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NEUROANATOMY OF THE MESOTHORACIC GANGLION OF THE COCKROACH *PERIPLANETA AMERICANA* (L.). II. MEDIAN NEURON CELL BODY GROUPS†

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[Plates 1–3; outrigger]

CONTENTS

The groups of neuron cell bodies in the midline of the mesothoracic ganglion of adult male *Periplaneta americana* (L.) were examined using Bodian silver-stained paraffin sections and toluidine blue-stained wholemounts to determine their general architecture, and axonal filling with Procion yellow or cobalt to study pathways of their neuron processes. Filling tracheae with trypan blue provided additional information on tracheation of the ganglion. Seven groups of somata were named according to position: the anterior median (AM), mid-dorsal median (MDM), posterior dorsal median (PDM), posterior median (PM), anterior ventral median (AVM), mid-ventral median (MVM) and posterior ventral median (PVM) groups. Each group is

† Paper I appeared in *Phil. Trans. R. Soc. Lond.* B **267**, 421–465 (1974).

characterized by general appearance and position, numbers and sizes of constituent somata, and numbers and pathways of fibre bundles. Groups consist largely of interneurons, with a few efferent, presumed motor, neuron somata present in some. Different functional types of neurons (that is, motoneurons and interganglionic and intraganglionic interneurons) do not appear to be strictly segregated into different groups. The AM, PM, AVM and MVM groups contain apparently only interneurons, either interganglionic (AM), intraganglionic (PM, AVM), or both together (MVM). In the MDM group one motoneuron to each side supplies the dorsal root of peripheral nerve 2, four or five PDM cells (equivalent to dorsal unpaired median (DUM) cells of other species) bifurcate to nerve 5 of both sides of the ganglion and some also branch to nerves 3, 4 and 6, and in the PVM group one cell to each side is the widespread common inhibitory motoneuron to nerves 3–6. Three other large, bifurcating neurons of the PDM group may be efferent but follow a somewhat different pathway and could not be traced into peripheral nerves. Numbers of somata in the seven groups total 200 or more, and intraganglionic interneurons seem greatly to outnumber interganglionic ones. The MDM, AVM, MVM and PVM groups show evidence of an apparently paired origin.

Introduction

Paper I (Gregory 1974*a*) described the general structure of the mesothoracic ganglion and the arrangement and composition of the nerve fibre bundles that form within it the roots of the peripheral nerves. Groups of neuron cell bodies (somata) that contribute efferent, presumed motor, fibres to these roots were also referred to briefly. This and the two subsequent papers (see below) describe the classification and characteristics of the groups of cell bodies, both efferent presumed motor, and interneuron, in more detail. Additional information is included about the presumed motoneurons and their pathways obtained from cobalt chloride-filled preparations (Pitman *et al.* 1972), not available when paper I was written, but as general descriptions of the motoneuron pathways were given in paper I they are not repeated. In that paper they were described in the direction in which they had been traced, from nerve base to cell body, but in the present group of papers pathways are described from the cell body outwards. These three papers also give a partial description of the courses of the fibre bundles of the interneurons. As the majority of these are intraganglionic, that is, do not send processes into the peripheral nerves or interganglionic connectives, they cannot be filled with stain except by injection into each individual cell, a very lengthy undertaking. However, their fibre bundles could be traced for some distance in silver preparations with reasonable confidence, so it seemed worthwhile to provide some account of them, even if incomplete, rather than wait until fuller information was available. It is hoped to give more detail of the pathways of the interganglionic interneurons in a future paper on the longitudinal nerve fibre tracts.

The general features of the cell bodies of *Periplaneta* were described by Pipa *et al.* (1959). Finer structure was studied by Hess (1958), Wigglesworth (1960) and Smith & Treherne (1963) and reviewed, with additions, by Guthrie & Tindall (1968). A general review of the fine structure of insect cell bodies was given by Lane (1974). Ashhurst (1961) and Pipa (1961, 1962) examined the cytology and cytochemistry of cell bodies in *Periplaneta*. Cohen & Jacklet (1967) mapped the motoneuron somata of the metathoracic ganglion 20 μm or more in diameter and Young (1969, 1972, 1973) mapped some of those of the mesothoracic ganglion, using as a marker the perinuclear ring of RNA produced in neurons after injury to their axons. Young was also able to trace a few in both meso- and metathorax to the muscles they innervate. Further

work, reviewed by Pipa & Delcomyn (1981), has been concerned mainly with identifying somata and mapping the processes of particular motoneurons, largely in the metathoracic ganglion (Rowe *et al.* 1969; Crossman *et al.* 1971; Iles & Mulloney 1971; Iles 1972*a*; Pearson & Bradley 1972; Pearson & Fourtner 1973, 1975; Denburg *et al.* 1977; Fourtner & Pearson 1977; Denburg 1982; Ritzmann *et al.* 1983) but also in the mesothoracic (Iles 1972*b*; Whitington 1979; Reep *et al.* 1980; Ritzmann *et al.* 1983) and prothoracic ganglia (Iles 1976; Reep *et al.* 1980). Pearson & Fourtner (1975) located the cell body of a metathoracic intraganglionic interneuron, and Reep *et al.* (1980) and Delcomyn (1983) have described some interganglionic interneurons, with somata in the pro- and mesothoracic, and meso- and metathoracic ganglia respectively. Recently attention has been given to mapping somata showing immunoreactive responses, either like the pentapeptide proctolin (Bishop & O'Shea 1982) or pancreatic polypeptide-like (Endo *et al.* 1982). However, so far no comprehensive account has been given of all the cell bodies of any ganglion or of the pathways of the majority of the fibre bundles that arise from them.

This paper describes the groups of cell bodies that lie in the midline of the ganglion. Further papers (III and IV) are in preparation dealing respectively with the anterior and posterior paired cell groups that lie on either side.

Materials and methods

Adult male *Periplaneta americana* (L.), 2–14 weeks after their adult moult, were used. Altogether around 300 specimens were studied. A wider range of methods than in the first paper (Gregory 1974*a*) was employed to display the various aspects of structure. General arrangement and appearance of the groups of neuron cell bodies was determined from reduced silver-stained sections; more detail of neuron pathways was obtained from Procion yellow or cobalt filled specimens; general disposition of the cell bodies was studied in toluidine blue-stained wholemounts; and some additional information on tracheation of the ganglion was gained by filling the tracheae with trypan blue.

For all methods except trypan blue tracheal filling, ganglia were dissected from CO_2-narcotized cockroaches under the saline of Yamasaki & Narahashi (1959). Those for silver staining were fixed in alcoholic Bouin (Duboscq-Brasil), previously 'aged' to improve its action (Gregory 1970), or in later work the synthetic mixtures derived from it (Gregory 1980*a*; Gregory *et al.* 1980). They were stained with eosin during dehydration, to aid orientation for sectioning, embedded in Gurr's Paramat (Searle Diagnostic, High Wycombe, Buckinghamshire, U.K.), and sectioned at 10–20 μm. Sections were stained by the Bodian (1936) protargol (silver–protein) method, usually in the Power (1943) double impregnation modification, but later using a single impregnation technique (Gregory 1980*b*). Full practical details are given elsewhere (Gregory 1980*c*). For double impregnation copper concentration in the impregnating baths was 1.3 or 2.6 g 65 ml^{-1}, and developers contained 10 g l^{-1} hydroquinone and 40–100 g l^{-1} sodium sulphite ($Na_2SO_3 . 7H_2O$), pure enough to give the required clear red stain (Gregory 1974*b*). For single impregnation 1.3 g of copper were used, and 25–100 g l^{-1} sulphite, depending on fixation.

The fluorescent dye Procion yellow M-4R (Imperial Chemical Industries Ltd, Manchester, U.K.) (Kravitz *et al.* 1968; Stretton & Kravitz 1968) was used to fill nerve axons either by an immersion or a two-bath method. In the former (Gregory 1973) freshly dissected ganglia,

with the nerve or connective to be filled cut short and all others left as long as possible, were immersed in a saturated solution of the dye (< 20 g l^{-1} at 2 °C) in cockroach saline diluted to maintain isotonicity. In the two-bath method, developed from the axonal iontophoretic technique of Iles & Mulloney (1971), ganglia were immersed in saline and the nerve or connective to be filled led across a barrier of sealant (petroleum jelly or similar material) into a saturated solution of the dye (about 6%) in distilled water. Full practical details of both methods are given by Gregory (1980*d*). After filling for the necessary time (about 1–2 h at 2 °C by immersion; from < 30 min to overnight at 2–37 °C for the two-bath method, depending on length and thickness of axons being filled) ganglia were rinsed in saline and fixed, dehydrated and embedded as for Bodian staining, except for treatment with eosin, which itself fluoresces. They were then sectioned at 10–30 μm and sections dewaxed in xylene and mounted in Fluormount (E. Gurr, London, U.K.). They were examined by fluorescence microscopy, using Schott BG12 and BG38 (red absorbing) exciter filters and a Zeiss 50 barrier filter.

Cobalt filling (Pitman *et al.* 1972) of neurons was by a two-bath technique like that used for Procion yellow, and similar to that described by Pearson & Fourtner (1973), using saline in one bath and 0.5 M cobaltous chloride solution in the other. Filling time varied according to axonal length and diameter from 15 min to > 4 h at 37 °C or overnight at room temperature (20–25 °C). Ganglia were then treated with dilute (2.25% by volume) ammonium sulphide solution, washed in saline and fixed in freshly mixed Carnoy (1886) (3:1 ethanol:acetic acid) for at least half an hour. They were then washed in 90% (by volume) ethanol containing one drop of 10% (by volume) ammonium hydroxide per four millilitres (equivalent to about 0.135%) to neutralize acid from the fixative, to reduce solution of the cobalt sulphide precipitate, and dehydrated with ordinary ethanol grades, cleared in xylene and mounted in neutral Canada balsam.

Cell bodies were stained with toluidine blue by the method of Altman & Bell (1973), discussed further by Altman (1980). Staining time in the borate buffered dye solution was 10–20 min at 37 °C and ganglia were then differentiated and fixed in the Bodian (1937) no. 2 mixture for 20–30 min at room temperature, depending on staining time and the type of result desired. They were then dehydrated in ethanol grades, cleared in xylene and mounted in neutral Canada balsam.

Tracheae were filled with trypan blue using the procedure of Hagmann (1940), in which air is evacuated from the tracheal system of the whole insect and replaced with dye solution by atmospheric pressure. Total staining time ranged from 20 to 45 min. Fixation overnight in a solution containing barium chloride then precipitates the dye in the tracheae. Ganglia were dissected out in 20% (by volume) ethanol and then dehydrated, cleared and mounted as usual. The method is fully described by Gregory (1980*e*).

Figures were drawn using a Zeiss camera lucida fitted to a Photomicroscope II. Coloured pens were used as in the previous study (Gregory 1974*a*) to assist in the mapping of details from successive sections. Orientation is marked on each figure. The numbers of neurons given for each cell body group are based on counts of both somata visible and the number of fibres in their fibre bundles. An Arnold (1969) portable electronic counter (Burkard Manufacturing Co. Ltd., Woodcock Hill, Rickmansworth, Hertfordshire, U.K.) was used as before (Gregory 1974*a*) to aid counting.

General structure and classification of neuron cell bodies

The unipolar cell bodies, mostly of efferent, presumed motoneurons and interneurons, lie peripherally in the ganglion, in the outer layer of glial cells around the central fibrous ganglion core. The cell bodies are ovate or pyriform in shape but vary in size and in the relative volumes of nucleus and cytoplasm. Pipa *et al.* (1959) distinguished two extreme types based on these criteria: large, ovate cells with relatively much cytoplasm; and small 'globuli' cells with little cytoplasm and relatively large nuclei. Ashhurst (1961) divided them similarly. Hess (1958) and Wigglesworth (1960) were able to distinguish two morphological types in thinner sections: 'dark cells', with dark-staining, electron-dense cytoplasm and few cytoplasmic spaces; and 'light cells', with pale, less dense cytoplasm containing many clear spaces. Smith & Treherne (1963) found gradations between these extremes and suggested that the differences might result from an unusually sensitive response of the cells to the preparative treatments used. Pipa (1961, 1962), using cytochemical methods, found that cells stained lighter or darker according to the degree of vacuolation of the cytoplasm and the pattern of distribution of its RNA. In the following account cell bodies are classified for descriptive purposes into three types, based primarily on size: large, with a maximum diameter, at right-angles to the long axis, of > 30 μm; medium, 20–30 μm; and small, < 20 μm. These divisions are somewhat arbitary but have some cytological basis. Sizes are those in fixed and stained material and make no allowance for shrinkage due to the methods of preparation. The large somata range in diameter up to 80 μm and though few in number are conspicuous. Their relatively large amount of cytoplasm stains deeply in Bodian silver preparations and has a vesicular appearance like that illustrated by Hess (1958), Wigglesworth (1960) and Pipa (1961, 1962) and interpreted as dictyosomes (Golgi bodies) – the clear, rounded spaces – with fine granules of RNA in between. The medium-sized cells are more numerous and their relatively smaller amount of cytoplasm stains less and appears faintly vesicular only in the larger cells of the type. The small cells far outnumber those of the other types – Cohen & Jacklet (1967) found that 3192 of the 3422 cell bodies they counted in the metathoracic ganglion were less than 20 μm in diameter. The small cells range in size down to 12 μm in diameter and have only a little, pale cytoplasm, which appears homogeneous. They are never as small or have so little cytoplasm as the globuli cell somata of the corpora pedunculata of the brain, however. Thus it is perhaps preferable not to extend the term 'globuli cells', with its connotations of special association function (Bullock & Horridge 1965), to the small cells of the thoracic ganglia, as did Pipa *et al.* (1959), at least until the functions of these are better known. The nuclei of all three cell types stain darkly in Bodian silver preparations and the chromatin is generally displaced to the inner side, an artifact presumably caused by the ethanol in the alcoholic Bouin fixative (Baker 1950; Hess 1958). Nuclear diameter ranges from about 35 μm in the largest cells down to 10 μm, but decreases more gradually than cell diameter, in accordance with the change in the ratio of nuclear to cytoplasmic volume. The processes that arise from the cell bodies vary in diameter from 10 μm down to 2 μm or less in the region nearest the cell body, the 'link segment' of Cohen (1970), but may be considerably bigger farther away from it. As noted by Pipa *et al.* (1959), larger cells generally have the thicker processes. In the descriptions of fibre pathways that follow, the same categories of fibre size are used as in the first paper (Gregory 1974*a*): giant, > 20 μm in diameter; large, 12–20 μm; medium, 5–12 μm; small, 2–5 μm; very small, < 2 μm.

The cell bodies are arranged mainly ventrally and laterally in the ganglion, with a small

number dorsally (figure 1; figure 4, plate 1). They are divisible into more or less well-defined groups according to where their processes enter the ganglion core, the cells of a group all contributing processes to one fibre bundle or, sometimes, to a few closely associated bundles. The cell bodies vary in their positions within a group but generally the points of entry of the fibre bundles into the core are more constant and reliable. The groups can be conveniently considered under three headings: median groups, in the midline between the halves of the ganglion core; and anterior and posterior paired groups on either side. For brevity, as in the first paper (Gregory 1974*a*), the cell groups and other structures will generally be referred to after the first mention only by their abbreviations. All are listed at the end of the paper.

The principal tracheae of the ganglion, which form useful landmarks, were briefly described and illustrated in a simplified drawing in the earlier paper (Gregory 1974*a*). A photograph of the ventral view of the tracheal system, filled with trypan blue, is included in the present account (figure 5, plate 1) the better to show its real appearance and for comparison with figures of the tracheation of the locust central nervous system, filled with cobalt (Burrows 1980). Trypan blue filling shows the ganglion to be even more highly tracheated than previously supposed from silver- and Procion yellow-stained sectioned material. The major tracheal branches are mostly arranged as in the earlier generalized drawing, but there seems always to be some variation from the basic plan, as illustrated by the absence of the anterior median trachea (AMTr) on the right hand side (true left) and the second median trachea (MTr2) on the left hand side (true right) in the present specimen. It is planned to discuss the extent of such variation, in this and the other ganglia of the ventral nerve cord, in a separate paper (G. E. Gregory, in preparation).

Median neuron cell body groups

Seven median cell body groups can be distinguished. They are named here according to position, the anterior median (AM), mid-dorsal median (MDM), posterior dorsal median (PDM), posterior median (PM), anterior ventral median (AVM), mid-ventral median (MVM) and posterior ventral median (PVM) groups (figures 1, 2). Some were illustrated, but not described, in paper I (Gregory 1974*a*) (figure 6, plate 21). In the following descriptions the characteristics of each group are given in much the same order: general appearance and position; number and sizes of constituent somata; number of fibre bundles; description and pathway of each bundle. Where more than one bundle arises from a cell group the bundles are numbered in the order most convenient for description, generally from anterior to posterior or dorsal to ventral. When they are referred to subsequently usually only the abbreviation for the cell group, followed by the bundle number in parentheses, is quoted: for example, PDM(1) is bundle 1 of the posterior dorsal median group. The position and limits of cell body groups and the courses of their fibre bundles are frequently described in relation to the longitudinal and transverse tracts or other major features of the ganglion (see Gregory 1974*a*), rather than by a series of measurements from particular reference points, for much of the information was gained from sectioned material, in which those features are very obvious. This should not prove a disadvantage to workers without access to such material for comparison, because the major tracts, tracheae and so on can still be seen, even when unstained, in cobalt or toluidine blue-stained wholemounts, if microscope illumination is suitably adjusted, usually simply by closing down the substage diaphragm.

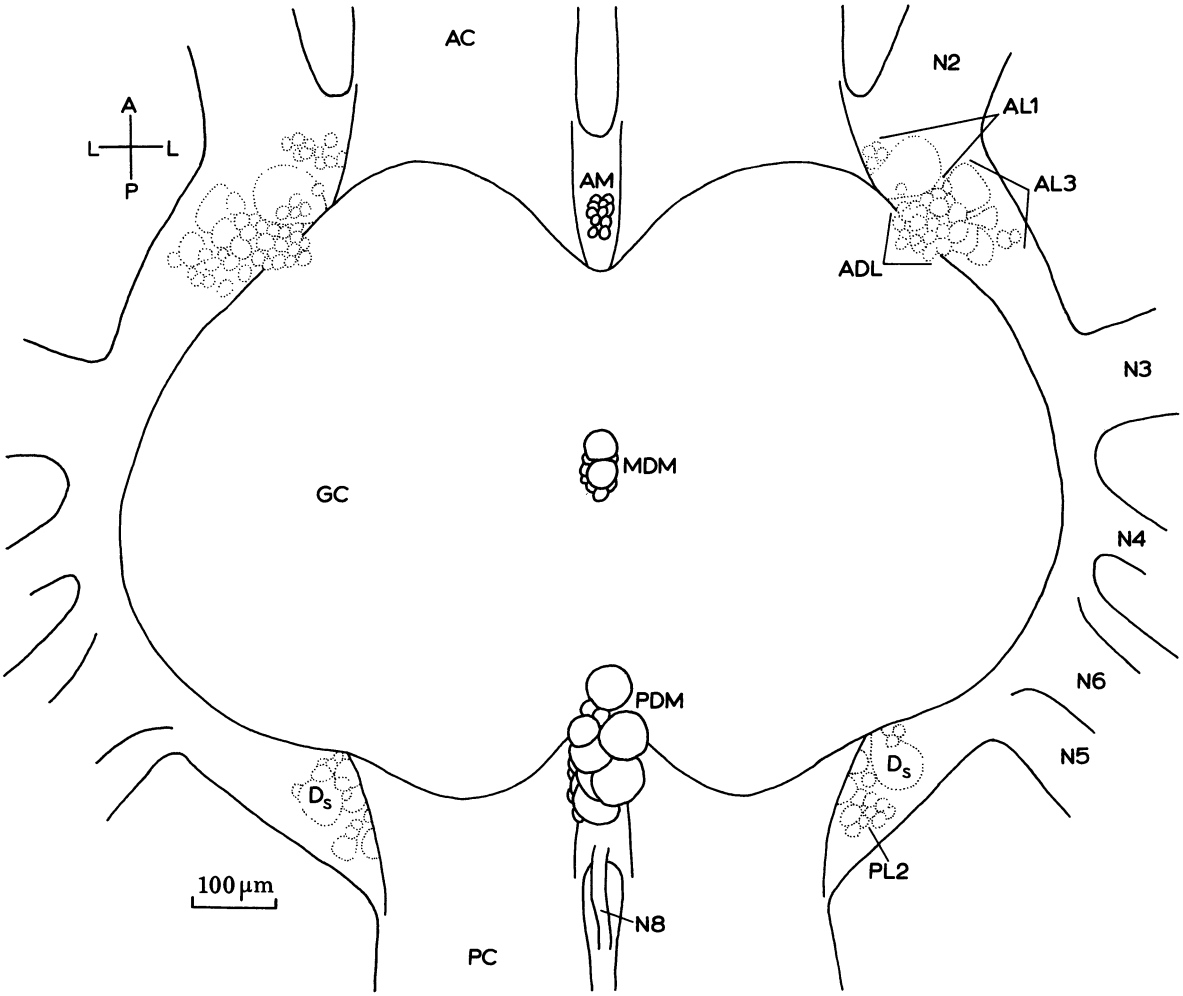

FIGURE 1. Arrangement of median cell body groups of mesothoracic ganglion visible in dorsal view of wholemount; paired cell body groups shown dotted.

Anterior median group

(AM; figures 1–3; figure 6, plate 2; figures 15, 19, plate 3; figure 26*a*.) A very small group of 10 or 11, occasionally as few as seven, small somata, which lies between the bases of the anterior connectives (AC). Its vertical position varies. Usually the cell bodies form a compact group between the dorsal and ventral median longitudinal tracts (DMTs, VMTs), but often they lie more ventrally, in front of the anterior mass (a. VAC) of the ventral association centre (VAC). Sometimes they are more scattered and some or most of the somata lie more dorsally, above the level of the DMTs. The very small fibres that arise from the cell bodies form a usually fairly tight bundle, which runs posteriorly in the midline between the two halves of the ganglion core, more or less horizontally. The fibres give off fine anterolateral branches to each side, which arborize close to the anterior core margins, into neuropil between the DMT, VMT and ventral intermediate tract (VIT). The main bundle passes below or through dorsal commissure I (DCI), occasionally above it when the somata are located more dorsally, and gives very small dorsal branches into neuropil towards dorsal commissure II (DCII). It then passes between

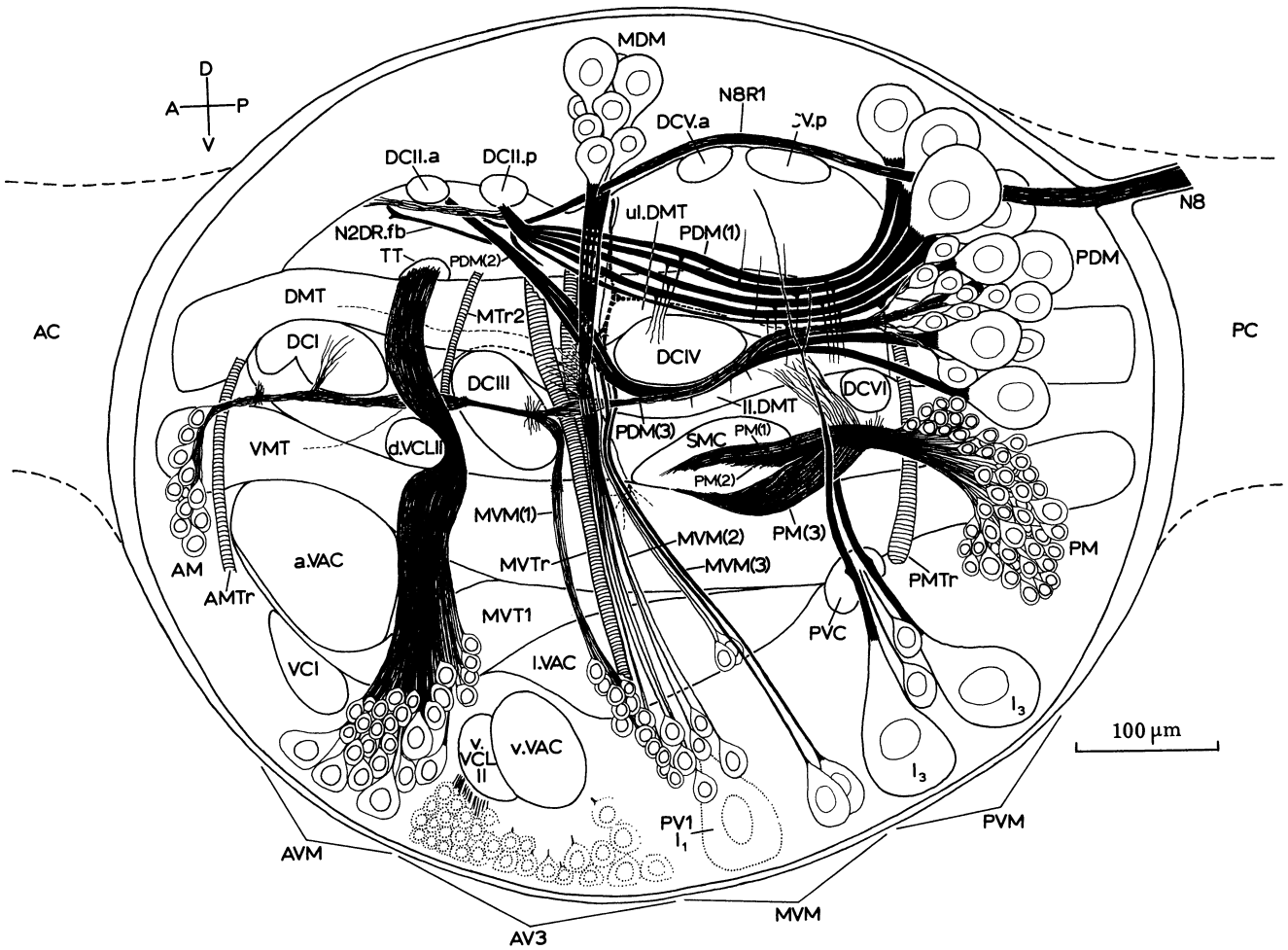

FIGURE 2. Arrangement of median cell body groups and neighbouring structures in midline region of ganglion.

the two ascending fibre bundles from the AVM cell body group that form part of the T-shaped tract (TT), to reach the anterior region of dorsal commissure III (DCIII). Here the fibres fork to give a group of branches to each side. These merge with two bundles of very small branches of the similarly forking fibres of the intermingled bundle 3 of the PDM cell body group and bundle 1 of the MVM group (figure 17, plate 3). The combined bundle of each side runs laterally in DCIII and then turns anterolaterally above the VIT to enter the mid-dorsal or dorsolateral side of this tract (figure 19, plate 3). Here it merges with a bundle of extremely fine fibres from posteriorly (FBP), which run in the upper mid-region of the VIT and leave the ganglion in the anterior connective. It was not, however, possible to be certain whether the AM–PDM–MVM fibres continue this far.

Mid-dorsal median group

(MDM; figures 1, 2; figure 7, plate 2; figures 13, 14; figure 15, plate 3; figure 26*b*.) This small group, easily identifiable by its central position in the dorsal side of the ganglion, lies

in the dorsal midline cleft (DMC) and is the most dorsal of all the cell groups. It is widely separated by glial areas from the AM group anteriorly and the PDM group posteriorly. Its size varies. It consists of two large somata and one medium-to-large one but between 4 and 11 small-to-medium sized ones; all are closely packed together. Their relative positions vary but the two large cell bodies normally lie either directly or diagonally closely one behind the other. The bundle of mainly small fibres runs vertically downwards between the DMTs, behind DCII and in front of dorsal commissure V (DCV). The processes of the two large cell bodies soon loop laterally and then dorsally again, one to each side of the ganglion, through the DMTs,

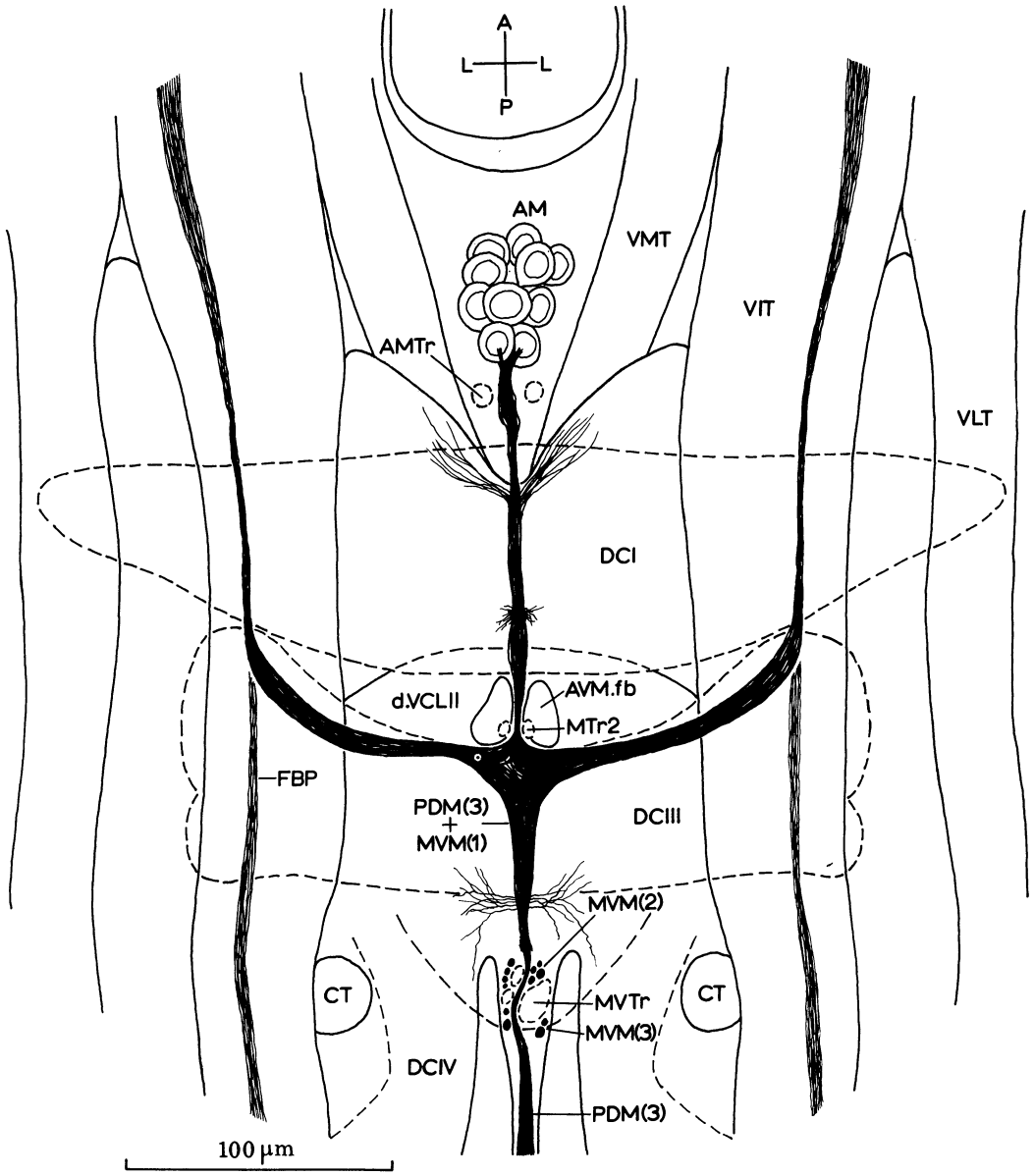

FIGURE 3. Pathways of fibres of anterior median (AM) cell body group and of bundle 1 of mid-ventral median group (MVM(1)) and bundle 3 of posterior dorsal median group (PDM(3)) in mid-region of ganglion core; frontal section, dorsal view. Positions of dorsal commissures I, III and IV, above other structures, shown in broken lines.

and follow the course described in paper I (Gregory 1974*a*) to form part of the dorsal root of nerve 2 (N2DR). The pathway of one is shown in figure 13. At or slightly below this point a few of the smaller MDM fibres also loop laterally, one or two to each side of the ganglion, and those of one side or the other usually pass under the ventral bundle of medium-sized fibres (bundle 2) from the PDM group. They then turn dorsally and run with the N2DR fibre through the DMT, but soon become confused with other, so far unidentified fibres and are lost. The rest of the MDM fibres continue ventrally, in front of or alongside the prominent mid-ventral tracheae (MVTr), at least as far as the ventral limit of the DMTs. Two certainly, one each side of the midline, continue downward, between DCIII in front and dorsal commissure IV (DCIV) behind, and then turn forward under DCIII to join the dorsal margins of the VMTs. They begin to run anteriorly in these but are soon lost among their many fibres. How far they continue is still unknown.

Posterior dorsal median group

(PDM; figures 1–3; figures 6–9, plate 2; figures 13, 14; figures 15–17, 19, plate 3; figure 26*a*, *c*.) This conspicuous group forms a narrow dorsoventral band between the bases of the posterior connectives (PC). It extends down posteriorly as far as, or a little below, the mid-level of the ganglion, where it abuts on the PM cell body group. It includes eight large cell bodies, one of which is often smaller than the rest, which correspond to the somata of the dorsal unpaired median (DUM) group of neurons reported in the metathoracic ganglion by Crossman *et al.* (1971), and between 6 and 12, most frequently eight to ten, small ones, grouped in a variable manner among the others. The root of the median nerve, nerve 8, (N8R1) passes forward between them. The neuron processes enter the ganglion core in the posterior midline between the DMTs and pass between DCV above and dorsal commissure VI (DCVI) below. They form three bundles, the pathways of the two largest of which around DCIV form a highly characteristic pattern (figure 2). This is repeated in the other ventral nerve cord ganglia and provides a valuable means of distinguishing individual ganglia in composite masses such as the suboesophageal ganglion and the terminal abdominal ganglion (G. E. Gregory, in preparation).

Bundle PDM(1)

The most dorsal bundle, of four medium-sized fibres, arranged for the most part one above the other, and one small one, usually below the others, runs forward immediately above DCIV. The fibres give off a succession of small and very small ventral and posteroventral branches to DCVI and neuropil in front of it, and to DCIV; also very small dorsal branches towards DCV. The main fibres then pass between the descending fibres of the MDM group and give off very small ventral branches. These run down with the MDM fibres and then, like some of them, loop laterally and then dorsally again, some to each side of the ganglion. Those of one or other side usually pass under the lower bundle (bundle 2) of medium-sized PDM fibres (see below), just as some of the MDM fibres do, but they are readily distinguished from the MDM fibres by being much finer. They pass up through the DMTs and seem to ramify into

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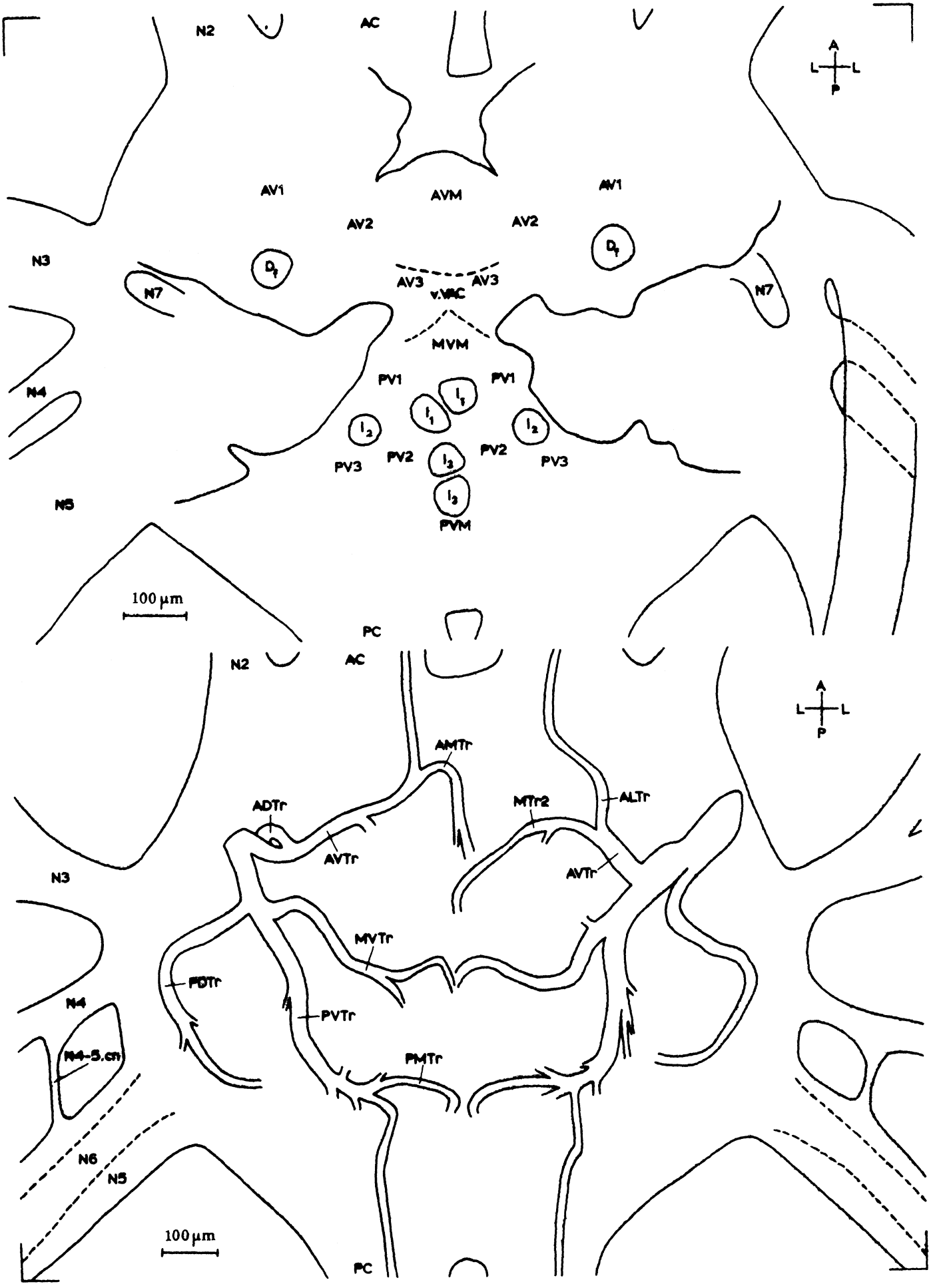
DESCRIPTION OF PLATE 1

FIGURE 4. Ventral view of whole mesothoracic ganglion stained with toluidine blue, showing limits of regions occupied by neuron cell bodies and positions of some identified cell bodies and groups.

FIGURE 5. Ventral view of whole ganglion with tracheal system filled with trypan blue.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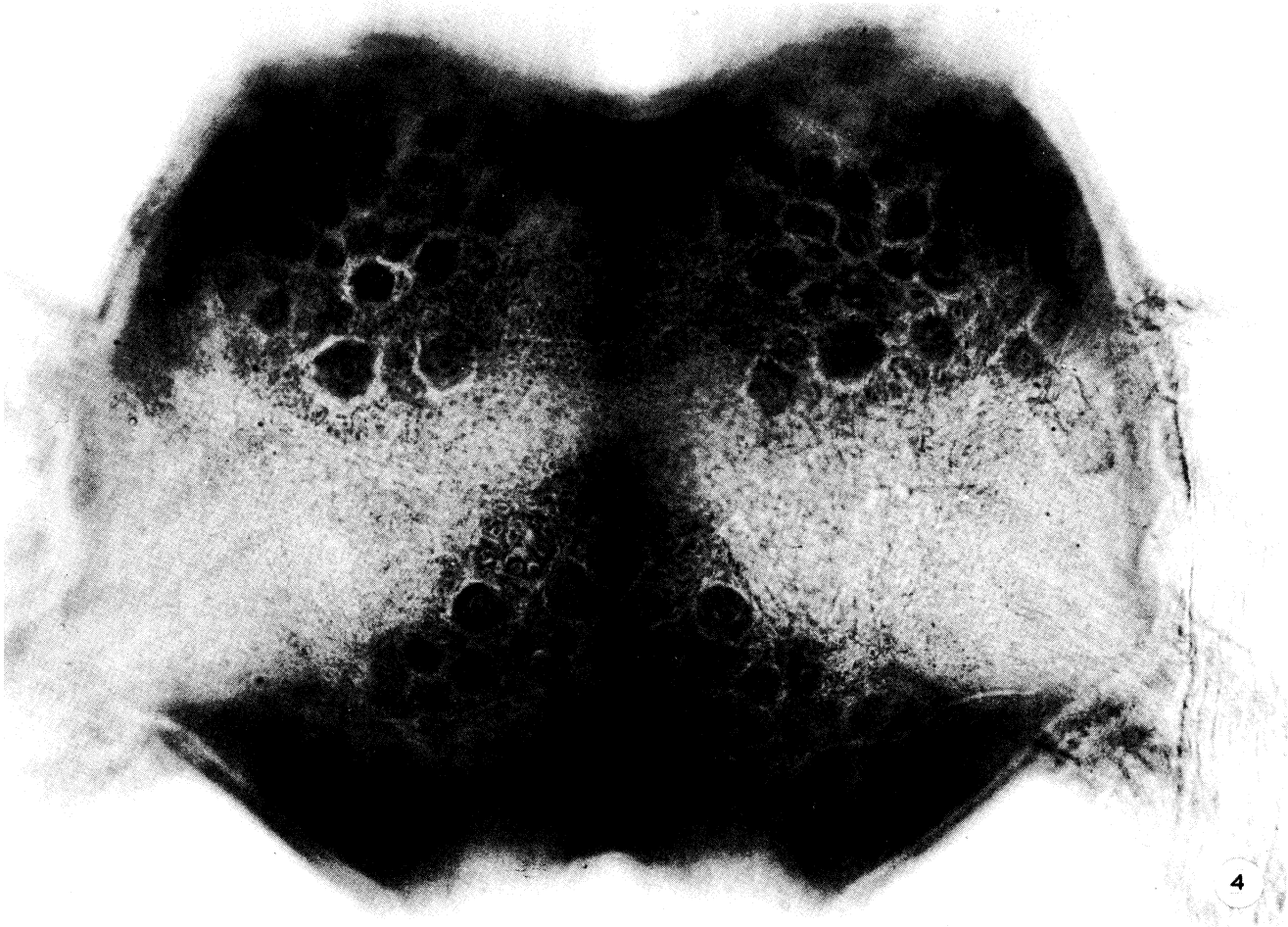

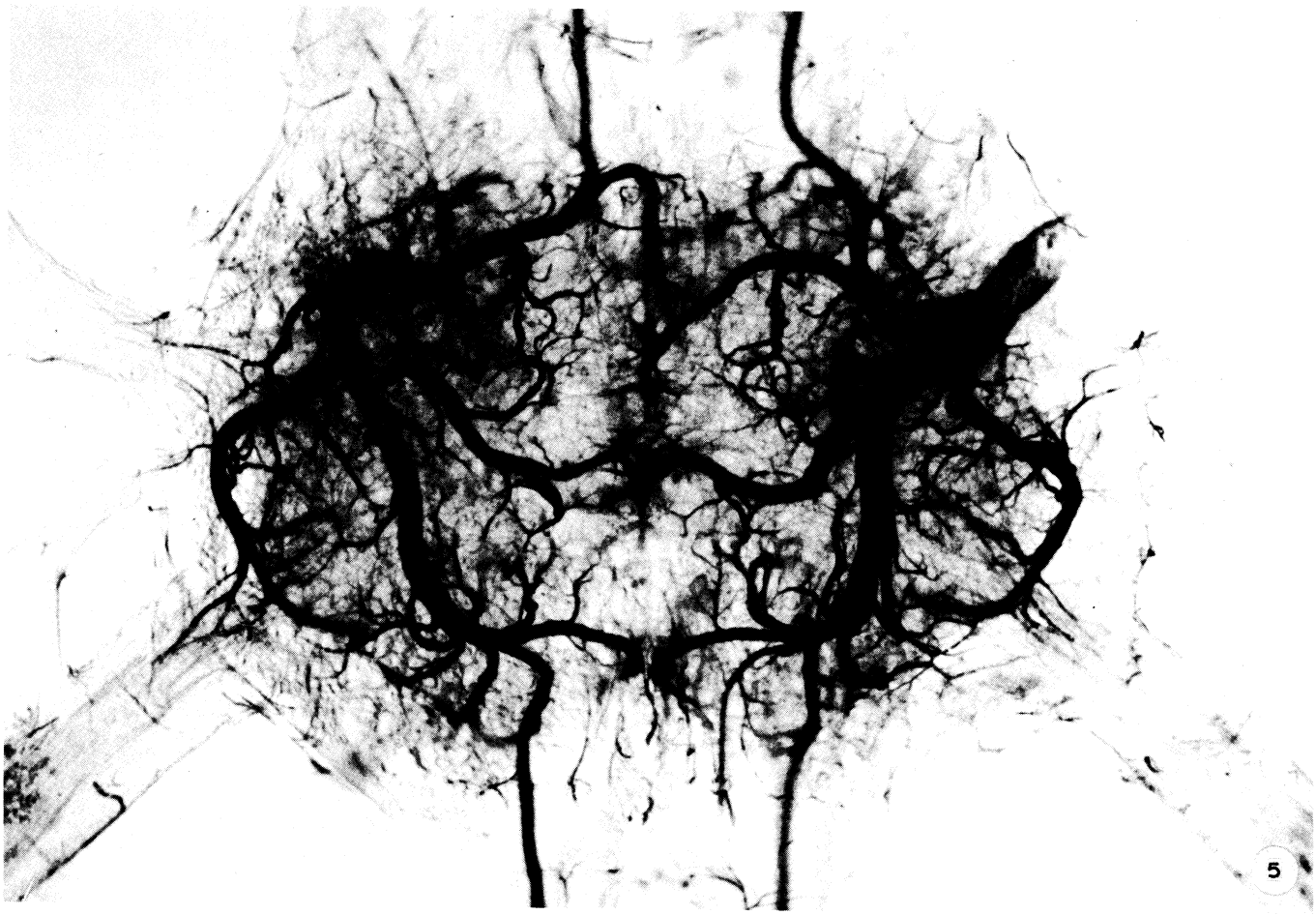

FIGURES 4 AND 5. For description see opposite.

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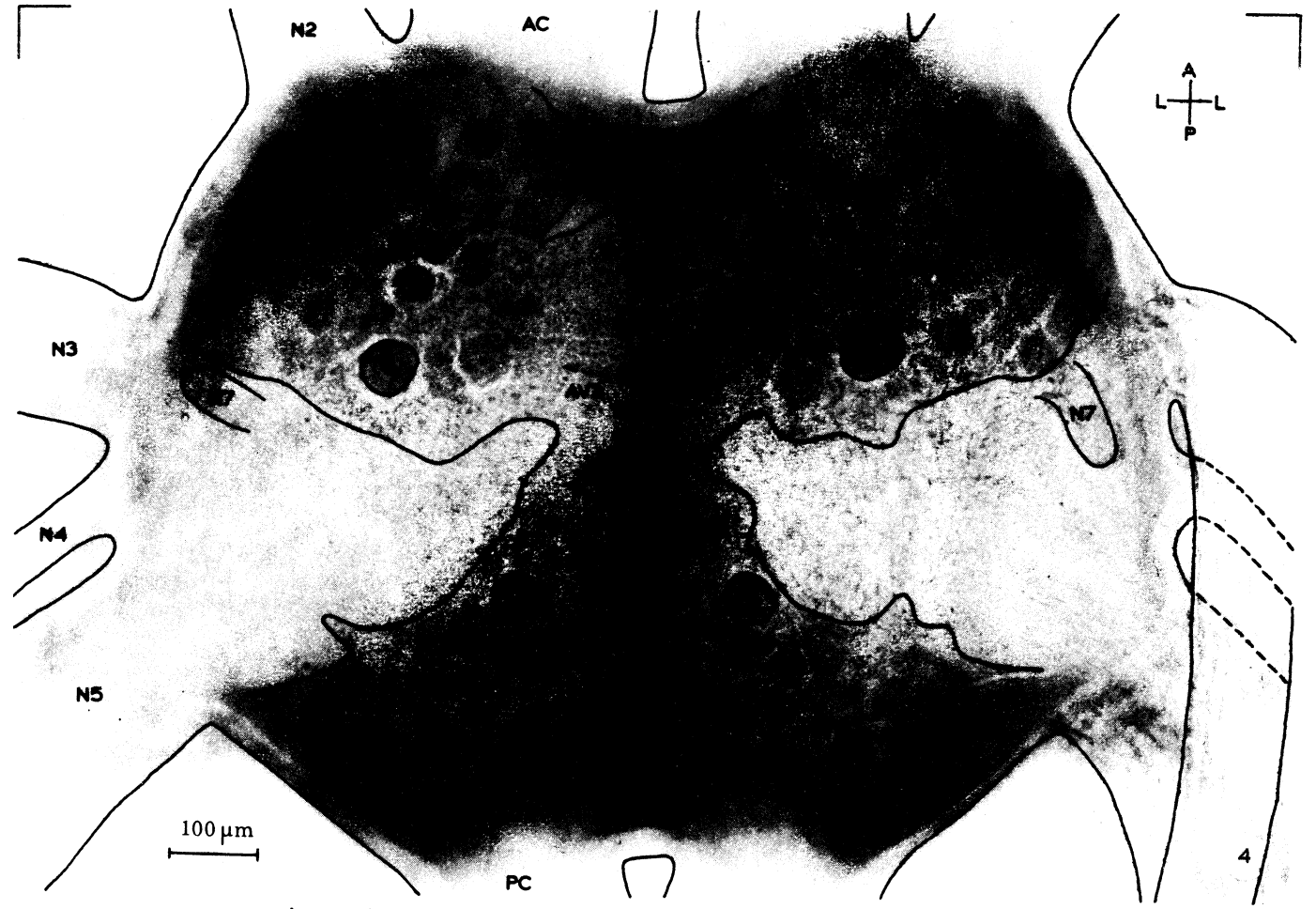

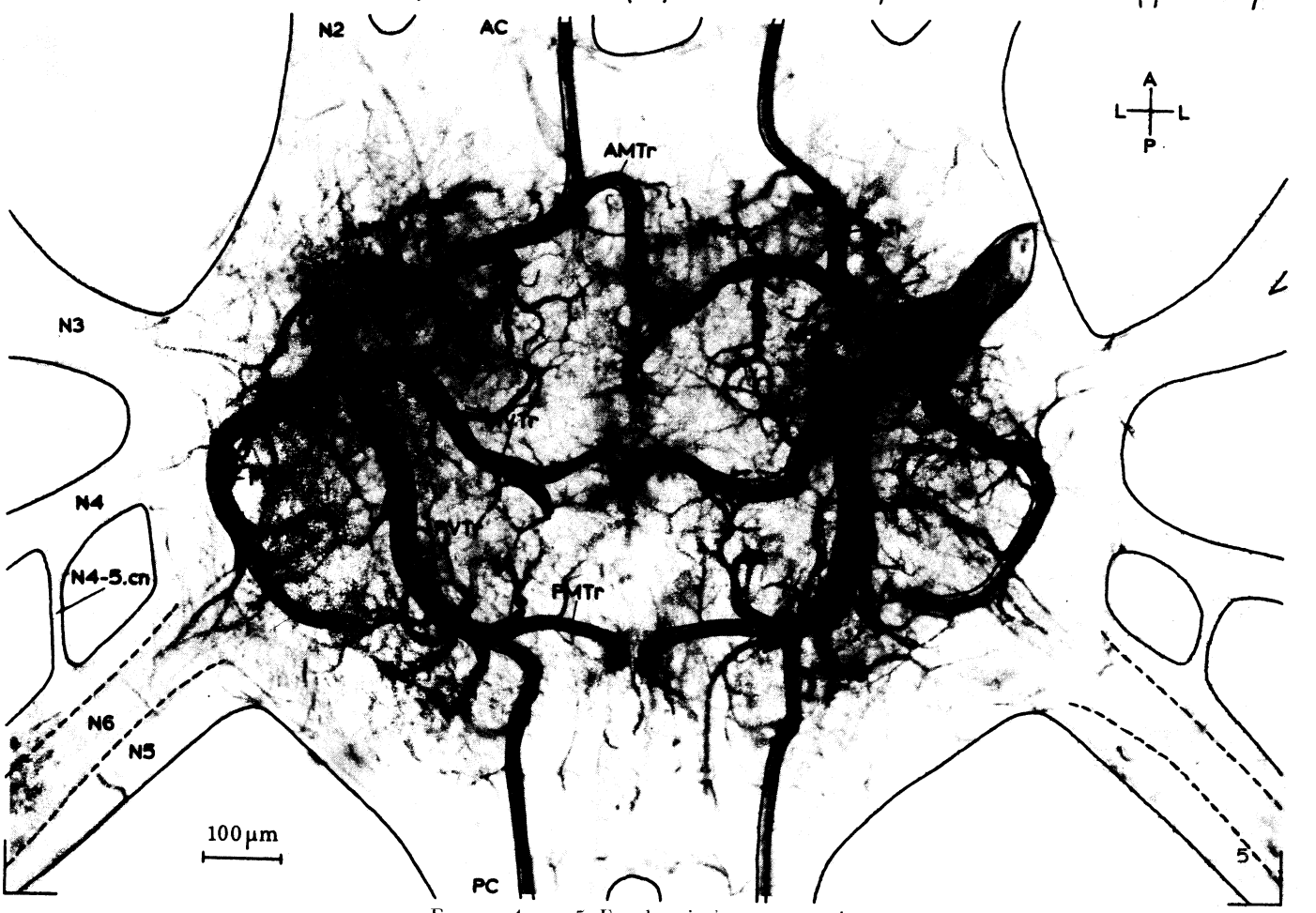

FIGURES 4 AND 5. For description see opposite.

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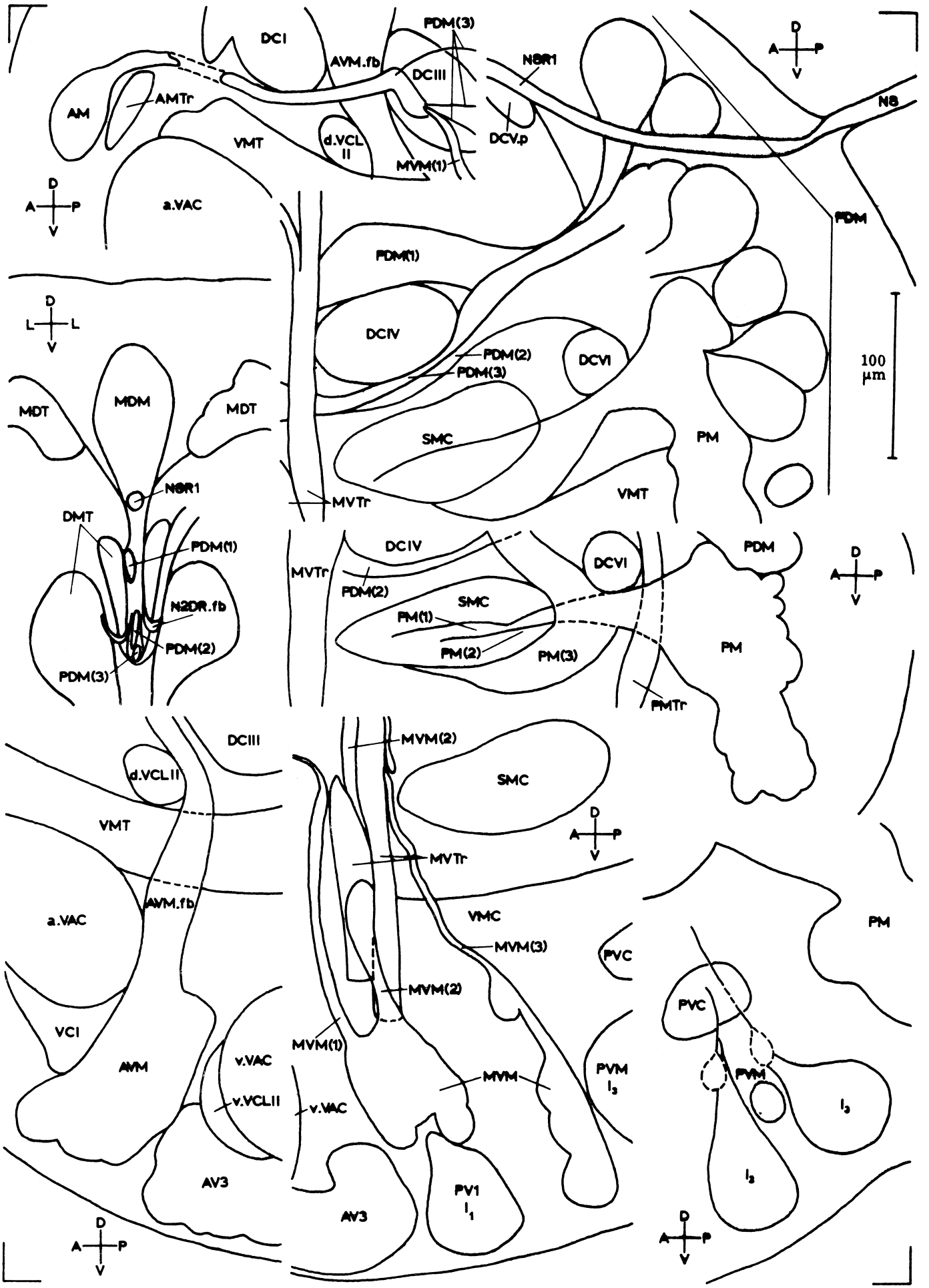
DCI
PDM(3)
AVM.fb
DCIII
NBR1
AM
AMTr
VMT
d.VCL II
MVM(1)
DCV.p
NB
a.VAC
PDM
PDM(1)
DCIV
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PDM(3)
DCVI
100 µm
MDT
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SMC
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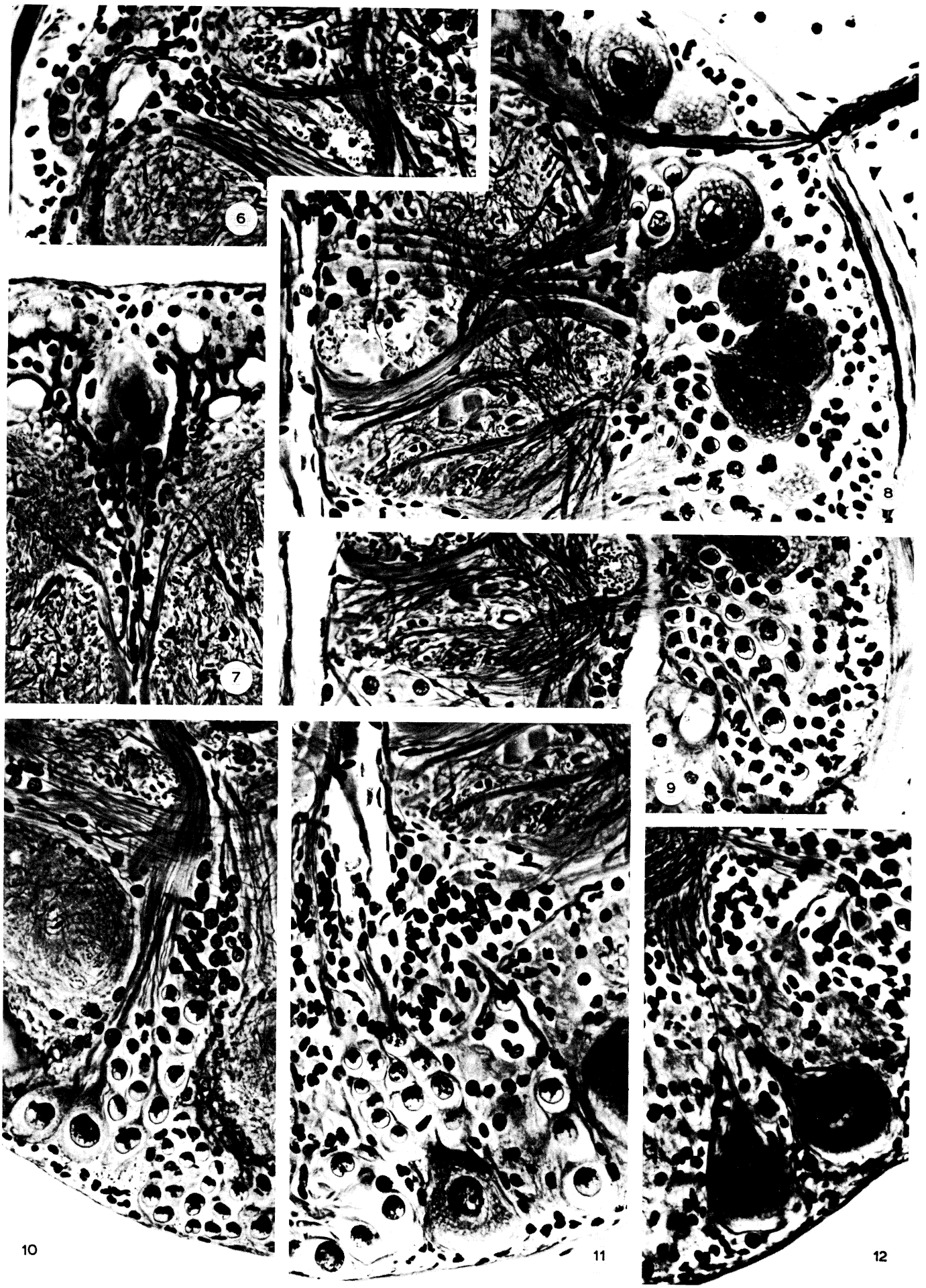
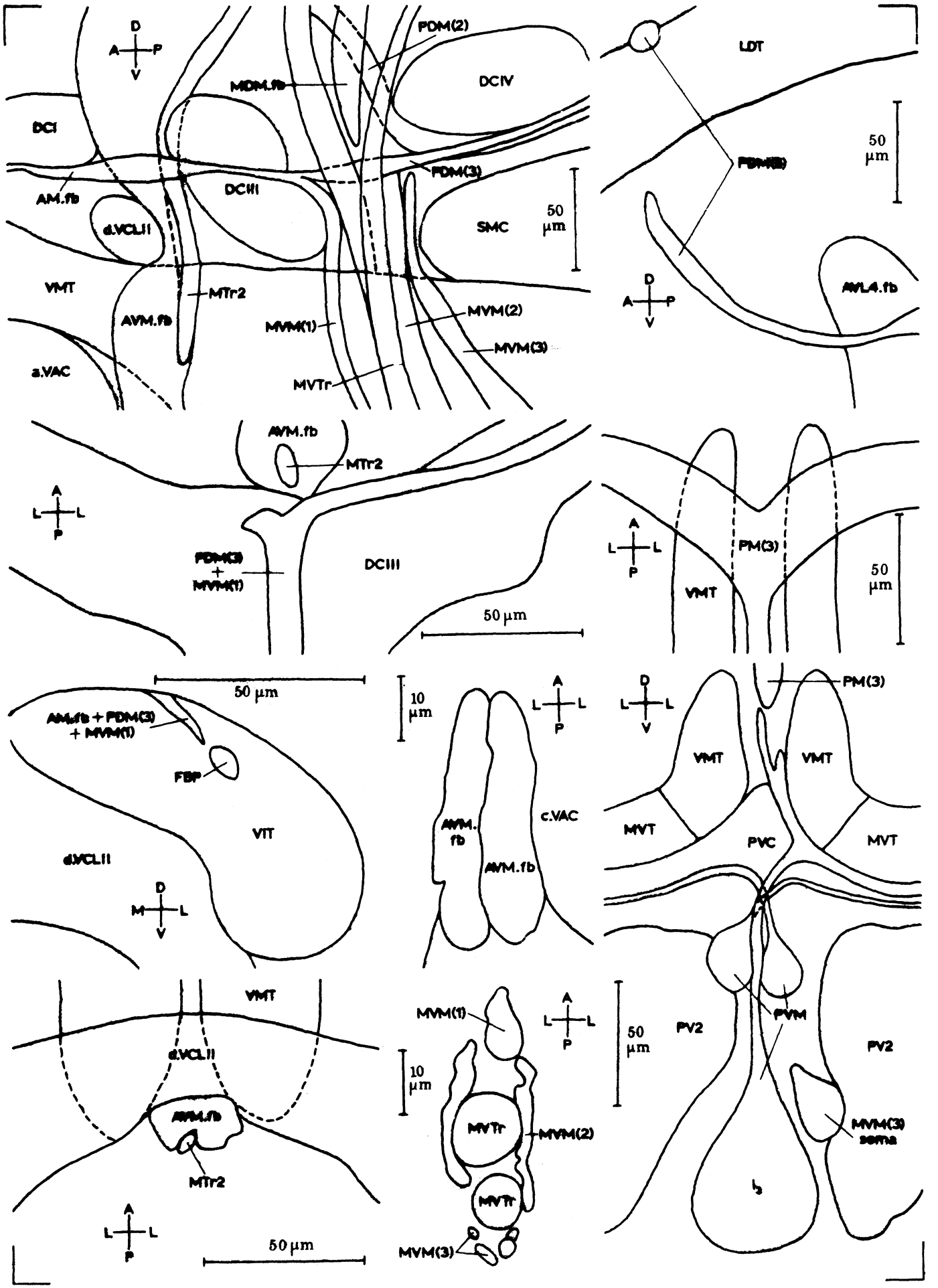
MVM(3)
MVM(2)
MVM(1)
v.VAC
MVM
PVM
I_3
AV3
PV1
I_1
PM
PVC
PVC
PVM
I_3
I_3



FIGURES 6–12. For description see opposite.

FIGURES 6–12. For description see opposite.


D
A
P
V
PDM(2)
MDM.fb
DCIV
DCI
PDM(3)
AM.fb
DCIII
SMC
50 µm
d.VCL.II
VMT
MTr2
AVM.fb
MVM(1)
MVM(2)
MVM(3)
a.VAC
MVTr
LDT
PDM(3)
50 µm
AVL4.fb
AVM.fb
MTr2
A
L
L
P
PDM(3) + MVM(1)
DCIII
50 µm
PM(3)
VMT
50 µm
50 µm
AM.fb + PDM(3) + MVM(1)
FBP
VIT
d.VCL.II
D
M
L
V
10 µm
AVM. fb
AVM.fb
c.VAC
PM(3)
VMT
VMT
MVT
PVC
MVT
VMT
d.VCL.II
AVM.fb
MTr2
MVM(1)
10 µm
MVTr
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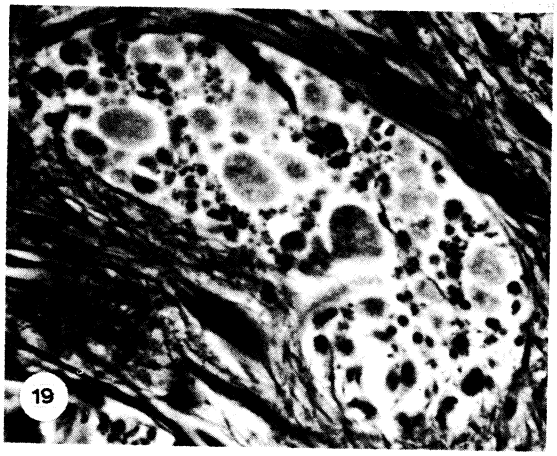
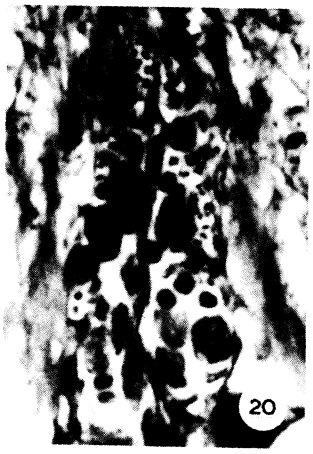
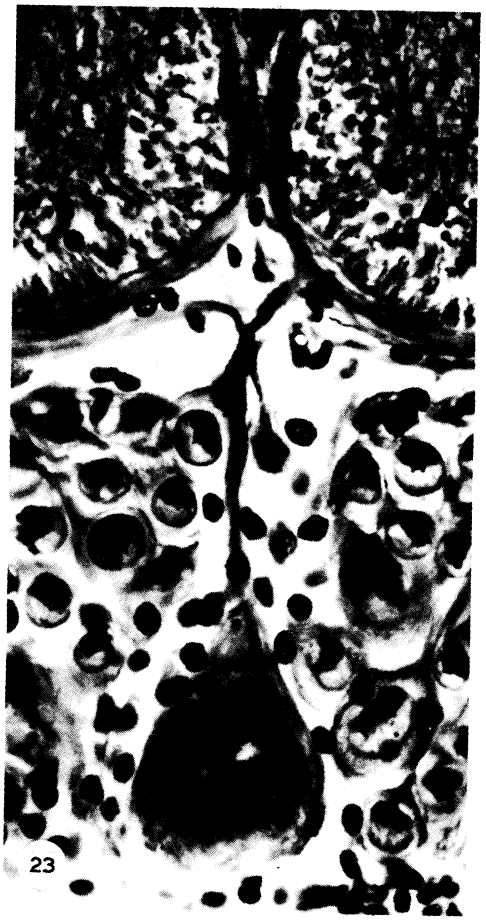
MVTr
MVM(3)
50 µm
PV2
PVM
PV2
MVM(3) sema
b







FIGURES 15–23. For description see opposite.

FIGURES 15–23. For description see opposite.

Description of plate 2

Median cell body groups, in Bodian silver preparations; all same scale (see figure 8).

Figure 6. Anterior median (AM) group; sagittal section of ganglion, 10 μm thick.

Figure 7. Mid-dorsal median (MDM) group; 10 μm transverse section of ganglion.

Figure 8. Posterior dorsal median (PDM) group; 10 μm sagittal section of ganglion.

Figure 9. Posterior median (PM) group; 10 μm sagittal section of ganglion.

Figure 10. Anterior ventral median (AVM) group; 10 μm sagittal section of ganglion

Figure 11. Mid-ventral median (MVM) group; 10 μm sagittal section of ganglion.

Figure 12. Posterior ventral median (PVM) group; 20 μm sagittal section of ganglion

neuropil between the DMTs and the median dorsal tracts (MDTs). The main fibres then fork to form two bundles of branches, one to each side of the ganglion; they also send very small branches anteriorly into neuropil above the DMTs. The main bundles diverge and turn anterodorsolaterally beneath the posterior part of DCII and pass above the diverging halves of N8R1. Each bundle then runs laterally, curving through the MDT and above the lateral dorsal tract (LDT), to the edge of the ganglion core. The four medium-sized fibres and one small one here lie side by side, one behind the other (figure 14). They follow the curve of the core margin ventrolaterally, then posteroventrally, and pass just outside nerve 6, dorsal root 1 (N6DR1) where it leaves the ganglion core. Here, just above where the widespread common inhibitory motoneuron, I_3 (Fourtner & Pearson 1977), branches to nerves 3 and 4 anteriorly and to join N6DR1 posteriorly (see paper I (Gregory 1974*a*), figure 24, where it is designated the posterior fibre of nerve 4, root 2 (N4R2.p)), some of the PDM(1) fibres give off very small branches that run posteriorly and slightly ventrally with nerve 6, dorsal root 2 (N6DR2), and perhaps also with nerve 6, dorsal root 3 (N6DR3), into the base of nerve 6. At least three of the main PDM(1) fibres then fork like the I_3 neuron, to give off very small anterior branches that seem to fork again to send extremely fine processes into the bases of nerves 3 and 4. Up to four, perhaps all five, of the main PDM(1) fibres, which are by this time small or very small, then continue posteroventrally and pass through the glial cell layer to the base of nerve 5. Here they join nerve 5, root 1 (N5R1) as an anterior component (N5R1.a), and leave the ganglion.

Bundle PDM(2)

The other three medium-sized fibres enter the core immediately below bundle 1 and then diverge from it to pass underneath DCIV. The fibres usually lie one above the other at first but then become more clumped together. They give off only a few very small dorsal and ventrolateral branches behind DCIV and then ventral and posterolateral ones beneath it.

Description of plate 3

Details of fibre bundles of median cell body groups; Bodian silver preparations.

Figure 15. Junction in dorsal commissure III of anterior median group fibres (AM.fb), bundle 3 of posterior dorsal median group (PDM(3)) and bundle 1 of mid-ventral median group (MVM(1)), and relationships with neighbouring bundles; 20 μm sagittal section of central region of ganglion core.

Figure 16. Bundle 2 of posterior dorsal median group (PDM(2)), lateral to lateral dorsal tract; 10 μm parasagittal section of anterolateral region of ganglion.

Figure 17. Forking of fibres of the combined bundle 3 of posterior dorsal median group (PDM(3)) and bundle 1 of mid-ventral median group (MVM(1)) in dorsal commissure III; 10 μm frontal section of anterior mid-region of ganglion core.

Figure 18. Fountain-like arrangement of fibres of bundle 3 of posterior median group (PM(3)) above ventral median tracts; 10 μm frontal section of posterior region of ganglion core.

Figure 19. Entry of combined bundle of fibres of anterior median group (AM.fb), bundle 3 of posterior dorsal median group (PDM(3)) and bundle 1 of mid-ventral median group (MVM(1)) into ventral intermediate tract; 10 μm transverse section of anterior mid-region of ganglion core.

Figure 20. Division of fibres of anterior ventral median group (AVM.fb) into paired bundles; 10 μm frontal section of anteroventral region of ganglion.

Figure 21. Compressed bundles of fibres of anterior ventral median group (AVM.fb) behind dorsal part of ventral commissural loop II; 20 μm frontal section of anterior mid-region of ganglion core.

Figure 22. Disposition of bundles 1–3 of mid-ventral median (MVM) group around mid-ventral tracheae; 10 μm frontal section of mid-ventral region of ganglion.

Figure 23. Pathways of fibres of posterior ventral median (PVM) group in posterior ventral commissure; 20 μm transverse section of posteroventral region of ganglion.

Under DCIV the fibres are tightly sandwiched between ventral fibres of the DMTs, which divide around DCIV into dorsal and ventral limbs. In front of DCIV the fibres rise anterodorsally to rejoin those of bundle 1 between the descending fibres of the MDM group. Here they usually pass above some of the very small, laterally looping MDM fibres and branches of bundle 1, as described above. The fibres continue anteriorly beyond those of bundle 1 and fork a little way in front of them, just behind the anterior part of DCII, to give a bundle of three branches to each side of the ganglion (figure 14). These lie in much the same transverse plane as the T-shaped tract that contains fibres from the AVM group. The PDM(2) branches arch through the MDT and above the LDT and are joined by a fourth, unidentified fibre (omitted from figure 14), which runs with them for the rest of their course. Like the lateral branches of bundle 1 the four fibres here run side by side. They run more anterolaterally than the lateral branches of bundle 1, crossing the LDT 100–120 μm in front of them. After passing above the LDT they turn ventrally around its lateral margin and then curve posteroventrally and finally posteriorly (figure 14; figure 16, plate 3), giving off various very small ventral, lateral and ventrolateral branches. They run back to the transverse level of DCIII, passing beneath the prominent bundle of fibres of anterior ventrolateral cell body group 4 (AVL4.fb), which contributes to nerve 3, root 3 (N3R3), nerve 4, root 1 (N4R1) and N6DR1. The PDM(2) fibres give dorsal and ventral branches to neuropil in front of and behind this bundle of fibres. They could not be traced to the base of any peripheral nerve.

Bundle PDM(3)

The very small fibres from the small cell bodies form a distinct, compact bundle, which follows a variable course anteriorly, sometimes passing with bundle 1 above DCIV, sometimes accompanying bundle 2 below it. Much of the way some slightly thicker fibres of unknown origin run with it. In either case, the bundle eventually passes beside or between the mid-ventral tracheae and then runs into the posterior region of DCIII, where it is joined by an equally small bundle of very small fibres of bundle MVM(1) from the MVM cell body group below (figure 15, plate 3). Rarely a few of the PDM(3) fibres separate from the rest and pass above DCIII to enter this commissure anteriorly. The intermingled bundles of PDM(3) and MVM(1) pass to the front part of DCIII, where their fibres fork to send lateral branches to both sides of the commissure (figure 17, plate 3). Each lateral bundle merges with the corresponding lateral bundle from the AM group, and the combined bundle runs into the dorsal side of the VIT, in which it continues anteriorly, as described under the AM cell body group above.

Posterior median group

(PM; figure 2; figures 8, 9, 12, plate 2; figures 18, 23, plate 3; figure 26*d*.) This compact, laterally compressed cluster of about 45–50 somata, which are mainly small, with a few medium-sized ones among them, lies between the bases of the posterior connectives immediately below the PDM group; some of its more dorsal cell bodies often mingle with the more ventral PDM ones. The neuron processes are mostly very small, with usually about four small ones lying more dorsally, and form a small, compact bundle that enters the ganglion core in the posterior midline between the ascending posterior median tracheae (PMTr). It passes under DCVI and runs forward in the midline, inclining slightly downwards, to enter the supra-median commissure (SMC). The more dorsal fibres seem to have few if any branches up to this point, but the rest branch below and a little in front of DCVI. Very small dorsolateral branches ramify

among the ventral fibres of DCVI where it extends laterally between the VIT, DMT and the dorsal intermediate tract (DIT), others incline more anteriorly into neuropil in front of DCVI, between it and DCIV and DCV, and a group of very fine branches goes more laterally, between the most dorsal fibres of the VMT, into neuropil behind the transverse level of DCVI, between the VIT, VMT and DIT. The main branches then thicken to become mostly small in size and curve anteroventrally into the SMC. This causes the whole bundle to spread dorsoventrally as it reaches the SMC, and its fibres become separated into three component bundles, one above the other. Their pathways become more difficult to follow, owing to the complexity of the SMC, but seem to be as follows.

Bundle PM(1)

The cylindrical dorsal bundle consists of about 15–20 very small fibres, together with a thicker, so far unidentified fibre not belonging to the PM group. They appear to be the continuations of the seemingly unbranched dorsal fibres more posteriorly. The bundle passes

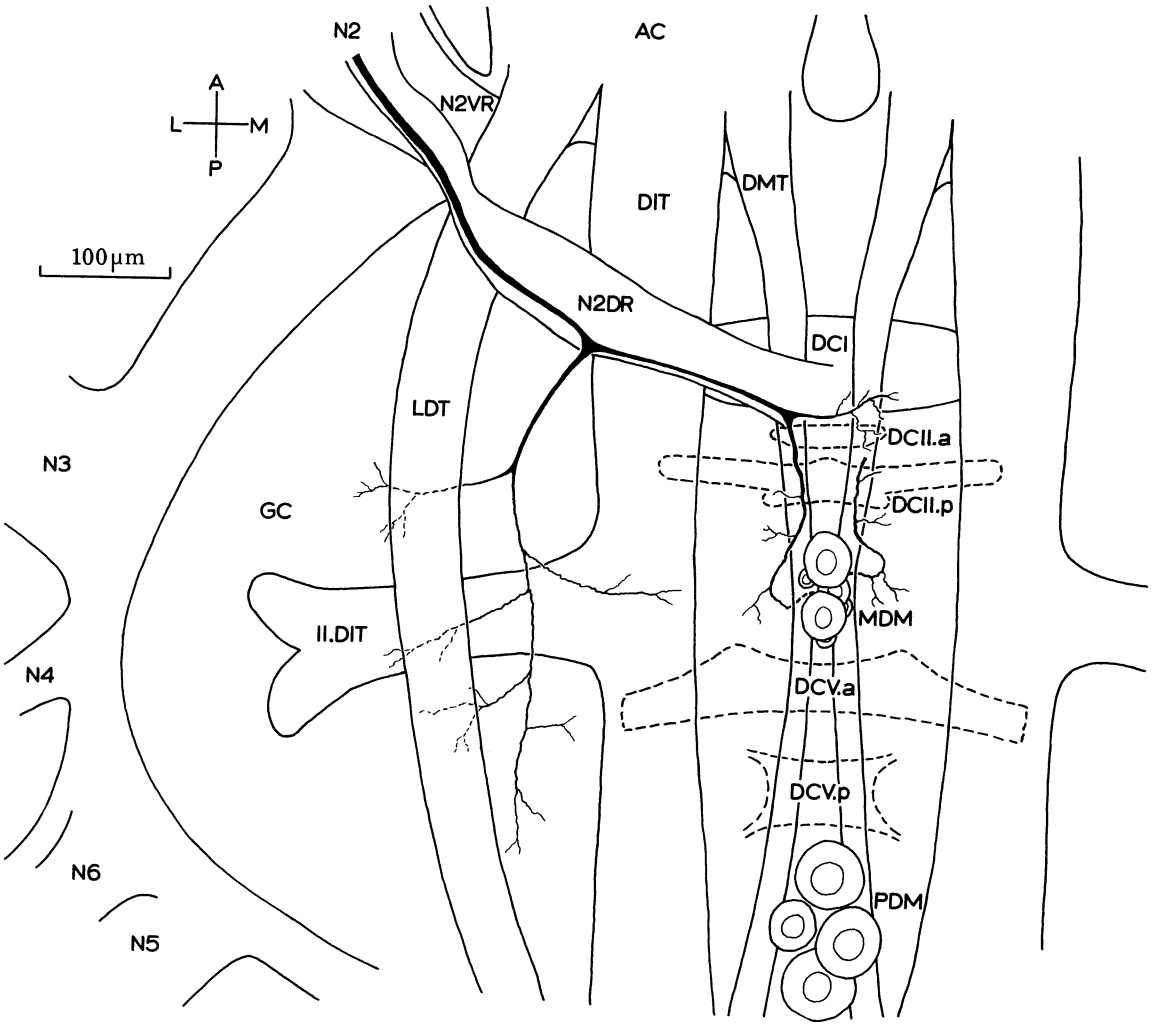


FIGURE 13. Pathway of neuron of mid-dorsal median (MDM) cell body group contributing to dorsal root of nerve 2; frontal section of dorsal region of ganglion, dorsal view. Positions of dorsal commissures II and V, above other structures, shown in broken lines.

immediately beneath some medium-sized transverse fibres at the posterior margin of the SMC and runs anteroventrally nearly to the front region of the SMC. There the fibres fork to send a lateral branch to each side. These branches soon become lost among anterolaterally curving fibres of a component of the posterior part of the ring tract (RT).

Bundle PM(2)

The middle bundle, of up to about ten mainly small fibres, gives off very small dorsolateral branches just behind the SMC, which run into neuropil between the DMT, DIT and VIT. It then appears to give a group of anterolateral branches to each side, which curve down to the outer margins of the VMTs, into neuropil lateral to these tracts. The main fibres then turn down anteroventrally and fork among the posterior SMC fibres. Lateral branches above the VMTs turn anteriorly to run to the front part of the SMC and probably into neuropil anterior to it.

Bundle PM(3)

The ventral bundle is a fairly compact group of up to about 20 fibres, many small but with very small ones ventrally. They curve down beneath the rear part of the SMC, between the upper parts of the VMTs, and gradually become narrower and form a cylindrical bundle. Each fibre then appears to fork to send an anterolateral branch to each side, just in front of the anterolateral branches of bundle 2, in a fountain-shaped arrangement (figure 18, plate 3) immediately above the VMTs. These branches taper into a complex of fibres lateral to the SMC, and some seem to pass among the posterior branches of the main bundle of nerve 7, root 2 (N7R2.mp) (see paper I (Gregory 1974*a*), figure 30).

Anterior ventral median group

(AVM; figures 2, 3; figure 4, plate 1; figures 6, 10, plate 2; figures 15, 17, 20, 21, plate 3; figure 26*d*.) An easily recognized group of about 100–125 cell bodies, mostly small but including eight to ten medium-sized ones, a few of which are almost large, which extends back from beneath the rear part of ventral commissure I (VCI) to the ventral part of ventral commissural loop II (v.VCLII) and laterally abuts on the paired anterior ventral cell body groups 1 and 2 (AV1, AV2) (to be described in a later paper). Glial cells clearly define its boundary anteriorly but less so laterally, and posteriorly it merges with the small cell bodies of the paired anterior ventral 3 groups (AV3). Some of its cells extend up into the ventral midline cleft (VMC) between the paired cylindrical regions of the ventral association centre (c.VAC) and so lie a little above v.VCLII. Its fibres run vertically up the midline just in front of the small second median trachea (MTr2) and pursue a slightly sinuous course. They pass behind the anterior mass of the VAC and between the median ventral tract 1s (MVT1s), the cylindrical halves of the VAC and the VMTs; then behind the dorsal part of ventral commissural loop II (d. VCLII) and between DCI in front and DCIII behind. At first the fibres form a comparatively wide, laterally flattened band but they are squeezed into a more cylindrical bundle behind the d.VCLII. They spread out again somewhat between DCI and DCIII. Though the cell group itself shows no obvious signs of being divided, the fibres are often, but not always, separated for the initial part of their course into two, bilaterally paired, bundles (figure 20, plate 3). Each is made up of one or two fibres that just reach medium size, six to ten small ones and about 45–55 very small ones; further dorsally they tend to become thicker. Generally

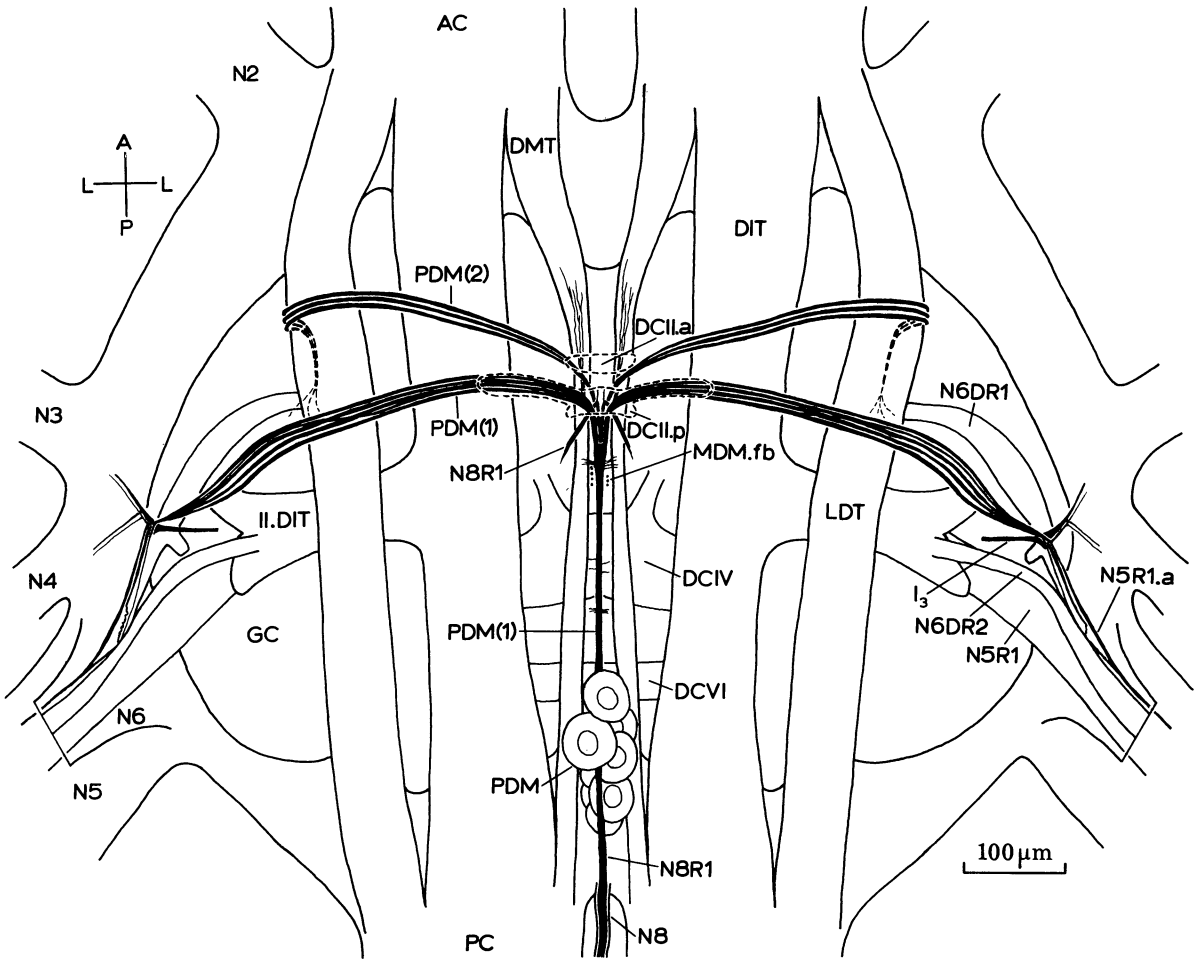


FIGURE 14. Pathways of fibres of bundles 1 and 2 of posterior dorsal median cell body group (PDM(1), PDM(2)) in dorsal region of ganglion; frontal section, dorsal view.

the very small fibres form the anterior and major part of each bundle, accompanied by the medium-sized fibres, and the small fibres are grouped behind them. Some other, unidentified, fibres run with them more dorsally. The two bundles, even when distinguishable ventrally, become compressed together behind the d . VCLII (figure 21, plate 3), but above this the fibres are again divided, apparently into the same paired bundles, by the fibres of the AM cell group passing between them. The bundles this time separate more widely. They continue upwards, pass between the DMTs and then turn laterally above these to form parts of the arms of the T-shaped tract, which run outwards above the DITs (see paper I (Gregory 1974*a*), figure 2). The various groups of fibres then follow different courses. Not all could be traced fully, however, for they are joined in the T-shaped tract by a confusing array of ventral and posterior fibres above the DMTs and of components of the posterior part of DCII above the DITs.

Small and very small fibres that lie anteriorly in the ascending bundle of each side form the largest and most easily followed group. Above the DMT they swing posterolaterally, between the coarser fibres, to lie posteriorly in the bundle above the DIT. Just before reaching the DIT they give off two groups of very small branches from much the same point. One runs down ventrally and ventrolaterally close to the medial side of the DIT to ramify into neuropil between

the DIT and DMT, above DCIII; the other runs posteriorly along the medial side of the DIT and breaks up into neuropil at or in front of the transverse level of the mid-ventral tracheae (MVTr). The main fibres continue over the top of the DIT and, although a few may go on laterally, most turn ventrally down the lateral margin of the DIT and seem to fan out medially and laterally into neuropil below it and above the ventral lateral tract (VLT).

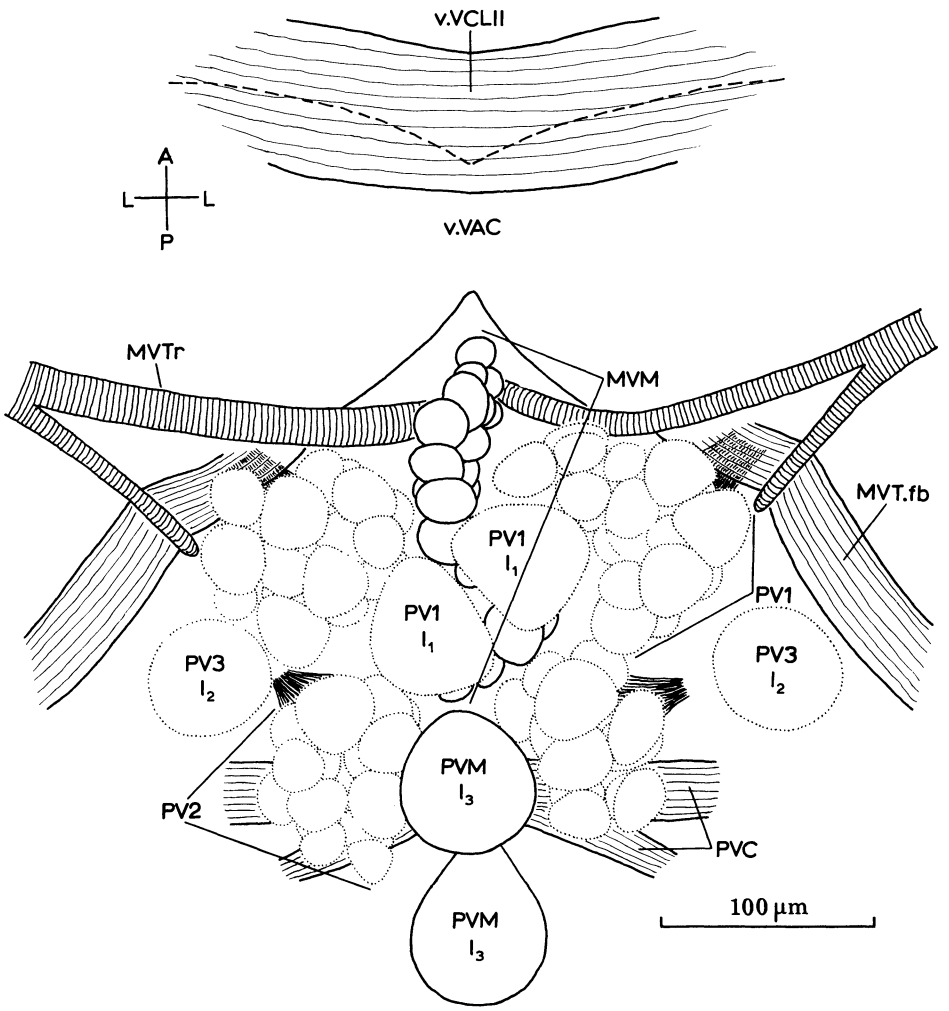


FIGURE 24. Relationships of mid-ventral median (MVM) and posterior ventral median (PVM) cell body groups to neighbouring, paired, cell body groups (shown dotted) and other structures of ventral region of ganglion, ventral view; cell bodies of paired anterior groups ventral to ventralmost region of ventral association centre (v.VAC) omitted.

Two medium-sized fibres that lie at the medial side of each ascending AVM bundle first give off anterior branches between the DMTs. One from each fibre runs slightly ventrally and crosses to the opposite (contralateral) side of the ganglion among the posterior components of DCI. The main fibres then fork and each sends a small branch across the midline above the contralateral DMT to ramify dorsolaterally into neuropil between the DMT, DIT and MDT. The main fibres then run laterally above the DMT and DIT of their own (ipsilateral) half of the ganglion. They appear to turn downwards around the lateral margin of the DIT and run

out into the ventrolateral region of the ganglion core, but they soon become confused with other fibre tracts running in the same direction and can no longer be followed.

Two other, slightly narrower, medium-sized fibres from each ascending AVM bundle run laterally behind the first two, but continue laterally after passing above the DIT. They then seem to run underneath the LDT and curve dorsally around its lateral margin, but become confused with other fibres following a similar course and are eventually lost.

Mid-ventral median group

(MVM; figures 2, 3; figure 4, plate 1; figures 6, 11, plate 2; figures 15, 19, 22, 23, plate 3; figures 24, 25, 26*a*, *e*.) An inconspicuous group of about 20–22 cell bodies, about half of which are medium-sized and the rest small, that extends back from behind the ventralmost region of the VAC (v . VAC) almost to the large somata (of the I_3 motoneurons of Fourtner & Pearson (1977)) of the PVM group. It forms a laterally compressed band, only one or two cells thick, sandwiched between the paired posterior ventral cell body groups 1 and 2 (PV1, PV2). Its most anterior and posterior somata tend to extend well up into the ventral midline cleft, between the halves of the posterior regions of the VAC. Anteriorly the group is usually well separated by glia from the paired AV3 cell groups that extend back beneath the ventralmost region of the VAC, but the separation is less easily seen in wholemounts than in sections because the posterior AV3 cells overlap the anterior MVM cells ventrally. Laterally the MVM cell bodies are difficult to distinguish from those of the PV1 and, particularly, the PV2 groups, which tend to mingle with them, but the directions taken by the neuron processes of the various groups are quite distinct. Those of the MVM cells run dorsally and somewhat anteriorly up the centre line between the two halves of the ganglion core and are at first rather scattered anterior to posteriorly, but then become gathered together into three bundles. These are grouped closely around the ascending mid-ventral tracheae (MVTr), together with a few other fibres (figure 22, plate 3).

Bundle MVM(1)

The most anterior group, of 10–12 very small fibres from the anterior somata, forms a small, compact bundle that runs up in front of the mid-ventral tracheae (MVTr) to the mid-level of the ganglion, where it turns forward (figure 15, plate 3) to merge with bundle PDM(3) in DCIII. The fibres often give off very small lateral branches between or just above the VMTs, about half the fibres branching to one side, the other half to the other side, and also more dorsally immediately behind DCIII. The more ventral branches fork anteriorly and posteriorly into neuropil lateral to the VMTs, between them and the nearby C-tracts (CT). The more dorsal branches ramify anteriorly and dorsally among the fibres of DCIII, and posteriorly into neuropil behind DCIII. Sometimes the MVM(1) fibres also appear to send very small branches anteriorly between the VMTs. In DCIII the combined MVM(1) and PDM(3) bundles divide into lateral branches to the VITs, together with branches from the AM group, as already described under the AM and PDM cell groups. Occasionally bundle MVM(1) inclines more anterodorsally to enter DCIII from below, just behind the ascending AVM bundles, and only then joins the AM and PDM(3) fibres.

Bundle MVM(2)

The six to eight small and very small fibres that lie behind bundle 1 run up close to the mid-ventral tracheae (MVTr), usually as paired bundles, one each side of the midline. They go farther dorsally than bundle 1 and pass between the lower limbs of the DMTs, where these divide around DCIV (see above, under PDM(2)). They then seem to branch and fan out anteriorly and dorsally, below the fibres of PDM(2). Some may run forward among the DMT fibres and others seem to pass posterodorsolaterally through the DMTs and give branches to neuropil lateral to them.

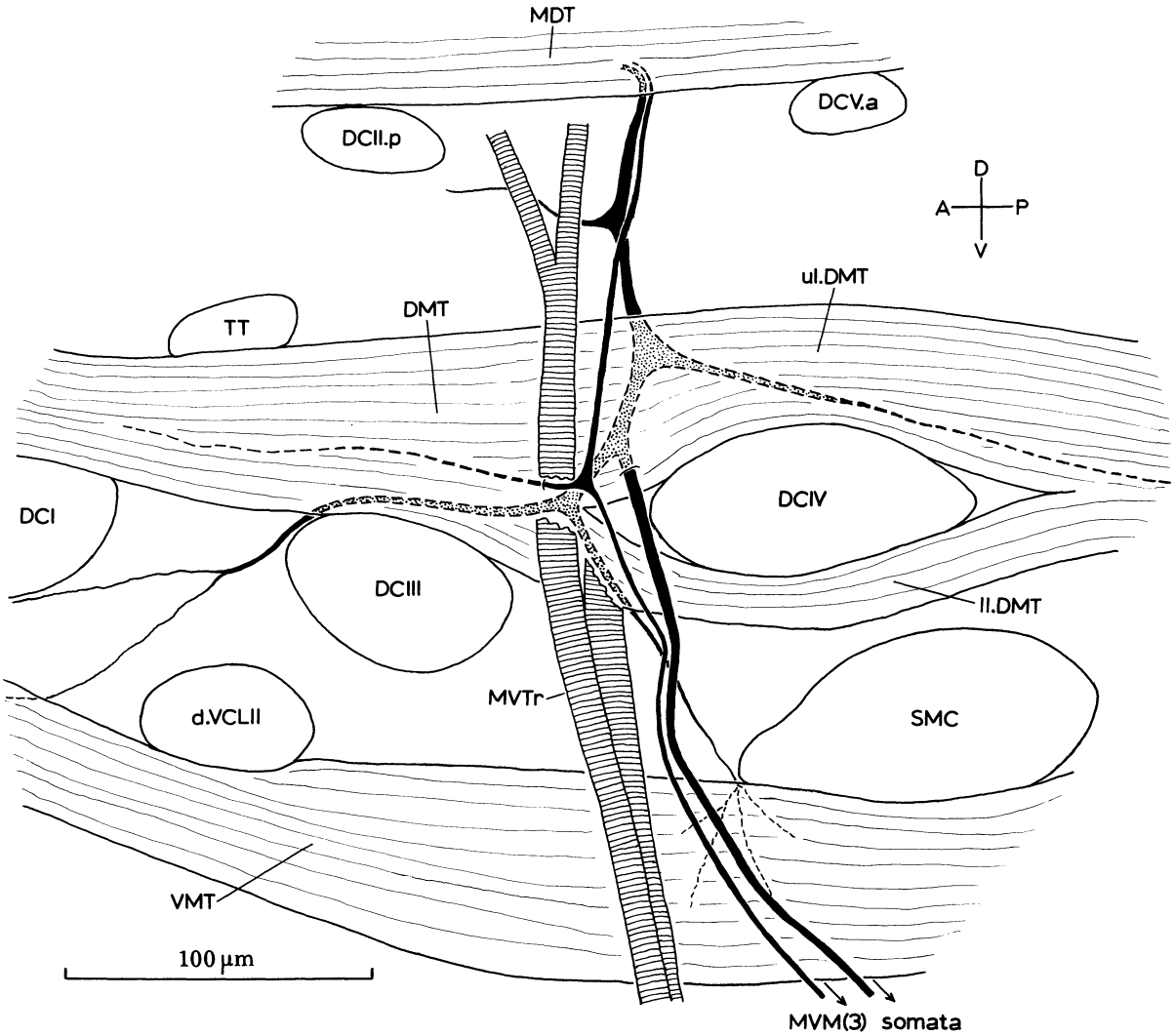


FIGURE 25. Branching of fibres of bundle 3 of mid-ventral median (MVM) cell body group, of one side, in parasagittal section of ganglion core close to midline; viewed from midline.

Bundle MVM(3)

The four most posterior fibres consist of two pairs, of one small and one very small fibre each side of the midline. They come from posterior cell bodies, often rather separated from the rest. The small fibres arise from two medium-sized cell bodies that lie in front of the more anterior of the two large (I_3) somata of the PVM group, and the very small fibres come from a pair

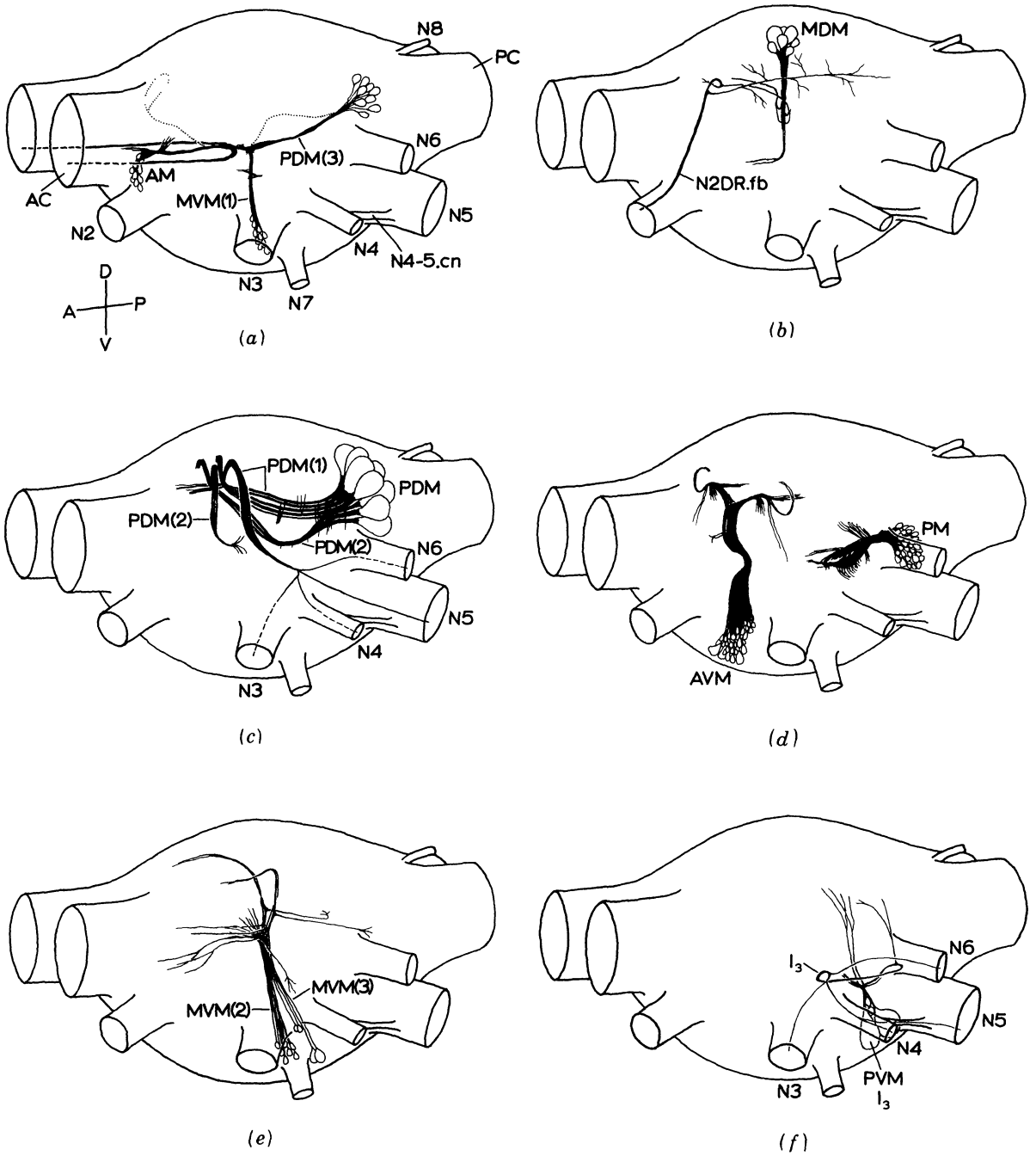


FIGURE 26. Three-dimensional reconstructions of median cell body groups and pathways of fibre bundles, as they would appear in whole ganglia; viewed from anterodorsolaterally. Alternative pathways shown dotted. (*a*) Anterior median (AM) group, bundle 3 of posterior dorsal median group (PDM(3)) and bundle 1 of mid-ventral median group (MVM(1)); (*b*) mid-dorsal median (MDM) group; (*c*) bundles 1 and 2 of posterior dorsal median group (PDM(1), PDM(2)); (*d*) anterior ventral median (AVM) and posterior median (PM) groups; (*e*) bundles 2 and 3 of mid-ventral median group (MVM(2), MVM(3)); (*f*) posterior ventral median (PVM) group.

of small cell bodies that lie more dorsally, usually well up in the ventral midline cleft. The two fibres each side of the midline run up almost to the dorsal surface of the ganglion core, and pass between the paired lower and upper limbs of the DMTs in front of DCIV. The smaller fibre here gives off a long anterior branch that runs forward with the ipsilateral DMT, at least as far as the transverse level of DCI. The other fibre enlarges between the DMTs and branches in a characteristic manner (figure 25). One, anteroventrolateral branch runs forward lateral to the DMT, above DCIII, and ramifies into neuropil below DCI and among the fibres of the ipsilateral VMT; a ventrolateral branch from it passes down between DCIII and the SMC to fan out into a considerable area of neuropil lateral to the VMT. Another branch runs back posteriorly and slightly laterally among the fibres of the upper limb of the DMT, above DCIV, and gives off very small medial branches. It passes above DCVI and then turns posterolaterally and branches into neuropil close to the posterior margin of the core. A third, more dorsal branch sometimes runs forward towards the posterior part of DCII. Both main fibres curve dorsolaterally through the upper limb of the DMT and then between the DIT and MDT. They turn upward into the MDT and run first anterolaterally and then anteriorly, but are eventually lost among the MDT fibres.

Posterior ventral median group

(PVM; figure 2; figure 4, plate 1; figures 11, 12, plate 2; figure 14; figure 23, plate 3; figures 24, 26*f*.) This consists of only two large cell bodies and two, sometimes three, small to medium-sized ones that lie below the posterior ventral commissure (PVC). They are fairly well separated by glia from the MVM group in front and the PM group behind them, but are tightly compressed between the paired PV2 and posterior ventral 4 (PV4) groups laterally. The large somata lie one behind the other, often slightly separated, but the smaller ones usually lie more dorsally, close to the PVC. The medium-sized processes from the large somata pass up into the PVC and turn laterally, crossing over each other, to run one to each side. They send dorsal branches up the midline, past the fibre bundles of the PM and PDM cell body groups, to ramify into neuropil below DCV. The further course of their main fibres was described (in the reverse direction) in paper I (Gregory 1974*a*), under N4R2 . p. They branch to nerves 3, 4 and 6, and to nerve 5 through the small connecting branch from nerve 4 (see paper I (Gregory 1974*a*), figure 8, plate 22). Each corresponds to the widespread common inhibitory motoneuron of the metathoracic ganglion, designated D_3 by Pearson & Fourtner (1975), CI by Fourtner & Drewes (1977) and I_3 by Fourtner & Pearson (1977). The processes of the smaller cells are small or very small and also run up into the PVC and turn laterally, similarly crossing over one another (figure 23, plate 3). Usually one goes to each side but when three are present two go to one side and one to the other. The fibres curve laterally at the ventral core margin with the PVC fibres, at least as far as the inner lateral ventral tracts (LVTs), but then become confused with the other PVC fibres and can no longer be identified. The entire bundle turns dorsolaterally into the core but the component fibres then fan out and pursue various courses in the lateral regions of the core.

Discussion

Neuron cell body groups

The concept of the neuron cell body groups adopted here is derived solely from their morphological arrangement in the ganglion. Mill (1964) used a similar approach to describe the arrangement of the cell bodies in the abdominal ganglia of *Aeschna* nymphs, defining a group as a collection of cell bodies, the processes from which pass into the same tract or tracts'.

However, he identified his groups by letters and numbers rather than names. Four groups of cell bodies lay either in the midline (groups N, P) or were paired and juxtaposed across it (groups L, M), but lack of sufficient detail makes it difficult to compare these with the present groups. However, group L, with its apparently T-shaped 'vertical fiber tract', is reminiscent of the AVM group; group M lies somewhat in the position of the MVM and PVM groups; group N occupies a similar position to the PDM group, and also has anteriorly running processes; and group P lies rather in the position of the AM group. Iles (1976), in cockroach, could reliably distinguish a number of cell groups in the prothoracic ganglion similar to some of those described here. Thus he found MDM, PDM and PVM groups in the midline, as well as PV1 and posterior ventral 3 (PV3) groups laterally. The anterior dorsal median (ADM) group, which he could also distinguish, occurs only in the prothoracic ganglion and does not seem homologous with the AM groups of the mesothoracic and metathoracic ganglia (G. E. Gregory, in preparation). The rest of the somata he classified only into geographical regions: anterolateral, anteroventral and posterolateral. No other authors have yet been found to have used the cell body group concept in describing the somata in the ventral nerve cord ganglia of insects, although in cockroach and locust (G. E. Gregory, in preparation) at least, the arrangement of the cell bodies in discrete groups is often strikingly obvious. The division of the cell bodies into groups offers a useful means for describing them, especially in locating them in the ganglion, but it may not be of great functional significance. Most of the cell groups defined here are mixtures of somata of various sizes and frequently include neurons of more than one functional type (see below).

Though each of the median cell groups appears as a single collection of somata, there is some evidence of their being originally paired groups at the median side of each half ganglion that have fused in the midline. The fibres of the AVM group are frequently divided into bilaterally paired bundles, and bundles 2 and 3 of the MVM group are both usually similarly split. The processes of some, at least, of the cells of the MDM group also separate, to supply individual halves of the ganglion, as do those of the PVM group. The remaining three cell groups (AM, PDM, PM) and bundle 1 of the MVM group contain neurons that supply both halves of the ganglion, often by way of commissures (those of the AM group, bundles PDM(3) and MVM(1) in DCIII; and of PM in the SMC). The neuron processes are usually more or less T-shaped, each main side branch running to one half of the ganglion. It is interesting to speculate whether these groups might also have had a paired origin. Certainly many of the neurons of the other median groups possess small contralateral branches in addition to their main, ipsilateral ones. Perhaps work on other insect species or embryological studies such as those of Goodman *et al.* (1979) and Goodman & Spitzer (1979) on grasshopper dorsal unpaired median (DUM) neurons, which correspond to the PDM group, will eventually shed light on this question. Mill (1964) found the midline cell groups of *Aeschna* nymphs also showed evidence of a paired origin.

Number and function of neurons

Table 1 summarizes the total numbers of somata found in each cell body group, together with the numbers of each functional type identified. All possible care was taken to obtain accurate counts but numbers, particularly of interganglionic and intraganglionic interneurons, must be regarded as provisional. However, until the neurons have been filled with dye and traced individually – a formidable undertaking – the present figures may be of value in giving some idea of the likely proportions of the different types.

The general impression obtained is that the median cell body groups are composed largely

TABLE 1. NUMBER AND LIKELY FUNCTION OF NEURONS IN MEDIAN CELL BODY GROUPS OF MESOTHORACIC GANGLION OF *PERIPLANETA AMERICANA*

		function and numbers of somata		
cell body group	total	efferent, presumed motor neurons	interganglionic interneurons	intraganglionic interneurons
AM	7–11	—	7–11	—
MDM	7–14	2	—	5–12
PDM	14–20	4 or 5	6–12	3 (?)
PM	45–50	—	—	45–50
AVM	100–125	—	—	100–125
MVM	20–22	—	10–12	10
PVM	4 or 5	2	—	2 or 3
total numbers	197–247	8 or 9	23–35	165–203

of interneurons, with a few, usually larger, efferent, presumed motoneuron somata present in some groups. Four groups (AM, PM, AVM, MVM) seem to contain only interneurons, either interganglionic (AM) or intraganglionic (PM, AVM) or both together (MVM). Thus the different functional classes of neuron do not appear to be strictly segregated into different groups. Unless interpretation has been seriously at fault, it appears, too, that intraganglionic interneurons far outnumber the interganglionic ones. Siegler & Burrows (1979), working on locust metathoracic ganglion, suggested that as many as 65 % of the neurons in a ganglion might be local, intraganglionic interneurons. The present results suggest a figure of around 80 %, but this is no doubt too high for the ganglion as a whole. Thus the three intraganglionic interneurons in the PDM group could well be efferent neurons, the axons of which were not traceable far enough to reveal their entries into peripheral nerves (see next section). More important, relatively few motoneurons seem to be present in these median groups, most being in the anterior and posterior paired groups, as described in paper I (Gregory 1974*a*) and to be considered in greater detail in papers III and IV (G. E. Gregory, in preparation). Preliminary results that include counts from these paired groups suggest that at least two-thirds of the somata in the ganglion are of intraganglionic interneurons, which agrees well with the percentage arrived at by Siegler & Burrows (1979). Here, as in paper I, efferent, 'motor' neurons will also include both neurosecretory cells that send their axons peripherally, and also any sensory neurons with central somata that do the same. Recently small numbers of the latter have been discovered in thoracic ganglia of cockroach, locust and other Orthoptera (Bräunig & Hustert 1980; Collin 1981; Bräunig 1982). However, their somata all lie in anterior paired cell groups and none has so far been found in the median groups. It thus seems reasonable to presume that most of the efferent neurons described in the present account are motor neurons. The distribution of neurosecretory cells has not yet been studied in detail. Previous accounts so far found give insufficient information on the positions of the cells to allow them to be assigned readily to particular cell body groups. Thus Füller (1960) places one B-type soma in the midline between the bases of the anterior connectives in the metathoracic ganglion but its vertical position is not indicated. It seems to lie in the area of the AM group. Geldiay (1962) shows two 'type I' (probably A-type (Delphin 1965)) midline cells anteriorly and two posteriorly in the thoracic ganglia but again their vertical level cannot be determined. The anterior ones may lie in the AM group and the posterior ones in the PDM group. In locusts and grasshoppers one, probably more, of the dorsal unpaired median (DUM) neurons, which are equivalent to part of the PDM

group, have been shown to be neurosecretory (Hoyle 1974; Hoyle *et al.* 1974), producing octopamine (Hoyle 1975; Hoyle & Barker 1975; Evans & O'Shea 1977, 1978), and some cockroach PDM somata have also been found to be octopaminergic (Dymond & Evans 1979). The neurons of this group are considered further below. De Bessé (1967) located 3–5 large C-type cells lying centrally in the midline in *Periplaneta* thoracic ganglia. If they are ventral they would seem to lie in the AVM or MVM group, but if dorsal, in the MDM group. Bishop & O'Shea (1982) found a few median cell bodies that showed proctolin (neuropeptide)-like immunoreactivity dorsally in the thoracic ganglia but it is difficult to relate these to cell groups. Two shown in the mesothoracic ganglion (their figure 8C) seem to be in the region of the MDM group. They found two near the PDM (DUM) group in the metathoracic ganglion, with four others more posteriorly. Endo *et al.* (1982) found pancreatic polypeptide-like activity in the thoracic ganglia only in paired groups of cell bodies.

Young (1969, 1973), using perinuclear RNA as a marker, mapped many of the major ventral motoneuron somata of the mesothoracic ganglion, but not the dorsal ones. Only two seem to belong to a midline cell body group: the more posterior pair of the posterior, unnumbered midline quartet in his earlier map (1969, figure 1) and the pair numbered 41 in the later version (1973, figure 2). Both appear to correspond to the widespread common inhibitory (CI) motoneuron somata, I_3, of the PVM group. Iles (1976) similarly concluded in the prothoracic ganglion that the soma of I_3 (D_3) was homologous with Young's cell 41.

Neuron pathways

Axonal filling with cobalt in the present study has confirmed and extended the descriptions in paper I (Gregory 1974*a*) of the pathways of the neurons of the MDM group to N2DR and of the CI motoneurons I_3 of the PVM group to nerve 3, nerve 4, root 2 (N4R2), nerve 5 and N6DR1. Also, four or five neurons of the PDM group have been traced to nerve 5 of both sides of the ganglion, as the small additional nerve root N5R1.a. At least three of these seem also to branch to nerves 3 and 4 of both sides, and some, which may or may not be the same fibres, seem to branch to nerve 6. Crossman *et al.* (1972) found electrophysiological evidence that suggested the existence of branches to nerves 3–6 in the metathoracic ganglia of cockroach and locust. Hoyle *et al.* (1974) and Hoyle (1978) studied the corresponding, DUM group of neurons intensively in locust and grasshopper metathoracic ganglia and found the eight, possibly nine, largest to be efferent and to give branches to nerves of both sides of the ganglion. One neuron (DUMDL), innervating the dorsal longitudinal flight muscles, emerged only through nerve 1 (the most anterior paired nerve, designated nerve 2 in cockroach), one only through nerve 3, one only through nerve 4, and one (DUMETi), supplying the jumping, extensor tibiae, muscles, only through nerve 5, while five others gave branches to both nerves 4 and 5; but none branched to nerve 6. The remaining cells of the group appeared to be interneurons. Denburg & Barker (1982), studying the innervation of cockroach coxal depressor muscles by neurons of the PDM (DUM) group, were able to fill single neurons with Lucifer Yellow CH (Stewart 1978) and illustrate one in the mesothoracic ganglion that branches to nerves 3–6 of both sides of the ganglion in a manner similar to those described here. However, they were not clear as to how many neurons followed this pathway. The present observations indicate that, although four or five of the largest PDM cells send their axons, in bundle PDM(1), directly to peripheral nerves, the other three, in bundle PDM(2), follow a somewhat different pathway into the lateral regions of the ganglion core. Here they could well supply branches to root

bundles of nerves and hence be efferent also, but until such branches can be traced the three cells must be tentatively classified as 'interneurons'. If such branches are present their fineness may prevent them filling with dye adequately from the cut ends of the nerves unless special methods are used (Hoyle 1978) and injection into the somata may be necessary to display them. The pathways of thoracic PDM (DUM) neurons traced in grasshopper embryos by Goodman *et al.* (1979) and Goodman & Spitzer (1979) resemble only those of bundle PDM(1) described here. Support for the idea that all eight neurons are efferent is perhaps given by the findings of Dymond & Evans (1979) that between five and eight of the largest PDM somata in the pro- and mesothoracic ganglia, and all eight in the metathoracic ganglion, appeared to be octopaminergic. In the prothoracic ganglion, Iles (1976) found an MDM and a PDM cell to supply axons to nerve 2, the PVM group I_3 (D_3) CI motoneurons to branch to nerves 3–6, and one PDM cell to send an axon into nerve 6Br4, but he recorded no PDM axons in nerve 5. The position and pathway of the DUMDL neuron of *Schistocerca* and *Romalea* (Hoyle 1978) (and also of the metathoracic dorsal median (DM) cell in the cricket *Teleogryllus* (Clark 1976)) bears an interesting resemblance to the cockroach MDM neurons described here that contribute to N2DR. However, in these other species the neuron gives axon branches to nerve 1 of both sides of the ganglion, whereas in *Periplaneta* two neurons are present, each sending an axon to nerve 2 of only one side.

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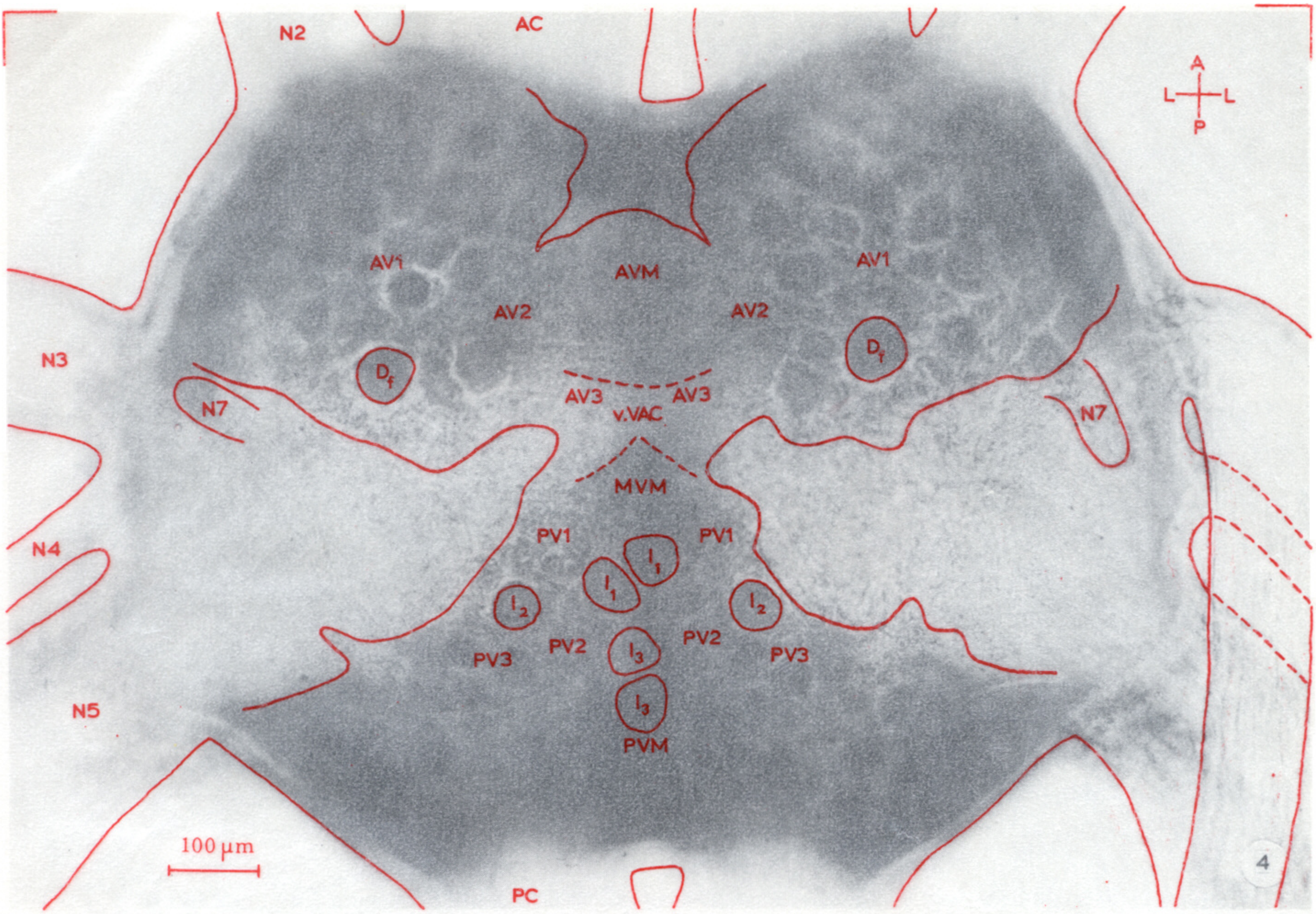
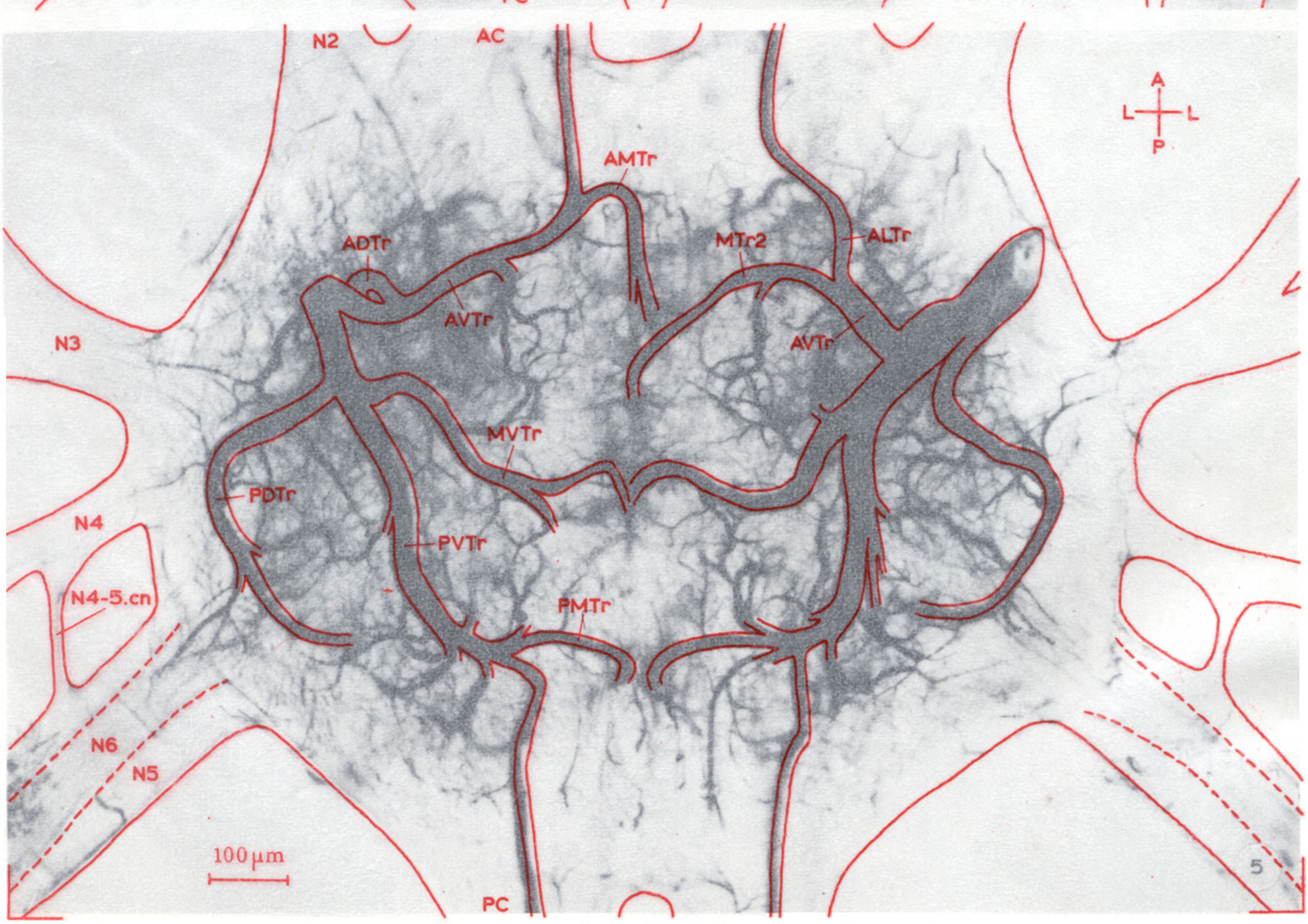
Explanation of abbreviations

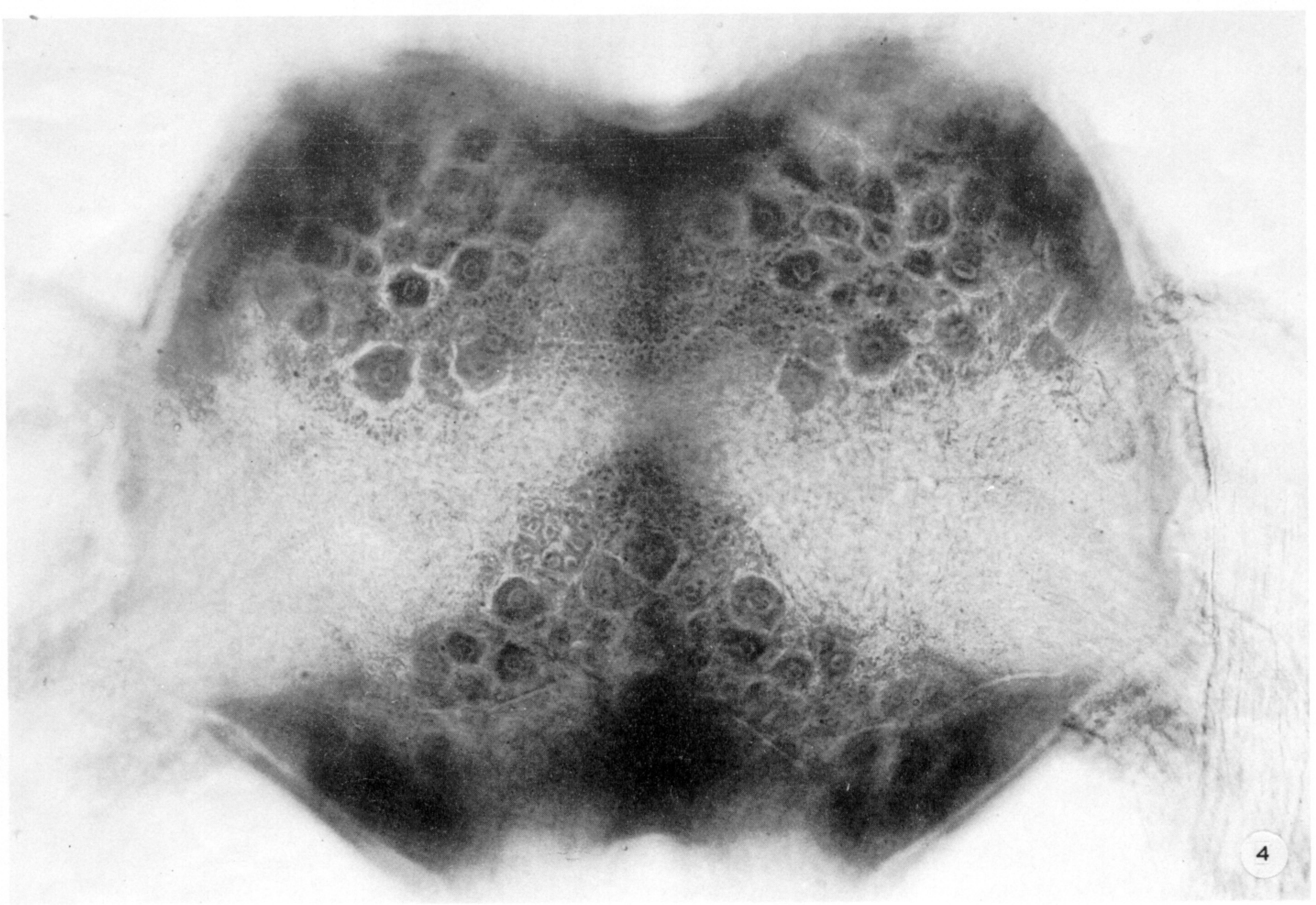
A	anterior
AC	anterior interganglionic connective
ADL	anterior dorsolateral cell body group
ADM	anterior dorsal median cell body group
ADTr	anterior dorsal trachea
AL1	anterior lateral cell body group 1
AL3	anterior lateral cell body group 3
ALTr	anterior lateral trachea
AM	anterior median cell body group
AM.fb	anterior median cell body group fibres
AMTr	anterior median trachea
AV1	anterior ventral cell body group 1
AV2	anterior ventral cell body group 2
AV3	anterior ventral cell body group 3
a.VAC	anterior mass of ventral association centre
AVL4.fb	fibre bundle of anterior ventrolateral cell body group 4
AVM	anterior ventral median cell body group
AVM.fb	anterior ventral median cell body group fibres
AVTr	anterior ventral trachea
CI	widespread common inhibitory motoneuron
CT	C-tract
c.VAC	cylindrical region of ventral association centre
D	dorsal
D_3	soma of widespread common inhibitory motoneuron
DCI	dorsal commissure I
DCII	dorsal commissure II
DCII.a	anterior part of dorsal commissure II
DCII.p	posterior part of dorsal commissure II
DCIII	dorsal commissure III
DCIV	dorsal commissure IV
DCV	dorsal commissure V
DCV.a	anterior part of dorsal commissure V
DCV.p	posterior part of dorsal commissure V
DCVI	dorsal commissure VI
D_f	cell body of fast extensor (depressor) of femur motoneuron
DIT	dorsal intermediate tract
DM	dorsal median neuron
DMC	dorsal midline cleft
DMT	dorsal median tract
D_s	cell body of slow extensor (depressor) of femur motoneuron
DUM	dorsal unpaired median neurons
DUMDL	dorsal unpaired median neuron innervating dorsal longitudinal flight muscles
DUMETi	dorsal unpaired median neuron innervating extensor tibiae muscles
d.VCLII	dorsal part of ventral commissural loop II
FBP	fibre bundle from posterior, in ventral intermediate tract
GC	ganglion core
I_1	soma of local common inhibitory motoneuron 1
I_2	soma of local common inhibitory motoneuron 2
I_3	soma of widespread common inhibitory motoneuron
L	lateral
LDT	lateral dorsal tract
ll.DIT	lateral limb of dorsal intermediate tract
ll.DMT	lower limb of dorsal median tract
l.VAC	ventrolateral extension of ventral association centre
LVT	lateral ventral tract
M	medial
MDM	mid-dorsal median cell body group
MDM.fb	mid-dorsal median cell body group fibres
MDT	median dorsal tract
MTr2	second median trachea
MVM	mid-ventral median cell body group
MVM(1)	fibre bundle 1 of mid-ventral median cell body group
MVM(2)	fibre bundle 2 of mid-ventral median cell body group
MVM(3)	fibre bundle 3 of mid-ventral median cell body group
MVT	median ventral tract
MVT1	median ventral tract 1
MVT.fb	median ventral tract fibres
MVTr	mid-ventral trachea
N2	nerve 2
N2DR	nerve 2, dorsal root
N2DR.fb	fibre contributing to nerve 2, dorsal root
N2VR	nerve 2, ventral root
N3	nerve 3
N3R3	nerve 3, root 3
N4	nerve 4
N4R1	nerve 4, root 1
N4R2	nerve 4, root 2
N4R2.p	posterior medium-sized fibre of nerve 4, root 2
N4–5.cn	connection between nerves 4 and 5
N5	nerve 5
N5R1	nerve 5, root 1
N5R1.a	anterior fibre bundle of nerve 5, root 1
N6	nerve 6
N6DR1	nerve 6, dorsal root 1
N6DR2	nerve 6, dorsal root 2
N6DR3	nerve 6, dorsal root 3
N7	nerve 7
N7R2.mp	posterior branches of main bundle of nerve 7, root 2
N8	nerve 8
N8R1	nerve 8, root 1
P	posterior
PC	posterior interganglionic connective
PDM	posterior dorsal median cell body group
PDM(1)	fibre bundle 1 of posterior dorsal median cell body group
PDM(2)	fibre bundle 2 of posterior dorsal median cell body group
PDM(3)	fibre bundle 3 of posterior dorsal median cell body group
PDTr	posterior dorsal trachea
PL2	posterior lateral cell body group 2
PM	posterior median cell body group
PM(1)	fibre bundle 1 of posterior median cell body group

PM(2)	fibre bundle 2 of posterior median cell body group
PM(3)	fibre bundle 3 of posterior median cell body group
PMTr	posterior median trachea
PV1	posterior ventral cell body group 1
PV2	posterior ventral cell body group 2
PV3	posterior ventral cell body group 3
PV4	posterior ventral cell body group 4
PVC	posterior ventral commissure
PVM	posterior ventral median cell body group
PVTr	posterior ventral trachea
RT	ring tract
SMC	supra-median commissure
TT	T-shaped tract
ul . DMT	upper limb of dorsal median tract
V	ventral
VAC	ventral association centre
VCI	ventral commissure I
VIT	ventral intermediate tract
VLT	ventral lateral tract
VMC	ventral midline cleft
VMT	ventral median tract
v . VAC	ventralmost region of ventral association centre
v . VCLII	ventral part of ventral commissural loop II





FIGURES 4 AND 5. For description see opposite.

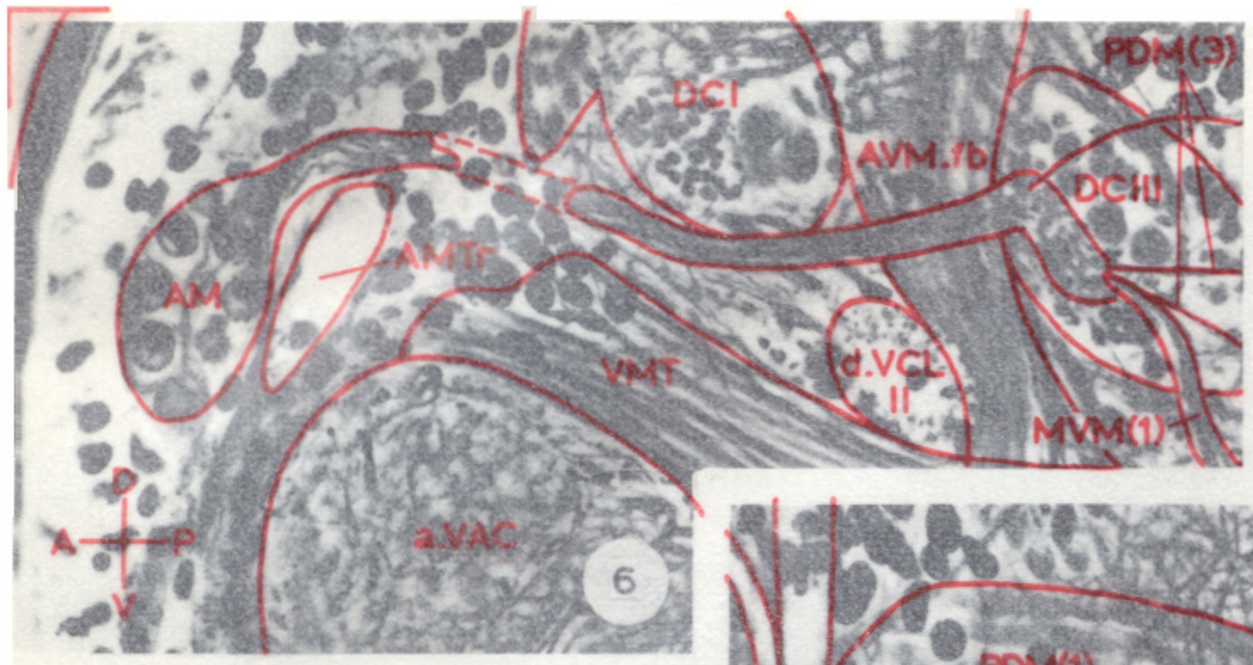


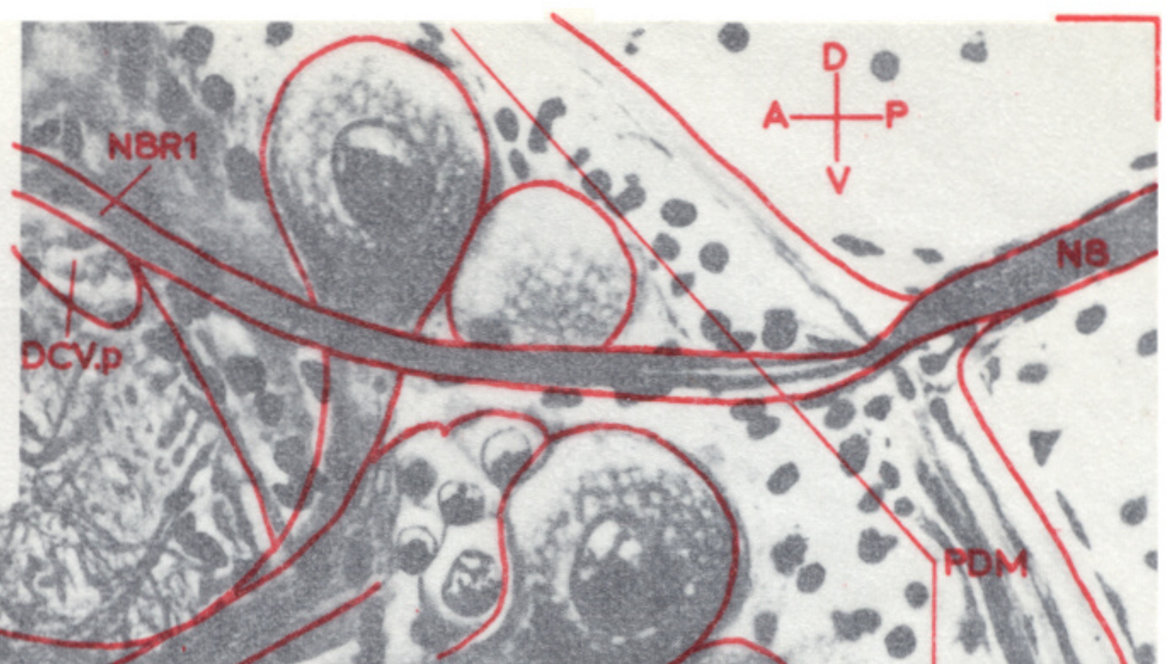
4

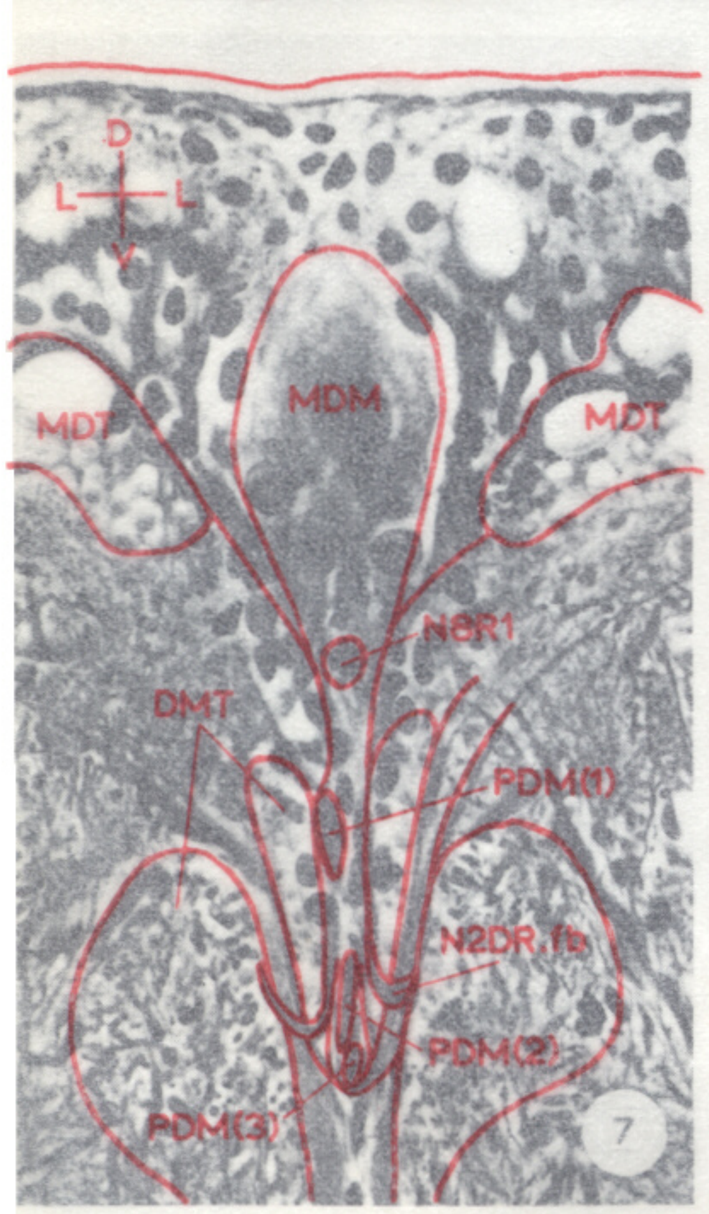
5

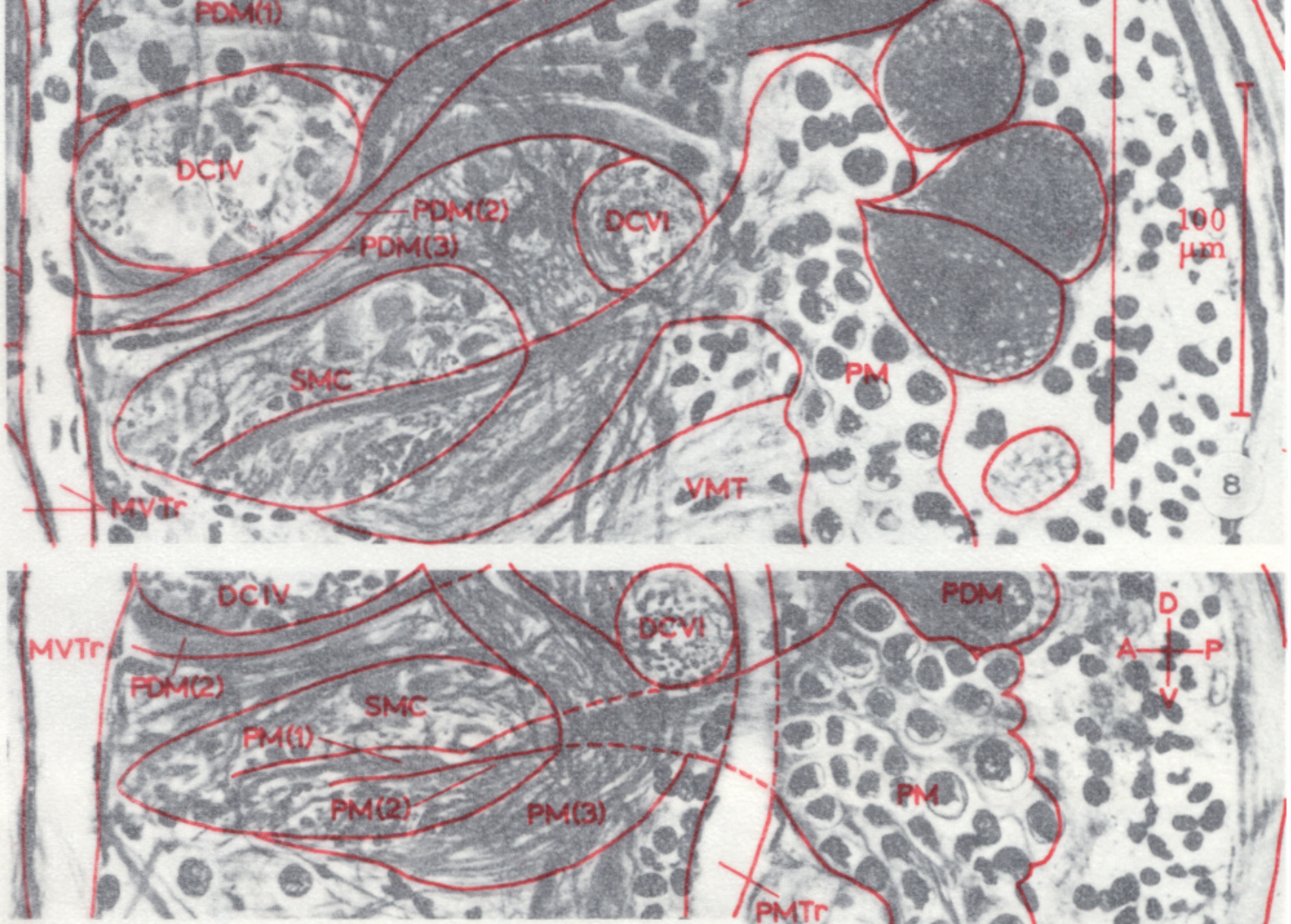
FIGURES 4 AND 5. For description see opposite.

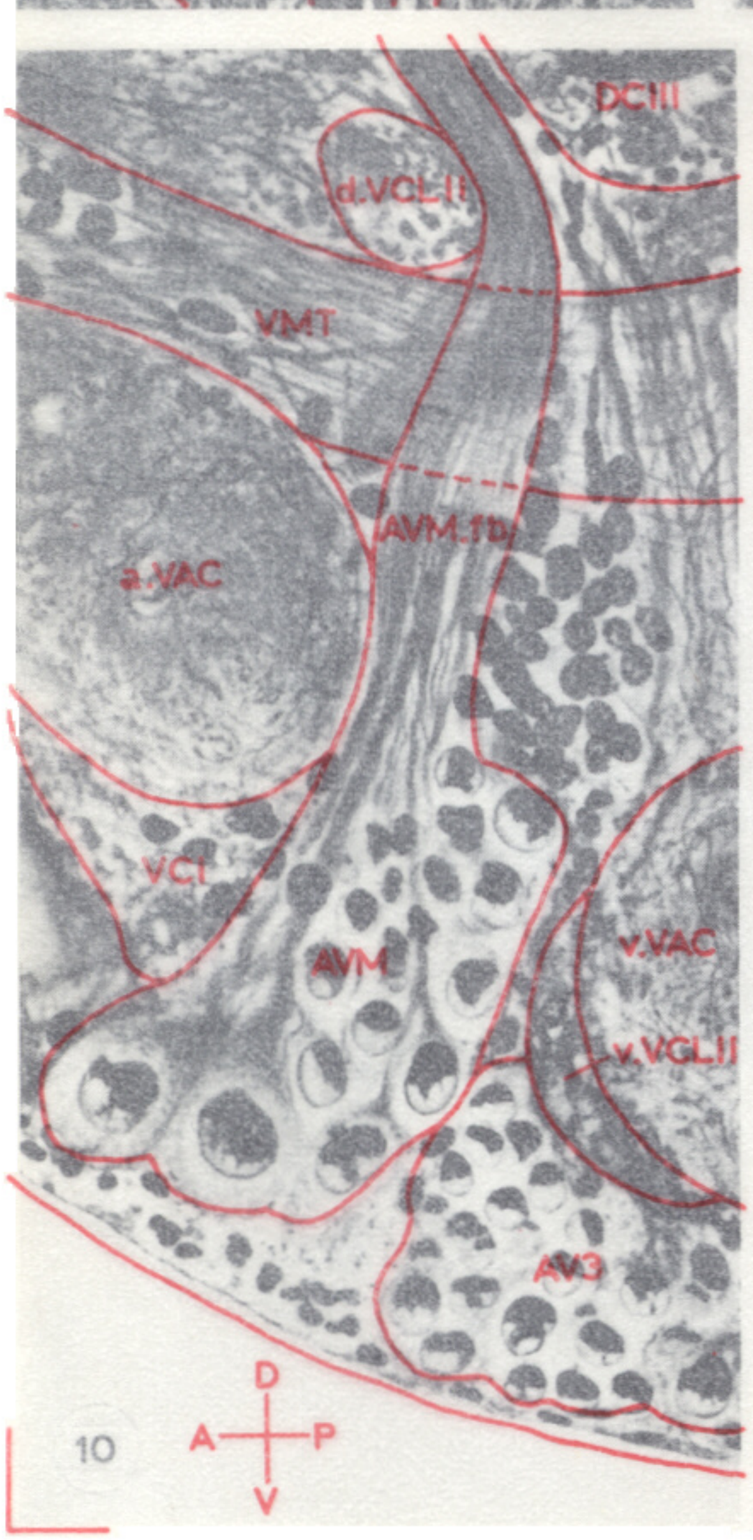
(*Facing p.* 200)

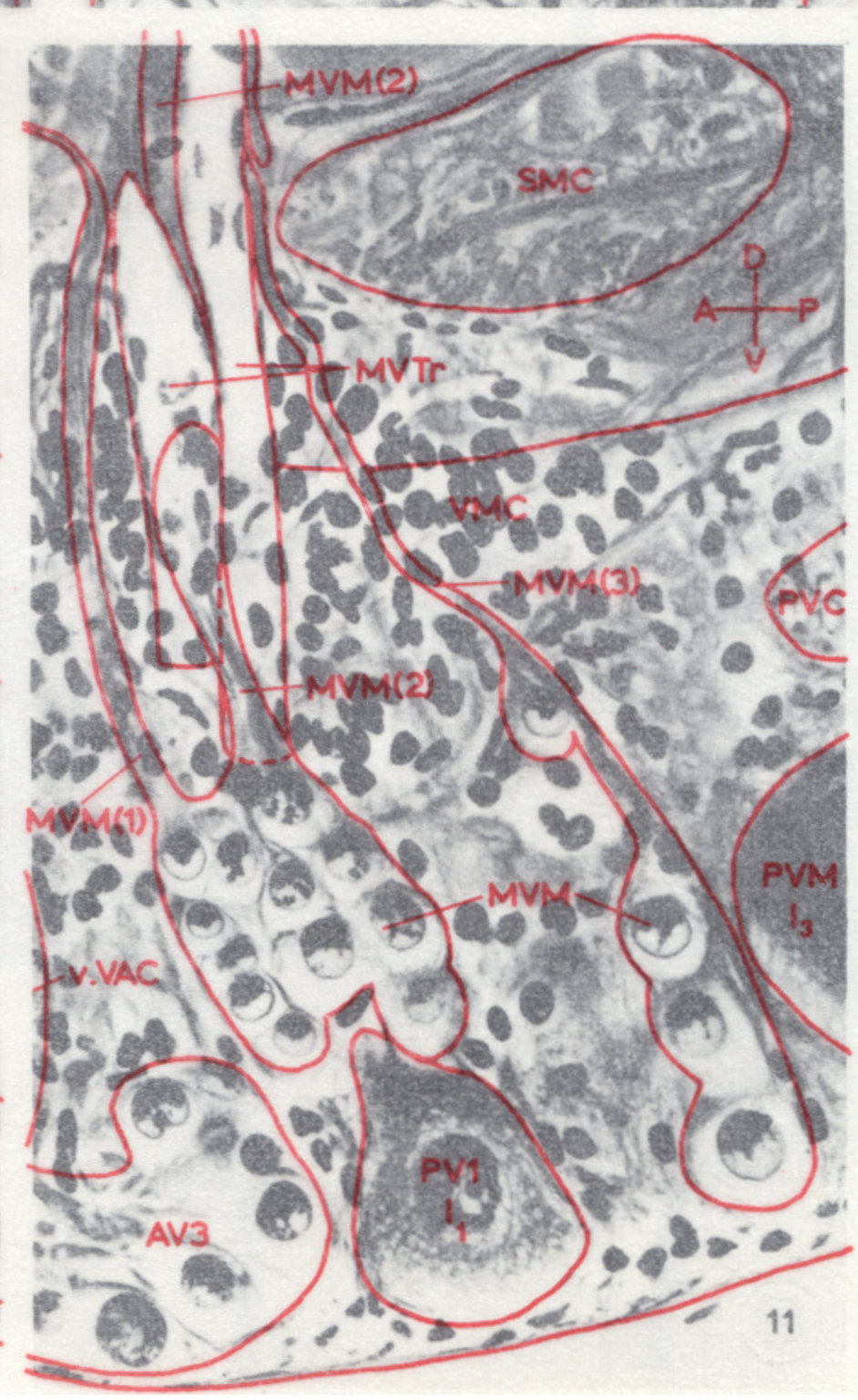


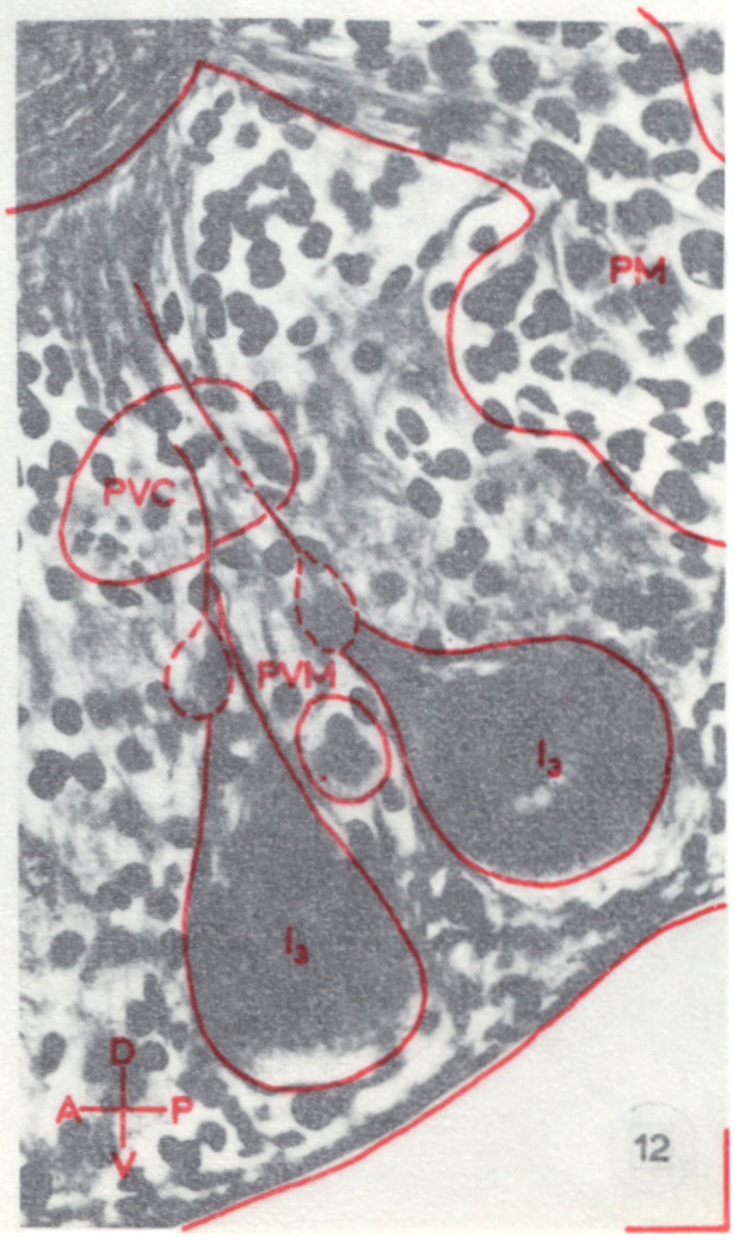




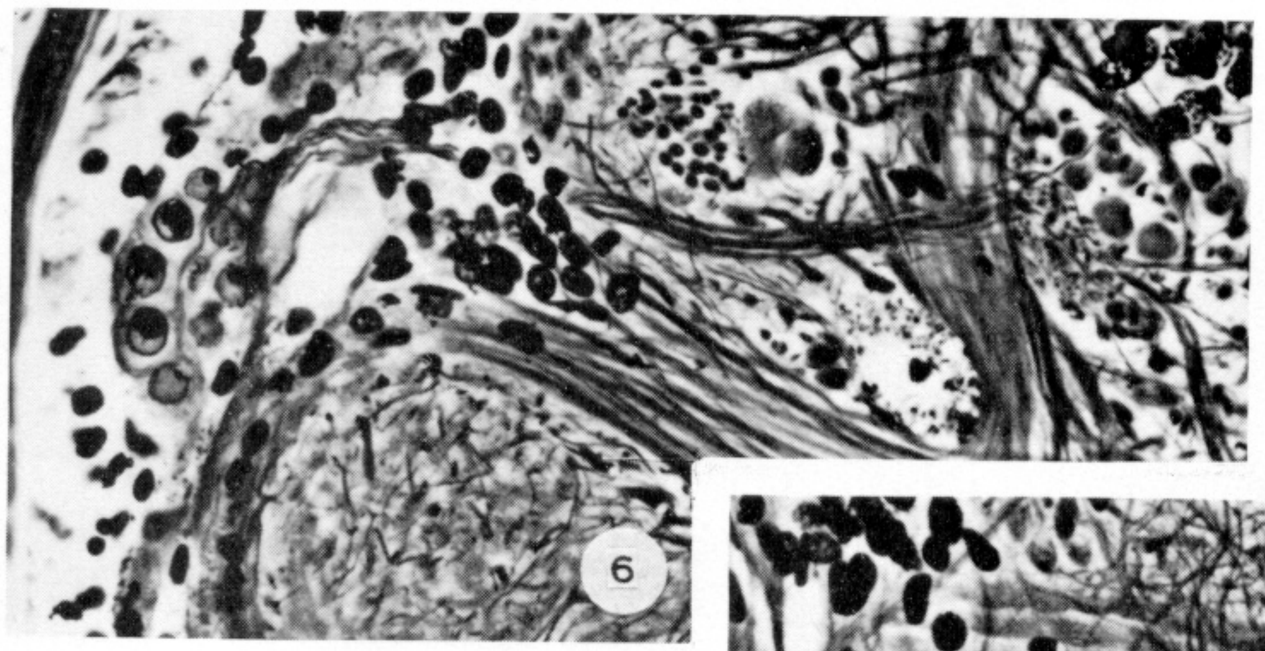


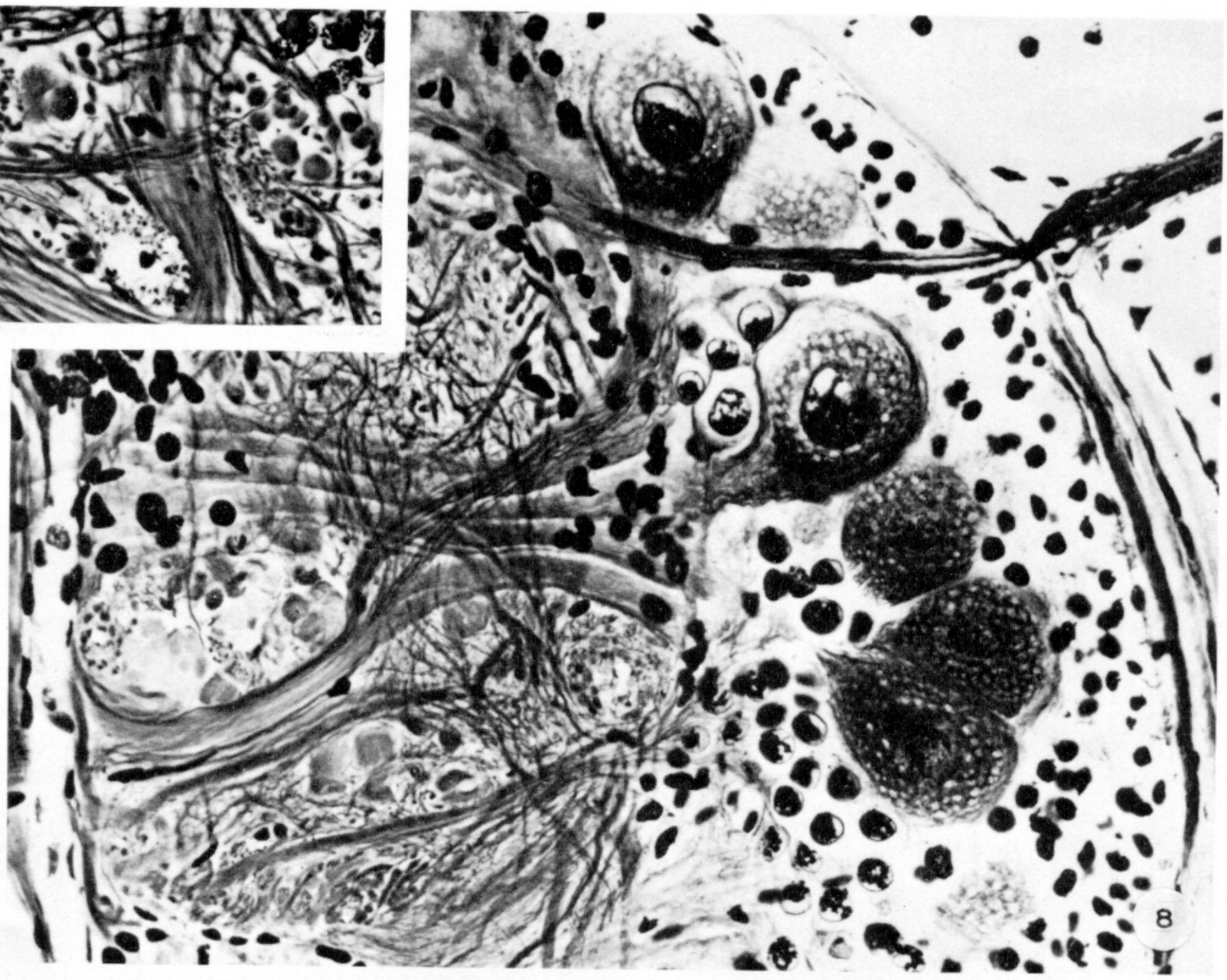


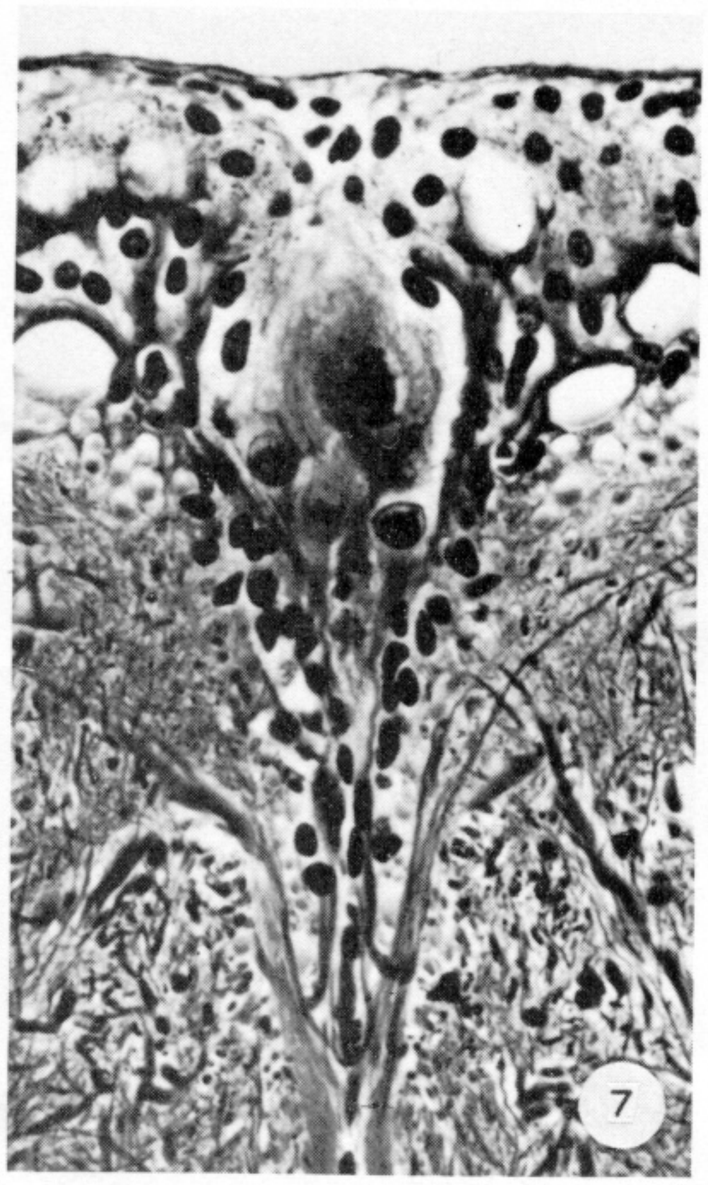


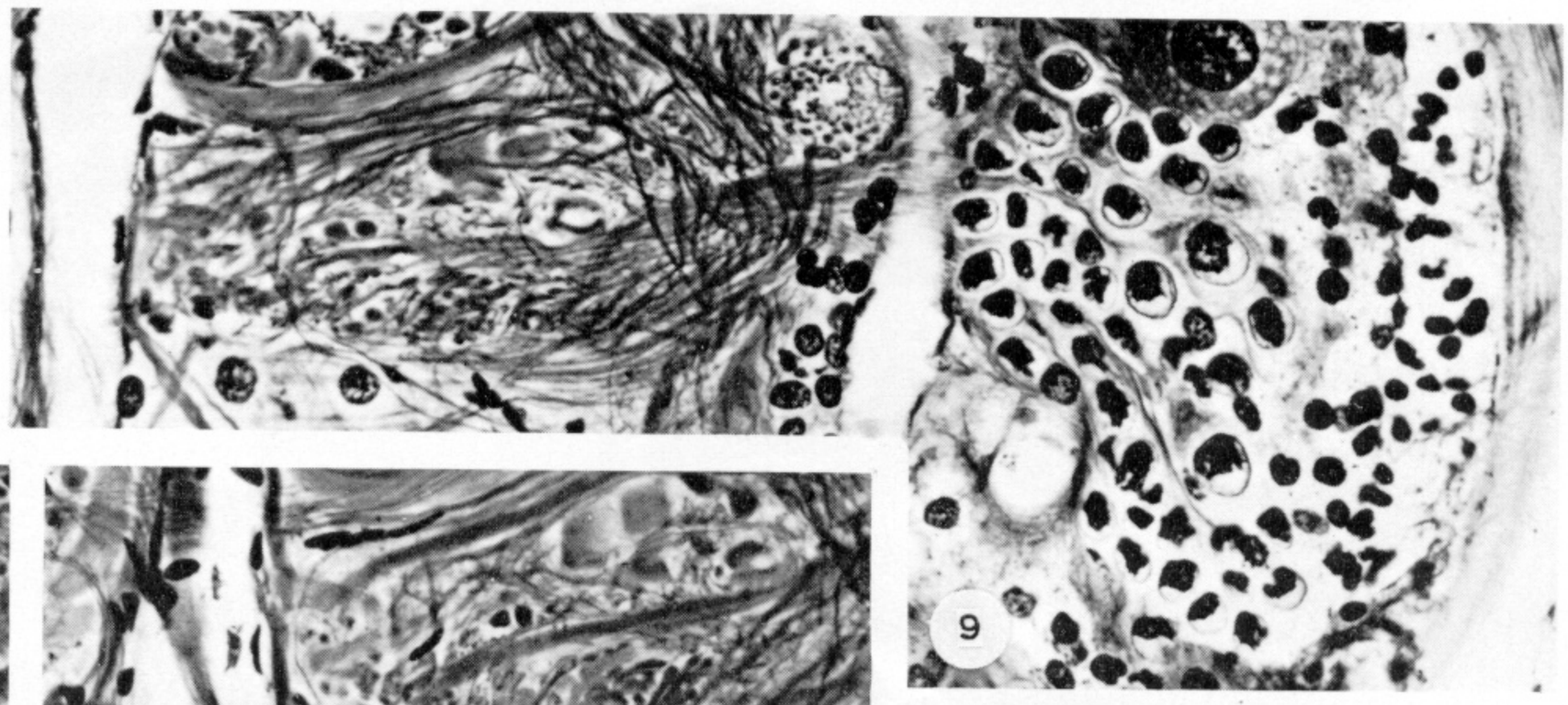


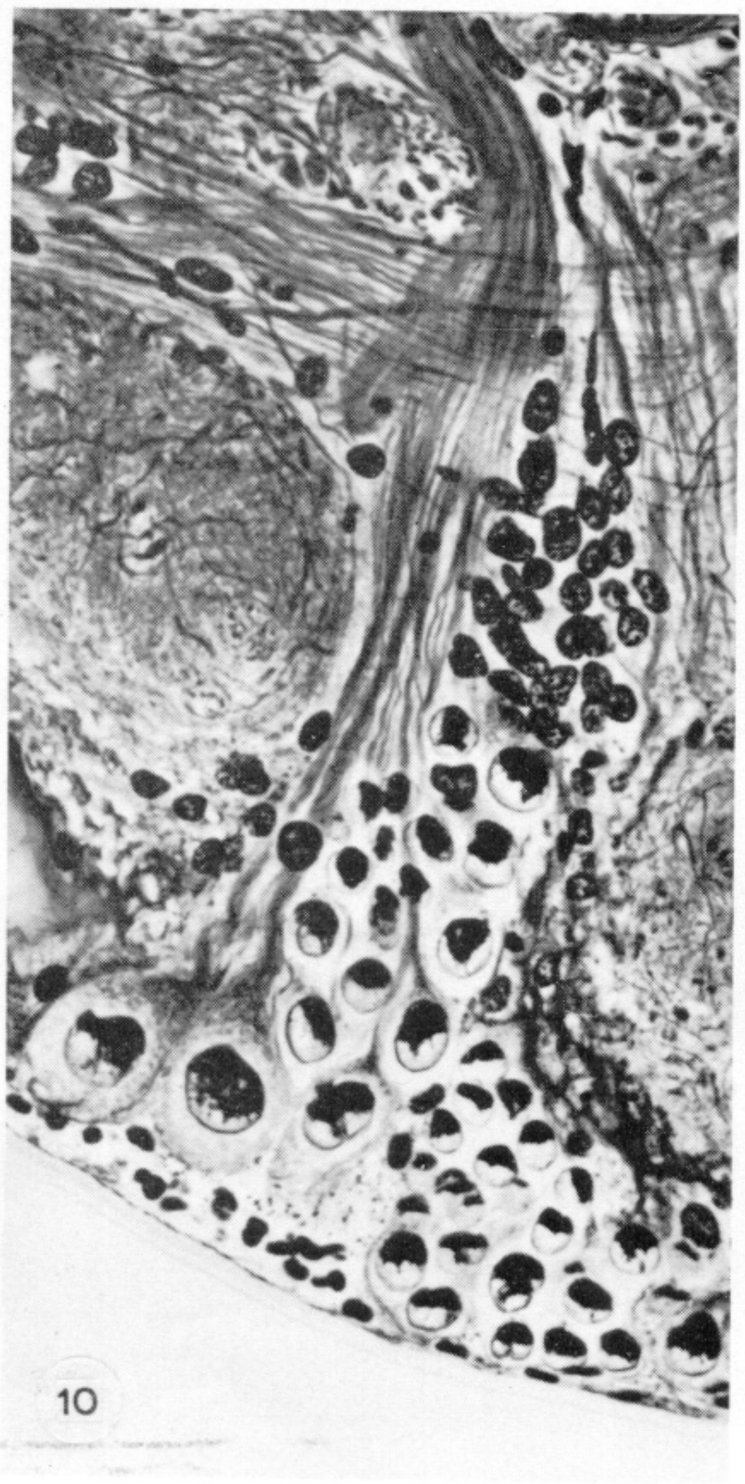
FIGURES 6–12. For description see opposite.

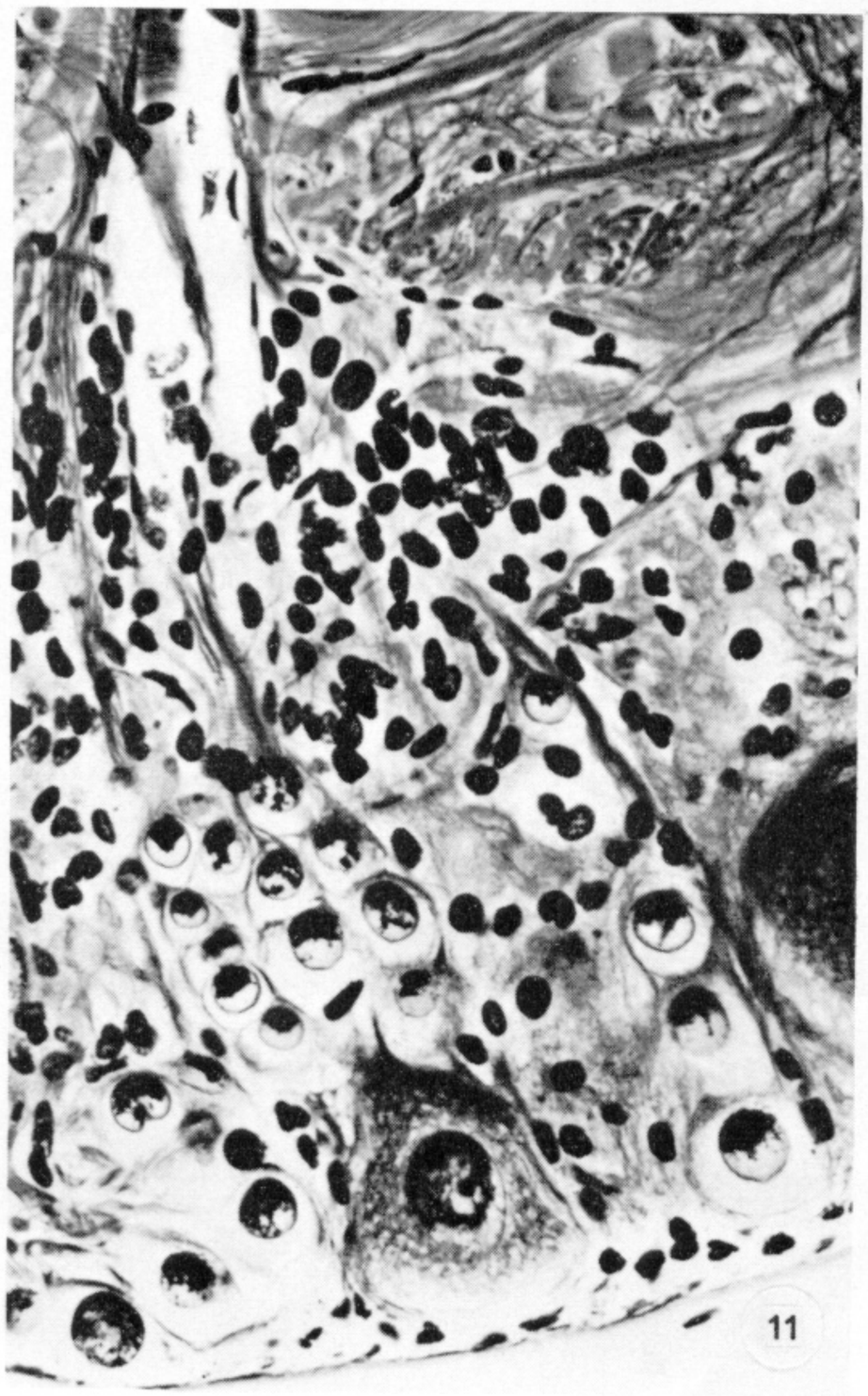


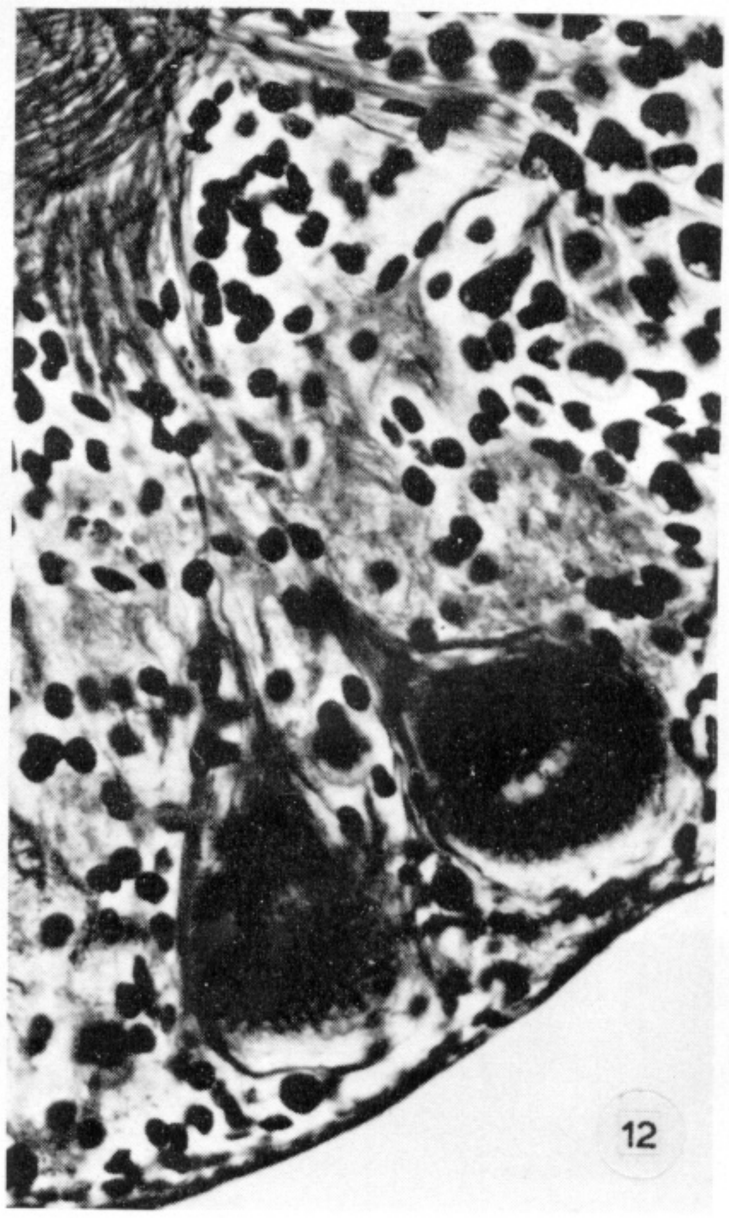




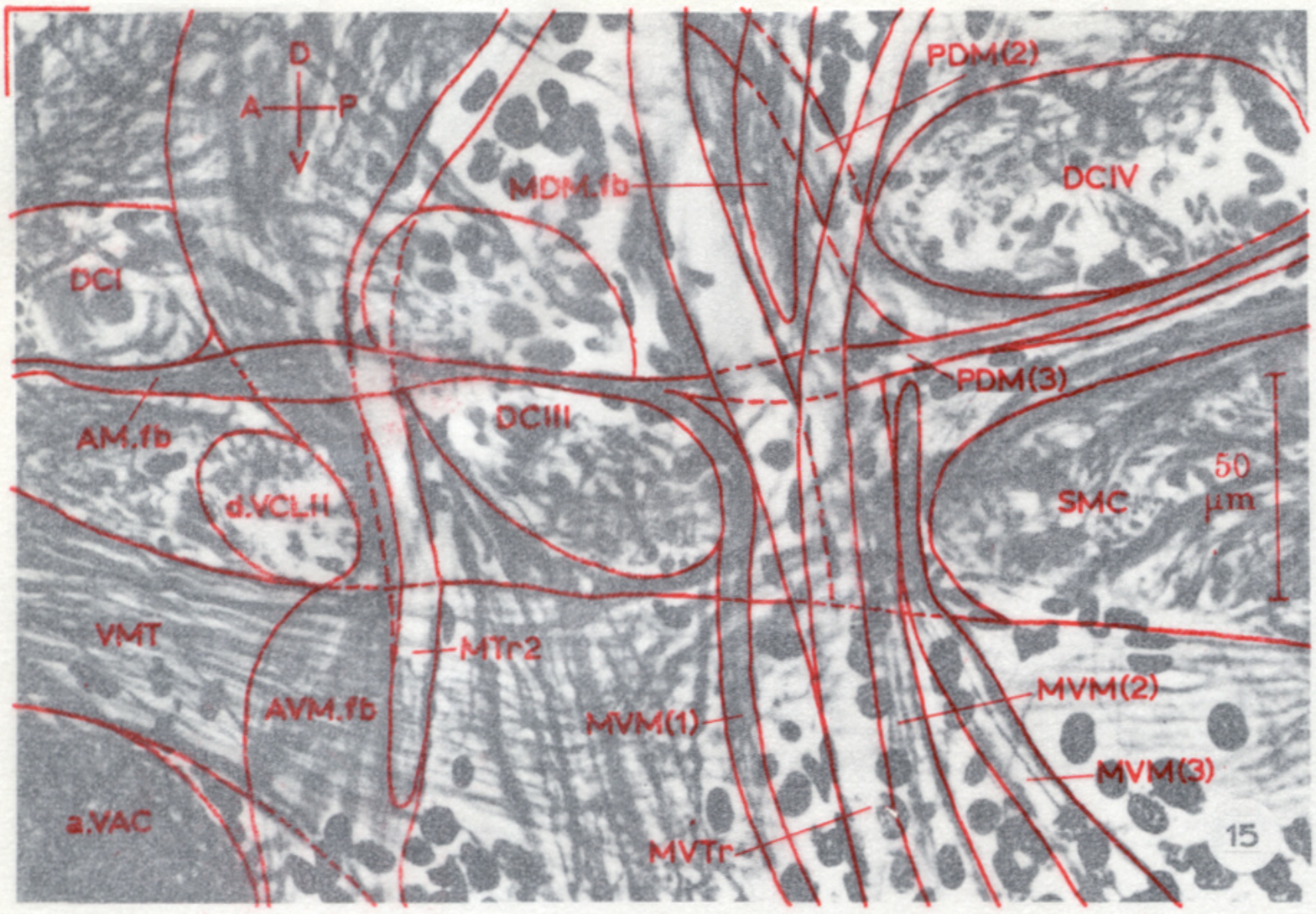


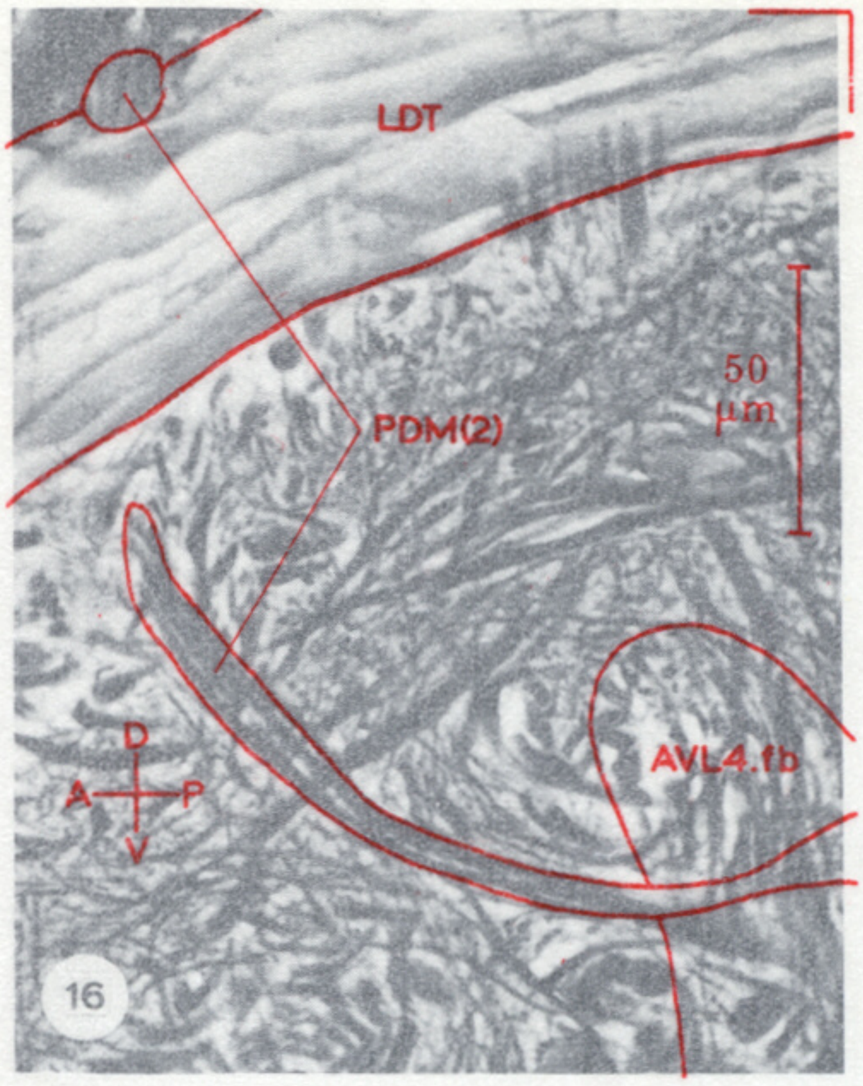


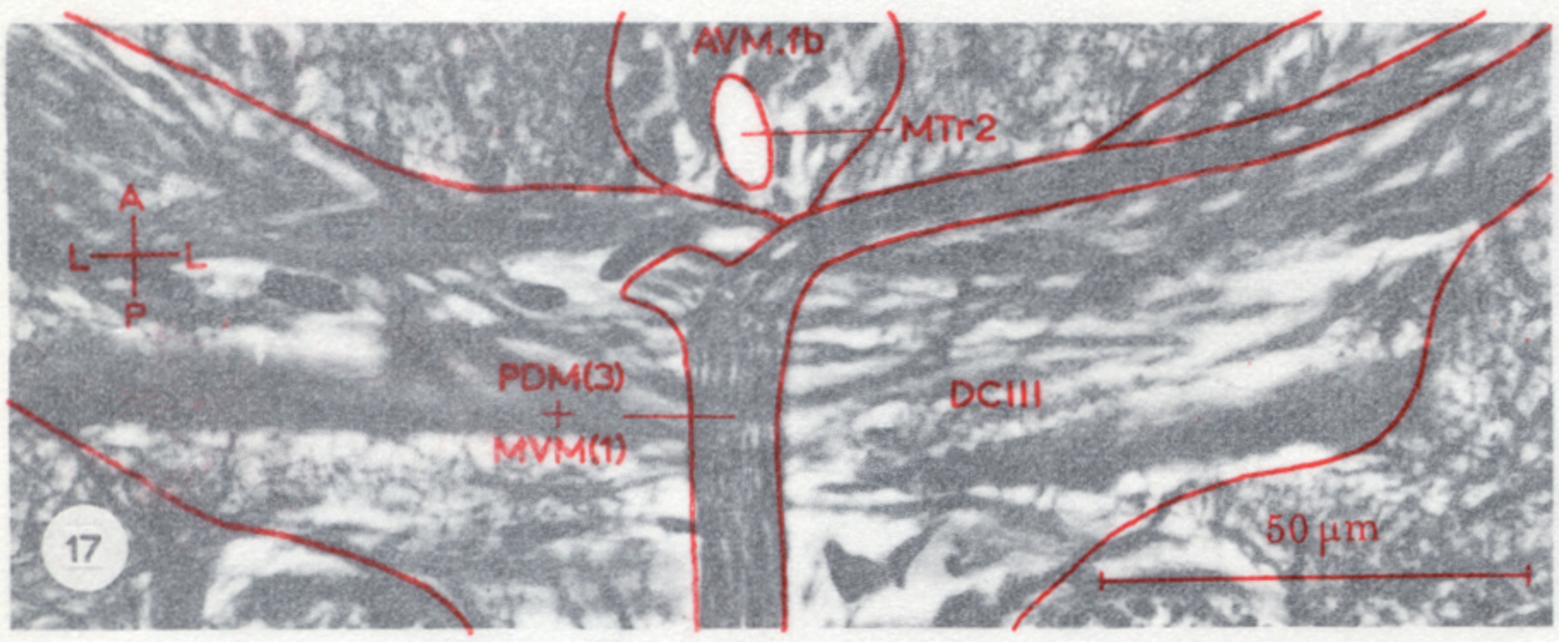


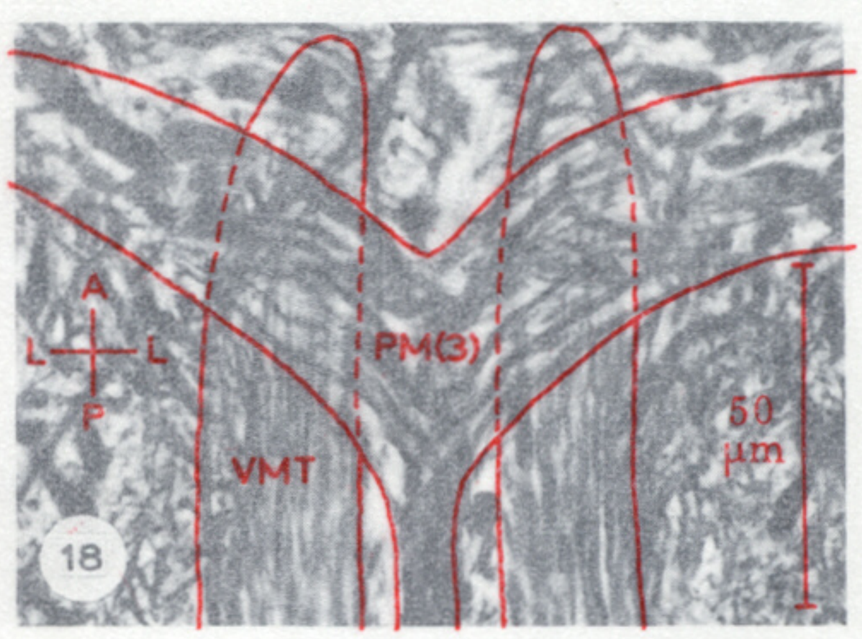


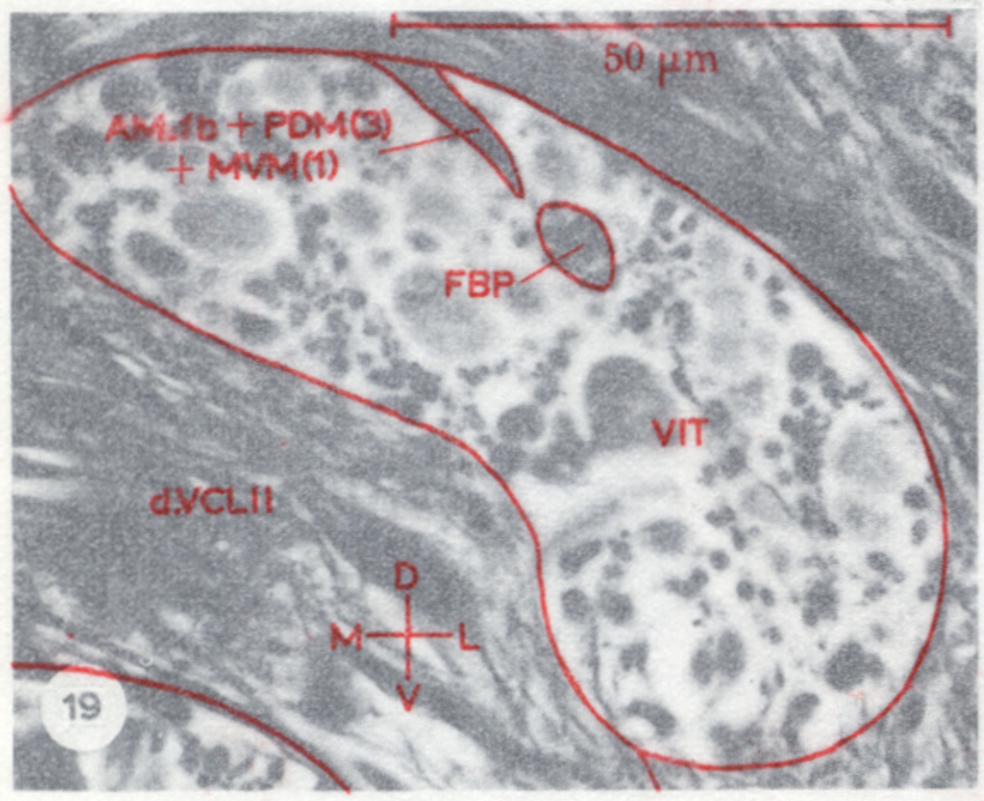
FIGURES 6–12. For description see opposite.

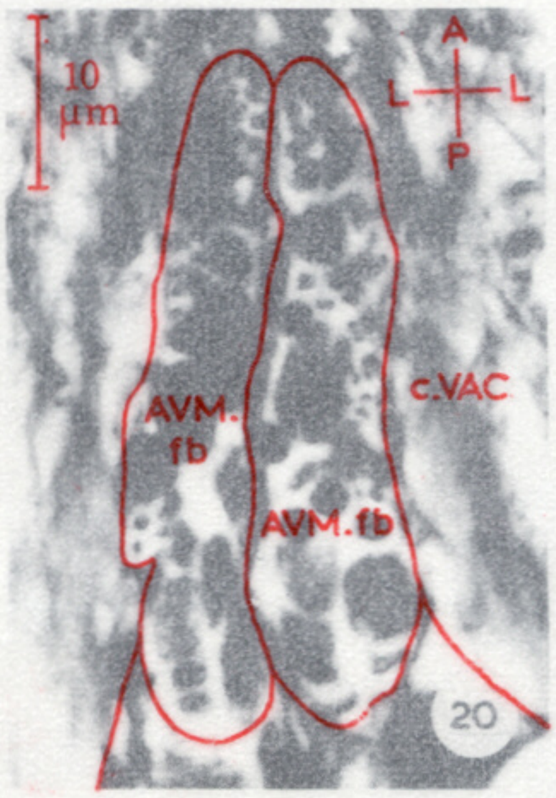


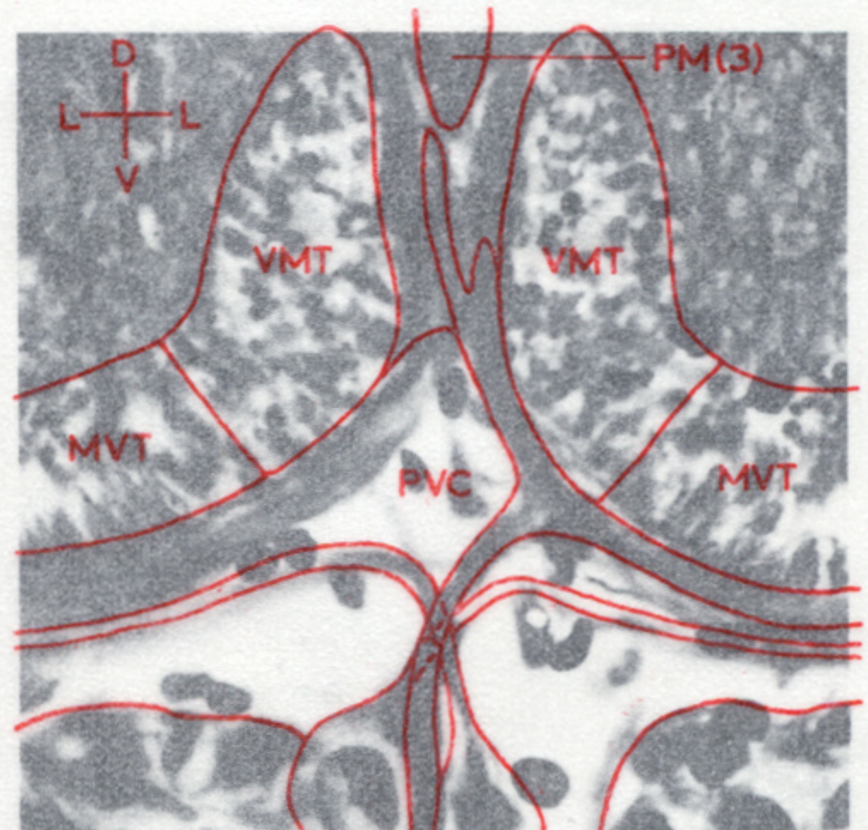


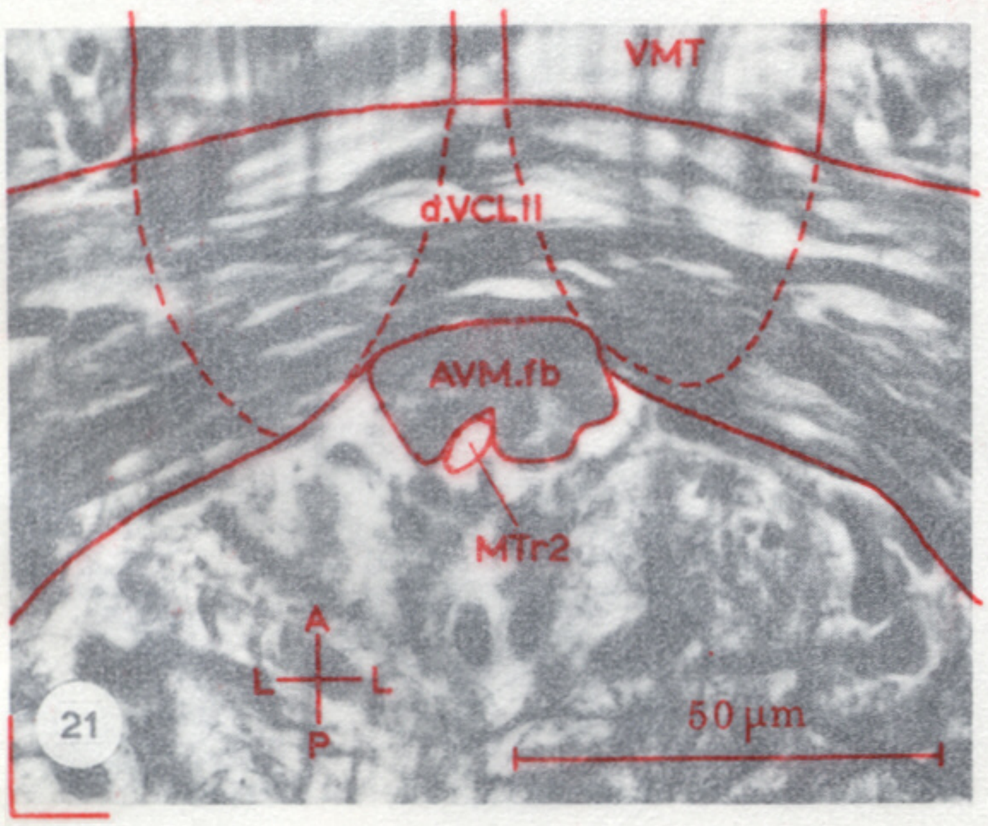


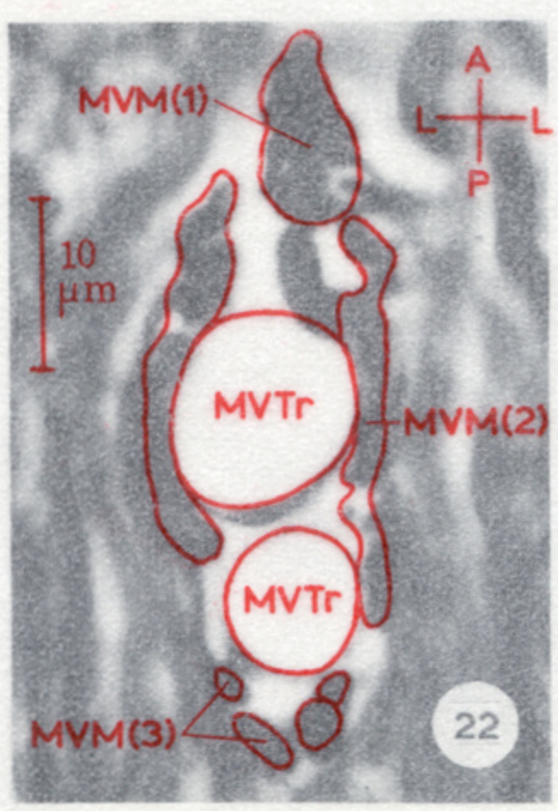


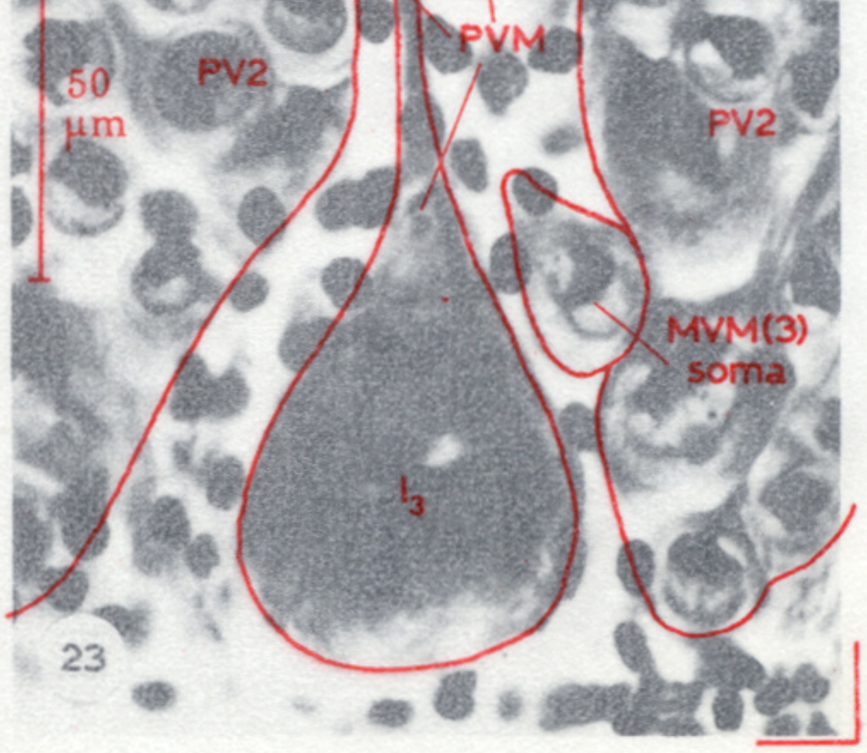




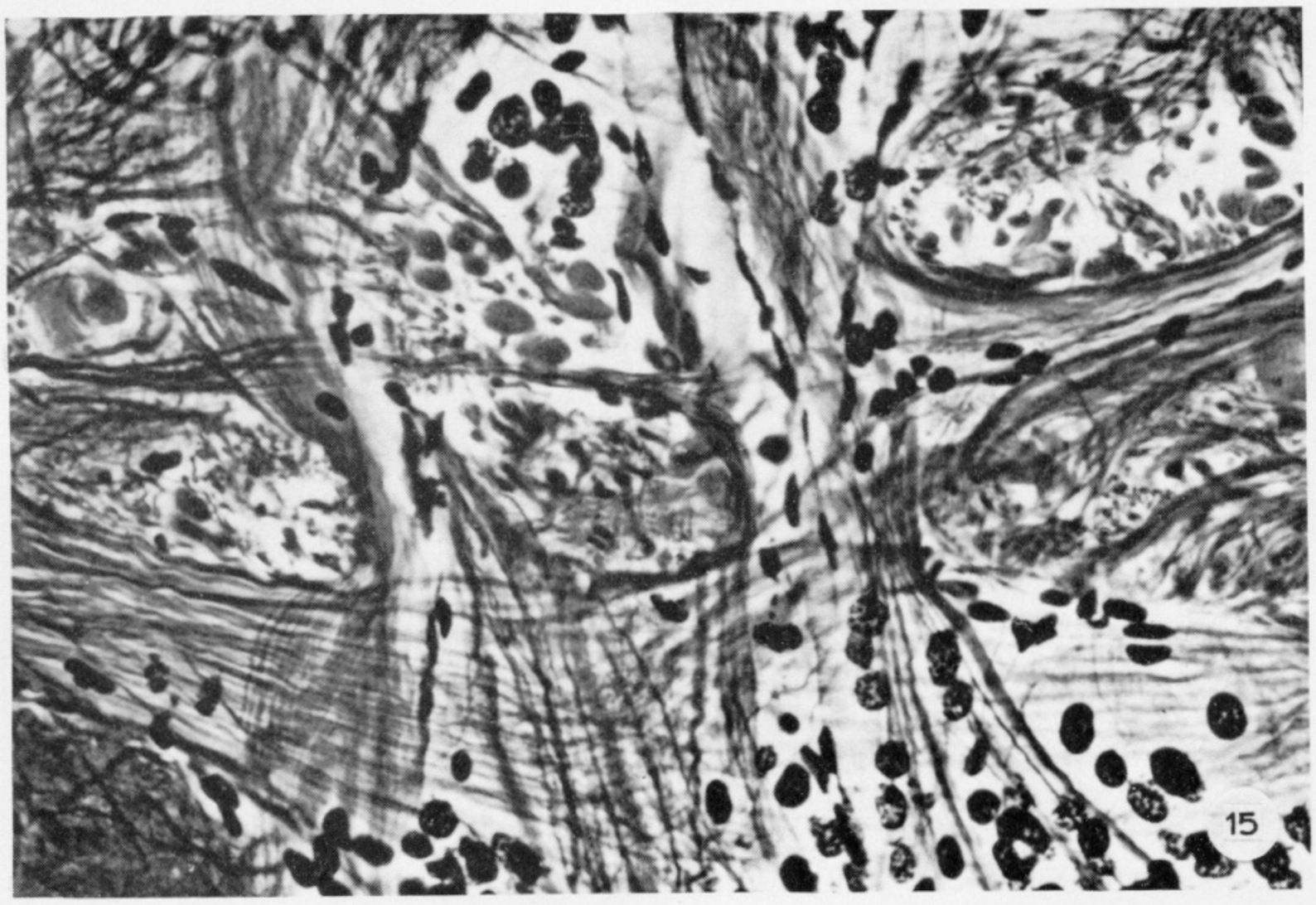


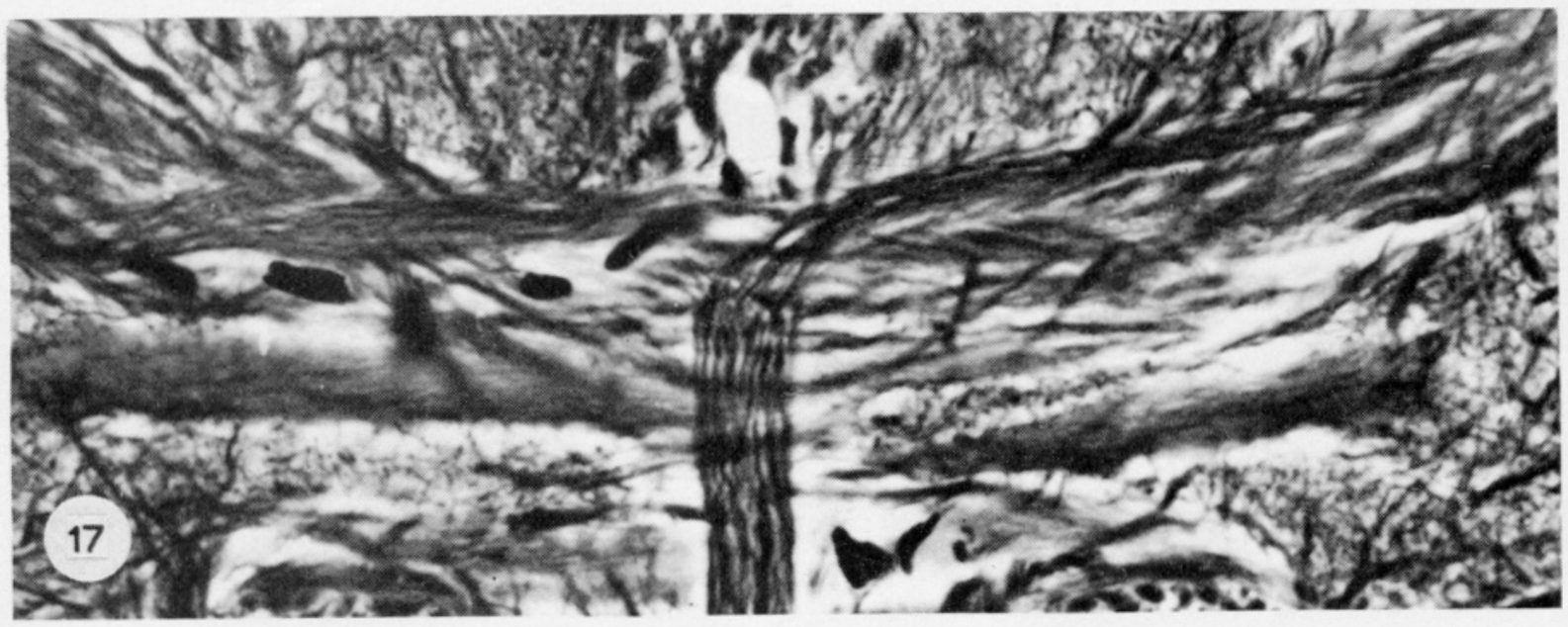


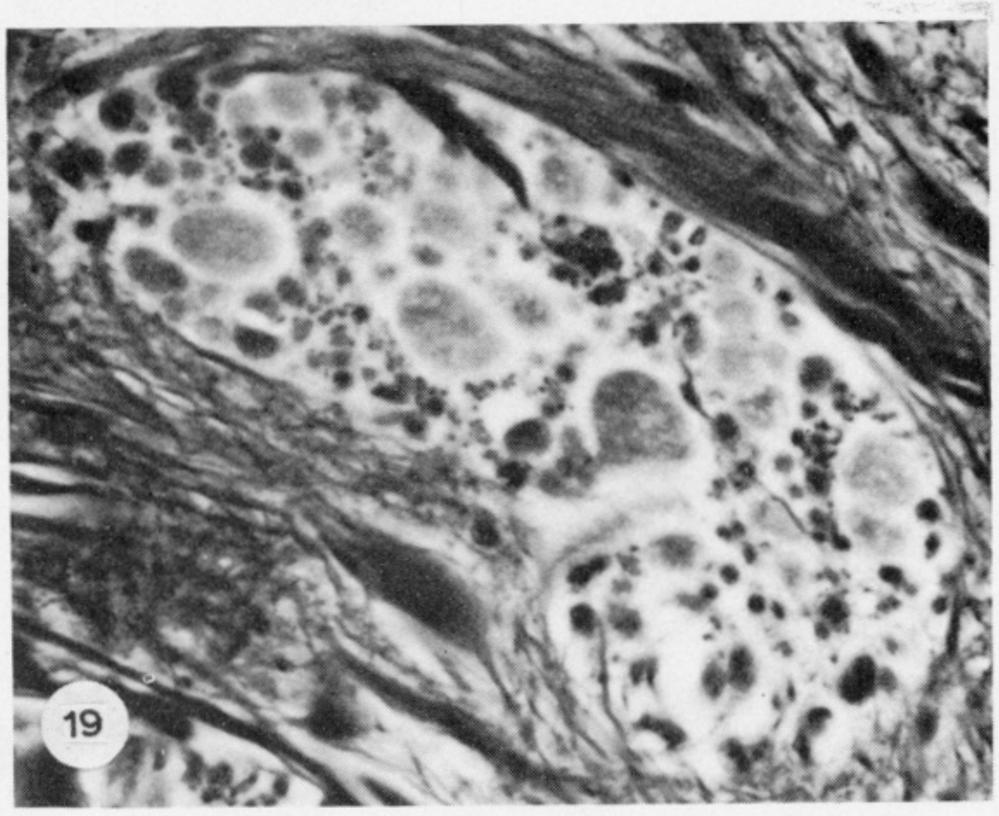


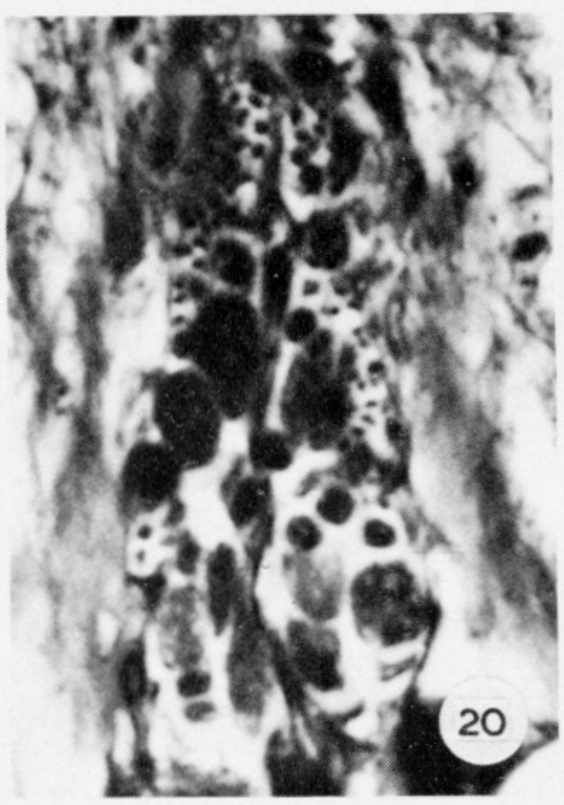


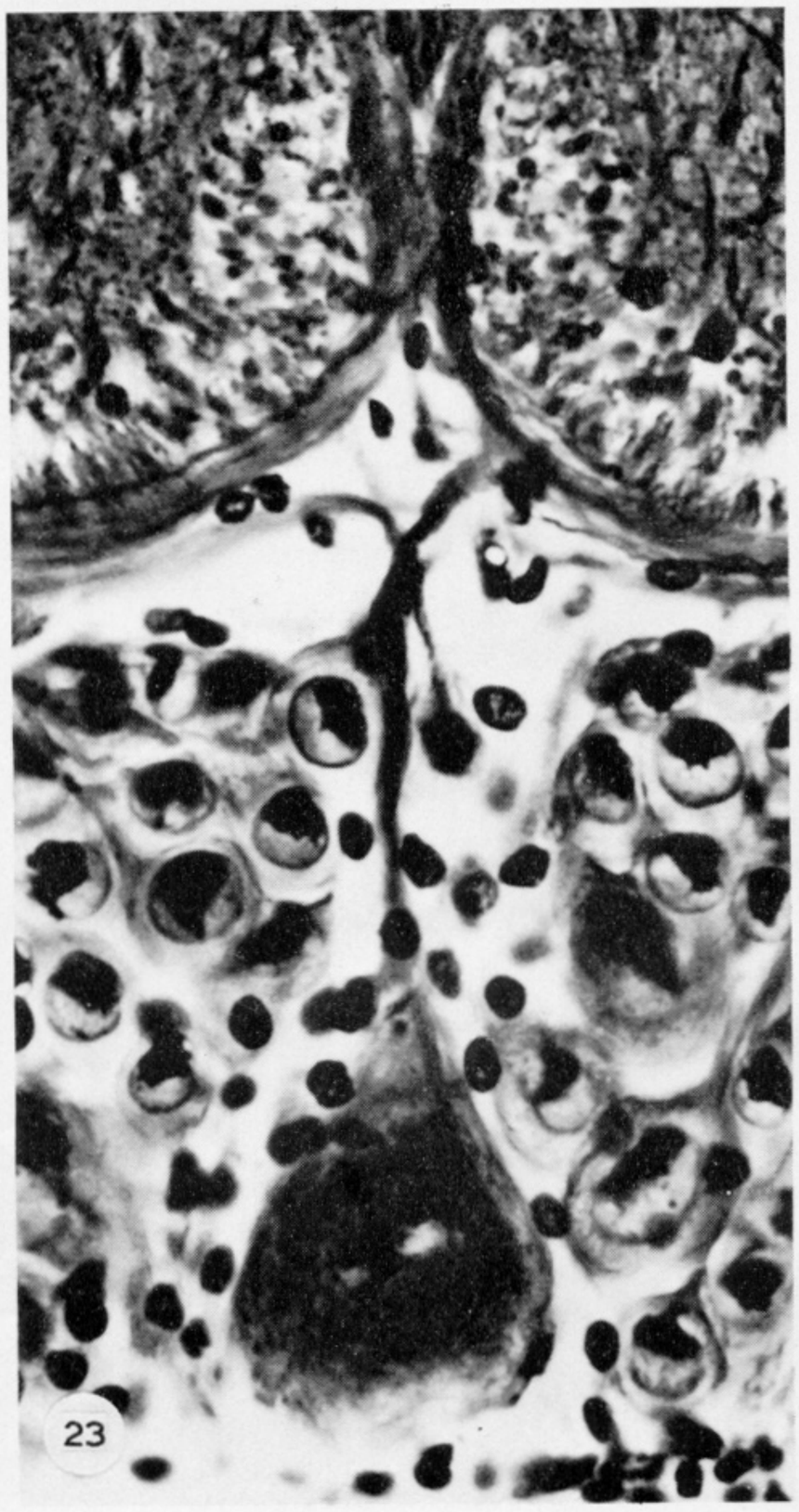
FIGURES 15–23. For description see opposite.

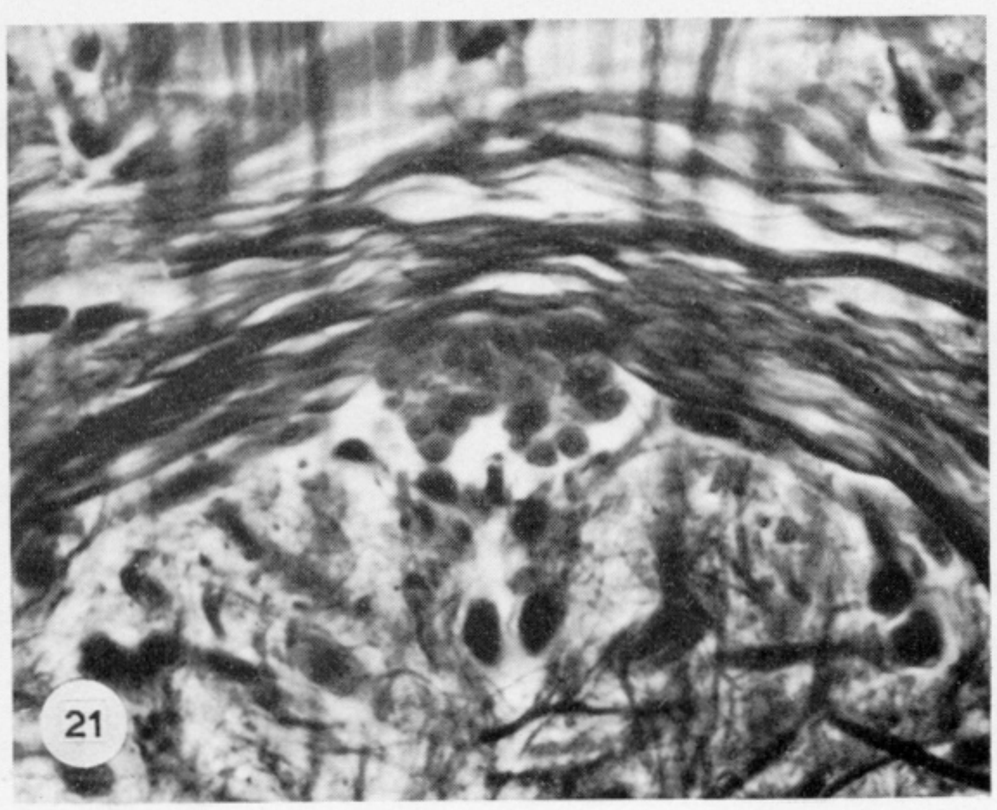












FIGURES 15–23. For description see opposite.