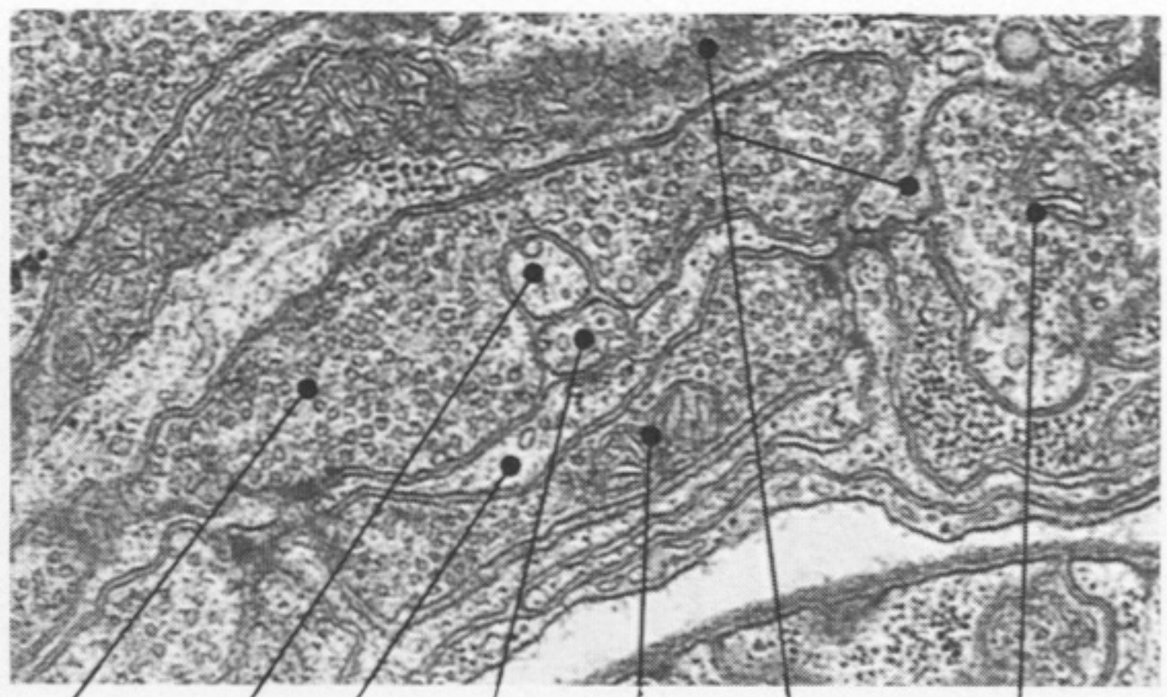
LUA

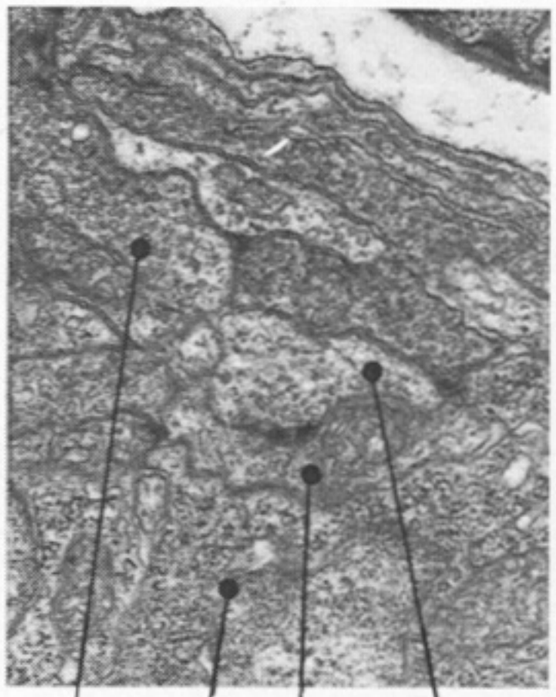

RIS
AVER
RIBL
OLLL
IL1VL
a
AVER
RIBL
SMDVR
OLLL
OLLR
RMEV
b
SMDDL
OLLR
CEPDR
AVEL
c
RMDDR
URYVR
AVEL
OLLR
d
OLLL
e

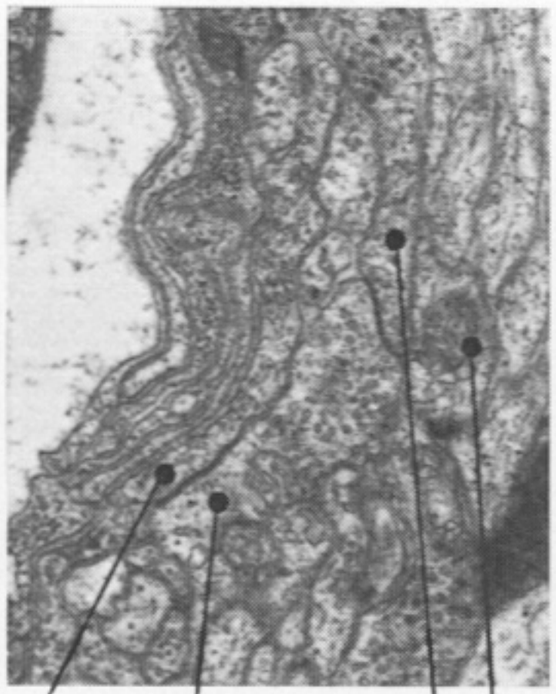
OLL

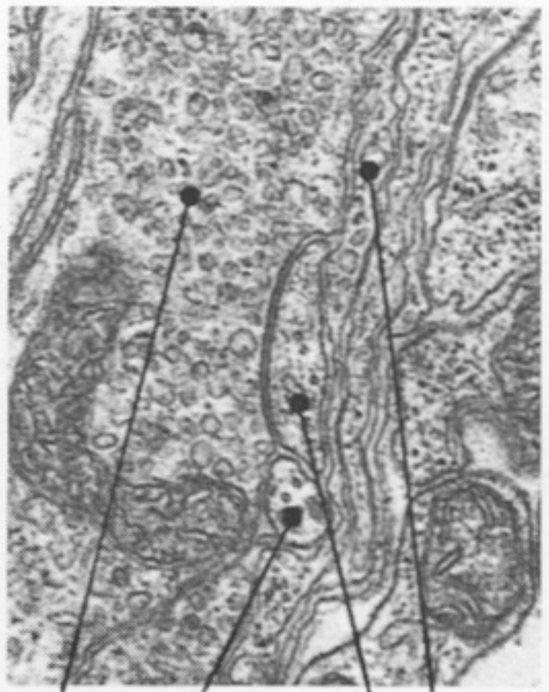

RICR
OLQDL
IL2DL
RIPL
IL1DL
a

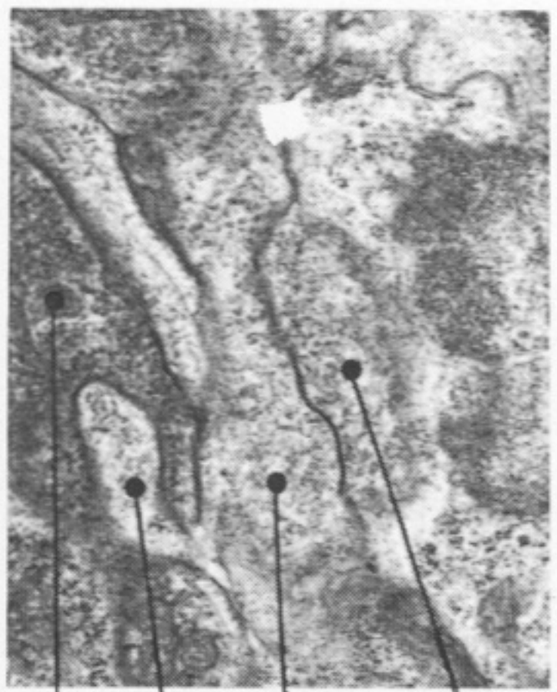

SIBDL
RMDR
RMDVR
OLQVL
b

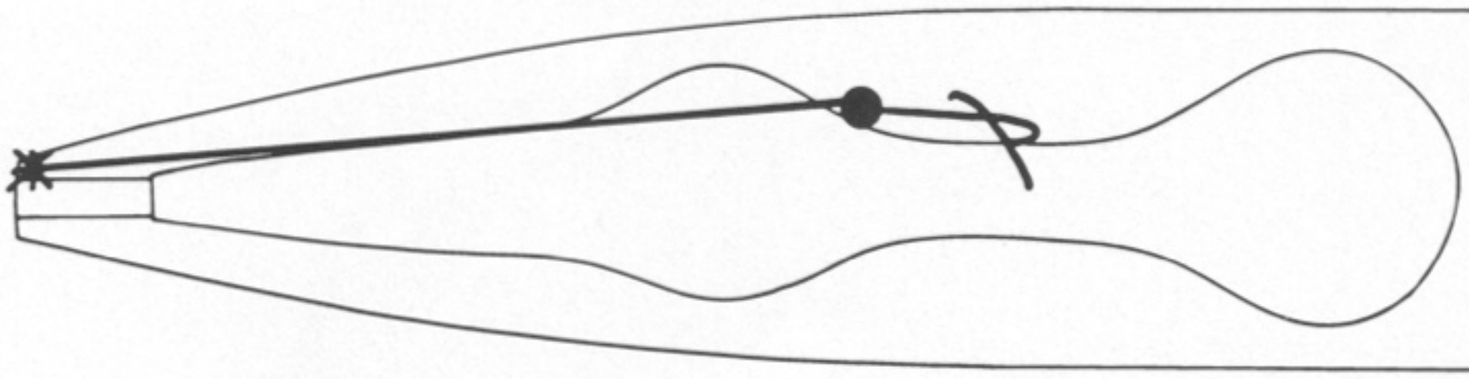

IL1DL
OLQDL
RIPL
IL2DL
URADL
RMDVL
RMDDR
c

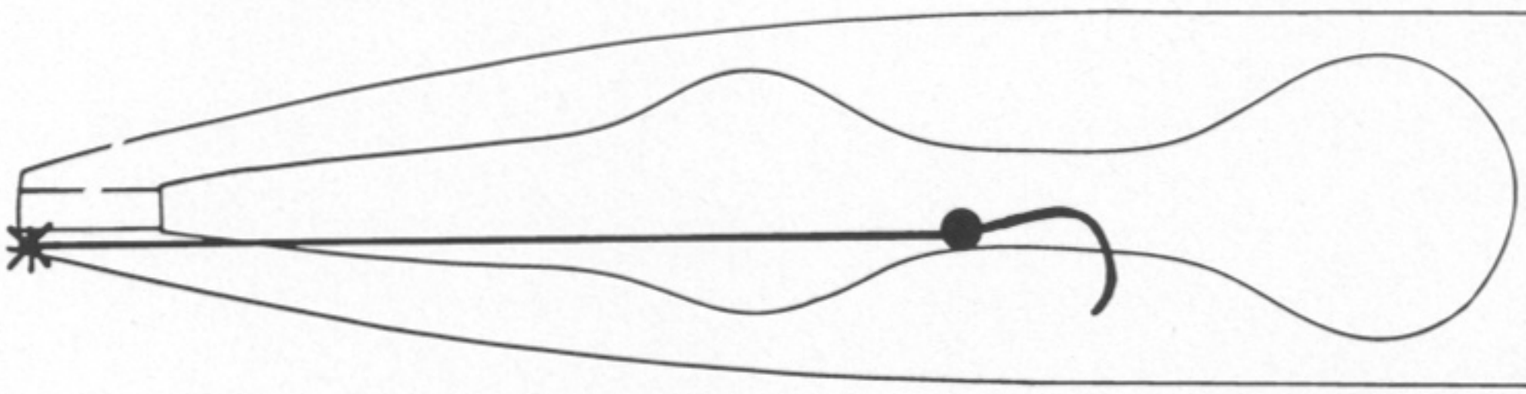

IL1VL
RIH
CEPVL
OLQVL
d


CEPVR
URBR
OLQVR
SIBDR
e

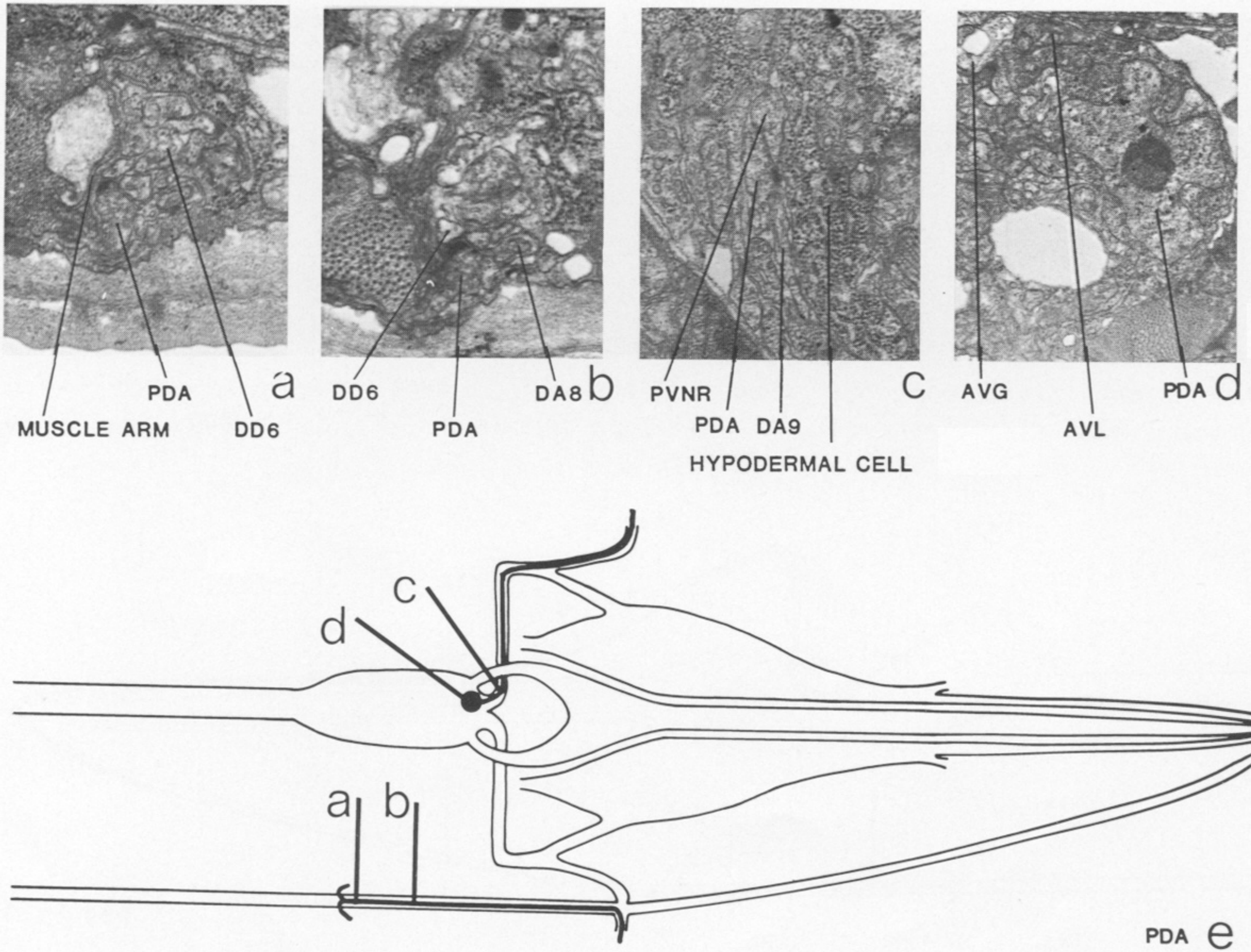

RIGR
URYVR
OLQVR
CEPshVR
f


IL2DR
RIPR
RIH
OLQDR
g

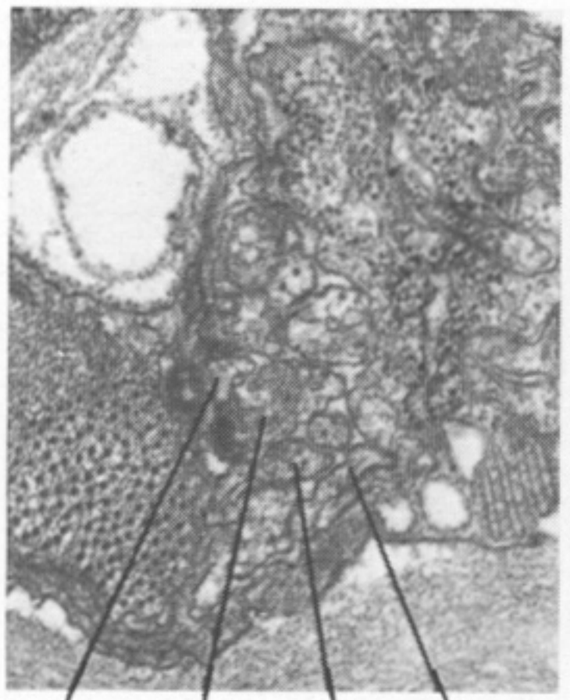

OLQDL
h

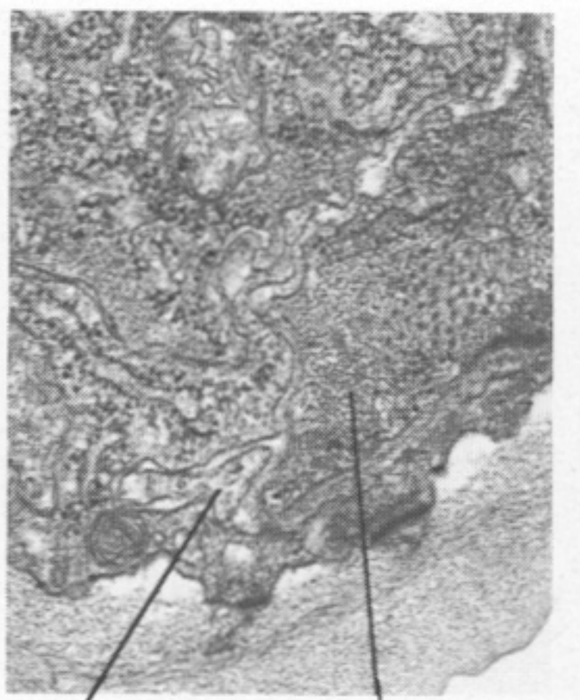

OLQVL
i

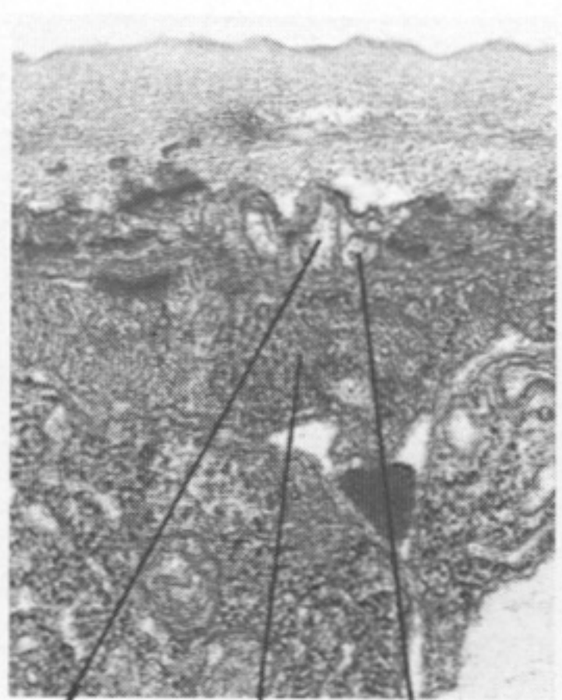
OLQ

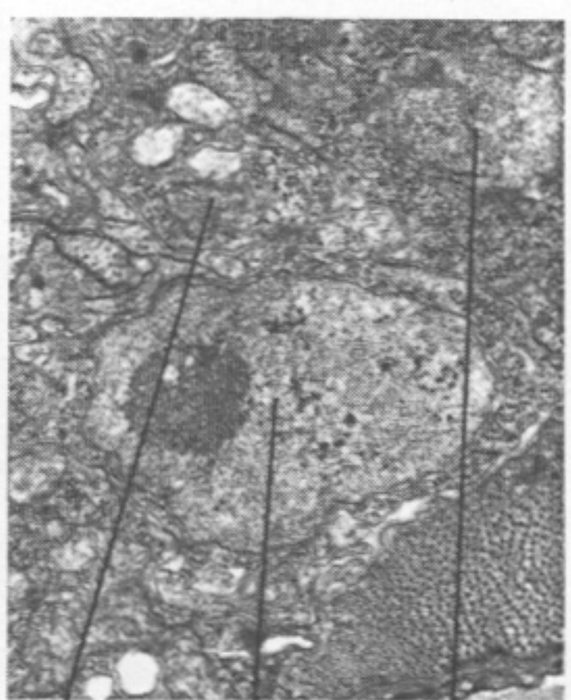

MUSCLE ARM
PDA
DD6
a
DD6
PDA
DA8
b
PVNR
PDA
DA9
HYPODERMAL CELL
c
AVG
AVL
PDA
d
c
d
a
b
PDA
e

PDA


DD6
PDB
PDA
DA8
a

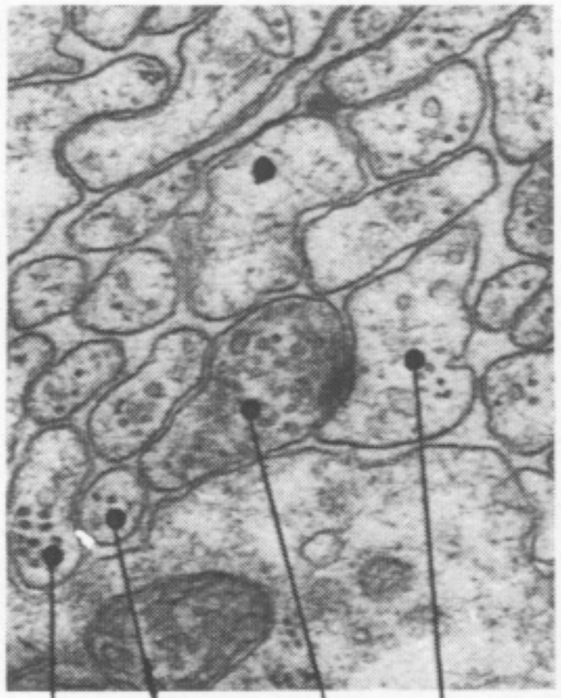

PDB
MUSCLE
b

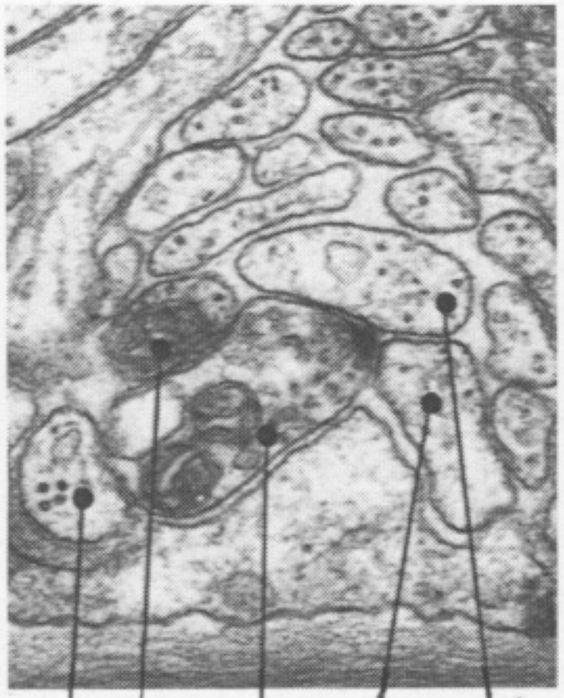

PDB
MUSCLE
DD6?
C

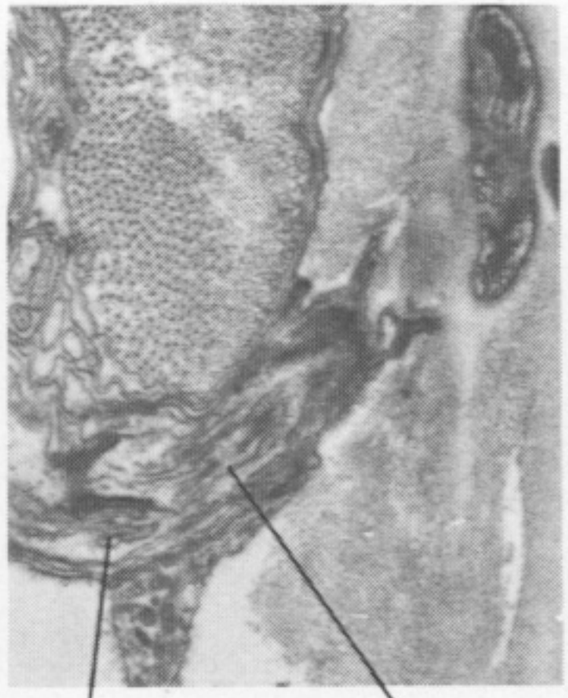

DA9
PDB
VD13
d

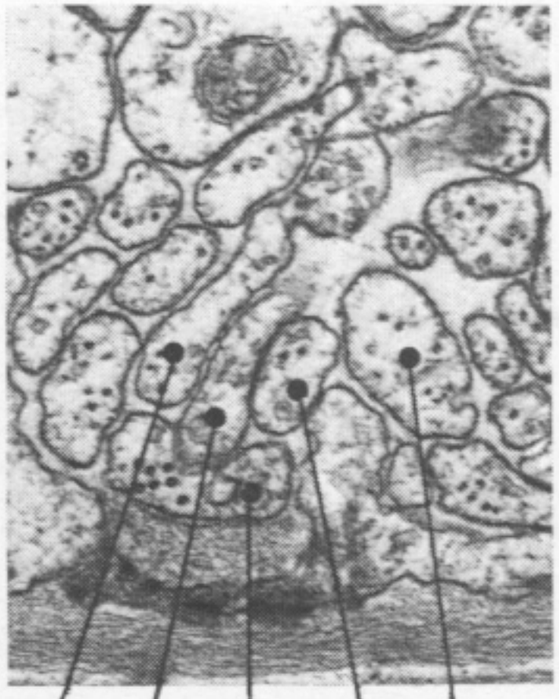
d
b
a
c
PDB
e

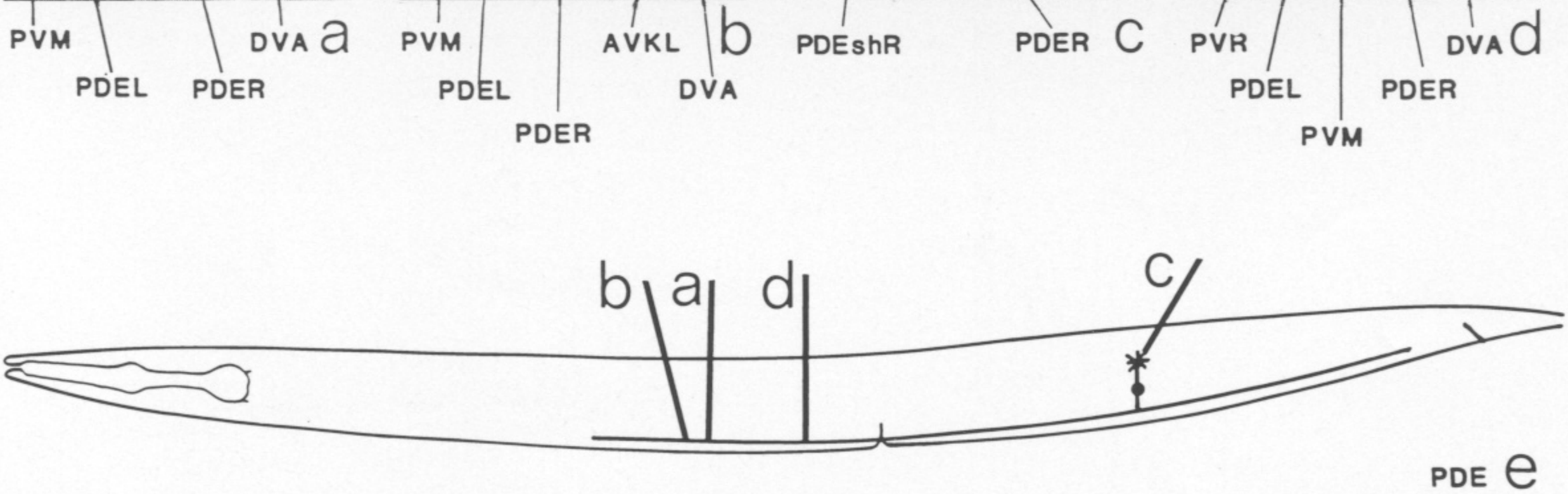
PDB


PVM
PDEL
PDER
DVA
a

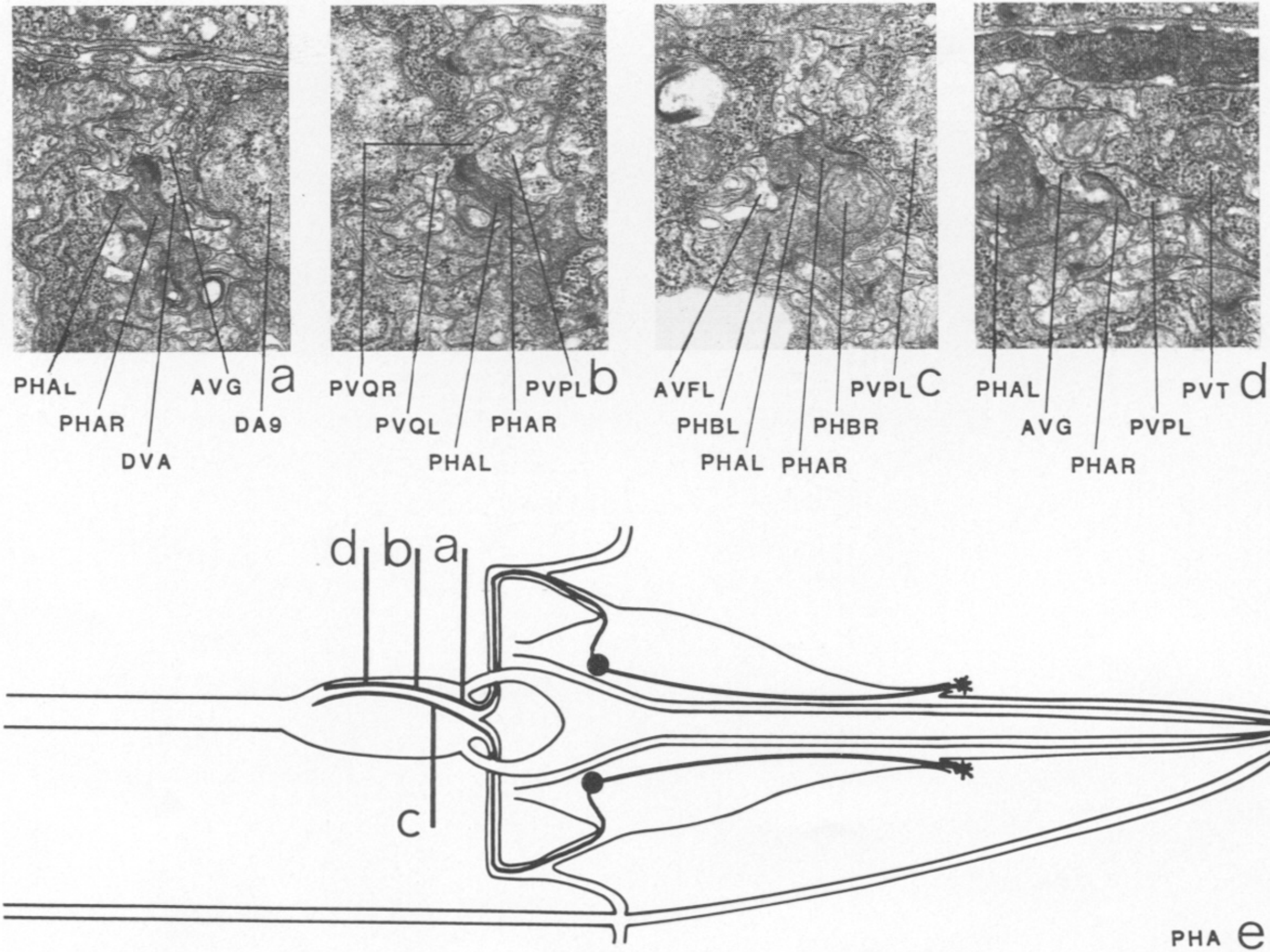

PVM
PDEL
AVKL
DVA
b


PDEshR
PDER
c

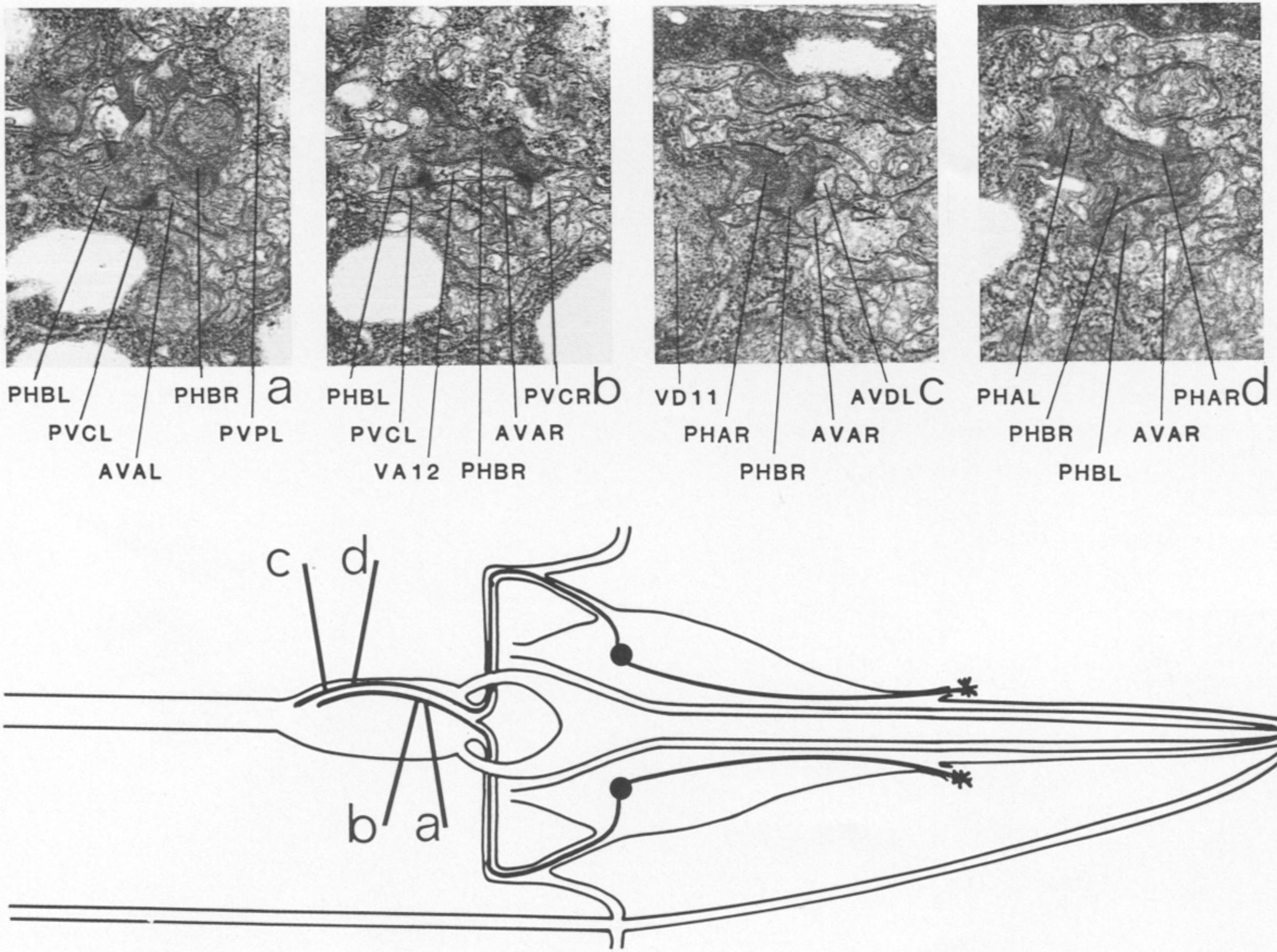

PVR
PDEL
PDER
DVA
d


PDER
PVM
b
a
d
c
PDE
e

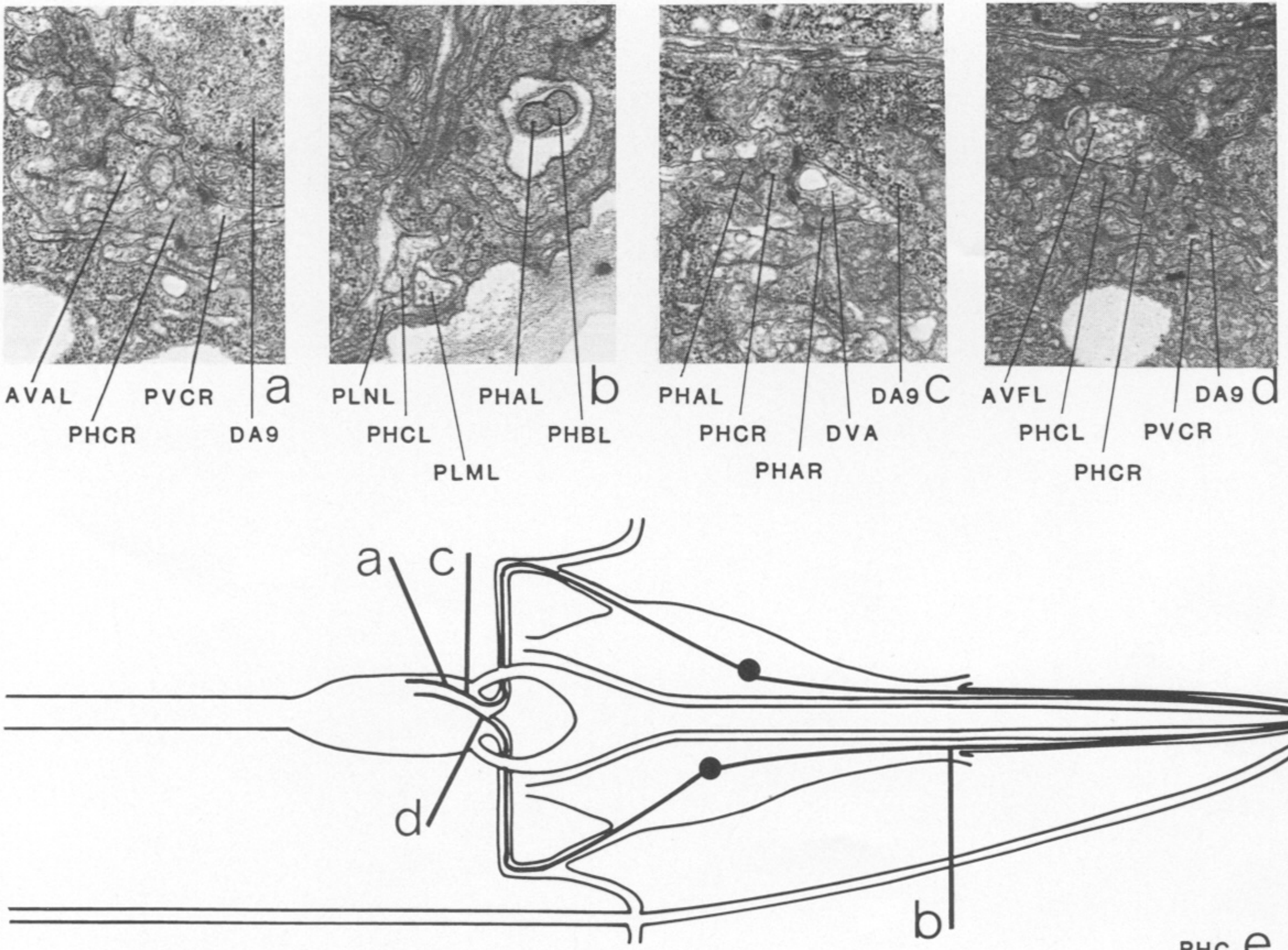
PDE


PHAL
PHAR
DVA
AVG
DA9
a
PVQR
PVQL
PHAL
PHAR
PVPL
b
AVFL
PHBL
PHAL
PHAR
PHBR
PVPL
C
PHAL
AVG
PHAR
PVPL
PVT
d
d
b
a
c
PHA
e

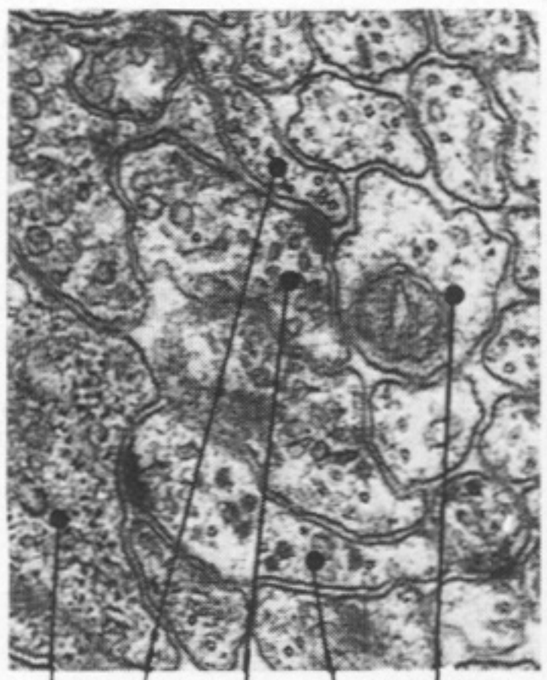
PHA


PHBL
PVCL
AVAL
PHBR
PVPL
a
PHBL
PVCL
VA12
PHBR
AVAR
PVCR
b
VD11
PHAR
PHBR
AVAR
AVDL
c
PHAL
PHBR
PHBL
AVAR
PHAR
d
c
d
b
a
PHB
e

PHB


AVAL
PHCR
PVCR
DA9
a
PLNL
PHCL
PLML
PHAL
PHBL
b
PHAL
PHCR
PHAR
DVA
DA9
c
AVFL
PHCL
PHCR
PVCR
DA9
d
a
c
d
b
PHC
e

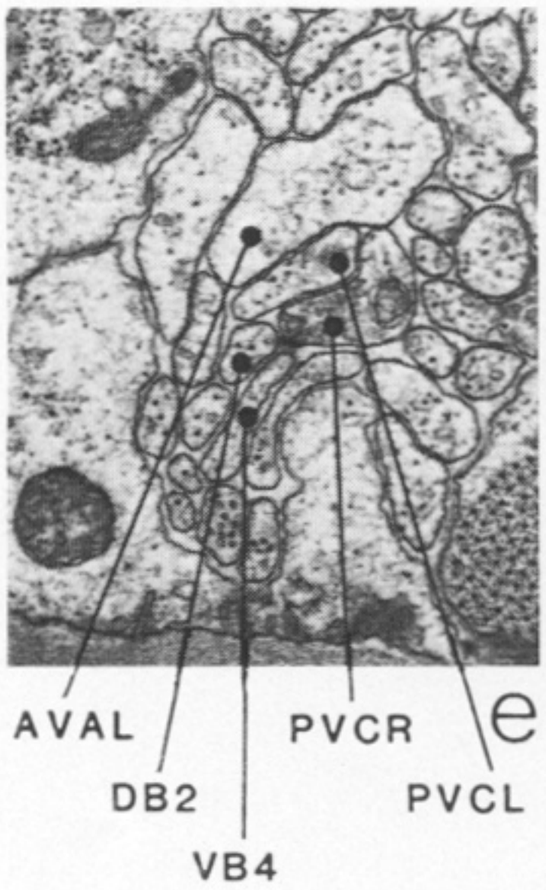
PHC

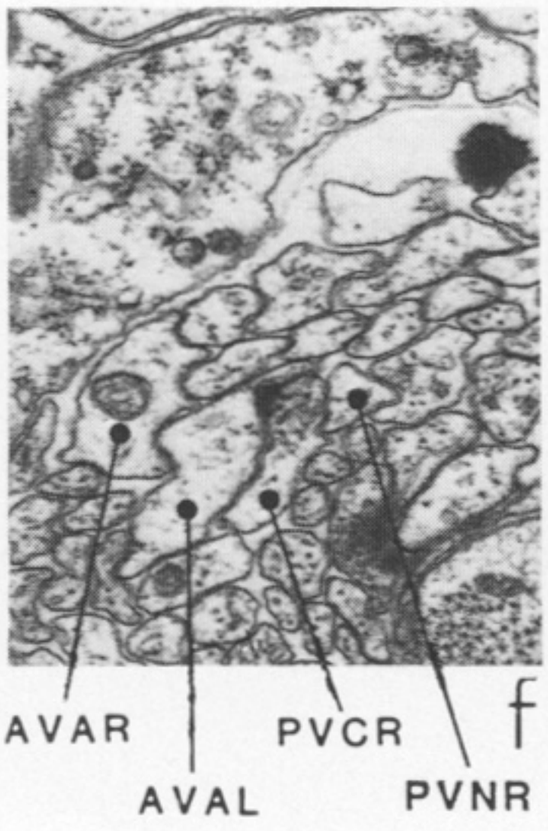

RIS
AVEL
PVCR
AVJL
AVBL
a

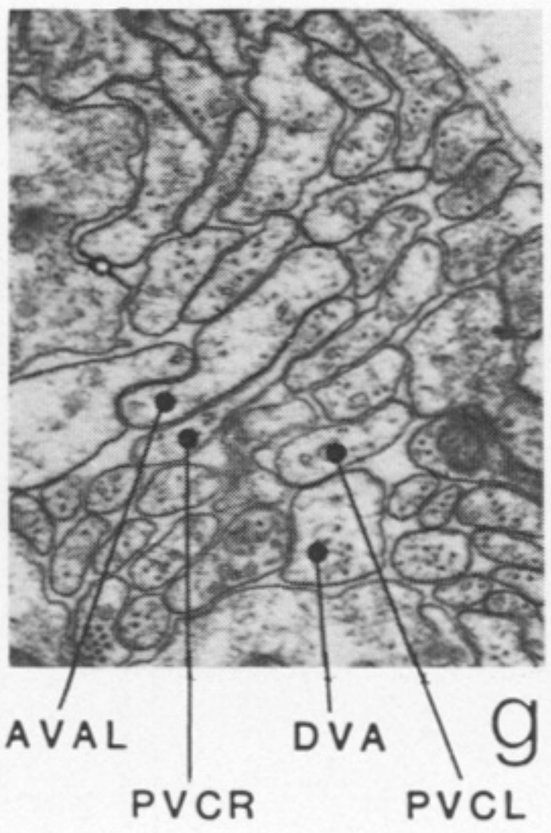

RIFL
AVBL
PVCL
AVBR
b

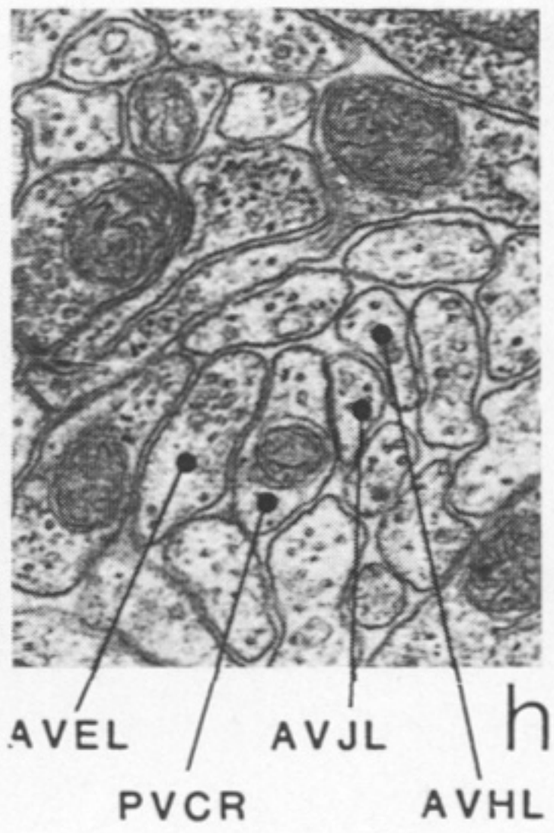

AVBR
PVCL
AVDR
SIBVR
RICR
c

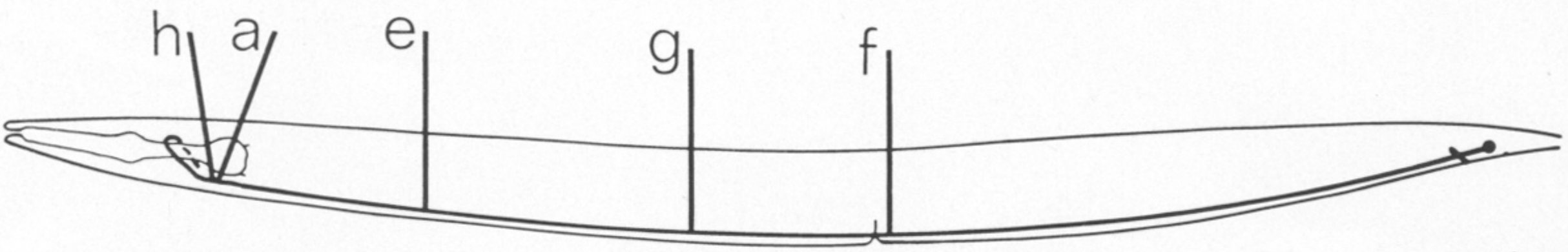

RID
AVBR
PVCR
AVDL
d

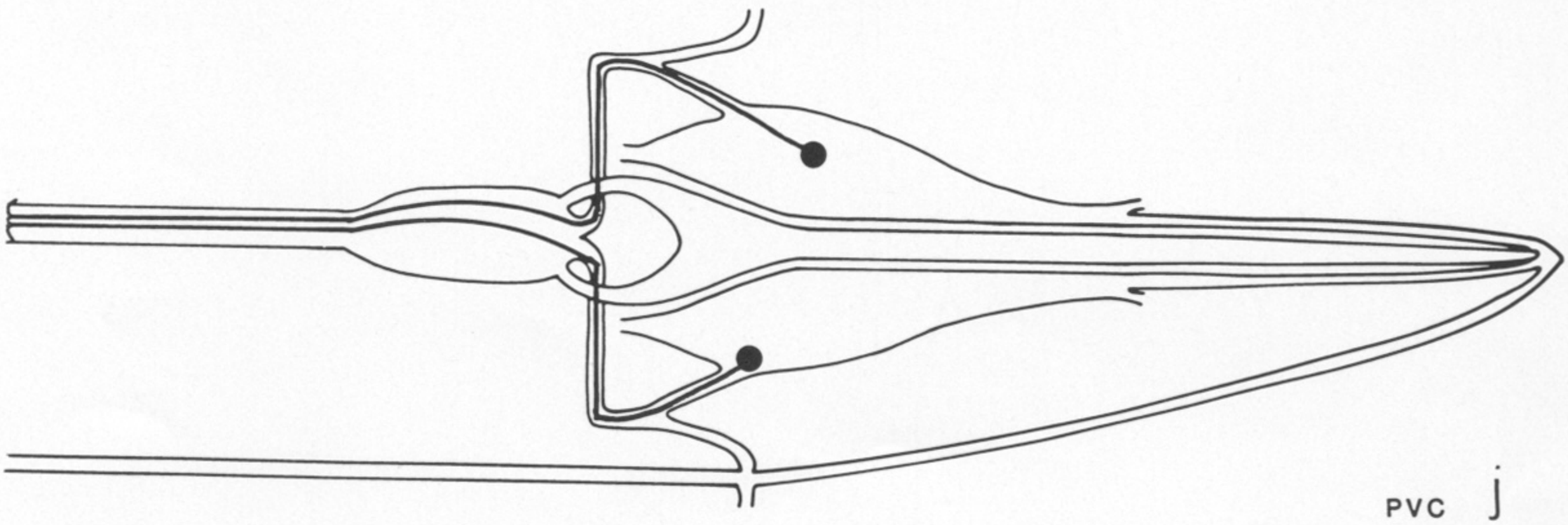

AVAL
DB2
VB4
PVCR
PVCL
e

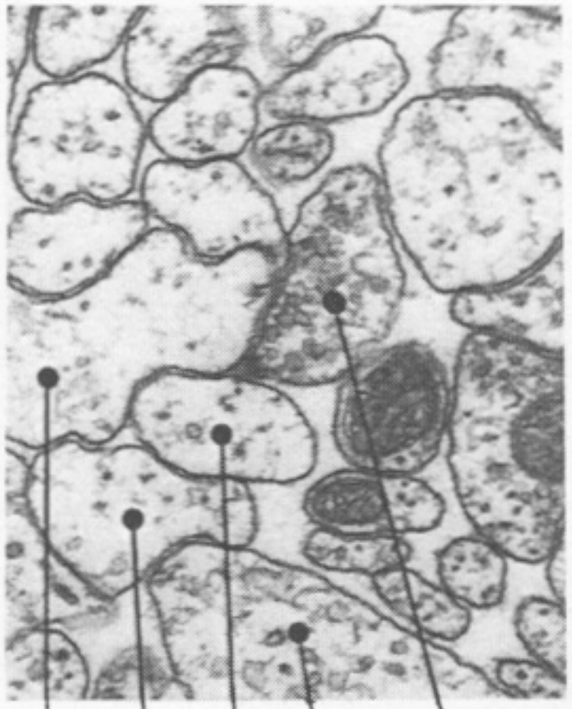

AVAR
AVAL
PVCR
PVNR
f

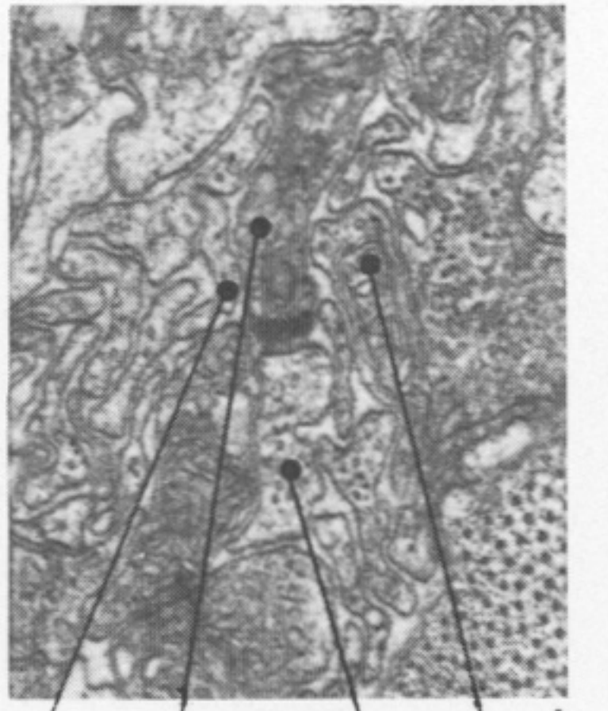

AVAL
PVCR
DVA
PVCL
g

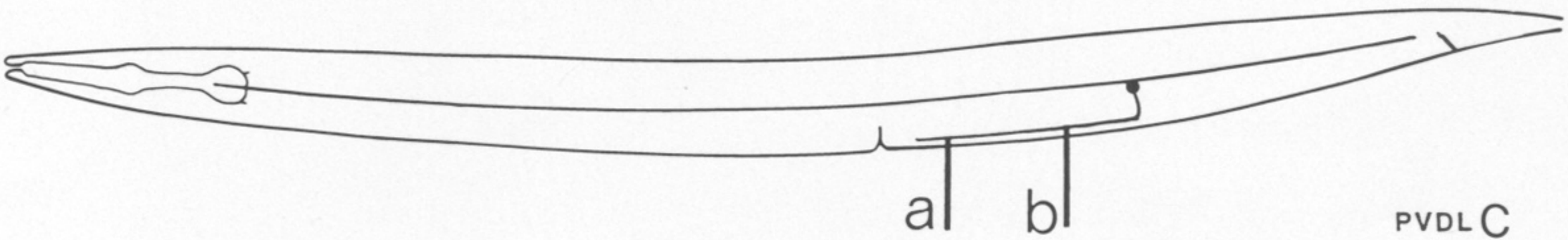

AVEL
PVCR
AVJL
AVHL
h


h
a
e
g
f
PVCL
i

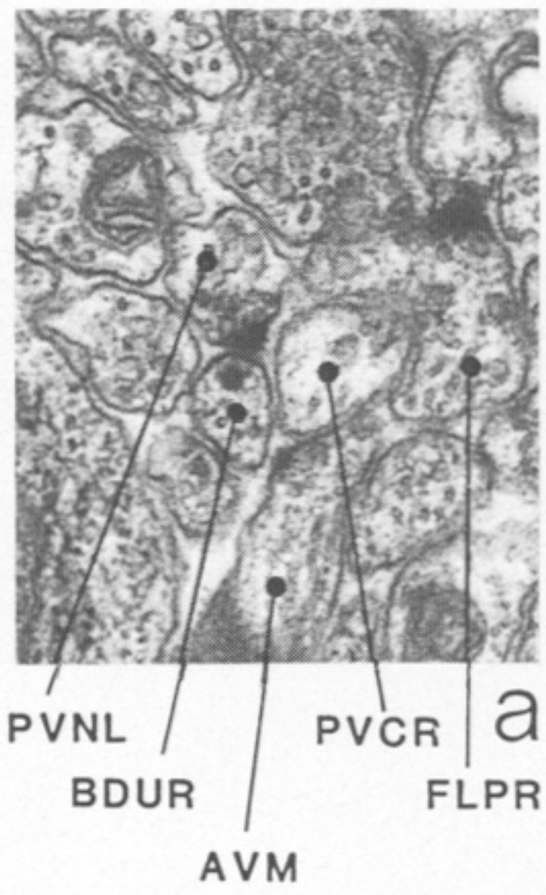

PVC
j

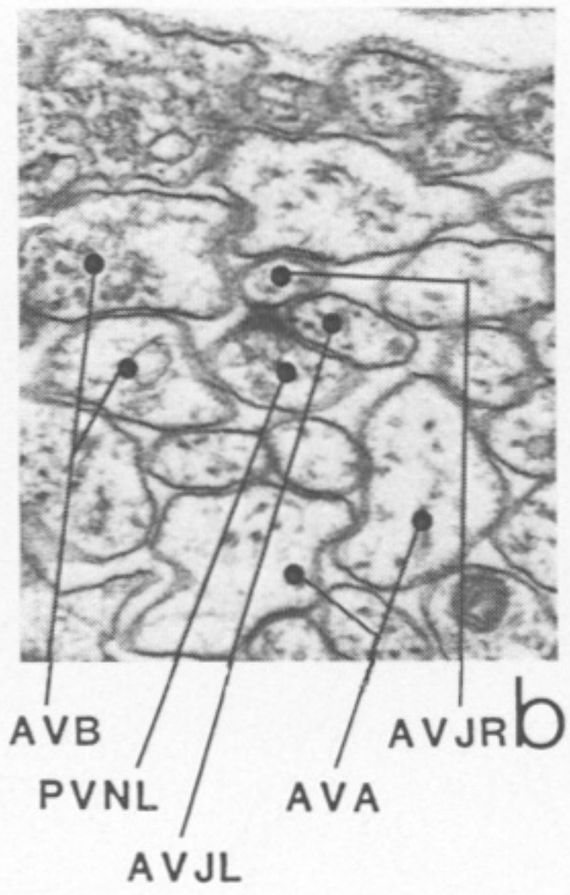


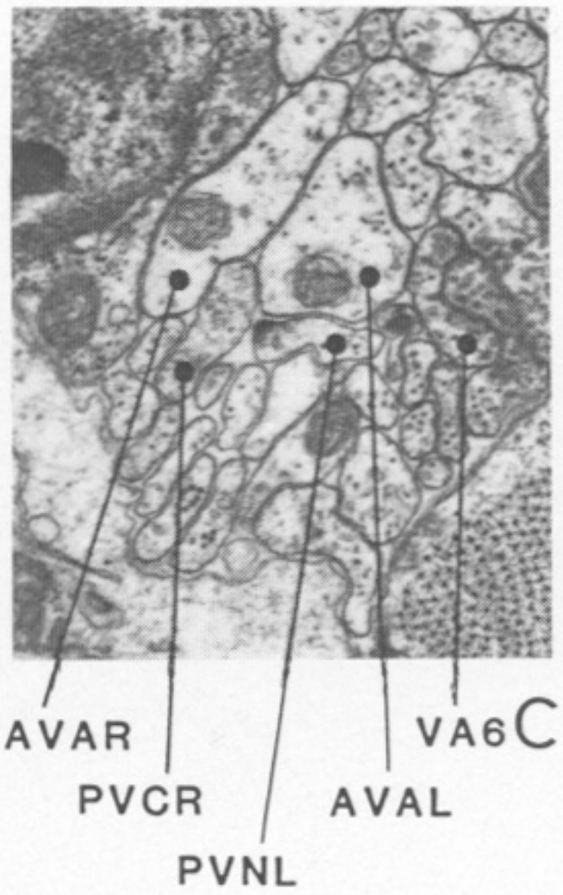


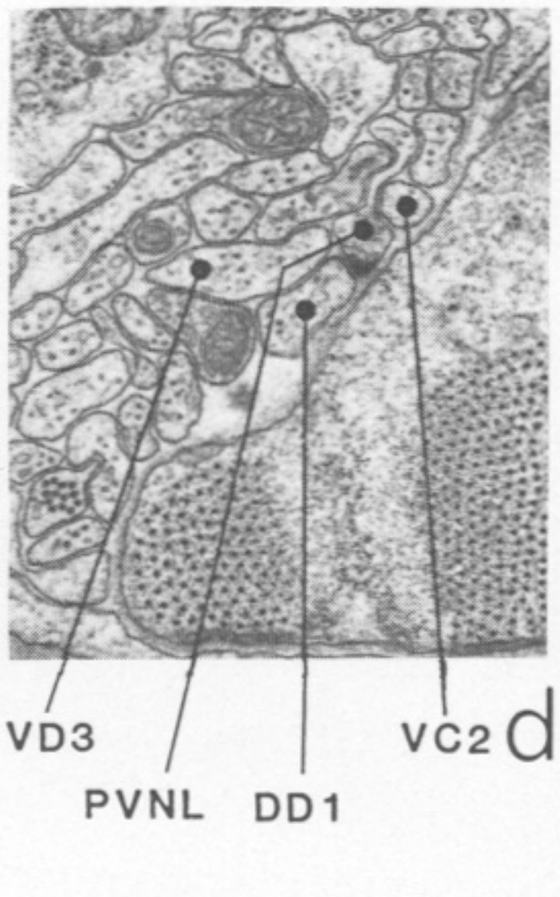


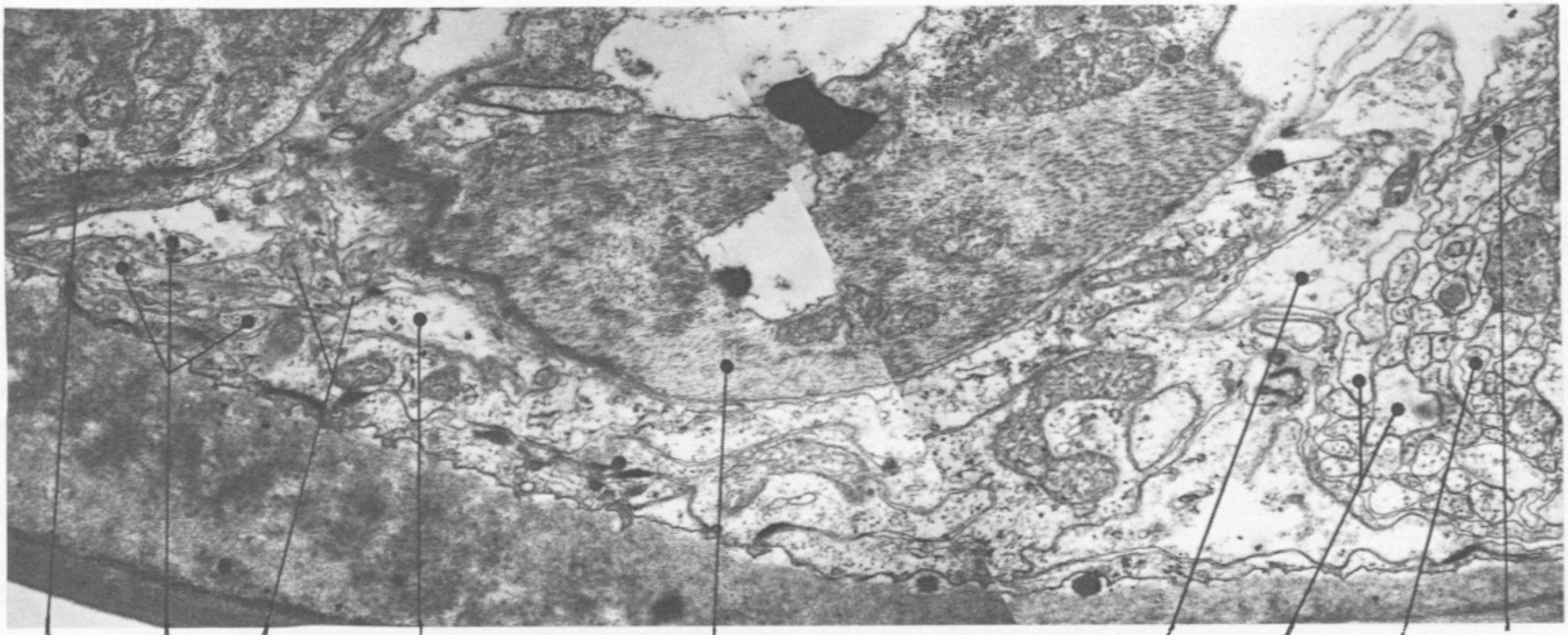
PVD

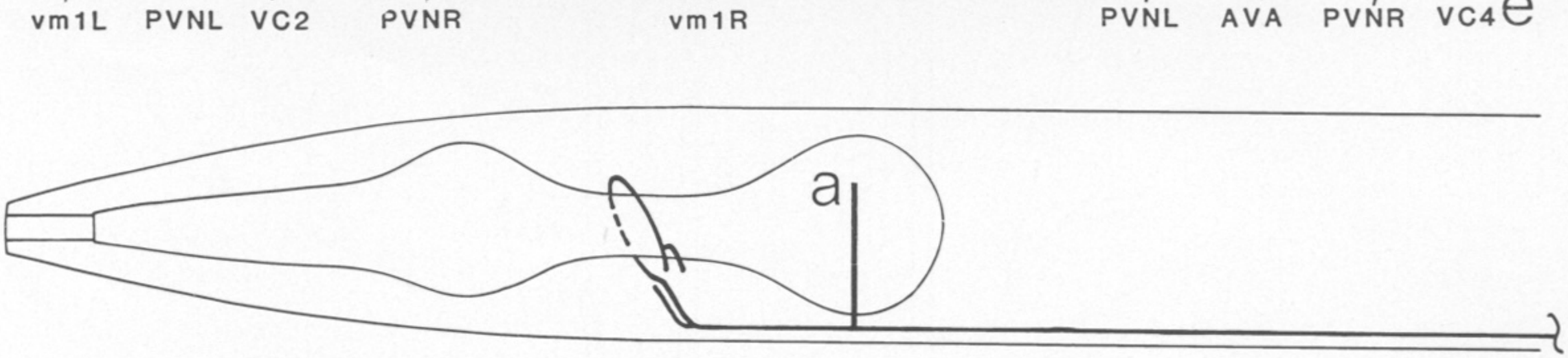

PVNL
BDUR
AVM
PVCR
FLPR
a

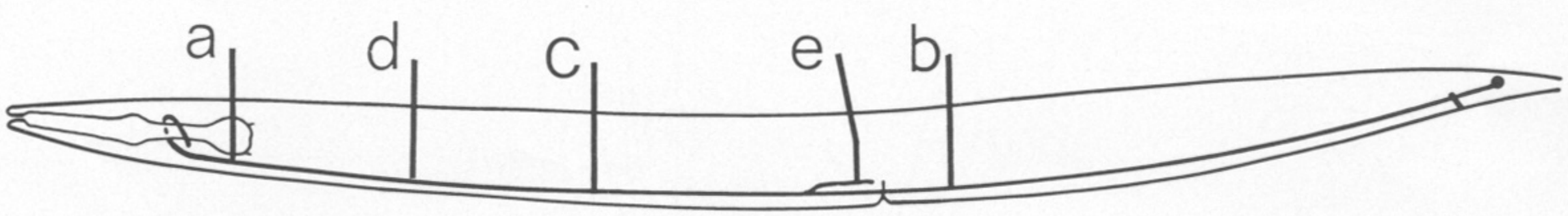

AVB
PVNL
AVJL
AVA
AVJR
b

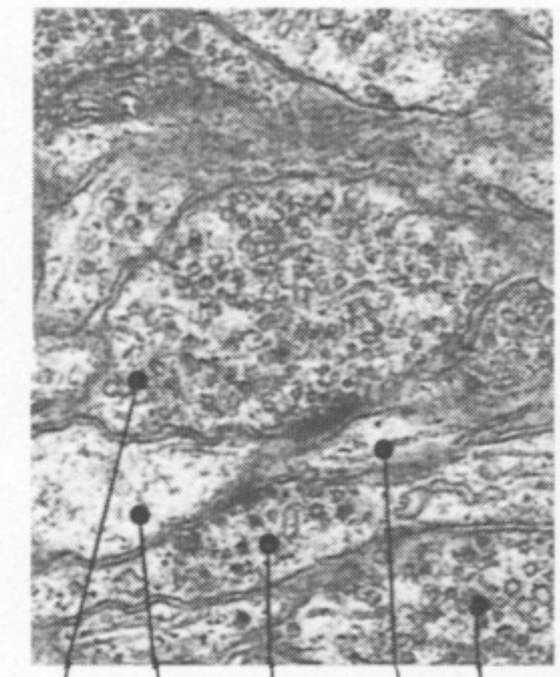

AVAR
PVCR
PVNL
AVAL
VA6
C

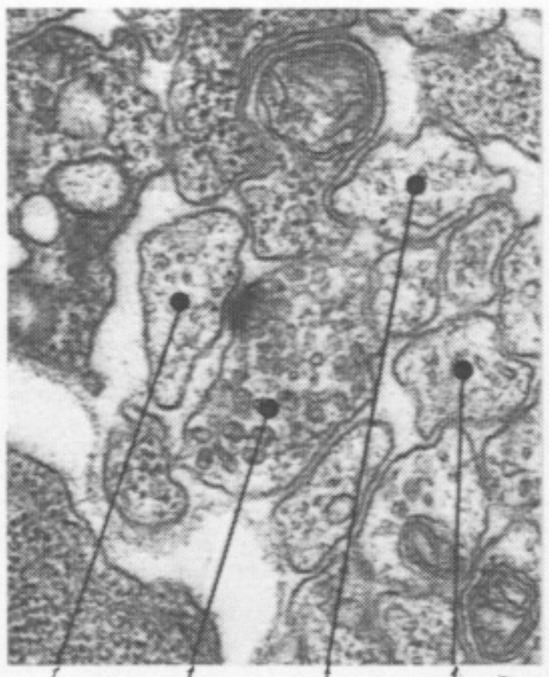

VD3
PVNL
DD1
VC2
d

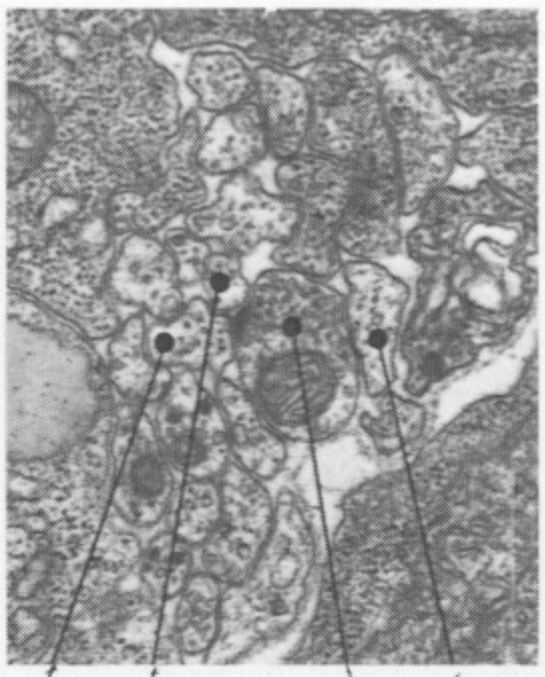

vm1L
PVNL
VC2
PVNR
vm1R
PVNL
AVA
PVNR
VC4
e

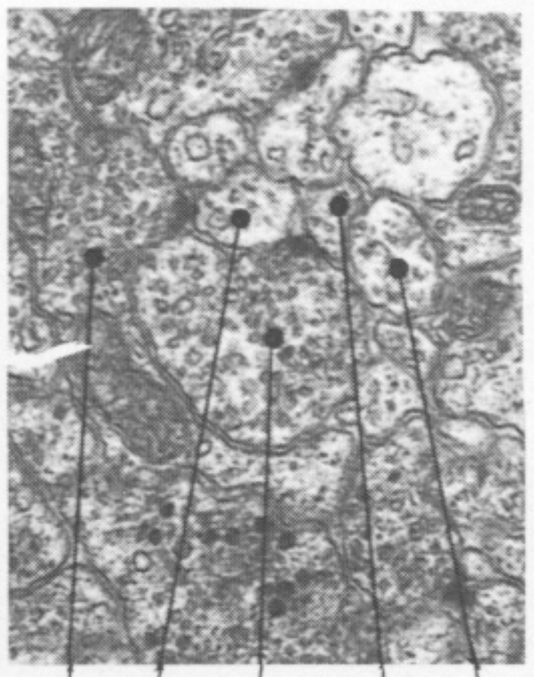

a
PVNR
f

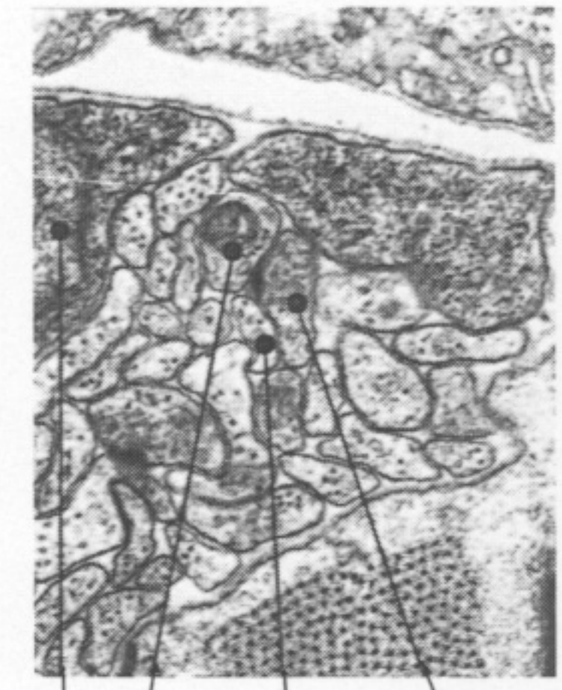

a
d
c
e
b
PVNR
g

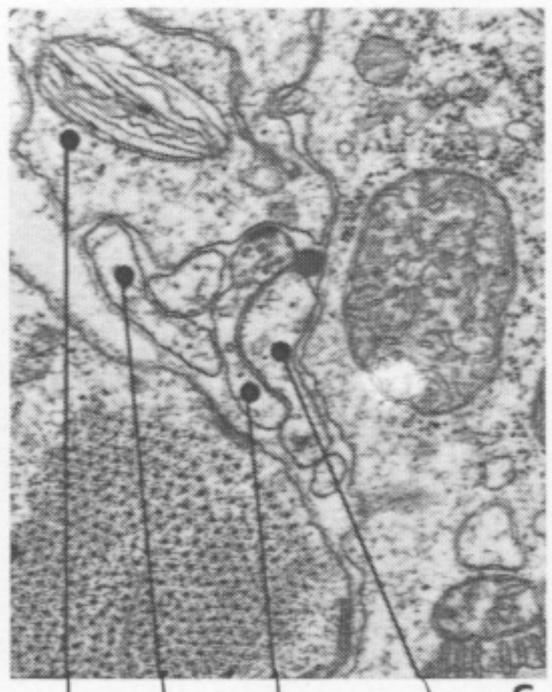

PVPR
AVBR
AVJL
PVCR
PVR
a

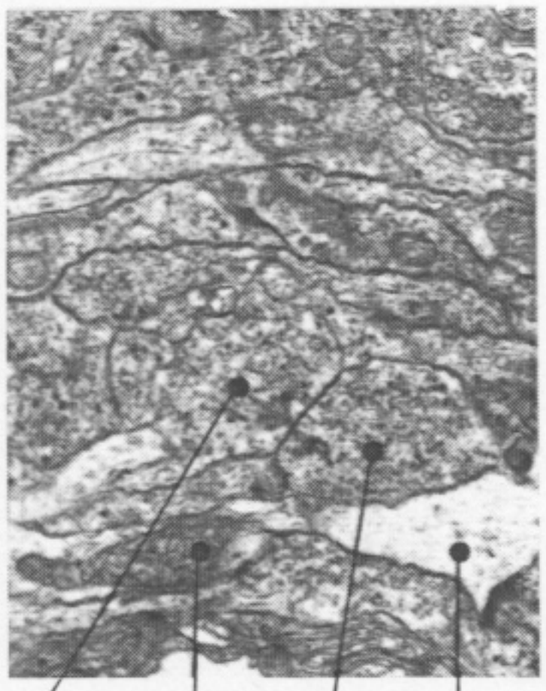

RIGL
PVPL
AVBR
AVAR
b

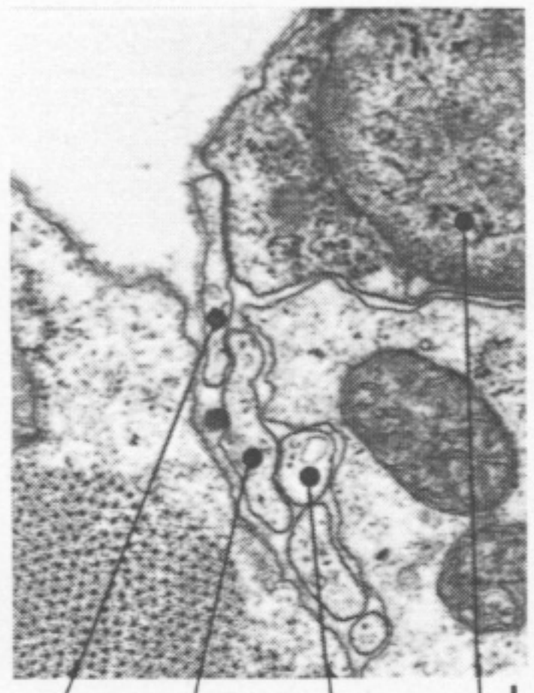

AVAL
AVHL
PVPR
RIGR
c

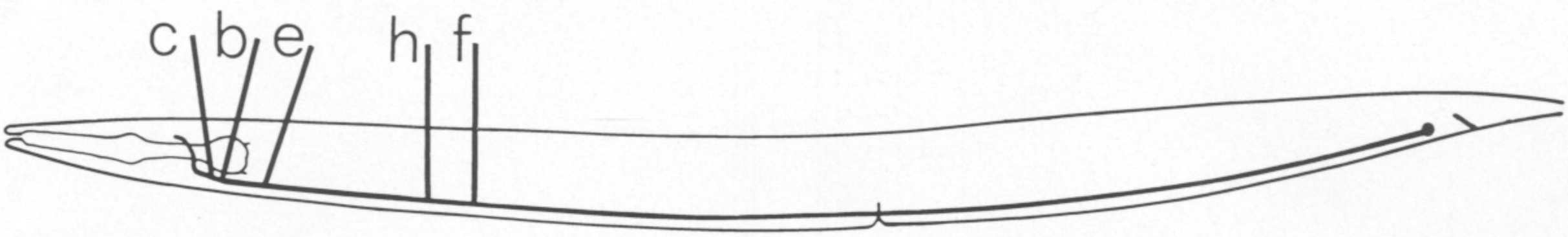

RIFL
AVBL
PVPL
AQR
DVA
d

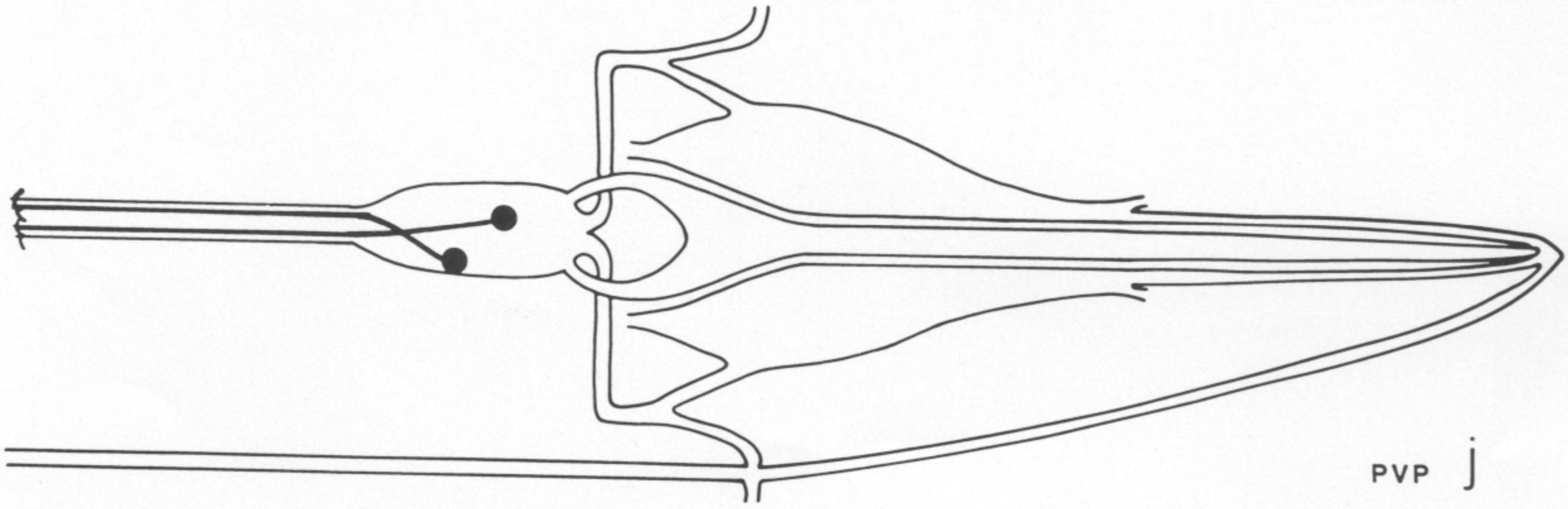

DB1
AVL
PVQR
PVPR
e

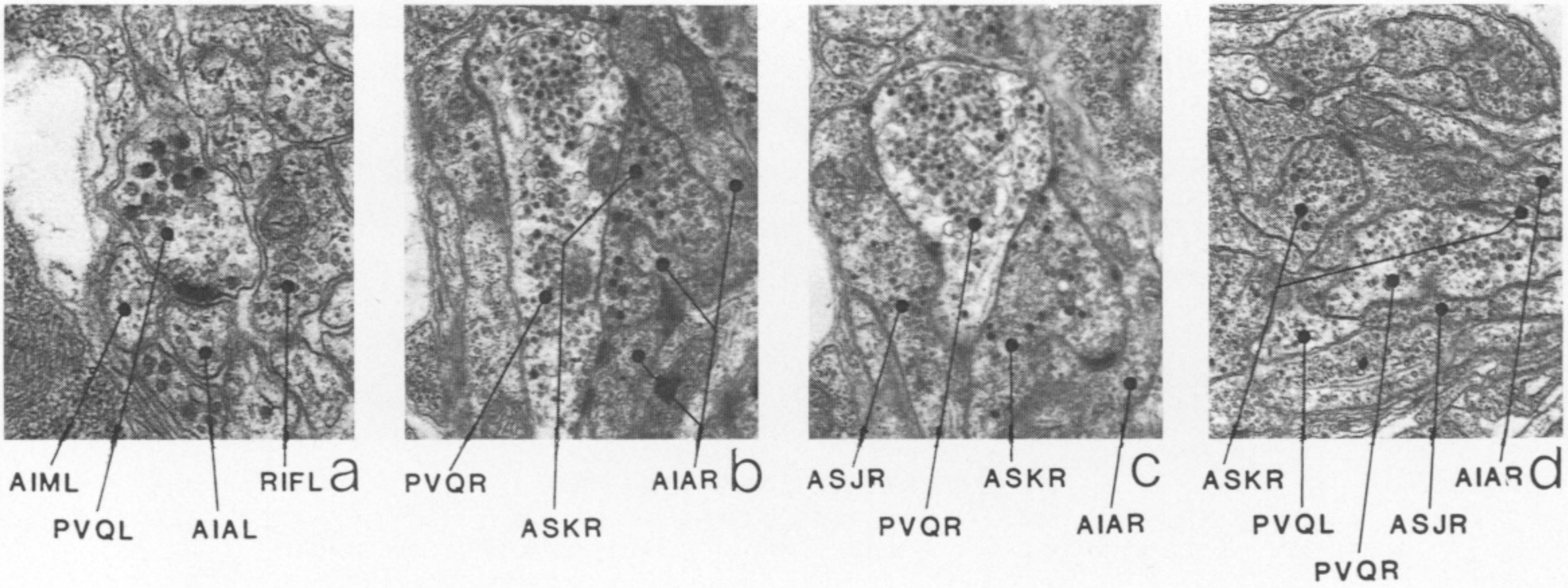

HSNL
AVKR
PVPL
HYPODERMIS
f

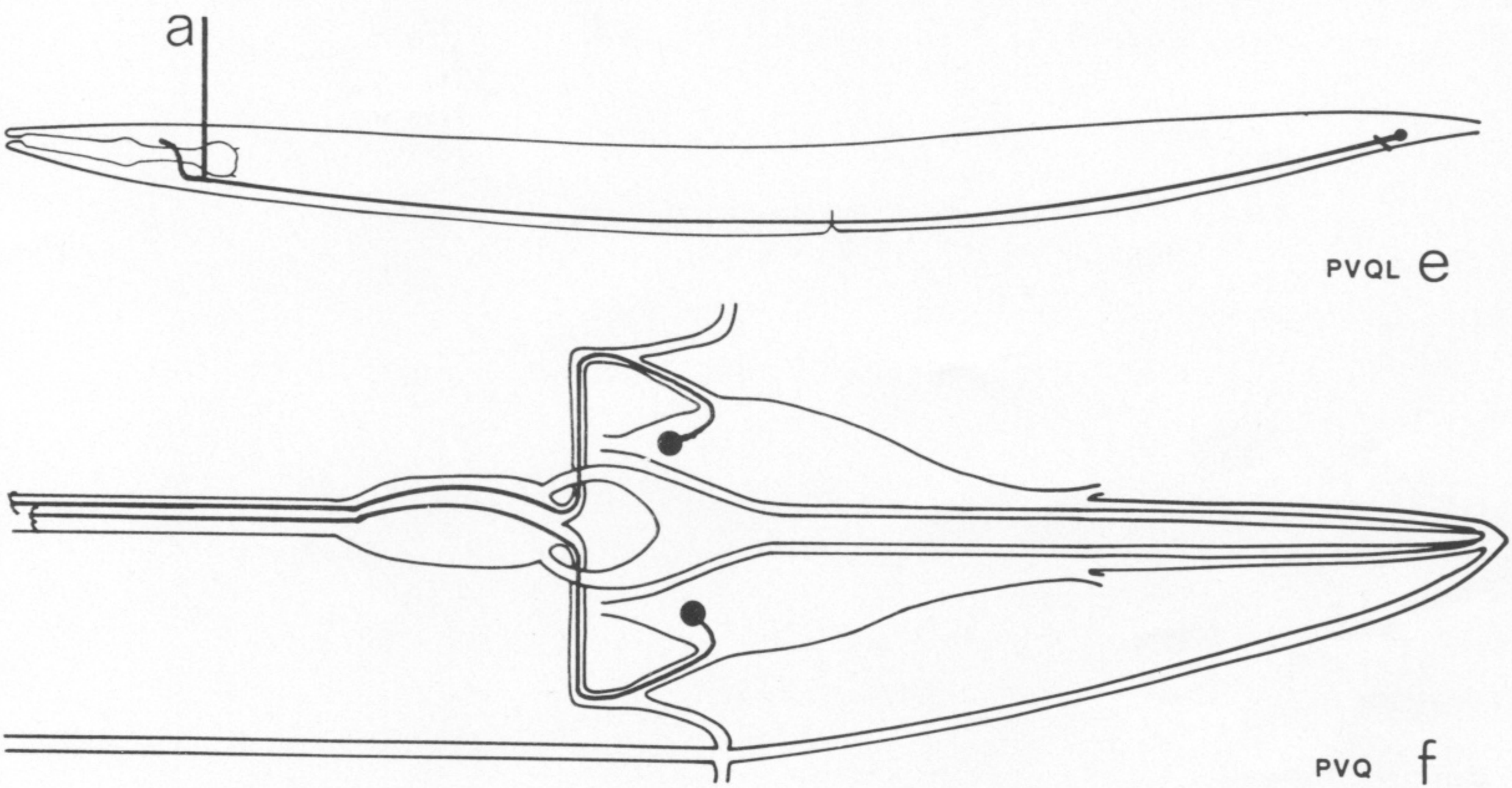

PVPL
PVPR
AVBR
AVBL
g


PVPL
PVQL
HSNL
VD3
h

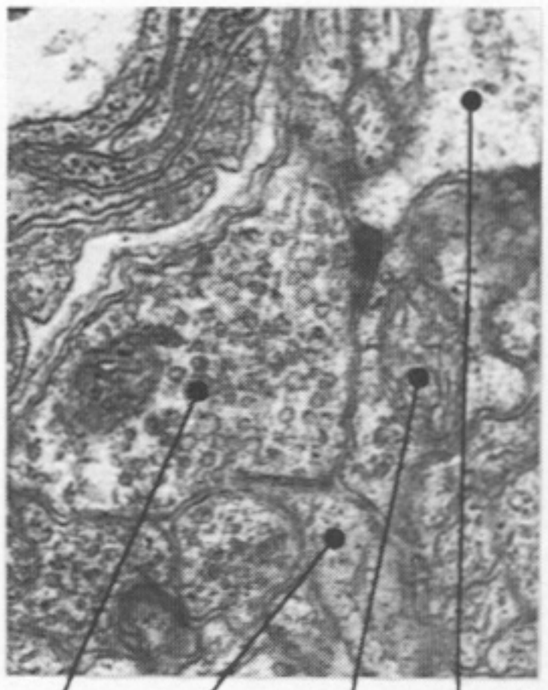

c
b
e
h
f
PVPL
i


PVP
j

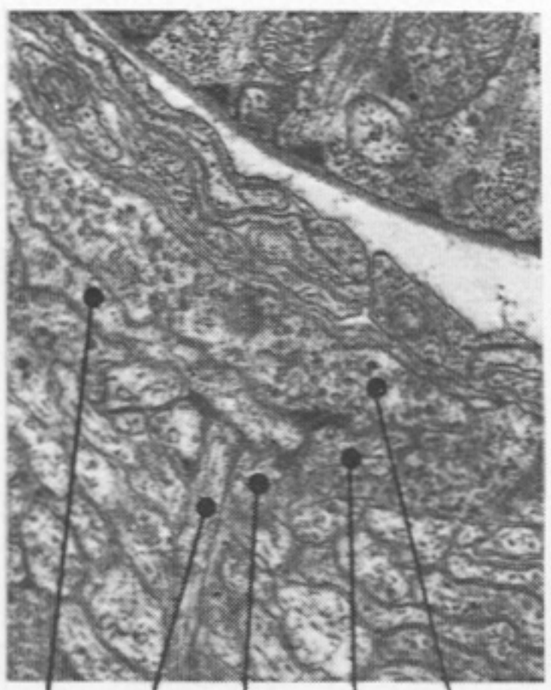

AIML
PVQL
AIAL
RIFL a
PVQR
ASKR
AIAR b
ASJR
PVQR
ASKR
AIAR c
ASKR
PVQL
PVQR
ASJR
AIAR d

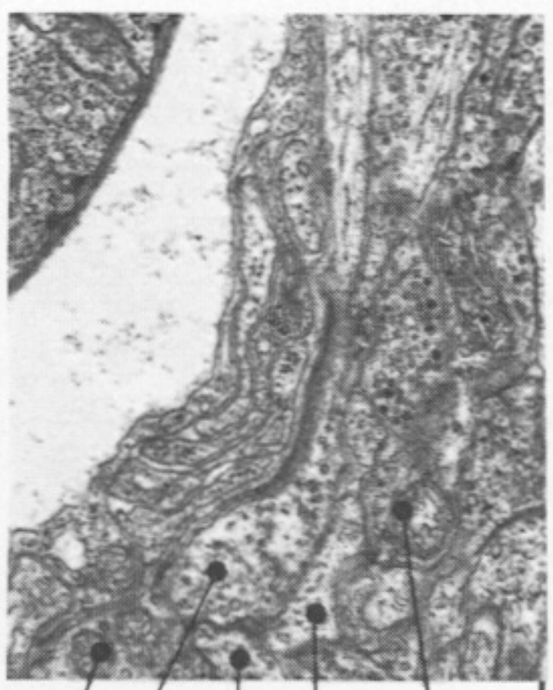

a
PVQL e
PVQ f

PVQ


PVR
IL1VR
RIPR
AVBR
a


PVPR
AVJL
PVR
AVBL
RIPR
ADAR
b

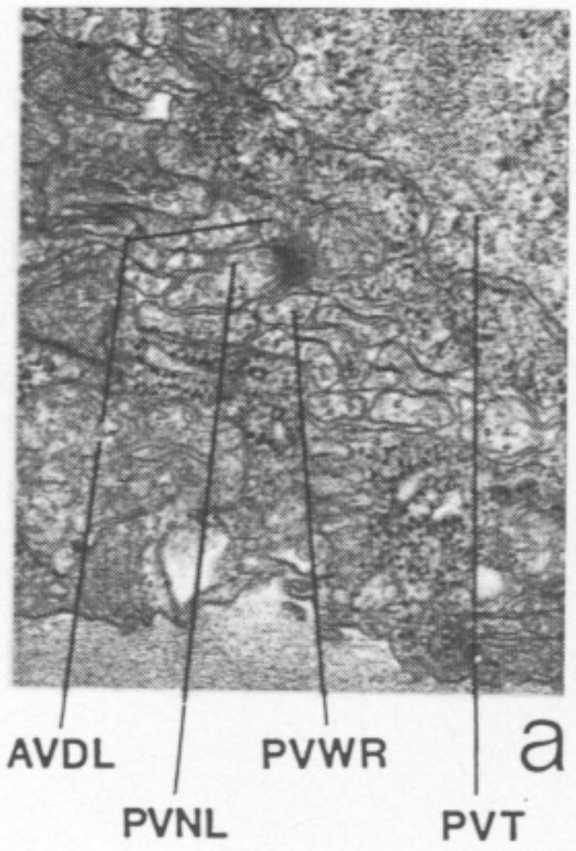

RIPL
URAVL
IL2VL
IL1VL
PVR
c

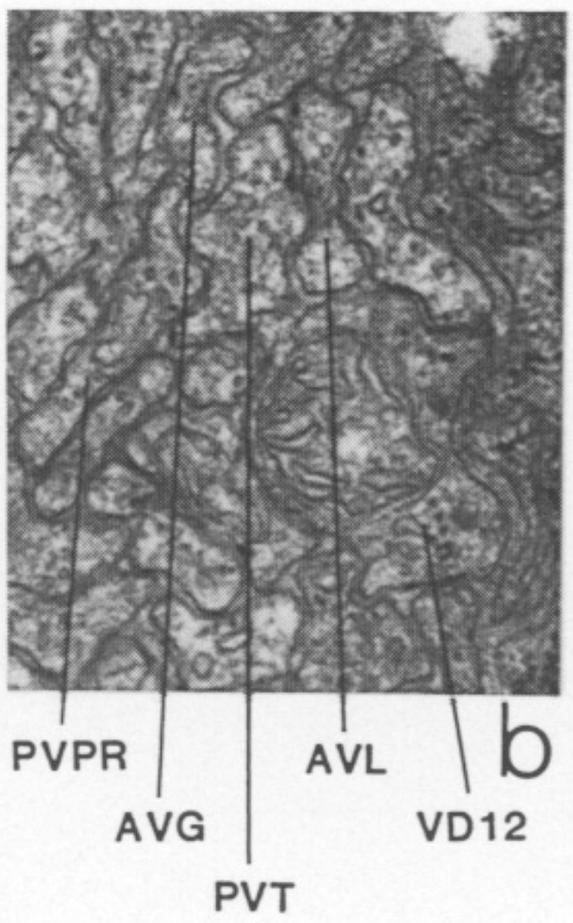

CEPVR
PVR
IL1VR
RIPR
ADAR
d

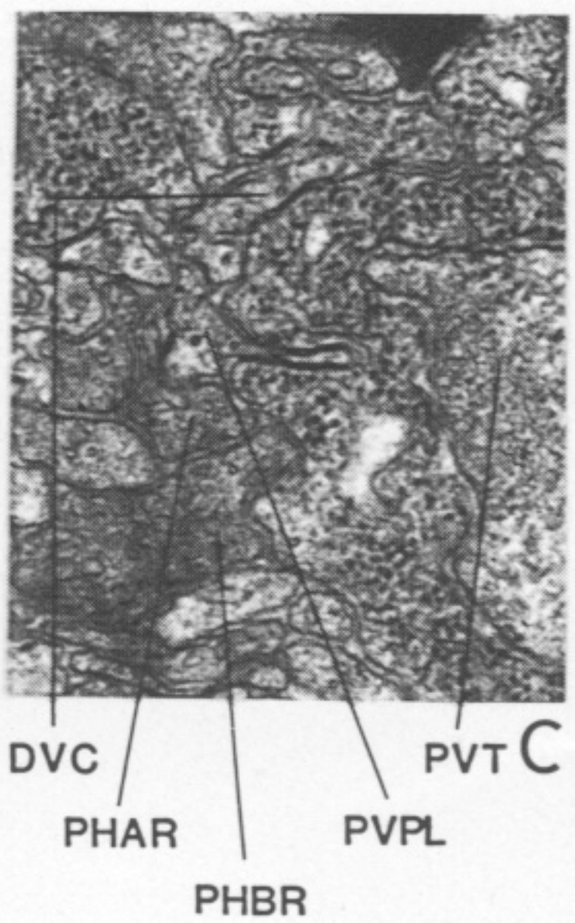

PVR
e

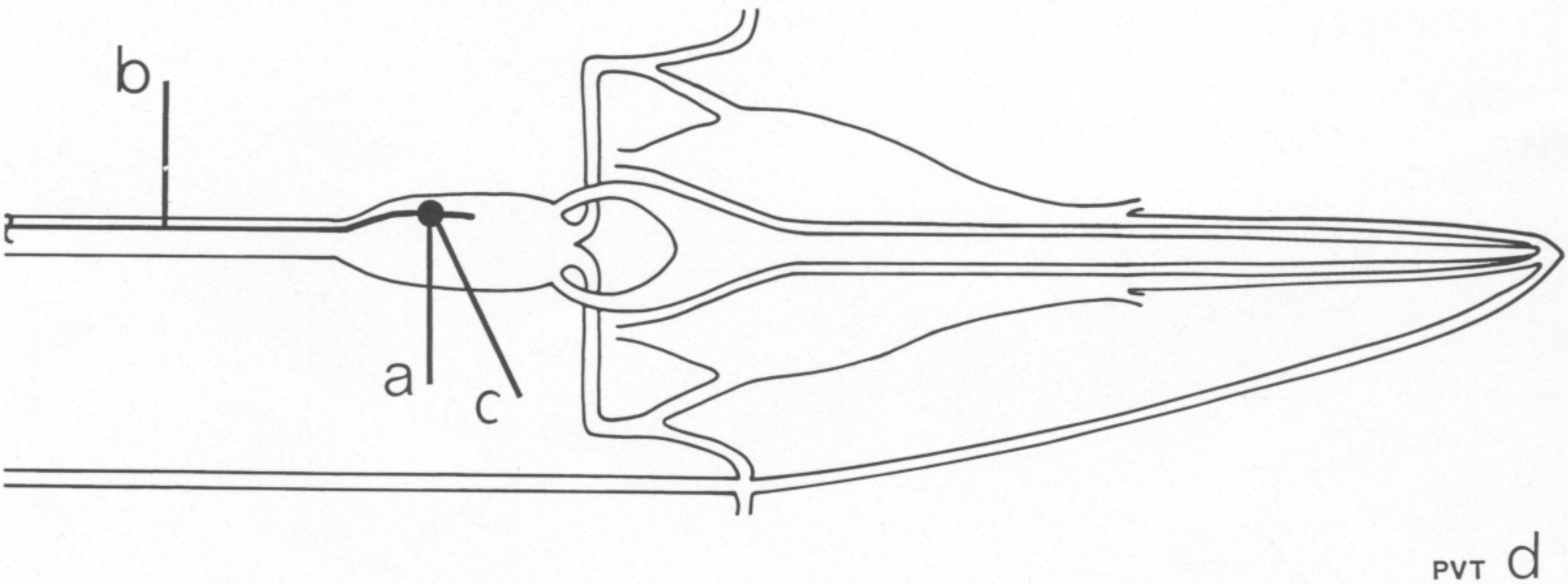
PVR
f

PVR

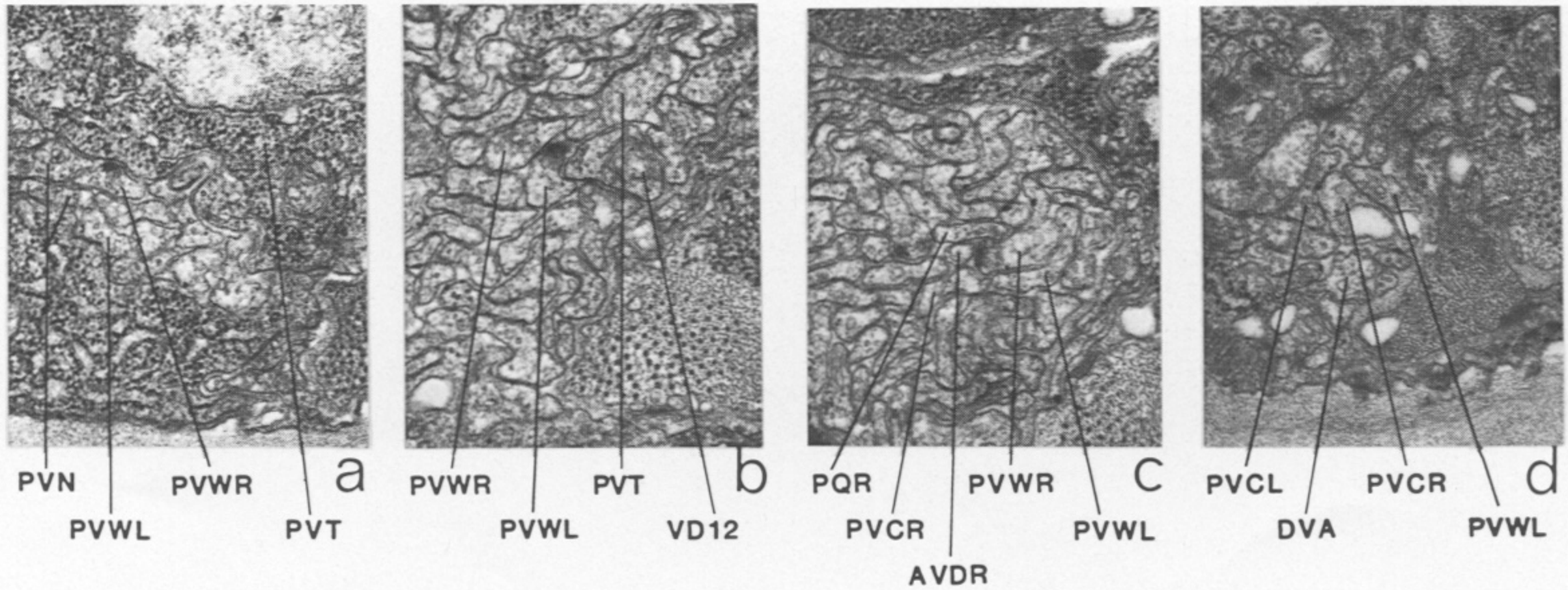

AVDL
PVNL
PVWR
PVT
a


PVPR
AVG
PVT
AVL
VD12
b

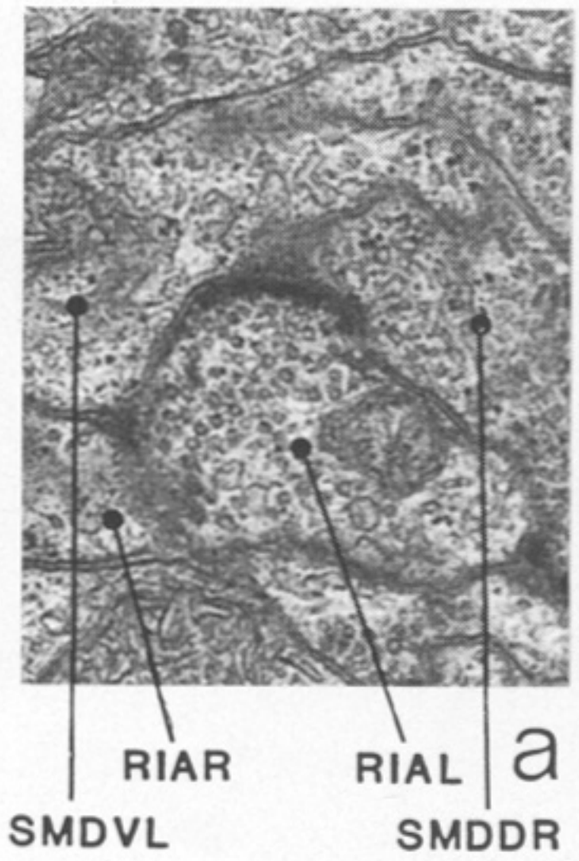

DVC
PHAR
PHBR
PVPL
PVT
C

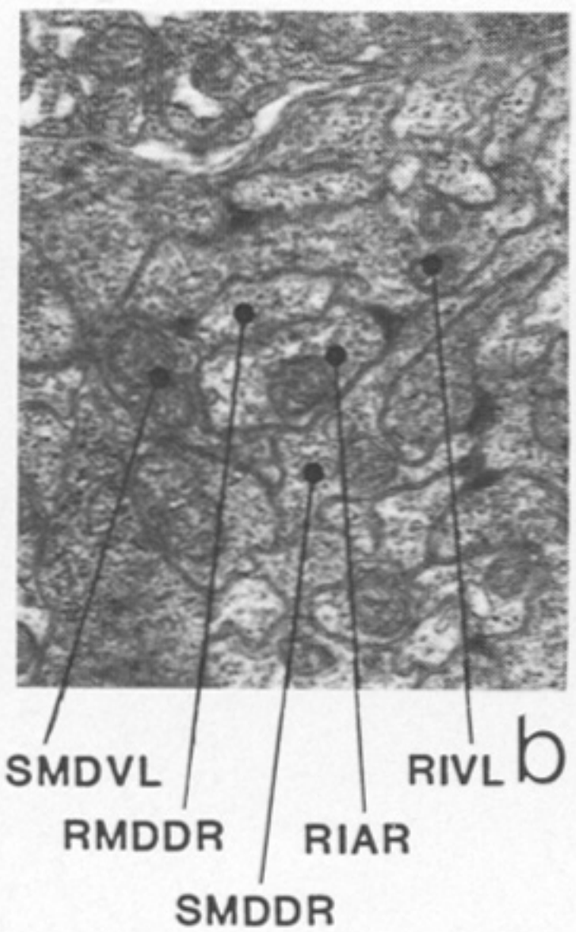

b
a
c
PVT
d

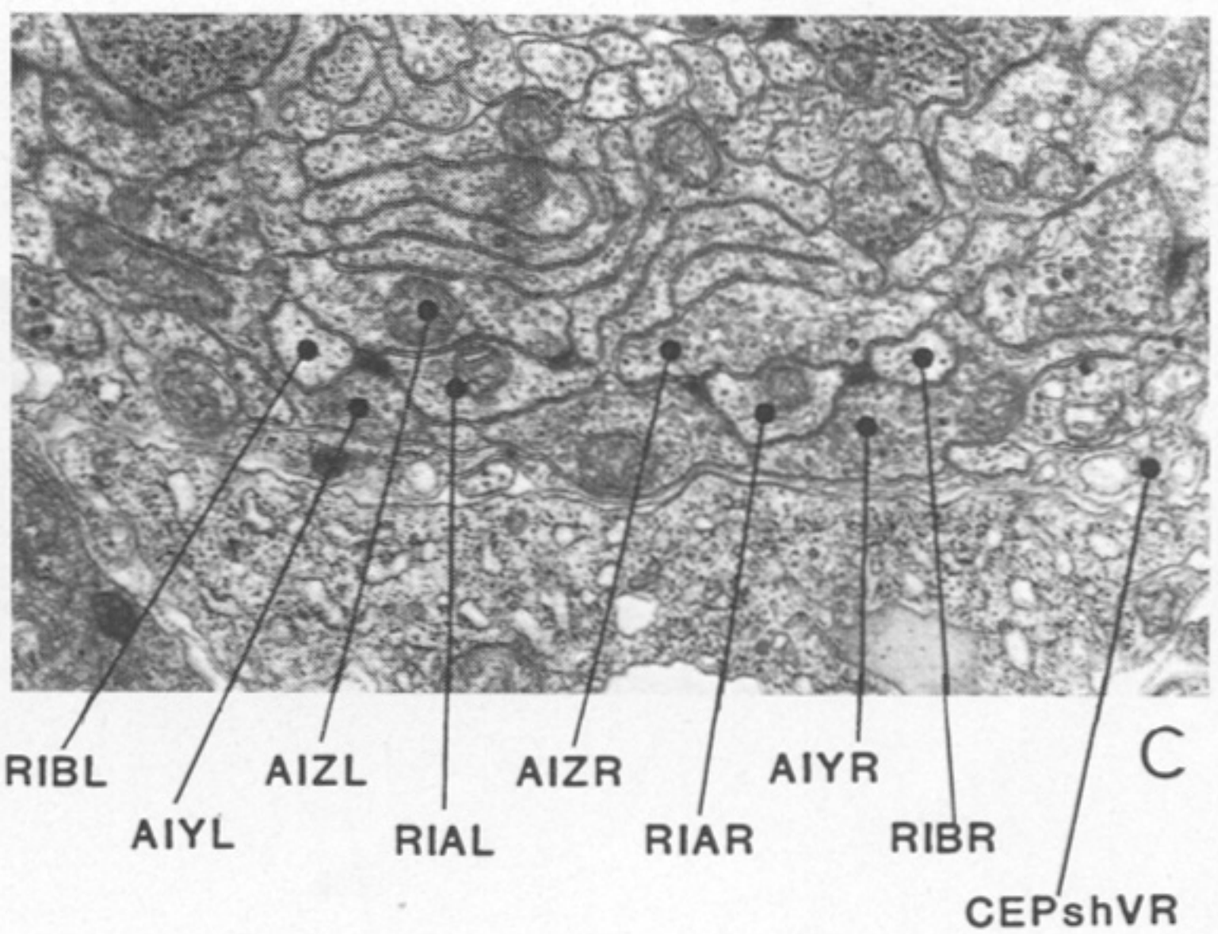
PVT


PVN
PVWL
PVWR
PVT
a
PVWR
PVWL
PVT
VD12
b
PQR
PVCR
AVDR
PVWR
PVWL
C
PVCL
DVA
PVCR
PVWL
d
c
a
b
d
PVW
e

PVW


RIAR
RIAL
SMDVL
SMDDR
a

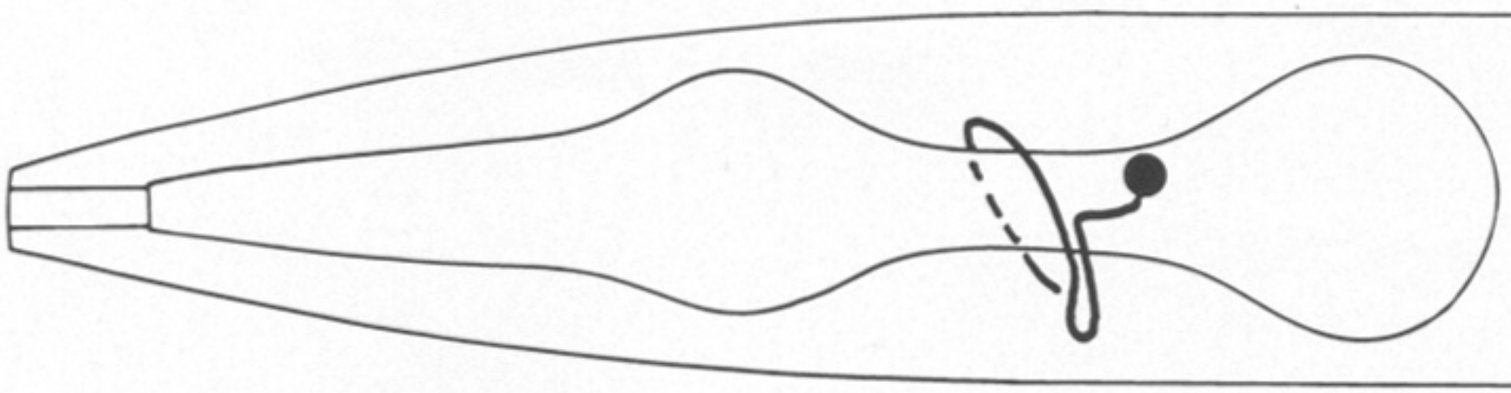

SMDVL
RIVL
RMDDR
RIAR
SMDDR
b


RIBL
AIZL
AIZR
AIYR
AIYL
RIAL
RIAR
RIBR
CEPshVR
c


SMDVL
RIAR
SMDDR
SIADR
d

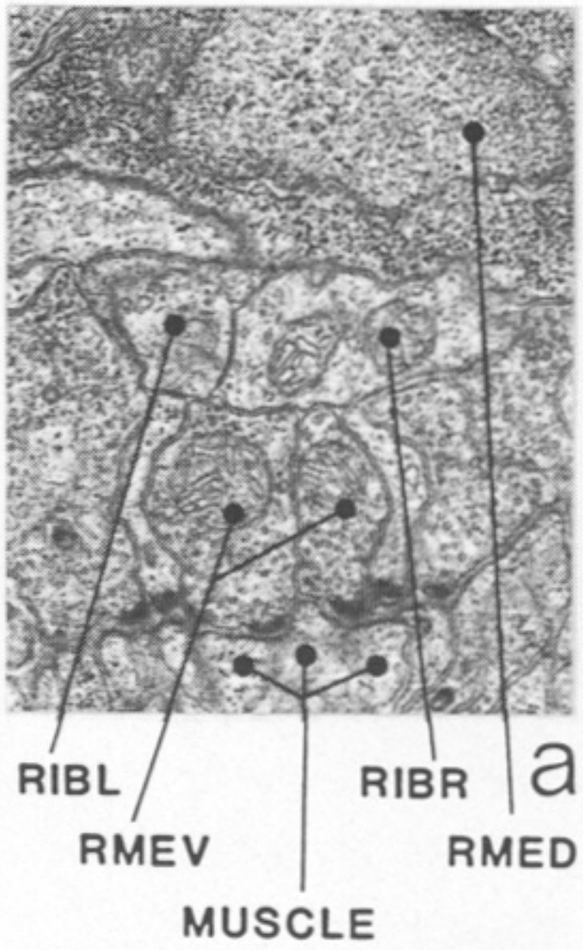

RMDR
RIAR
RIAL
RMDL
e

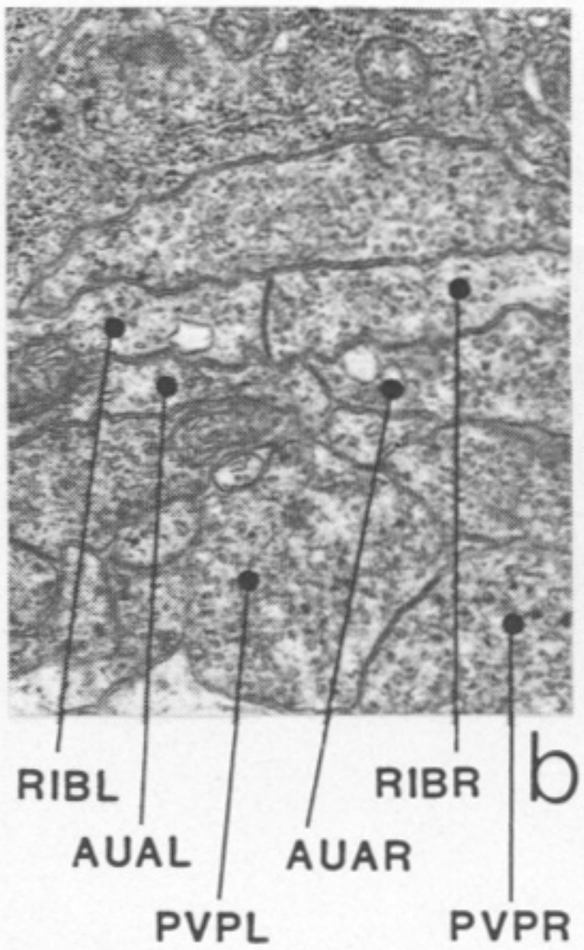

SMDDR
SMDVL
RIAL
SMDVR
RMDVR
MUSCLE
RMDDL
SMDDL
SMBDL
f

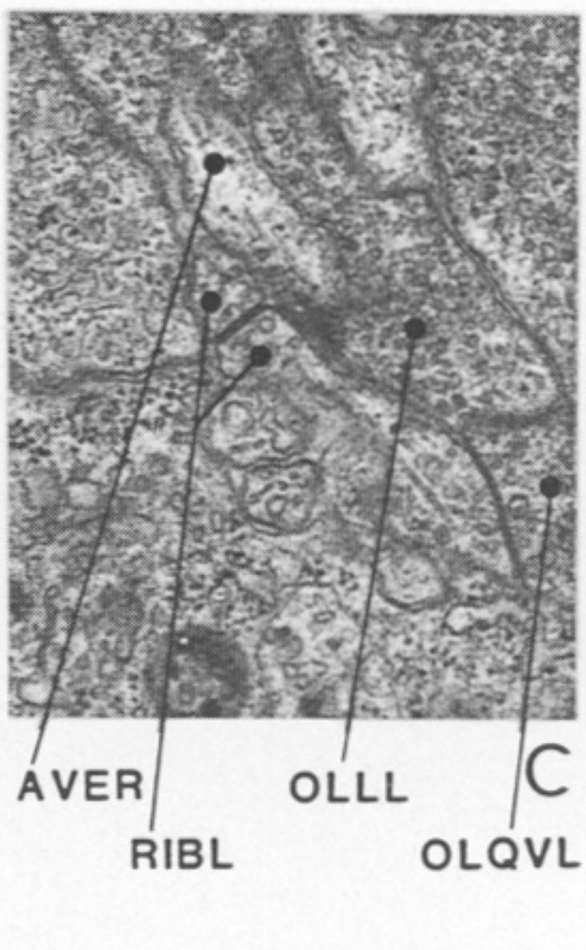


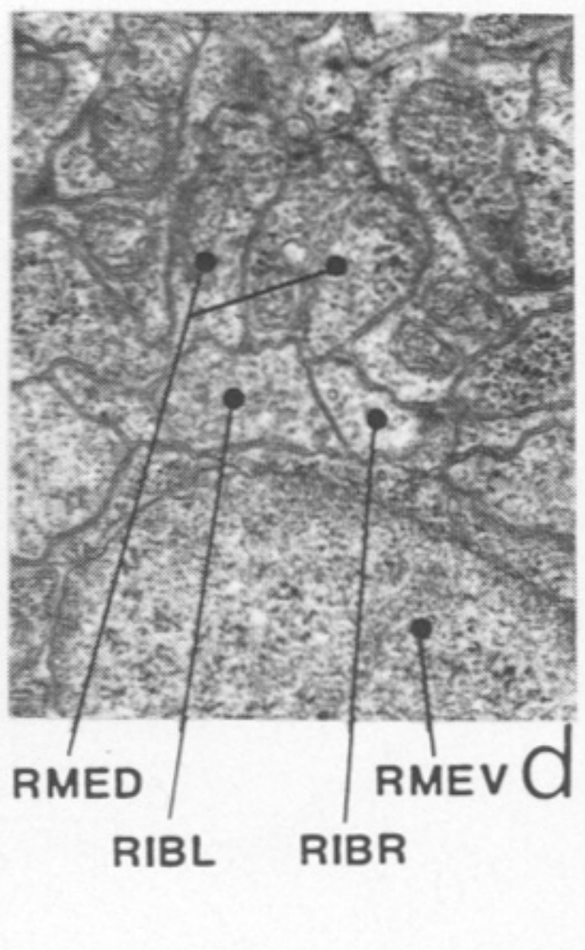
RIAL g

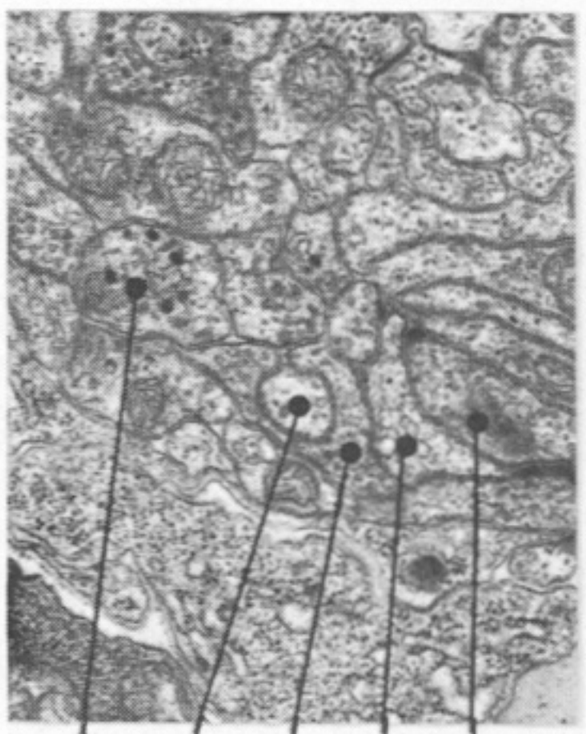
RIA

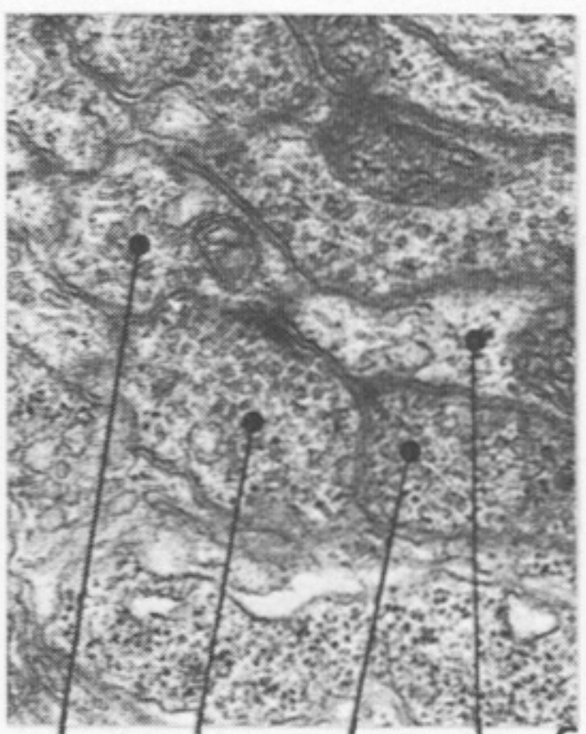

RIBL
RMEV
MUSCLE
RIBR
RMED
a

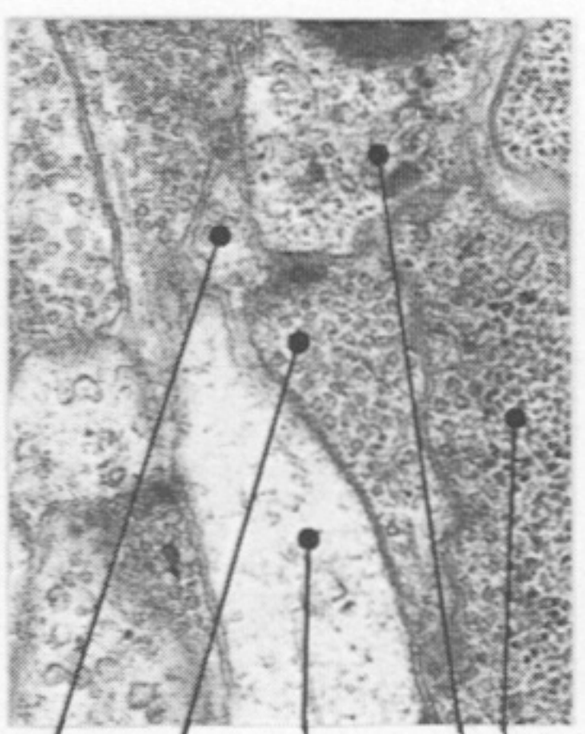

RIBL
AUAL
PVPL
AUAR
RIBR
PVPR
b

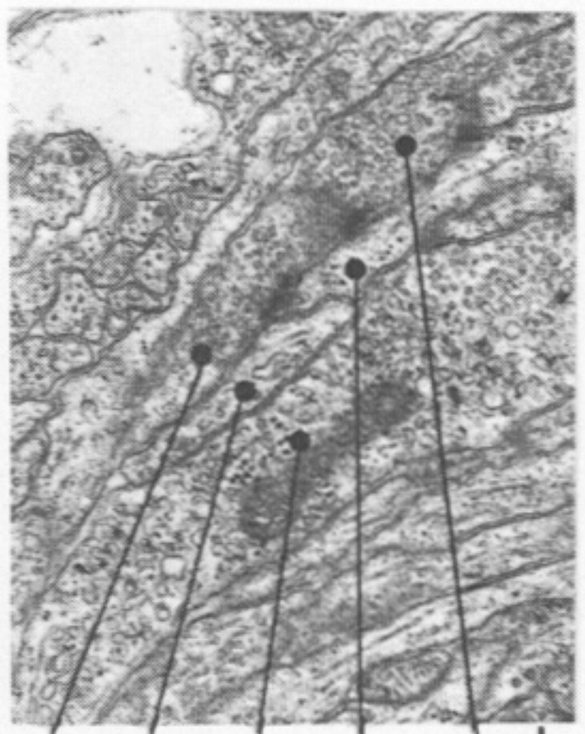

AVER
RIBL
OLLL
OLQVL
c

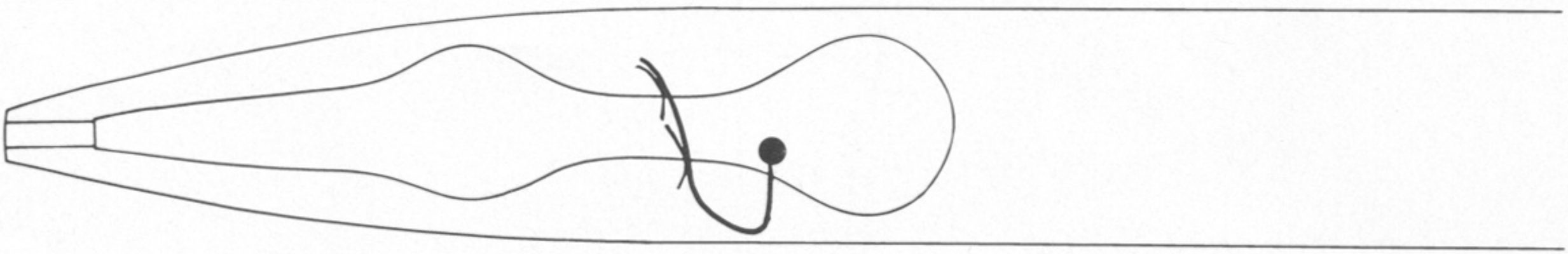

RMED
RIBL
RIBR
RMEV
d


AWAL
RIBL
AIYL
RIAL
AIZL
e

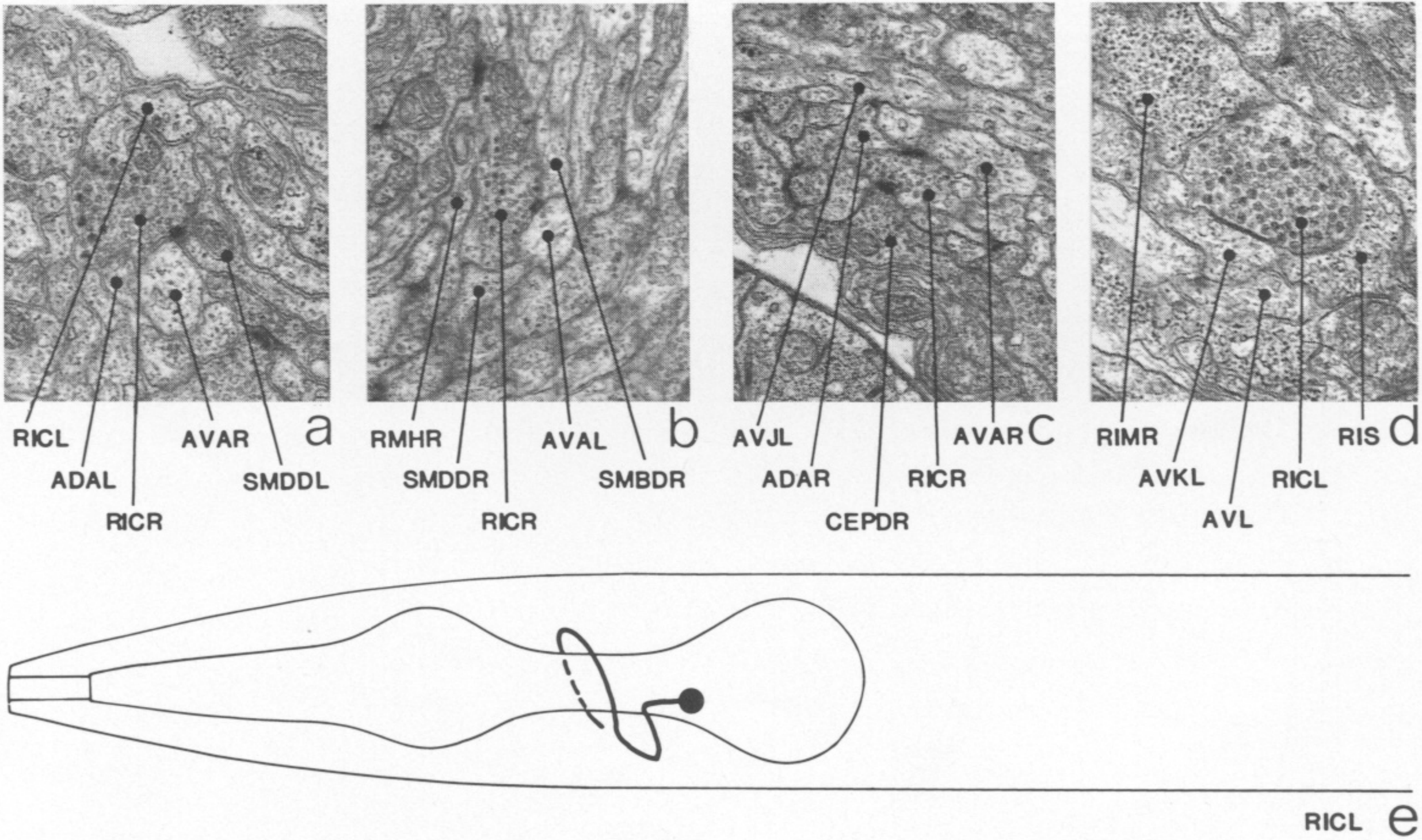

AUAL
RIBL
RIH
RIAL
f


BAGL
RIBR
AVBL
AVAR
RIMR
g

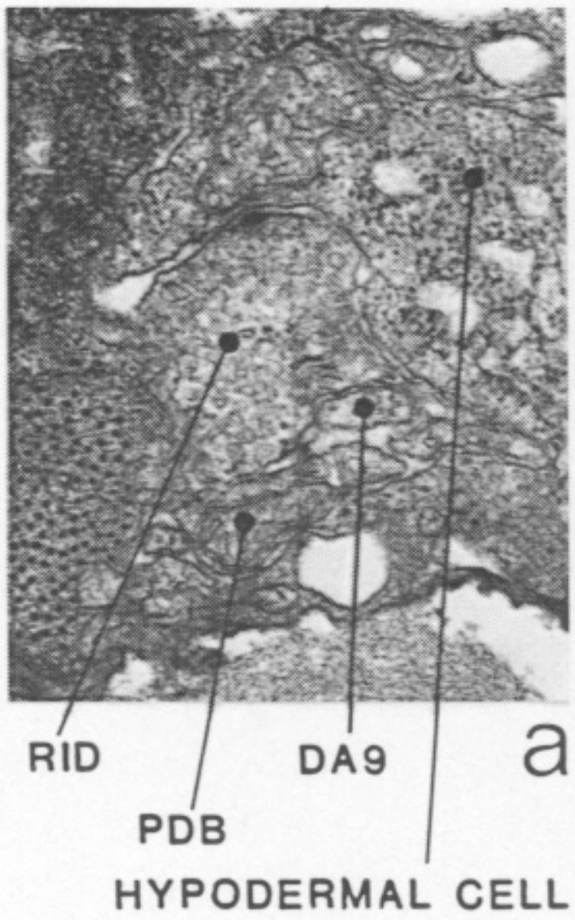

RIBL
AIZL
DVA
AVEL
BAGR
h

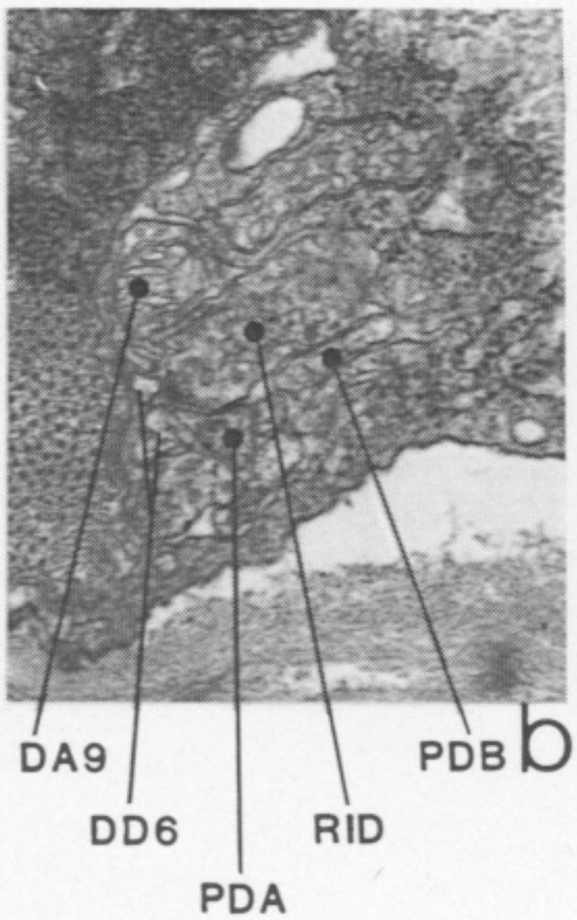

RIBL
i

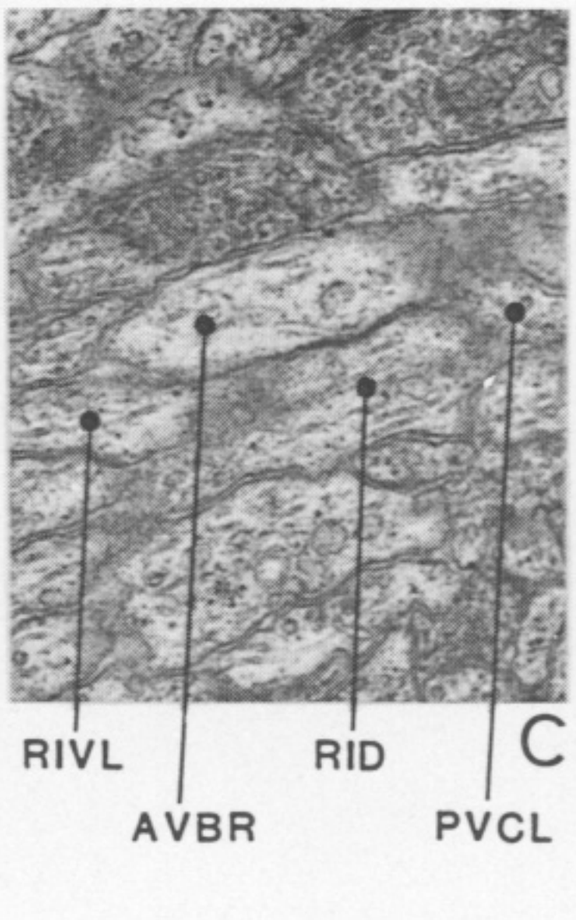
RIB

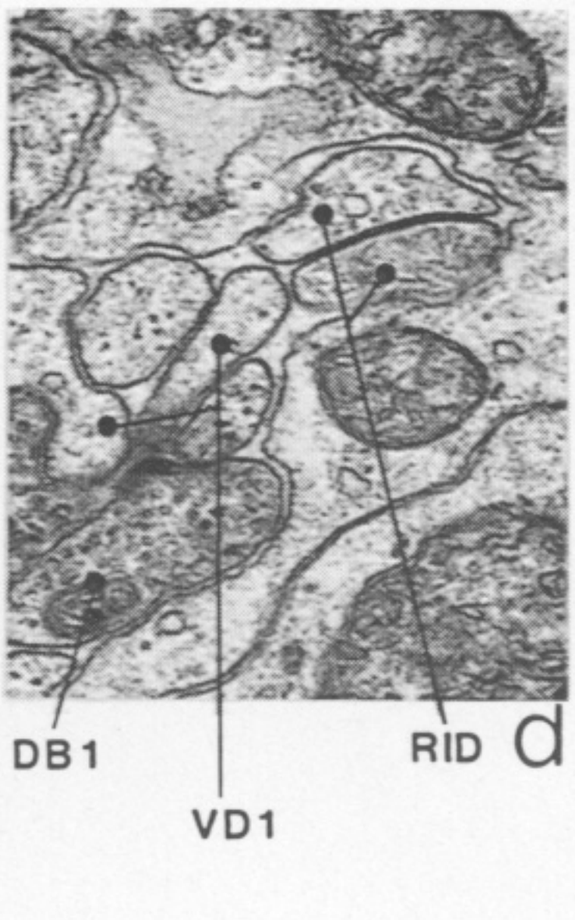

RICL
ADAL
RICR
AVAR
SMDDL
a
RMHR
SMDDR
RICR
AVAL
SMBDR
b
AVJL
ADAR
CEPDR
RICR
AVAR
c
RIMR
AVKL
AVL
RICL
RIS
d
RICL
e

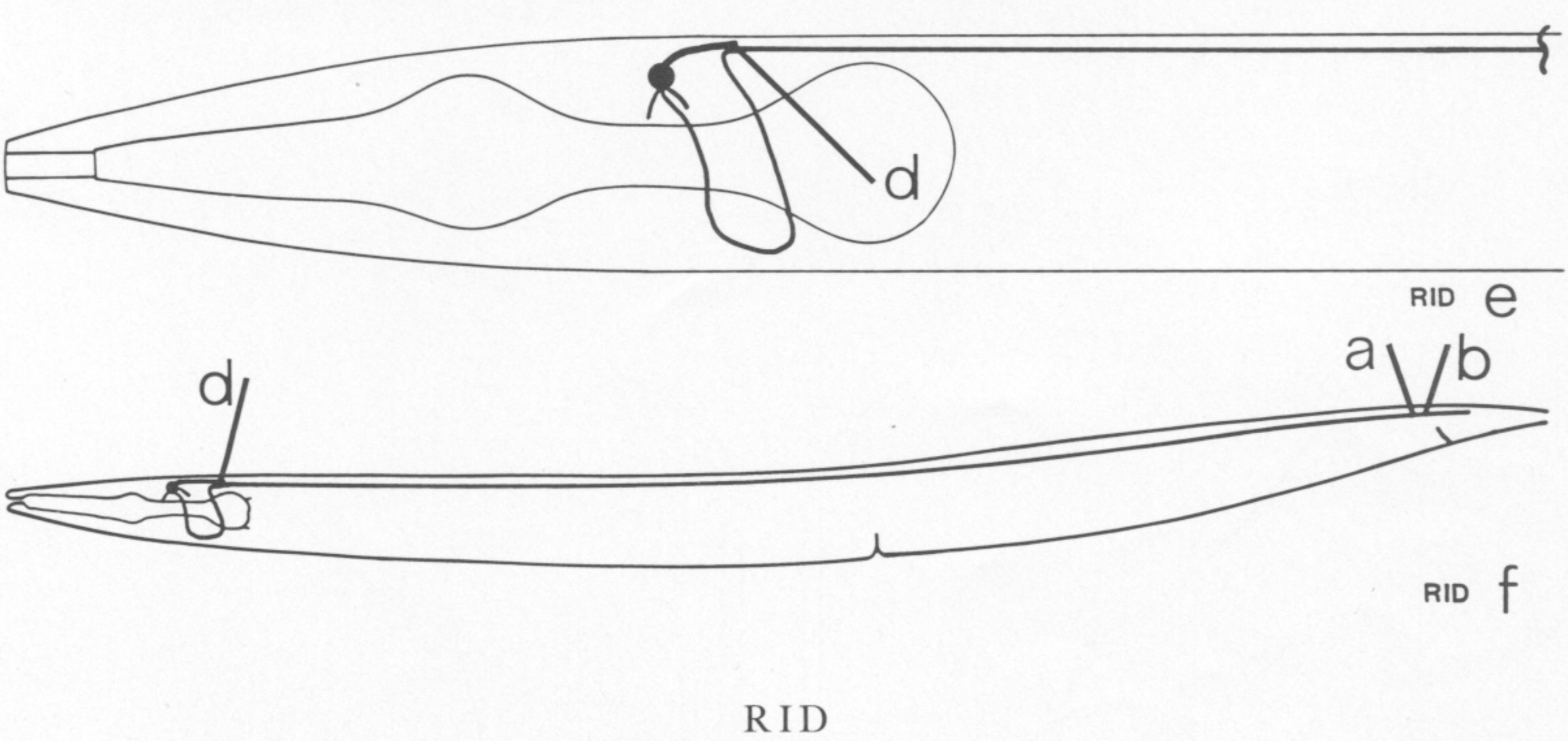
RIC


RID
PDB
DA9
HYPODERMAL CELL
a

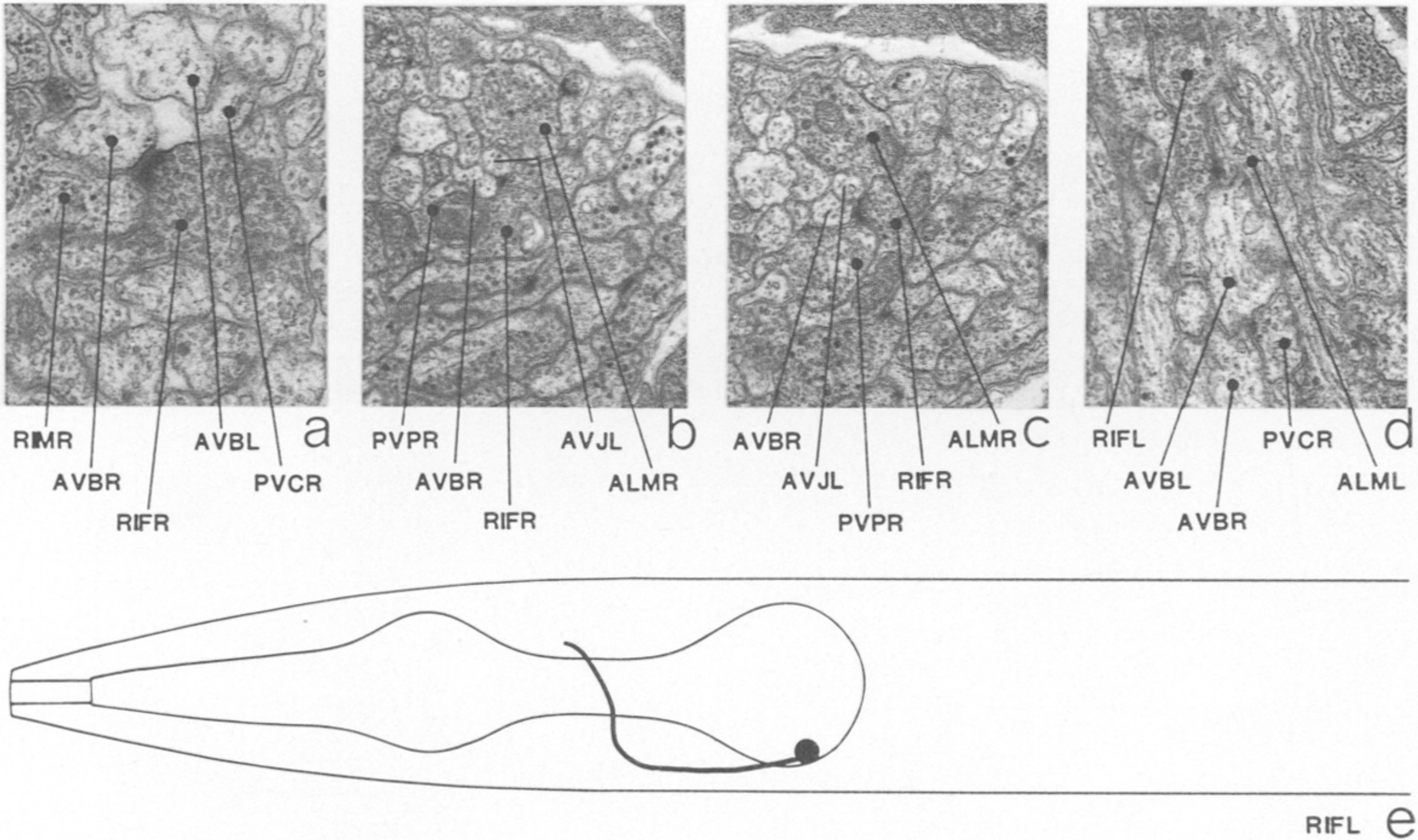

DA9
DD6
PDA
RID
PDB
b


RIVL
AVBR
RID
PVCL
C

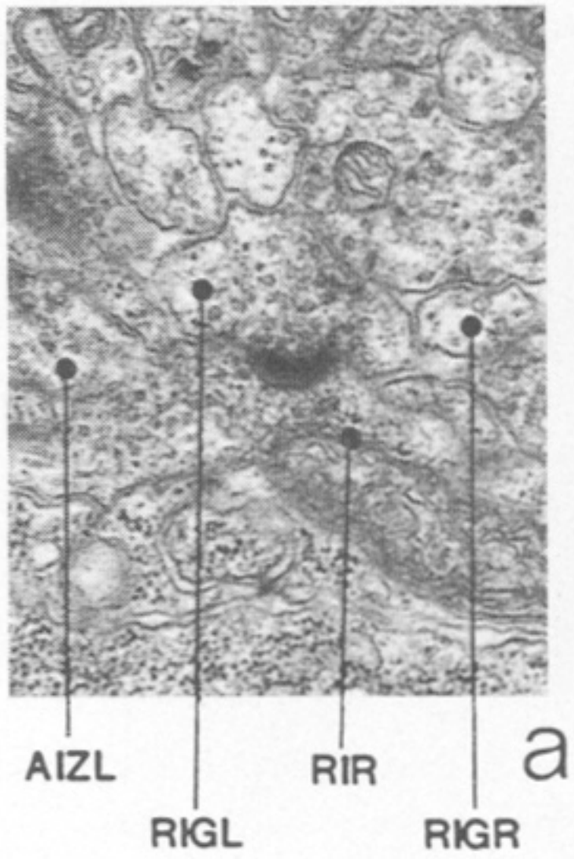

DB1
VD1
RID
d


d
RID
e
a
b
d
RID
f

RID


RIMR
AVBR
AVBL
PVCR
a
PVPR
AVBR
RIFR
AVJL
ALMR
b
AVBR
AVJL
RIFR
ALMR
c
RIFL
AVBL
PVCR
ALML
d
RIFL
e

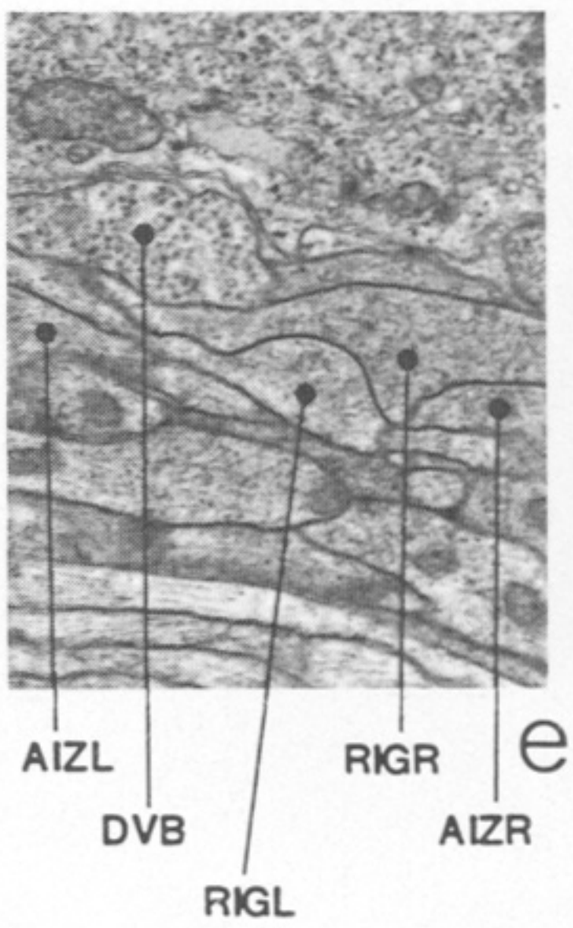
RIF

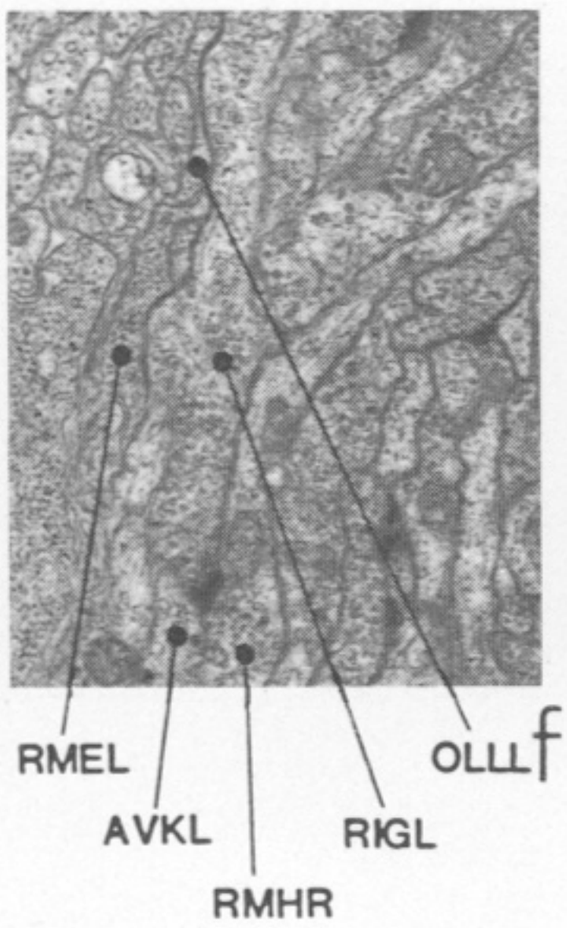

AIZL
RIGL
RIR
RIGR
a

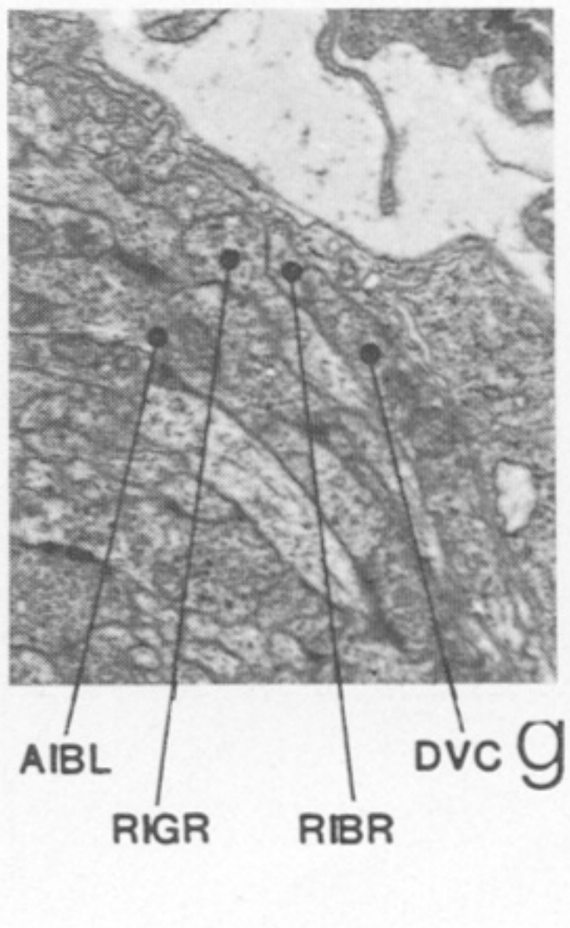

RIGR
RMHL
AVKL
DVB
DVC
b

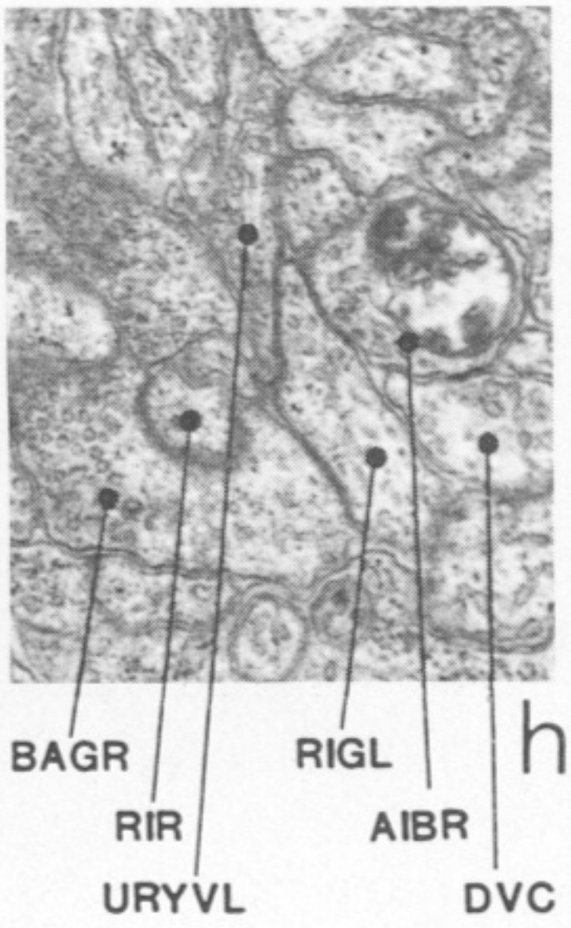

URYDL
AIBR
AVEL
AIZL
RIGL
RIML
c

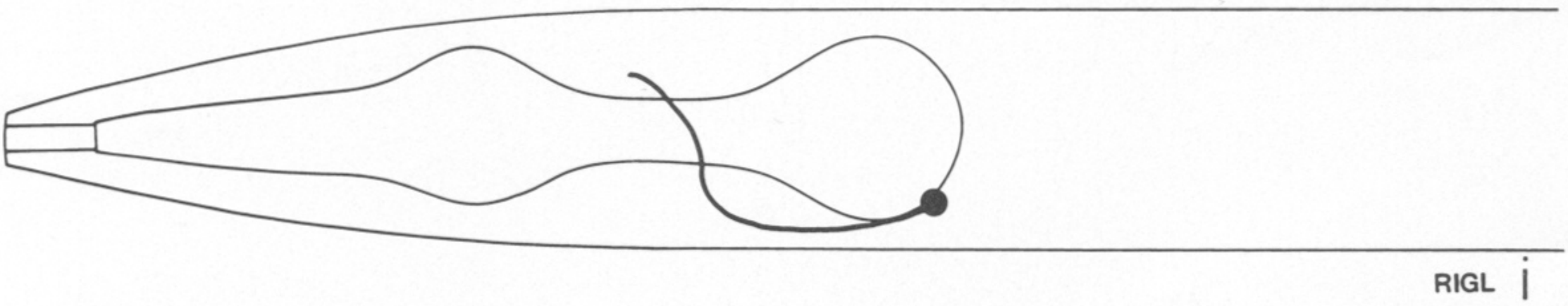

BAGR
RIBL
RIGL
DVB
DVC
d


AIZL
DVB
RIGL
RIGR
AIZR
e

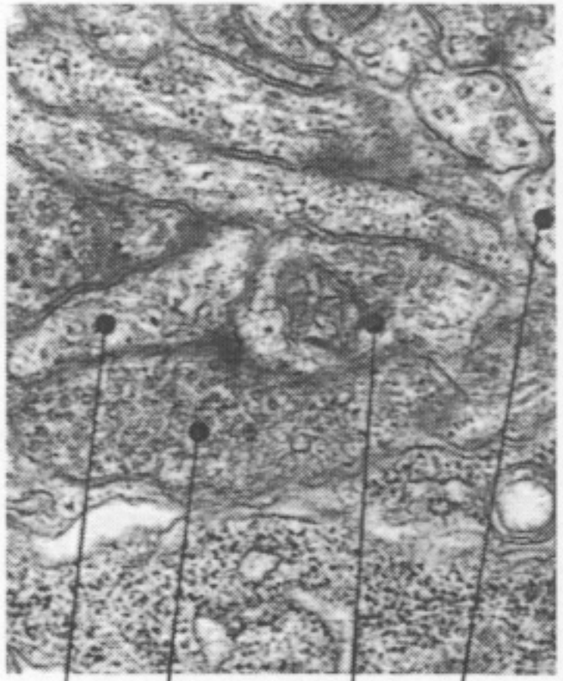

RMEL
AVKL
RMHR
RIGL
OLLL
f

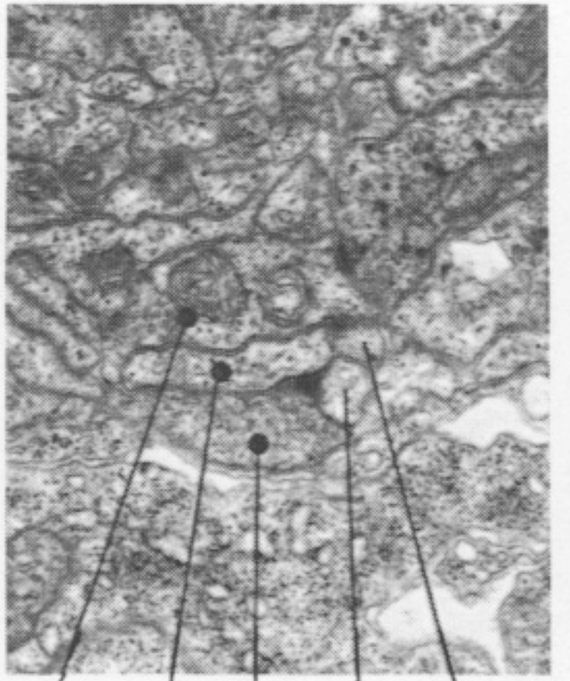

AIBL
RIGR
RIBR
DVC
g

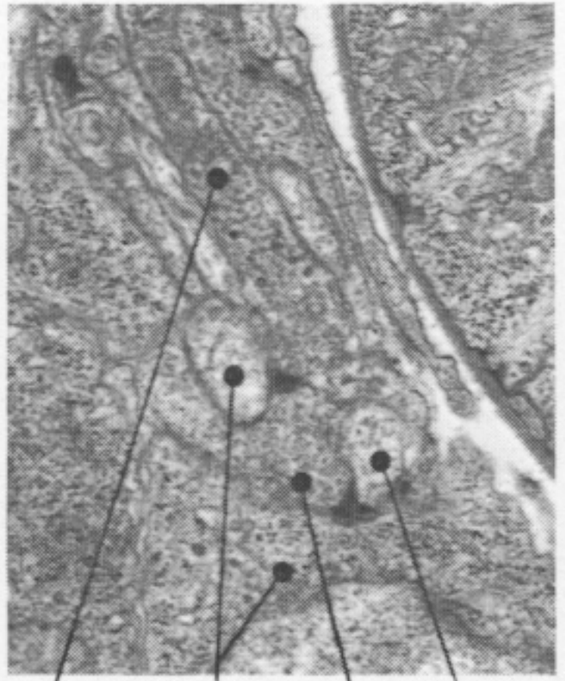

BAGR
RIR
URYVL
RIGL
AIBR
DVC
h

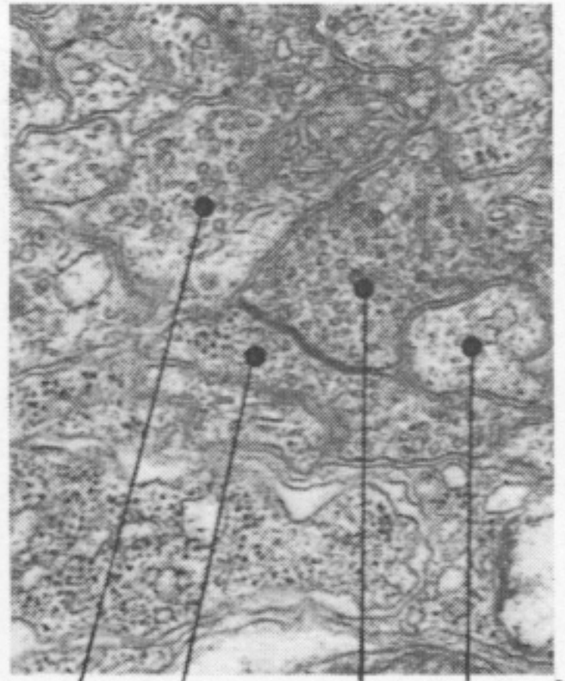

RIGL
i

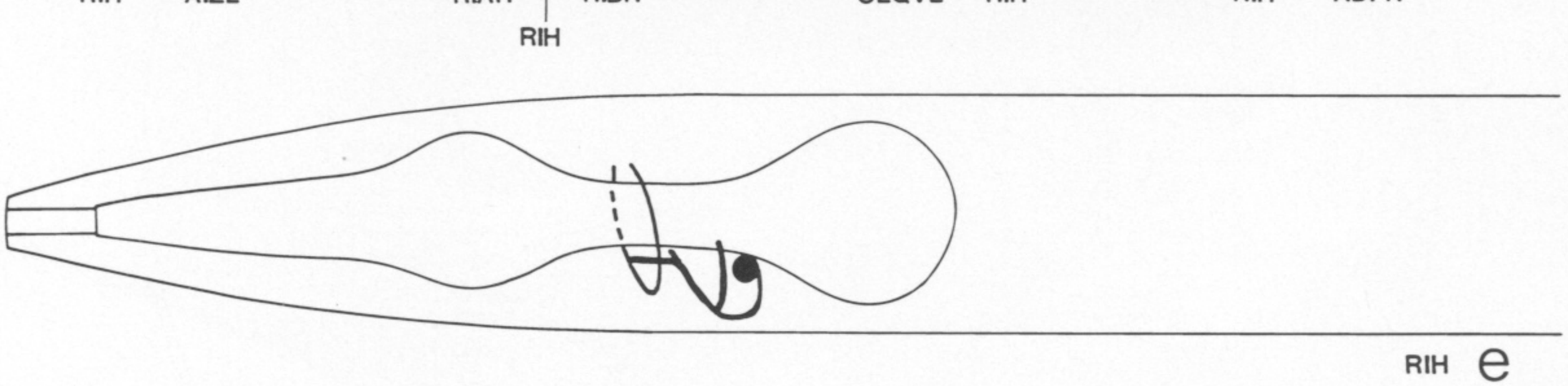
RIG


RIAL
RIH
AIZL
RIGL
a

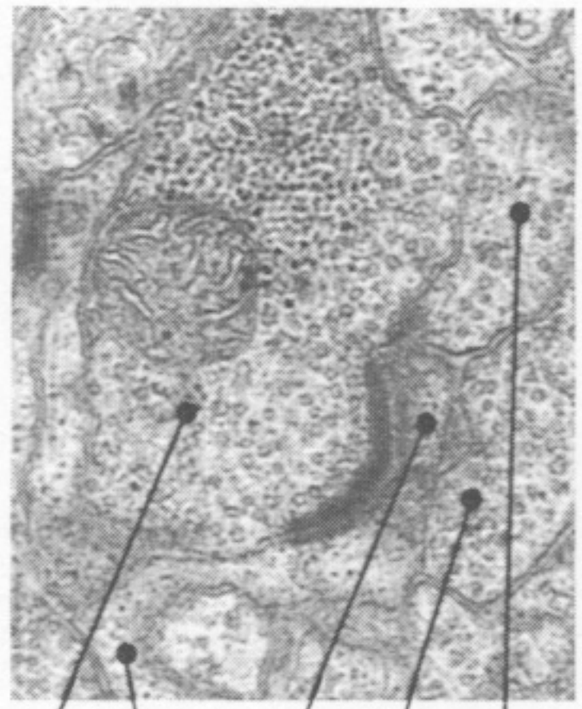

AIZR
RIAR
RIBR
AIYR
b

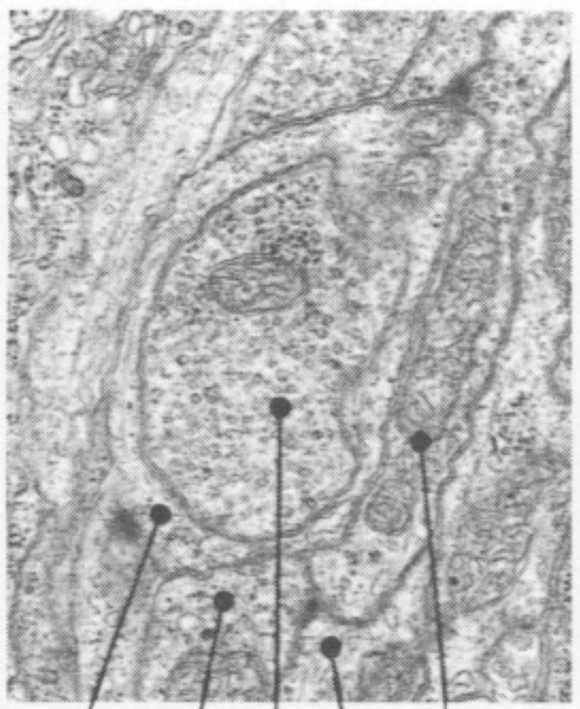

IL2L
OLQVL
RIH
RIPL
C

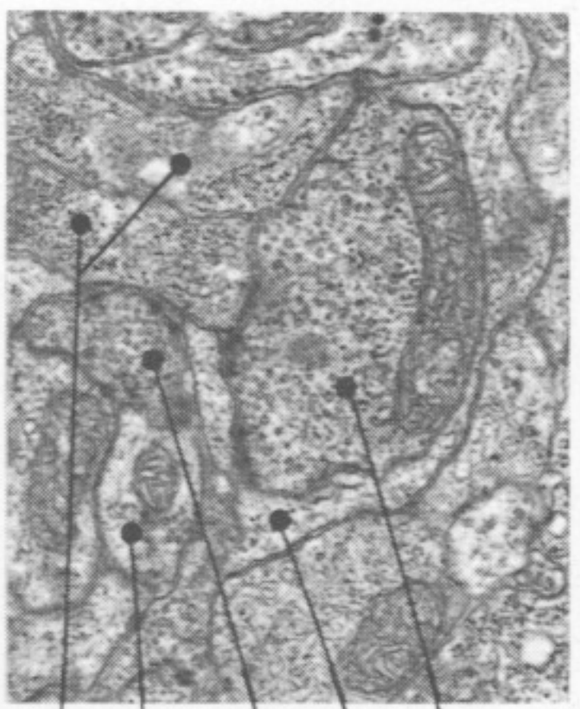

AIZR
RIH
ADFR
RIAR
d


RIH
RIH
e

RIH



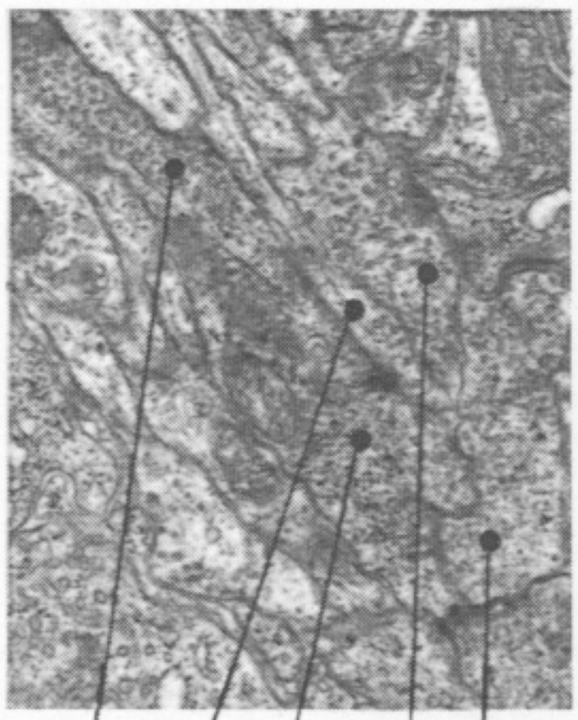


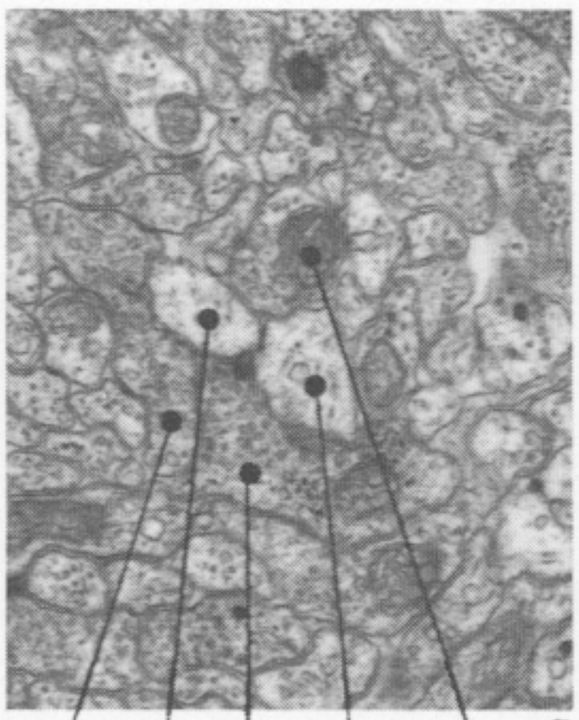


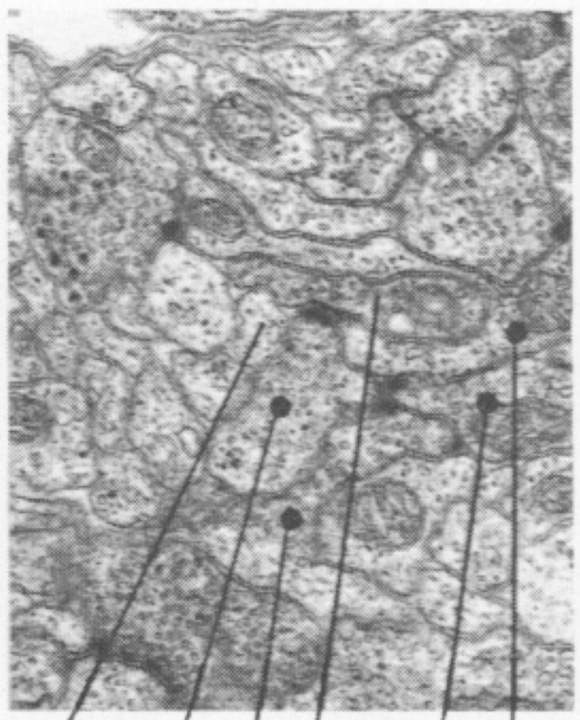
MUSCLE

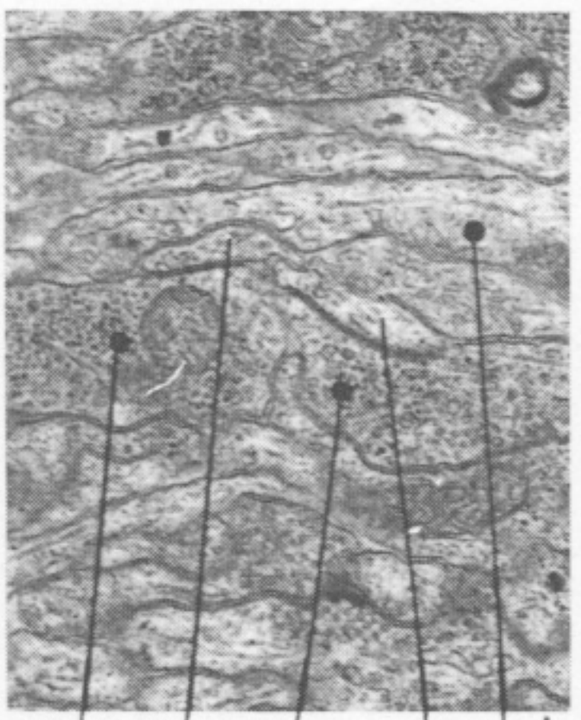
RIMR

MUSCLE ARMS

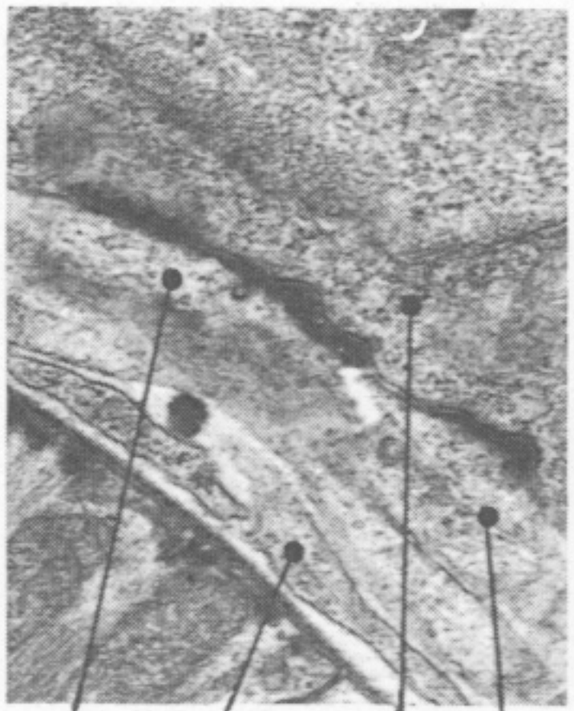


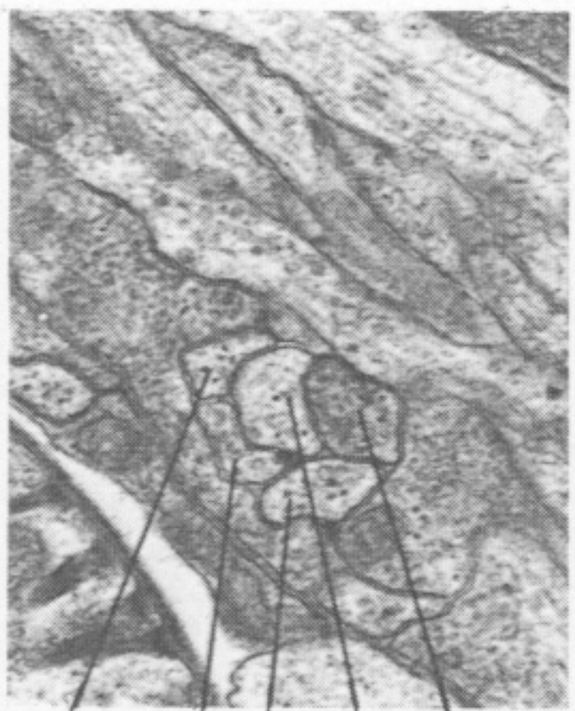


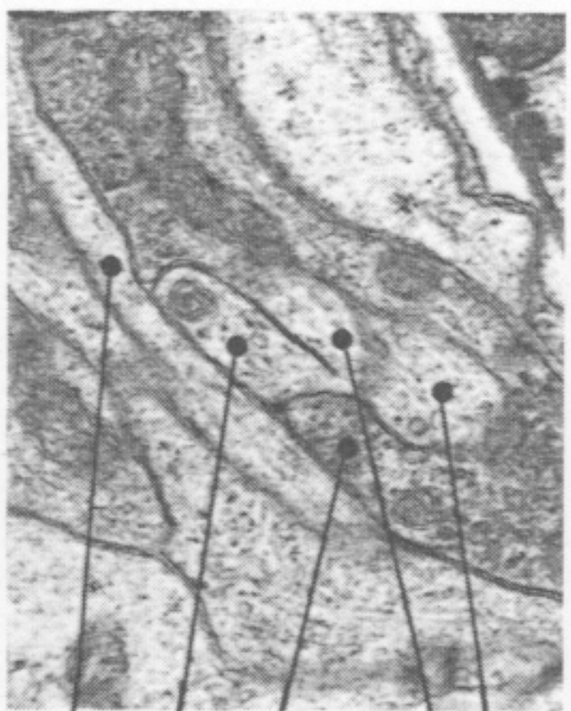


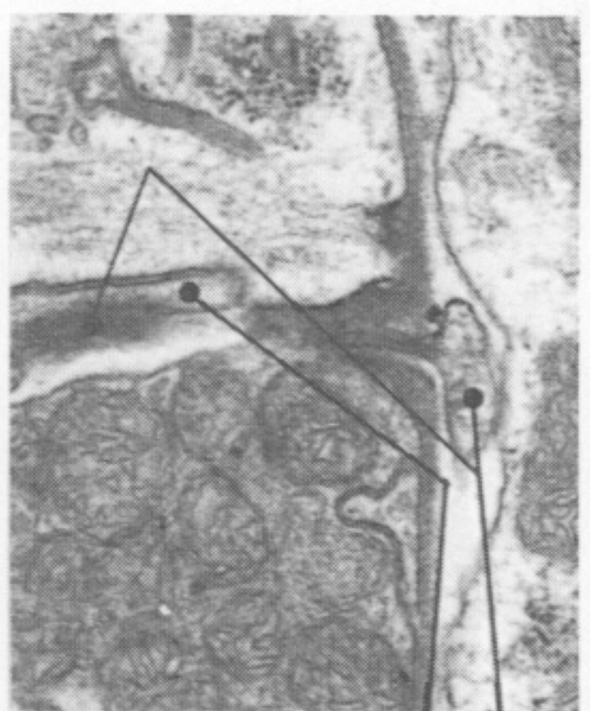


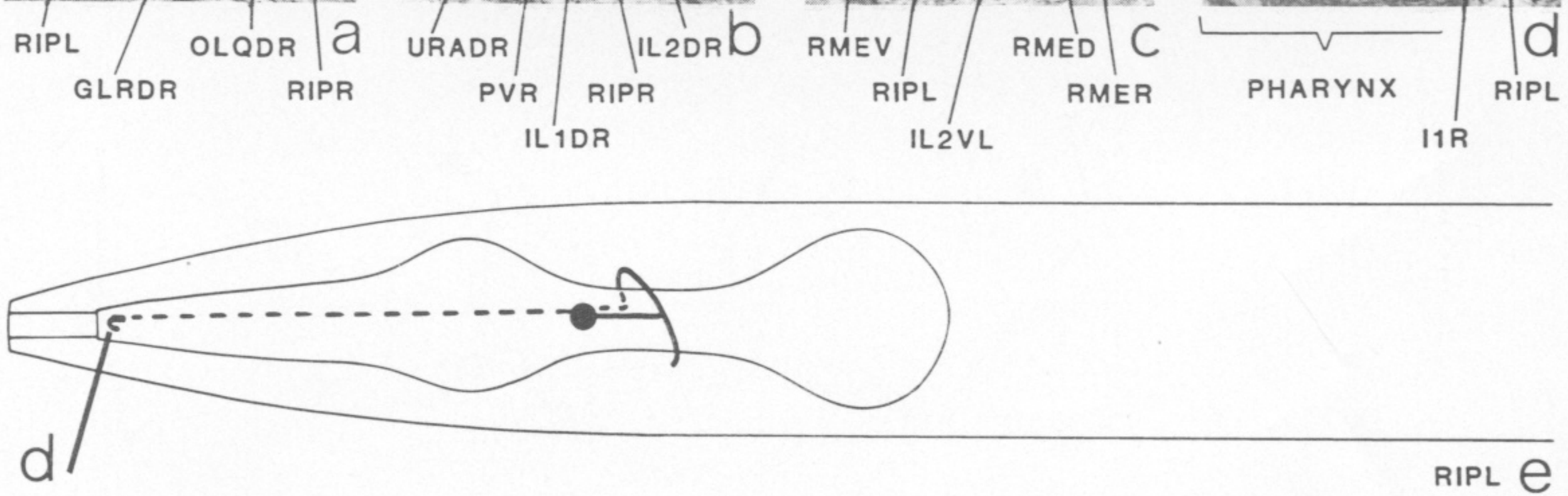
RIM


RIPL
GLRDR
OLQDR
RIPR
a

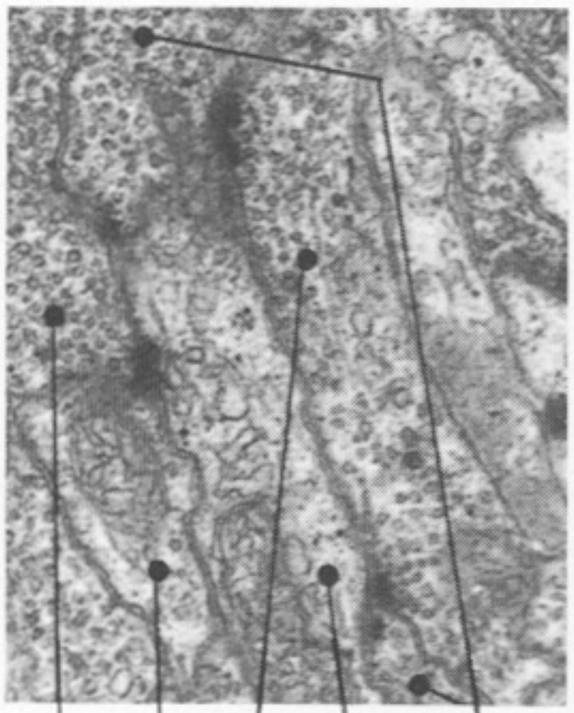

URADR
PVR
RIPR
IL2DR
b

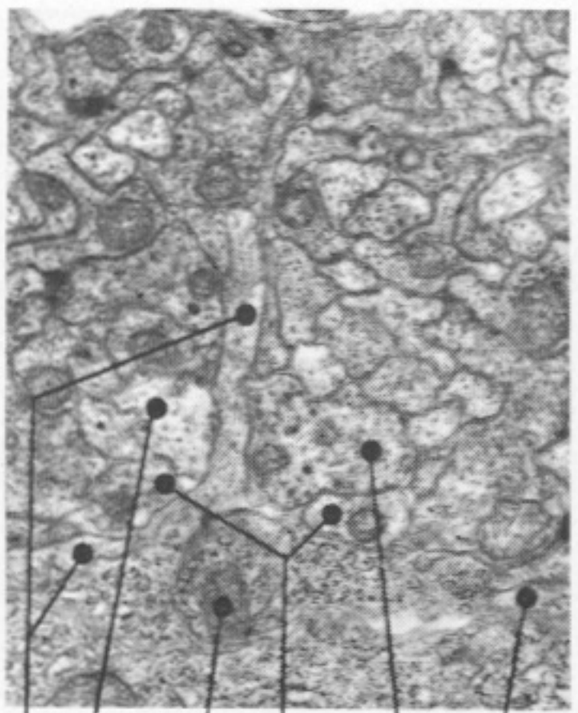

RMEV
RIPL
RMED
RMER
c

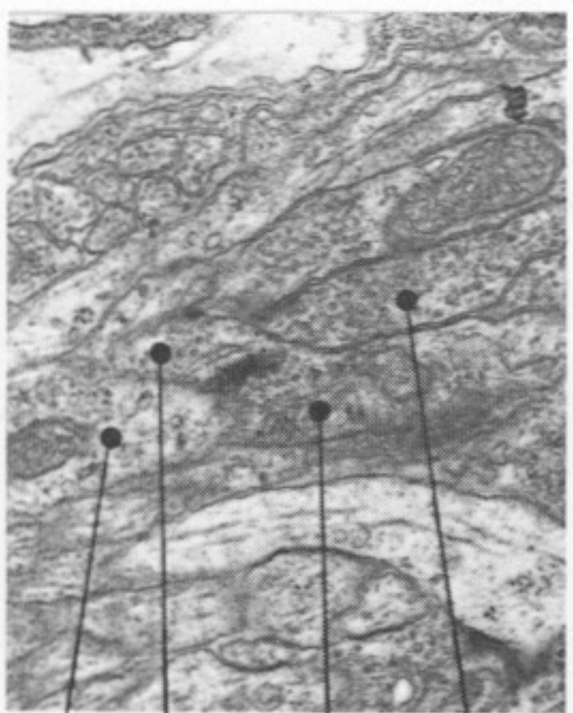

PHARYNX
RIPL
d

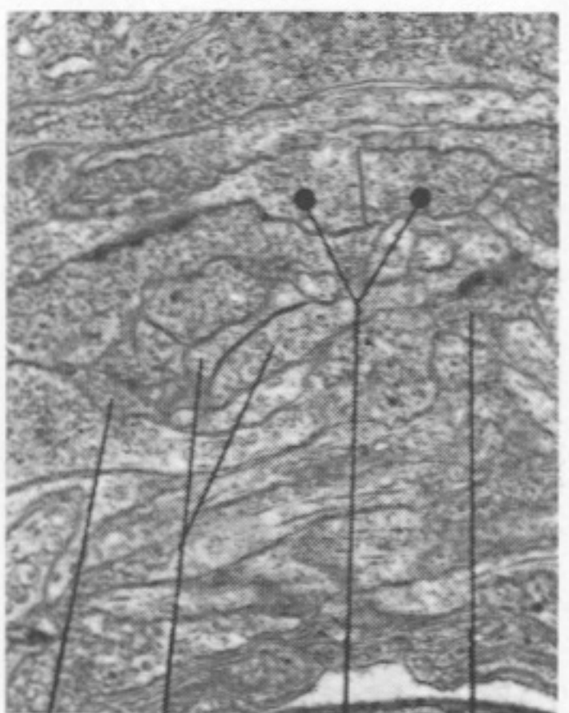

IL1DR
IL2VL
I1R
d
RIPL
e

RIP


AUAL
RIBL
RIR
RIAL
URXL
a

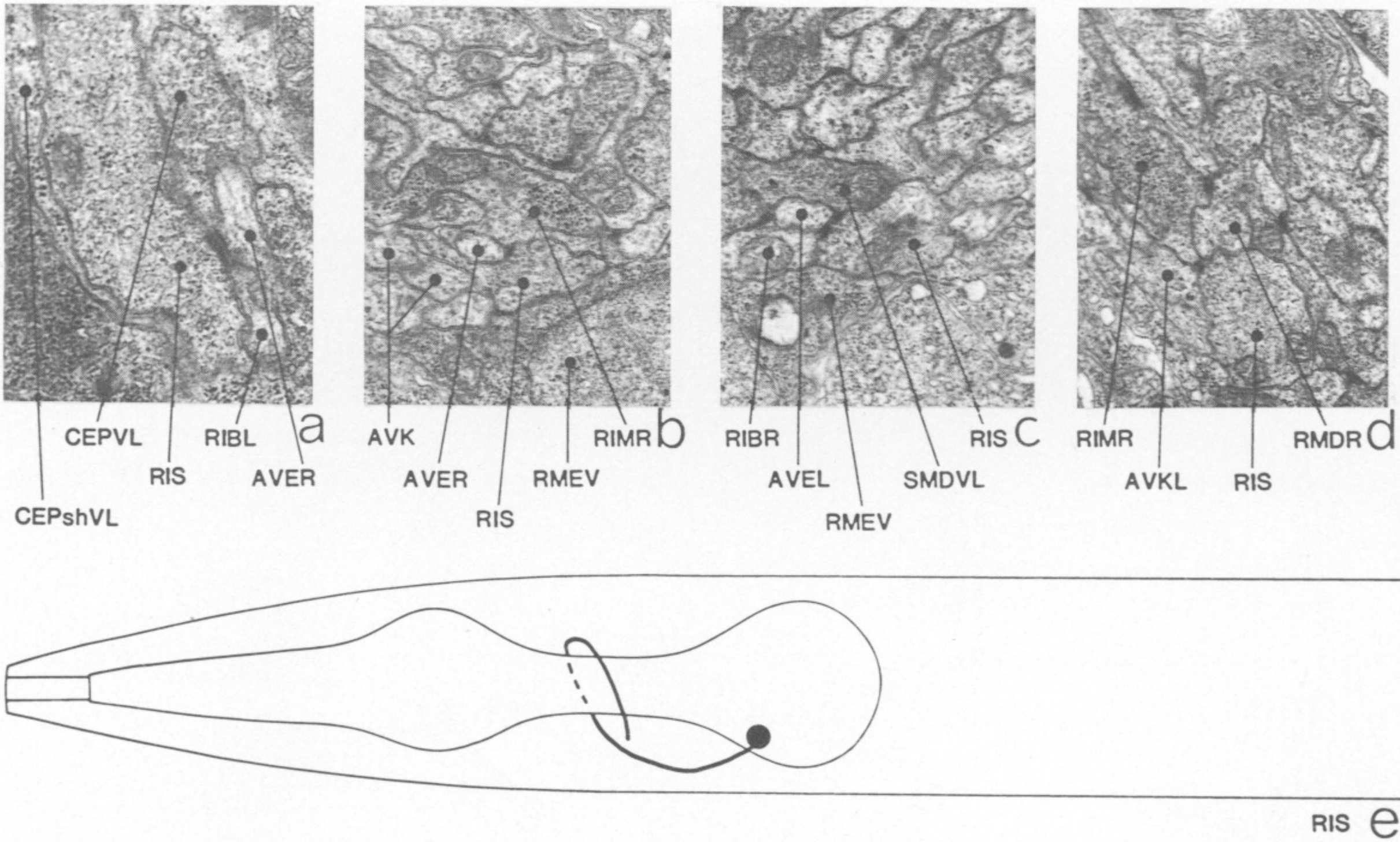

RIR
DVB
RMEV
RIG
DVB
RIR
b


DVA
AIZL
RIR
AUAL
C


RIR
AIZ
RIB
RIR
d

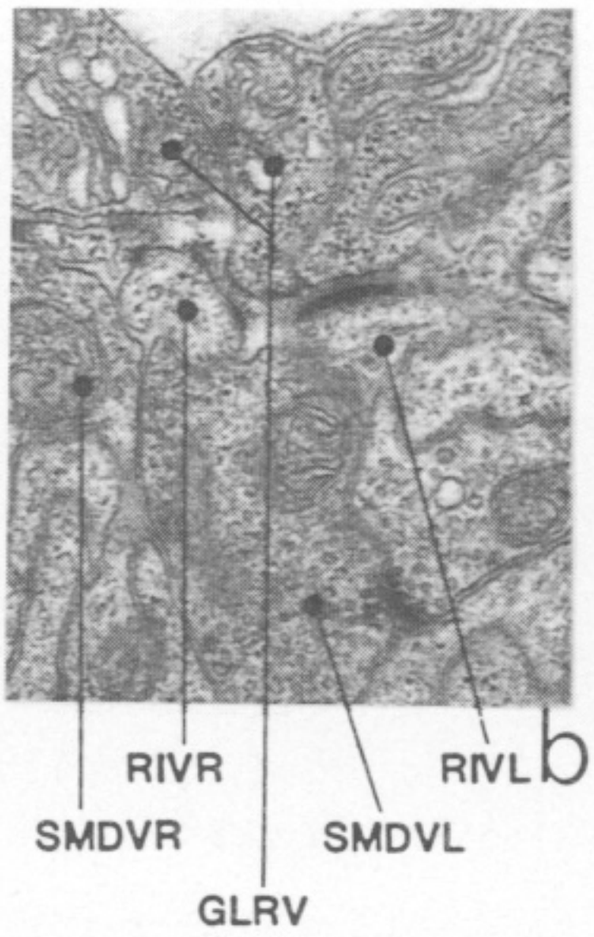
RIR
e

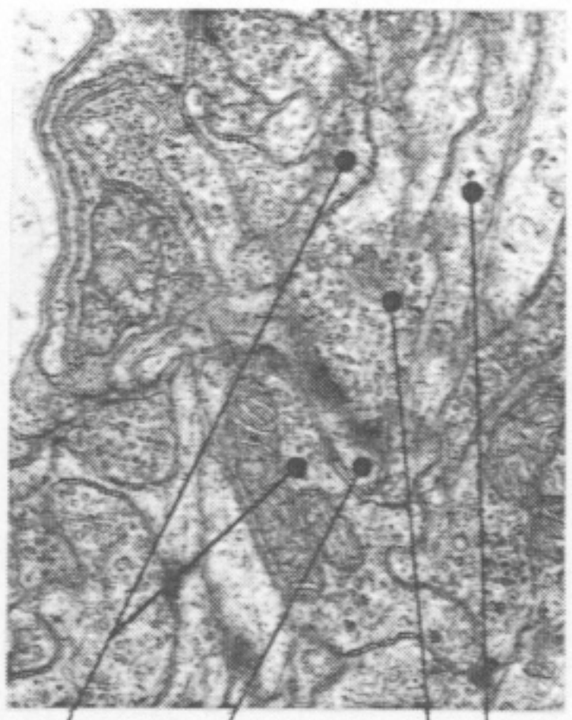
RIR

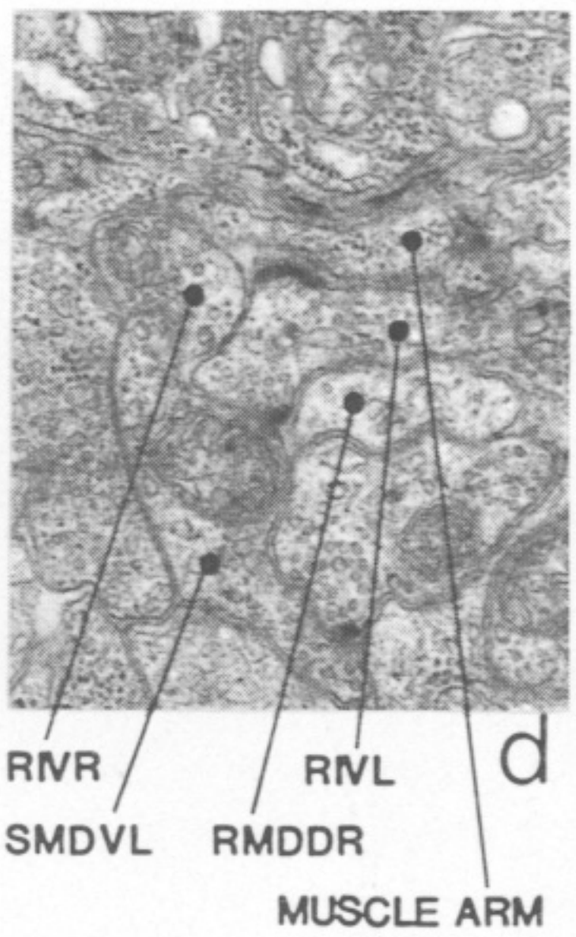

CEPVL
RIS
RIBL
AVER
a
AVK
AVER
RMEV
RIMR
b
RIBR
AVEL
SMDVL
RIS
c
RIMR
AVKL
RIS
RMDR
d
CEPshVL
RIS
RMEV
RIS
e

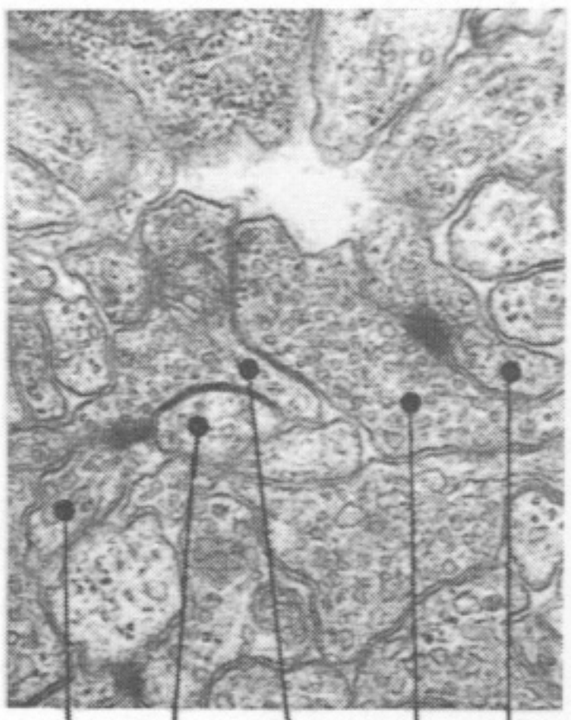
RIS

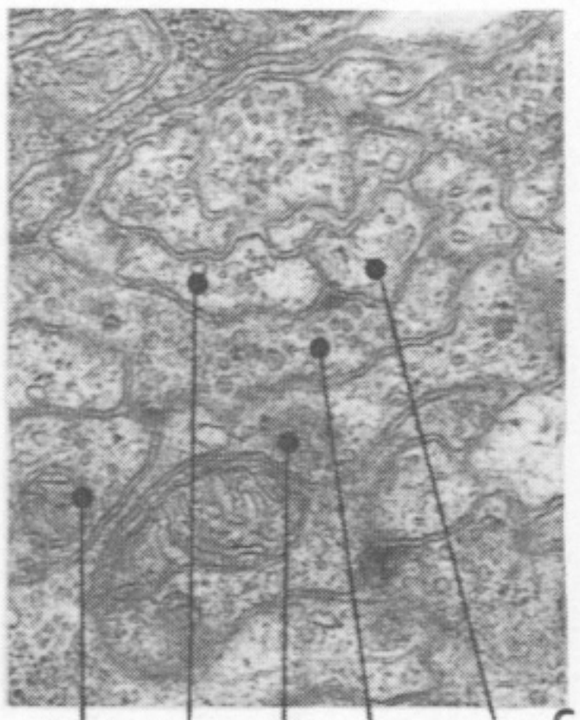

SAADL
RIVR
SDQR
RIH
a

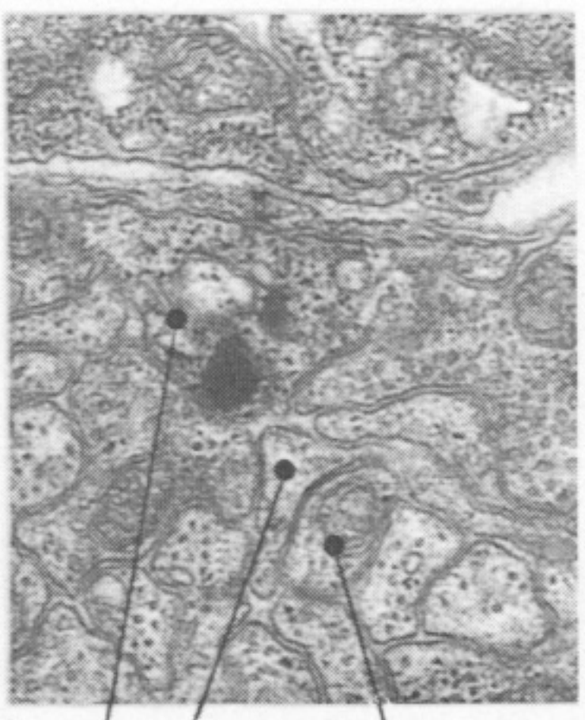

RIVR
RIVL
b
SMDVR
SMDVL
GLRV

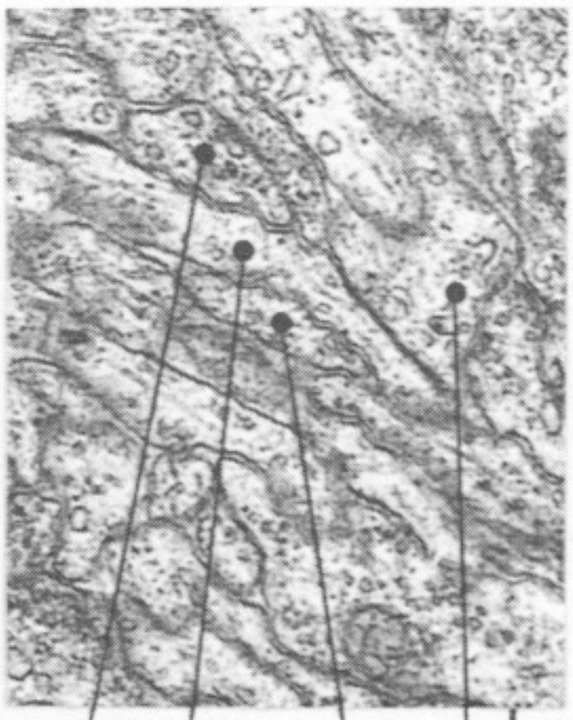

RMDL
RIVL
c
MUSCLE ARM
SMDDR

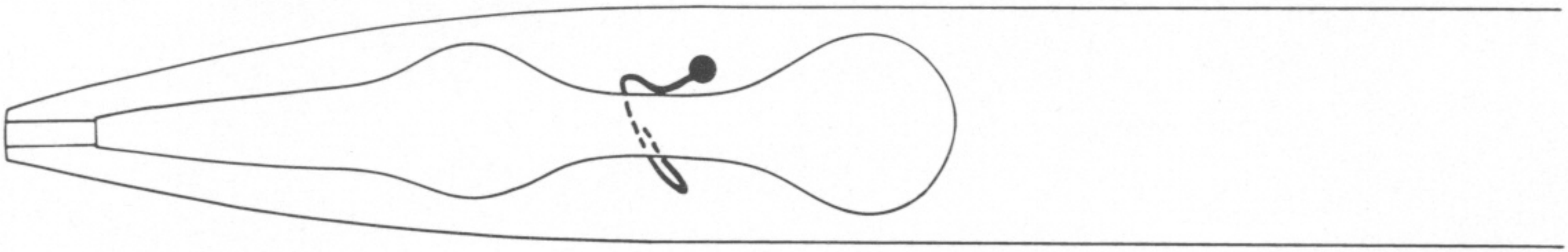

RIVR
RIVL
d
SMDVL
RMDDR
MUSCLE ARM


RIAL
RIVL
e
SDQR
SAADR
RIVR

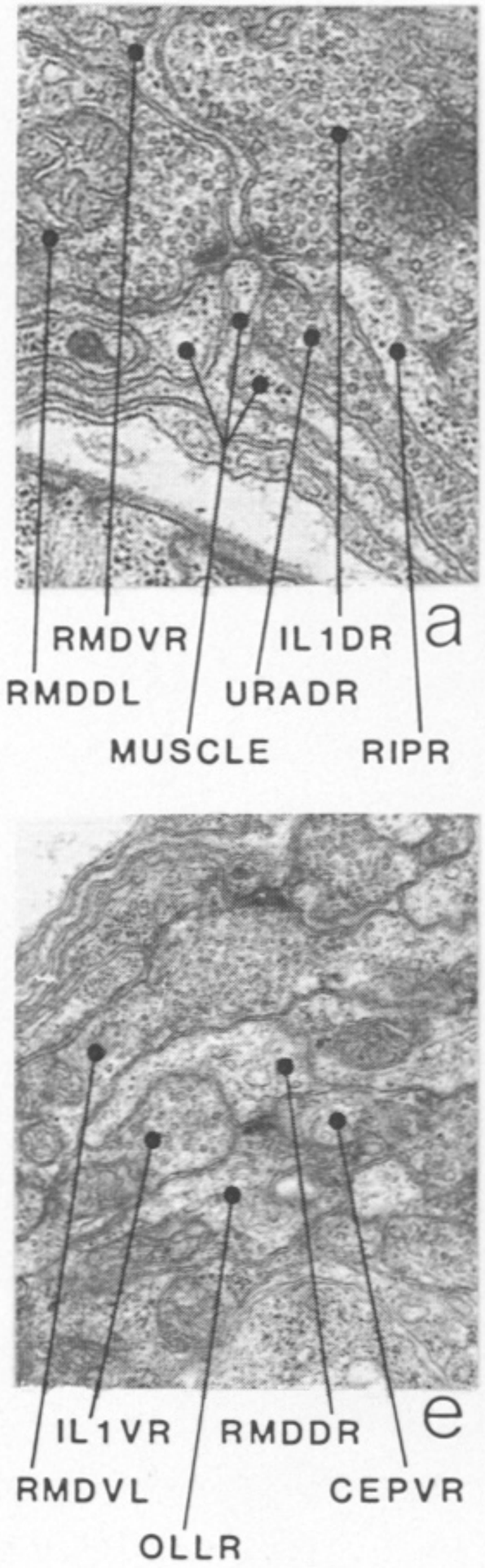

RIAR
SIAVR
f
RMDVL
RIVL
SMDDR

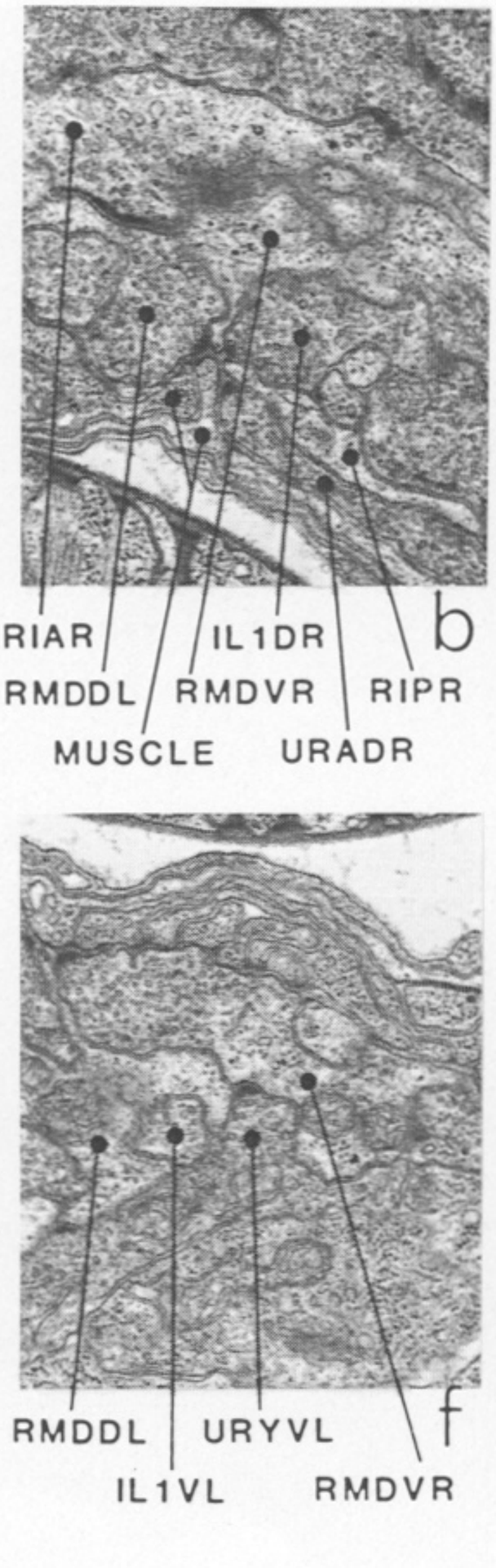

RIVL
SMDVL
g
EXCRETORY GLAND

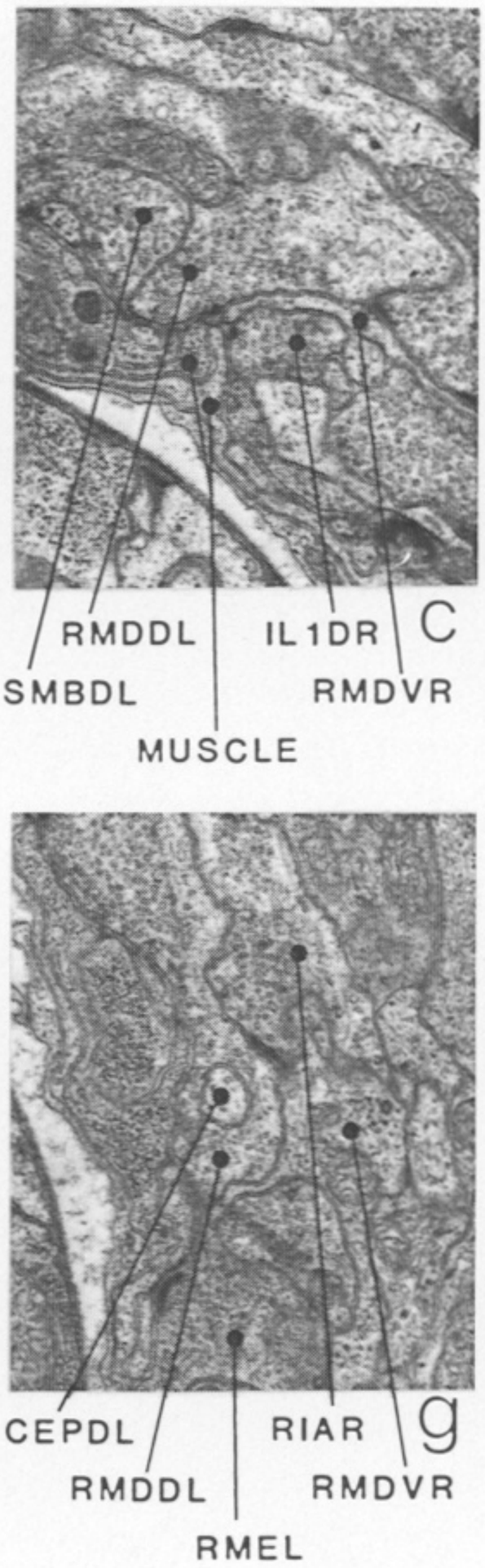

SMDVR
AIBL
h
RIVL
SAAVR

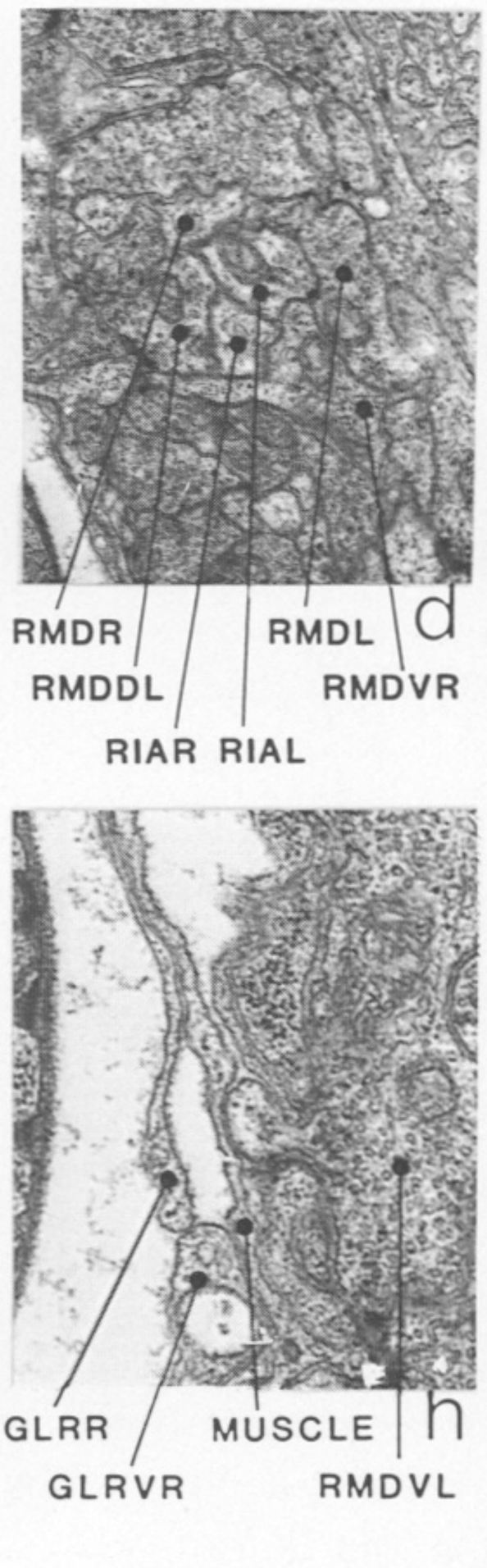

RIVL
j

RIV


RMDVR
IL1DR
a
RMDDL
URADR
MUSCLE
RIPR


RIAR
IL1DR
b
RMDDL
RMDVR
RIPR
MUSCLE
URADR


RMDDL
IL1DR
c
SMBDL
RMDVR
MUSCLE

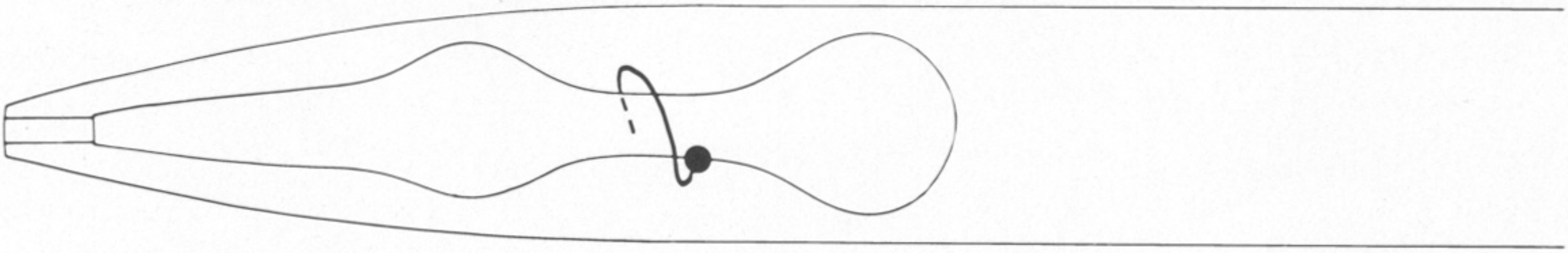

RMDR
RMDL
d
RMDDL
RMDVR
RIAR
RIAL

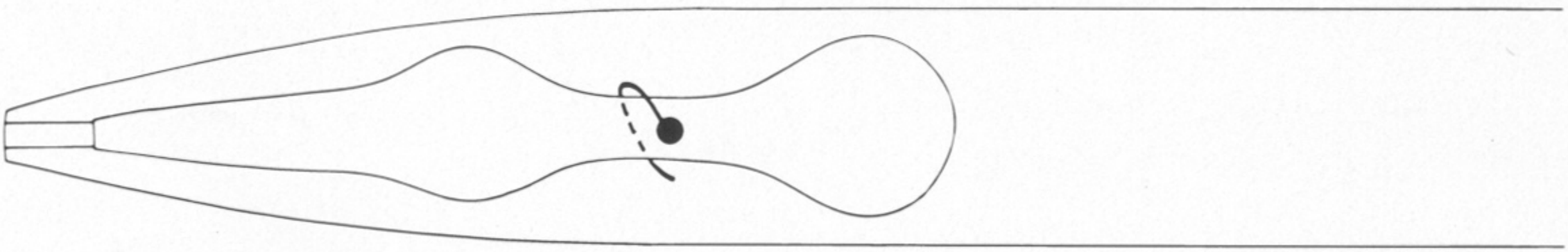
IL1VR
RMDDR
e
RMDVL
CEPVR
OLLR

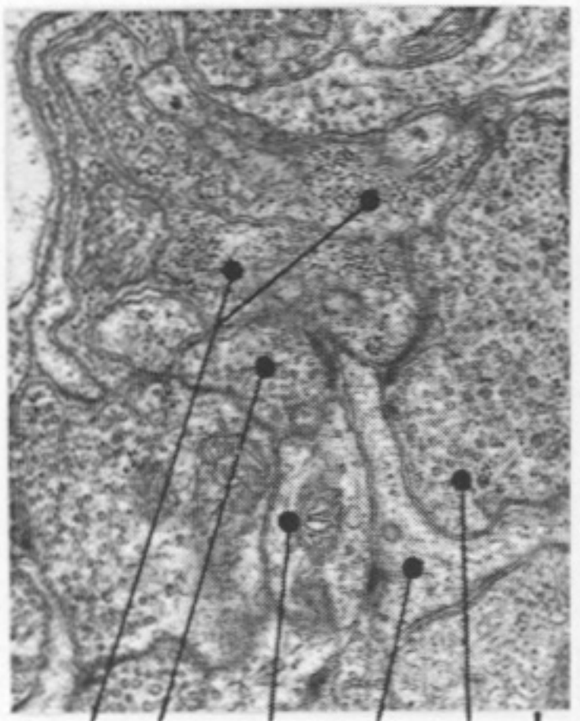
RMDDL
URYVL
f
IL1VL
RMDVR

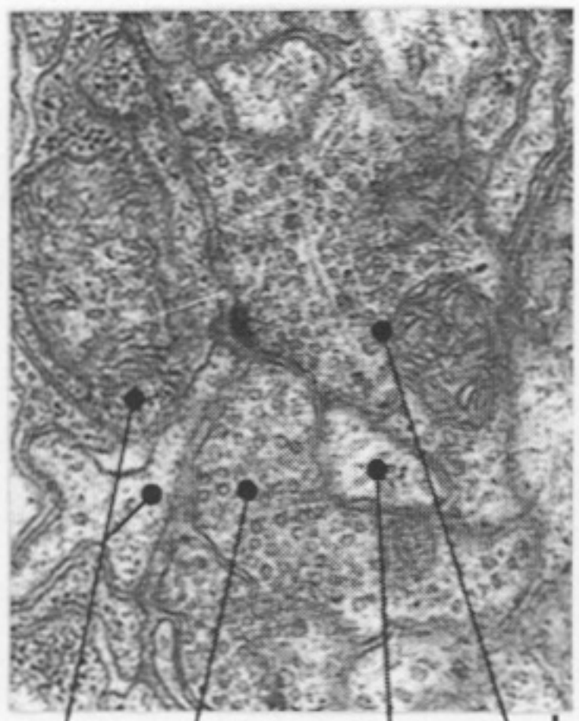
CEPDL
RIAR
g
RMDDL
RMDVR
RMEL

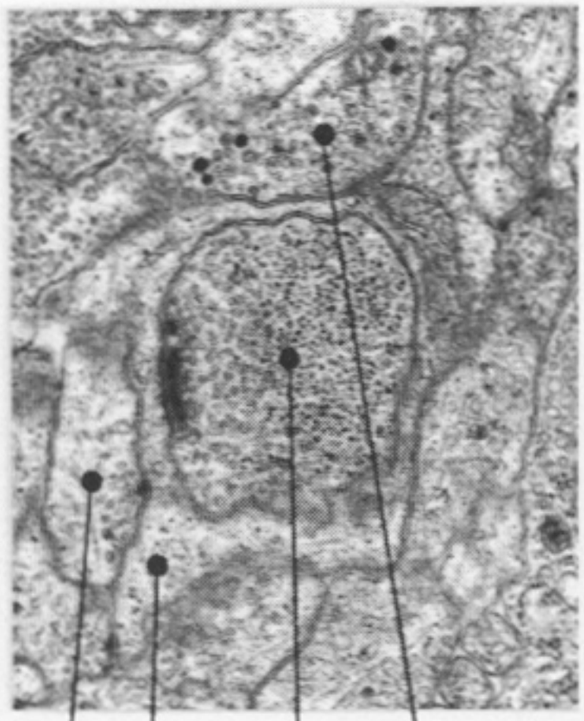
GLRR
MUSCLE
h
GLRVR
RMDVL

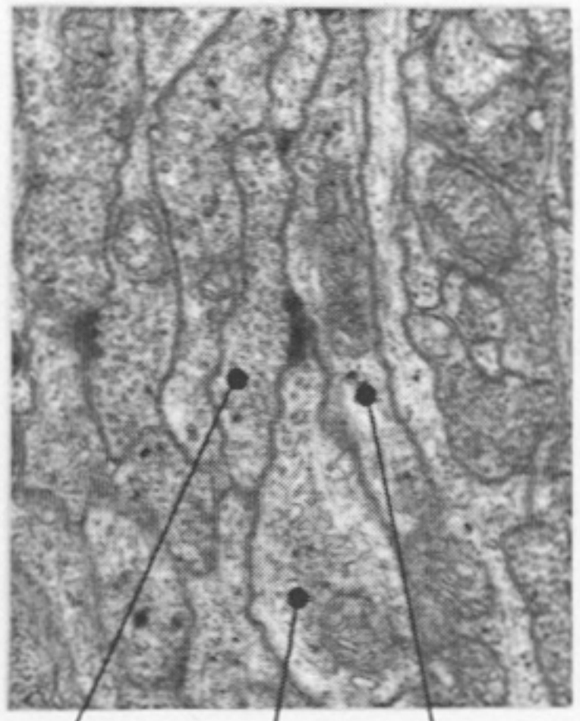

RMDDL
i

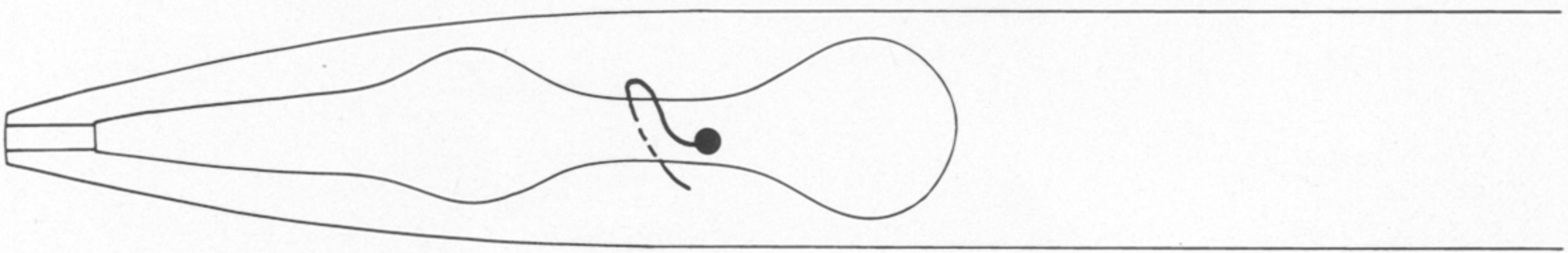

RMDVL
j


RMDL
MUSCLE
RMDR
RIML
RIAL
k

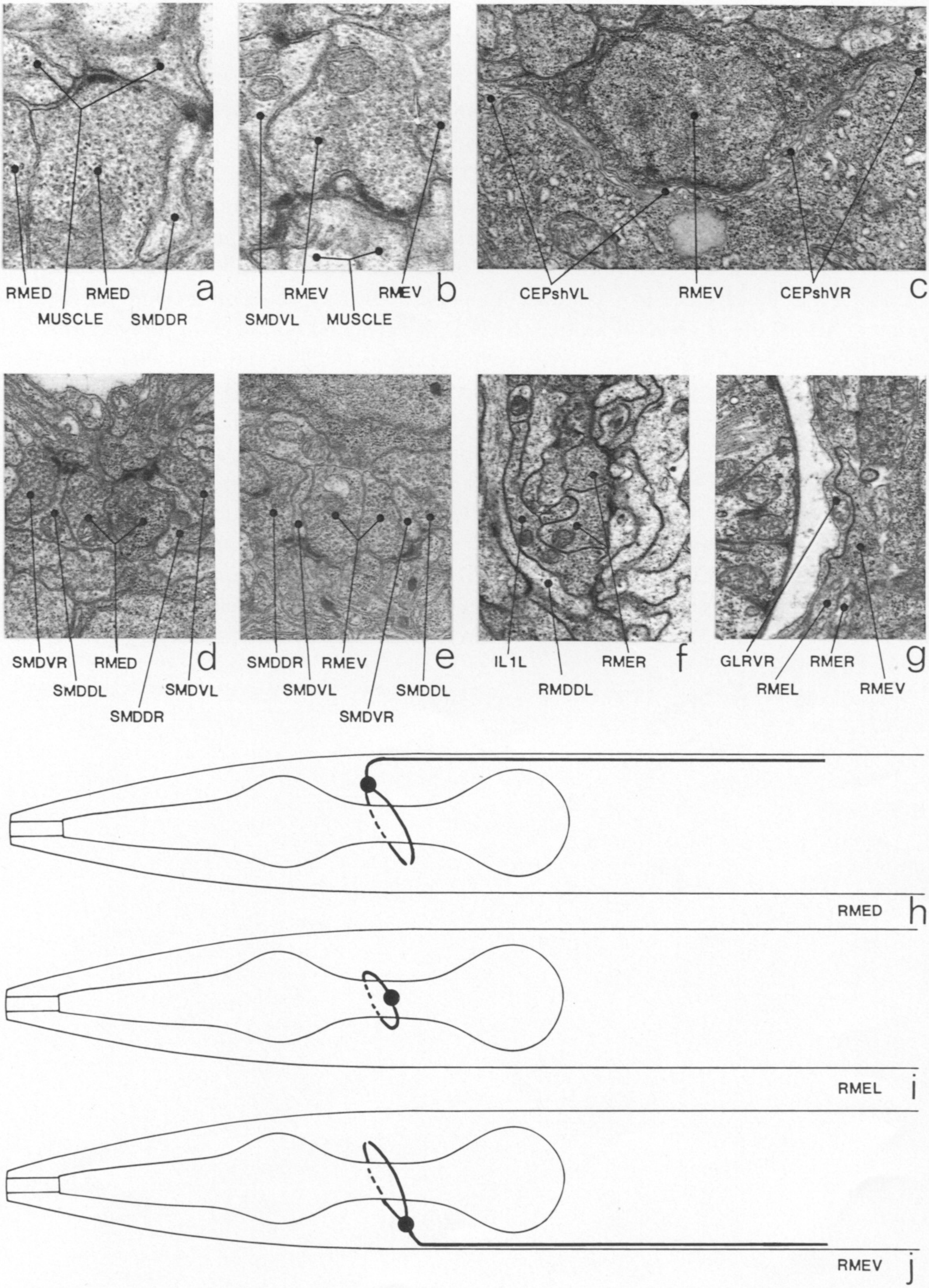

RMHL
RMDR
MUSCLE
RMDL
l

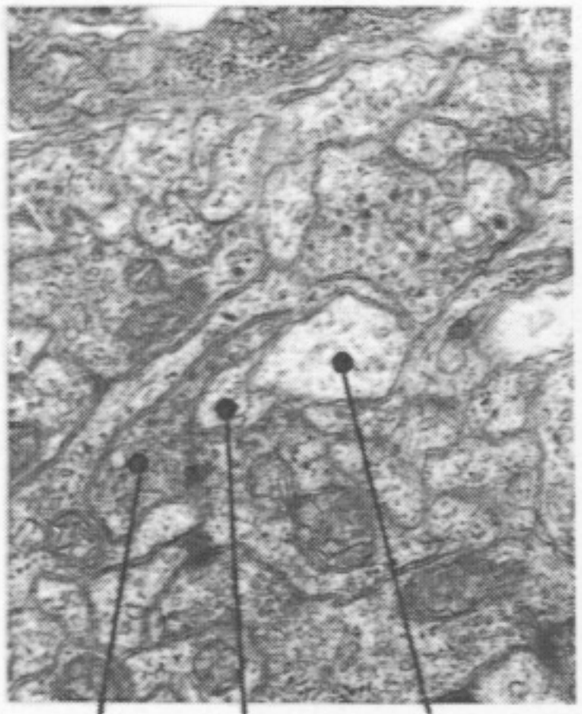

RIAL
RMGR
m
RMDR
RIML

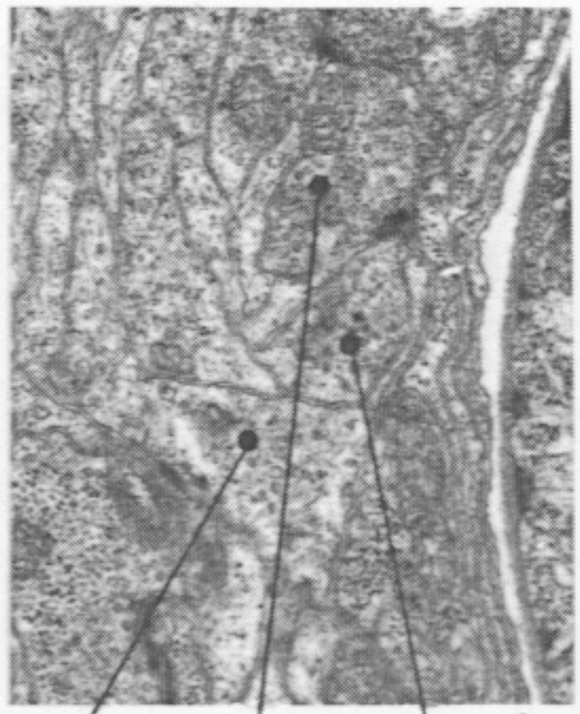

RMDR
RIAR
n
RIAL

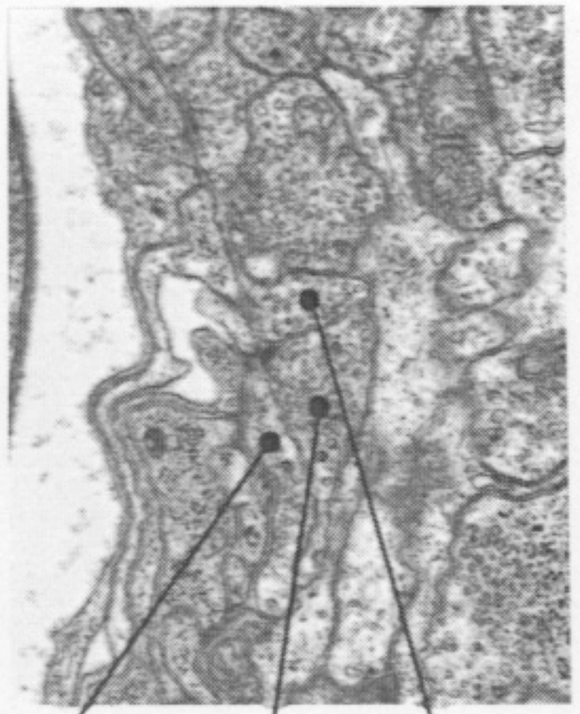

RMDL
O

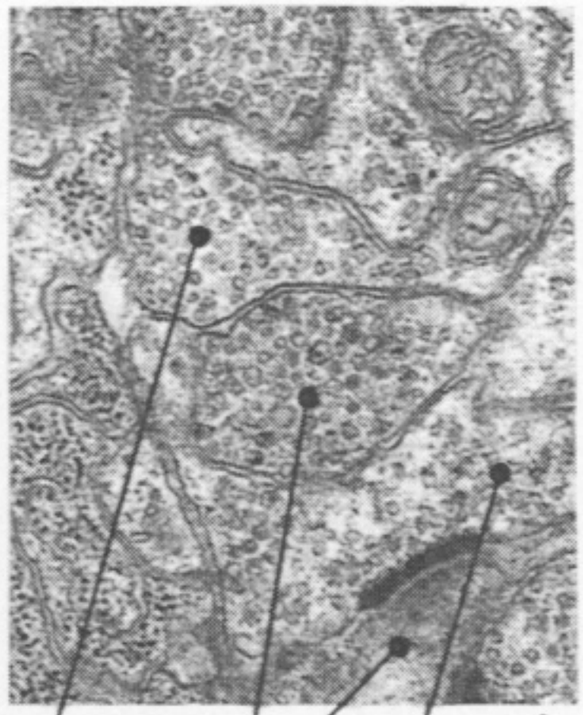
RMD


RMED
RMED
a
RMEV
RMEV
b
CEPshVL
RMEV
CEPshVR
c
MUSCLE
SMDDR
SMDVL
MUSCLE
SMDVR
RMED
SMDDL
SMDVL
SMDDR
d
SMDDR
RMEV
SMDVL
SMDDL
SMDVR
e
IL1L
RMER
RMDDL
f
GLRVR
RMER
RMEL
RMEV
g
RMED
h
RMEL
i
RMEV
j

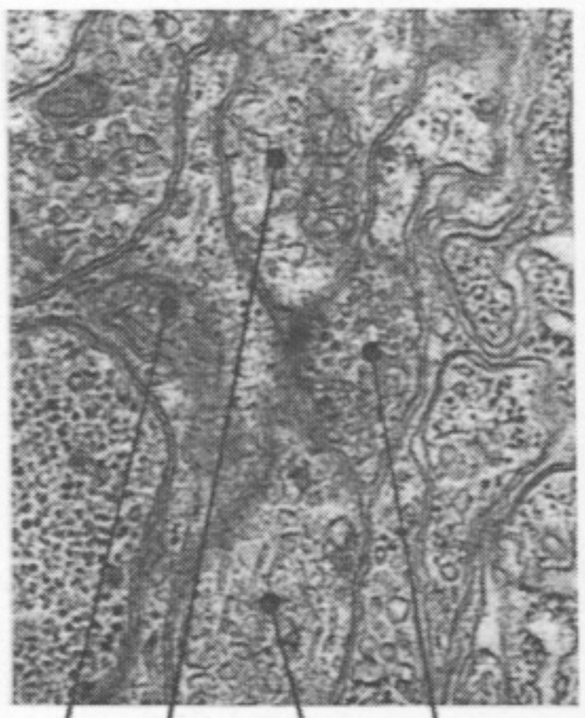


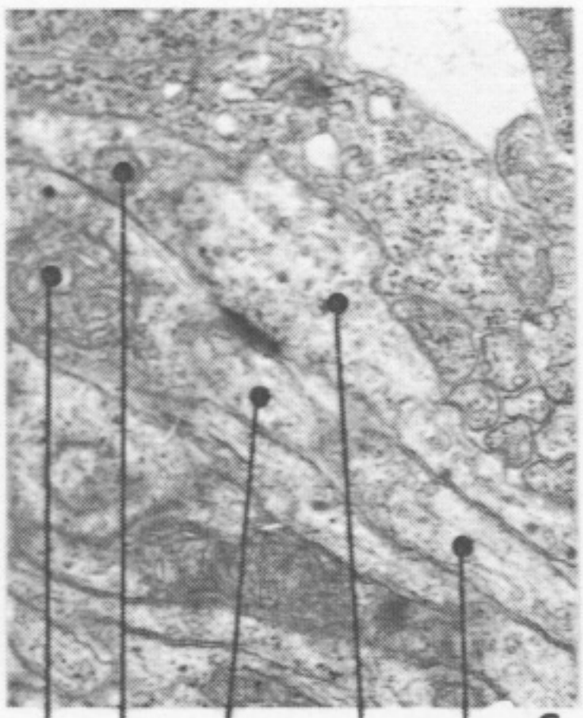


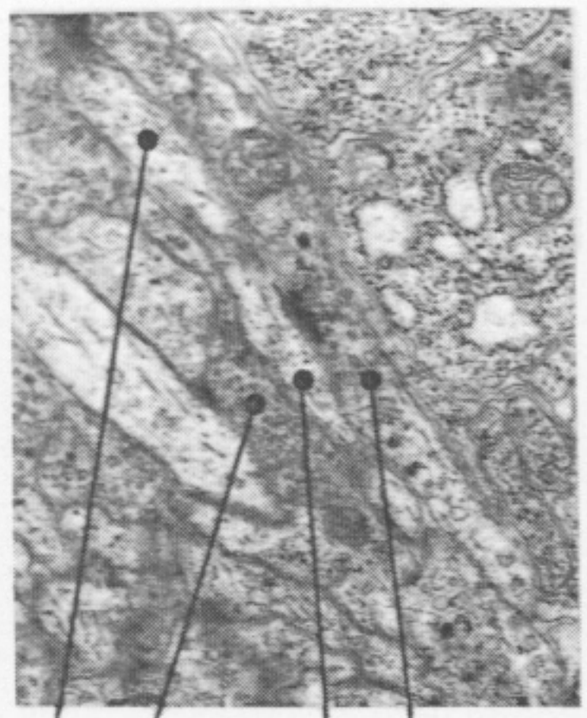


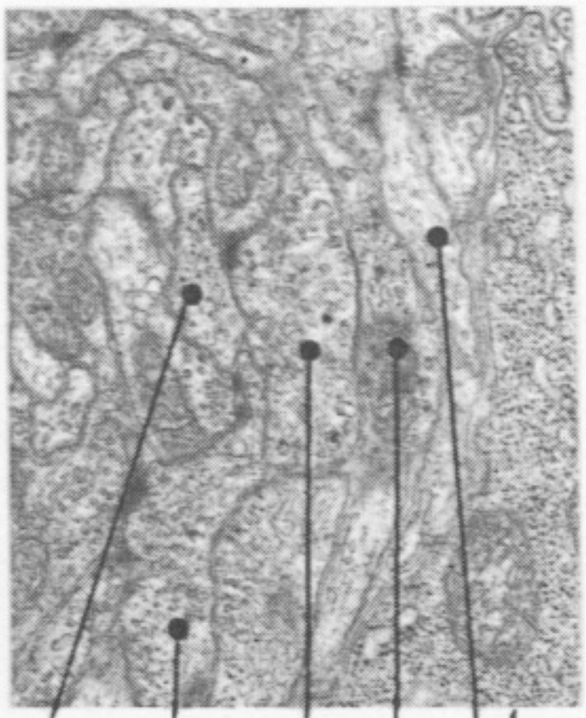


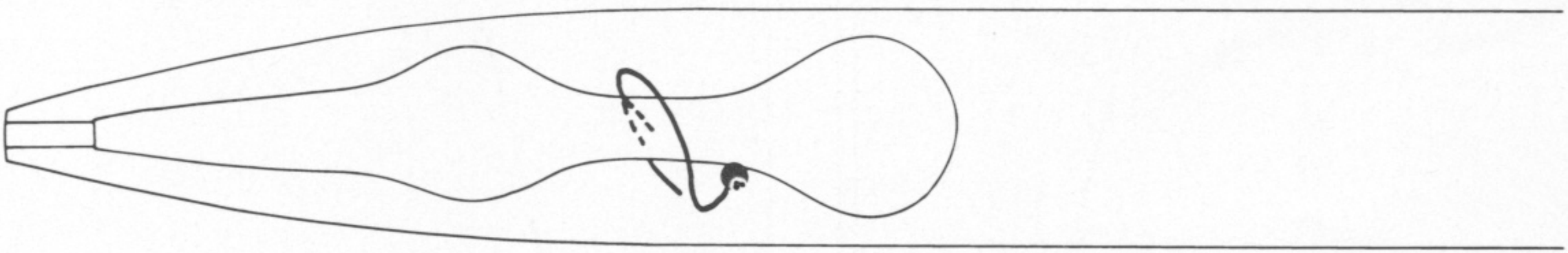
MUSCLE ARMS



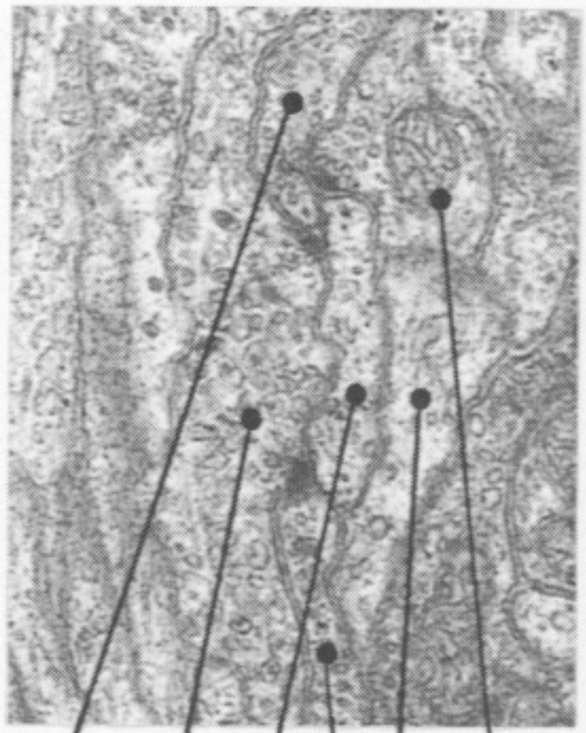


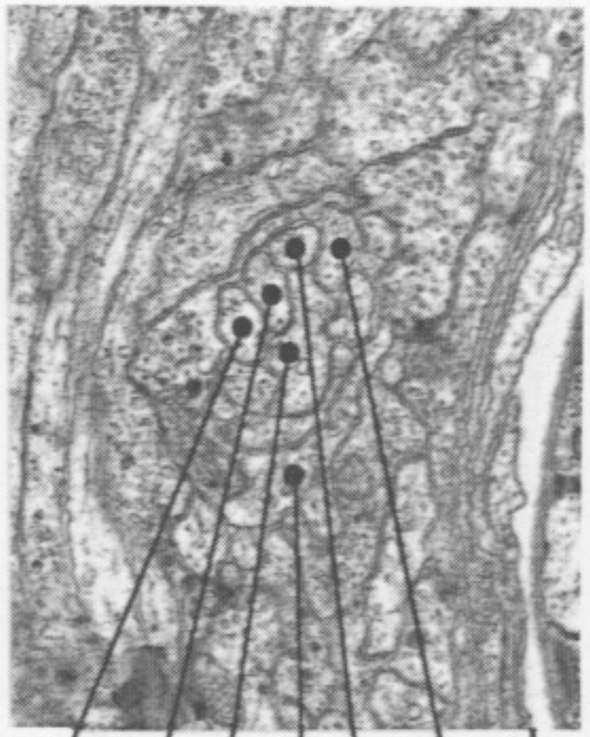


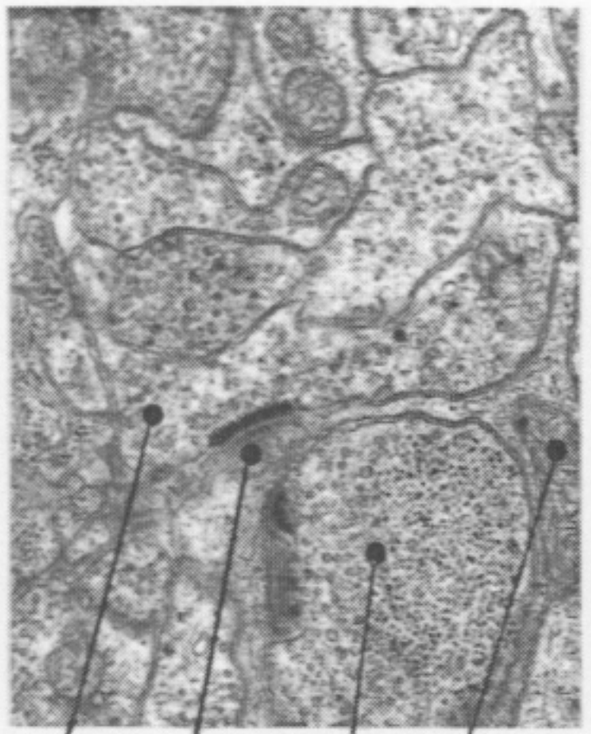


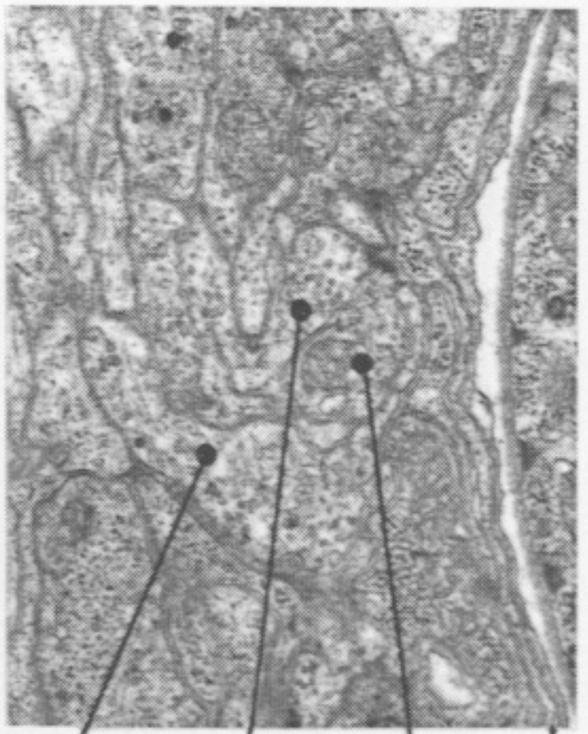


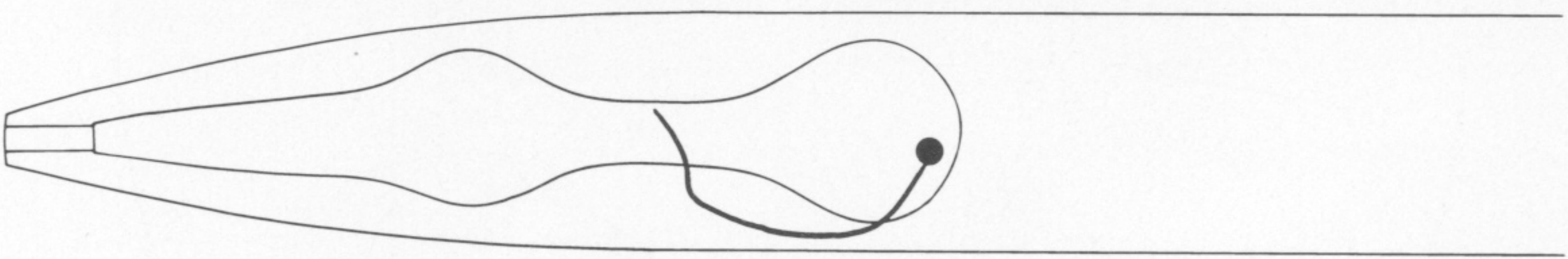
RMF


RMDR
RMGL
RIAL
RIAR
a
RMDVL
RMDR

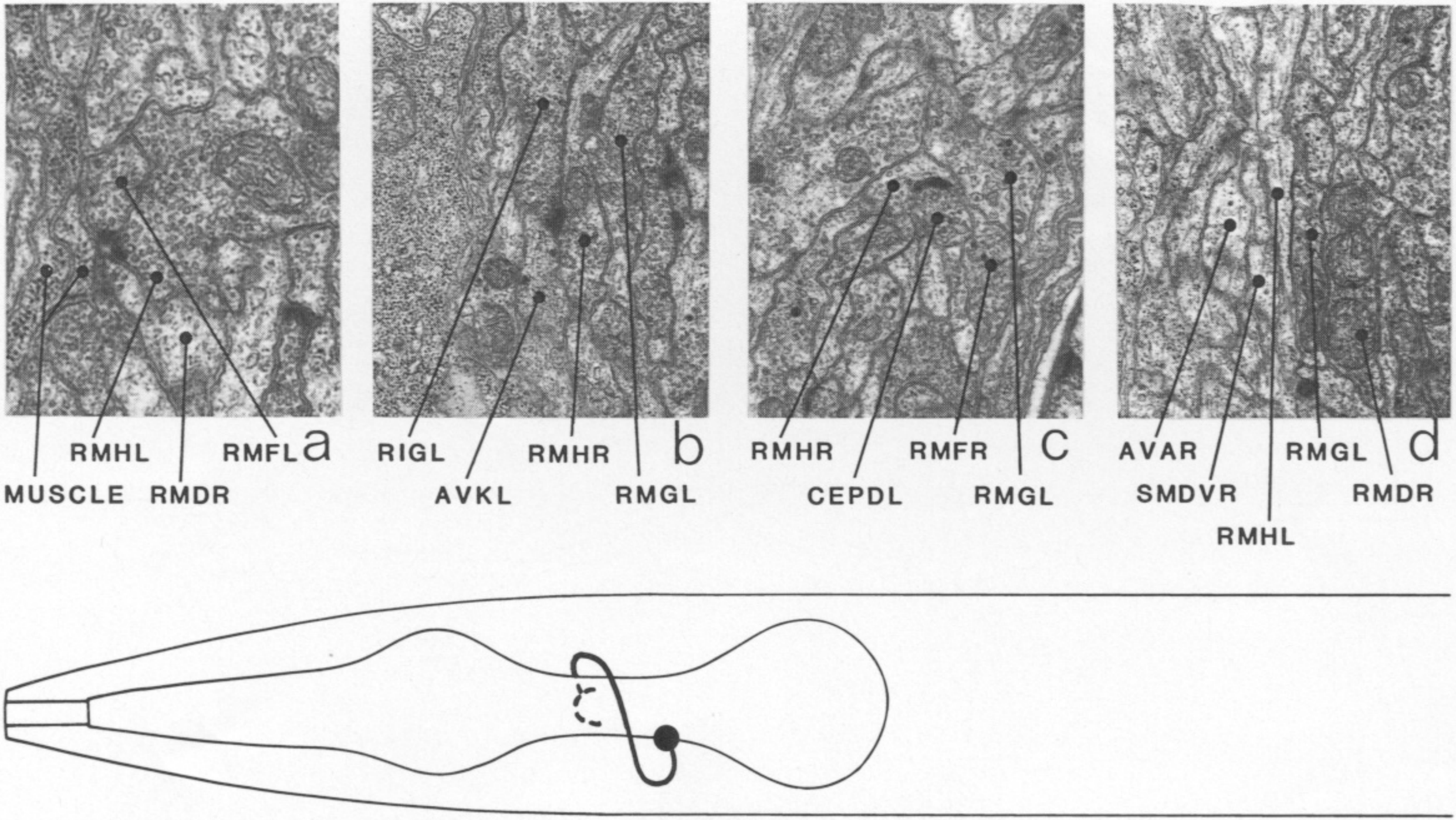

ALNL
SMDDR
SIBDR
SIADR
b
RMDDR
RMGL


RMGR
MUSCLE
RIML
RMDR
c

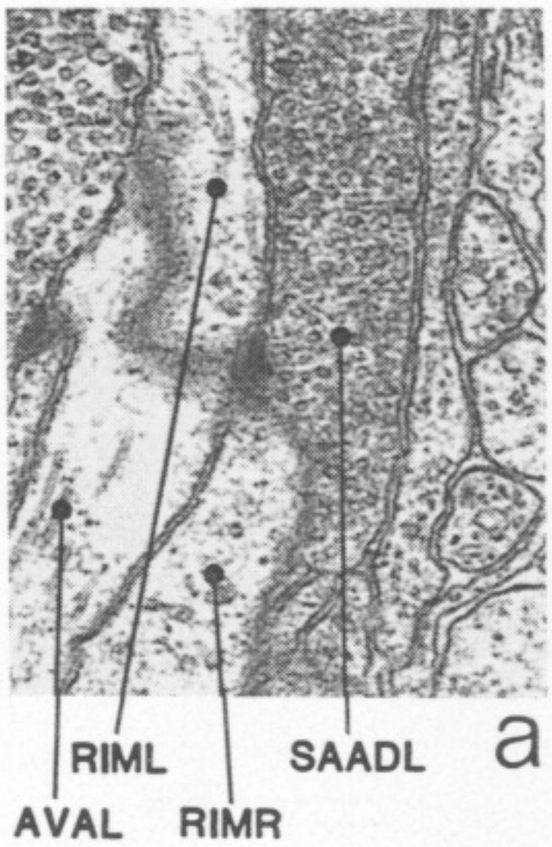

RMGL
RMHR
RMFR
d

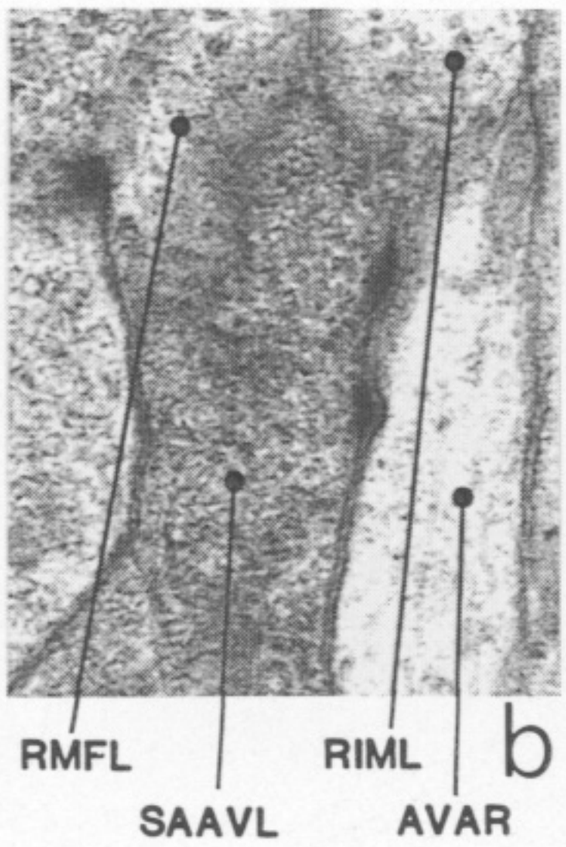

RMGL
e

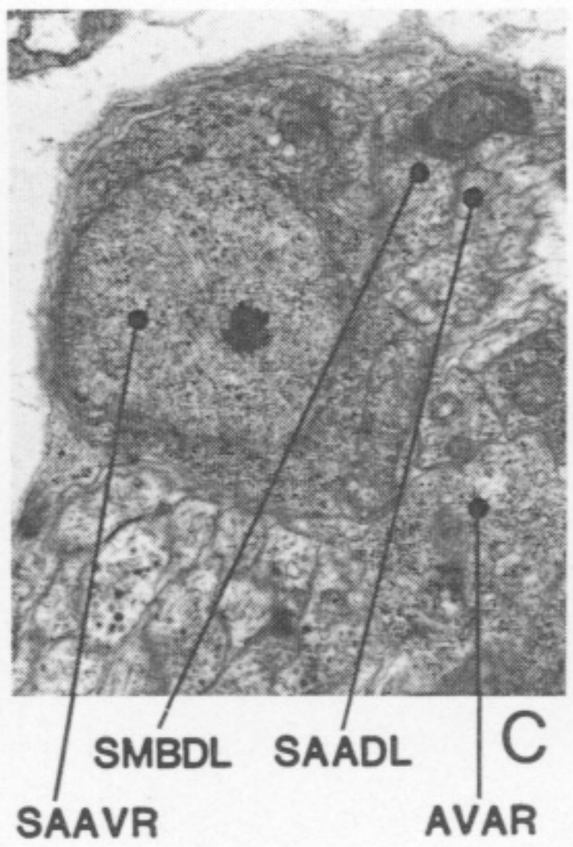
RMG

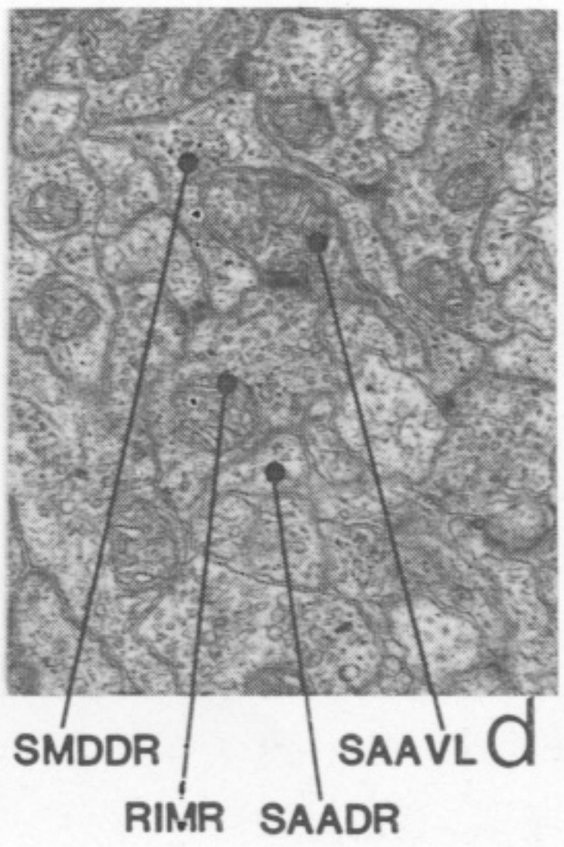

RMHL
RMFL
a
MUSCLE
RMDR
RIGL
RMHR
b
AVKL
RMGL
RMHR
RMFR
c
CEPDL
RMGL
AVAR
RMGL
d
SMDVR
RMDR
RMHL
RMHL
e

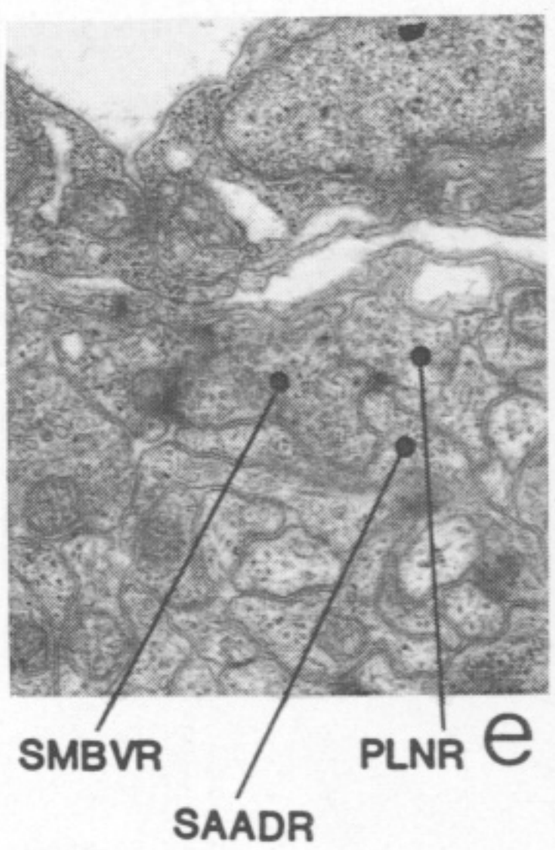
RMH

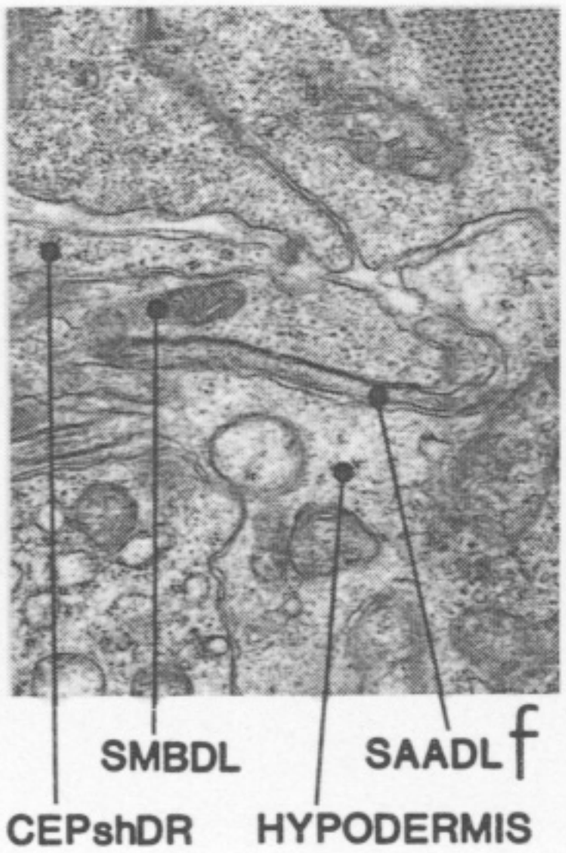

RIML
SAADL
AVAL
RIMR
a

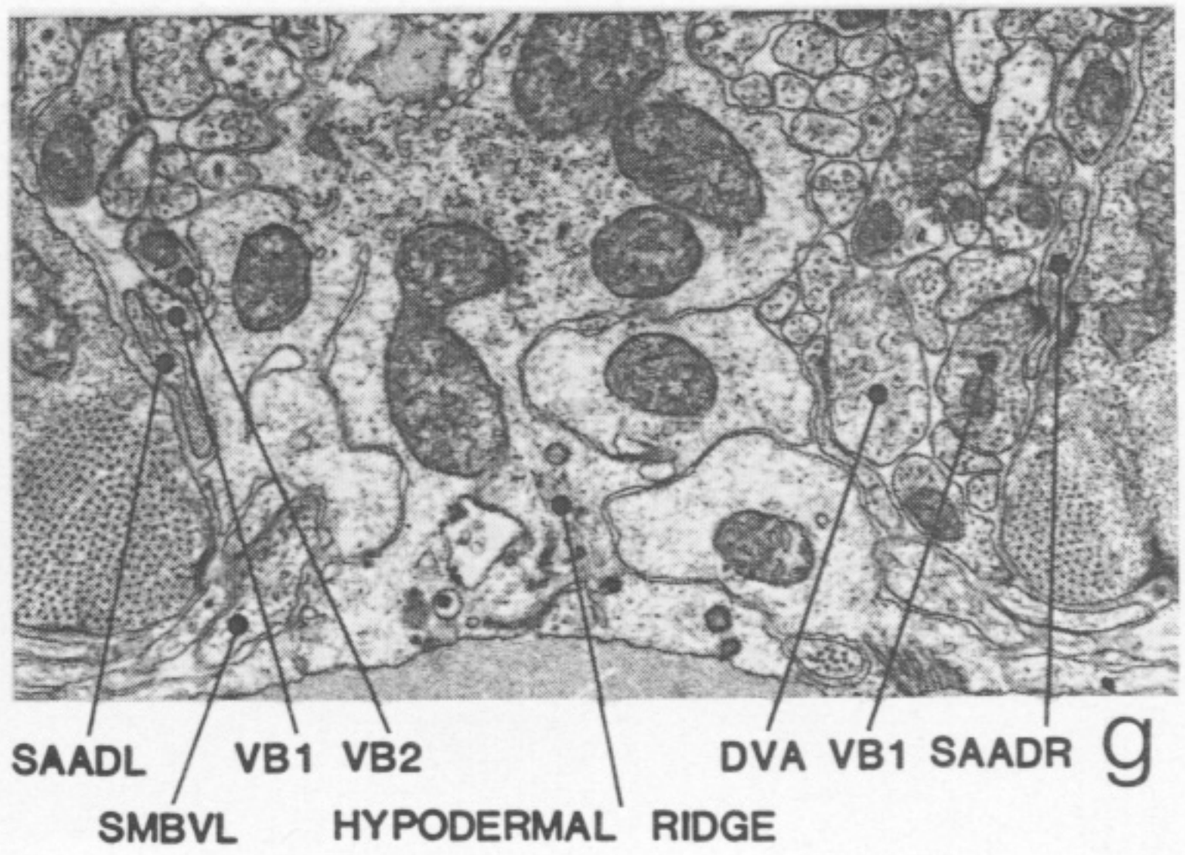

RMFL
RIML
SAAVL
AVAR
b

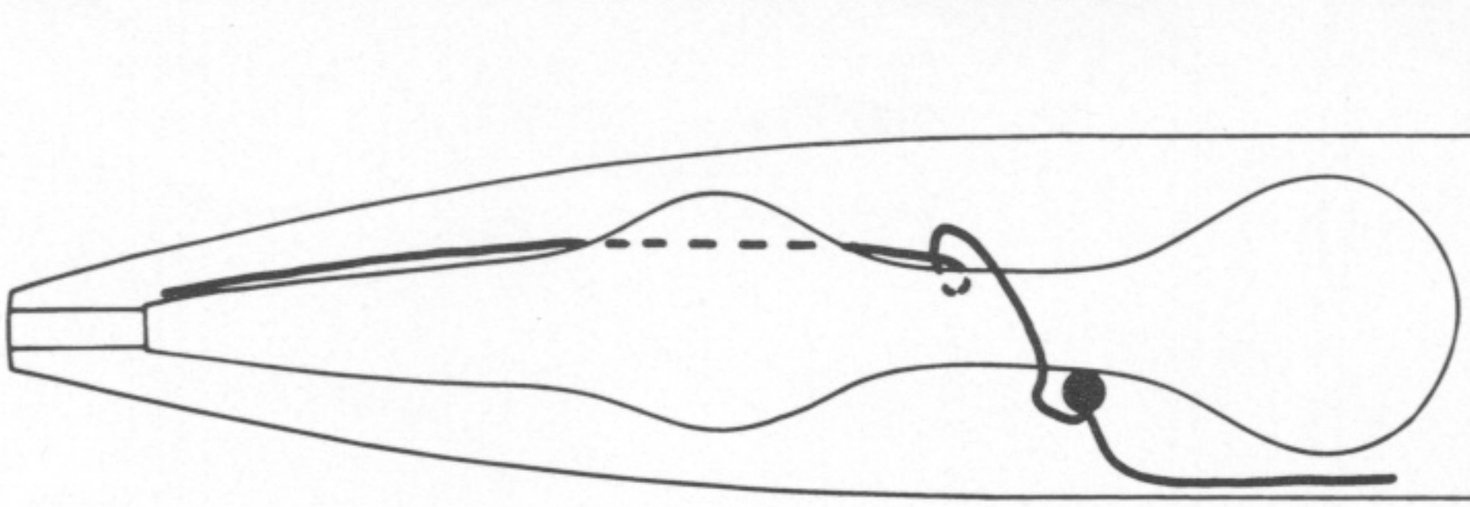

SMBDL
SAADL
SAAVR
AVAR
c

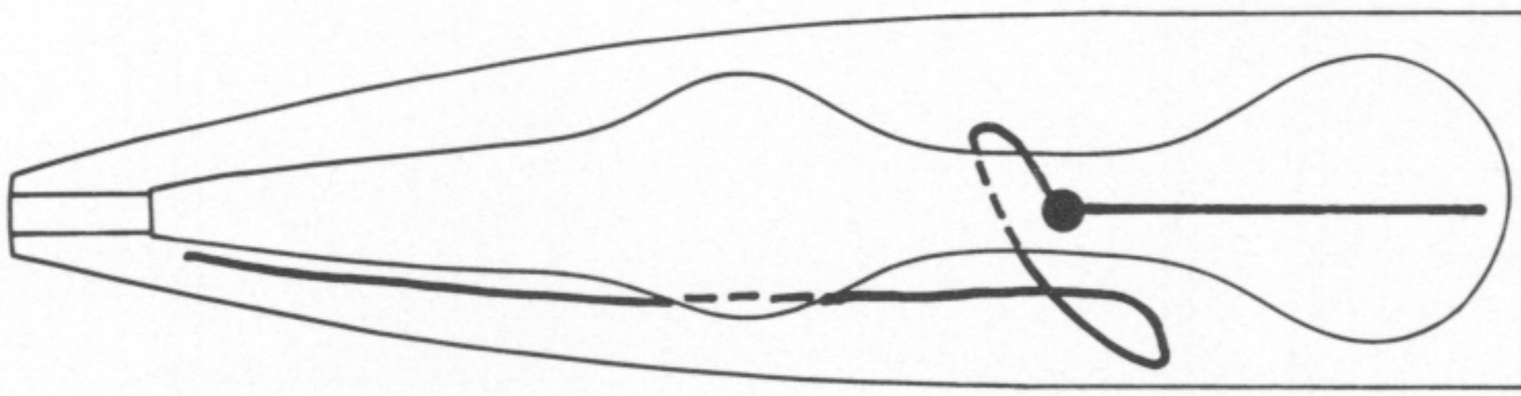

SMDDR
SAAVL
RIMR
SAADR
d


SMBVR
PLNR
SAADR
e

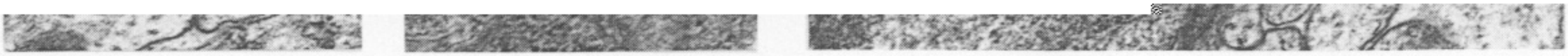

SMBDL
SAADL
CEPshDR
HYPODERMIS
f

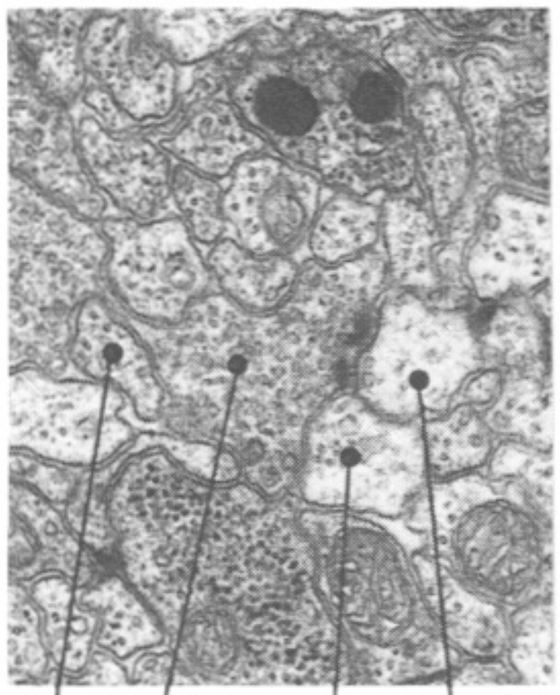

SAADL
VB1
VB2
DVA
VB1
SAADR
SMBVL
HYPODERMAL
RIDGE
g

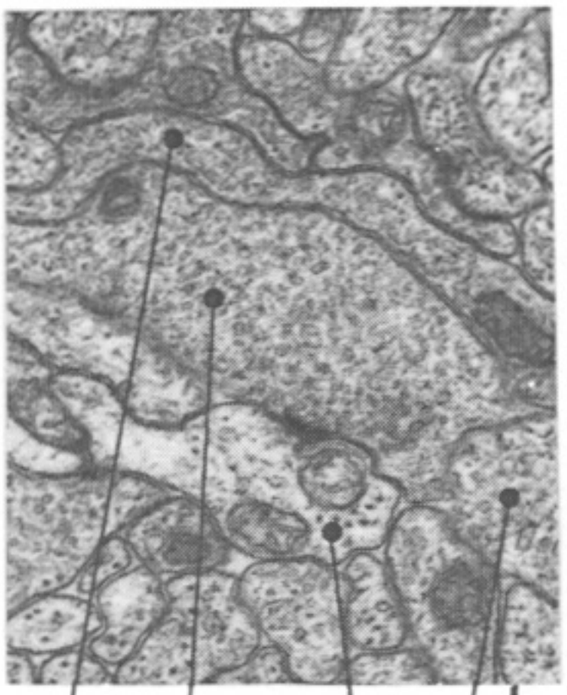

SAADL
h

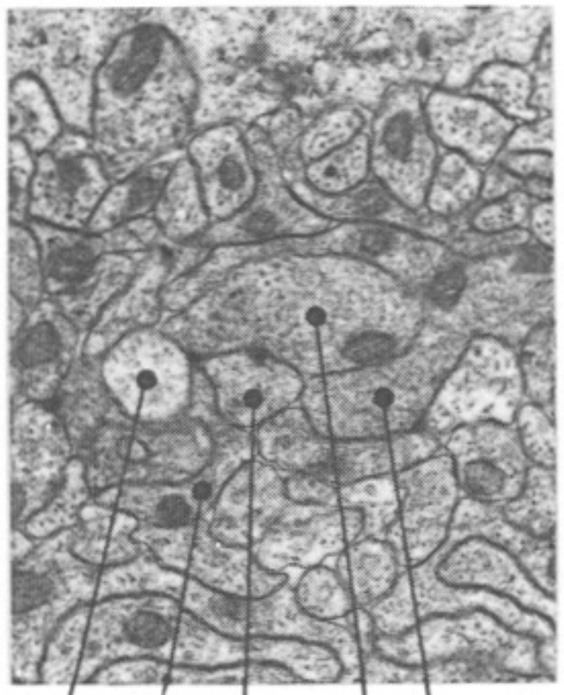

SAAVL
i

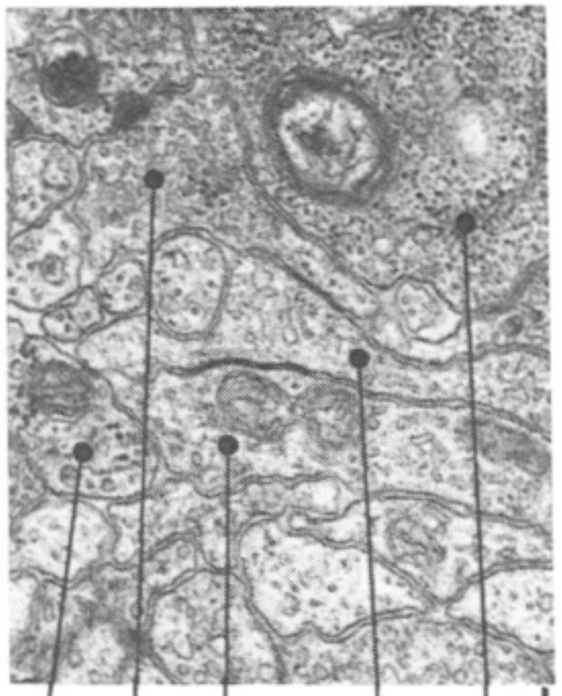
SAA

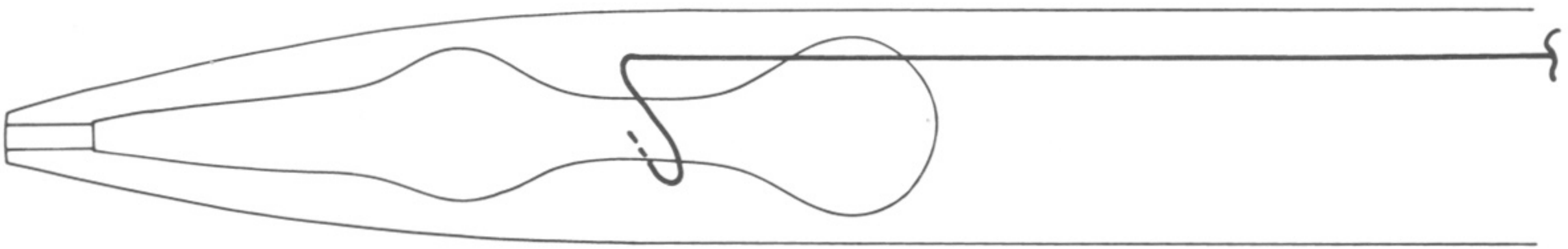


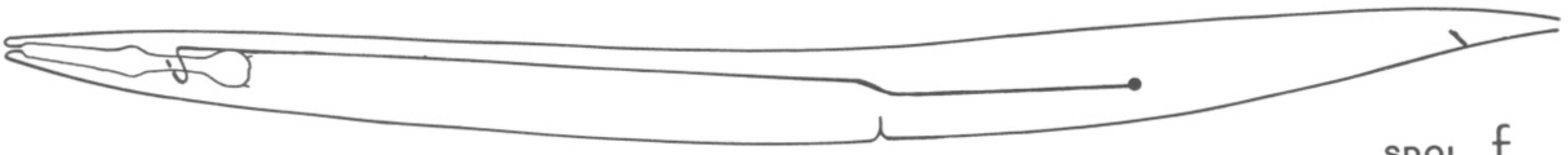

RIAR
SDQR
DVA
AVBL
a

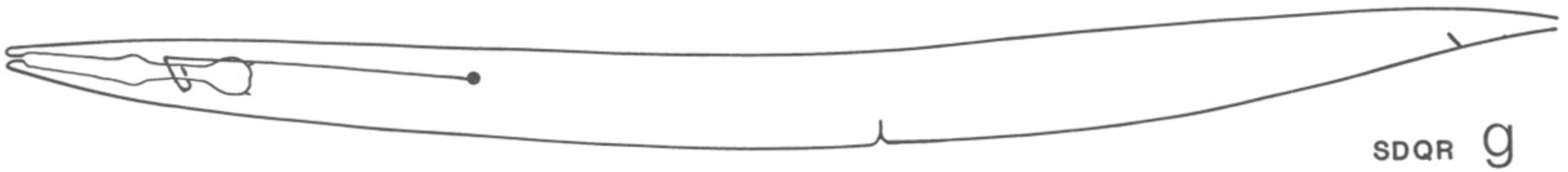

SDQR
SDQL
AVAL
DVA
b


AVAR
AIBR
RIS
SDQL
SDQR
C

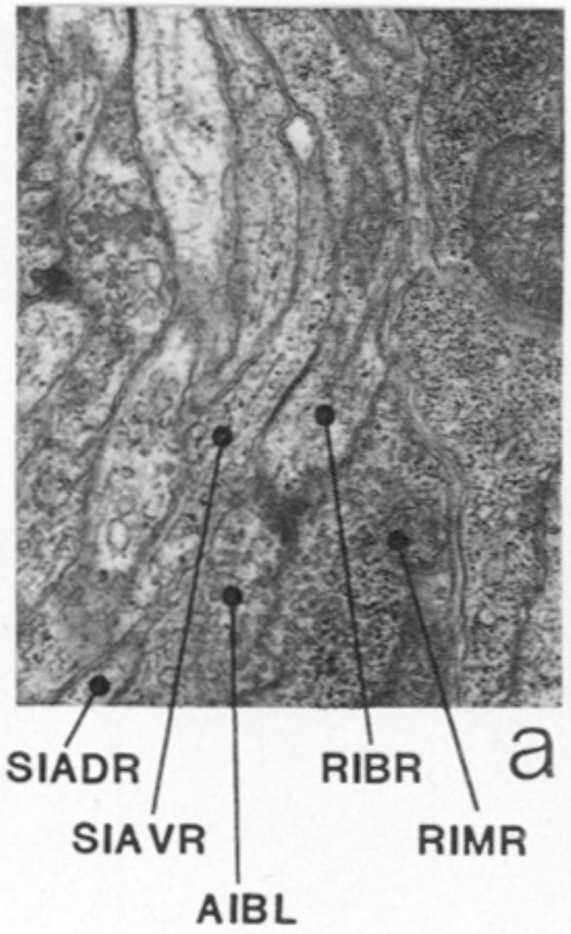

DVA
RIVR
SDQL
SDQR
RIH
d

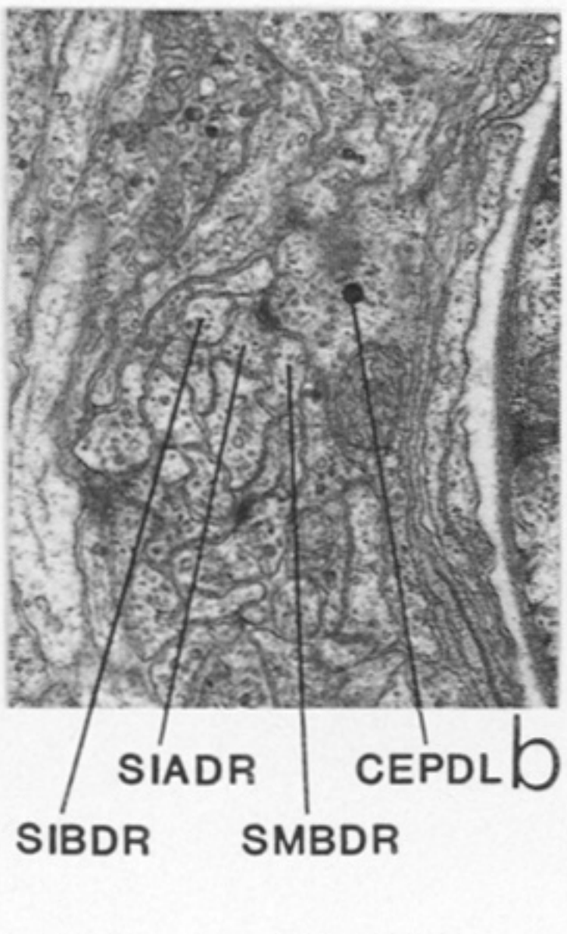

SDQL e

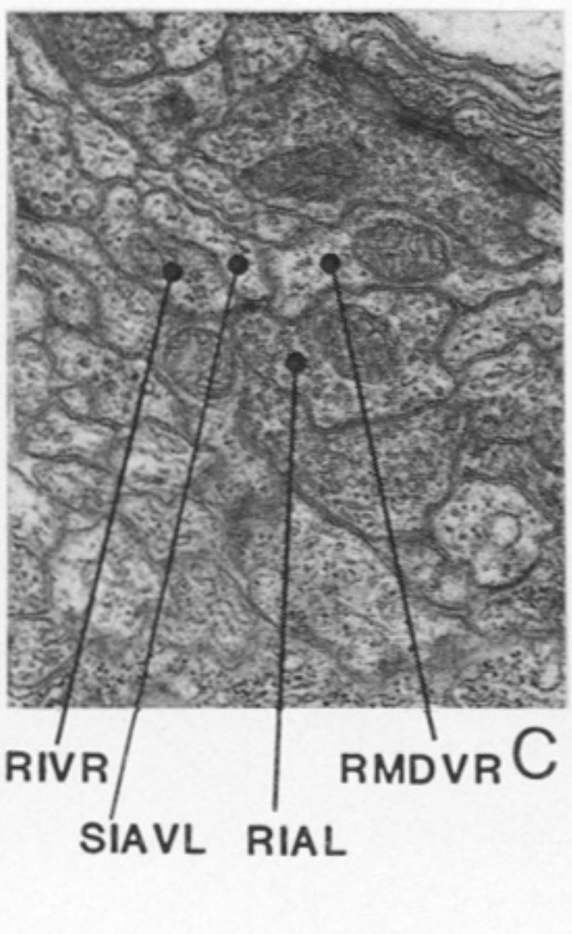

SDQL f


SDQR g

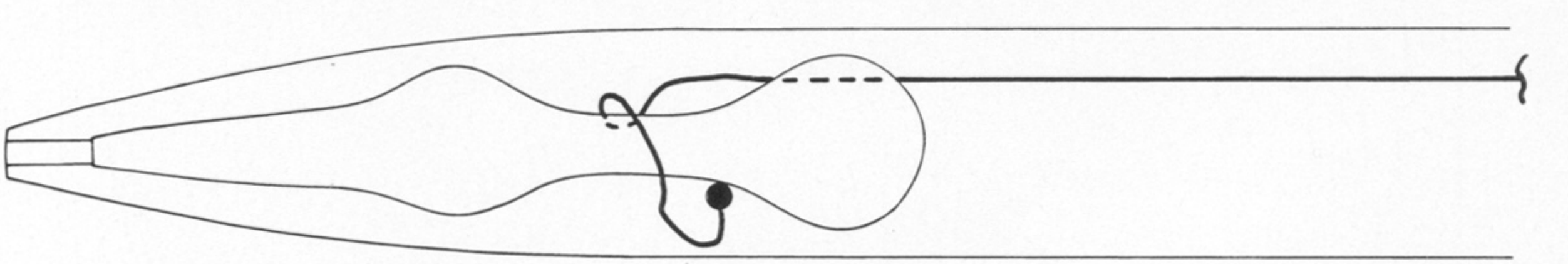
SDQ

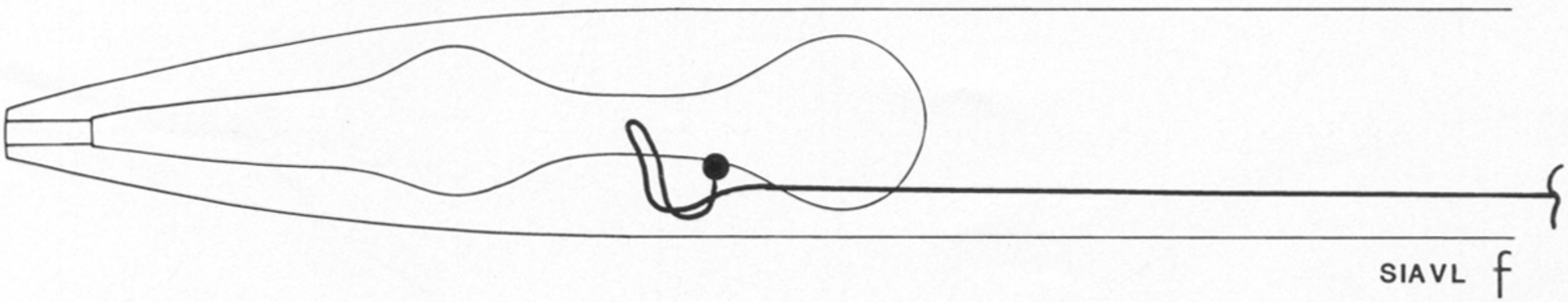

SIADR
SIAVR
AIBL
RIBR
RIMR
a


SIADR
CEPDL
SIBDR
SMBDR
b

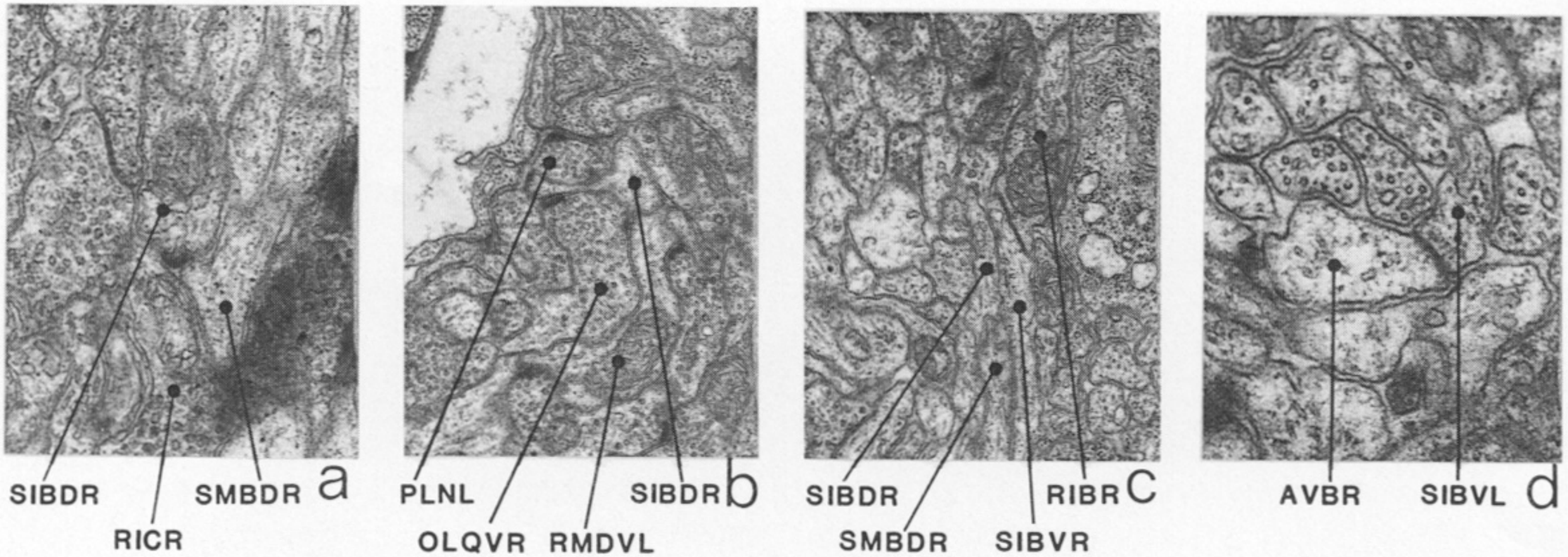

RIVR
RMDVR
SIAVL
RIAL
c


SIAVL
SIBVL
SIADL
SIBVR
SMBDL
SAADL
d

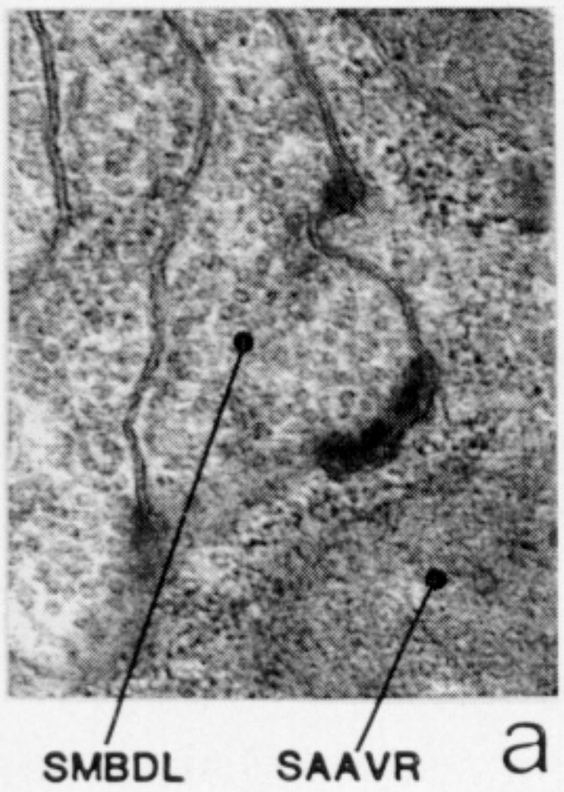

SIADL
e

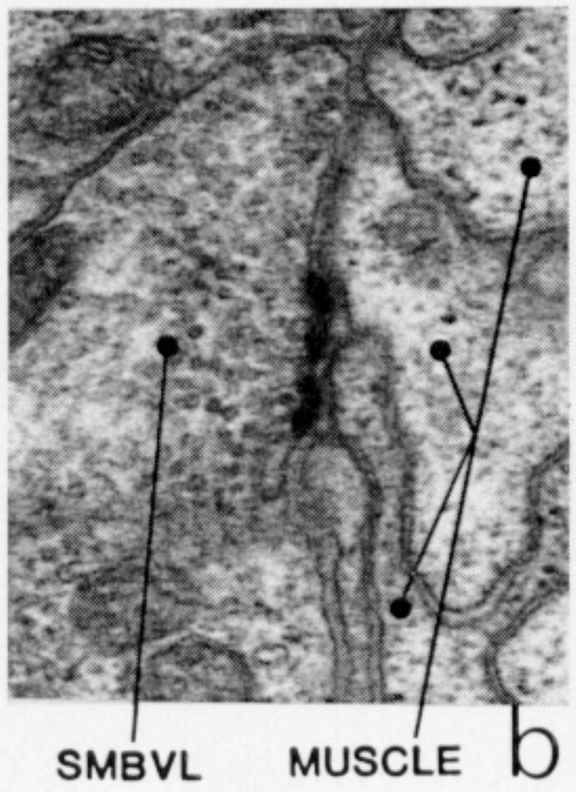

SIAVL
f

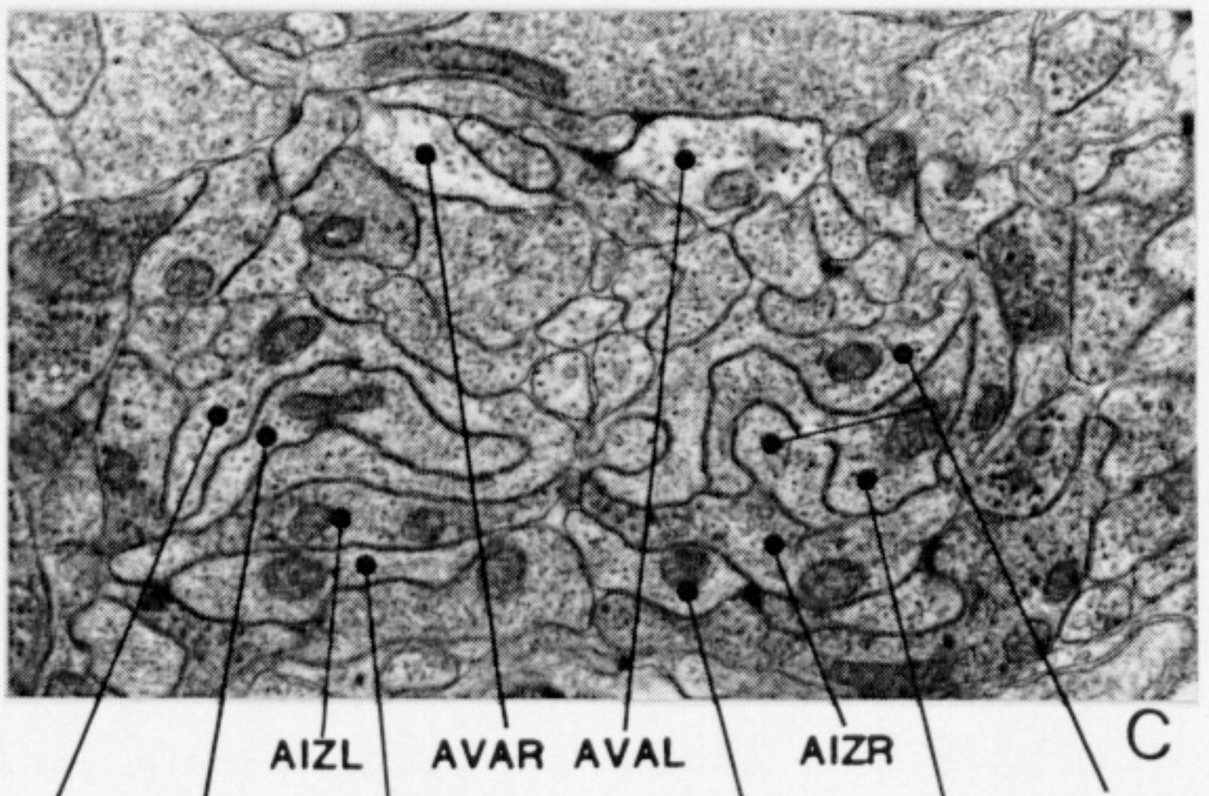
SIA

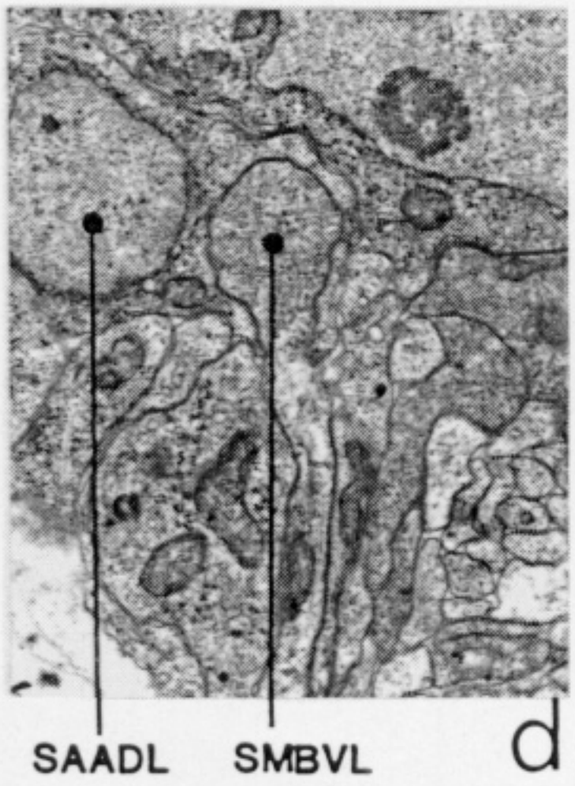

SIBDR
RICR
SMBDR
a
PLNL
OLQVR
RMDVL
SIBDR
b
SIBDR
SMBDR
SIBVR
RIBR
c
AVBR
SIBVL
d
SIBDL
e
SIBVL
f

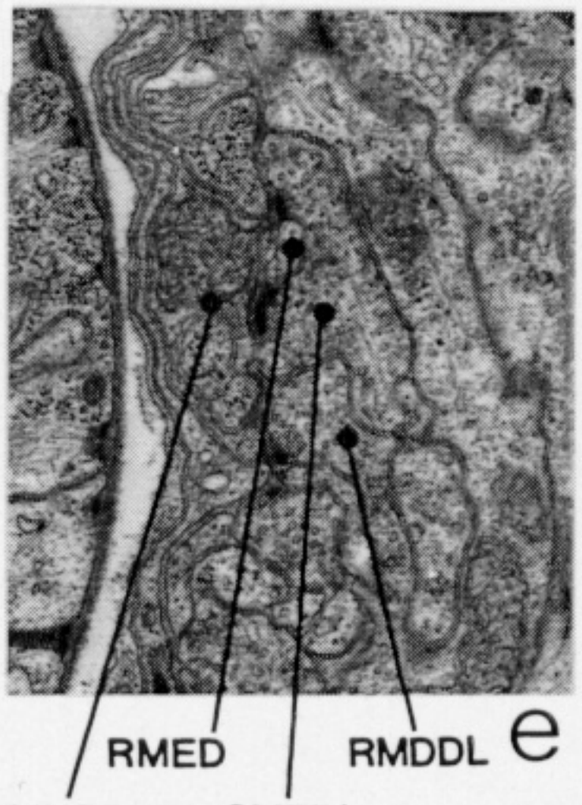
SIB

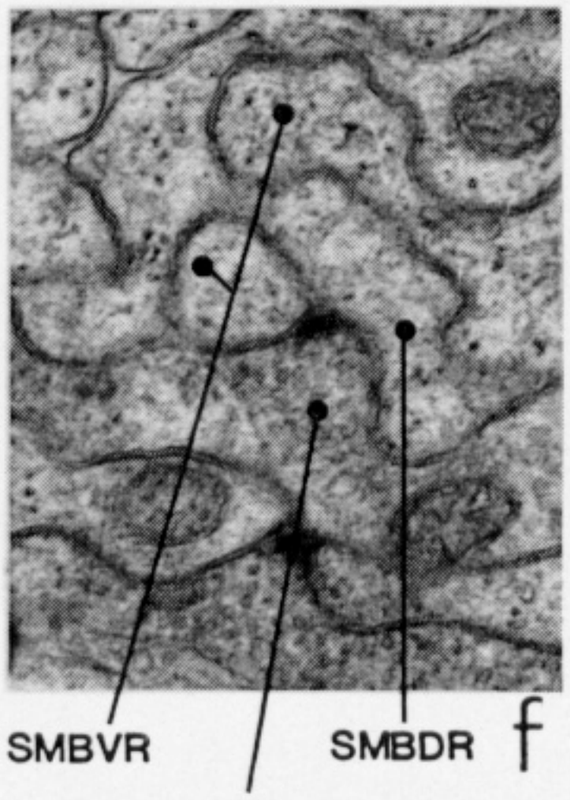

SMBDL
SAAVR
a

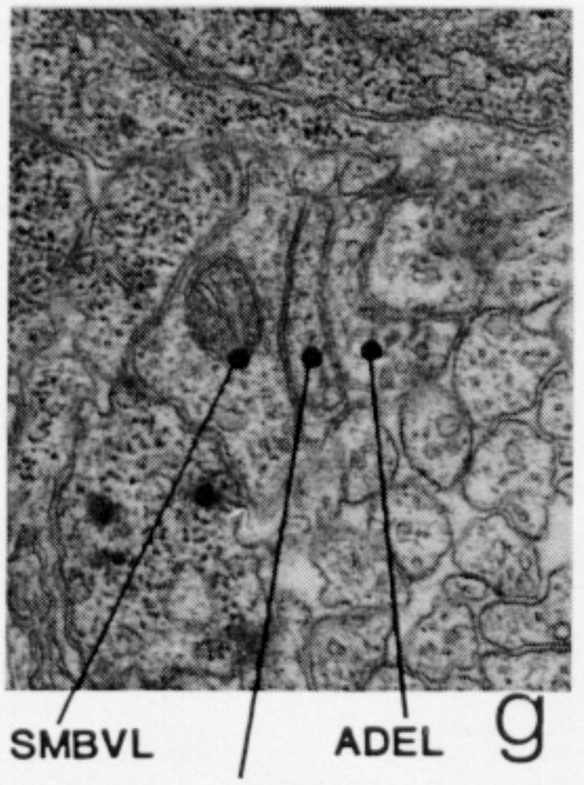

SMBVL
MUSCLE
b

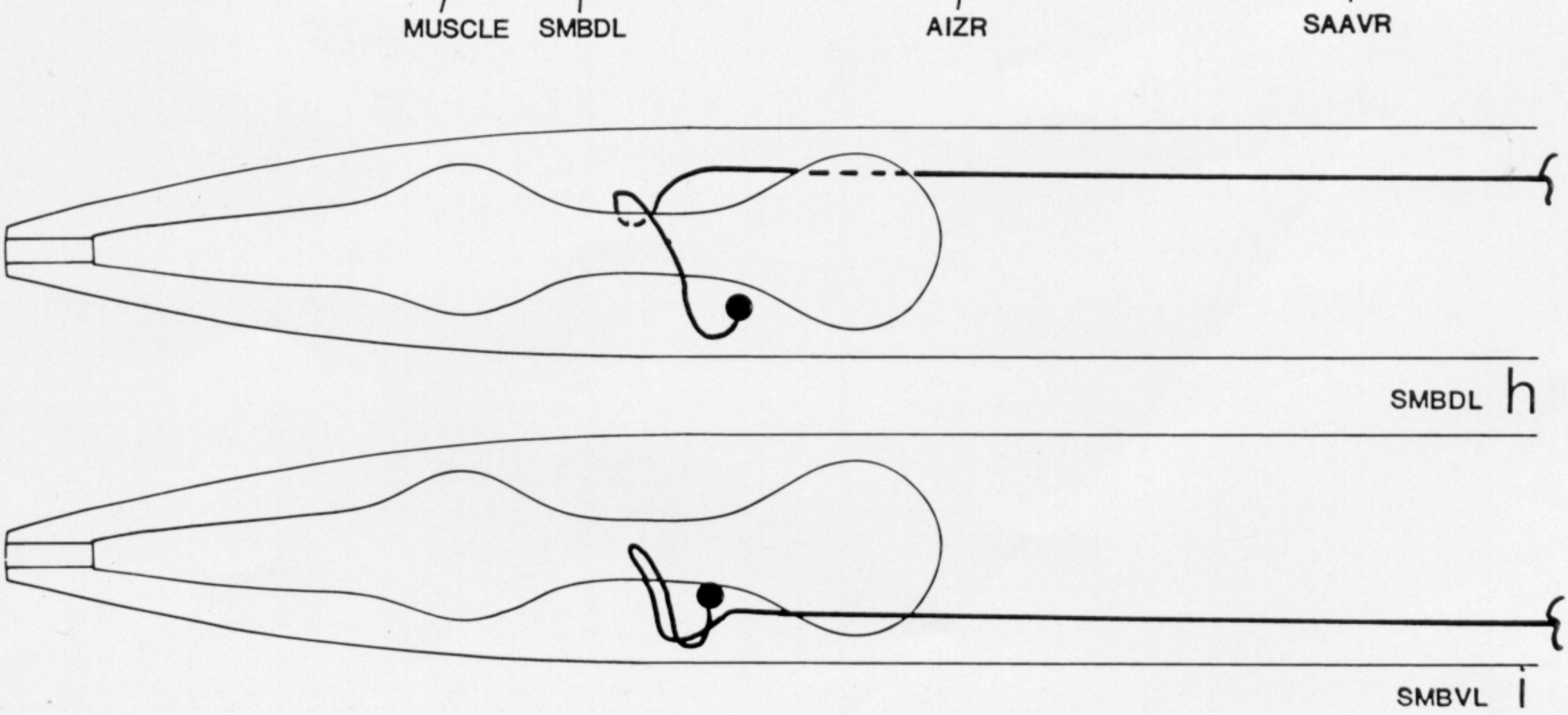

SMBDL
SMBVL
AIZL
RIAL
AVAR
AVAL
RIAR
AIZR
SMBVR
SMBDR
c


SAADL
SMBVL
d

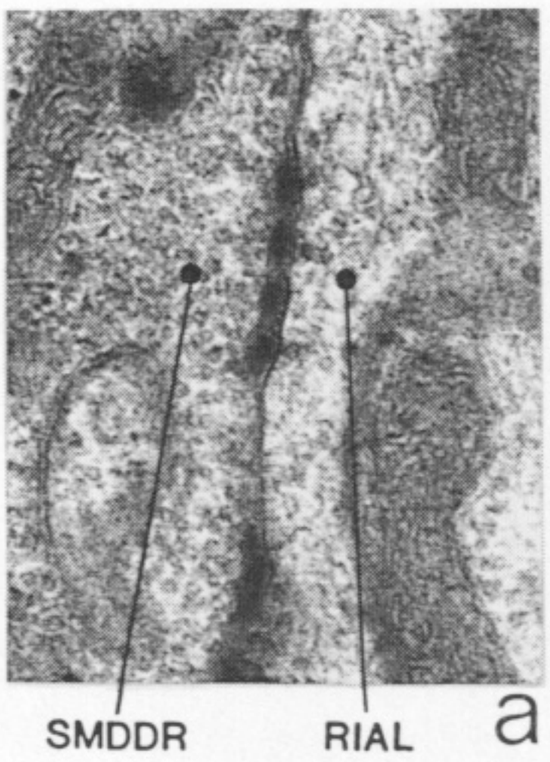

RMED
RMDDL
e
MUSCLE
SMBDL

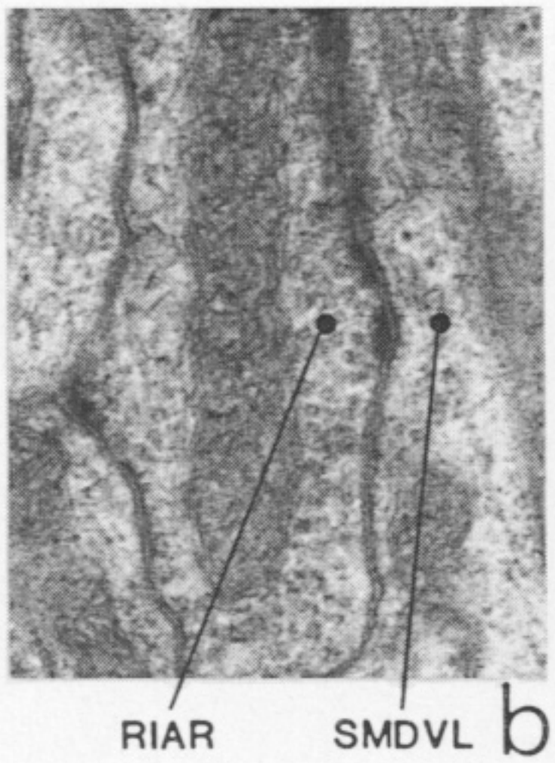

SMBVR
SMBDR
f
AIZR

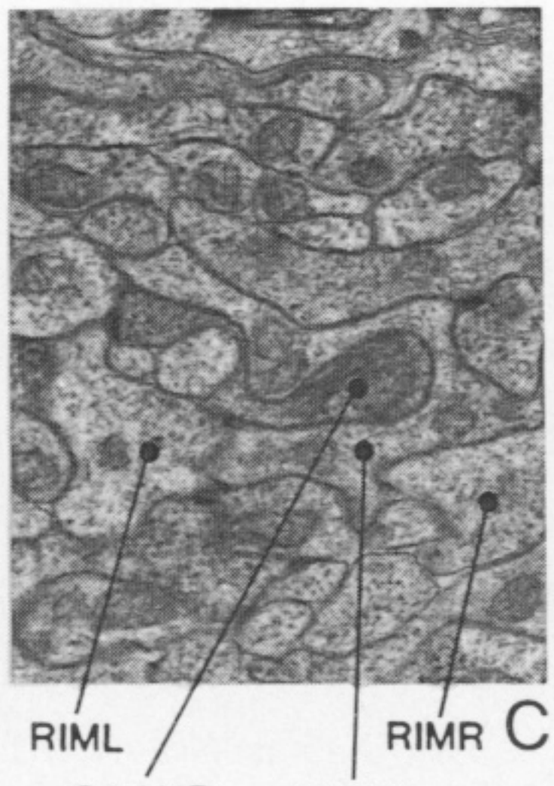

SMBVL
ADEL
g
SAAVR

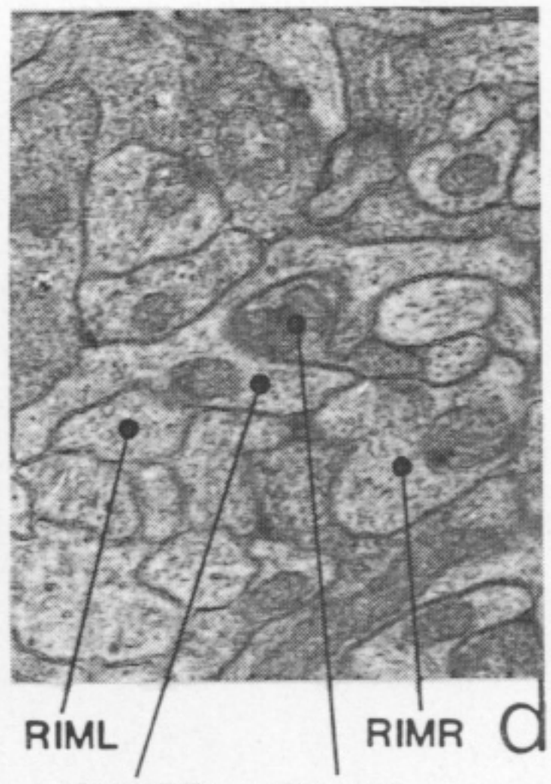

SMBDL
h
SMBVL
i

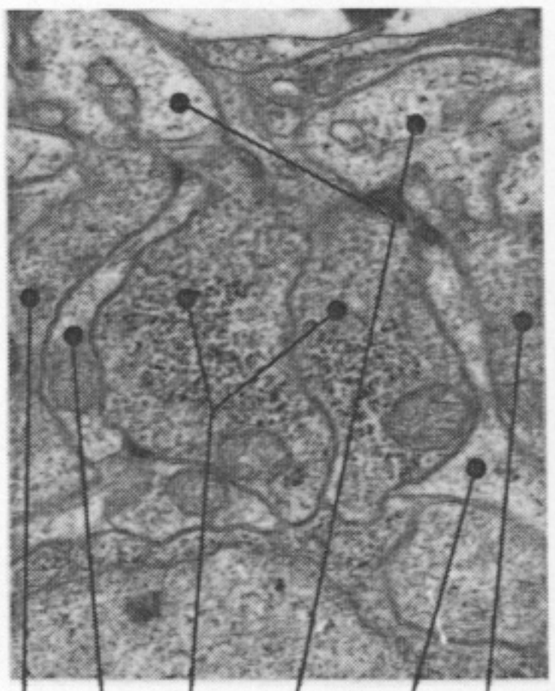
SMB

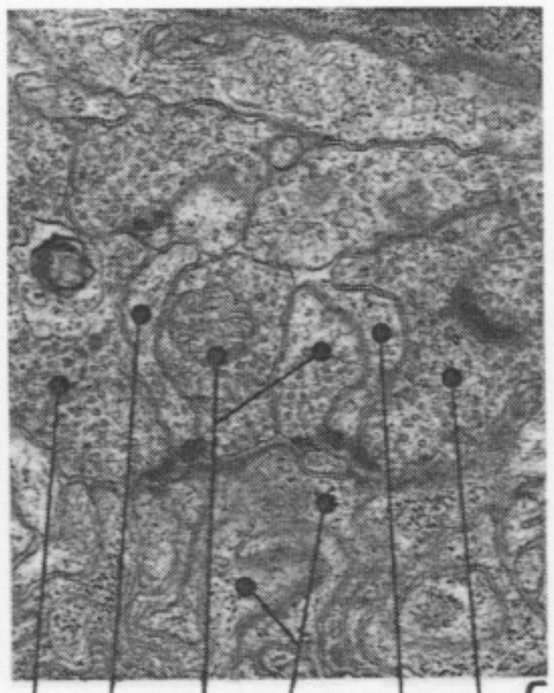

SMDDR
RIAL
a

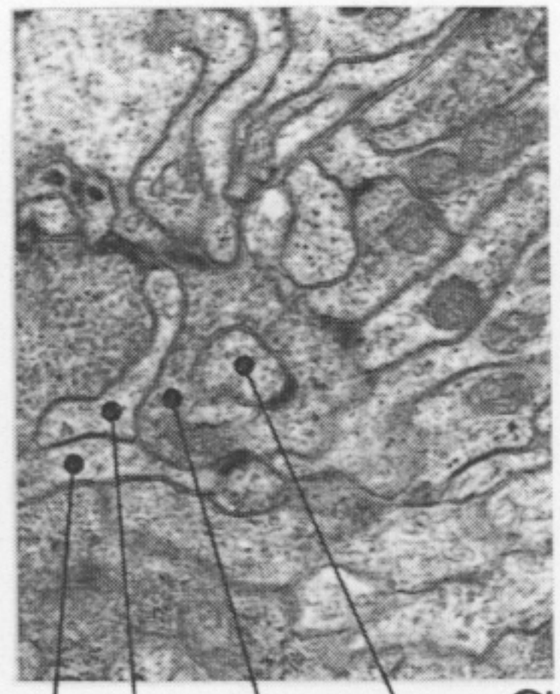

RIAR
SMDVL
b

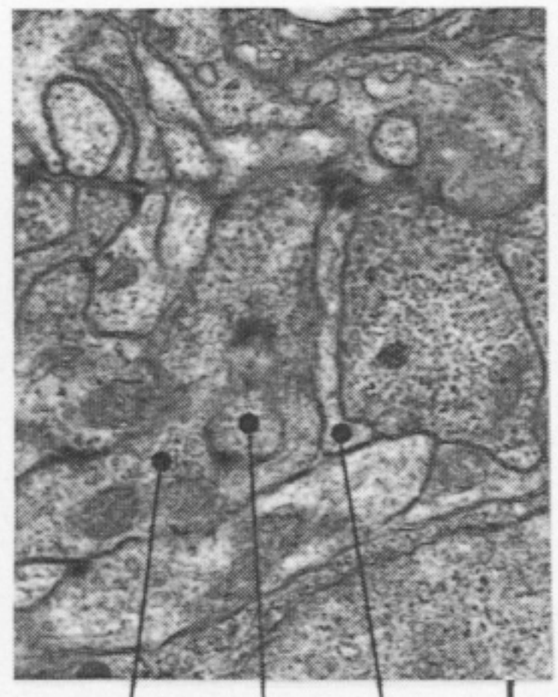

RIML
SAAVR
SMDDL
RIMR
c

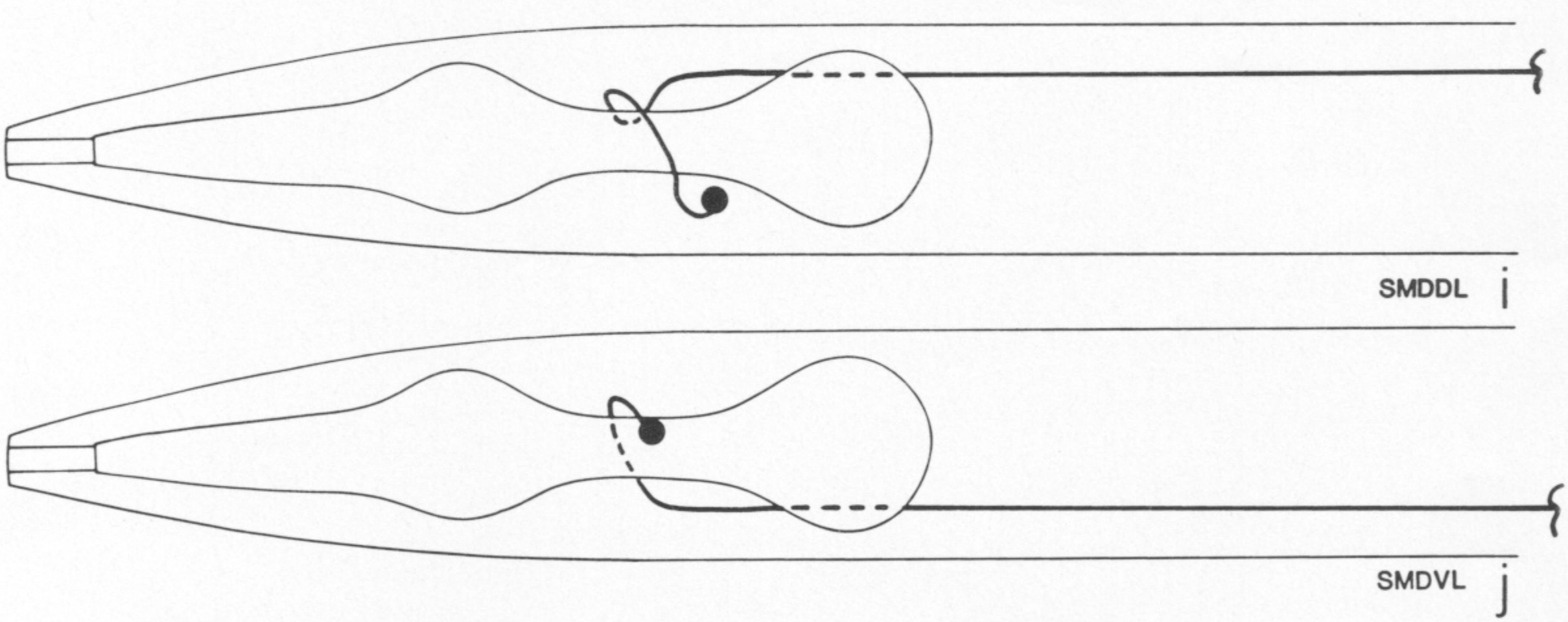

RIML
SMDDR
SAAVL
RIMR
d


SMDDL
MUSCLE
SMDVR
RMED
SMDVL
SMDDR
e

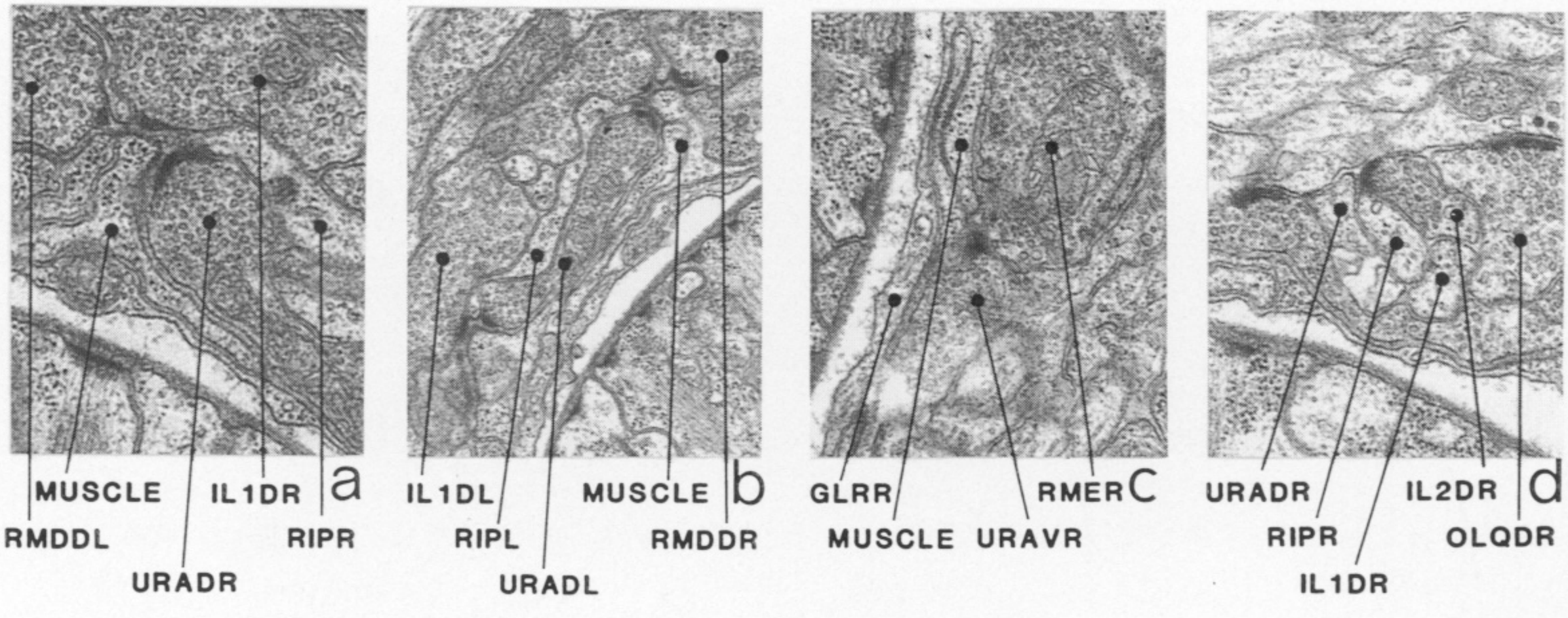

SMDVL
MUSCLE
f
SMDDR
RMEV
SMDVR
SMDDL


SMDDR
OLLR
g
RIBR
SMDVL

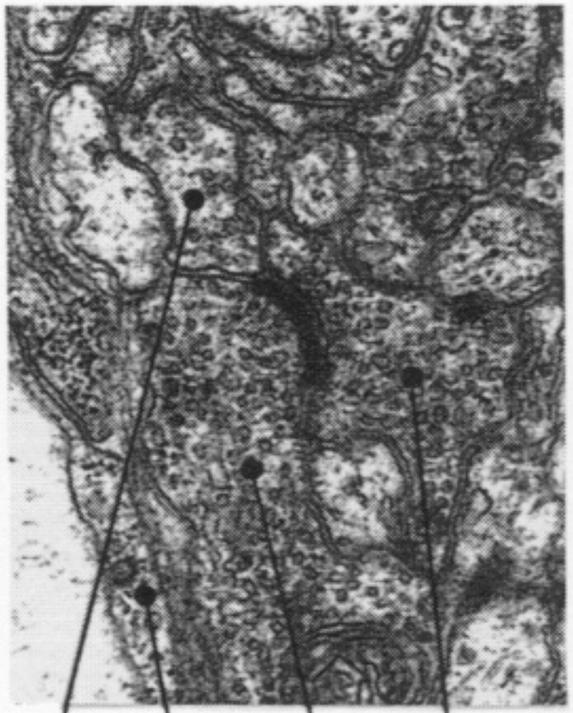

SMDVR
SMDDL
h
OLLL


SMDDL
i
SMDVL
j

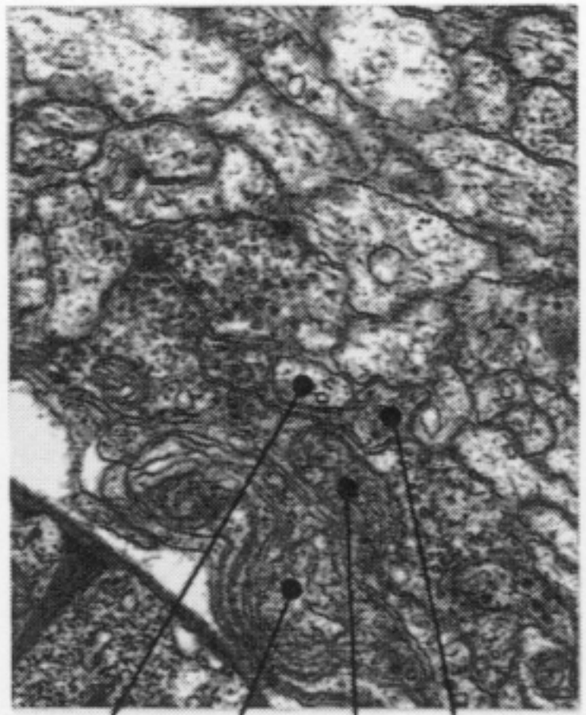
SMD

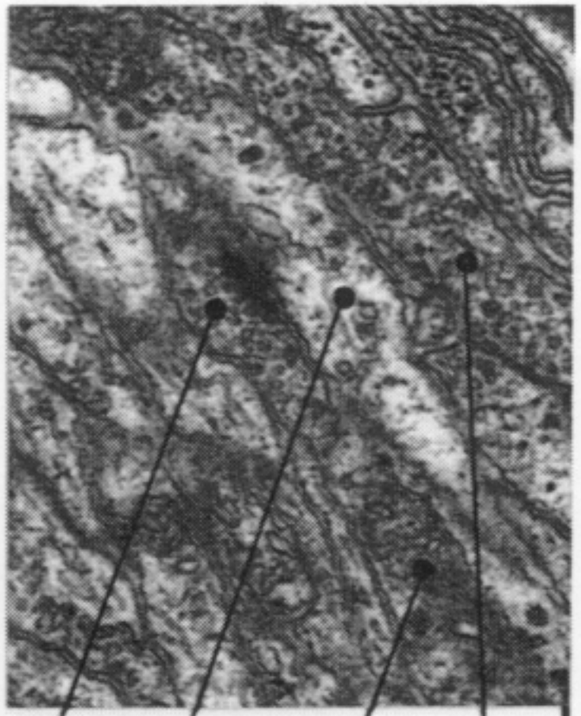

MUSCLE
IL1DR
a
RMDDL
RIPR
URADR
IL1DL
MUSCLE
b
RIPL
RMDDR
URADL
GLRR
RMERC
MUSCLE
URAVR
URADR
IL2DR
d
RIPR
OLQDR
IL1DR
URADL
e
URAVL
f

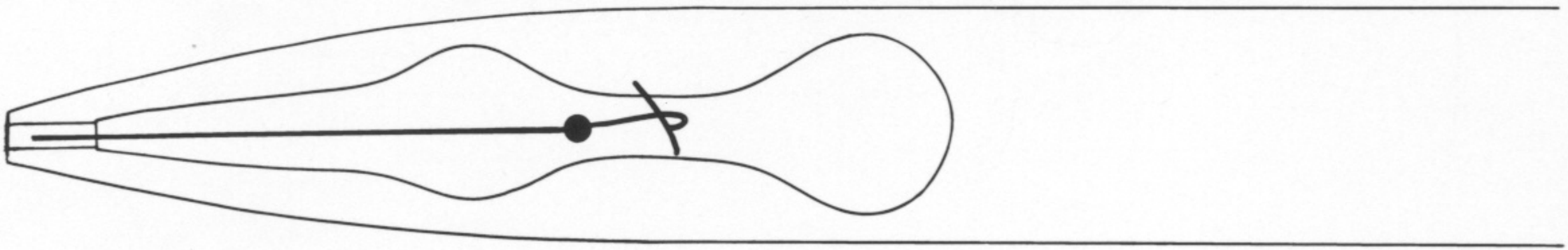
URA


RMHL
GLRR
URBR
URXR
a

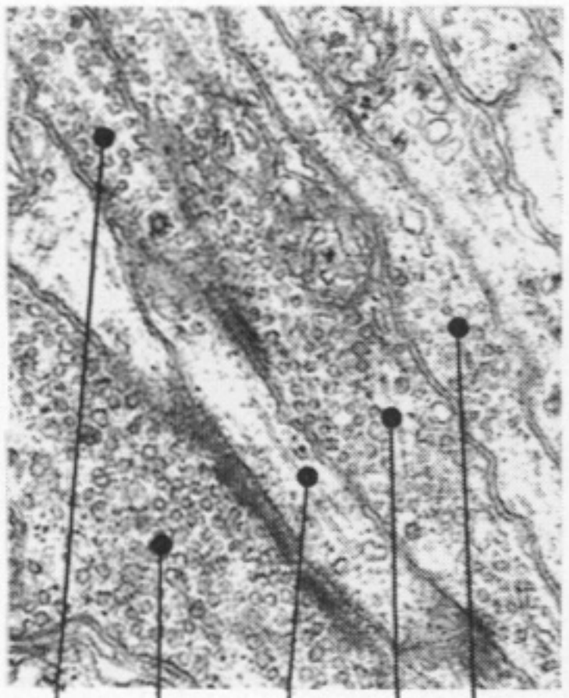

GLRR
CEPDR
RMHL
URBR
b

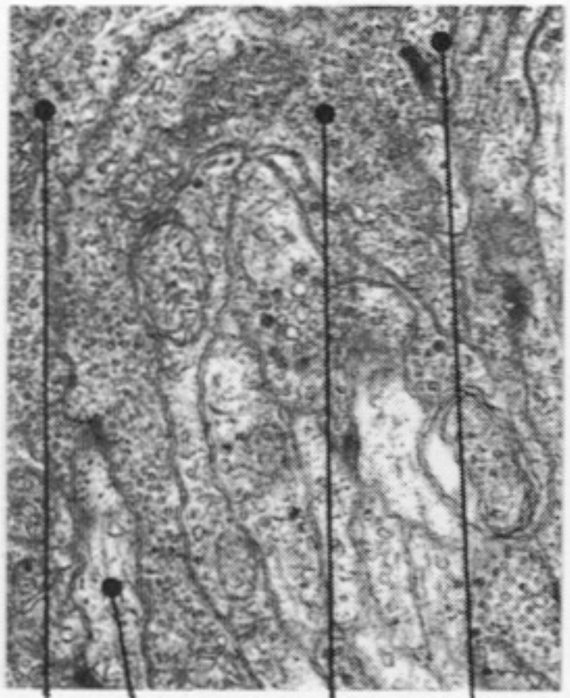

SMBDL
MUSCLE
CEPDR
URBR
c

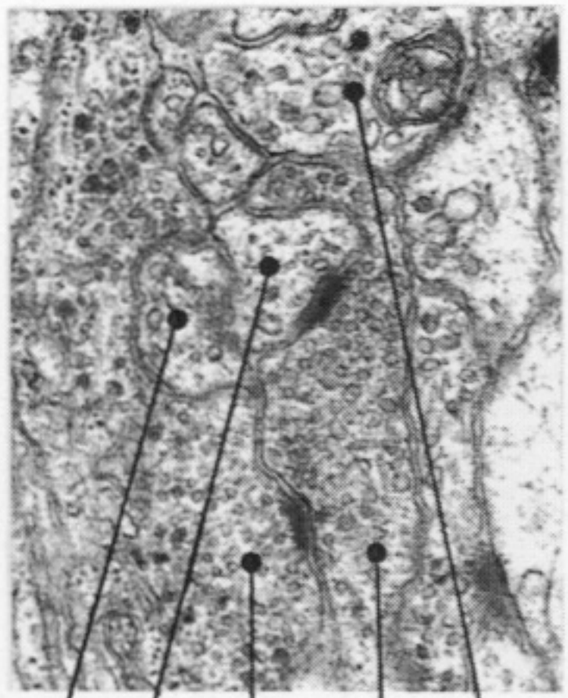

URBL
RICR
RICL
CEPVL
d

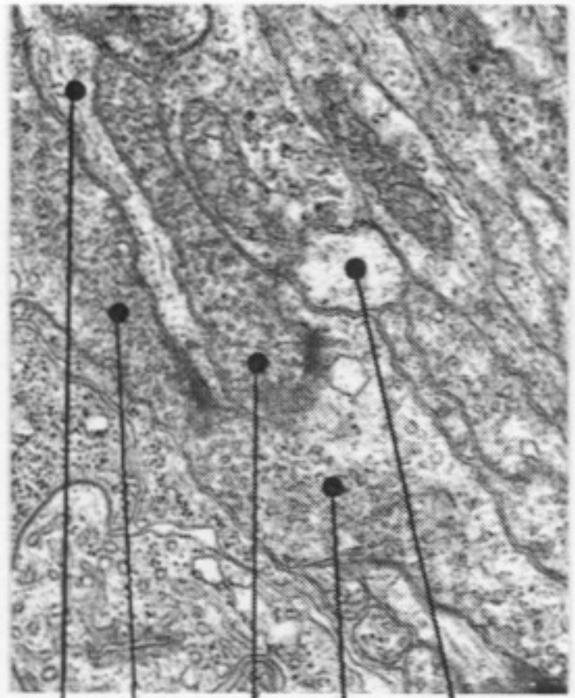

URBL
e

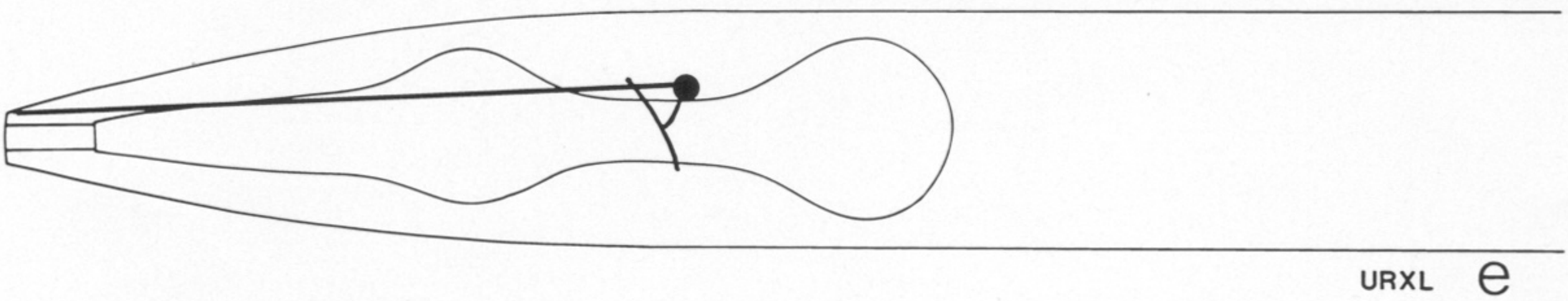
URB


AUAL
BAGR
RIAL
URXL
RIR
a

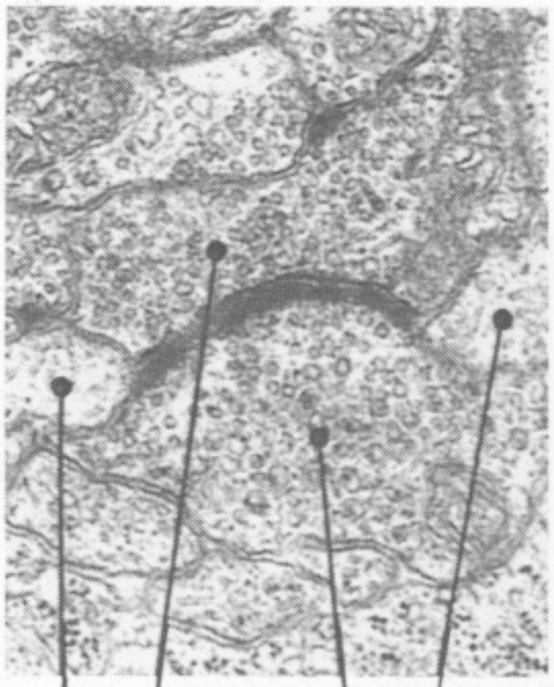

AUAL
RIAR
URXL
AVEL
b

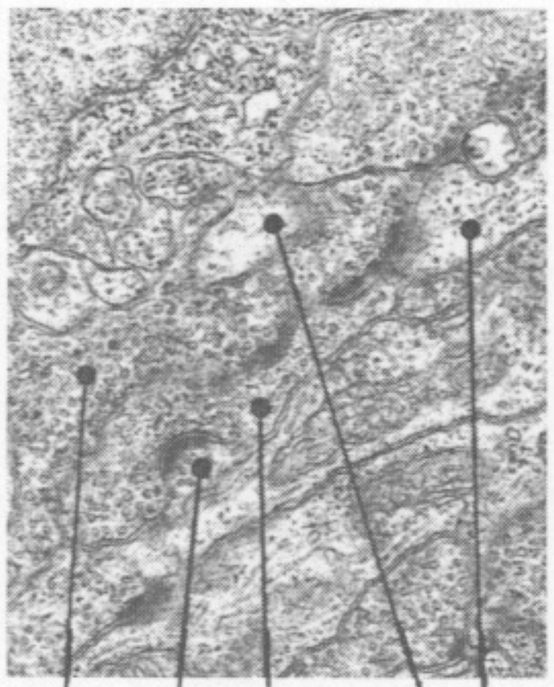

IL1R
AVER
URBR
URXR
RMGR
c

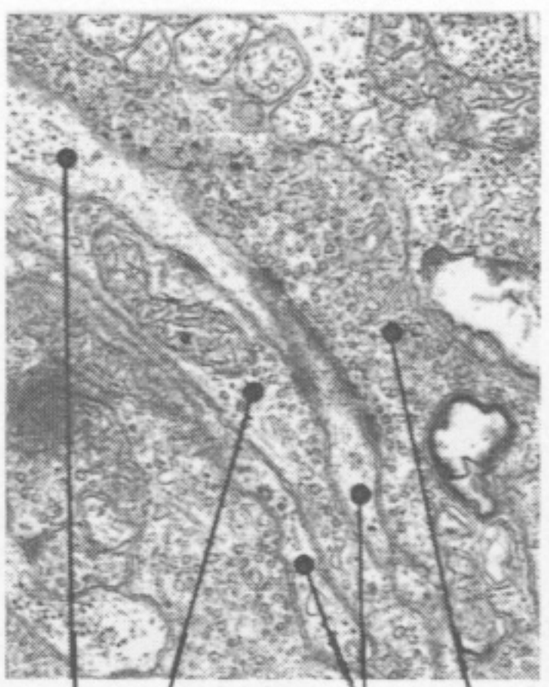

RIAL
BAGR
RIGL
AVBR
d

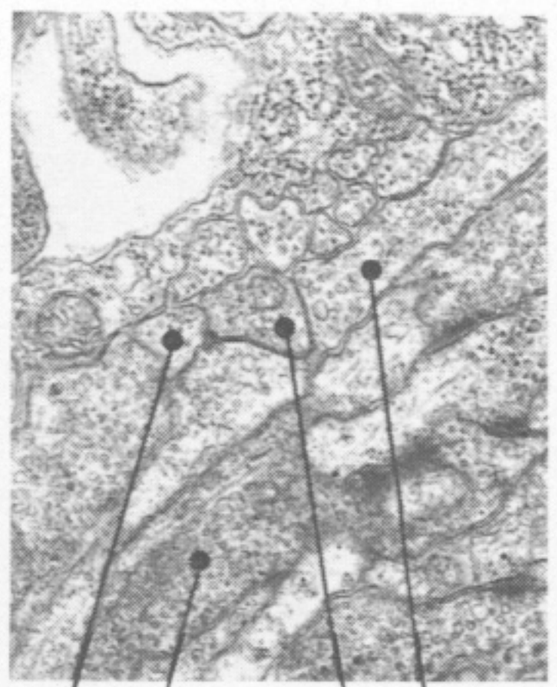

URXL
e

URX


AVEL
SMDVL
URYVR
RIBR
a

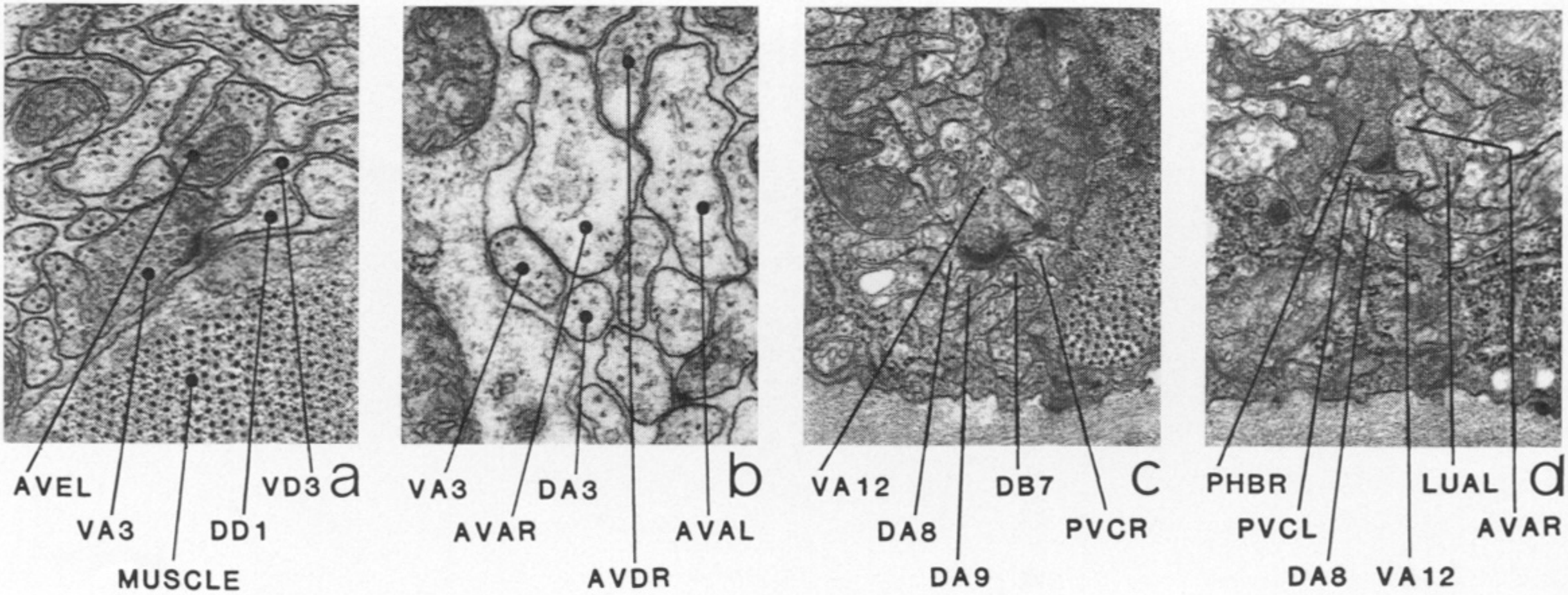

URYDL
OLLL
SMDDR
RIBL
AVER
b


AVEL
OLLR
RMDVR
URYDR
c

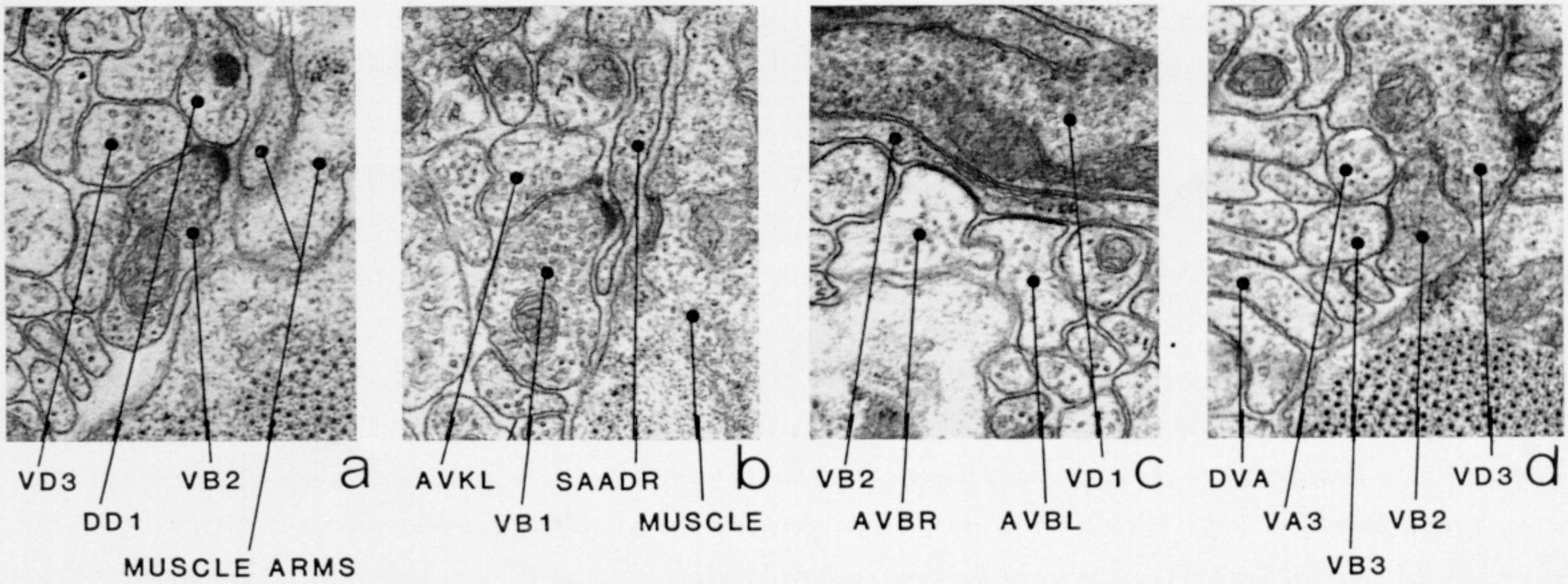

RIBL
SAADR
URYDL
RIGL
d

URYDL
e
URYVL
f

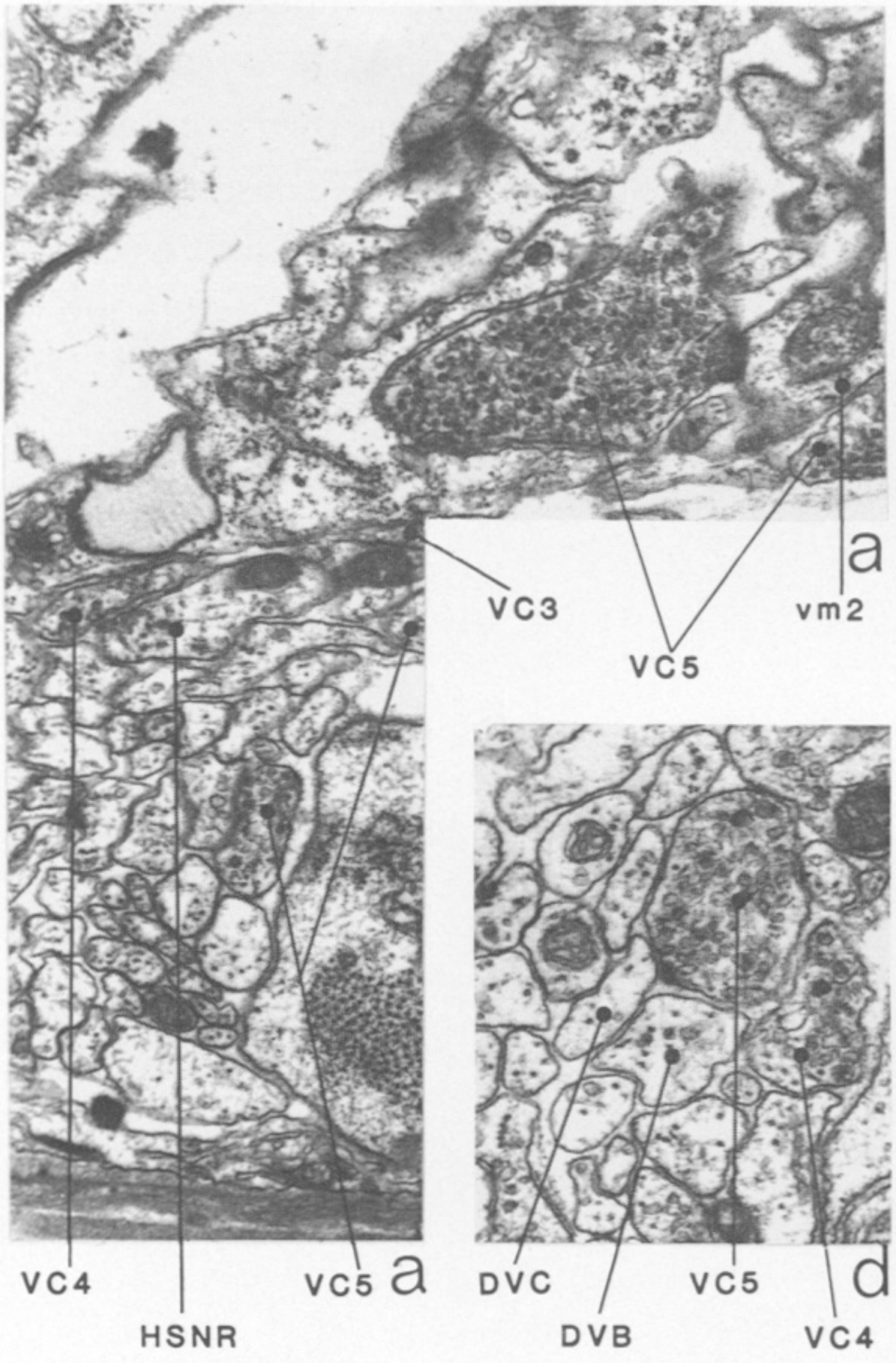
URY

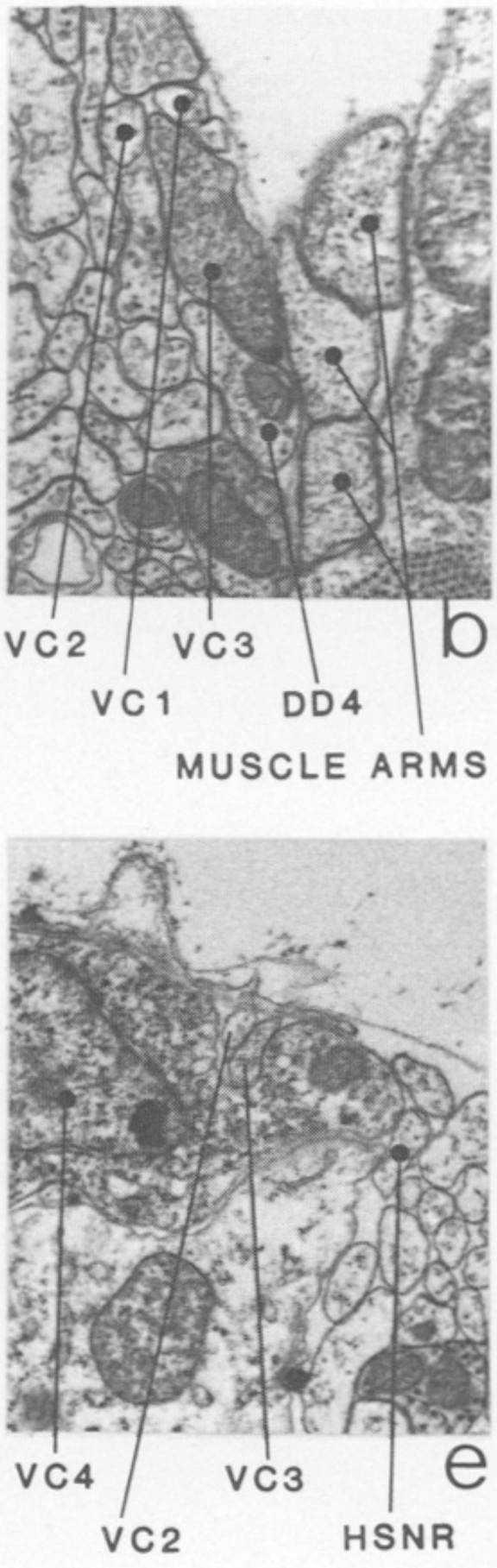

AVEL
VA3
MUSCLE
DD1
VD3
a
VA3
AVAR
DA3
AVDR
AVAL
b
VA12
DA8
DA9
DB7
PVCR
c
PHBR
PVCL
DA8
VA12
LUAL
AVAR
d
VA1
e
a
b
VA3
f
c
d
VA12
g

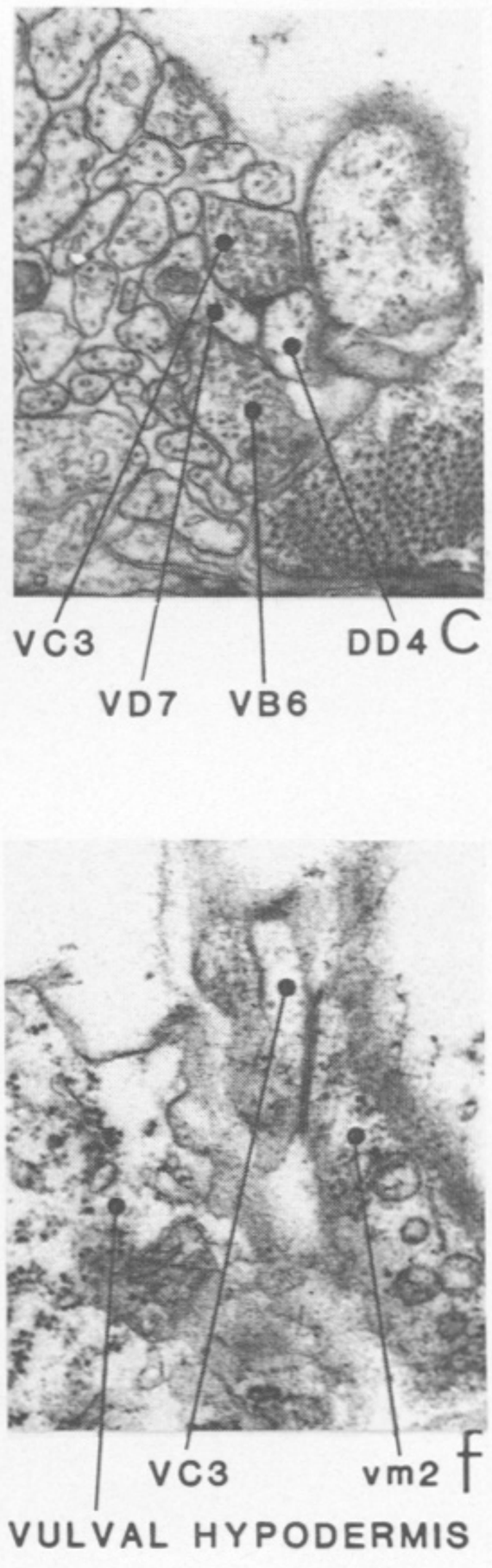
VAn


VD3
DD1
VB2
MUSCLE ARMS
a
AVKL
VB1
SAADR
MUSCLE
b
VB2
AVBR
AVBL
VD1
C
DVA
VA3
VB3
VB2
VD3
d
b
VB1 e
b
VB1 f
c
a
d
VB2 g
VB4 h

VBn


VC3
VC5
vm2
a
VC4
HSNR
VC5
a


VC2
VC1
VC3
DD4
b
MUSCLE ARMS


VC3
VD7
VB6
DD4
C

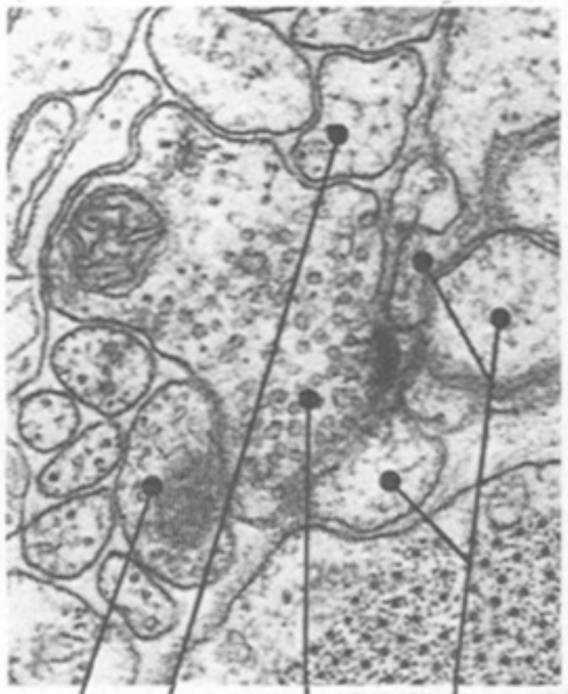
DVC
DVB
VC5
VC4
d

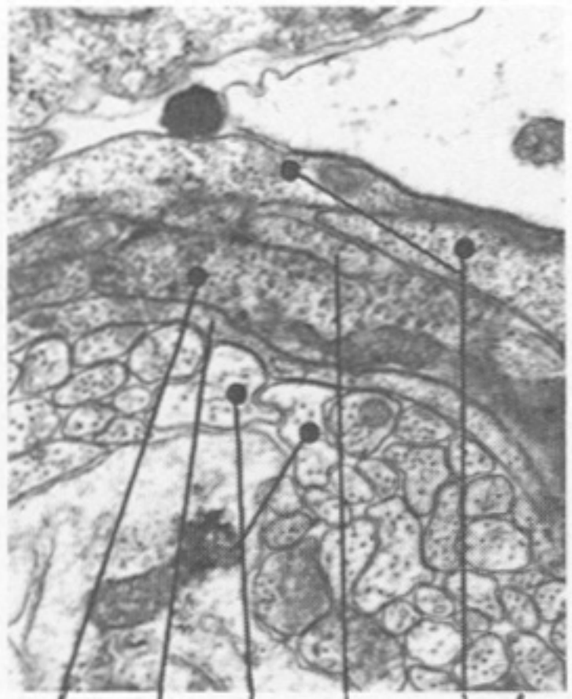
VC4
VC2
VC3
HSNR
e

VC3
vm2
f
VULVAL HYPODERMIS

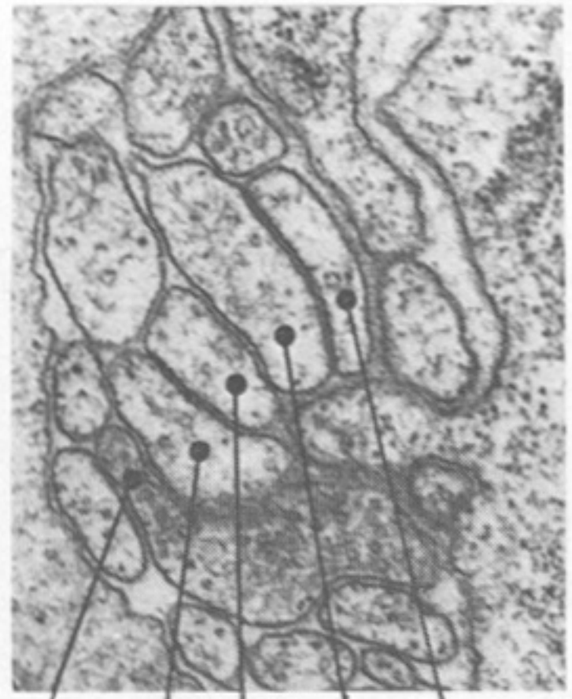
b
c
f
e
VC3
g
d
a
VC5
h

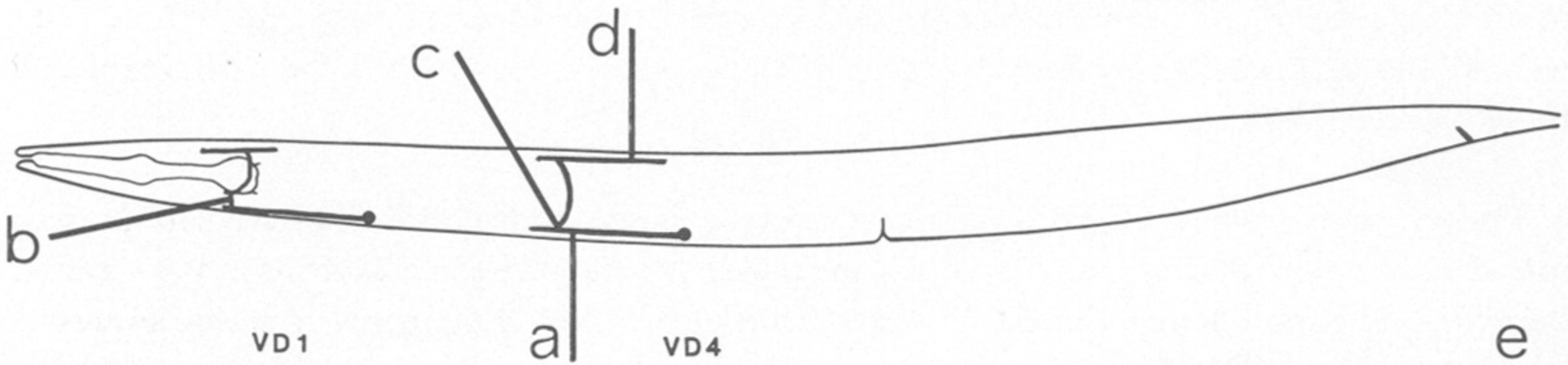
VCn


VB3
DD2
VD4
a
MUSCLE ARMS


VD1
VB2
AVB
VA1
b
MUSCLE ARMS


AVA
AVM
VD4
C
VD4 COMMISSURE


DB3
DD2
DD3
VD4
VD5
d


c
d
b
a
VD1
VD4
e

VDn