

NEUROANATOMY OF THE MESOTHORACIC GANGLION
OF THE COCKROACH *PERIPLANETA AMERICANA* (L.).
I. THE ROOTS OF THE PERIPHERAL NERVES

BY G. E. GREGORY

*Department of Insecticides and Fungicides, Rothamsted Experimental Station,
Harpenden, Hertfordshire, AL5 2JQ*

(Communicated by L. Fowden, F.R.S. — Received 1 October 1973)

[Plates 21–23]

CONTENTS

	PAGE		PAGE
INTRODUCTION	422	Nerve 4	436
MATERIALS AND METHODS	423	Nerve 5	439
GENERAL STRUCTURE OF THE MESOTHORACIC GANGLION	424	Nerve 6	448
ORGANIZATION OF THE GANGLION CORE	428	Nerve 7	449
ROOTS OF THE PERIPHERAL NERVES	430	Nerve 8	450
Nerve 2	431	DISCUSSION	451
Nerve 3	433	REFERENCES	460
		EXPLANATION OF ABBREVIATIONS	464

Bodian silver-stained sections and Procion Yellow impregnation were used to examine the general neuroanatomy and details of the nerve roots in the mesothoracic ganglion of adult males of *Periplaneta americana* (L.). General structure of the ganglion is summarized and the basic plan of its tracheation outlined. Fresh details are given of the seven paired longitudinal fibre tracts and ten transverse commissures, and three new oblique tracts of characteristic shape are described: the ring tract, C-tract and I-tract. Regions of the ventral association centre are briefly described. Groups of neuron cell bodies, which lie peripherally in the ganglion, are designated according to position. The fibre bundles that form the roots of each of the six paired peripheral nerves (nerves 2–7) and the single median nerve (nerve 8) are numbered from dorsal to ventral and their courses and fibre composition described. In all, 30 roots are characterized on each side of the ganglion, containing over 150 efferent, presumed motor, fibres and over 2000 afferent, presumed sensory, fibres. Function and fibre diameter are not consistently related and almost all sizes of both motor and sensory fibres occur. Nerves 2 and 6 divide into distinct dorsal and ventral roots; the roots of nerves 4 and 8 are dorsal and of nerve 7 solely ventral; roots of nerves 3 and 5 form fairly continuous series from dorsal to ventral. The more dorsal nerve roots tend to be motor in function and the ventral roots sensory. Nearly all motor cell bodies are located ventrally or ventrolaterally and their processes run more or less dorsally to give off dendritic branches into dorsal or lateral neuropile before sending axons peripherally in the nerve trunks. Cell bodies of nerves 3–6, except for one in the midline, are ipsilateral, those of nerves 3 and 4 lying almost wholly anteriorly and of nerves 5 and 6 both anteriorly and posteriorly. Cell bodies of nerve 2 are contralateral and anterior except for one in the dorsal midline. Nerve 8 receives axons from posterior cell bodies of both sides. An apparently common inhibitory motoneuron branches to nerves 3–6. The topology of some other motoneurons, chiefly of nerves 4 and 5, is outlined and the probable correspondence of some of them with previously identified metathoracic neurons is discussed. Sensory roots, predominantly of very small fibres, of nerves 2, 3 and 5–7 enter the ventral association centre. Mainly coarser sensory fibres branch into mid-level neuropile or below, though some of those of nerves 2, 3 and 7 ascend more dorsally.

INTRODUCTION

'This research was extremely laborious and tedious on account of its novelty, as well as the minuteness, fragility, and intricacy of the parts, which required a special manipulation; so that when I had toiled for many months at this incessant and fatiguing task, I was plagued next autumn with fevers and inflammation of the eyes. Nevertheless, such was my delight in the work, so many unsuspected wonders of nature revealing themselves to me, that I cannot tell it in words.'

MARCELLO MALPIGHI (1669), quoted from Miall & Denny (1886).

Recent years have seen an increasing demand, especially from neurophysiologists (Hughes 1965; Roeder 1965; Hoyle 1970), for detailed studies of the neuroanatomy of the insect central nervous system (c.n.s.), for these have lagged far behind experimental studies. Roeder, in particular, lamented that 'perhaps this sort of work should have been done fifty years ago and it is now too late'. One aspect of this problem became highlighted during histochemical investigations, following on from those of Burt, Gregory & Molloy (1966, 1967), into the sites of action of insecticides in the c.n.s. of the cockroach *Periplaneta americana* (L.). Further progress was halted by ignorance of the structure of the ventral nerve cord ganglia.

Numerous workers have studied particular aspects of the histology of the cockroach ventral nerve cord, such as the giant internuncial fibres (Roeder 1948; Hess 1958*a*; Farley & Milburn 1969; Spira, Parnas & Bergmann 1969*a, b*; Dagan & Parnas 1970; Dagan 1971; Parnas & Dagan 1971) and neurosecretory cells (Füller 1960; Geldiay 1962; de Bessé 1967; Brady 1967; Smalley 1970; Farley & Evans 1972), but the only account of general neuroanatomy remains that by Pipa, Cook & Richards (1959), summarized, with additions, by Guthrie & Tindall (1968). Pipa *et al.* described the basic architecture of the three thoracic ganglia, naming the principal nerve tracts and outlining the structure of neuron cell bodies (somata) and the surrounding glial cells. More recently, Cohen & Jacklet (1967), by the novel use of perinuclear RNA as a marker, were able to map the major motor neuron somata of the fused metathoracic and first abdominal ganglia, and Young (1969, 1973), who helped develop the method, has mapped some of those of the mesothoracic ganglion. The advent of the Procion Yellow fluorescence technique for displaying neuron geometry (Kravitz, Stretton, Alvarez & Furshpan 1968; Stretton & Kravitz 1968) opened the way for a new wave of investigations. These were at first confined to detailed studies of only a few neurons (Rowe, Moberly, Howard & Cohen 1969; Crossman, Kerkut, Pitman & Walker 1971; Harris & Smyth 1971; Milburn & Bentley 1971; Crossman, Kerkut & Walker 1972; Iles 1972*a, b*), but Hoyle & Burrows (1970, 1973*a, b*) and Burrows & Hoyle (1973) have lately begun systematically mapping the metathoracic motor neurons of the locust *Schistocerca gregaria* Forskål. The recently introduced cobalt chloride staining method (Pitman, Tweedle & Cohen 1972) allows still more detail of neuron branching patterns to be seen, and Burrows (1973*a-c*) and Tyrer & Altman (1974) have now used it to map thoracic neurons in the locust *Chortoicetes terminifera* (Walker).

The present account seeks to cover a wider field at the less detailed level required for interpreting histochemical preparations of the c.n.s. It results from the application of an improved (Bodian) silver technique and a new use of Procion Yellow to display whole tracts of nerve fibres instead of single ones. The existence of the description by Pipa *et al.* as a starting-point and the close correspondence between the functional condition of the thoracic ganglia and the state of poisoning of the whole insect after treatment with insecticide (Burt *et al.* 1966) made the thoracic ganglia, despite their relative complexity, an obvious first choice for investigation, and of them the mesothoracic ganglion was examined in most detail. This paper is the first in

a projected series, in which it is hoped to examine the neuroanatomy from four main viewpoints: (1) the roots of the peripheral nerves; (2) neuron cell body groups; (3) longitudinal, and (4) transverse nerve fibre tracts. It is hoped the whole will provide a medium-scale atlas of the mesothoracic ganglion that will form a useful basis for electrophysiological and more detailed neuroanatomical studies as well as for histochemical work.

In the present paper, to avoid confusion, generally only first- and second-order branches of dendritic trees are shown; further detail may be included in subsequent papers.

MATERIALS AND METHODS

Adult male cockroaches, 2 to 14 weeks after their final moult, were used. Basic neuroanatomy was determined from silver-stained sections of more than 60 specimens and these observations were verified and amplified by fluorescence studies of material stained with Procion Yellow M-4R (Imperial Chemical Industries Ltd, Manchester, England) (24 specimens). In both techniques cockroaches were narcotized with CO₂ and ganglia removed under the saline of Yamasaki & Narahashi (1959) within 2–3 min.

For silver staining, ganglia were fixed immediately in alcoholic Bouin (Duboscq-Brasil), previously 'aged' for at least 40 days at 60 °C to improve preservation (Gregory 1970). They were stained with eosin in absolute ethanol (Pantin 1948) during dehydration to allow them to be oriented for sectioning, and embedded in Paramat (G. T. Gurr, London). Sections were cut at 10–20 µm in transverse, frontal and sagittal planes, and in many oblique planes to show particular structures. Stains tried included the Holmes (1943) silver nitrate method and its Blest (1961) and Rowell (1963) modifications, but best results were given by the Bodian (1936) protargol (silver-protein) technique, as modified by Power (1943). In this, sections are impregnated twice in protargol solutions containing metallic copper, each followed by development in a hydroquinone-sodium sulphite solution. The stain is finally intensified with gold chloride and oxalic acid. Results at first were inconsistent, as found by previous users (Power 1943; Rowell 1963), but a study of factors controlling the stain (Gregory 1970) made it possible to improve reliability and to vary the pattern of staining to suit the work being done. Between 0.5 and 5 g of copper per 65 ml of 2% protargol solution were used for impregnation and 0.25–1% hydroquinone in 5–10% Na₂SO₃·7H₂O was used for development, depending on section thickness and the intensity and selectivity of staining required.

Procion Yellow was used as a saturated solution in cockroach saline diluted to maintain isotonicity. Dye concentration was < 2% at 2 °C. It was made to diffuse along nerve fibres not by the usual intracellular injection techniques (Stretton & Kravitz 1968; Bentley 1970) or by electrophoresis (Iles & Mulloney 1971), but more simply by immersing whole ganglia in it (Gregory 1973). Each ganglion was dissected with pro- and metathoracic ganglia attached and all mesothoracic peripheral nerves as long and undamaged as possible. A peripheral nerve or branch was then cut off close to the ganglion and the whole thoracic nerve cord immersed in stain for 1–2 h at 2 °C. Dye diffused into all cut nerves and tracheae and into the superficial layers of the ganglion, but staining time was adjusted so that it entered the central fibrous region of the ganglion only along the fibres of the shortened nerve or branch, which thus became preferentially stained. The other two ganglia prevented it entering along the interganglionic connectives. Ganglia were washed in cockroach saline and fixed, dehydrated and embedded as above, except that eosin treatment was omitted because eosin itself fluoresces. Pro- and

metathoracic ganglia were cut away before embedding. Sections were cut at 10–30 μm , dewaxed in xylene and mounted in Fluormount (E. Gurr, London). They were examined by fluorescence microscopy, with the use of Schott BG 12 and BG 38 exciter filters and a Zeiss 50 barrier filter.

Tracheation was examined in whole, fresh ganglia under saline and in sections. It showed particularly well in understained Procion Yellow preparations (figure 16, plate 23).

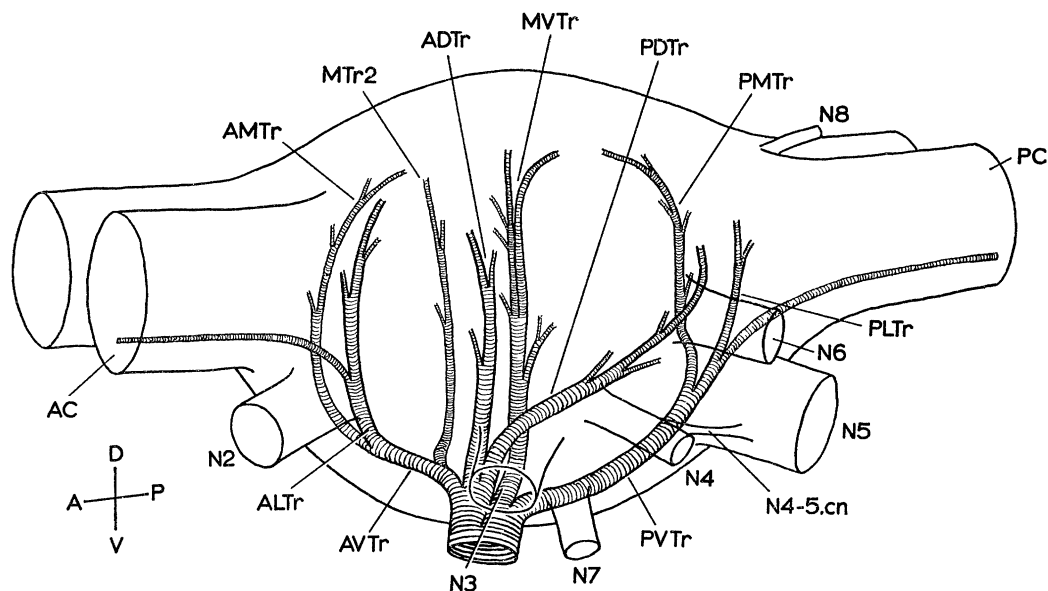


FIGURE 1. Mesothoracic ganglion, perspective view showing bases of peripheral nerves and interganglionic connectives, and principal tracheae of left half.

Figures were constructed by means of a Zeiss camera lucida fitted to a Photomicroscope II, by carefully superimposing relevant features from successive sections. Felt-tipped pens in a wide range of colours made this easier: in the initial sketches a different colour was used for each section; as knowledge increased, a different colour could be used for each nerve fibre or group of fibres. For simplicity, only the nerve roots are shown in full depth in the figures, other structures being outlined only in the plane of the nearest relevant nerve root. Occasionally features, such as some nerve cell bodies, are included which are in a plane considerably removed from that of the rest of the figure. Orientation is marked on each figure.

An Arnold (1969) portable electronic counter was used to count the large numbers of small nerve fibres. The counter probe was viewed superimposed on the microscope image by means of the camera lucida and fibres were counted by touching the tip of the probe against the drawing easel at the position of each fibre. The use of a felt-tipped pen as the probe enabled fibres to be marked off on paper as they were counted, to avoid counting any twice. Nevertheless, counts given are usually only approximate because of the difficulty of distinguishing between small fibres packed closely together.

GENERAL STRUCTURE OF THE MESOTHORACIC GANGLION

The mesothoracic ganglion (figure 1) consists, like most other ventral nerve cord ganglia, of a pair of ganglia fused in the midline and linked with those anterior and posterior to them by

cells that are flattened, cuboidal or columnar in different parts of the ganglion and which contain distinctive mitochondria (Hess 1958*c*) and much glycogen (Wigglesworth 1960; Ashhurst 1961). Their fine structure was described by Maddrell & Treherne (1967). The neural lamella and perineurium together form the 'perilemma' of Scharrer (1939). They are thinner in the peripheral nerves and connectives and the perineurium cells differ cytologically from those in the ganglion (Hess 1958*c*; Smith & Treherne 1963). Below the perineurium are the glial cells. In the ganglion they are incompletely divided into an outer and inner layer (o.GL, i.GL) by the 'glial lacunar system' (GLS) (Wigglesworth 1960) of intercellular spaces. The cells of the outer layer invest the neuron cell bodies (cb) and form small interdigitations with their plasma membranes. The cells of the inner layer surround the central fibrous region of the ganglion and send complex processes into it. These ensheath the nerve fibres of the central region in one or more spirally-arranged layers, the mesaxon folds, between which is the mesaxon invagination, an extracellular channel 10–15 nm wide (Smith & Treherne 1963). The glial cells of the peripheral nerves and connectives are likewise produced into processes that ensheath the nerve fibres. These processes have a similar appearance in overstained Bodian preparations to the 'interaxonic supporting tissue' of Pipa *et al.* (1959), which therefore seems likely to be composed of them, perhaps together with amorphous matter between the glial folds (Guthrie & Tindall 1968). Pipa (1961) investigated the histochemistry of the glia. The cell bodies of unipolar motor and interneurons form more or less well-defined groups (cbg) in the outer glial layer, the cells of each group contributing their fibres to a common fibre bundle (fb) or a few closely associated bundles. Most groups lie ventrally or laterally in the ganglion, with a few mid-dorsally. They are classified in a subsequent account (in preparation) according to their position, into anterior or posterior, dorsal, dorsolateral, lateral, ventrolateral, ventral and median groups. Where several groups occur in a given area they are numbered from anterior to posterior. Their fibre bundles run into the central fibrous region of the ganglion, the ganglion core (GC) (Bullock & Horridge 1965). This is composed largely of fibre tracts and areas of neuropile. The tracts include, in addition to the bundles of fibres from cell body groups, sensory fibres from peripheral nerves and internuncial fibres from other ganglia. Neuropile is an imprecisely defined term (Maynard 1962) often applied loosely to the whole ganglion core, but it is usefully restricted to the fine fibrous regions that lie between the tracts, and composed of their interlacing branches, terminal arborizations and synapses. The core is partially divided into right and left halves, the cores of the two component ganglia, by dorsal and ventral midline clefts (DMC, VMC), which contain glia, neuron cell bodies and tracheae. The two halves are connected across the midline by transverse fibre tracts (commissures).

The ganglion is well supplied with small tracheae (tre). All originate from a single trachea each side that branches from the middle of the large tracheal trunk linking the two thoracic spiracles. It enters the ganglion ventrolaterally in front of nerve 7 and divides into two dorsal and three ventral branches, 25–30 μm in diameter. These run through the glial cell layer at or near the surface of the ganglion core and, with their major branches, form a system of tracheae sufficiently constant in general arrangement to provide useful landmarks (figure 1; figure 16, plate 23). Each trachea gives off innumerable small branches, most of which ramify into the core but which vary from individual to individual. Smith & Treherne (1963) discuss their fine structure. The anterior dorsal trachea (ADTr, figure 1) ascends in front of nerve 3 and follows the margin of the core to the dorsal midline. It gives branches to the anterior lateral and anterior dorsal parts of the core. The posterior dorsal trachea (PDTr) passes behind or through

the base of nerve 3 and between the bases of nerves 5 and 6, and then curves up to the dorsal midline. It supplies the posterior lateral and posterior dorsal regions of the core. The anterior ventral trachea (AVTr) usually divides into three branches, which supply the anterior and anterodorsal regions of the core and the anterior connective. The two most anterior branches, the anterior lateral and anterior median tracheae (ALTr, AMTr), arise behind or beneath the base of nerve 2 and ascend lateral to the base of the anterior connective and close to the anterior

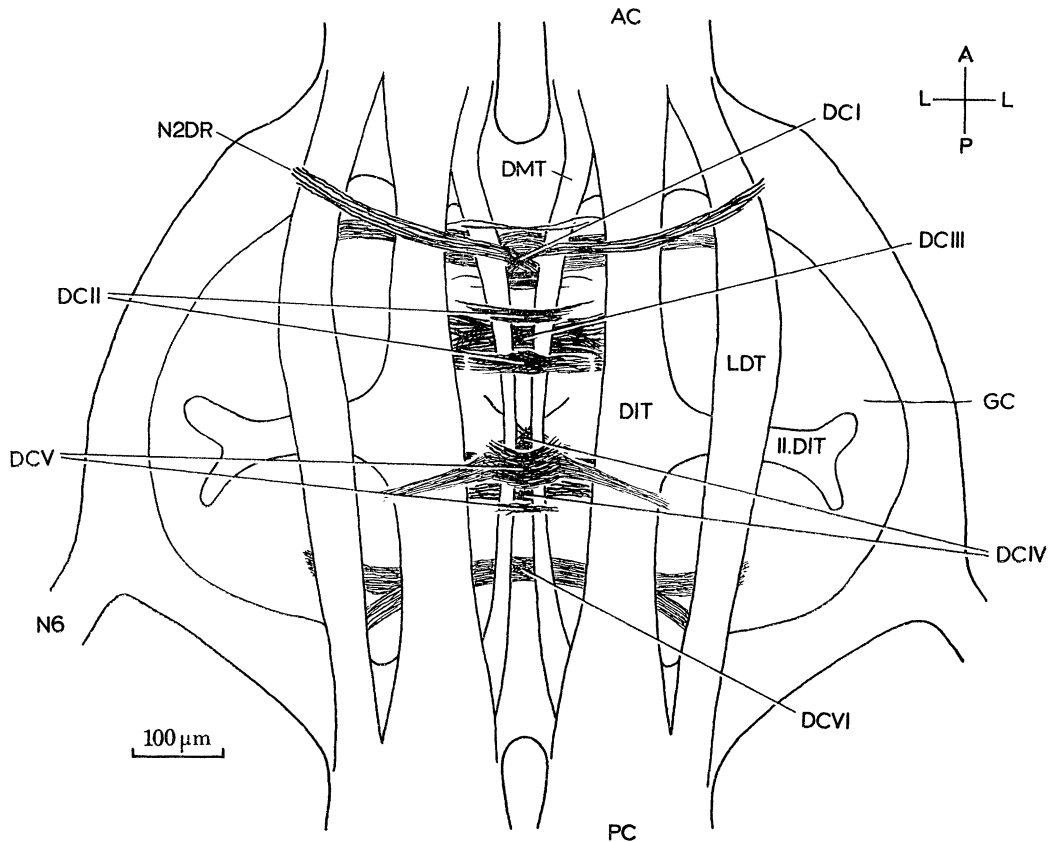


FIGURE 3. Dorsal half of ganglion, showing dorsal longitudinal fibre tracts and commissures; dorsal view, median dorsal tracts omitted.

midline respectively. The lateral branch sends one, sometimes two, small tracheae forward ventrally in the anterior connective. The third branch, usually smaller than the others, which forms the second median trachea (MTr2), runs medially to the ventral midline cleft and ascends between the halves of the core a little forward of the middle of the ganglion. The mid-ventral trachea (MVTr) also runs to the ventral midline cleft and then ascends between the halves of the core in the centre of the ganglion. It sends branches into the central and mid-dorsal regions of the core. The posterior ventral trachea (PVTr) supplies the posterior and posterodorsal parts of the core and the posterior connective. It runs posteromedially along the ventral surface of the core and then sends two branches dorsally, and one posteriorly into the posterior connective. The dorsal branches, the posterior median and posterior lateral tracheae (PMTr, PLTr), ascend close to the posterior midline and lateral to the base of the connective respectively. The medial branch sometimes connects dorsally with a branch of the mid-ventral trachea or even with the anterior median trachea (figure 16).

ORGANIZATION OF THE GANGLION CORE

Despite its initially confusing appearance, the ganglion core possesses a fairly straightforward basic pattern of organization. Most of its nerve fibres are gathered together for some part of their course into reasonably clearly defined tracts, the more conspicuous of which form useful landmarks for locating less obvious structures.

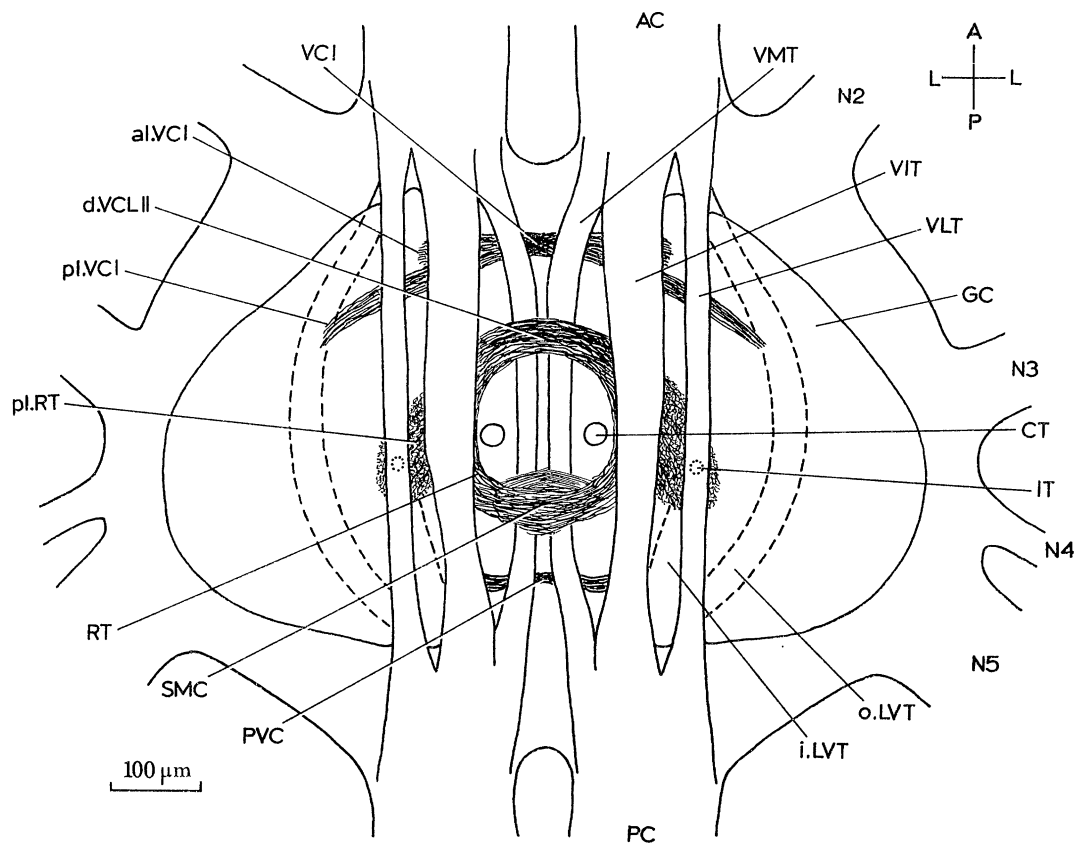


FIGURE 4. Ventral half of ganglion, showing ventral longitudinal fibre tracts and commissures and positions of C-tract and I-tract; dorsal view, median ventral tracts and ventral association centre omitted.

The most prominent are the longitudinal and transverse tracts recognized by Pipa *et al.* (1959) (figures 2–5; figures 6, 7, plate 21), whose terminology is retained. Apart from the first mention, major tracts and other structures will generally be referred to by their abbreviations, and all abbreviations are listed at the end of the paper. Seven longitudinal tracts run through each half of the core between the anterior and posterior connectives. They are, from dorsal to ventral, the dorsal tract (DT), dorsal intermediate tract (DIT), dorsal median tract (DMT), ventral lateral tract (VLT), ventral intermediate tract (VIT), ventral median tract (VMT) and ventral tract (VT). The DT comprises two regions, the median dorsal tract (MDT) and lateral dorsal tract (LDT). The VT consists of two well-defined lateral bundles, here termed the outer and inner lateral ventral tracts (o.LVT, i.LVT), and three more median, looser collections of fibres, termed median ventral tracts 1–3 (MVT1, MVT2, MVT3). The DIT gives off a large bundle of branches, the lateral limb of the DIT (ll.DIT), into the middle of its own half of the core. The transverse tracts, which link the two halves of the core, comprise six dorsal commissures

numbered from anterior to posterior (DCI to DCVI), and four ventral commissures – ventral commissure I (VCI), ventral commissural loop II (VCLII), the supra-median commissure (SMC) and the posterior ventral commissure (PVC). DCII and DCV are groups of fibre bundles at the dorsal margin of the core. Associated with DCII is a prominent tract (TT, figures 2, 5, 6), T-shaped in transverse sections of the ganglion, composed of fibres of the anterior

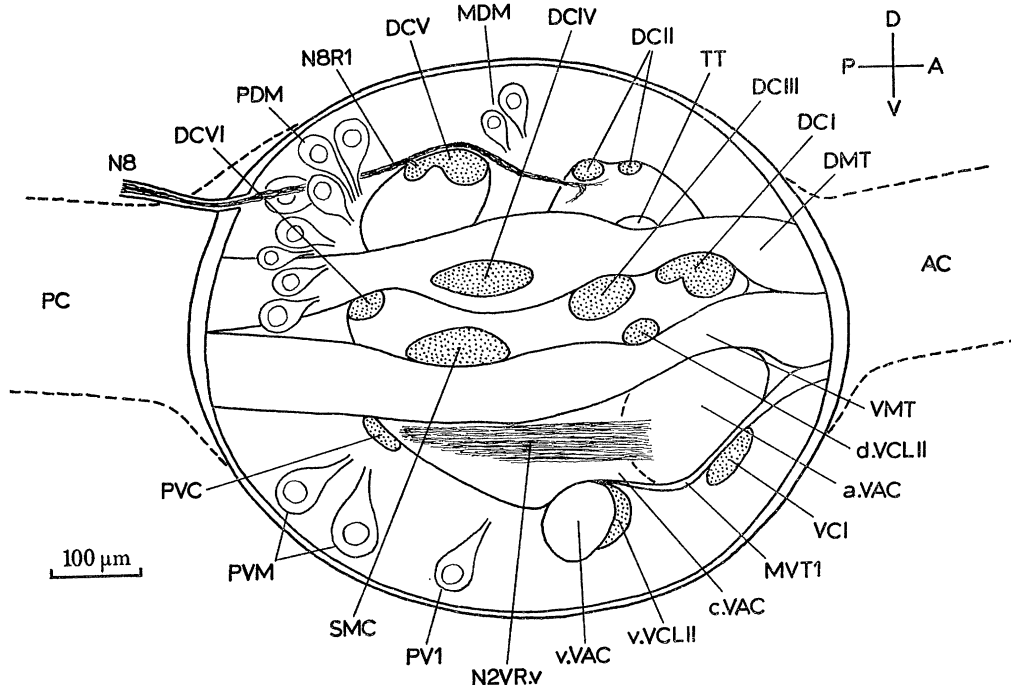


FIGURE 5. Parasagittal section of ganglion close to midline, showing positions of commissures, ventral association centre and large median cell bodies, and root of nerve 8; viewed from midline.

ventral median cell body group (AVM, figures 6, 7, plate 21). It runs vertically up the midline and sends a lateral limb above the DIT of each half of the core. VCI extends laterally as two bundles, the anterior and posterior lateral limbs of VCI (al.VCI, pl.VCI, figures 4, 14). The loop of VCLII crosses the midline twice and so includes two commissures, the dorsal and ventral parts of VCLII (d.VCLII, v.VCLII, figures 2, 4–7).

The ganglion core also contains many vertical and oblique tracts, composed largely of fibre bundles from the surrounding cell body groups and peripheral nerves. Three are important as landmarks. They are termed here, because of their characteristic shapes, the ring tract, C-tract and I-tract. The ring tract (RT, figure 4; figures 9, 11, 12, plate 22; figures 30, 32) is a conspicuous horizontal ring of fibres that extends back from the dorsal part of VCLII, beneath the VITs, and is completed posteriorly by components of the SMC. From its sides a poorly delimited zone of much-branched fibres, the posterolateral limb of the ring tract (pl.RT, figure 4; figures 10–12, plate 22; figures 30, 32), spreads laterally towards the base of nerve 5. The C-tract (CT, figures 4, 9–11; figure 22, plate 23; figures 25, 29–32) is a distinctive vertical bundle, C-shaped in transverse sections of the ganglion, in the mid-region of each half of the core close to the midline where the mid-ventral trachea ascends. It curves between the VMT and MVT2 and then dorsally between the DIT and VIT. It is composed chiefly of fibres from cell bodies of anterior ventrolateral group 2 (AVL2, figures 23,

25). The I-tract (IT, figures 4, 9, 10, 12, 25, 26, 29–31) lies a little behind the level of the C-tract and lateral to it. It is a cylindrical bundle, which widens above and below and appears I-shaped in parasagittal sections of the ganglion. It runs vertically up from a ventral, longitudinal bundle of fibres of anterior ventral cell body group 4 (AV4) and fans out dorsally among the fibres of the VLT.

The neuropile between the tracts forms the chief synaptic field of the ganglion. Often it is not clearly demarcated from the tracts where they break up into it. A region of especially fine neuropile occurs ventrally in each half of the core. Pipa *et al.* (1959) termed this the ventral association centre (VAC), because it receives the main sensory inputs from several peripheral nerves. Anteriorly, it consists of two rounded masses fused in the midline and bounded by the MVT1s below, the VMTs and MVT2s above, and the anterior lateral limbs of VCI laterally (a.VAC, figures 5, 6, 14, 16, 25, 28, 29, 31). The two masses become separated nearer the centre of the ganglion by the ventral midline cleft, in which run the ascending fibres of the AVM cell body group. Here the two halves of the VAC narrow and become cylindrical, and pass within the loop of VCLII (c.VAC, figures 2, 5, 7). The cylindrical regions then widen and their boundaries become less definite. Ventrolateral extensions of them (l.VAC, figure 32) are linked across the midline immediately behind the ventral part of VCLII by a transverse bridge of neuropile, which forms the ventralmost region of the VAC (v.VAC, figures 5, 6, 16, 32). Behind this the ventral midline cleft again divides the VAC into right and left halves, each of which forms the ventromedial margin of its half of the core. Posteriorly they narrow to strips along the borders of the widening ventral cleft and are then broken up by fibre bundles of ventral cell body groups entering the core. They cease to be distinguishable by the level of the PVC.

ROOTS OF THE PERIPHERAL NERVES

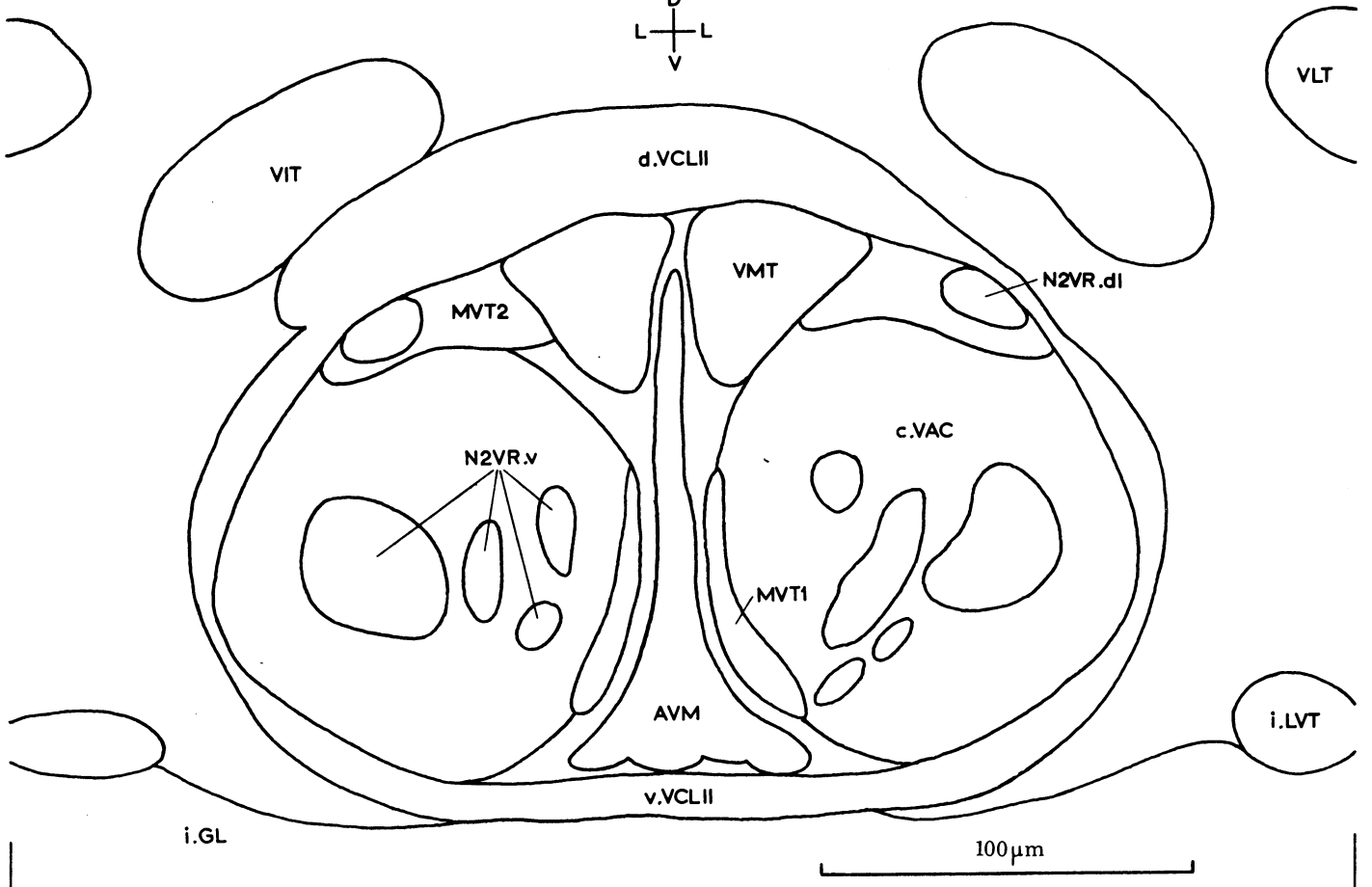
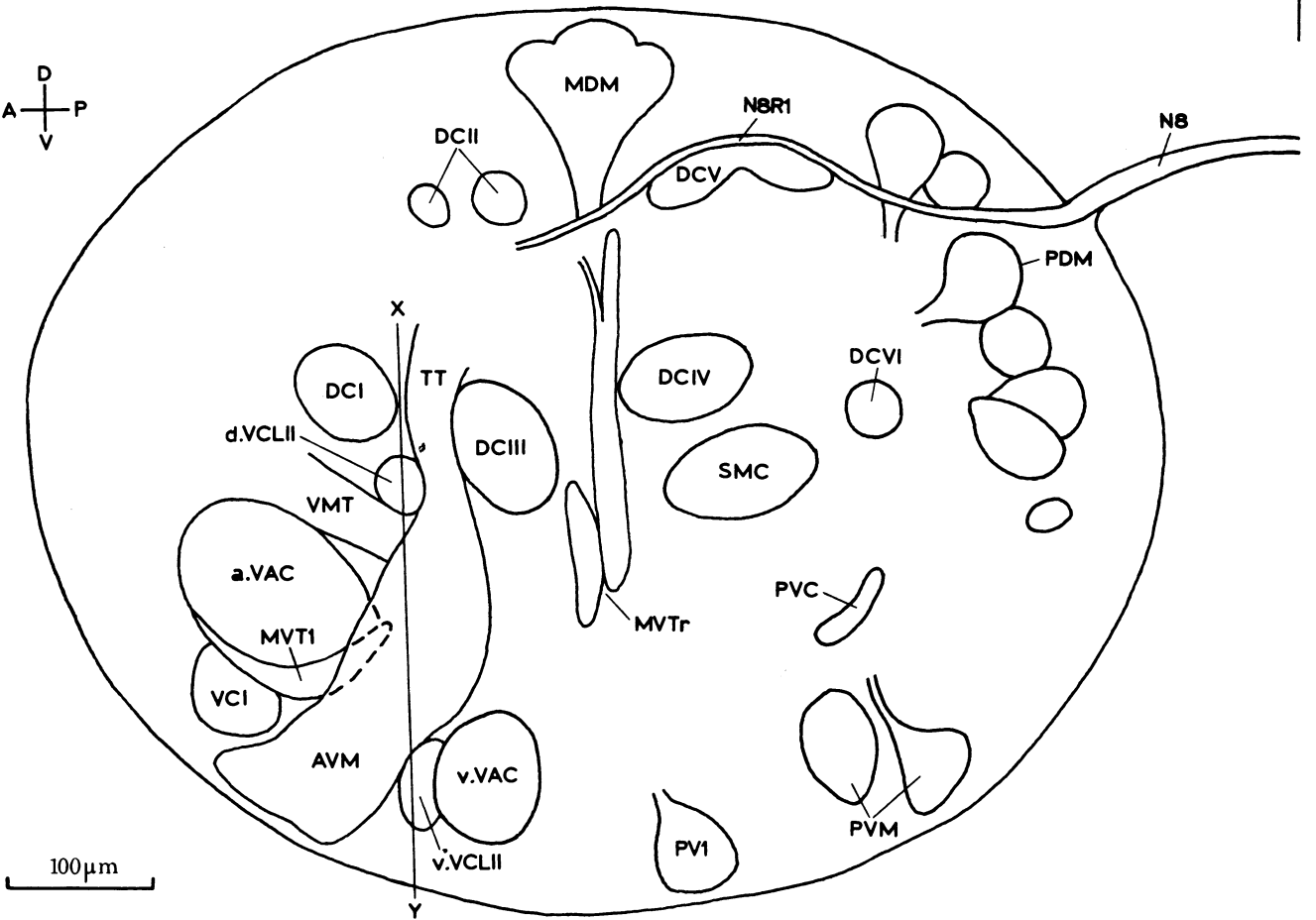
Upon entering the ganglion each peripheral nerve except the median nerve 8 divides into a number of bundles of fibres, the nerve roots. In this account those of each nerve are numbered from dorsal to ventral or, if they are in much the same horizontal plane, from anterior to posterior. The abbreviation 'R' is used for 'root', to distinguish it from 'r', generally used for the branch or ramus of a peripheral nerve. Their courses are followed in the direction in which they were originally traced – from the nerve inwards – though in many this is the reverse of the presumed direction of conduction of impulses. To describe roots in the direction of conduction, which would normally be preferable, would frequently mean describing different roots of the same nerve in opposite directions, which would unduly complicate the account, and in those roots that contain fibres running in two directions would lead to confusion. To give some idea of the composition of each root bundle, fibres are classified by diameter into arbitrary size-groups, modified from Nijenhuis & Dresden (1952), though fibres vary in diameter along their length, usually being largest in the nerve trunk, narrowing in the glial cell layer, and often en-

DESCRIPTION OF PLATE 21

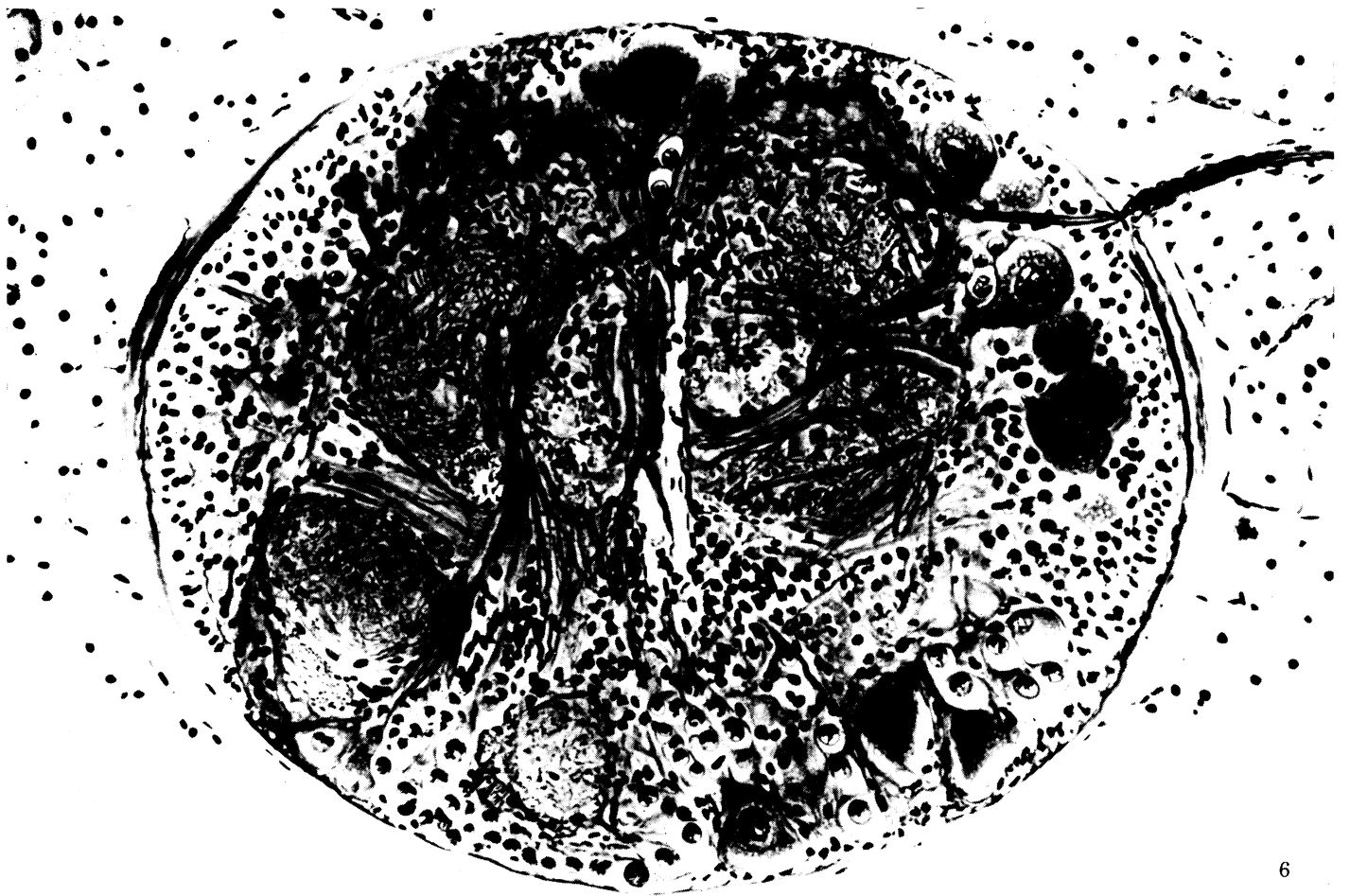
Bodian silver preparations

FIGURE 6. Sagittal (midline) section of ganglion, 10 μm thick, showing commissures, ventral association centre, some median cell body groups and root of nerve 8. Black dots within ganglion are nuclei of glial cells and (peripherally) perineurium; outside ganglion are nuclei of fat-body cells. Line XY shows plane of figure 7.

FIGURE 7. Part of 10 μm transverse section of ganglion along plane XY in figure 6, showing ventral commissural loop II and associated structures.



FIGURES 6 AND 7. Overlay.



6



7

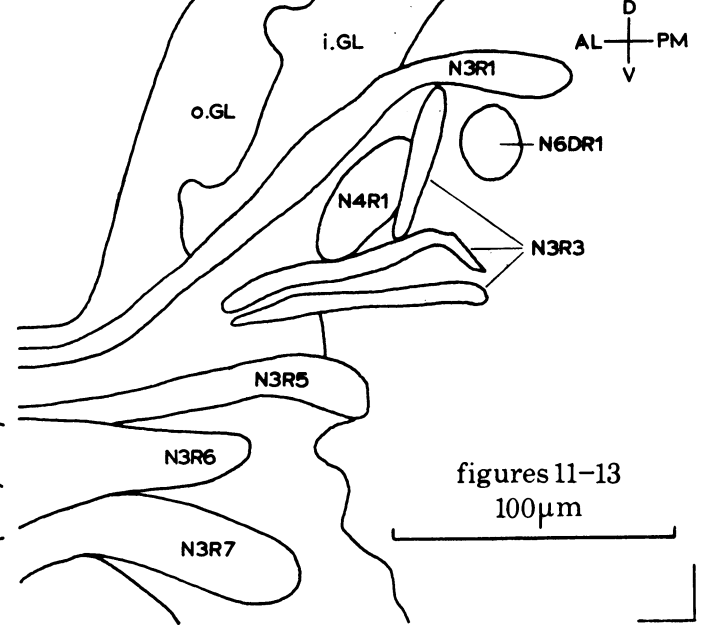
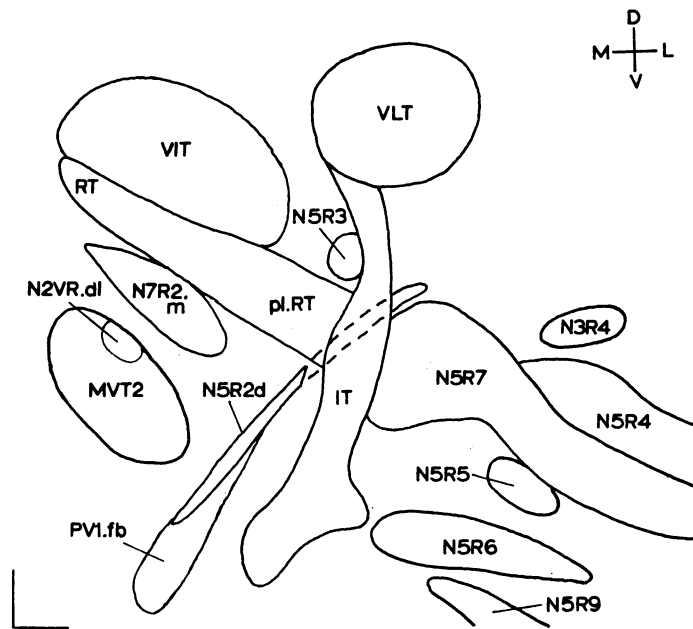
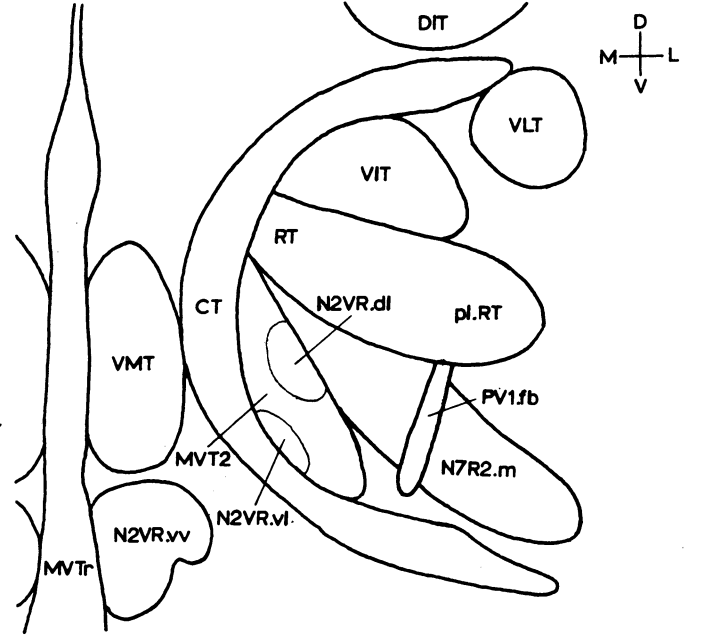
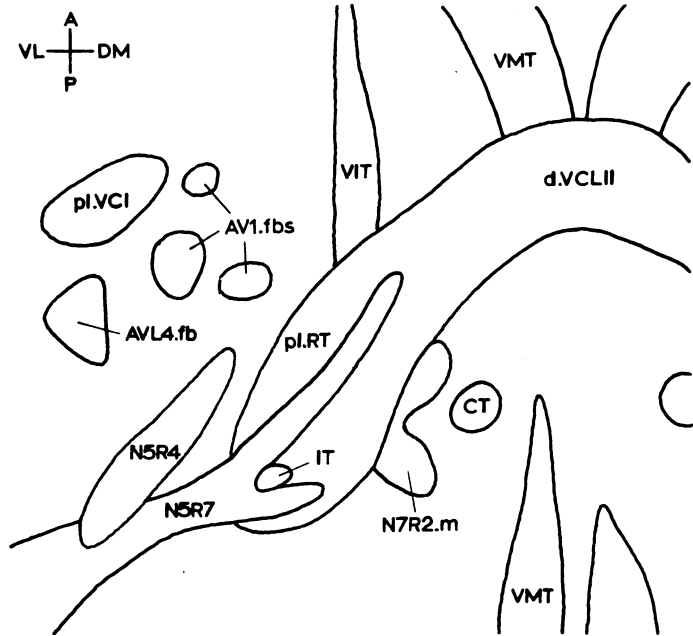
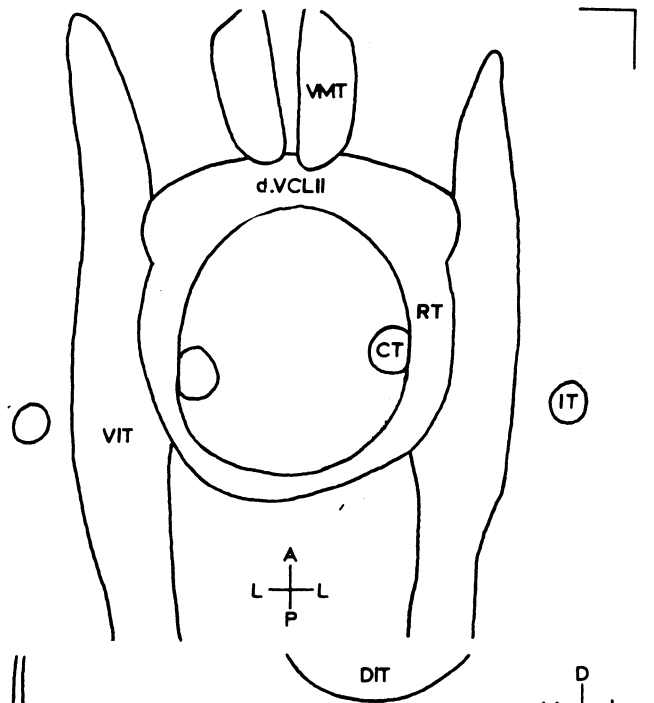
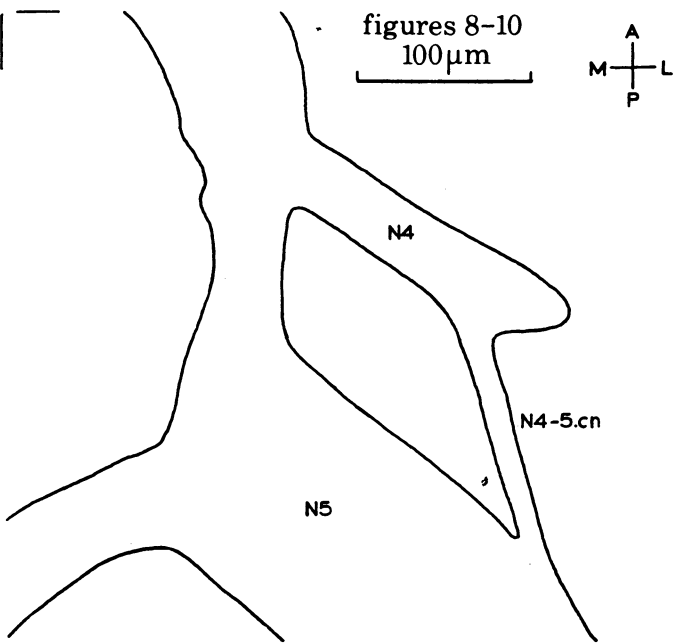
FIGURES 6 AND 7. For description see opposite.

(Facing p. 430)



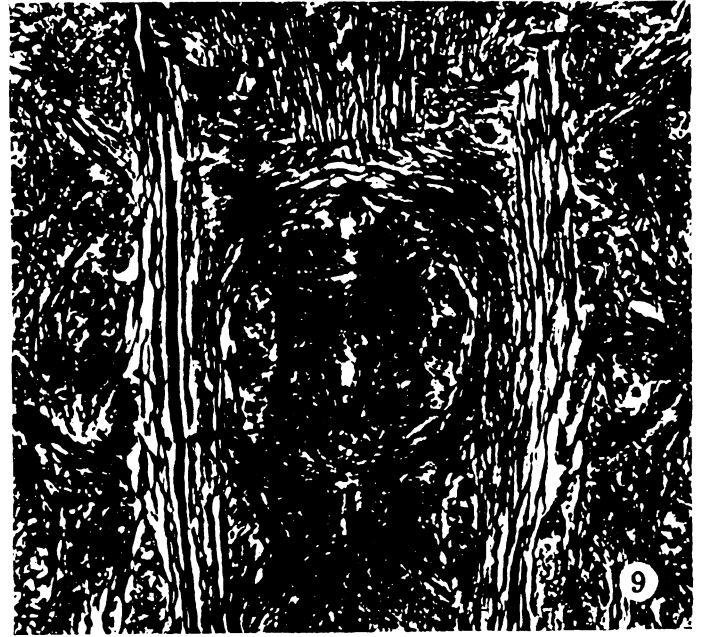
FIGURES 6 AND 7. Overlay.

figures 8-10
100µm

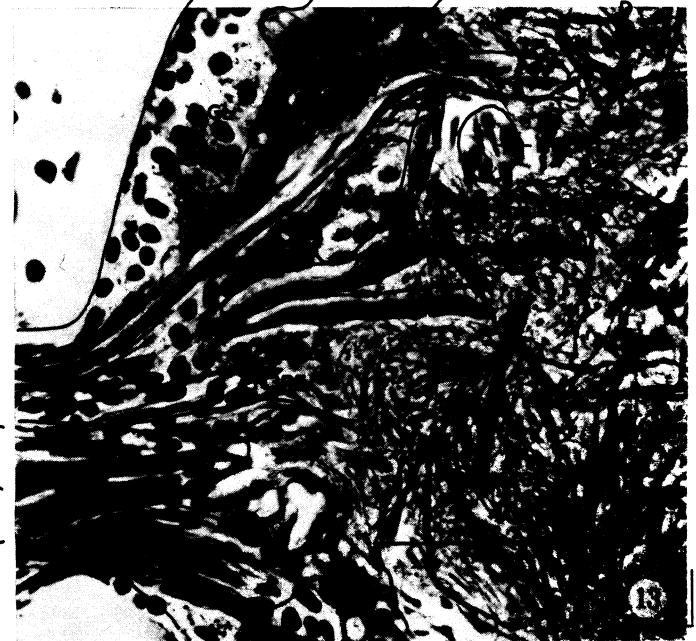
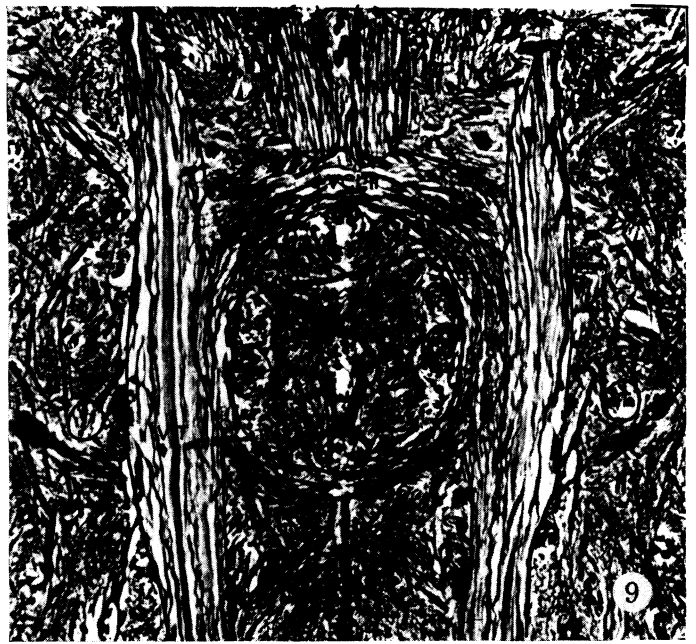
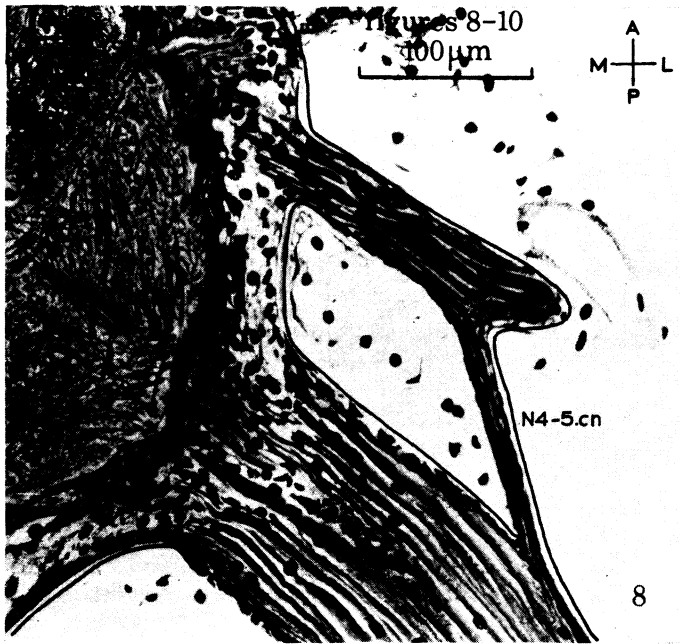


figures 11-13
100µm

FIGURES 8-13. Overlay.



FIGURES 8-13. For description see opposite.



FIGURES 8-13. Overlay.

larging for some distance within the ganglion core. The groups adopted are: very small, $< 2 \mu\text{m}$ in diameter; small, 2 to $5 \mu\text{m}$; medium, 5 to $12 \mu\text{m}$; large, 12 to $20 \mu\text{m}$; giant, $> 20 \mu\text{m}$. Sizes are those in silver-stained sections and make no allowance for shrinkage due to preparative treatments or the swelling sometimes caused by Procion Yellow staining. The interganglionic connectives are not considered here because they consist almost entirely of the fibres of the longitudinal tracts and are best described with them.

Nerve 2

This is 90 to $110 \mu\text{m}$ in diameter where it joins the ganglion at the base of the anterior connective. It is composed of about 700 very small fibres with about twelve medium-sized and about 140 small fibres scattered among them, and a group of 16 to 20 small and medium-sized fibres dorsally. Within the ganglion the fibres separate into a distinct dorsal and ventral root.

Dorsal root (N2DR; figures 3, 14, 23)

The dorsal group of four medium-sized and 12 to 16 small fibres runs from the base of the nerve dorsomedially through the glial cell layer to enter the ganglion core through the MDT, close to the LDT. Six or seven of the fibres are by this time medium-sized. The more anterior ones give off ventral dendritic branches that break up into neuropile laterally, between the LDT and DIT, and the posterior fibres send small branches posteriorly below the MDT. The fibres then run posteromedially above the DMT of their own (ipsilateral) side. Four anterior fibres turn ventrally and cross the midline to pass beneath the DMT of the other (contralateral) side, as a component of DCI. They then merge with the fibre bundles of the anterior dorsolateral and anterior lateral 3 cell body groups (ADL, AL3, figure 14), and run to cell bodies of group AL3. One of the more posterior fibres crosses the midline above both DMTs, immediately behind the anterior median tracheae at the dorsal boundary of the core, and passes above the contralateral DIT. It then runs anteroventrally to a cell body above the ventral root of nerve 2 (N2VR), probably of anterior lateral cell body group 1 (AL1). A second fibre may follow a similar course, but this is still uncertain. The remaining posterior fibre gives off a small branch, which ramifies above the contralateral DMT, and the main fibre then runs posteriorly above the ipsilateral DMT. Finally it loops towards the midline and goes to a cell body of the mid-dorsal median group (MDM, figures 5, 6, 14). One of the most anterior of the small fibres of N2DR leaves the larger ones posteroventrally after they have branched into lateral neuropile and runs posteriorly in the ipsilateral DMT, close to the most dorsal bundle of N2VR (see below). The remaining 8 to 13 small fibres seem to ramify ventrally into neuropile close to the ventral branches of the larger fibres, between the LDT and DIT.

DESCRIPTION OF PLATE 22

Bodian silver preparations

FIGURE 8. Branch connecting nerves 4 and 5; frontal section of ganglion. All sections are $10 \mu\text{m}$ thick.

FIGURE 9. Ring tract, in frontal section of central region of ganglion.

FIGURE 10. Posterolateral limb of ring tract and neighbouring structures, in oblique frontal section of ganglion.

FIGURE 11. C-tract and associated nerve fibre bundles, in transverse section of ganglion.

FIGURE 12. I-tract and associated structures; transverse section of ganglion.

FIGURE 13. Base of nerve 3 and neighbouring roots of nerves 4 and 6, in laterally oblique transverse section of ganglion.

Ventral root (N2VR; figure 5; figure 7, plate 21; figures 11, 12, plate 22; figure 14; figure 17, plate 23; figures 23, 25, 26, 28, 32)

This is composed of the very small fibres that form the bulk of nerve 2, plus some small and medium-sized ones. The large, cylindrical bundle enters the ganglion core horizontally in a posteromedial direction and passes in front of the anterior lateral limb of VCI. It then divides

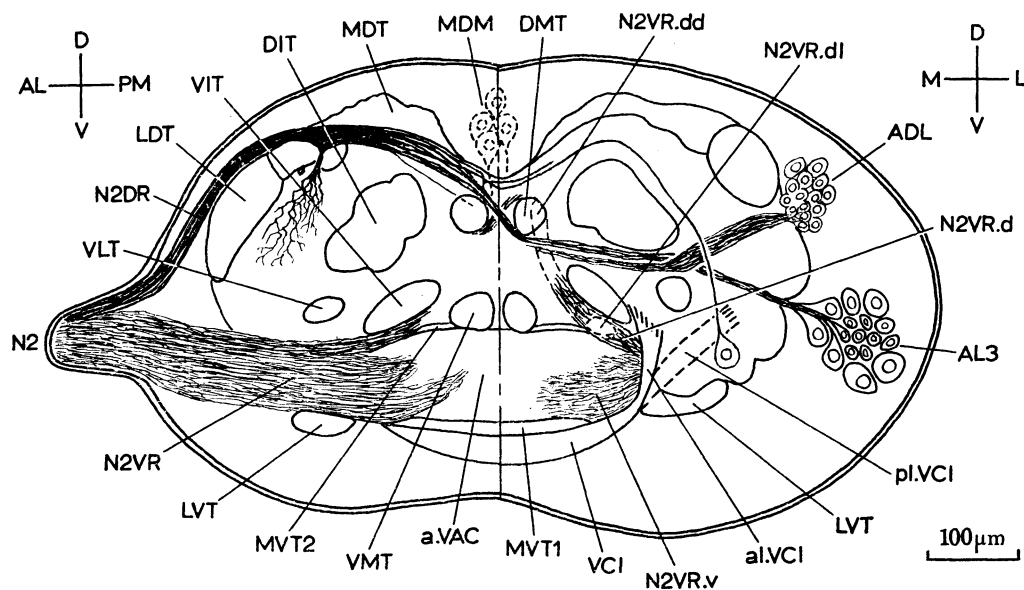


FIGURE 14. Composite of halves of laterally oblique transverse section of ganglion (left) and transverse section (right), to show dorsal and ventral roots of nerve 2; anterior view. Single ventral cell body on right and anterior dorsolateral cell body group (ADL) are in front of plane of rest of section, structures shown dashed are behind it.

into a small dorsal and larger ventral bundle, some of the fibres giving branches to both. The dorsal bundle (N2VR.d) contains mainly small fibres. It passes beneath the VIT, to which it gives a few very small fibres that run posteriorly, and then divides into two. The upper bundle (N2VR.dd), the most dorsal bundle of N2VR, ascends posterodorsally behind DCI and runs posteriorly lateral to the DMT; it sends very small branches into dorsal neuropile above DCI, DCIII and DCIV. It merges with the DMT posteriorly but can be traced nearly to the posterior limit of the ganglion core, where it breaks up into several groups of very small branches that arborize below and behind DCV. The other, lower bundle (N2VR.dl) runs posteriorly with MVT2. It sends very small branches dorsally behind DCIII and itself turns dorsally behind DCIV to ramify between the DIT and DMT. The large, ventral bundle of N2VR (N2VR.v) consists chiefly of very small fibres. It continues into, and largely forms, the anterior mass of the VAC. It then runs posteriorly, breaking up into a maximum of about six poorly defined bundles that fuse and separate in a complex manner. In the cylindrical region of the VAC a few lateral fibres (N2VR.vl) diverge dorsally from the rest and run for a short distance beneath MVT2, passing with it within the curve of the C-tract, before rejoining the others beneath the SMC. At the level of the C-tract the more ventral fibres form a single compact bundle (N2VR.vv, figures 11, 32). The bundles are finally lost at the posterior margin of the core, among fibres from the posterior connective that form the MVT.

Nerve 3

This is also 90 to 110 μm in diameter at its base. It contains fibres of all sizes from medium to very small, numbering about 90 medium to small ones and over 180 very small ones. Most or all of the very small fibres enter nerve 3B, but both nerves 3A and 3B contain small and medium-sized fibres. In the ganglion nerve 3 divides into seven bundles (figure 15) – one anterior

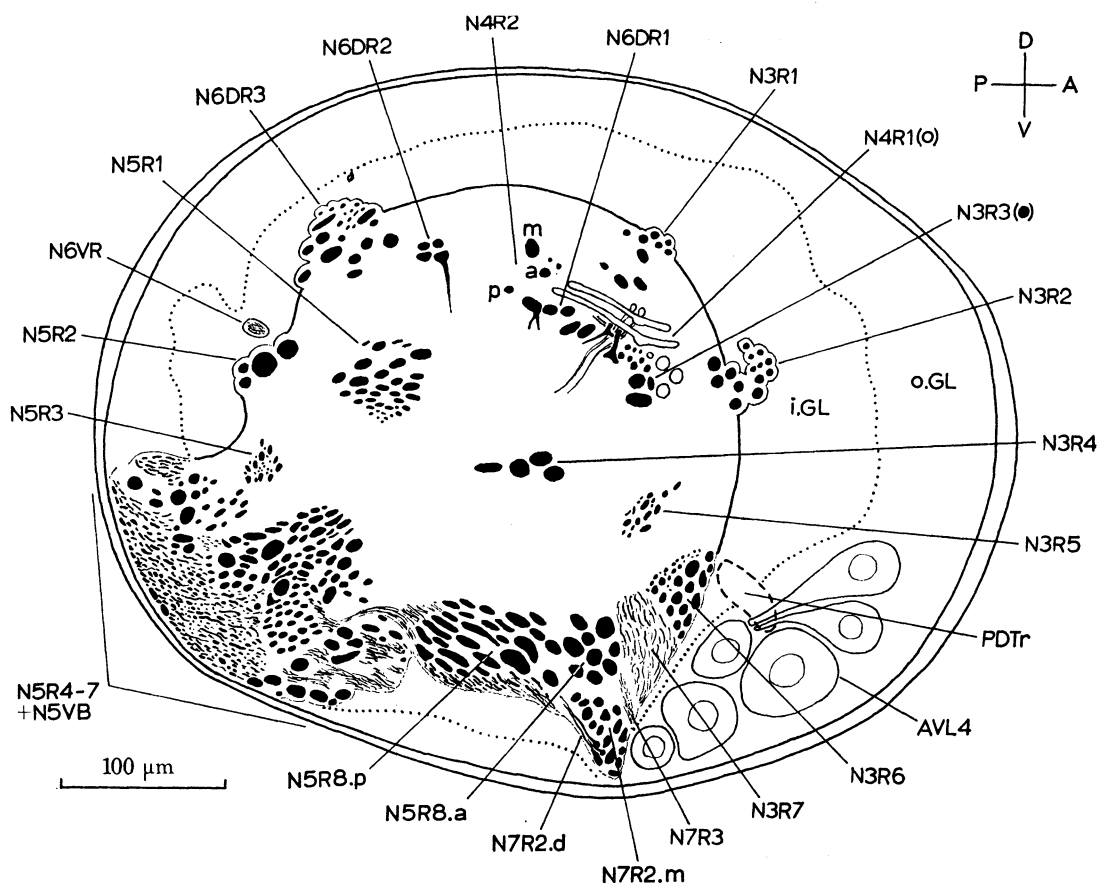


FIGURE 15. Roots of nerves 3 to 7, in parasagittal section close to surface of ganglion core; lateral view.

(root 2), one posterior (root 4), and five in much the same vertical plane in between. Nerve 3A, which forms the anterodorsal region of the base of the nerve, receives roots 1 and 2 and contributes the most posterior fibres of root 7 and perhaps a fibre or two to root 6; nerve 3B comprises all the rest. The courses of the roots in the ganglion are complex because of frequent changes of direction, and are further confused by fibres of nerves 4 and 6 running among them.

Root 1 (N3R1; figure 13, plate 22; figures 15, 23, 24, 32)

This consists of about ten small to medium-sized fibres. They run posterodorsally through the glial cell layer to enter the ganglion core above nerve 4, root 1 (N4R1). In the core three of the fibres enlarge more than the rest (figure 15). They all pass above nerve 6, dorsal root 1 (N6DR1), where the three largest fibres give off a posterior branch, and then give anteroventral branches to the anterolateral region of the core. The three most dorsal fibres then turn forward,

while the rest curve medially and give off small dorsal branches. The most dorsal of the three largest fibres then turns anteriorly to accompany the three dorsal fibres (figures 24, 32). They and the posterior fibres all give off dorsomedial branches (omitted from the posterior fibres to simplify figure 24), which ramify between the LDT and DIT, and the main fibres then run ventrally to cell bodies of anterior ventral group 1 (AV1).

Root 2 (N3R2; figures 15, 23, 24, 26, 32)

This contains 12 to 14 medium-sized fibres. They tend to split into two groups in the ganglion core, five usually diverging medially from the others. All give off small posterior branches (N3R2.p), which arborize into neuropile, and the main fibres then run anteromedially. They incline slightly dorsally, close to the core margin, and give off small dorsomedial branches that break up into neuropile below the LDT and MDT. At the transverse level of DCI the main fibres give off small anterodorsal branches and then turn ventrally to cell bodies of anterior ventrolateral group 1 (AVL1).

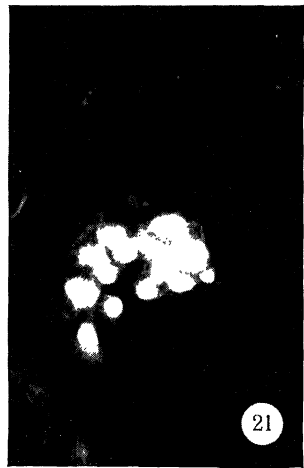
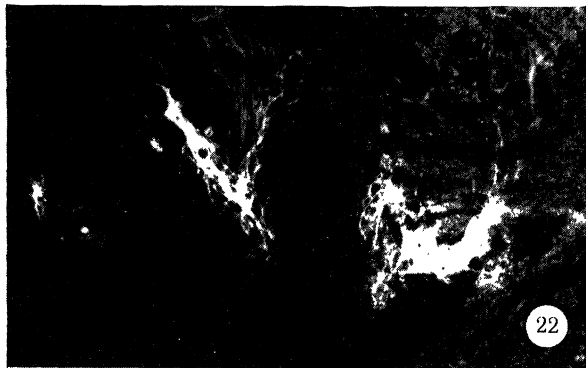
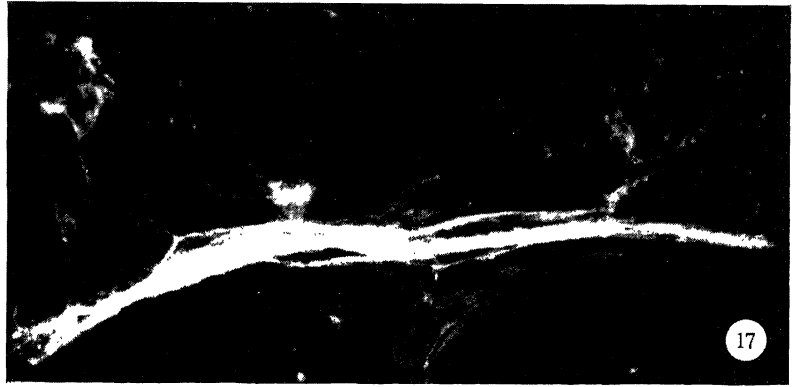
Root 3 (N3R3; figure 13, plate 22; figures 15, 23–26, 32)

About 15 mainly medium-sized fibres enter the core in a posteromedial direction below N3R1 and pass under N4R1; all except two posterior fibres then fork characteristically (figure 26) to give off small posterior branches. The main branches (N3R3.a, figures 24, 32) of all except the most ventral fibre then curve anterodorsomedially, passing in front of N6DR1 and the posterior fibres of N3R1, and behind N4R1. They send small dorsal branches into neuropile ventrolateral to the LDT and then fork below the LDT. Small branches run posterodorsally to

DESCRIPTION OF PLATE 23

Procion Yellow preparations

- FIGURE 16. Understained sagittal (midline) section of ganglion, 20 μm thick, showing anterior (left) and posterior median tracheae, here joining dorsally; and mid-ventral tracheae (centre). Also visible are commissures, anterior and ventralmost regions of ventral association centre, and median cell body groups (see figure 6, plate 21). Magn. $\times 140$.
- FIGURE 17. Part of dorsalmost bundle of ventral root of nerve 2, where it passes above dorsal commissures III and IV, showing three groups of very small branches extending into dorsal neuropile. Parasagittal section of ganglion, 20 μm thick. Anterior to the left, magn. $\times 400$.
- FIGURE 18. Nerve 3, root 4, entering base of nerve 3 (top left); 10 μm frontal section of ganglion. Anterior at top, magn. $\times 350$. (Compare with figure 25.)
- FIGURE 19. Nerve 3, root 6, showing anteromedial bundle (top) and posterior bundle accompanied by posteromedial branches of anterior bundle of nerve 5, root 8 (below); 10 μm frontal section of ganglion with nerves 3 and 5 stained. Also visible are parts of anterior and medial branches of nerve 5, root 10 (centre and right) and part of nerve 5, root 4 (diagonally across centre) (see figures 25, 29). Anterior at top, lateral to the left, magn. $\times 350$.
- FIGURE 20. Posterolateral region of 10 μm frontal section of ganglion with nerves 3, 5 and 7 stained, showing nerve 3, root 6 (top right), nerve 7, root 2 (top left), nerve 5, roots 4 and 5, with root 7 (little stained) between, and small parts of anterior branches of root 10 (centre); also nerve 5, root 10, dividing into anterior and medial branches (bottom) (see figures 29, 30). Anterior at top, lateral to the right, magn. $\times 350$.
- FIGURE 21. Composite bundle of nerve 5, root 8 (above, unstained), and nerve 7, root 2 (below), in 20 μm parasagittal section of ganglion with only nerve 7 stained. Dorsal at top, anterior to the left, magn. $\times 700$.
- FIGURE 22. Anterior (far left), dorsal and posterior branches of main bundle of nerve 7, root 2, in 20 μm parasagittal section of ganglion. Small group of anterior branches lies immediately in front of dorsal part of ventral commissural loop II; dorsal branches ramify among fibres of dorsal commissure III (upper left), posterior branches among fibres of supra-median commissure (lower right) and behind dorsal commissure IV (above); between dorsal and posterior branches are unstained vertical fibres of C-tract. Dorsal at top, magn. $\times 280$.



FIGURES 16-22. For description see opposite.

ramify between the LDT and DIT, while the main fibres turn ventrally. They curve down to cell bodies of anterior ventrolateral group 4 (AVL4) as part of its fibre bundle (AVL4.fb, figure 32), which passes between roots 6 and 7 of nerve 3 (N3R6, N3R7). The main branch of the most ventral fibre of N3R3 (N3R3.v, figures 25, 26, 32) runs more anteriorly than the others. It passes above the two ventralmost fibres of N4R1 and then curves anteromedially, giving off a dorsal branch and several very small lateral and medial branches. Finally it forks to give a very small anterior branch lateral to the VLT and then runs ventrally to a cell body of the AVL1 group. The two small posterior fibres of N3R3 (N3R3.p, figure 24) curve medially some way behind the others. They pass above N6DR1 and then run beneath N3R1. They give off posteromedial branches into dorsal neuropile in front of the lateral limb of the DIT and then turn ventrally, giving off very small anterodorsal branches, and run to the AVL4 cell body group.

Root 4 (N3R4; figure 12, plate 22; figure 15; figure 18, plate 23; figures 23, 25, 28, 32)

This consists of three medium-sized fibres and one small one, from the posterior sector of the nerve. They send small anterior branches into superficial neuropile where they enter the core and then run posteromedially nearly halfway to the midline, before turning anteriorly round a vertical bundle of small fibres (PL1.fb, figure 25) from the posterior lateral 1 (PL1) cell body group. Near here the N3R4 fibres give off very small posterior and medial dendritic branches. They then run forward, medial to the fibre bundles of cell body group AV1 (AV1.fbs, figure 25) and the posterior lateral limb of VCI. They reach the anterolateral margin of the core close to the ventralmost fibre of N3R3 and go to cell bodies of the same group, AVL1.

Root 5 (N3R5; figure 13, plate 22; figures 15, 23, 25, 28, 32)

About eight medium-sized fibres from the posterodorsal sector of the nerve enter the core below N3R3. At first they run posteroventromedially, above the posterior bundle of N3R6, but then turn anteriorly. They run parallel with and at first lateral to N3R4 and give off very small medial branches. Like N3R4 they then pass medial to the fibre bundles of the AV1 cell body group and the posterior lateral limb of VCI. They reach the margin of the ganglion core just anterior to N3R4 and go to cell bodies of the same group, AVL1.

Root 6 (N3R6; figure 13, plate 22; figure 15; figures 19, 20, plate 23; figures 23, 25, 28–30, 32)

This, the largest root of nerve 3, contains about 36 fibres, of which about 15 are medium-sized and the rest small or very small. In the glial cell layer they give off small to very small posterodorsal branches, which break up into superficial neuropile above the base of nerve 5. N3R6 enters the core together with N3R7, which then diverges ventrally. N3R6 runs medially for a short distance and then its fibres fork into two bundles. The smaller, anteromedial one (N3R6.am) soon forks again and its branches ramify in front of the posterior lateral limb of VCI and among the fibre bundles of the AV1 cell body group. The much larger posterior bundle (N3R6.p), which is an important landmark in the posteroventral region of the core, gives off a few very small medial branches below N3R5 and then passes between roots 3 (above) and 4 (below) of nerve 5 (N5R3, N5R4) (figure 28). It then forks into very small medial and posterolateral branches. These ramify respectively among the ascending fibre bundles of the posterior cell body groups, chiefly posterior ventral group 3 (PV3.fbs, figure 25), and close to the posteroventral boundary of the core above nerve 5, root 10 (N5R10).

Root 7 (N3R7; figure 13, plate 22; figures 15, 23, 28, 31, 32)

This is composed of about nine small fibres and 150 to 200 very small ones. It follows the margin of the ganglion core ventromedially after leaving N3R6 and passes in front of the prominent tract composed of the main bundles of nerve 5, root 8, and nerve 7, root 2 (N5R8.p,

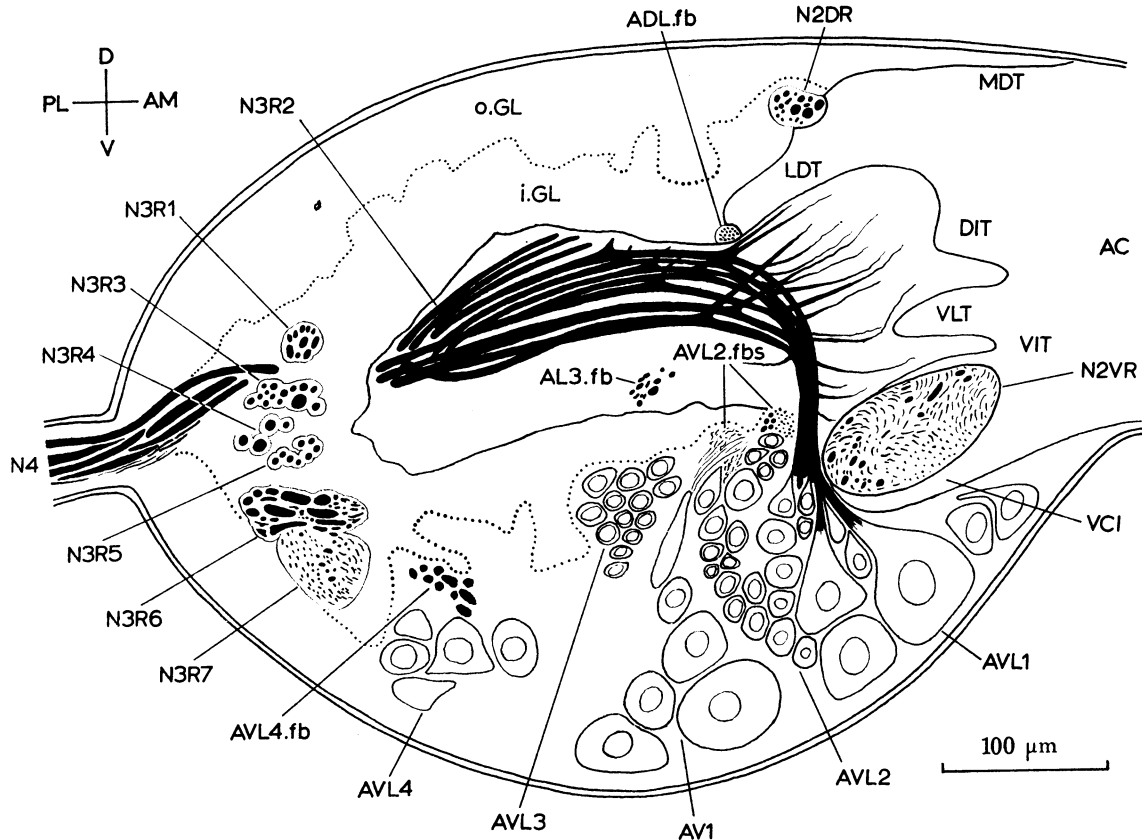


FIGURE 23. Roots of nerves 2 to 4, in oblique section through surface of ganglion core between anterior connective and base of nerve 4.

N7R2.m, figure 32). Here nerve 7, root 3 (N7R3) merges with N3R7 and the combined bundle continues along the margin of the core medially and a little posteriorly, at the anterior edge of a ventral sheet of fibres, which forms nerve 5, root 11 (N5R11). The combined bundle passes immediately above, rarely below, the outer LVT and above the inner LVT and then turns dorsomedially into the lateral extension of the middle region of the VAC, above the ventralmost part. Here it divides into several small bundles, which fan out anteriorly and posteriorly close beneath the ventral bundles of N2VR.

Nerve 4

This small nerve is 50–55 μm in diameter at its base and consists of about 20 fibres, eight of which are usually medium-sized and the rest small or very small (figures 23, 27). Seven or eight of the smallest fibres, which lie in the posterior sector of the nerve, pass by way of the connecting branch or branches near the base of the nerve into nerve 5, in which they run distally. One of them forks in nerve 4 to give a branch to both nerve 4 and 5. Two small fibres from the distal part of nerve 4 also pass into nerve 5 by this route. The connexions between nerves 4 and 5 may

differ on the two sides of the ganglion. Normally only one branch connects them (figure 8), but occasionally up to four of the fibres form a second branch, which either runs independently to nerve 5, medial to the other branch, or joins the other branch at some point between the nerves. Rarely nerves 4 and 5 fuse at their bases, connecting branches then being absent. In the ganglion, nerve 4 divides into two groups of fibres.

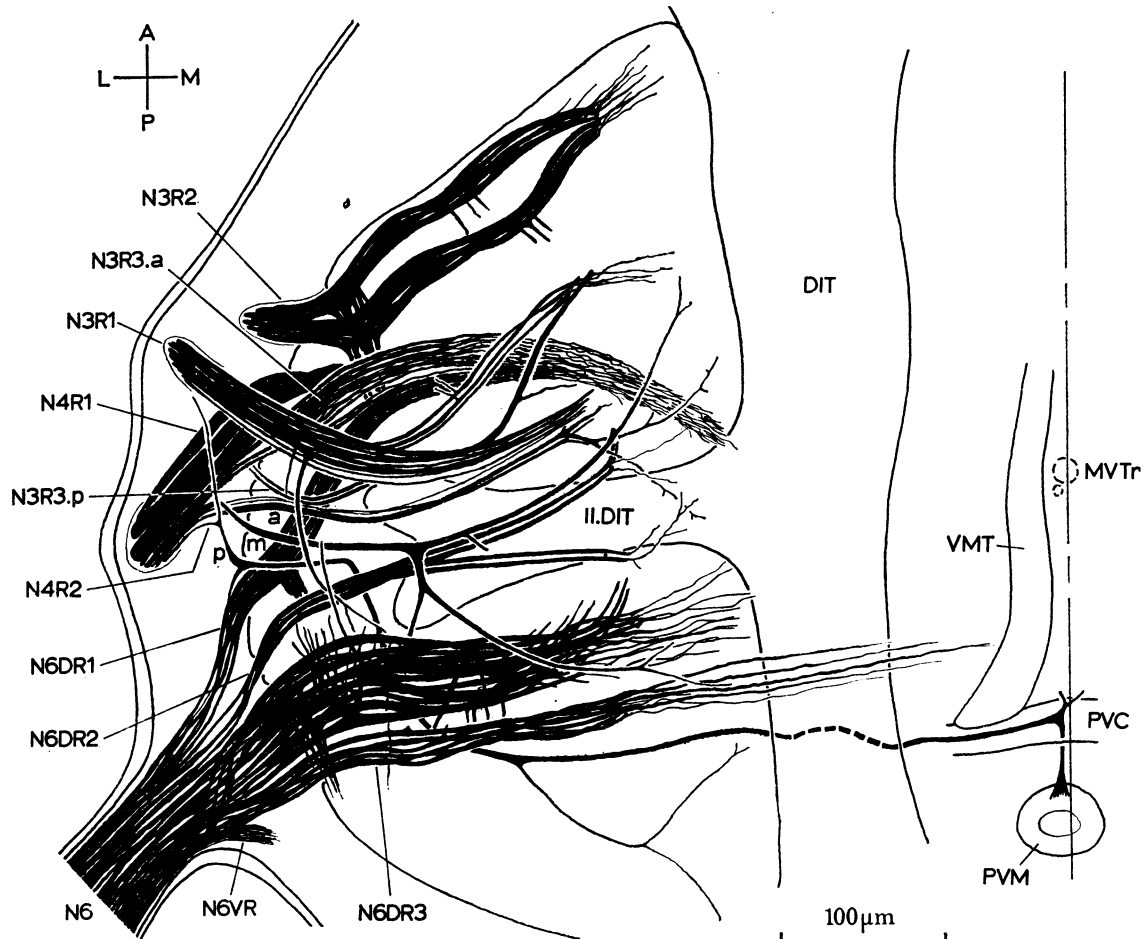


FIGURE 24. Roots of nerves 3, 4 and 6 in dorsal region of ganglion core; frontal section, dorsal view. Structures near midline are well below plane of rest of section.

Root 1 (N4R1; figure 13, plate 22; figures 15, 24–26, 32)

This is composed of the eight medium-sized fibres. They run anterodorsally through the glial cell layer and curve medially into the core above the base of nerve 3, between N3R1 and N3R3. The two smallest, most dorsal, fibres give off long posteroventral branches (figure 15) and then they and another small fibre turn dorsally and run with the anterodorsomedial bundle of N3R3 (figure 24), which goes to cell body group AVL4. The remaining five fibres enlarge and separate into two groups, the two dorsal fibres (N4R1.d) turning into the core in front of the other three (figure 26). The two dorsal fibres give off posterior branches close to the margin of the core above N6DR1 (figures 15, 26) and then pass above the posterior branches of N3R2 and run anteromedially. They give off posterior, ventral, dorsal and anterior branches into neighbouring areas of neuropile and posterodorsal and anterodorsal branches that ramify between the LDT

and DIT. The main fibres then turn ventrally to cell bodies of group AL3. The other three, more posterior fibres run medially under N6DR1 and give off small posterodorsal, ventral, posterior, anterior and dorsal branches into nearby neuropile and larger posterodorsal branches that ramify beneath nerve 6, dorsal root 3 (N6DR3). The most dorsal of the three fibres (N4R1.m) then turns anteriorly and joins the two anterior fibres. Like them it gives off an anterodorsal branch and then runs ventrally, but to a cell body of anterior ventrolateral group 2 (AVL2). The two ventralmost fibres (N4R1.vv) continue medially and send dorsomedial branches between the LDT and DIT, each of which divides into anterior and posterior branches that ramify above and lateral to the DIT. The main fibres run anteroventrally, lateral to the ascending fibres of cell body group AVL4 (AVL4.fb, figure 32), and give off an anterior branch to dorsal neuropile. They then curve ventrally and afterwards anteriorly, close to the ventrolateral margin of the core, and go to cell bodies of the AL1 group above and behind N2VR.

Root 2 (N4R2; figures 15, 24, 32)

This consists of 10 to 12 small, or very small, fibres from the posterior sector of the nerve, most of which originate from nerve 5. In the glial cell layer they diverge dorsally from N4R1 along the boundary of the core to enter it behind N4R1, just above the level of N6DR1. Three of the fibres then enlarge to medium size. The most anterior fibre (N4R2.a) runs dorsomedially close behind N3R1, accompanied by one of the smaller fibres, and both fork below the LDT to give off dorsomedial branches that ramify between the LDT and DIT. The main fibres then turn ventrally and the larger one sends an anterior branch into dorsal neuropile in front of the level of DCI. The main fibres finally run to the AV1 cell body group. Another small fibre also runs dorsomedially close to the larger anterior fibre but merges with the posterior fibres of N3R1 and presumably runs to the AV1 cell body group with them. The middle medium-sized fibre (N4R2.m) also runs dorsomedially but dorsal to the anterior fibre. It comes to lie close above the two anterior fibres of nerve 6, dorsal root 2 (N6DR2) and here gives off a posterior branch, which ramifies above and below the fibres of N6DR3, and then a dorsal branch that ascends lateral to the LDT, turns medially above it, and ramifies between the LDT and DIT. The main fibre passes above the lateral limb of the DIT, sends an anteromedial branch between the DIT and LDT, and curves ventrally with the anterior N6DR2 fibres (figure 32) to the AV1 cell body group. The anterior and middle fibres cross at the boundary of the core so the middle fibre in the core becomes the anterior one in the glial cell layer. Here the most posterior fibre (N4R2.p) gives a branch to nerve 3 and another that forms the most dorsal fibre of N6DR1. It then runs ventromedially, sometimes directly below the middle fibre. It turns sharply posteriorly to pass beneath nerve 5, root 1 (N5R1) and then swings posteromedially and gives off a posterodorsomedial branch, which ramifies between the LDT and DIT. The main fibre runs medially and then ventromedially, beneath the VLT, to the PVC. Here it gives off two dorsal branches, which ascend one each side of the midline between the VMTs and DMTs in front of DCVI, to ramify into neuropile dorsally. The main fibre then goes ventrally or posteroventrally to one of a pair of large cell bodies of the posterior ventral median group (PVM, figure 5; figure 6, plate 21). The other fibres of N4R2 remain small. Two seem to ascend dorsomedially above the posterior fibres of N3R1 and then run forward lateral to the LDT as far as the level of DCII before disappearing. Two more, very small fibres, apparently from N4R2, run anteriorly in the glial cell layer towards nerve 3 but could not be traced further. The remaining untraced fibres may

(roots 1–3) and a broad zone along the ventral margin of the core (figure 15). Four more bundles (roots 4–7) then separate dorsally from the middle of this ventral zone (figure 27), which finally breaks up into four further groups of fibres (roots 8–11). The posterior bundle of N3R6 passes at right angles between the roots and forms a useful landmark, roots 1–3 lying above it and roots 4–11 below (figure 28).

Root 1 (N5R1; figures 15, 26–28, 32)

This is the largest of the dorsal bundles and contains about 17 medium-sized and about 15 small fibres. It runs in a straight line anteromedially into the ganglion core, parallel with and posterior to N4R1. Some of its fibres send small branches dorsally and ventrally. It passes close beneath the lateral limb of the DIT and in front of this mainly the small fibres give off a bundle of small dorsal branches that fork and ramify anteriorly and posteriorly lateral to the LDT. It then gives off a second bundle of small dendritic branches, mostly from the larger fibres, which ramify between the LDT and DIT and above the DIT. The main branches then turn anteroventrally and pass to cell body group AV1.

Root 2 (N5R2; figure 12, plate 22; figures 15, 25–32)

This comprises four fibres that enter the core behind N5R1. Two (a, b) are more anterior and larger (8–10 μm in diameter) than the other two (c, d) (5–6 μm). All run anterodorsomedially for a short distance but then branch and follow different courses. Fibre c usually lies above d at first but then moves behind it.

N5R2a, the most anterior fibre, gives off a short posteroventromedial branch and two anterior branches. The latter pass above N5R1 and the more lateral one curves ventrally, lateral to the lateral limb of the DIT, and sends one or two anterior branches towards N4R1. Further ventrally it gives off an anteromedial branch in front of N3R4 and then turns more posteriorly, giving off a posteroventral branch and finally breaking up into small branches lateral to the posterior bundle of N3R6. The main part of N5R2a follows a straight course anterodorsomedially and gives off anterior, median and posterior branches close behind the lateral limb of the DIT. These break up into dorsal neuropile, above N4R1 and the DIT and posteriorly. The main fibre turns anteroventrally, beneath N5R1, to pass down to the largest cell body of the AV1 group.

Fibre b gives off a small anterior branch, which ramifies above N5R1, and then gives off an anteroventral and an anterodorsal branch. The former passes under N5R1 and runs anteriorly in a complex of coarse longitudinal fibres in the lateral part of the core. It gives off a lateral branch and then, in front of the level of nerve 4, forks into two long anterior branches that ramify into neuropile medial to where N3R2 enters the core. The anterodorsal branch ascends behind N5R2a and sends a branch anteriorly, immediately ventrolateral to the LDT, to ramify into neuropile lateral to and beneath the LDT, at the transverse level of DCIII, and another medially, into neuropile above the DIT. The main part of fibre b curves posteriorly, giving off anterior and median branches and then a dorsal and ventral branch. The dorsal branch runs dorsally or dorsomedially and ramifies beneath the LDT or between the LDT and DIT; the ventral branch breaks up into neuropile near the posteroventral core margin. The main fibre finally goes to a large cell body associated with posterior lateral groups 1 and 2 (PL1, PL2).

Fibres c and d both give off small posterodorsomedial branches, which ramify into neuropile

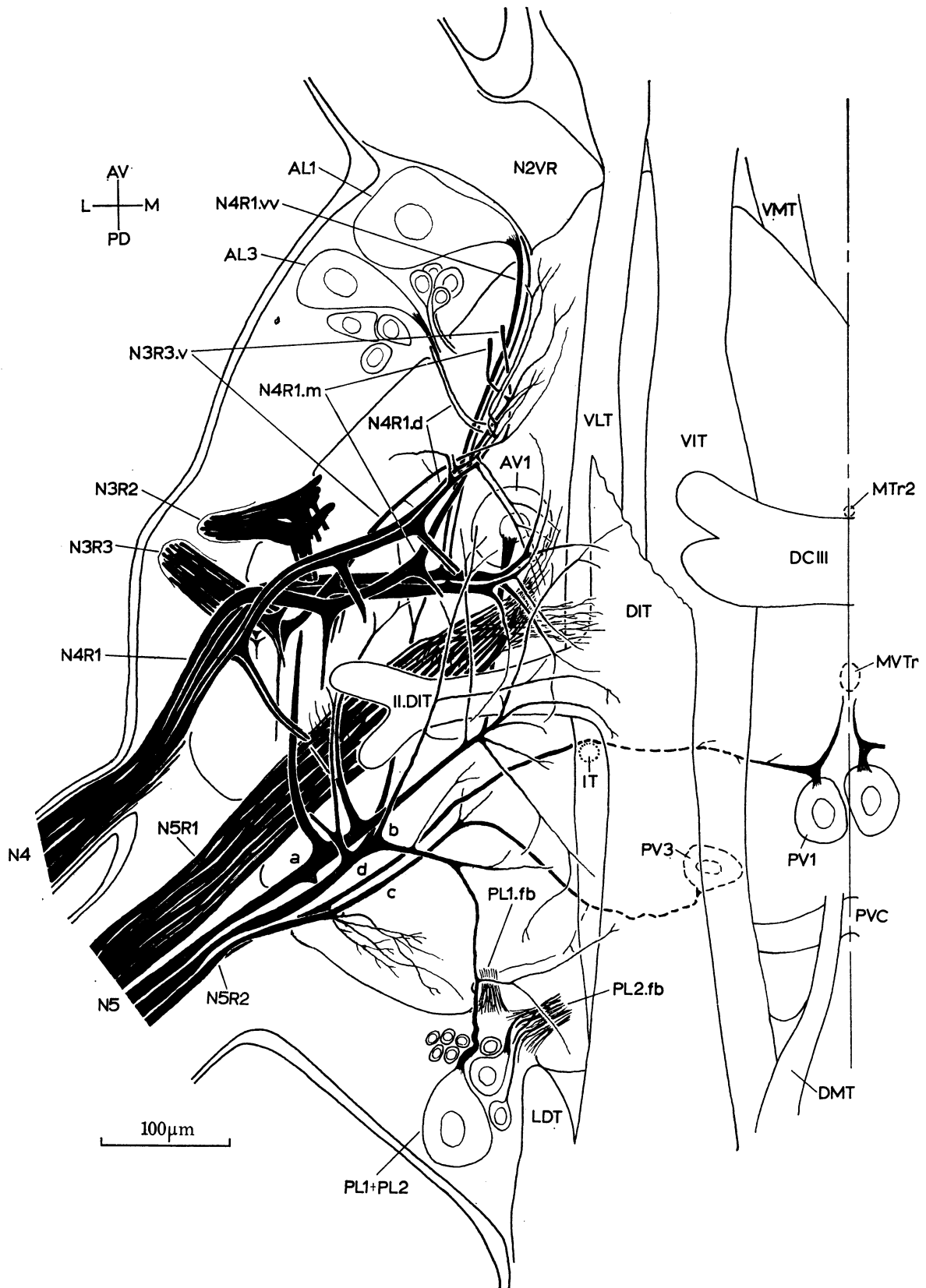


FIGURE 26. Roots of nerves 2-5, in oblique frontal section of mid-region of ganglion core between levels of figures 24 and 25; dorsal view. Cell bodies of anterior ventral group 1 (AV1) and posterior ventral groups 1 and 3 (PV1, PV3) are well below plane of rest of section.

lateral to the LDT. The main fibres then turn ventrally through the complex of longitudinal fibres in the lateral part of the core, after which they diverge. Fibre c gives off very small anterior branches and then turns posteroventromedially to run to a large cell body associated with the PV3 group. Fibre d runs ventrally and then ventromedially. It passes immediately in front of, occasionally behind, the I-tract and joins the fibre bundle of the posterior ventral 1

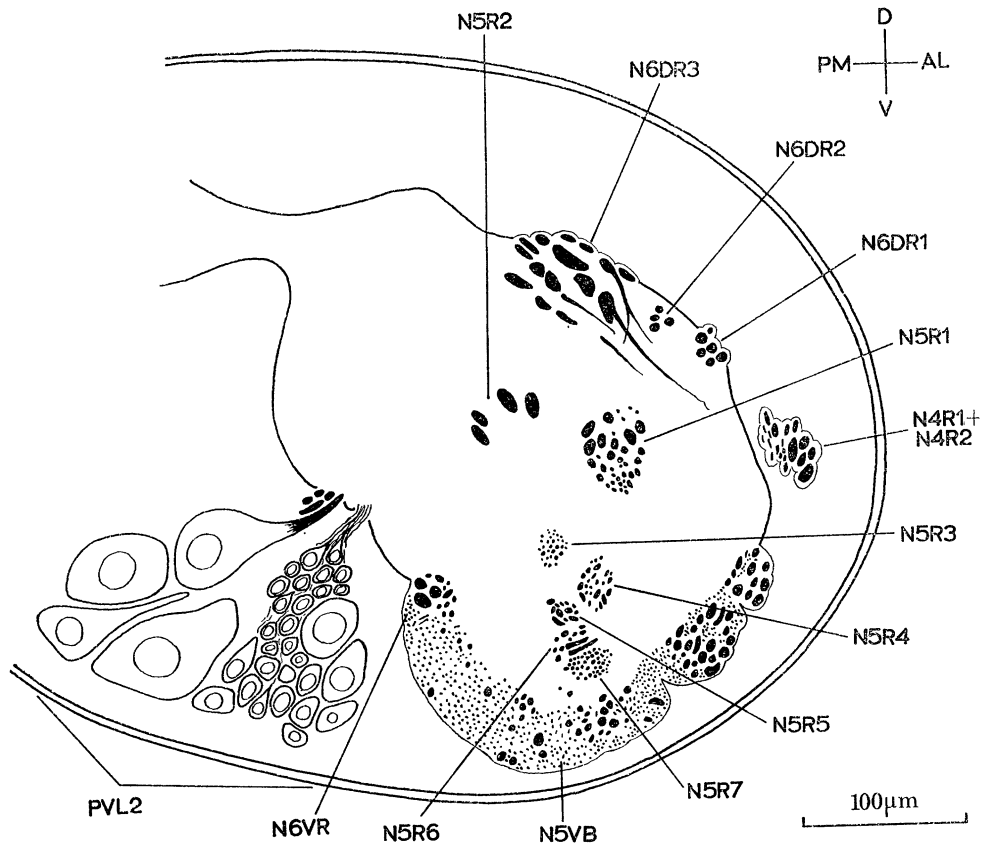


FIGURE 27. Roots of nerves 4 to 6, in oblique section, at right angles to axis of nerve 5, through superficial region of ganglion core close to base of nerve 5.

(PV1) cell body group (PV1.fb, figures 11, 12). It crosses the region of the VAC that forms the ventromedial margin of the core and goes to the largest cell body of group PV1 (figures 5, 6, 26), beside the ventral midline. Another branch from this cell body ascends vertically in the midline and breaks up into small branches immediately behind the mid-ventral tracheae at the horizontal level of the VITs.

Root 3 (N5R3; figure 12, plate 22; figures 15, 25, 27, 28)

This contains 25–30 fibres, of which 12–15 are small and the rest very small. The coarser fibres fork at the margin of the core into anterior and anteromedial branches. The former run along the core margin for a short distance and then curve medially to ramify behind N3R4. The anteromedial branches and the smaller fibres form the main bundle of the root. They fork into small or very small medial branches and larger ones that continue anteromedially. The former turn anteriorly lateral to the VIT and ramify below the VLT, behind the I-tract. The anteromedial branches run forward in a straight line, pass above the posterior bundle of N3R6

and below N3R4 and 5, and fork immediately behind the thickest fibre from the AV1 cell body group, which gives rise to N5R2a. Short anterior and longer dorsomedial branches ramify between the fibre bundles of the AV1 cell body group and below the VLT respectively.

Root 4 (N5R4; figures 10, 12, plate 22; figures 19, 20, plate 23; figures 27–29)

This comprises about 25 fibres, two or three of which are medium-sized and the rest small. Immediately after diverging from the ventral zone of fibres they give off small dorsal branches (figure 28), which fork beneath N5R1 and ramify in front of and behind it. The main fibres run

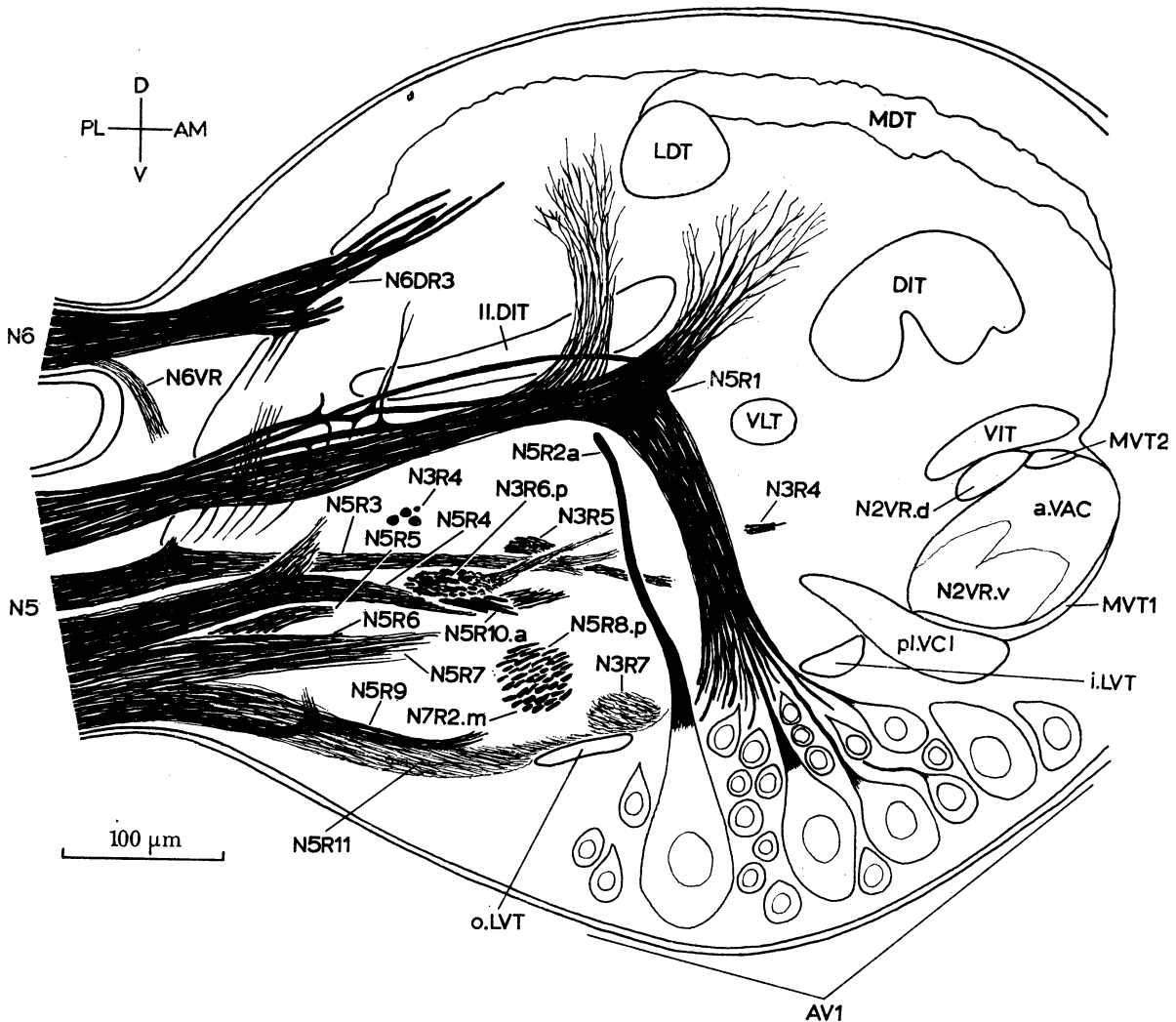


FIGURE 28. Nerve 5, root 1, and neighbouring roots of nerves 2, 3, and 5 to 7, in laterally oblique transverse section of ganglion, parallel to axis of nerve 5; anterolateral view.

anteromedially below N5R3. They give off very small anterior branches into neuropile near the base of nerve 3 and then pass under the anterior branches of N5R10, where they nearly merge with roots 5 and 7 of nerve 5 (N5R5, N5R7) behind and below (figure 20). They then divide into two bundles and some very small branches that run a little way posterodorsomedially before breaking up into neuropile. The larger bundle, of coarser fibres, turns anteriorly and breaks up into very small branches between MVT2 and the fibre bundles of the AV1 cell body

group; it also seems to send some very delicate branches behind the I-tract. The other, rather insignificant bundle, of very small fibres, continues anteromedially close above N5R7 and ramifies around and in front of the I-tract, to form part of the posterolateral limb of the ring tract.

Root 5 (N5R5; figure 12, plate 22; figure 20, plate 23; figures 27–29)

This is the smaller and more dorsal of two bundles of fibres, the other being the combined roots 6 and 7 (N5R6, N5R7), that leave the ventral mass of fibres close together immediately below N5R4. It contains about 12 small fibres. It runs anteromedially and comes to lie behind N5R4. After passing under the posterior bundle of N3R6 its fibres fork. Anterior branches pass between N5R6 and 7 to ramify above the combined bundle of N5R8 and N7R2, and the other, smaller branches ramify into neuropile dorsally.

Root 6 (N5R6; figure 12, plate 22; figures 27, 28, 30)

This and N5R7 leave the the remaining ventral band of fibres immediately below N5R5, at first as a single bundle. The dorsal part, which constitutes N5R6, consists of six or seven medium-sized fibres from the posterior sector of the nerve. Most of them soon give off anterior branches into neuropile behind the combined bundle of N5R8 and N7R2 (figure 30). The main fibres then run anteromedially below N5R4 and move to the ventral side of the bundle. They then leave N5R7 and form a separate bundle below. This continues anteromedially, passing under the posterior bundle of N3R6, where it gives off very small anterior branches, and its fibres finally break up into neuropile lateral to the I-tract, behind and above the combined bundle of N5R8 and N7R2.

Root 7 (N5R7; figures 10, 12, plate 22; figure 20, plate 23; figures 27, 28, 30)

This consists of 50–55 fibres that form the rest of the composite bundle with N5R6. They are recognizable by being mostly of uniform, small size, but include some very small ones anteriorly. After passing beneath the posterior bundle of N3R6 they almost merge with N5R4 and 5 above for a little way (figure 20). They continue anteromedially after separating from N5R6 below and some fork upon reaching the I-tract to give off very small medial branches that ramify behind it. Most fibres pass in front of the I-tract and divide into very small branches that extend forward above the combined bundle of N5R8 and N7R2 to the level of the dorsal part of VCL II. They form a major part of the posterolateral limb of the ring tract.

Root 8 (N5R8; figure 15; figures 19, 21, plate 23; figures 25, 28–32)

The ventral band of fibres that remains after the separation of roots 1 to 7 (N5VB, figure 27) contains about 40 medium-sized, 70 to 80 small fibres and over 650 very small ones. The different-sized fibres are mixed together near the base of the nerve but deeper within the ganglion the larger ones move to the dorsal margin of the band. Some of these larger fibres branch into the ventral region of the core singly but the rest aggregate into three bundles, one each at the anterior and posterior limits of the band and one in the centre. The smaller, ventral fibres continue at the margin of the core. The four groups of fibres diverge to pursue different courses within the core and are conveniently described as separate roots (8 to 11), but this interpretation is arguable in view of their coalescence nearer the base of the nerve.

The anterior bundle, root 8, contains about 20 medium-sized fibres and some 16 small ones. They run anteromedially from the base of the nerve close to the lateral margin of the core and give off short dorsal branches that fork and then break up in superficial neuropile in front of the more dorsal roots of nerve 5. The bundle then turns medially and divides into a smaller, anterior bundle above the base of nerve 7 and a larger one behind it, separated by dorsal branches of

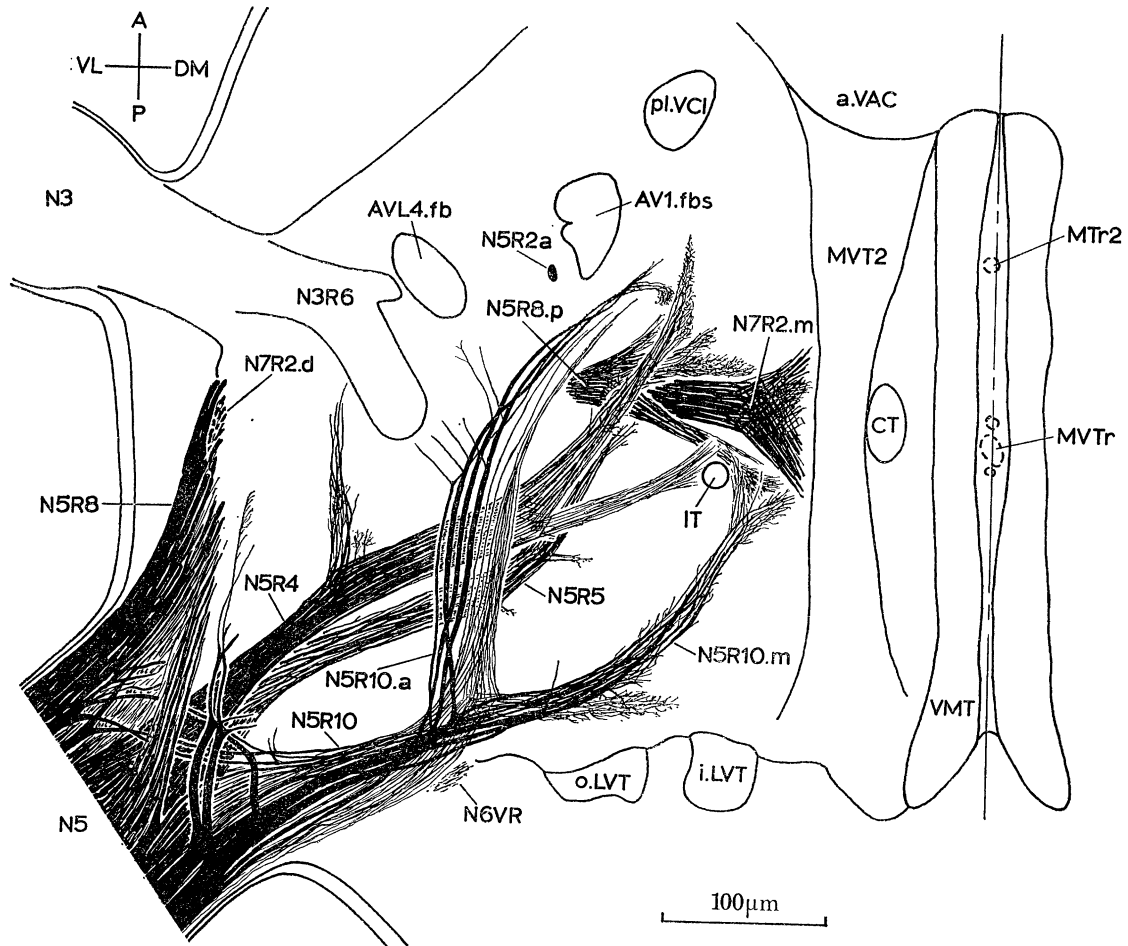


FIGURE 29. Nerve 5, roots 4, 5 and 10, and associated roots of nerves 3, and 5-7, in oblique frontal section of ventral region of ganglion core; dorsal view.

N7R2 (N7R2.d, figure 31). The fibres of the anterior bundle (N5R8.a) fork into posteromedial branches (N5R8.apm), which run above the posterior bundle of N3R6 and follow a similar course to ramify into the posterior region of the core, and medial branches (N5R8.am), which pass between N3R6 and 7 and ramify above N3R7. The larger, posterior bundle of fibres (N5R8.p) turns dorsomedially and runs together with and mainly above the main bundle of N7R2 (figure 21) towards the centre of the ganglion, the two forming a very prominent feature. The fibres of N5R8 give off two groups of small anteromedial branches, which ramify above, behind and medial to the medial branches of the anterior bundle, and then fork. Anteromedial branches ramify lateral to MVT2 beneath the posterolateral limb of the ring tract; posteromedial branches fan out between MVT2 and the I-tract.

bundle then runs medially along the posteroventral margin of the core. After a short distance all the fibres except a few small ones fork into anterior and medial branches. The anterior branches (N5R10.a) run forward between the posterior bundle of N3R6 above and N5R4 below. They give off very small anterolateral branches, which break up into neuropile beneath the posterior bundle of N3R6, and then curve anteromedially beneath the anteromedial branches of N5R3

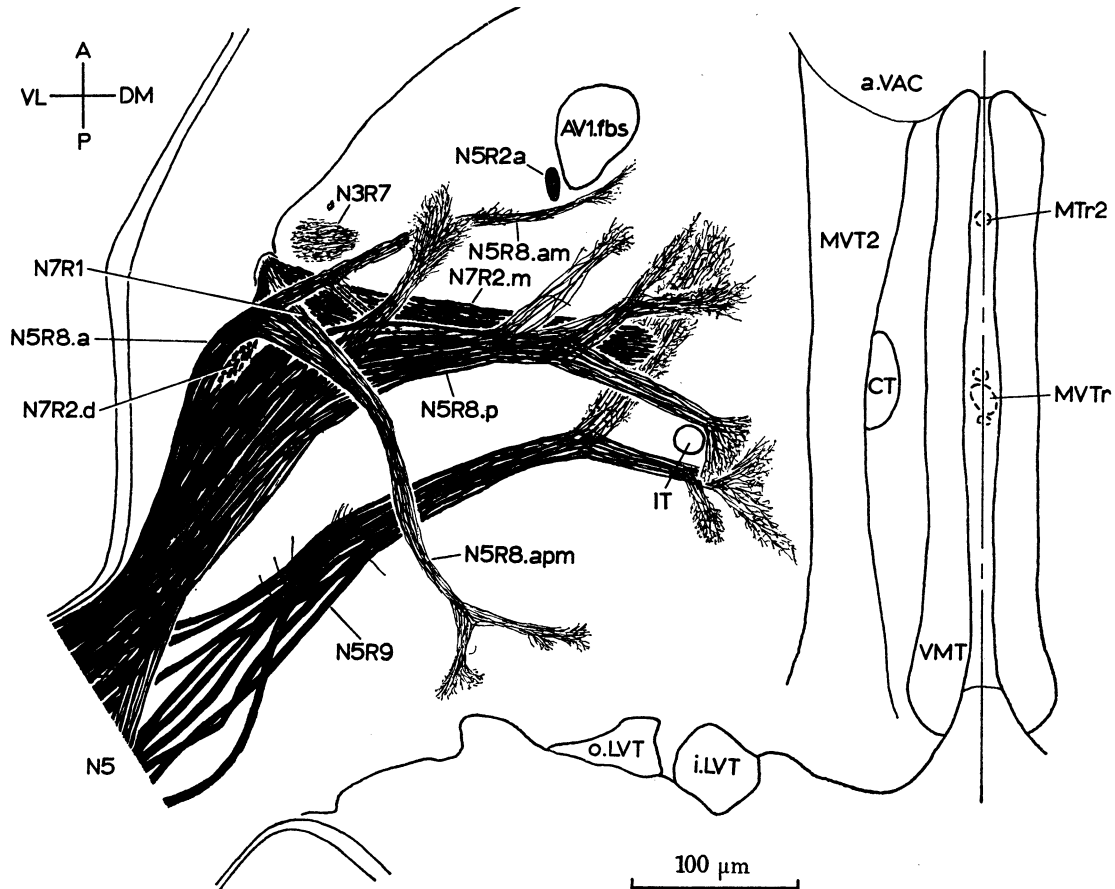


FIGURE 31. Nerve 5, roots 8 and 9, and associated roots of nerves 3 and 7, in oblique frontal section of ventral region of ganglion core; dorsal view.

and ramify in front of the combined bundle of N5R8 and N7R2. The medial branches (N5R10.m) continue with the small unforked fibres and separate dorsally from the remainder of the ventral band, which forms root 11. The medium-sized and small fibres then curve anteromedially and ramify lateral to MVT2, behind N5R4 and 7. The very small fibres continue medially to ramify close to the posteroventral core margin.

Root 11 (N5R11; figure 28)

The smaller fibres of the ventral band cover the whole of the ventral surface of the postero-lateral part of the core and are a mixture of small and very small fibres. They run mainly anteromedially and give off numerous very small dorsal branches near the base of the nerve. More medially the sheet of fibres splits into several poorly-defined bundles. All except the most posterior one run anteromedially and fan out into the ventrolateral extension of the mid-region of the VAC. The most posterior bundle, with which merges the ventral root of nerve 6 (N6VR),

runs at first medially along the posterior core margin below N5R10. It passes dorsal to the outer LVT but ventral to the inner LVT before fanning out anteriorly and anteromedially into the ventrolateral extension of the mid-region of the VAC close behind and below the branches of N3R7.

Nerve 6

This is 60–80 μm in diameter at its base and contains about 20 medium-sized and 30 small fibres, together with a group of 50–60 very small fibres in the middle or posteroventral sector of the nerve. It divides within the ganglion into distinct dorsal and ventral roots. The medium-sized and most of the small fibres form three dorsal roots – two small anterior ones close together and a larger one posteriorly – and six or so small fibres and the group of very small ones diverge posteroventromedially, in one specimen anteroventromedially, to form a ventral root.

Dorsal root 1 (N6DR1; figure 13, plate 22; figures 15, 24, 27, 32)

The most anterior root consists of six fibres, five medium-sized and one small, from the anterior sector of the nerve. They run forward in the glial cell layer, at first accompanied by N6DR2, for a short distance before curving anteromedially into the ganglion core, parallel with and posteromedial to N4R1. The single small dorsal fibre then joins with a branch to N4R2 and nerve 3; its further course is described under N4R2 (N4R2.p). The five medium-sized fibres give off posteromedial and posteroventrolateral branches, which run respectively beneath N6DR2 and 3 and between the dorsalmost roots of nerve 5. The main fibres then continue anteromedially, giving off small ventral branches above N3R4, and pass between N3R1 above and N4R1 below. They then curve medially, behind and parallel with the anterior branches of N3R3, which are distinguishable by being thinner, and, like these, fork below the LDT. Long dorso-medial branches ramify between the LDT and DIT, while the main fibres turn ventrally to cell body group AVL4, forming the posterior part of its fibre bundle.

Dorsal root 2 (N6DR2; figures 15, 24, 27, 32)

This consists of four medium-sized fibres. After running forward a little way with N6DR1 they turn medially into the core behind it and give off small ventral branches. The fibres then separate into two pairs. The two anterior, dorsalmost fibres (N6DR2.a) run anteromedially with the middle medium-sized fibre of N4R2 (N4R2.m) above the lateral limb of the DIT, where they give off very small dorsal branches, and then turn ventrally in front of it and fork. Small medial branches run towards the DIT and the main, ventral, branches run down lateral to the VLT, close to the medial side of N5R1. They send small branches in front of N5R1 into the lateral region of the core, and then continue to the AV1 cell body group. The two posterior fibres of N6DR2 give off very small dorsal branches and then curve down behind the lateral limb of the DIT. Here one sends a very small dorsomedial branch between the DIT and LDT, and the other, perhaps both, sends a branch anteromedially through the lateral limb of the DIT and then anteriorly close to the lateral side of the DIT. The main fibres then run ventrally and a little posteriorly to cell bodies of posterior ventrolateral group 1 (PVL1).

Dorsal root 3 (N6DR3; figures 15, 24, 27, 28)

This includes all the remaining small and medium-sized fibres apart from the few that run ventrally. Those of N6DR3 run anterodorsomedially in the glial cell layer after N6DR1 and 2 have separated from them. Upon entering the ganglion core they give off posterior branches

the anterior margin, which separate into two groups a little way from the ganglion. The fibres divide within the ganglion into one large root and two small ones. A fluorescence micrograph of them was included in a previous paper (Gregory 1973).

Root 1 (N7R1; figures 31, 32)

A group of about 15 small and very small fibres runs dorsally from the base of the nerve. The small fibres give off very small branches that run laterally for a short distance above the dorsal branches of N7R2 before ramifying into superficial neuropile above N3R7. The main small and very small fibres fork beneath N3R6 into very small branches that ramify lateral to the posterior bundle of N3R6 and slightly less fine branches that run posteriorly with it and the postero-medial branches of N5R8.a. A few very delicate branches also seem to pass anterodorsally in front of N3R6.

Root 2 (N7R2; figures 10–12, plate 22; figure 15; figures 20–22, plate 23; figures 28–32)

This, the largest root, contains all the medium-sized fibres. They fork in the glial cell layer to give off small dorsal branches (N7R2.d), which run along the core margin between the anterior and posterior bundles of N5R8 and then fork and fan out in superficial neuropile between the bases of nerves 4 to 6, below the posterodorsal branches of N3R6. The main bundle of N7R2 (N7R2.m) enters the core behind N3R7 and runs dorsomedially in a straight line, forming a conspicuous tract together with and mainly below the posterior bundle of N5R8. The N7R2 fibres continue medially beyond where those of N5R8 fork and themselves fork close to MVT2. Small anterior branches (N7R2.ma) run beneath the ring tract and ramify at the front of the dorsal part of VCLII (figure 22). Coarser posterior branches (N7R2.mp) turn dorsally to ramify in front of and behind the posterior region of the ring tract among the fibres of the SMC and behind DCIV. Between the anterior and posterior branches two groups of very small dorsal branches (N7R2.md) ascend in front of the C-tract and ramify among the fibres of DCIII and in the neuropile above.

Root 3 (N7R3; figures 15, 32)

About 20 of the very small fibres of nerve 7 run medially into the core behind N3R7, with which they mingle. They pass among the N3R7 fibres into the lateral extension of the mid-region of the VAC, where they fork into medial, dorsal, and perhaps also anterior branches, which ramify in the VAC.

Nerve 8

The median nerve is the smallest peripheral nerve and the only unpaired one. A little way from the ganglion, where it divides into two branches, it is surrounded by what is probably neurohaemal tissue (de Bessé 1966, 1967; Brady & Maddrell 1967). It is only 16 to 24 μm in diameter at its base and contains eight to ten small or very small fibres. These enter the ganglion as a single root in or near the midline, just above the bases of the posterior connectives (figure 1).

Root 1 (N8R1; figure 5; figure 6, plate 21)

Inside the ganglion the small bundle passes between the large cell bodies of the posterior dorsal median group (PDM) and runs anteriorly in the glial cell layer in the mid-dorsal cleft. Two very small fibres leave it ventrally above the posterior part of DCV and run laterally, one to each side. Each curves over the ipsilateral DIT and then turns ventrally. It merges with

a fibre bundle that passes between the VIT and VLT from posterior ventral cell body group 2 (PV2), which itself lies between the PV3 group and the midline, just in front of the level of the PVC. However, the fibre could not be traced with certainty to a cell body. Branches to the posterior connectives, shown by Guthrie & Tindall (1968, figure 8.27), were not seen. The other fibres of N8R1 dip anteroventrally in front of DCV beside the prominent mid-ventral tracheae and continue forward in the glial layer. They divide beneath the posterior part of DCII into two bundles, each of three or four fibres, and one or two very small branches each side, which continue into the core anterolaterally. Each bundle turns posterolaterally on its own side and enters the core at the side of the dorsal cleft. It runs posteroventrolaterally to pass under the DIT at the transverse level of DCIV and above the VLT. Finally it turns posteroventrally and its fibres go to cell bodies of the PVL1 group.

DISCUSSION

General neuroanatomy

The general neuroanatomical organization of the mesothoracic ganglion has proved to be gratifyingly consistent from one individual to another, though the details, such as the relative positions of fibres within a tract, cell bodies within a group, or the points of branching of individual fibres, vary. Cohen & Jacklet (1967) and Young (1969) noted a similar consistency of arrangement among the larger neuron somata of the meta- and mesothoracic ganglia respectively, as did Kendig (1967) in fibre groups of the crayfish *Procambarus clarkii* (Girard), Bentley (1970) and Burrows & Hoyle (1973) among flight and leg muscle motoneuron somata of the locust *Schistocerca*, and Tyrer & Altman (1974) among both motor and sensory flight neurons of the locust *Chortoicetes*. The position of tracheal branches varies more, however.

The present study has substantiated most of the observations of Pipa *et al.* (1959) that relate to the longitudinal and transverse fibre tracts of the mesothoracic ganglion. However, their description of the DT, DMT, VMT, and VT as forming for the most part a continuous arc, only arbitrarily subdivided into regions, has not been borne out. These tracts come together anteriorly and posteriorly as part of the connectives, but they were clearly separated throughout most of the ganglion in the specimens studied here. This is also true of the pro- and meta-thoracic ganglia; it is hoped to describe the gross neuroanatomy of these, for comparison, in a future publication. Pipa *et al.* mentioned the roots of the peripheral nerves only briefly, in connexion with the presumed sensory input to the VAC. However, they stated that, as well as the fibres from nerves 2, 3 and 5, all those of nerve 7 enter this zone, whereas in this study only the most ventral root (N7R3) has been found to do so, the other two roots ascending more dorsally. They could not trace any of the mainly coarse fibres of nerves 4 and 6 into the VAC, which agrees with the present observations, but evidently did not see the small, easily missed bundle, N6VR.

Guthrie, in the summary of the results of Pipa *et al.* (1959) by Guthrie & Tindall (1968), re-examined the structure of the mesothoracic ganglion. However, he reported finding the fibre tracts difficult to identify because many of the labels in the photographic illustrations of Pipa *et al.* were imprecisely located, and he could not find DCIII or, with certainty, VCLII. This explains some confusion in the labelling of two of his three illustrations (figures 8.8, 8.10, pp. 175, 177). Guthrie shows DCI as two bundles, the lower of which, as is clear from the micrograph in figure 8.8, is the missing (dorsal) VCLII (compare with present figure 6, plate 21).

Commissure 'd.c.4', immediately behind this, is the untraced DCIII. Bundle 'd.c.6' in micrograph 8.8 is in the characteristic position of and shows the typical coarse fibres of the SMC, while above it an unlabelled pale-stained area is almost certainly the true DCIV – in any sagittal section close to the midline, as this is, all commissures can be expected to be readily distinguishable. DCVI is correctly labelled in micrograph 8.9 (page 176) but in diagram 8.10 is shown unusually far forward, between DCV above and the SMC below, close to the typical position of DCIV, instead of in its usual position vertically above the PVC. This diagram, and micrograph 8.8, also show what Guthrie describes as another, anterior glomerulus, additional to the VAC. However, this is the anterior fused region of the VAC, described by Pipa *et al.* as very conspicuous anteriorly, lying beneath the VMT and receiving the broad tracts of fine fibres from nerve 2 (i.e. N2VR). VCI ('v.c.l.1') is shown behind it, though this commissure normally lies ventral to the anterior VAC (figures 5, 6). However, the lateral limbs of VCI do extend behind N2VR and would give this appearance away from the midline. VCLII is tentatively indicated in diagram 8.10 as 'v.c.l.2(?)', but the ventral part of the commissure lies rather below this position, in front of the ventralmost region of the VAC (figures 5–7).

In the same study Guthrie also examined the axon groups of mesothoracic nerve 5, which he labelled a to j, and gives diagrams (figure 8.11, A, B, page 178) of their positions in the base of the nerve and in a transverse section of the ganglion. In comparing these with the present results (figures 26 to 31, especially 28) it must be remembered that the relative positions of axons within nerve trunks are usually rather variable, so more significance should probably be attached to their arrangement within the ganglion. However, the positions of groups a, g and i in the ganglion are not indicated, as they were not observed as distinct tracts (D. M. Guthrie, personal communication). Their positions in the nerve suggest that group a may correspond to N5R1, group g to part of N5R10 or 11, and group i to N5R8. The ventralmost group, j, clearly resembles N5R11, perhaps together with N5R9. Comparison of the other groups with the present results is difficult because it is hard to correlate their arrangement in the nerve with that in the ganglion; their distribution differs in a number of respects from that described here.

Nerve root function

The likely function of the fibres that compose the nerve roots is indicated by whether they are efferent or afferent, i.e. arise from central cell bodies or not. Sensory neurons with central cell bodies have been found in crustaceans (Alexandrowicz & Whitear 1957; Roberts & Bush 1971), leeches (Nicholls & Baylor 1968) and other annelids (reviewed by Mill (1974)), but not so far in insects. In the present account, therefore, efferent fibres are presumed to be motor and afferent fibres sensory, though motor is used here in the broadest sense, to include excitatory and inhibitory fibres to effectors, and any of the small number of neurosecretory cells (de Bessé 1967) that may send axons peripherally. Ignoring neurosecretion, table 1 summarizes the present results and compares them with the previously reported functions of the peripheral nerves. These are quoted from Nijenhuis & Dresden (1952, 1955*a, b*) (nerves 3–6), Pipa & Cook (1959) (nerves 2, 7 and 8) and Case (1957) (nerve 8); all are reviewed by Guthrie & Tindall (1968). The present study was of tracts rather than of individual neurons and so it is always possible that an apparently motor tract might contain undetected sensory fibres, or a sensory tract might include motor fibres that have not been followed assiduously enough to their cell bodies. However, fluorescent staining greatly reduces this danger and table 1 probably gives a substantially accurate picture. Note that one fibre of N6DR1 (shown in curved brackets in the table) is

a branch of the probable common inhibitory neuron N4R2.p, as discussed below. Three groups of fibres remain of doubtful function, shown by square brackets in the table. Those of N2DR are probably mainly or all sensory but could not be traced confidently to areas of arborization. The 5 to 7 fibres of N4R2 are of more doubtful function. They may all be sensory but some may have been confused with the posterior fibres of N3R1 and be motor. The six or so small fibres

TABLE 1. COMPARISON OF FUNCTION OF PERIPHERAL NERVES AND ROOTS IN THE MESOTHORACIC GANGLION OF *PERIPLANETA AMERICANA*

nerve	reported function	root	function and approximate number of units		neuron cell body groups contributing to root
			motor	sensory	
2	m, s	N2DR	6-7	[9-14]	AL1?, AL3, MDM
		N2VR	—	850	—
3	m, s	N3R1	10	—	AV1
		N3R2	12-14	—	AVL1
		N3R3	15	—	AVL1, AVL 4
		N3R4	4	—	AVL1
		N3R5	8	—	AVL1
		N3R6	—	36	—
		N3R7	—	150-200	—
4	m	N4R1	8	—	AL1, AL3, AVL2, AVL4
		N4R2	5	[5-7]	AV1, PVM
5	m, s	N5R1	32	—	AV1
		N5R2	4	—	AV1, PL1 + 2, PV1, PV3
		N5R3	—	25-30	—
		N5R4	—	25	—
		N5R5	—	12	—
		N5R6	—	6-7	—
		N5R7	—	50-55	—
		N5R8	—	36	—
		N5R9	—	9	—
		N5R10	—	23-27	—
		N5R11	—	700	—
6	m, s	N6DR1	5 (+1)	—	AVL4, (PVM)
		N6DR2	4	—	AV1, PVL1
		N6DR3	34	—	PVL2
		N6VR	—	50-60 [+6]	—
7	s	N7R1	—	15	—
		N7R2	—	20	—
		N7R3	—	20	—
8	m	N8R1	4-5†	—	PVL1, PV2?
		Totals	151-155	2,027-2,102 + [20-27]	—

m, motor; s, sensory; †, from each side of ganglion; [], function uncertain; (), shared with N4R2.

of N6VR are probably sensory but, like those of N2DR, could not be traced far enough to be certain. The inferred functions of the nerve root components tally well with the previously reported functions of the nerves, except for the possibly sensory component in root 2 of the motor nerve 4. However, this anomaly, if real, can readily be explained by the fact that N4R2 receives many of its fibres from the predominantly sensory nerve 5, through the small branch that connects them.

Several workers have argued a possible relation between fibre diameter and function. Dresden & Nijenhuis (1958) noted that in nerves 3 to 6 the motor fibres were usually thicker than the

sensory ones, and Guthrie (1962) assumed in nerve 5 that fibres more than 5 μm in diameter were mainly motor and smaller ones mainly sensory. Chapman & Pankhurst (1967) disputed this, estimating some sensory fibres at about 10 μm in diameter, and Pearson, Stein & Malhotra (1970) similarly reported motor fibres much narrower than 5 μm , although Pearson & Iles (1971) found that a large number of axons less than 4 μm in diameter in a branch of nerve 5 were

TABLE 2. COMPARISON OF FIBRE COUNTS IN PERIPHERAL BRANCHES OF NERVES 3-6 (DRESDEN & NIJENHUIS 1958) AND PRESENT COUNTS IN NERVE ROOTS CLOSE TO BASES OF NERVES

nerve	motor fibres		sensory fibres	
	Dresden & Nijenhuis	present count	Dresden & Nijenhuis	present count
3	36	49-51	59-64	186-236
4	10	13	0	[5-7]
5	26†	36	137	886-901
6	31	44	2	50-60 [+ 6]

† Includes 8 fibres shared with nerve 3; [] function uncertain.

probably sensory. The present observations have shown that almost all sizes of both motor and sensory fibres occur, and the impression that sensory fibres are finer is due rather to the far greater numbers of small sensory fibres than to any consistent relation between diameter and function. All that can be said with certainty is that the smallest fibres are nearly all sensory and that most motor fibres are noticeably larger.

Many more fibres are listed here in nerves 3-6 than were found in the peripheral branches of these nerves by Dresden & Nijenhuis (1958), who counted 102 motor axons and about 200 sensory ones. Table 2 compares results in detail. The numbers of motor axons, extracted from tables I to VI of Dresden & Nijenhuis, total 103, not 102. Careful checking failed to explain the one additional medium-sized fibre found in the tables. Strict comparison of results is complicated because Dresden & Nijenhuis omitted fibres of nerve 5 to the distal parts of the leg; also nerves 3 and 5, as well as 6, receive a branch from a fibre of nerve 4, seven or eight fibres of nerve 4, probably including the 5-7 fibres of doubtful function, run peripherally in nerve 5, and two peripheral fibres of nerve 4 pass to the base of nerve 5. Nevertheless, it is clear that the present work has revealed not only some additional motor fibres but a great many more sensory ones. This no doubt reflects the better histological techniques now available. Many of the sensory fibres are very small (< 2 μm in diameter) and, though most fibres enlarge somewhat in the nerve trunks, are still difficult to count even with improved methods, so it would not be surprising if some had been missed by earlier workers. That Dresden & Nijenhuis counted only five very small fibres in all four nerves together seems to substantiate this. More recent workers have recorded larger numbers: Guthrie (1962) counted over 80 large and at least 350 'very fine' fibres in mesothoracic nerve 5; Pearson *et al.* (1970), in a micrograph of a branch of metathoracic nerve 6, showed many very small, presumed sensory, axons; and Milburn & Bentley (1971) reported 1000 and 2500 sensory fibres in the two cercal nerves of the last abdominal ganglion. The discrepancies between the present counts of motor fibres and those of Dresden & Nijenhuis are smaller but may also be due to improved technique, for some motor fibres are small, as noted above.

The cell body groups so far found to contribute to each nerve root are also summarized in table 1. All somata of nerves 3 to 6, except that of neuron N4R2.p in the midline PVM group,

are ipsilateral, nerve 8 receives axons from both sides of the ganglion, while one of the somata of nerve 2 lies in the midline and five or six are contralateral. In the metathoracic ganglion Cohen & Jacklet (1967) likewise found that all somata they could connect with nerves 3–6 were ipsilateral, though all eight associated with nerve 2 were contralateral and none in the midline. In *Schistocerca* also, Bentley (1970) found that all mesothoracic flight neuron somata were ipsilateral, except possibly those contributing to the most anterior nerve (nerve 1). Tyrer & Altman (1974) report that in both meso- and metathoracic ganglia of *Chortoicetes* one flight neuron soma contributing to nerve 1 is also contralateral. The total of over 150 motoneurons counted here considerably exceeds the 100 and 103 cell bodies 20 μm or more in diameter recorded on the two sides of the mesothoracic ganglion by Young (1969) and the 103 counted on each side of the metathoracic ganglion by Cohen & Jacklet (1967), though neither study included dorsal, midline cells. The differences between these and the present figures imply that a good proportion of motoneuron somata must be less than 20 μm in diameter, and indeed Cohen & Jacklet estimated that the entire metathoracic ganglion contains, in addition to about 230 cells larger than 20 μm , about 3192 smaller ones. These authors drew attention to the similarity between their total of 103 cell bodies each side and the 102 motor axons counted by Dresden & Nijenhuis (1958) as substantiating the idea that the large somata probably have a motor function. This conclusion is not disputed, but it should be remembered that Cohen & Jacklet's total included an average of eight somata contributing to nerve 2, not studied by Dresden & Nijenhuis, so the comparable total of cell bodies should be nearer 95.

Earlier workers (Hilton 1911; Zawarzin 1924; Wigglesworth 1959) tended to the idea that motor fibres in insect peripheral nerve roots generally lie dorsally and sensory fibres ventrally, the reverse of the position in the vertebrate spinal cord. Fielden (1963) showed this electrophysiologically in the dragonfly *Anax imperator* Leach, but Hoyle (1970) did not think this isolated example typical. The present results (table 1) provide another example. Most roots are either motor or sensory (allowing for possibly undetected fibres of the other type, noted above), except for the apparently mixed N2DR and N4R2, and in general the motor roots lie dorsal to the sensory roots. However, only in nerve 6 are the two types distinctly separated, and even here the six or so fibres of uncertain function leave an element of doubt. In nerve 3, and less so in nerve 5, motor and sensory roots form a continuous series. The wholly sensory nerve 7 and the motor nerve 8 fit the scheme better, being clearly ventral and dorsal respectively. Nerves 2 and 4 need further study. The sensory N2VR enters the ganglion ventrally but N2DR, which should, according to the scheme, be entirely motor, appears to include sensory fibres. Nerve 4 is complicated by the presence of apparently sensory fibres from nerve 5, but N4R1 and 2 seem otherwise to be wholly motor and both leave the ganglion core fairly dorsally. Hoyle (1970) also expressed surprise that motor elements should lie dorsal to sensory ones if, as was presumed, motor cell bodies are located ventrally. Evidence is increasing (Pyle 1941; Bentley 1970; Iles 1972*a, b*; Burrows 1973*a, c*; Burrows & Hoyle 1973) that this is nevertheless often so, though Crossman *et al.* (1971, 1972) found what may be motor cell bodies located dorsally in the metathoracic and last abdominal ganglia, and two (one in the MDM group, contributing to N2DR, and that of neuron N5R2b, associated with groups PL1 and 2) are reported here. In the present study all other motoneuron somata so far found lie ventrally or laterally, and their processes run more or less dorsally before leaving the ganglion along a nerve trunk. Many (especially of N4R1, N5R1 and 2, figures 26, 28) show well-defined link segments (Cohen 1970) running from the soma, and integrating segments (Sandeman 1969), which give off dendritic branches, into

usually dorsal or lateral neuropile. The ventral location of most of the sensory elements is partly associated with the position of the VAC, which receives predominantly very small fibres from N2VR, N3R7, N5R11, N6VR and N7R3. The other, chiefly coarser, sensory fibres branch into mid-level neuropile or below, but some (the most dorsal bundle of N2VR, posterodorsal branches of N3R6, N7R2, and the possibly sensory fibres of N2DR and N4R2) ascend more dorsally. The arborizations of sensory axons, insofar as they have yet been examined, give an impression of being more localized than the widely spreading dendrites of many of the motor fibres, which might mean that particular regions of neuropile are concerned with particular receptor fields. However, it may simply be that the further extensions of the sensory fibres were too fine to be seen with Procion Yellow. Cobalt chloride staining (Pitman *et al.* 1972), which fills small branches more completely (Burrows 1973*a*), may resolve this. Using this method, Tyrer & Altman (1974) have found that axons from wing sense organs of *Chortoicetes* also arborize into well-defined regions of neuropile.

Neuron topology

This study was not primarily concerned with individual neuron pathways, which are receiving increasing attention from other workers, but a handful have been outlined and some of these can be compared with other authors' descriptions.

Pearson & Bergman (1969) reported the first common inhibitory (CI) motoneuron to be discovered in insects in the locusts *Locusta migratoria* L. and *Schistocerca* and in *Periplaneta*. In the metathoracic ganglion of *Periplaneta* they were able to identify its axon branches electrophysiologically in nerves 3 to 6 and, with less certainty, in the anterior and posterior connectives. They also found a similar CI neuron in the mesothoracic ganglion. Pearson & Fournier (1973), using cobalt chloride staining, have recently identified the soma of this neuron, now designated the widespread CI neuron, D₃, in the metathoracic ganglion and traced its axon branches into nerves 3 to 6, but could not stain branches to the connectives. The existence of such branches therefore remains in doubt, though Burrows (1973*a*) found in *Chortoicetes* that a fine branch, 1.5 μm in diameter, of the metathoracic CI neuron runs to the mesothoracic ganglion along the ipsilateral connective. It seems certain that neuron N4R2.p in the present account is the mesothoracic counterpart of the metathoracic widespread CI neuron. Its soma, in the PVM group, lies in much the same position in or near the ventral midline and its axon gives branches to nerves 3, 4 and 6. Though no branch could be traced directly to nerve 5, one fibre of nerve 4 gives a branch to nerve 5 along the connexion between the two nerves, exactly as described by Pearson & Fournier in the metathoracic ganglion. Cobalt staining has now shown this to belong to neuron N4R2.p (unpublished observations). No branches to the connectives have yet been found. The axonal pathway of the metathoracic widespread CI neuron corresponds precisely with that of N4R2.p (K. G. Pearson, personal communication) and examination of the metathoracic ganglia of the present specimens (unpublished observations) confirms this. Young (1973) thought it very probable that the cells newly numbered 40 to 46 in his latest cell map of the mesothoracic ganglion include the soma of the CI neuron, and the present results support this. It appears from its position that his cell 41 is the soma of the widespread mesothoracic CI neuron, N4R2.p.

Pearson & Iles (1971) reported two more CI neurons, D₁ and D₂, in branches of metathoracic nerve 5, but could not find branches of them in any other ipsilateral nerves; they did not examine the connectives. So far, the present work has likewise revealed no mesothoracic neurons other than N4R2.p branching to more than one nerve. Pearson & Fournier (1973) identified

the somata of these two neurons, finding that of D_1 in the ventral midline at the transverse level of the posterior edge of nerve 3 and D_2 a little posterolateral to it. In the present study the only cell bodies in this region found to contribute to mesothoracic nerve 5 are those in the PV1 and PV3 groups (figure 5; figure 6, plate 21; figure 26), belonging to neurons N5R2d and N5R2c respectively. The large somata of neurons corresponding to these two are easily identified in the metathoracic ganglion (unpublished observations) and send their processes to nerve 5 along pathways similar to those in the mesothoracic ganglion. The somata lie in much the same positions as described by Pearson & Fournier for D_1 and D_2 and there thus seems every likelihood that neuron N5R2d corresponds to D_1 and N5R2c to D_2 . The equivalent somata in Young's (1973) cell map seem to be numbers 40 (N5R2d) and, probably, 44 (N5R2c).

Two other metathoracic neurons have been intensively studied by previous workers, the fast and slow coxal depressor motoneurons D_f and D_s (Pearson & Iles 1970). The soma of D_f is now known to be metathoracic cell 28 of Cohen & Jacklet (1967) (Iles 1972*a*; Young 1972; Pearson & Fournier 1973) and that of the corresponding mesothoracic neuron, cell 30 of Young (1969) (Young 1972), which is characterized by its large size and its position at the rear of the main anterior group of ventral cell bodies. The soma of neuron N5R2a described here is similarly one of the largest in the ganglion and lies to the back of the large AV1 group of cell bodies, and there seems little doubt that it corresponds to Young's cell 30, and hence to neuron D_f . In support of this, micrographs of metathoracic neuron 28 injected with cobalt chloride (Pitman *et al.* 1972, figure 2) show branching patterns strikingly similar to those of neuron N5R2a (figure 26 here), including the two lateral, anterior branches and a more medial anterior one, and several medial branches. The soma of neuron D_s lies posteriorly and dorsally (Iles 1972*a*), 130 to 230 μm behind nerve 3, 220 to 310 μm from the midline (Pearson & Bradley 1972; Pearson & Fournier 1973). In the mesothoracic ganglion only one soma contributing to nerve 5 has been found in this region in the present study, that of neuron N5R2b, associated with cell body groups PL1 and 2. The soma of the corresponding neuron in the metathoracic ganglion is easily recognizable (unpublished observations). It lies in a position similar to that of D_s and is relatively further forward than in the mesothoracic ganglion, as is the soma of D_s (J. F. Iles, personal communication), presumably because the metathoracic ganglion incorporates the first abdominal ganglion posteriorly. Neuron N5R2b thus seems likely to be equivalent to D_s . This is supported by the fact that the branching pattern of D_s , shown by filling with cobalt chloride, is similar to that of N5R2b (K. G. Pearson, personal communication). The soma of N5R2b, in both meso- and metathoracic ganglia, is unmistakably characterized in silver preparations by being much larger than neighbouring cell bodies. This conflicts with the original findings of Pearson & Bradley (1972) that the soma of D_s was only 25 μm in diameter – though Iles (1972*a*) gave the diameter as 50 μm – and indistinguishable morphologically from other similar-sized somata very close to it. However, Pearson & Bradley have now been able to identify the soma of D_s unambiguously and find its diameter 55 to 65 μm (K. G. Pearson, personal communication), close to the size found here (see below). The corresponding soma of Young (1969, 1973) is cell 56, as thought by D. Young (personal communication) and mentioned by Iles (1972*a*). Figure 3 of Young (1969) shows it clearly.

Figure 33*a, b* shows the positions of all these somata in the fused metathoracic and first abdominal ganglia of two individuals, for comparison with the present figures 24, 26 of the mesothoracic ganglion and with figure 2 of Pearson & Fournier (1973). These authors could not estimate sizes of the somata reliably because of swelling caused by the cobalt chloride stain. In

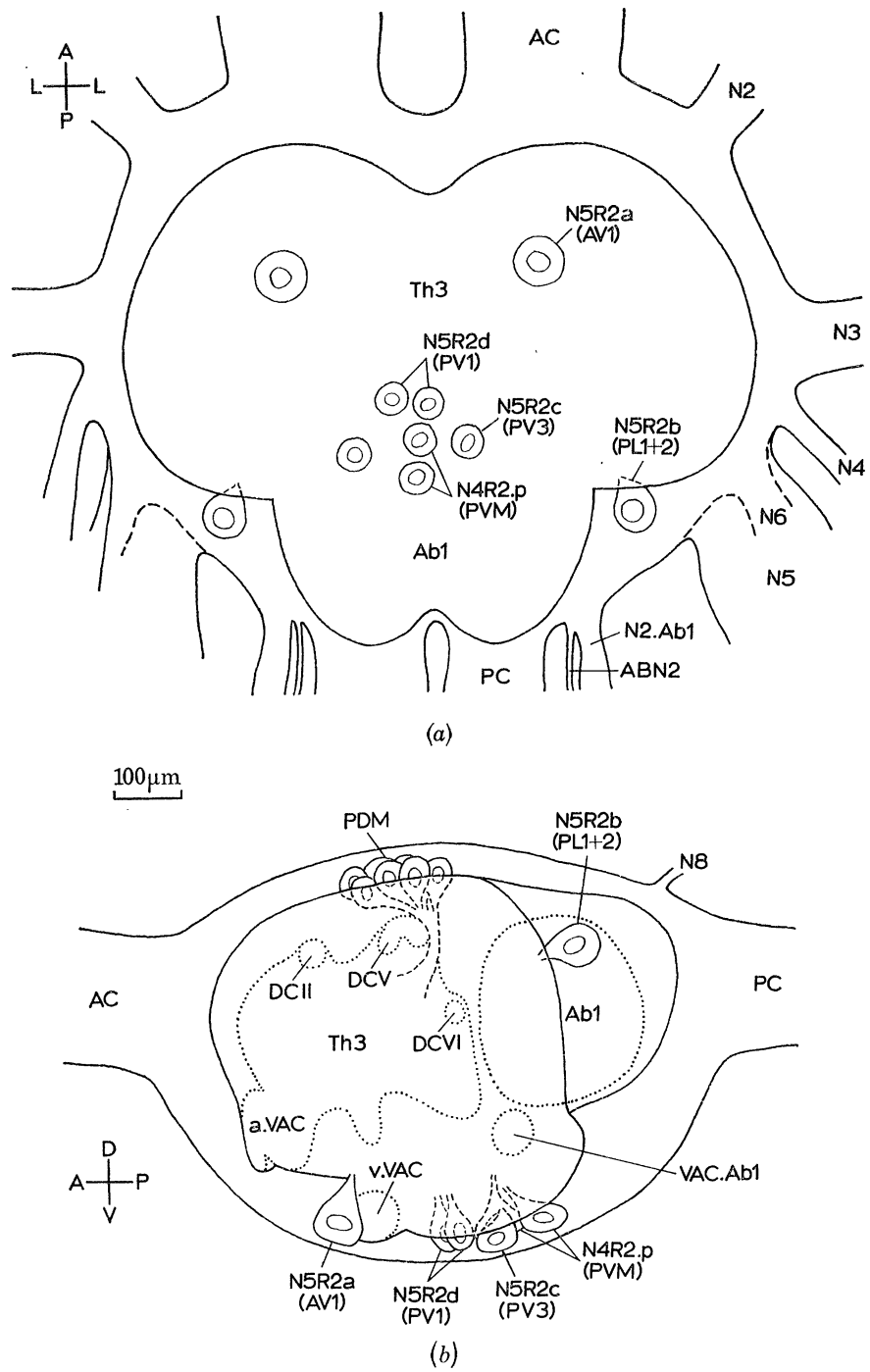


FIGURE 33. Positions of identified cell bodies of nerves 4 and 5, and of posterior dorsal median group, in fused metathoracic and first abdominal ganglia of two individuals. (a) Reconstructed from 20 µm frontal sections, ventral view; (b) from 20 µm sagittal sections, lateral view. Maximum limits of ganglion cores, solid line; limits of cores in midline, dotted line.

the present silver preparations all except the large soma of N5R2a are much the same size, those of the metathoracic ganglion being generally slightly the larger. Approximate mean diameters in the meso- and metathoracic ganglia respectively are: N4R2.p (D₃), 54, 56 μm ; N5R2a (D₁), 70, 78 μm ; N5R2b (D₈), 58, 66 μm ; N5R2c (D₂), 50, 54 μm ; N5R2d (D₁), 48, 54 μm .

Pearson & Fourtner (1973) also identified ten ventral somata sending axons into a branch (Br4) of metathoracic nerve 6, and an additional one contributing either to this or, more probably, to branch Br2. Seven of the somata were located laterally, anterior to nerve 3, two or three posteriorly, lateral to the abdominal connective, and one, apparently that of the widespread CI neuron, D₃, in or near the midline. Iles & Mulloney (1971) found six somata of nerve 6Br4 anteriorly and three posteriorly in the metathoracic ganglion, and Iles (1972*b*) found two anteriorly and three posteriorly in the mesothoracic ganglion. In the present study the five fibres composing N6DR1 and two of those of N6DR2 were found to originate from anterior, ventral cell bodies, in groups AVL4 and AV1 respectively; no other fibres of nerve 6 did so. In the metathoracic ganglion (unpublished observations) these roots contain the same numbers of fibres and follow similar courses. There seems little doubt, therefore, that their cell bodies correspond to the seven anterior somata of Pearson & Fourtner and include the six found by Iles & Mulloney and the two found by Iles. Likewise, the two posterior, ventral somata of Pearson & Fourtner seem likely to be those giving rise to the two posterior fibres of N6DR2, in the PVL1 group. More recent studies with cobalt chloride staining have confirmed both these conclusions (K. G. Pearson, personal communication). The two posterior somata may well correspond with two of those found by Iles & Mulloney and Iles. The third posterior soma found by these workers and by Pearson & Fourtner is presumably one of those in the PVL2 group, contributing fibres to nerve 6 along N6DR3.

Crossman *et al.* (1971, 1972) reported electrophysiological evidence that a group of eight mediadorsal cells in the metathoracic ganglion give axon branches to nerves 3 to 6 and to the anterior and posterior connectives of both sides of the ganglion. By injecting Procion Yellow into the cell bodies they were able to trace the main axons to both sides of the ganglion and in one instance follow an axon branch into nerve 5 of one side of the ganglion, in another into nerve 5 of both sides. Pearson & Fourtner (1973), however, found no staining of any of the dorsal cell bodies after diffusing cobalt chloride into branches of nerves 5 and 6, though electrical evidence suggested that two small axons in nerve 6Br4 of both sides might belong to two of these cells. The eight mediadorsal somata are easily identifiable as corresponding to those of the PDM group in the present account (figures 5, 6). Though these lie posteriorly in the mesothoracic ganglion they appear mid-dorsal in the metathoracic because the first abdominal ganglion, fused to it posteriorly, displaces them forward (figure 33*b*). Nevertheless, their processes enter the core of what is strictly the metathoracic ganglion as they do in the mesothoracic ganglion, posterodorsally, between DCV and DCVI. They then run forward and seem to bifurcate beneath DCII. Afterwards the fibres run laterally, near the dorsal margin of the core, as described by Crossman *et al.*, but could not be traced in silver preparations to any of the nerves or to the connectives. None of the fibres stained in any of the Procion Yellow preparations of the mesothoracic ganglion.

I wish to express my sincere thanks to Dr J. S. Altman, Dr P. J. Mill, Dr K. G. Pearson, Dr N. M. Tyrer and Dr D. Young for allowing me to see copies of papers before publication, and to Dr D. M. Guthrie and Dr J. F. Iles, as well as most of the foregoing, for reading the manuscript and for their helpful and encouraging comments.

Note added in proof, 1 February 1974. Diffusion filling of nerves with cobalt chloride has confirmed most of the present observations. N2DR seems to contain six motor units rather than seven (table 1), and the rest appear to be sensory. The fibres of doubtful function in N6VR also seem to be sensory, but those of N4R2 have yet to be examined. Only about 23 somata have so far been found to contribute to N6DR3, so the figures of 34 motor units in this root (table 1) and 44 in nerve 6 altogether (table 2) may be too large and may include some sensory fibres.

REFERENCES

- Alexandrowicz, J. S. & Whitear, M. 1957 Receptor elements in the coxal region of Decapoda Crustacea. *J. mar. biol. Ass. U.K.* **36**, 603–628.
- Arnold, A. J. 1969 Portable counter with keyboard and probes. *Lab. Pract.* **18**, 444–445.
- Ashhurst, D. E. 1959 The connective tissue sheath of the locust nervous system: a histochemical study. *Q. Jl microsc. Sci.* **100**, 401–412.
- Ashhurst, D. E. 1961 A histochemical study of the connective-tissue sheath of the nervous system of *Periplaneta americana*. *Q. Jl microsc. Sci.* **102**, 455–461.
- Bentley, D. R. 1970 A topological map of the locust flight system motor neurons. *J. Insect Physiol.* **16**, 905–918.
- de Bessé, N. 1966 Recherche des organes neurohémaux associés à la chaîne nerveuse ventrale de deux Blattes, *Leucophaea maderae* et *Periplaneta americana*. *C. r. hebdom. Séanc. Acad. Sci., Paris, D* **263**, 404–407.
- de Bessé, N. 1967 Neurosécrétion dans la chaîne nerveuse ventrale de deux Blattes, *Leucophaea maderae* (F.) et *Periplaneta americana* (L.). *Bull. Soc. zool. Fr.* **92**, 73–86.
- Blest, A. D. 1961 Some modifications of Holmes's silver method for insect central nervous systems. *Q. Jl microsc. Sci.* **102**, 413–417.
- Bodian, D. 1936 A new method for staining nerve fibers and nerve endings in mounted paraffin sections. *Anat. Rec.* **65**, 89–97.
- Brady, J. 1967 Histological observations on circadian changes in the neurosecretory cells of cockroach suboesophageal ganglia. *J. Insect Physiol.* **13**, 201–213.
- Brady, J. & Maddrell, S. H. P. 1967 Neurohaemal organs in the medial nervous system of insects. *Z. Zellforsch.* **76**, 389–404.
- Bullock, T. H. & Horridge, G. A. 1965 *Structure and function in the nervous systems of invertebrates*, 2 volumes. San Francisco: W. H. Freeman and Co.
- Burrows, M. 1973a Physiological and morphological properties of the metathoracic common inhibitory neuron of the locust. *J. comp. Physiol.* **82**, 59–78.
- Burrows, M. 1973b The role of delayed excitation in the co-ordination of some metathoracic flight motoneurons of a locust. *J. comp. Physiol.* **83**, 135–164.
- Burrows, M. 1973c The morphology of an elevator and a depressor motoneuron of the hindwing of a locust. *J. comp. Physiol.* **83**, 165–178.
- Burrows, M. & Hoyle, G. 1973 Neural mechanisms underlying behavior in the locust *Schistocerca gregaria* III. Topography of limb motoneurons in the metathoracic ganglion. *J. Neurobiol.* **4**, 167–186.
- Burt, P. E., Gregory, G. E. & Molloy, F. M. 1966 A histochemical and electrophysiological study of the action of diazoxon on cholinesterase activity and nerve conduction in ganglia of the cockroach *Periplaneta americana* L. *Ann. appl. Biol.* **58**, 341–354.
- Burt, P. E., Gregory, G. E. & Molloy, F. M. 1967 The activation of diazinon by ganglia of the cockroach *Periplaneta americana* L. and its action on nerve conduction and cholinesterase activity. *Ann. appl. Biol.* **59**, 1–11.
- Case, J. F. 1957 The median nerves and cockroach spiracular function. *J. Insect Physiol.* **1**, 85–94.
- Chapman, K. M. & Pankhurst, J. H. 1967 Conduction velocities and their temperature coefficients in sensory nerve fibres of cockroach legs. *J. exp. Biol.* **46**, 63–84.
- Cohen, M. J. 1970 A comparison of invertebrate and vertebrate central neurons. In *The neurosciences* (ed. F. O. Schmitt), vol. 2, pp. 798–812. New York: Rockefeller University Press.
- Cohen, M. J. & Jacklet, J. W. 1967 The functional organization of motor neurons in an insect ganglion. *Phil. Trans. R. Soc. Lond. B* **252**, 561–572.
- Crossman, A. R., Kerkut, G. A., Pitman, R. M. & Walker, R. J. 1971 Electrically excitable nerve cell bodies in the central ganglia of two insect species *Periplaneta americana* and *Schistocerca gregaria*. Investigation of cell geometry and morphology by intracellular dye injection. *Comp. Biochem. Physiol.* **40A**, 579–594.
- Crossman, A. R., Kerkut, G. A. & Walker, R. J. 1972 Electrophysiological studies on the axon pathways of specified nerve cells in the central ganglia of two insect species, *Periplaneta americana* and *Schistocerca gregaria*. *Comp. Biochem. Physiol.* **43A**, 393–415.
- Dagan, D. 1971 Neuronal basis for the escape response of the cockroach *Periplaneta americana*. Ph.D. thesis, Hebrew University of Jerusalem. (In Hebrew with English summary.)

- Dagan, D. & Parnas, I. 1970 Giant fibre and small fibre pathways involved in the evasive response of the cockroach, *Periplaneta americana*. *J. exp. Biol.* **52**, 313–324.
- Dresden, D. & Nijenhuis, E. D. 1958 Fibre analysis of the nerves of the second thoracic leg in *Periplaneta americana*. *Proc. K. ned. Akad. Wet. C* **61**, 213–223.
- Farley, R. D. & Evans, S. J. 1972 Neurosecretion in the terminal ganglion of the cockroach, *Periplaneta americana*. *J. Insect Physiol.* **18**, 289–303.
- Farley, R. D. & Milburn, N. S. 1969 Structure and function of the giant fibre system in the cockroach, *Periplaneta americana*. *J. Insect Physiol.* **15**, 457–476.
- Fielden, A. 1963 The localization of function in the root of an insect segmental nerve. *J. exp. Biol.* **40**, 553–561.
- Füller, H. B. 1960 Morphologische und experimentelle Untersuchungen über die neurosekretorischen Verhältnisse im Zentralnervensystem von Blattiden und Culiciden. *Zool. Jb.* **69**, 223–250.
- Geldiay, S. 1962 Histophysiological studies on the neurosecretion of *Blaberus craniifer* Burm. and *Periplaneta americana* L. *Sci. Rep. Fac. Sci. Ege Univ.* **3**, 1–59. (In Turkish with English summary.)
- Gregory, G. E. 1970 Silver staining of insect central nervous systems by the Bodian protargol method. *Acta zool., Stockh.* **51**, 169–178.
- Gregory, G. E. 1973 Simple fluorescence staining of insect central nerve fibres with Procion yellow. *Stain Technol.* **48**, 85–87.
- Guthrie, D. M. 1962 Regenerative growth in insect nerve axons. *J. Insect Physiol.* **8**, 79–92.
- Guthrie, D. M. & Tindall, A. R. 1968 *The biology of the cockroach*. London: Edward Arnold (Publishers) Ltd.
- Harris, C. L. & Smyth, T., Jr. 1971 Structural details of cockroach giant axons revealed by injected dye. *Comp. Biochem. Physiol.* **40A**, 295–303.
- Hess, A. 1958a Experimental anatomical studies of pathways in the severed central nerve cord of the cockroach. *J. Morph.* **103**, 479–502.
- Hess, A. 1958b The fine structure and morphological organization of the peripheral nerve-fibres and trunks of the cockroach (*Periplaneta americana*). *Q. Jl microsc. Sci.* **99**, 333–340.
- Hess, A. 1958c The fine structure of nerve cells and fibers, neuroglia, and sheaths of the ganglion chain in the cockroach (*Periplaneta americana*). *J. biophys. biochem. Cytol.* **4**, 731–742.
- Hilton, W. A. 1911 Some remarks on the motor and sensory tracts of insects. *J. comp. Neurol.* **21**, 383–395.
- Holmes, W. 1943 Silver staining of nerve axons in paraffin sections. *Anat. Rec.* **86**, 157–187.
- Hoyle, G. 1952 High blood potassium in insects in relation to nerve conduction. *Nature, Lond.* **169**, 281–282.
- Hoyle, G. 1970 Cellular mechanisms underlying behaviour – neuroethology. *Adv. Insect Physiol.* **7**, 349–444.
- Hoyle, G. & Burrows, M. 1970 Intracellular studies on identified neurons of insects. *Fedn Proc. Fedn Am. Socs exp. Biol.* **29**, 589.
- Hoyle, G. & Burrows, M. 1973a Neural mechanisms underlying behavior in the locust *Schistocerca gregaria* I. Physiology of identified motoneurons in the metathoracic ganglion. *J. Neurobiol.* **4**, 3–41.
- Hoyle, G. & Burrows, M. 1973b Neural mechanisms underlying behavior in the locust *Schistocerca gregaria*. II. Integrative activity in metathoracic neurons. *J. Neurobiol.* **4**, 43–67.
- Hughes, G. M. 1965 Neuronal pathways in the insect central nervous system. In *The physiology of the insect central nervous system* (ed. J. E. Treherne and J. W. Beament), pp. 79–112. London: Academic Press.
- Iles, J. F. 1972a Structure and synaptic activation of the fast coxal depressor motoneurone of the cockroach, *Periplaneta americana*. *J. exp. Biol.* **56**, 647–656.
- Iles, J. F. 1972b Electrophysiological investigations of insect nerve and muscle. D.Phil. thesis, Oxford.
- Iles, J. F. & Mulloney, B. 1971 Procion Yellow staining of cockroach motor neurones without the use of micro-electrodes. *Brain Res.* **30**, 397–400.
- Kendig, J. J. 1967 Structure and function in the third abdominal ganglion of the crayfish *Procambarus clarkii* (Girard). *J. exp. Zool.* **164**, 1–20.
- Kravitz, E. A., Stretton, A. O. W., Alvarez, J. & Furshpan, E. J. 1968 Determination of neuronal geometry using an intracellular dye injection technique. *Fedn Proc. Fedn Am. Socs exp. Biol.* **27**, 749.
- Maddrell, S. H. P. & Treherne, J. E. 1967 The ultrastructure of the perineurium in two insect species, *Carausius morosus* and *Periplaneta americana*. *J. Cell Sci.* **2**, 119–128.
- Maynard, D. M. 1962 Organization of neuropil. *Am. Zool.* **2**, 79–96.
- Miall, L. C. & Denny, A. 1886 *The structure and life-history of the cockroach (Periplaneta orientalis)*. London: Lovell Reeve and Co.
- Milburn, N. S. & Bentley, D. R. 1971 On the dendritic topology and activation of cockroach giant interneurons. *J. Insect Physiol.* **17**, 607–623.
- Mill, P. J. 1974 The organization of the nervous system in annelids. In *'Simple' nervous systems* (ed. P. N. R. Usherwood and D. R. Newth). London: E. J. Arnold. (In the Press.)
- Nicholls, J. G. & Baylor, D. A. 1968 Specific modalities and receptive fields of sensory neurones in CNS of the leech. *J. Neurophysiol.* **31**, 740–756.
- Nijenhuis, E. D. & Dresden, D. 1952 A micro-morphological study on the sensory supply of the mesothoracic leg of the American cockroach, *Periplaneta americana*. *Proc. K. ned. Akad. Wet. C* **55**, 300–310.
- Nijenhuis, E. D. & Dresden, D. 1955a On the topographical anatomy of the nervous system of the mesothoracic leg of the American cockroach (*Periplaneta americana*). I. *Proc. K. ned. Akad. Wet. C* **58**, 121–130.

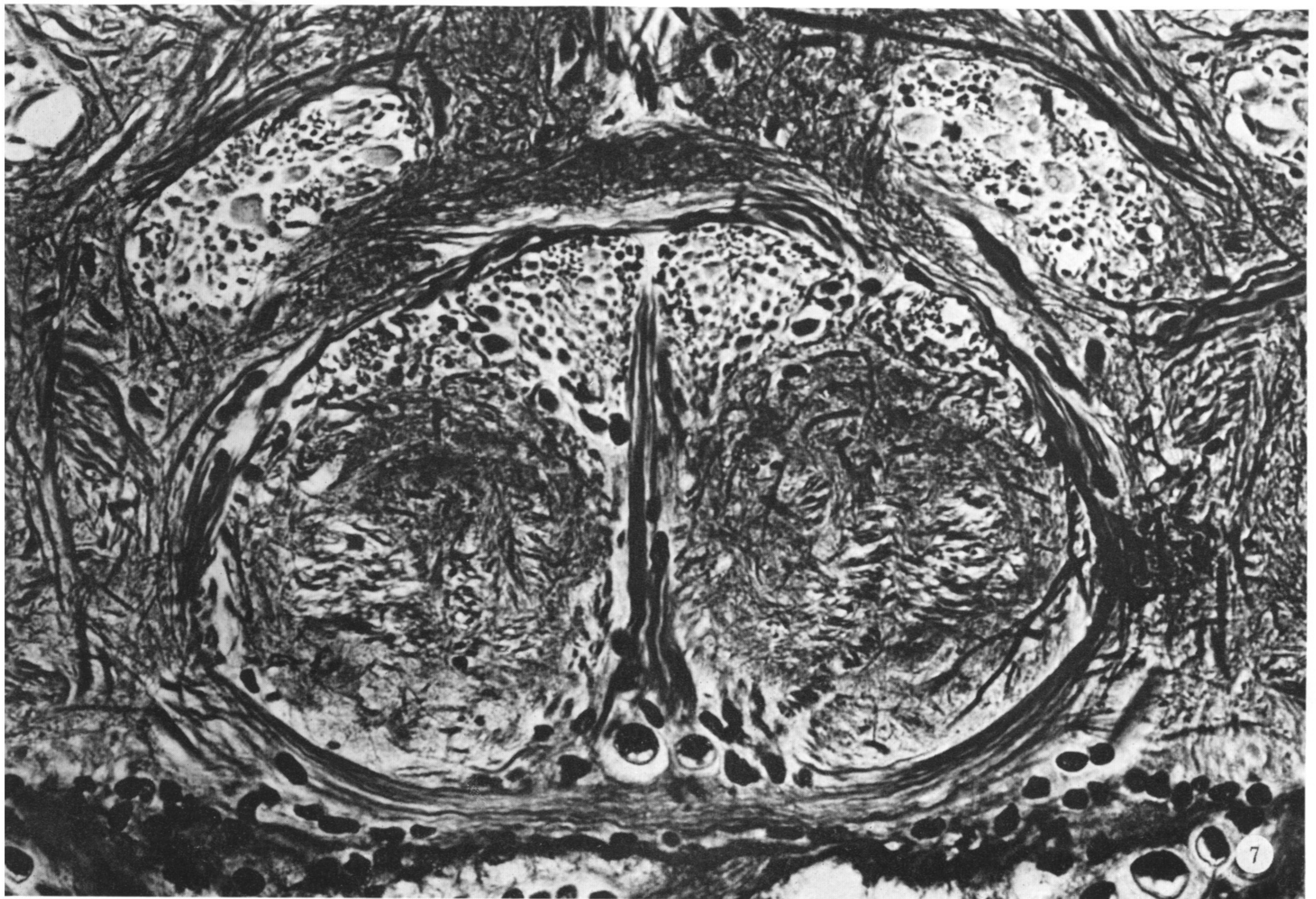
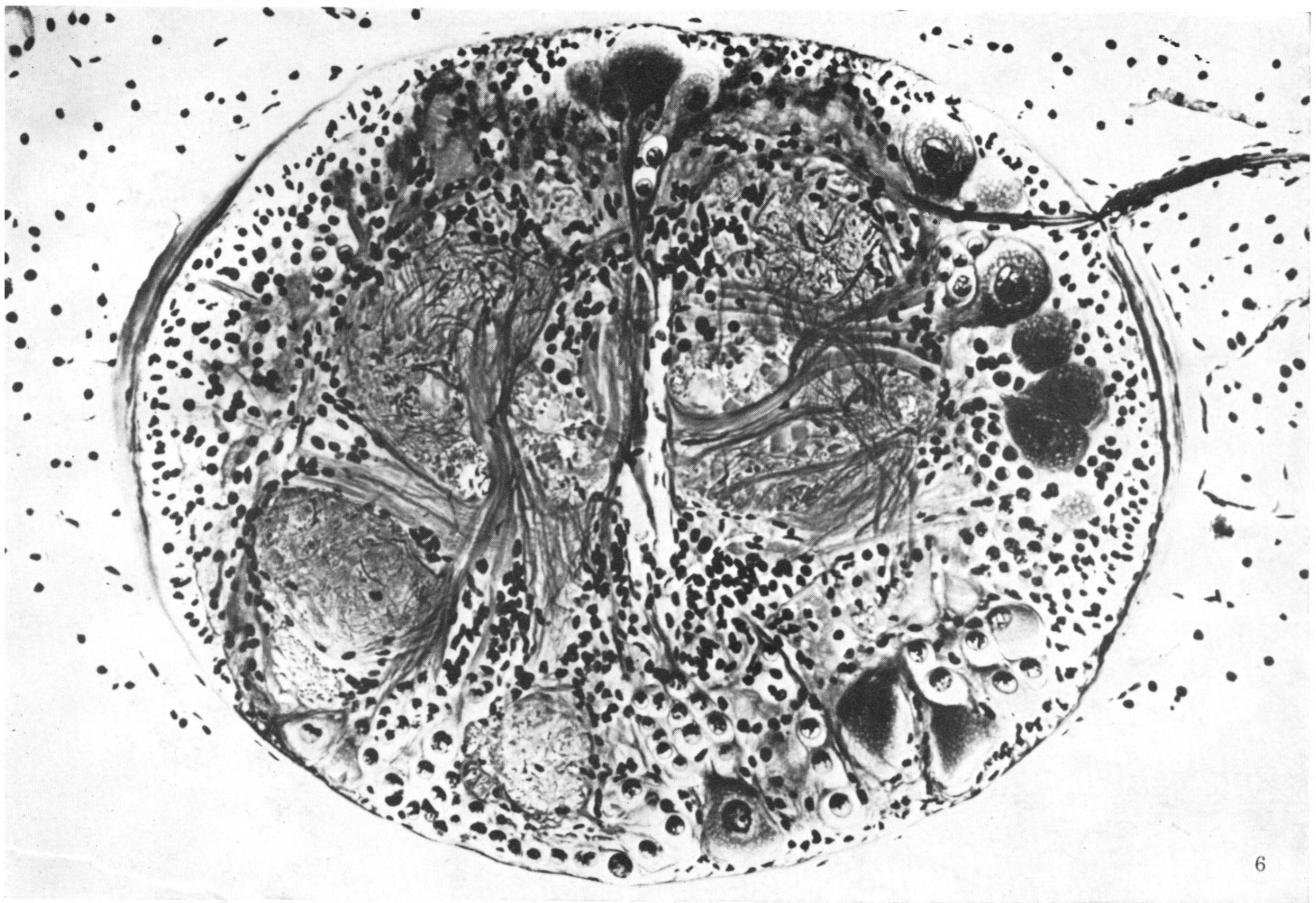
- Nijenhuis, E. D. & Dresden, D. 1955*b* On the topographical anatomy of the nervous system of the mesothoracic leg of the American cockroach (*Periplaneta americana*). II. *Proc. K. ned. Akad. Wet. C* **58**, 131–136.
- Pantin, C. F. A. 1948 *Notes on microscopical technique for zoologists*. Cambridge University Press.
- Parnas, I. & Dagan, D. 1971 Functional organizations of giant axons in the central nervous system of insects: new aspects. *Adv. Insect Physiol.* **8**, 95–144.
- Pearson, K. G. & Bergman, S. J. 1969 Common inhibitory motoneurons in insects. *J. exp. Biol.* **50**, 445–471.
- Pearson, K. G. & Bradley, A. B. 1972 Specific regeneration of excitatory motoneurons to leg muscles in the cockroach. *Brain Res.* **47**, 492–496.
- Pearson, K. G. & Fournier, C. R. 1973 Identification of the somata of common inhibitory motoneurons in the metathoracic ganglion of the cockroach. *Can. J. Zool.* **51**, 859–866.
- Pearson, K. G. & Iles, J. F. 1970 Discharge patterns of coxal levator and depressor motoneurons of the cockroach, *Periplaneta americana*. *J. exp. Biol.* **52**, 139–165.
- Pearson, K. G. & Iles, J. F. 1971 Innervation of coxal depressor muscles in the cockroach, *Periplaneta americana*. *J. exp. Biol.* **54**, 215–232.
- Pearson, K. G., Stein, R. B. & Malhotra, S. K. 1970 Properties of action potentials from insect motor nerve fibres. *J. exp. Biol.* **53**, 299–316.
- Pipa, R. L. 1961 Studies on the hexapod nervous system. III. Histology and histochemistry of cockroach neuroglia. *J. comp. Neurol.* **116**, 15–26.
- Pipa, R. L. & Cook, E. F. 1959 Studies on the hexapod nervous system. I. The peripheral distribution of the thoracic nerves of the adult cockroach, *Periplaneta americana*. *Ann. ent. Soc. Am.* **52**, 695–710.
- Pipa, R. L., Cook, E. F. & Richards, A. G. 1959 Studies on the hexapod nervous system. II. The histology of the thoracic ganglia of the adult cockroach, *Periplaneta americana* (L.). *J. comp. Neurol.* **113**, 401–433.
- Pitman, R. M., Tweedle, C. D. & Cohen, M. J. 1972 Branching of central neurons: intracellular cobalt injection for light and electron microscopy. *Science, Wash.* **176**, 412–414.
- Power, M. E. 1943 The brain of *Drosophila melanogaster*. *J. Morph.* **72**, 517–559.
- Pringle, J. W. S. 1939 The motor mechanism of the insect leg. *J. exp. Biol.* **16**, 220–231.
- Pyle, R. W. 1941 The fiber tracts of the fused thoracic ganglia of the adult *Ephesia kuehniella* Zeller (Lepidoptera Pyralidae). *Psyche* **48**, 123–128.
- Roberts, A. & Bush, B. M. H. 1971 Coxal muscle receptors in the crab: the receptor current and some properties of the receptor nerve fibres. *J. exp. Biol.* **54**, 515–524.
- Roeder, K. D. 1948 Organization of the ascending giant fiber system in the cockroach (*Periplaneta americana*). *J. exp. Zool.* **108**, 243–261.
- Roeder, K. D. 1965 Epilogue. In *The physiology of the insect central nervous system* (ed. J. E. Treherne and J. W. Beament), pp. 247–252. London: Academic Press.
- Rowe, E. C., Moberly, B. J., Howard, H. M. & Cohen, M. J. 1969 Morphology of branches of functionally-identified motoneurons in cockroach neuropile. *Am. Zool.* **9**, 1107.
- Rowell, C. H. F. 1963 A general method for silvering invertebrate central nervous systems. *Q. Jl microsc. Sci.* **104**, 81–87.
- Sandeman, D. C. 1969 Integrative properties of a reflex motoneuron in the brain of the crab *Carcinus maenas*. *Z. vergl. Physiol.* **64**, 450–464.
- Scharrer, B. C. J. 1939 The differentiation between neuroglia and connective tissue sheath in the cockroach (*Periplaneta americana*). *J. comp. Neurol.* **70**, 77–88.
- Schneider, K. C. 1902 *Lehrbuch der vergleichenden Histologie der Tiere*. Jena: Fischer.
- Shankland, D. L. 1966 Nerves and muscles of the pregenital abdominal segments of the American cockroach, *Periplaneta americana* (L.). *J. Morph.* **117**, 353–386.
- Smalley, K. N. 1970 Median nerve neurosecretory cells in the abdominal ganglia of the cockroach, *Periplaneta americana*. *J. Insect Physiol.* **16**, 241–250.
- Smith, D. S. & Treherne, J. E. 1963 Functional aspects of the organization of the insect nervous system. *Adv. Insect Physiol.* **1**, 401–484.
- Spira, M. E., Parnas, I. & Bergmann, F. 1969*a* Organization of the giant axons of the cockroach *Periplaneta americana*. *J. exp. Biol.* **50**, 615–627.
- Spira, M. E., Parnas, I. & Bergmann, F. 1969*b* Histological and electrophysiological studies on the giant axons of the cockroach *Periplaneta americana*. *J. exp. Biol.* **50**, 629–634.
- Stretton, A. O. W. & Kravitz, E. A. 1968 Neuronal geometry: determination with a technique of intracellular dye injection. *Science, Wash.* **162**, 132–134.
- Tyrer, N. M. & Altman, J. S. 1974 Motor and sensory flight neurones in a locust demonstrated using cobalt chloride. (in the Press).
- Wigglesworth, V. B. 1959 The histology of the nervous system of an insect, *Rhodnius prolixus* (Hemiptera). II. The central ganglia. *Q. Jl microsc. Sci.* **100**, 299–313.
- Wigglesworth, V. B. 1960 The nutrition of the central nervous system in the cockroach *Periplaneta americana* L. The role of the perineurium and glial cells in the mobilization of reserves. *J. exp. Biol.* **37**, 500–512.

- Yamasaki, T. & Narahashi, T. 1959 The effects of potassium and sodium ions on the resting and action potentials of the cockroach giant axon. *J. Insect Physiol.* **3**, 146–158.
- Young, D. 1969 The motor neurons of the mesothoracic ganglion of *Periplaneta americana*. *J. Insect Physiol.* **15**, 1175–1179.
- Young, D. 1972 Specific re-innervation of limbs transplanted between segments in the cockroach, *Periplaneta americana*. *J. exp. Biol.* **57**, 305–316.
- Young, D. 1973 Specificity and regeneration in insect motor neurons. In *Developmental neurobiology of arthropods* (ed. D. Young), pp. 179–202. Cambridge University Press.
- Zawarzin, A. 1924 Zur Morphologie der Nervenzentren. Das Bauchmark der Insekten. Ein Beitrag zur vergleichenden Histologie (Histologische Studien über Insekten VI). *Z. wiss. Zool.* **122**, 323–424.

EXPLANATION OF ABBREVIATIONS

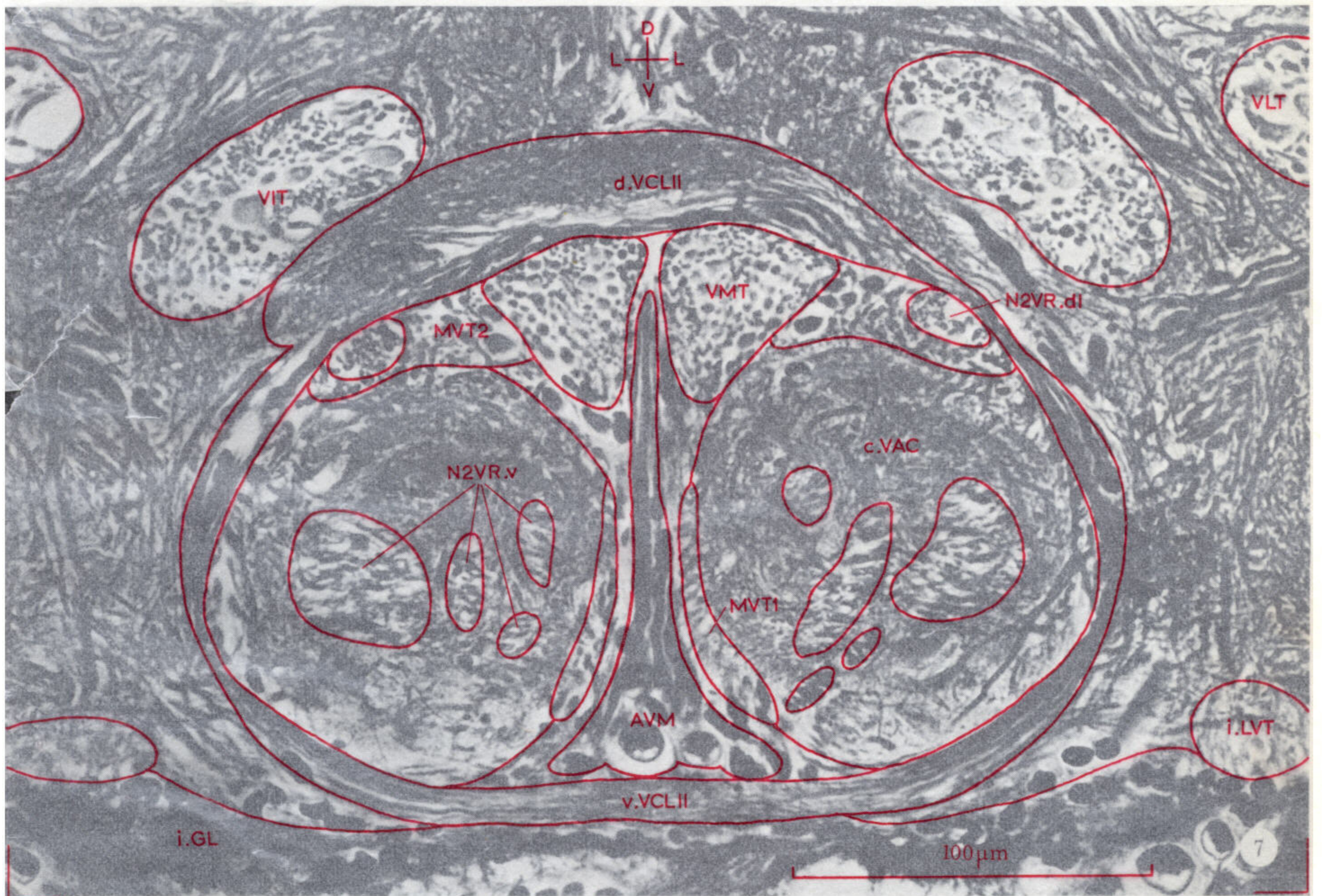
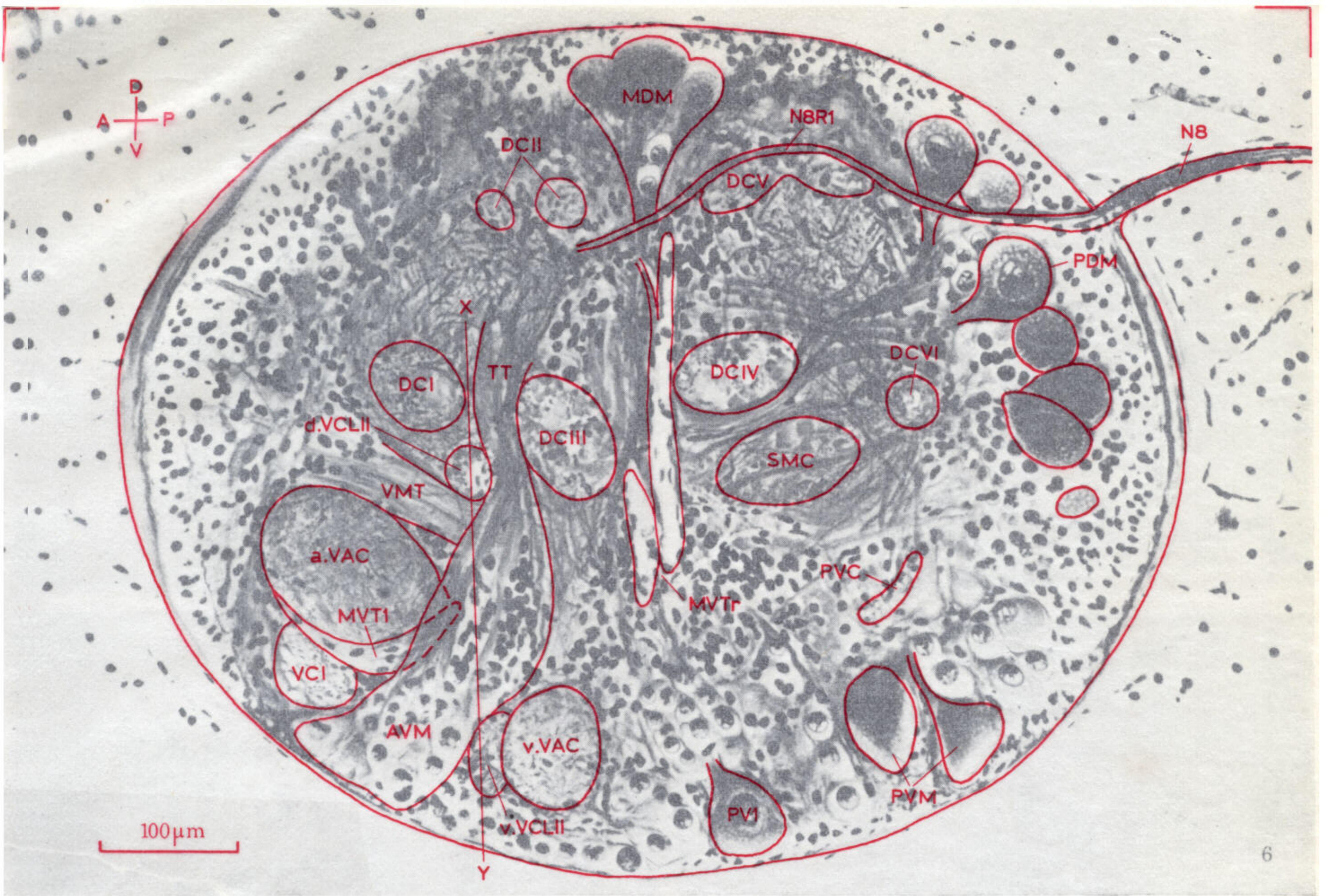
A	anterior	L	lateral
Ab1	first abdominal ganglion	LDT	lateral dorsal tract
ABN2	second nerve of first abdominal ganglion	ll.DIT	lateral limb of dorsal intermediate tract
AC	anterior interganglionic connective	l.VAC	ventrolateral extension of ventral association centre
ADL	anterior dorsolateral cell body group	LVT	lateral ventral tract
ADL.fb	fibre bundle of anterior dorsolateral cell body group	M	medial
ADTr	anterior dorsal trachea	MDM	mid-dorsal median cell body group
AL	anterolateral	MDT	median dorsal tract
AL1	anterior lateral cell body group 1	MTr2	second median trachea
AL3	anterior lateral cell body group 3	MVT1	median ventral tract 1
AL3.fb	fibre bundle of anterior lateral cell body group 3	MVT2	median ventral tract 2
ALTr	anterior lateral trachea	MVT3	median ventral tract 3
al.VCI	anterior lateral limb of ventral commissure I	MVTr	mid-ventral trachea
AM	anteromedial	N2	nerve 2
AMTr	anterior median trachea	N2Ab1	nerve 2 of first abdominal ganglion
AV	anteroventral	N2DR	nerve 2, dorsal root
AV1	anterior ventral cell body group 1	N2VR	nerve 2, ventral root
AV1.fbs	fibre bundles of anterior ventral cell body group 1	N2VR.d	dorsal bundle of nerve 2, ventral root
AV4	anterior ventral cell body group 4	N2VR.dd	dorsalmost bundle of nerve 2, ventral root
a.VAC	anterior mass of ventral association centre	N2VR.dl	lower dorsal bundle of nerve 2, ventral root
AVL1	anterior ventrolateral cell body group 1	N2VR.v	ventral bundle of nerve 2, ventral root
AVL2	anterior ventrolateral cell body group 2	N2VR.vl	lateral fibres of ventral bundle of nerve 2, ventral root
AVL2.fbs	fibre bundles of anterior ventrolateral cell body group 2	N2VR.vv	ventral fibres of ventral bundle of nerve 2, ventral root
AVL3	anterior ventrolateral cell body group 3	N3	nerve 3
AVL4	anterior ventrolateral cell body group 4	N3R1	nerve 3, root 1
AVL4.fb	fibre bundle of anterior ventrolateral cell body group 4	N3R2	nerve 3, root 2
AVM	anterior ventral median cell body group	N3R2.p	posterior branches of nerve 3, root 2
AVTr	anterior ventral trachea	N3R3	nerve 3, root 3
cb	neuron cell body	N3R3.a	anterior branches of nerve 3, root 3
cbg	neuron cell body group	N3R3.p	posterior fibres of nerve 3, root 3
c.n.s.	central nervous system	N3R3.v	ventralmost fibre of nerve 3, root 3
CT	C-tract	N3R4	nerve 3, root 4
c.VAC	cylindrical region of ventral association centre	N3R5	nerve 3, root 5
D	dorsal	N3R6	nerve 3, root 6
DCI	dorsal commissure I	N3R6.am	anteromedial bundle of nerve 3, root 6
DCII	dorsal commissure II	N3R6.p	posterior bundle of nerve 3, root 6
DCIII	dorsal commissure III	N3R7	nerve 3, root 7
DCIV	dorsal commissure IV	N4	nerve 4
DCV	dorsal commissure V	N4R1	nerve 4, root 1
DCVI	dorsal commissure VI	N4R1.d	dorsal larger fibres of nerve 4, root 1
DIT	dorsal intermediate tract	N4R1.m	middle larger fibre of nerve 4, root 1
DM	dorsomedial	N4R1.vv	ventralmost fibres of nerve 4, root 1
DMC	dorsal midline cleft	N4R2	nerve 4, root 2
DMT	dorsal median tract	N4R2.a	anterior medium-sized fibre of nerve 4, root 2
DT	dorsal tract	N4R2.m	middle medium-sized fibre of nerve 4, root 2
d.VCLII	dorsal part of ventral commissural loop II	N4R2.p	posterior medium-sized fibre of nerve 4, root 2
fb	fibre bundle (of neuron cell body group)	N4-5.cn	connexion between nerves 4 and 5
GC	ganglion core	N5	nerve 5
GLS	glial lacunar system	N5R1	nerve 5, root 1
i.GL	inner glial cell layer	N5R2	nerve 5, root 2
i.LVT	inner lateral ventral tract	N5R2a	fibre a of nerve 5, root 2
IT	I-tract	N5R2b	fibre b of nerve 5, root 2
		N5R2c	fibre c of nerve 5, root 2

N5R2d	fibre d of nerve 5, root 2	PDTr	posterior dorsal trachea
N5R3	nerve 5, root 3	PL	posterolateral
N5R4	nerve 5, root 4	PL1	posterior lateral cell body group 1
N5R5	nerve 5, root 5	PL1.fb	fibre bundle of posterior lateral cell body group 1
N5R6	nerve 5, root 6	PL2	posterior lateral cell body group 2
N5R7	nerve 5, root 7	PL2.fb	fibre bundle of posterior lateral cell body group 2
N5R8	nerve 5, root 8	PLTr	posterior lateral trachea
N5R8.a	anterior bundle of nerve 5, root 8	pl.RT	posterolateral limb of ring tract
N5R8.am	medial branches of anterior bundle of nerve 5, root 8	pl.VCI	posterior lateral limb of ventral commissure I
N5R8.apm	posteromedial branches of anterior bundle of nerve 5, root 8	PM	posteromedial
N5R8.p	posterior bundle of nerve 5, root 8	PMTr	posterior median trachea
N5R9	nerve 5, root 9	PN	perineurium
N5R10	nerve 5, root 10	PV1	posterior ventral cell body group 1
N5R10.a	anterior branches of nerve 5, root 10	PV1.fb	fibre bundle of posterior ventral cell body group 1
N5R10.m	medial branches of nerve 5, root 10	PV2	posterior ventral cell body group 2
N5R11	nerve 5, root 11	PV3	posterior ventral cell body group 3
N5VB	ventral band of fibres of nerve 5 (giving rise to roots 8 to 11)	PV3.fbs	fibre bundles of posterior ventral cell body group 3
N6	nerve 6	PVC	posterior ventral commissure
N6DR1	nerve 6, dorsal root 1	PVL1	posterior ventrolateral cell body group 1
N6DR2	nerve 6, dorsal root 2	PVL2	posterior ventrolateral cell body group 2
N6DR2.a	anterior fibres of nerve 6, dorsal root 2	PVM	posterior ventral median cell body group
N6DR3	nerve 6, dorsal root 3	PVTr	posterior ventral trachea
N6VR	nerve 6, ventral root	RT	ring tract
N7	nerve 7	SMC	supra-median commissure
N7R1	nerve 7, root 1	Th3	metathoracic ganglion
N7R2	nerve 7, root 2	tre	tracheae
N7R2.d	dorsal branches of nerve 7, root 2	TT	T-shaped tract
N7R2.m	main bundle of nerve 7, root 2	V	ventral
N7R2.ma	anterior branches of main bundle of nerve 7, root 2	VAC	ventral association centre
N7R2.md	dorsal branches of main bundle of nerve 7, root 2	VAC.Ab1	ventral association centre of first abdominal ganglion
N7R2.mp	posterior branches of main bundle of nerve 7, root 2	VCI	ventral commissure I
N7R3	nerve 7, root 3	VCLII	ventral commissural loop II
N8	nerve 8	VIT	ventral intermediate tract
N8R1	nerve 8, root 1	VL	ventrolateral
NL	neural lamella	VLT	ventral lateral tract
o.GL	outer glial cell layer	VMC	ventral midline cleft
o.LVT	outer lateral ventral tract	VMT	ventral median tract
P	posterior	VT	ventral tract
PC	posterior interganglionic connective	v.VAC	ventralmost region of ventral association centre
PD	posterodorsal	v.VCLII	ventral part of ventral commissural loop II
PDM	posterior dorsal median cell body group		

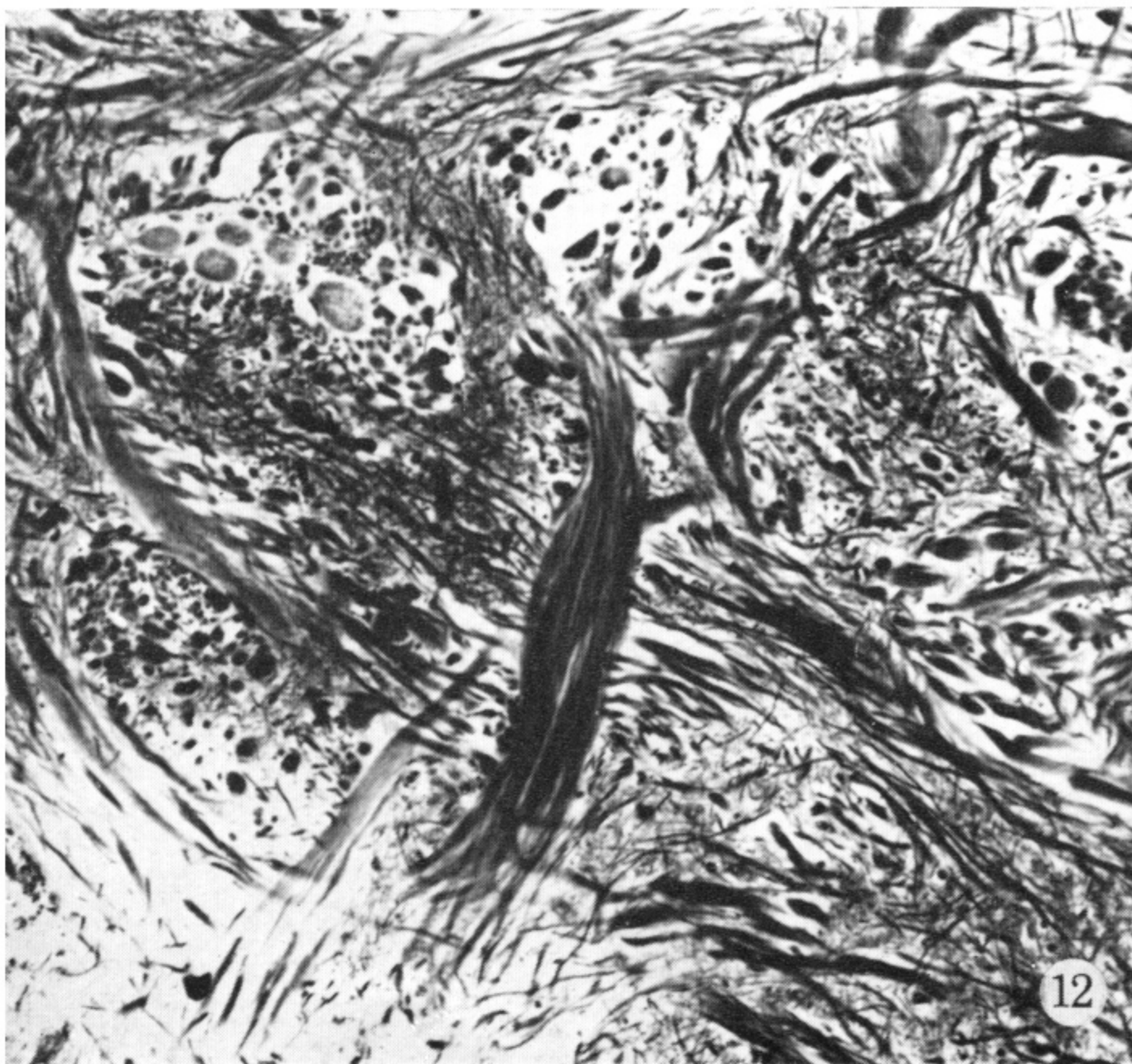
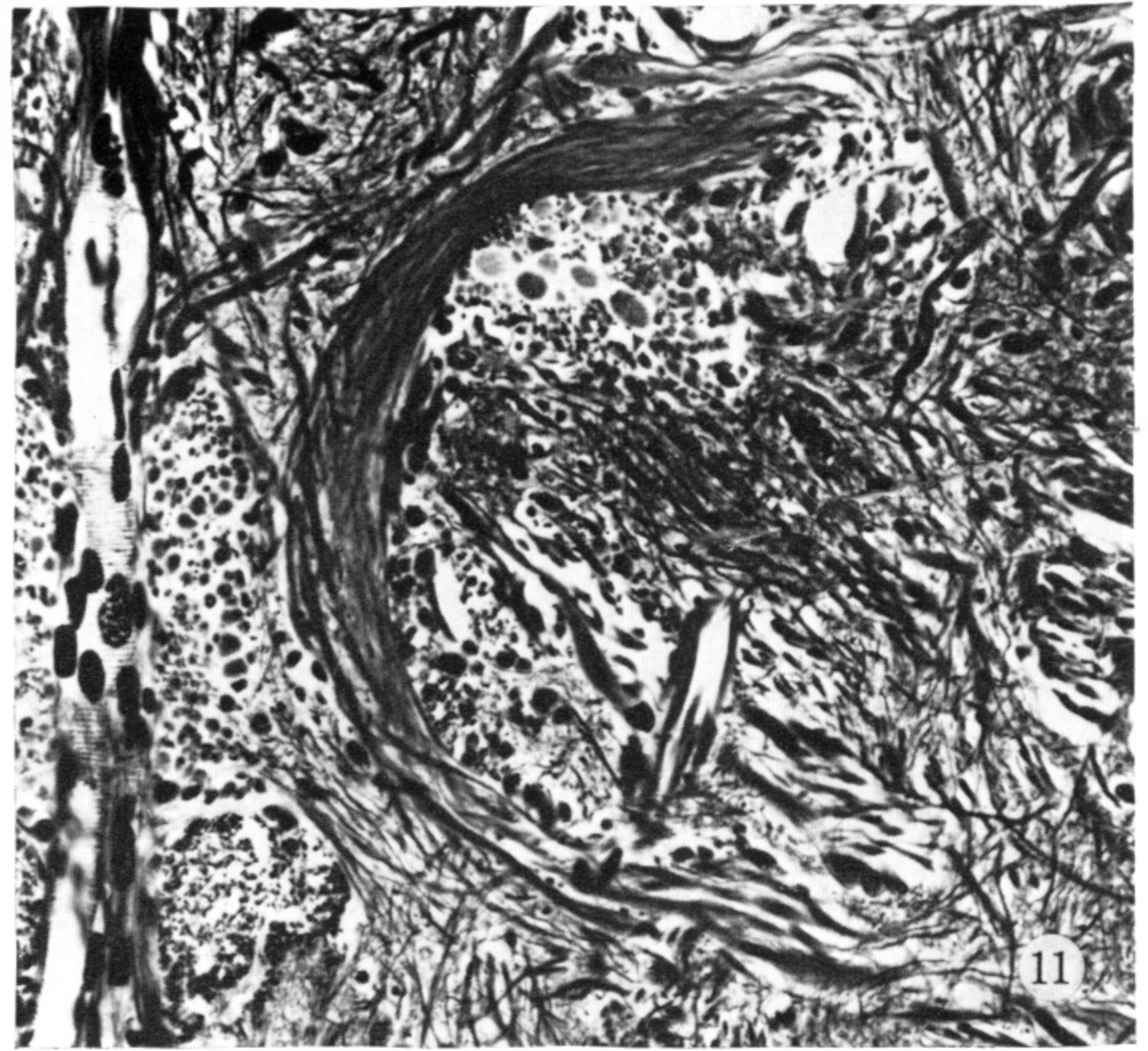
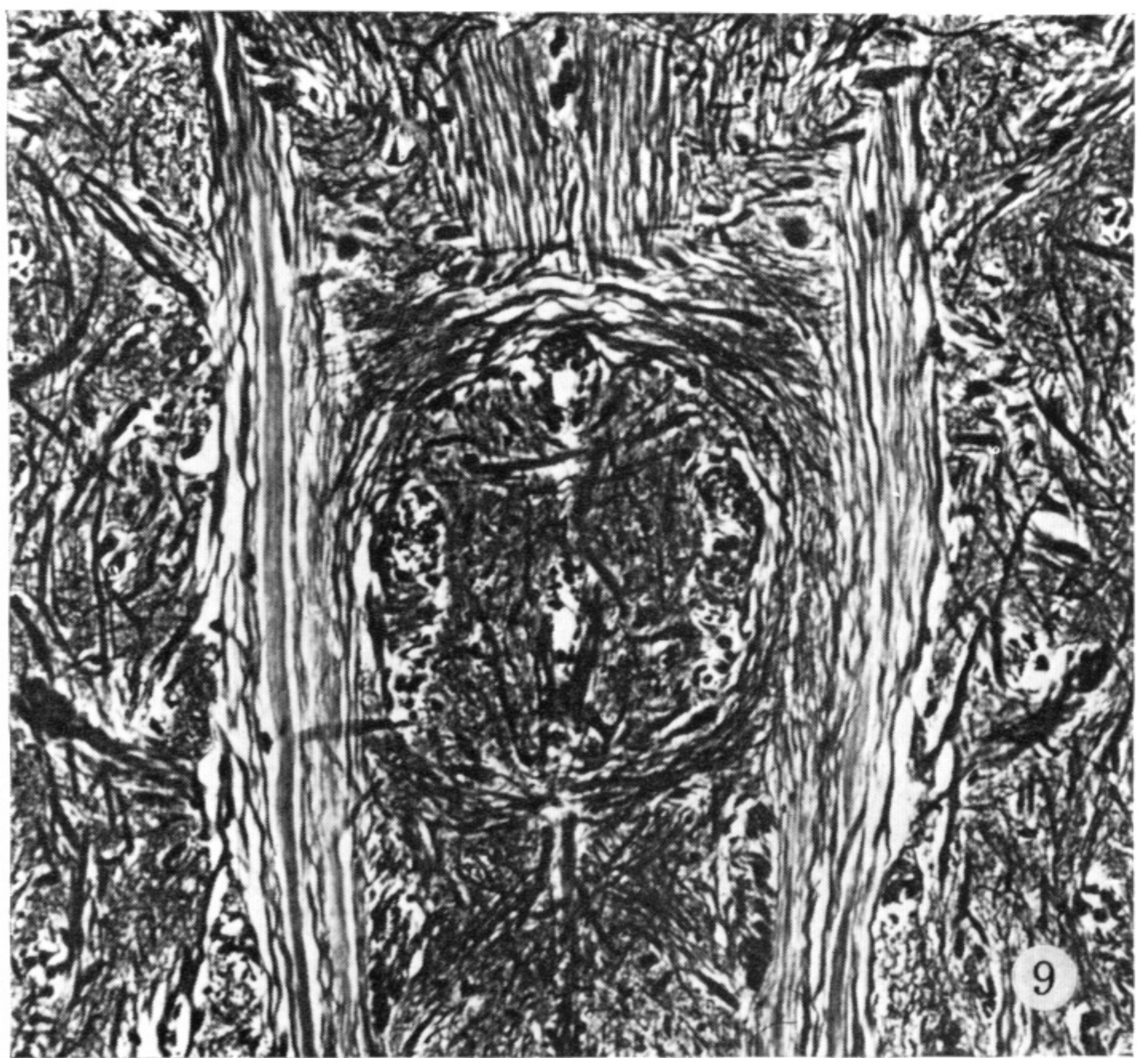
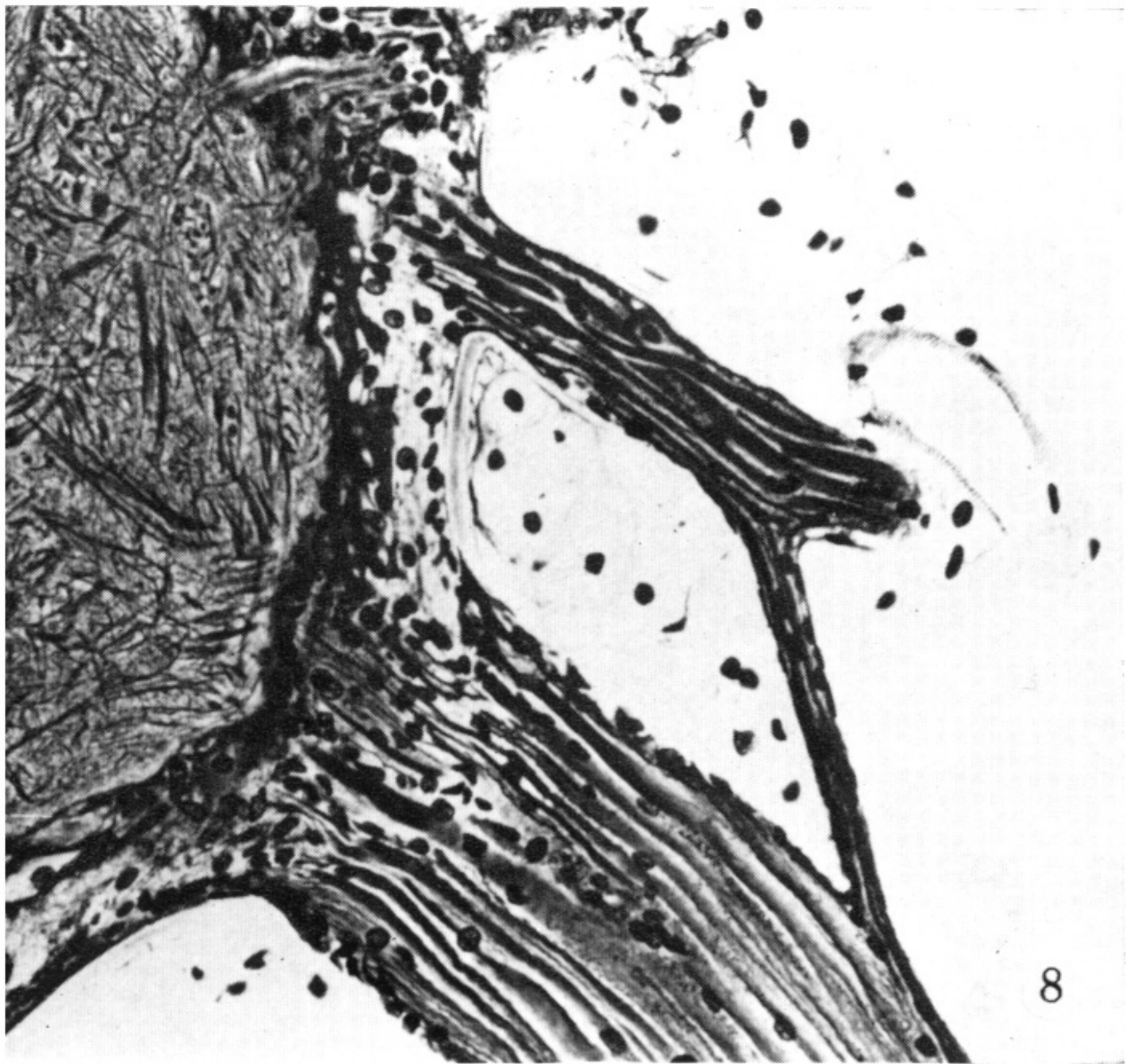


FIGURES 6 AND 7. For description see opposite.

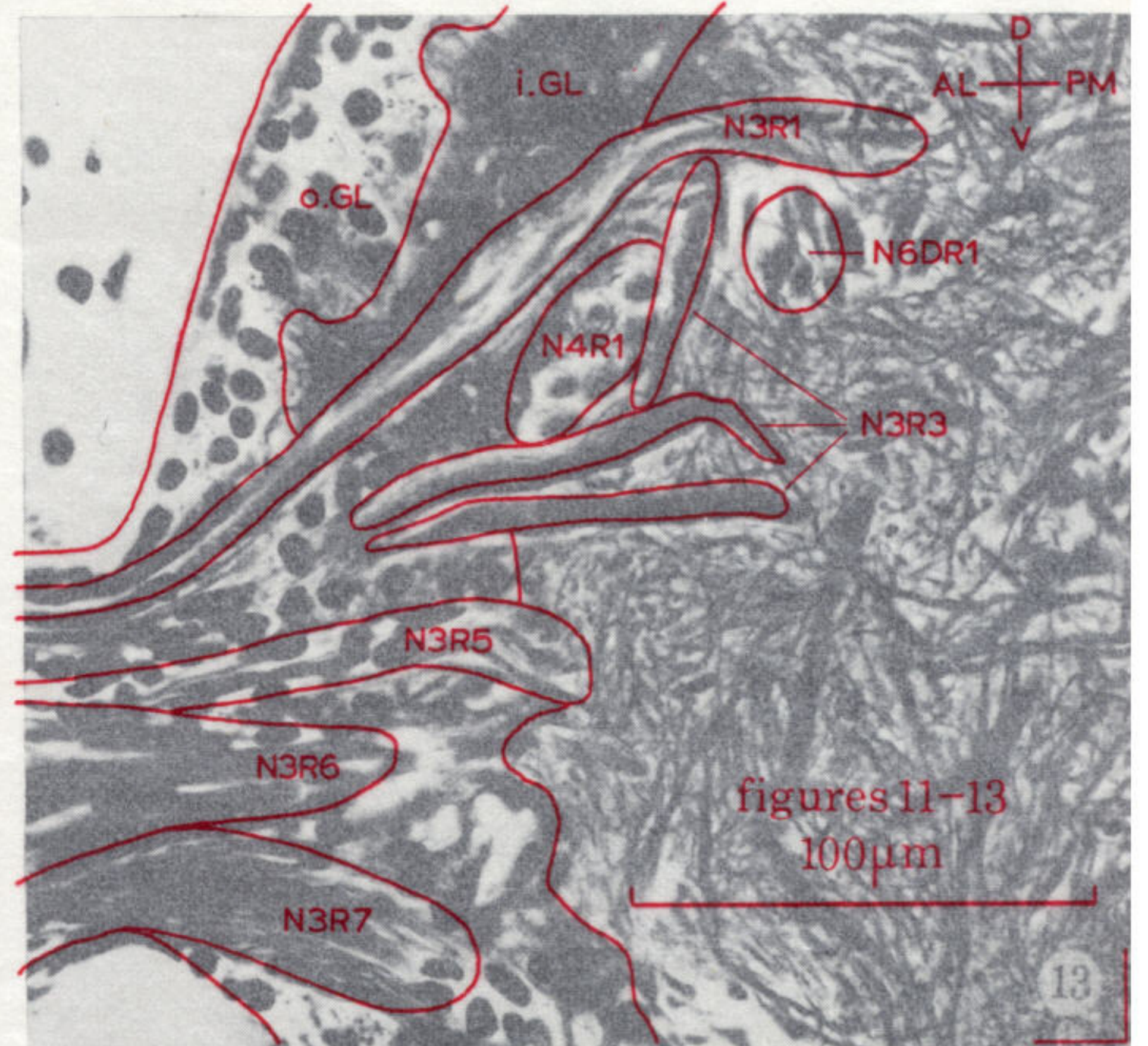
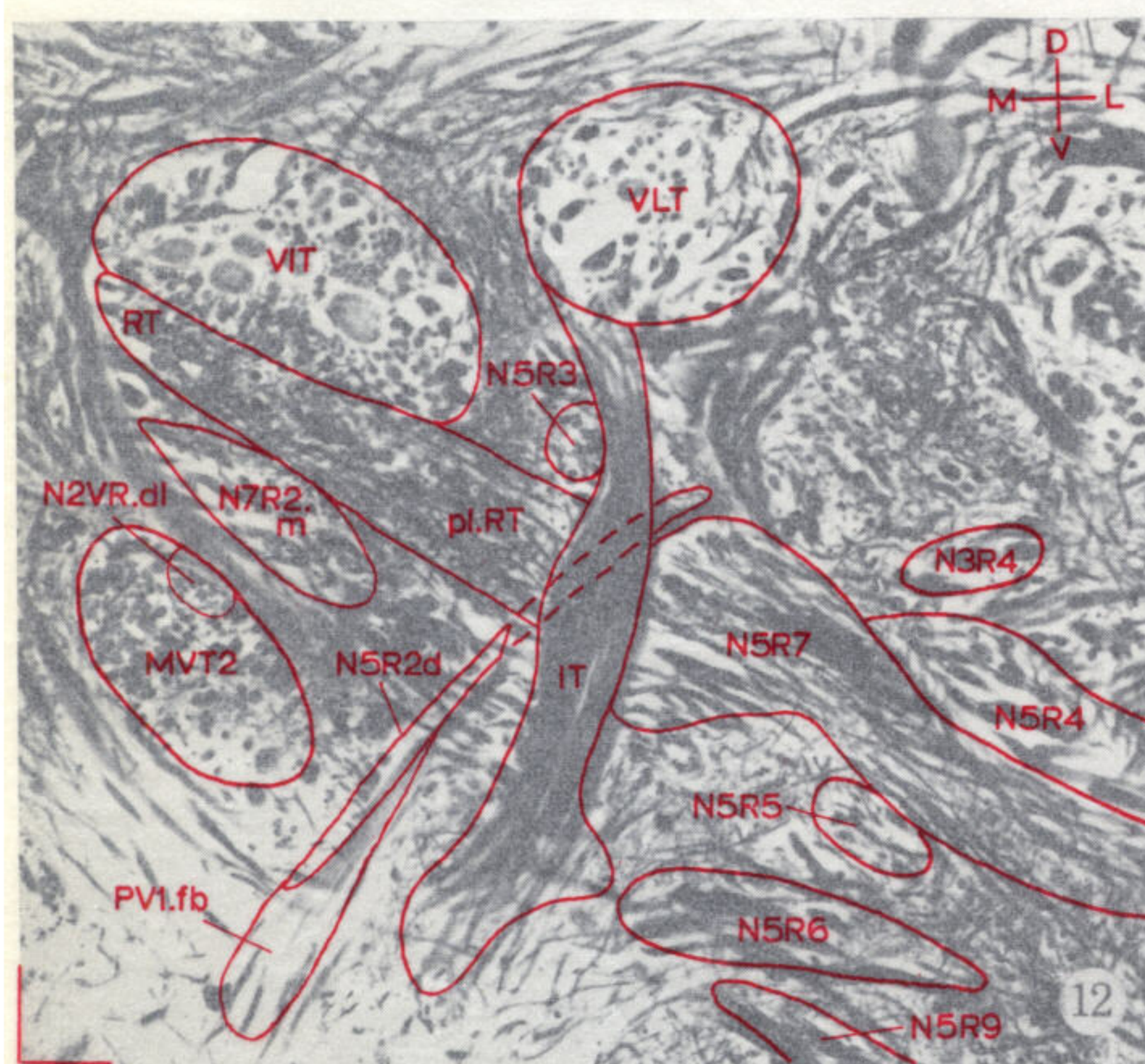
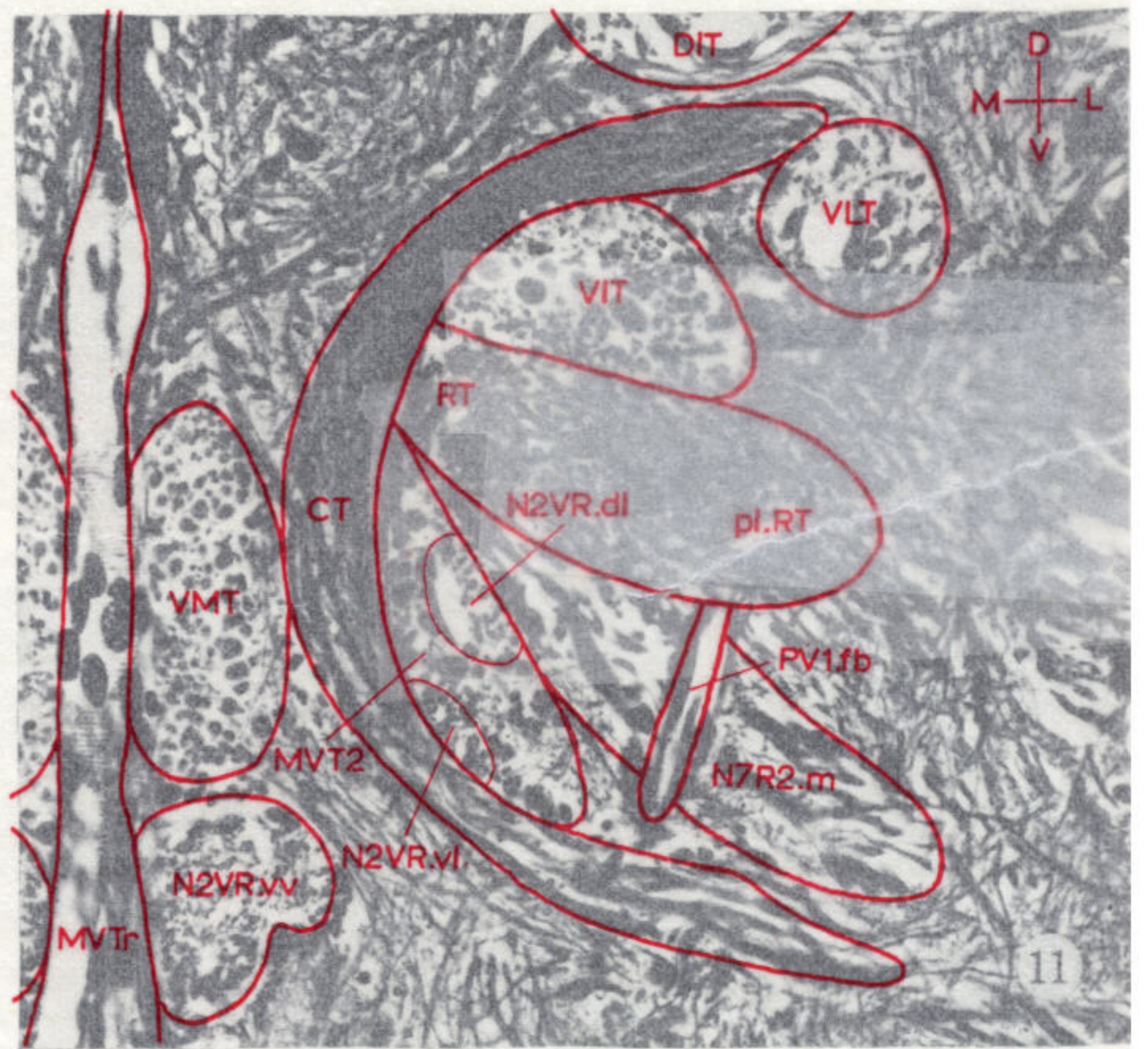
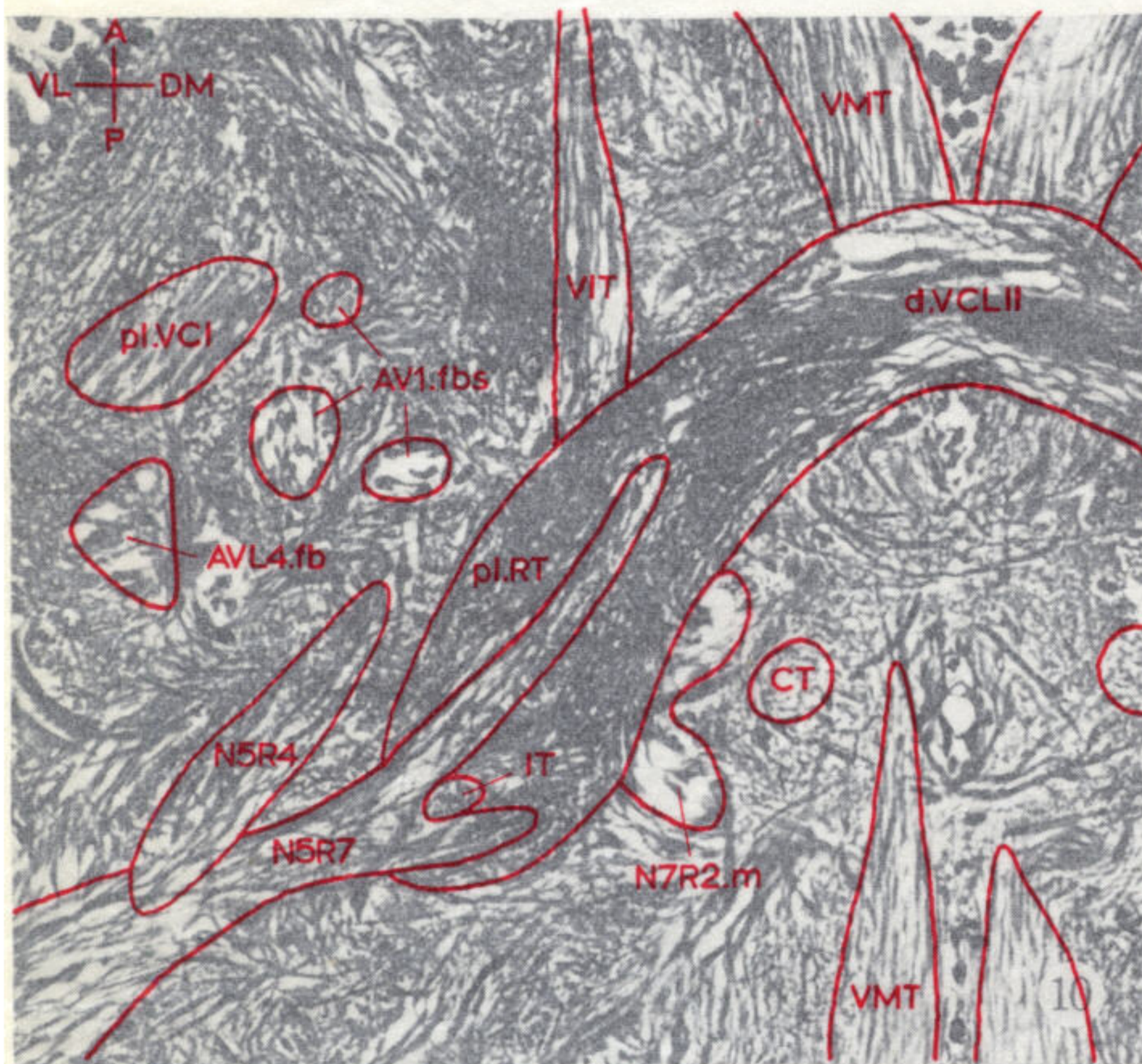
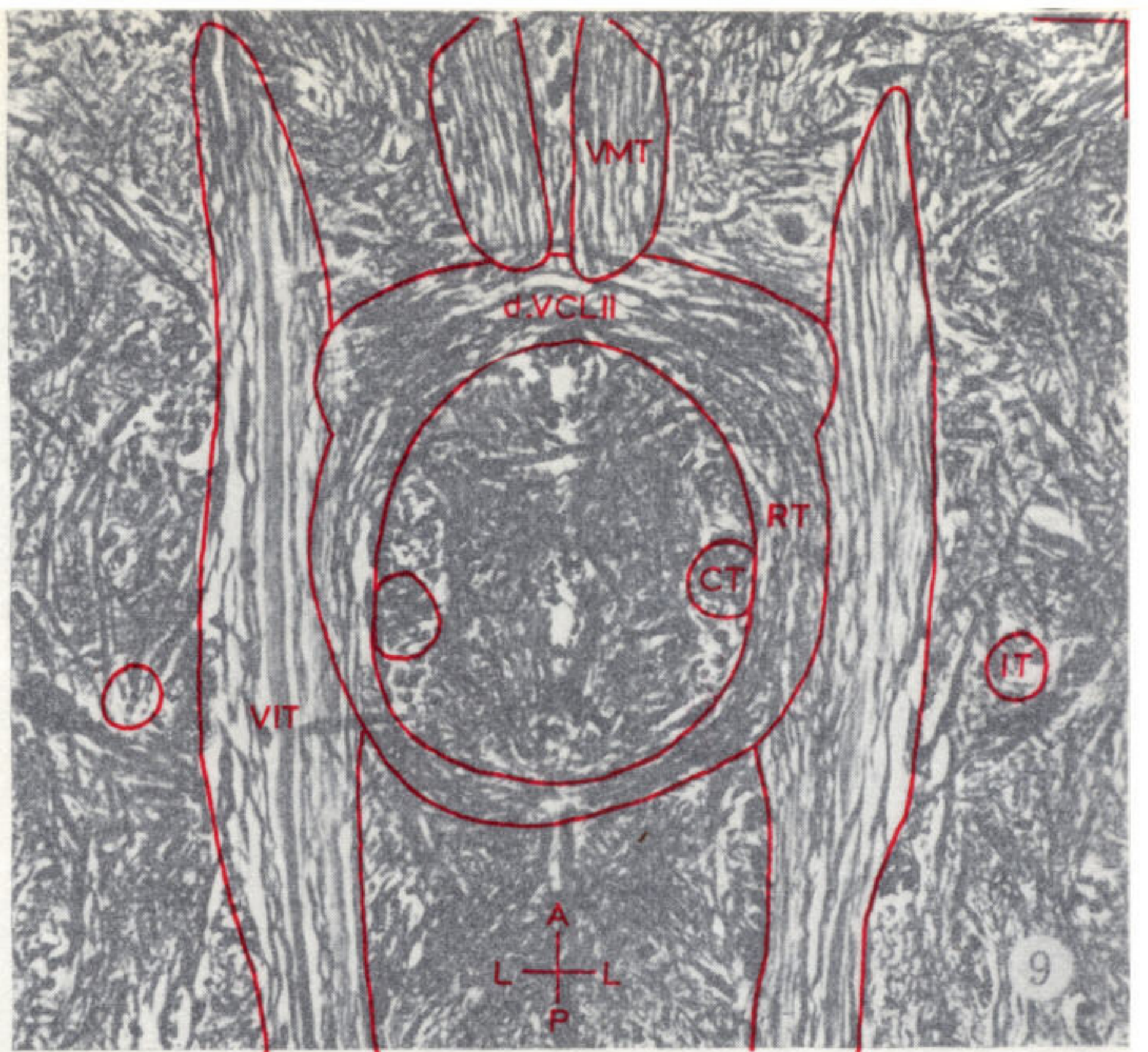
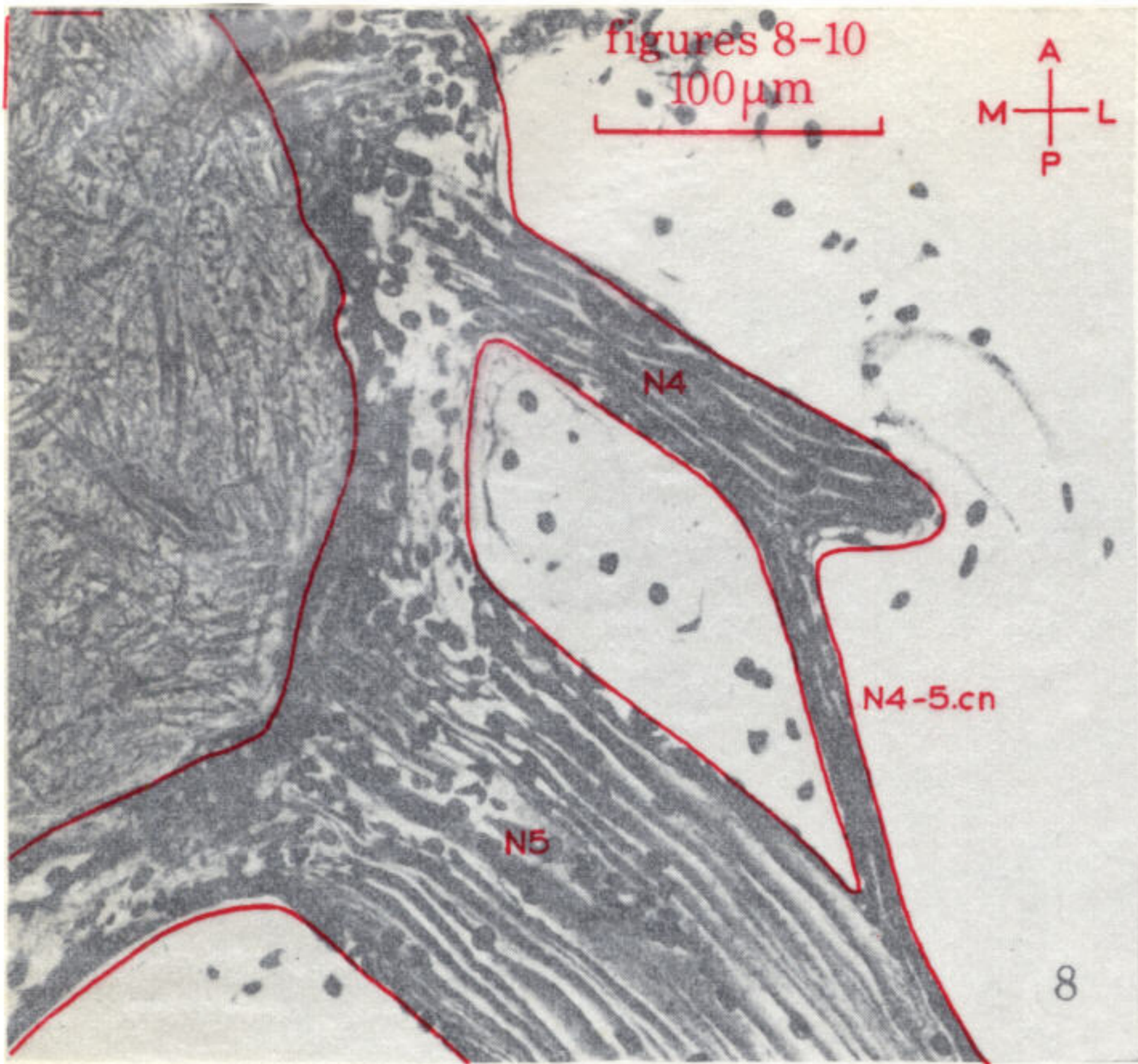
(Facing p. 430)



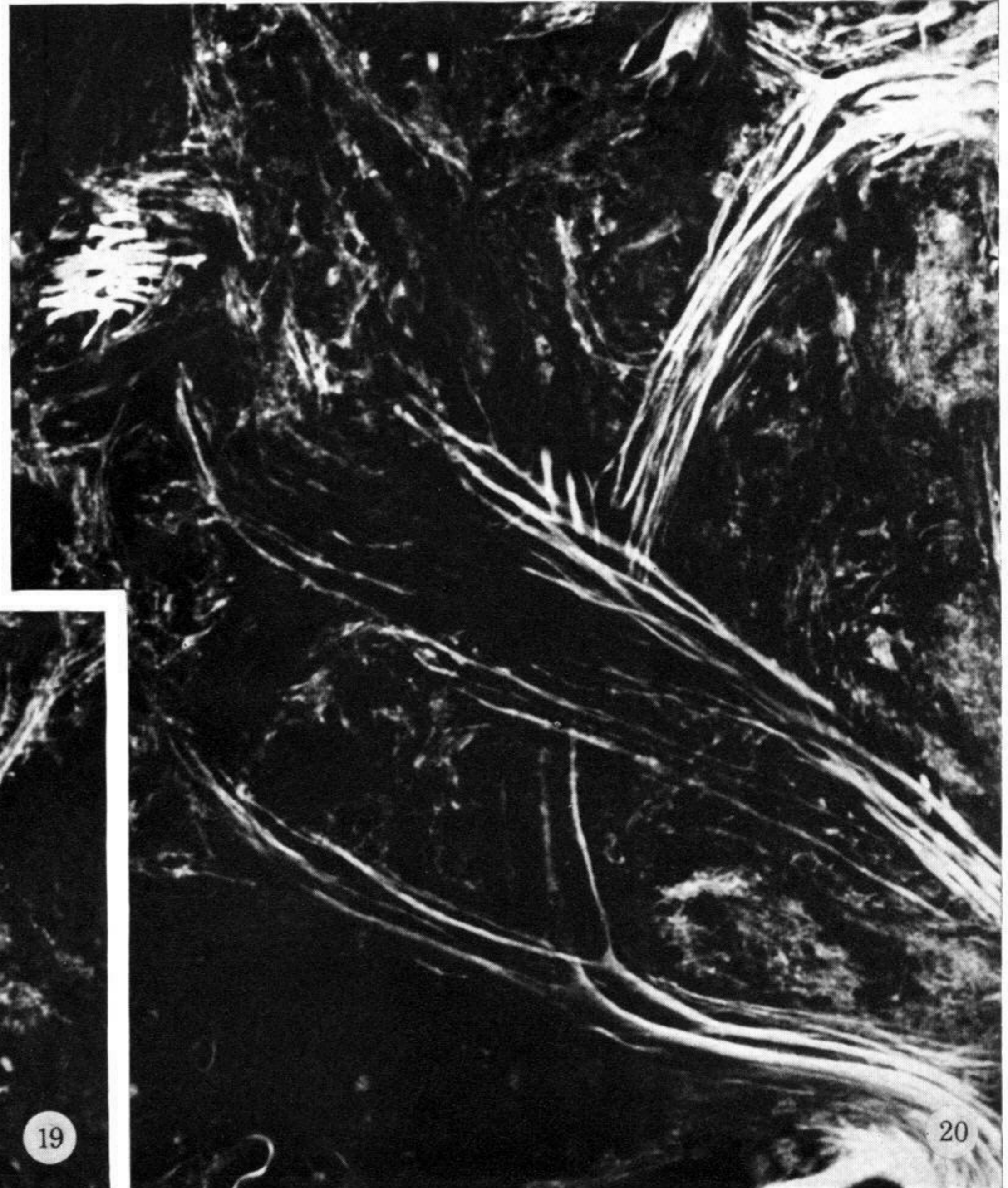
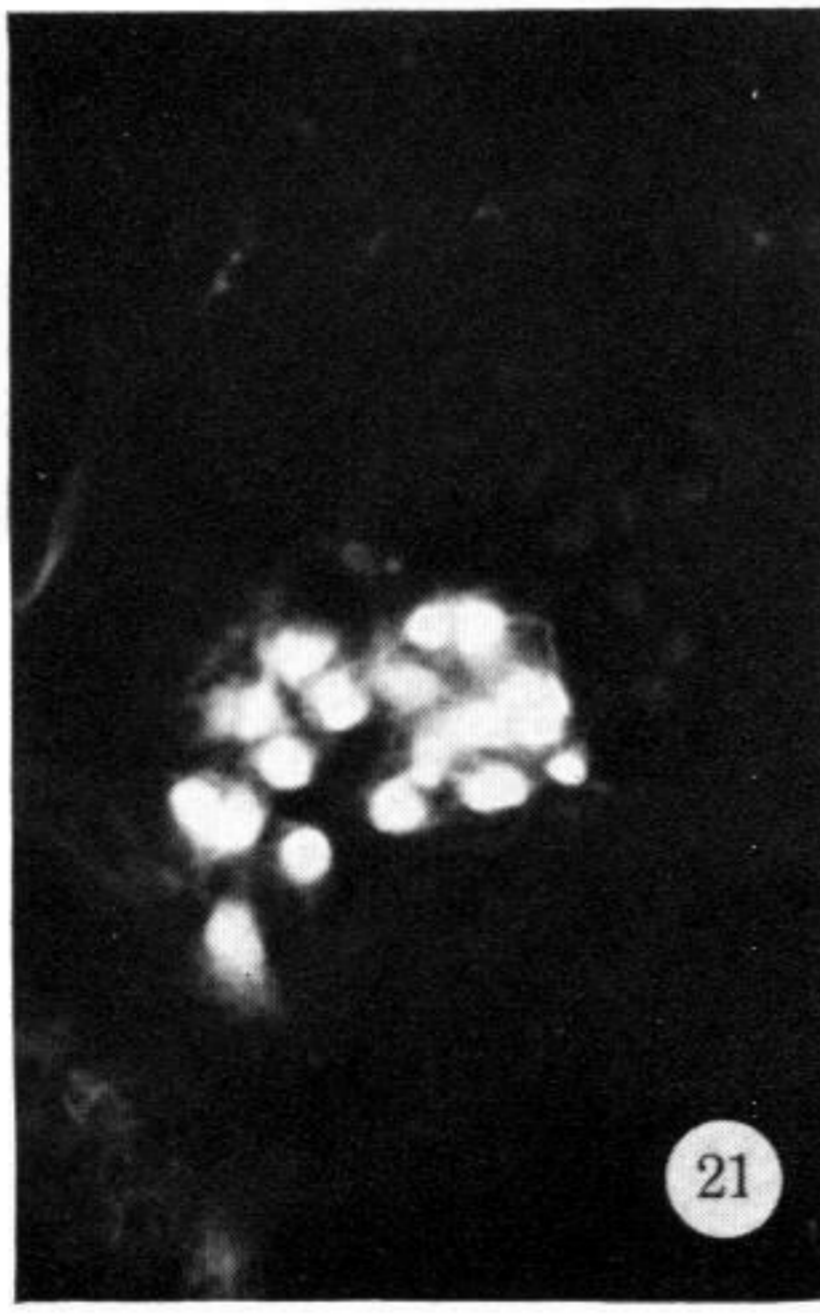
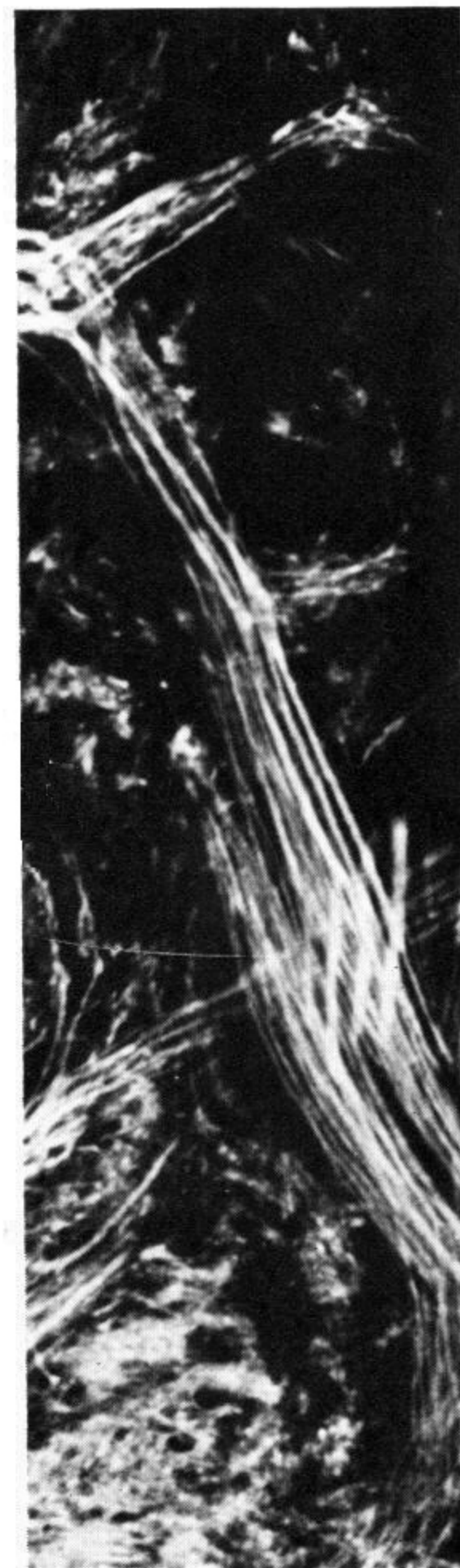
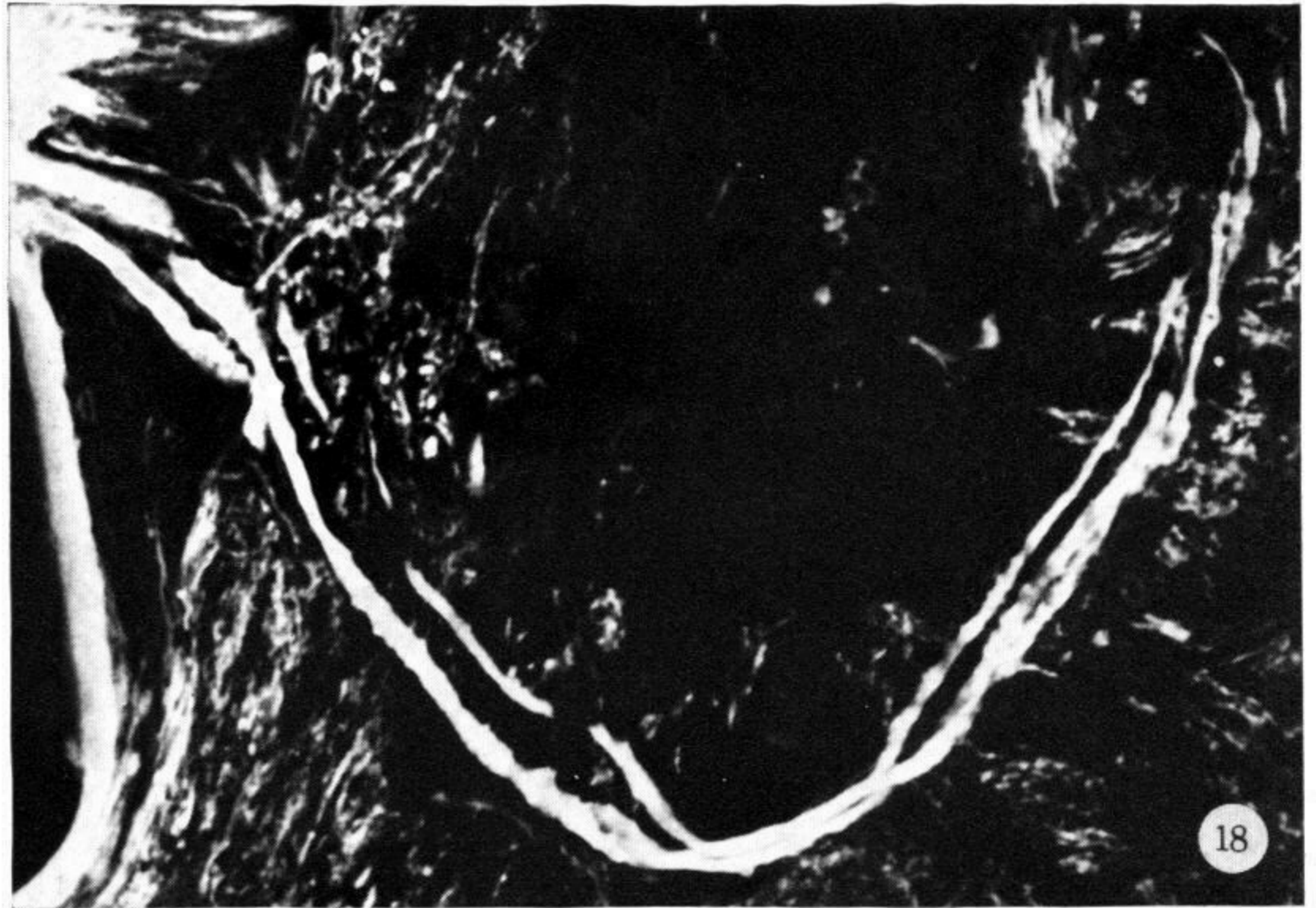
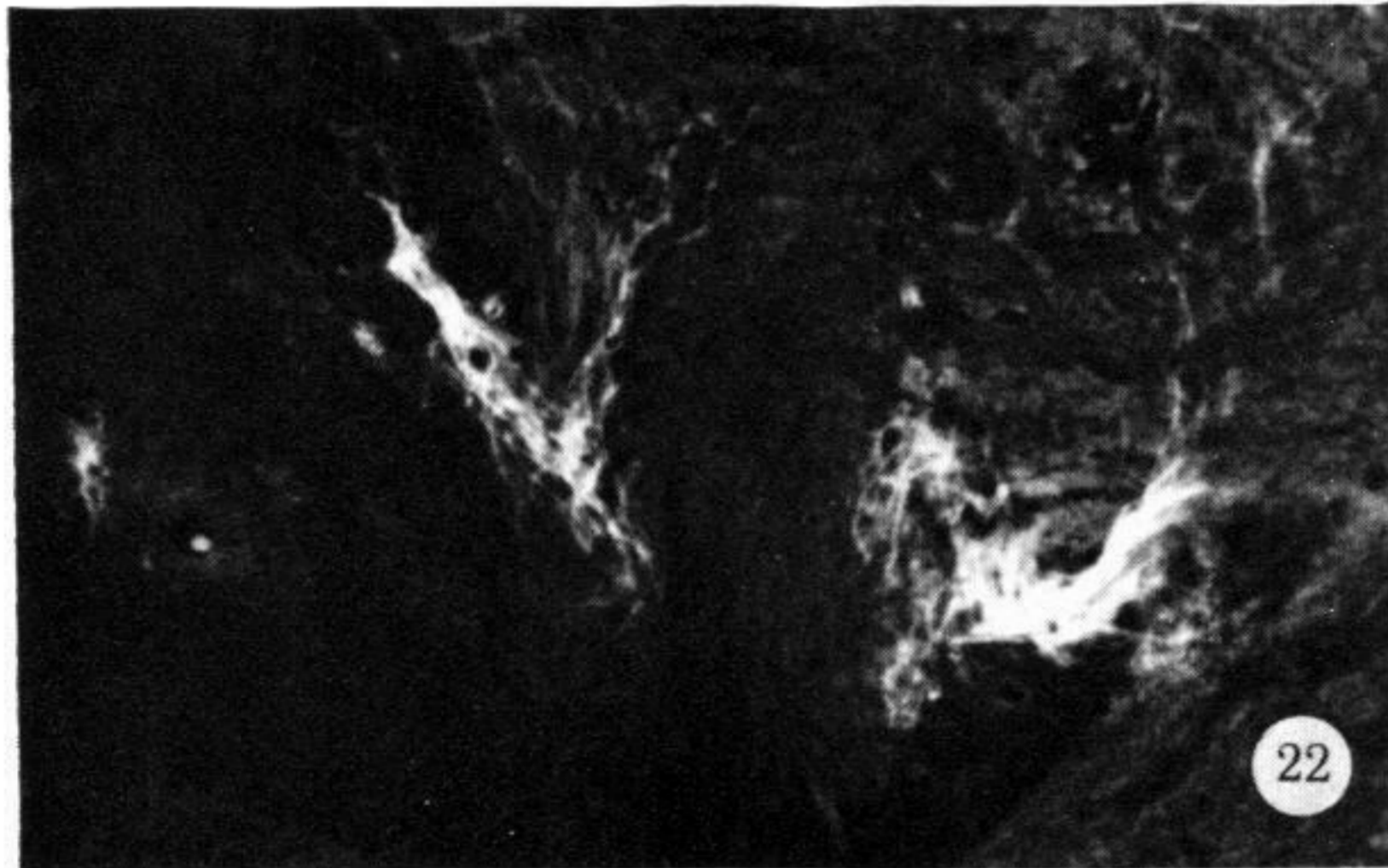
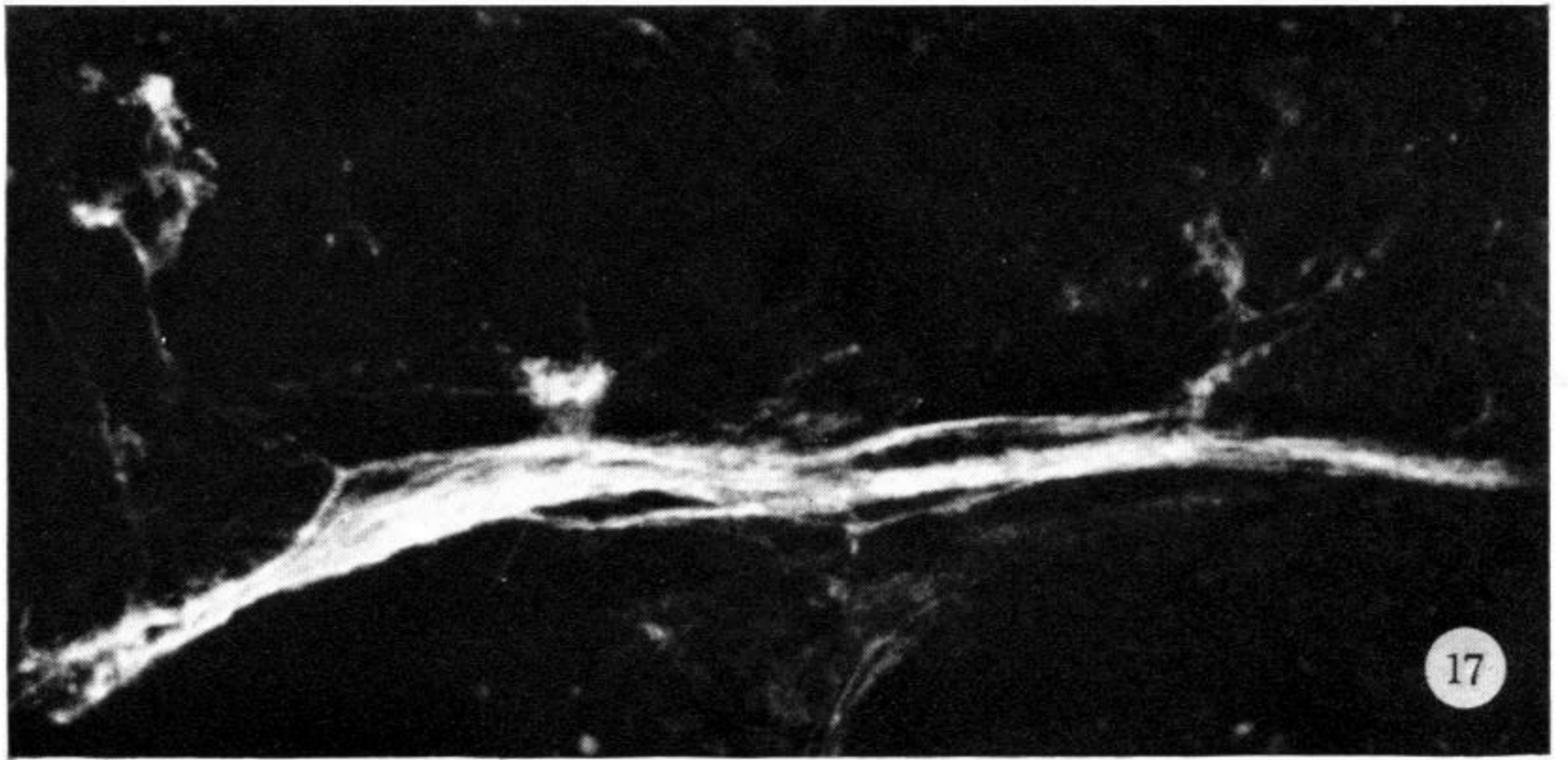
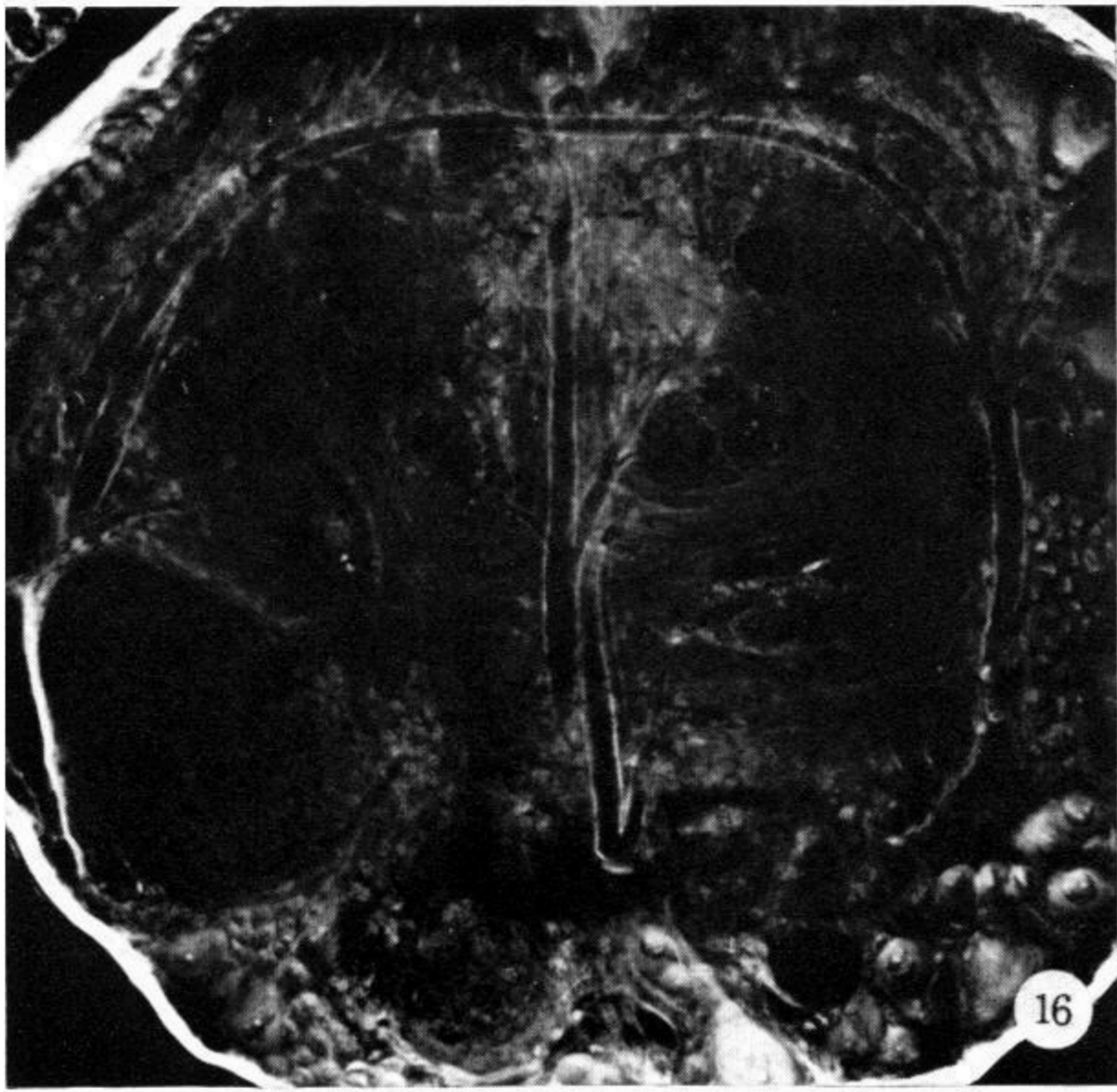
FIGURES 6 AND 7. Overlay.



FIGURES 8-13. For description see opposite.



FIGURES 8-13. Overlay.



FIGURES 16-22. For description see opposite.