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THE ORGANIZATION OF MECHANOSENSORY NEUROPILES IN LOCUST THORACIC GANGLIA

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[Plates 1–12]

CONTENTS

This paper describes the neuropilar areas of the thoracic ganglia of locusts (*Locusta migratoria*) in which projections from mechanoreceptors terminate.

Reference transverse, sagittal and parasagittal sections through a meso- and metathoracic ganglion illustrate the relation of these neuropiles to known structures such as longitudinal tracts and commissures.

The ventral association centres (VAC), divided into anterior (aVAC), medial (mVAC), ventralmost (vVAC) and lateral (lVAC) parts, receive terminals from

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tactile hairs (H; aVAC, vVAC and lVAC) and chordotonal organs (CO; mVAC). Newly defined neuropilar areas are the lateral association centres (LAC) which are divided into an anterior (aLAC) and posterior part (pLAC). These receive projections from hair plates (HP), campaniform sensilla (CS), multipolar sensory cells (MS), strand receptors (SR) and chordotonal organs (CO). In contrast to the VACs they also contain fibres of motorneurons.

Introduction

Locust thoracic ganglia are one of the most thoroughly studied parts of arthropod central nervous systems. The structures of identified neurons have been studied in detail by staining them either intracellularly or by backfilling using various dyes, in particular cobalt salts (Pitman *et al.* 1972) with subsequent silver intensification (Tyrer & Bell 1974; Bacon & Altman 1977). The first achievements of these techniques were 'neuronal maps' of thoracic ganglia showing the locations of cell bodies of many identified motorneurons (Bentley 1970; Burrows & Hoyle 1973; Tyrer & Altman 1974; Wilson 1979) and interneurons (Burrows & Siegler 1984; Siegler & Burrows 1979, 1984; Wilson 1981; Wilson & Phillips 1982).

Backfilling the cut dendrites or axons of sensory neurons (axonal diffusion technique) has revealed the central projections of sensory receptors within thoracic ganglia: wing stretch receptor (Burrows 1975; Altman & Tyrer 1977*a*, *b*), multipolar sensilla and strand receptors of the legs (Bräunig & Hustert 1980; Bräunig 1982*a*, *b*), wing tegula (Kien & Altman 1979; Bräunig *et al.* 1983), hairs and hair plates (Hustert 1978; Pflüger 1980; Pflüger *et al.* 1981; Johnson & Murphey 1985), cervical hair plate (Kien 1980), windsensitive head hairs (Tyrer *et al.* 1979), campaniform sensilla (Hustert 1978; Hustert *et al.* 1981), chordotonal organs (Hustert 1978; Bräunig *et al.* 1981; Burrows 1987), subgenual organ (Grosch *et al.* 1985) and tympanal organ (Rehbein 1973; Rehbein *et al.* 1974; Eibl & Huber 1979; Ball & Field 1981; Oldfield 1983; Römer 1983, 1985; Römer & Marquart 1984; Miller 1983; Wohlers & Huber 1985).

For a precise description of specific features of a neuron, its structure has to be described in relation to the architectural framework of the ganglion. For that reason Tyrer & Gregory (1982) developed a useful anatomical guide for the locust thoracic nervous system which is based on the anatomical studies of the cockroach nervous system by Pipa *et al.* (1959) and Gregory (1974). Since its publication this guide has been widely used and neurons can now be described in relation to commissures and prominent longitudinal tracts which coalesce to form the connectives (Tyrer 1983; Burrows & Siegler 1984; Siegler & Burrows 1984; Watson & Burrows 1982, 1983; Watson *et al.* 1985; Watkins *et al.* 1985; Pflüger *et al.* 1986). A further conspicuous structural feature in sections of ganglia is the unstructured, 'amorphous' neuropiles formed by areas of densely packed small diameter fibres. The density of fibres in these neuropiles is greater than anywhere else in the ganglia and staining methods using osmium as a lipophilic agent show them as dark areas (Wigglesworth 1957, 1959; Wohlers & Huber 1985).

The ventral neuropiles are thought to be predominantly sensory (Binet 1894; Zawarzin 1924; Pipa *et al.* 1959; Gregory 1974; Altman 1980; Pflüger *et al.* 1981; Johnson & Murphey 1985) whereas the dorsal neuropiles contain a mixture of mechanosensory, motor, interneuronal and neurosecretory fibres (Tyrer & Altman 1974; Altman & Tyrer 1977*a*; Altman 1980; Watson 1984).

This paper attempts to show the extent to which different sensory modalities project to specific areas of neuropile. It is an extension of the anatomical guides published by Pipa *et al.* (1959), Gregory (1974, 1985) and Tyrer & Gregory (1982). Central projections of tactile hairs (H, 'bristles', Johnson & Murphey (1985)), hair plates (HP), campaniform sensilla (CS), chordotonal organs (CO), multipolar sensory cells (MS) and strand receptors (SR) are described. In representative cross sections the neuropilar areas in which their afferents terminate are shown and their branching patterns are described in relation to ganglionic landmarks.

Materials and methods

In locusts (*Locusta migratoria*) of either sex, specific populations of thoracic mechanoreceptors were stained by backfilling their axons with solutions of cobalt chloride (15–60 g l^{-1}) ($CoCl_2$ or $Co(NH_4)_6Cl_2$, hexaminecobaltic chloride). The procedures for staining particular receptor projections can be found in Bräunig *et al.* (1981), Pflüger *et al.* (1981), Hustert (1978) and Hustert *et al.* (1981). After backfilling, the thoracic ganglia were dissected, cobalt ions precipitated as cobalt sulphide with ammonium sulphide (1 % by volume), $(NH_4)_2S$, and fixed in alcoholic Bouin or neutral formaldehyde (4 % by volume) (10 g $CaCl_2$ and $CaCO_3$ powder to saturation added to 1 l solution). Wholemounts were silver intensified (Bacon & Altman 1977), dehydrated, and cleared in methyl salicylate. Central projections of sensory fibres were drawn with the aid of a drawing tube attached to a Leitz microscope. Subsequently, specimens were embedded in soft Durcupan (Fluka-Chemie) and serially sectioned (10–20 μm).

To gain further insight into the distribution of tracts, commissures and neuropiles, meso- and metathoracic ganglia were stained by using the osmium and ethyl-gallate procedure of Wigglesworth (1957, 1959). Ganglia were prefixed in glutaraldehyde (2.5 % by volume) in phosphate buffer (pH 7.2) for 3 h and then fixed in OsO_4 (1 % by volume) in phosphate buffer for 2 h at 4 °C. Then ganglia were transferred to a saturated ethyl gallate solution for 2–3 h, dehydrated and embedded in soft Durcupan and later serially sectioned (16 μm). All sections were drawn and photographed with a Zeiss photo microscope.

A complete list of all abbreviations used in the text and figures is given at the end of this paper (see also Tyrer & Gregory 1982; Siegler & Burrows 1984).

Results

Description of principal neuropiles

Ventral neuropiles have clearly defined borders already recognized by early anatomists. Binet (1894) described the ventral regions of a ganglion of a beetle as 'sensory association centres'. Corresponding regions of neuropile have been described as 'darkly stained' serving as 'synaptic regions' in *Rhodnius* (Wigglesworth 1959) and as 'sensory neuropiles' in various insect species (Plotnikova 1979). We shall use the term 'ventral association centre' for this most conspicuous ventral neuropile, a term introduced by Pipa *et al.* (1959) for the description of cockroach ganglia and later adopted for locust ganglia (Tyrer & Gregory 1982). We shall also introduce several new names for neuropile regions, as a logical extension of the existing terminology. This is necessary for understanding the descriptions of the projection patterns of sensory afferents. Figures 1 and 2† show selected 16 μm-sections from osmium and ethyl-gallate

† Figures 1–4 appear on plates 1–12.

stained meso- (figure 1*a–m*) and metathoracic ganglia (figure 2*a–k*) to illustrate our terminology. Sections in which prominent features such as neuropiles and commissures can be identified are shown. We recommend the following procedure for identification of structures in transverse sections of these ganglia according to Tyrer & Gregory (1982).

Identification of ganglionic structures

DCI is the most anterior dorsal commissure, which is composed of two bundles of fibres that cross the midline dorsal (dDCI) or ventral (vDCI) to DMT and two bundles of fibres that cross diagonally between the DMTs (figures 1*e, f* and 2*c, d*). DCII is less pronounced as it consists of several smaller parts lying anterior to the midline trachea and to the division of the two neuropilar halves. All its bundles lie between MDT/LDT and DMT/DIT (figures 1*h, i* and 2*e*).

The T-tracts lying anterior of DCII are recognized by their clear features as running posteriorly between aVAC and vVAC (figures 1*e–h* and 2*d–f*) and ascend dorsally in the midline of the ganglion to diverge to the lateral neuropiles. The T-tracts run in front of the large DCIII, which lies between DMT/DIT and VIT. A next landmark is the division of the two halves of the ganglion by the midline trachea, separating DCIII/DCII and DCIV (m.tr., figures 1*i* and 2*g*). At the same level the conspicuous C-tracts emerge ventrally and ascend median to MVT before turning laterally between VIT and DIT. More posteriorly is the bell-shaped DCIV, which splits laterally into a ventral bundle median to VIT, and into a lateral bundle running between DMT/DIT and VIT. DCIV also divides DMT into a dorsal (dDMT) and ventral part (vDMT). Ventral to DCIV and above VMT/MVT is the prominent SMC (figures 1*j* and 2*h, i*). DCV can also be easily identified by its dorsal location between MDT and DMT/DIT, and because the DUM-tract runs through it (figures 1*k, l* and 2*h*). The most posterior dorsal commissure is DCVI, which lies between DMT/DIT and VIT/MVT (figures 1*m* and 2*i*). The ventral commissures, VCI (figures 1*b* and 2*b*) and VCII (figures 1*d* and 2*d*) can be easily found lying rather anteriorly, in contrast to the PVC (figure 1*l*) which is always difficult to identify.

Compared with the mesothoracic ganglion the metathoracic one is distorted by the fusion with the first three abdominal ganglia. In principle, however, the abdominal neuromeres have the same landmarks as those just described. This applies also to the unfused abdominal ganglia (Watson & Pflüger 1987).

The ventral association centre (VAC)

Morphological criteria allow the VAC to be subdivided into anterior, medial, ventral and lateral parts (aVAC, mVAC, vVAC and lVAC).

Both the prominent aVAC (figures 1*c–f* and 2*b–e*) and mVAC (figures 1*e–h* and 2*b–f*)

DESCRIPTION OF PLATE 1

FIGURE 1. (*a*) Ventral view of a mesothoracic ganglion cut into 16 μm transverse sections starting with section 1 (first cell bodies visible) ending with section 53 (last cell bodies visible). Prominent neuropiles, commissures and other structures in the sections are indicated as black bars. Thickness of bars gives a relative measure of the size of the structures in the sections. (*b–m*) Camera lucida drawings (left) and photographs (right) of selected sections of a mesothoracic ganglion stained with osmium and ethyl-gallate. Numbers in brackets refer to section numbers in (*a*). Calibration 100 μm; abbreviations: see List of abbreviations used.

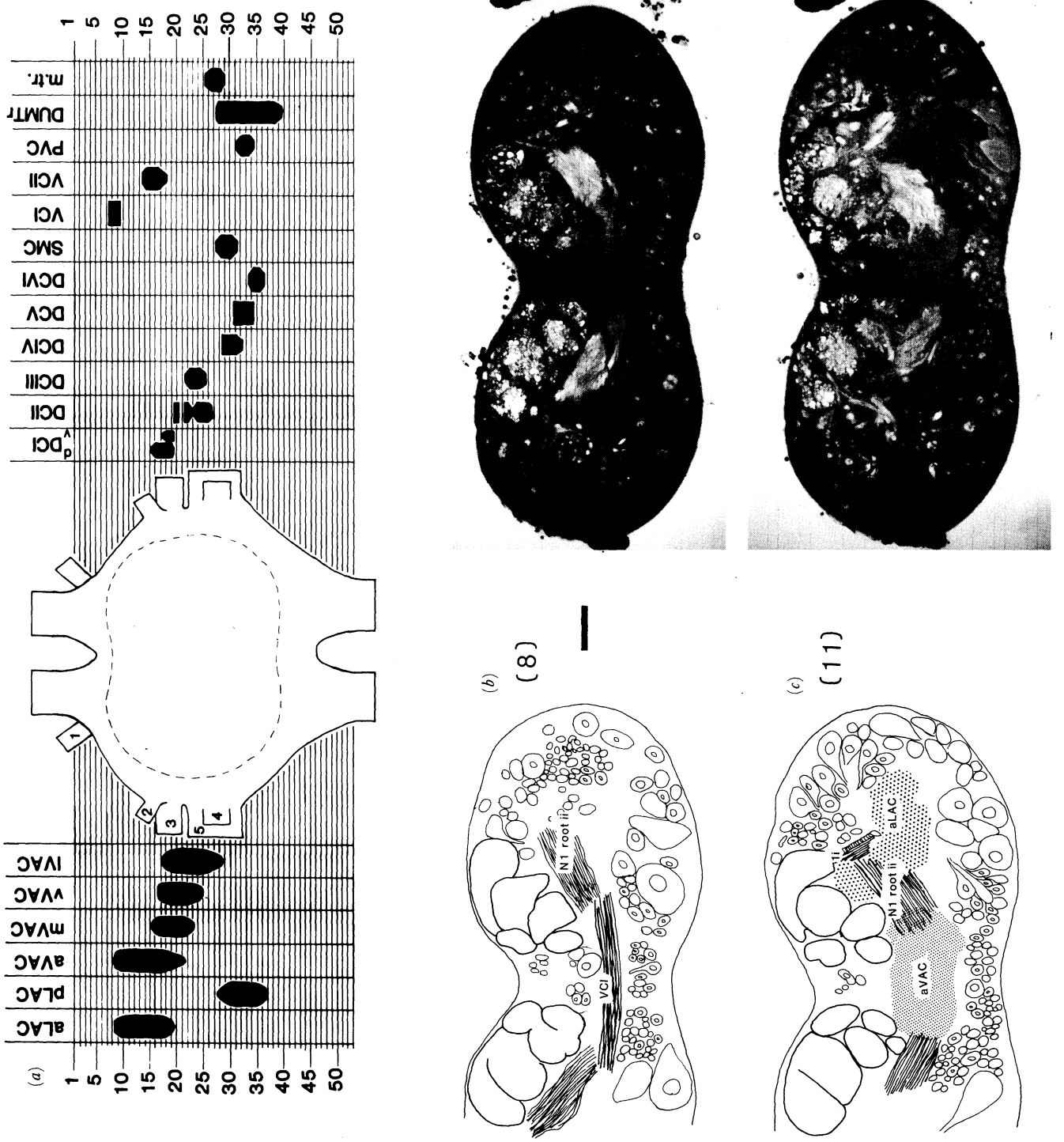


FIGURE 1*a–c*. For description see opposite.

(*Facing p.* 4)

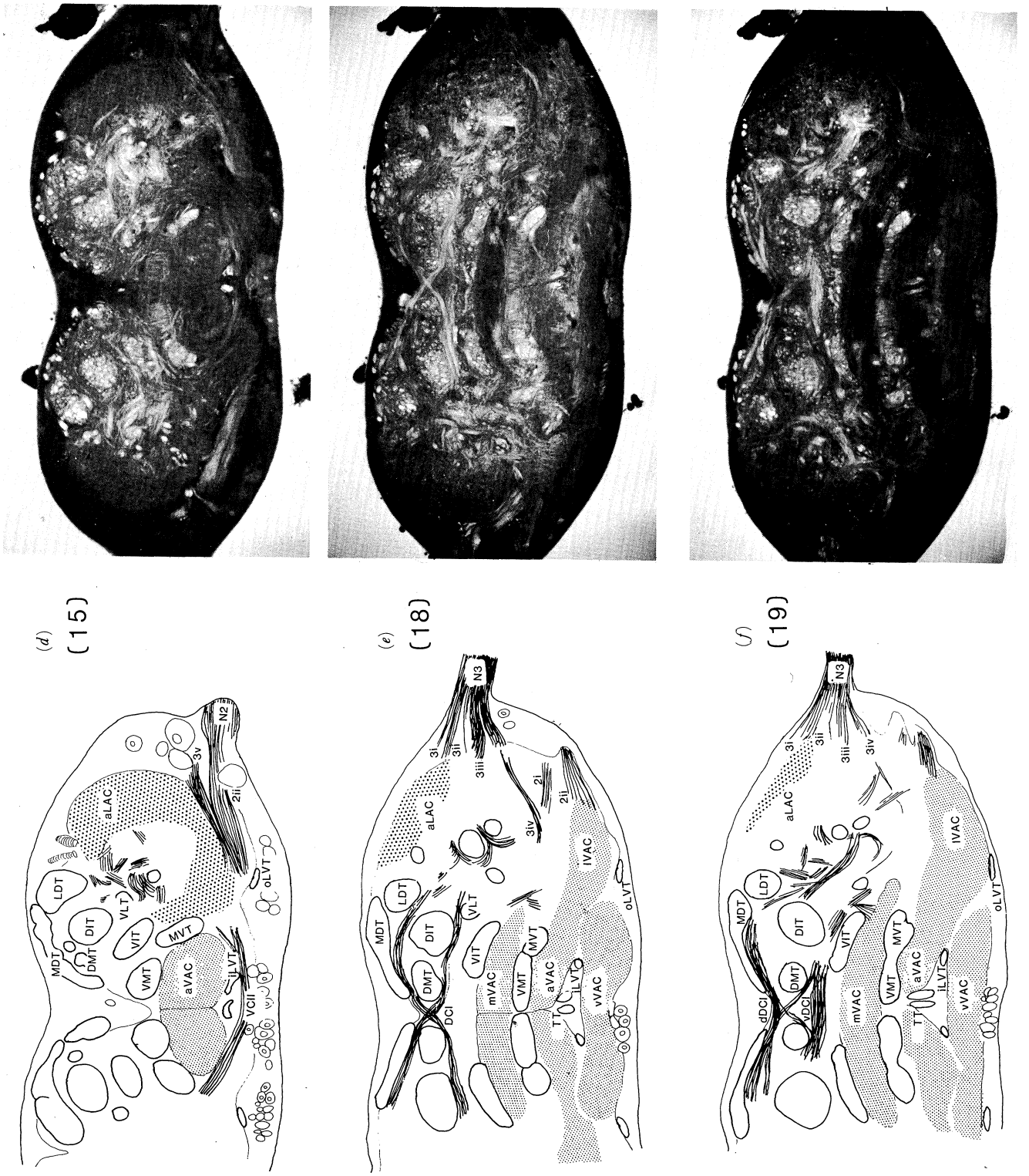


FIGURE 1*d–f*. For description see p. 4.

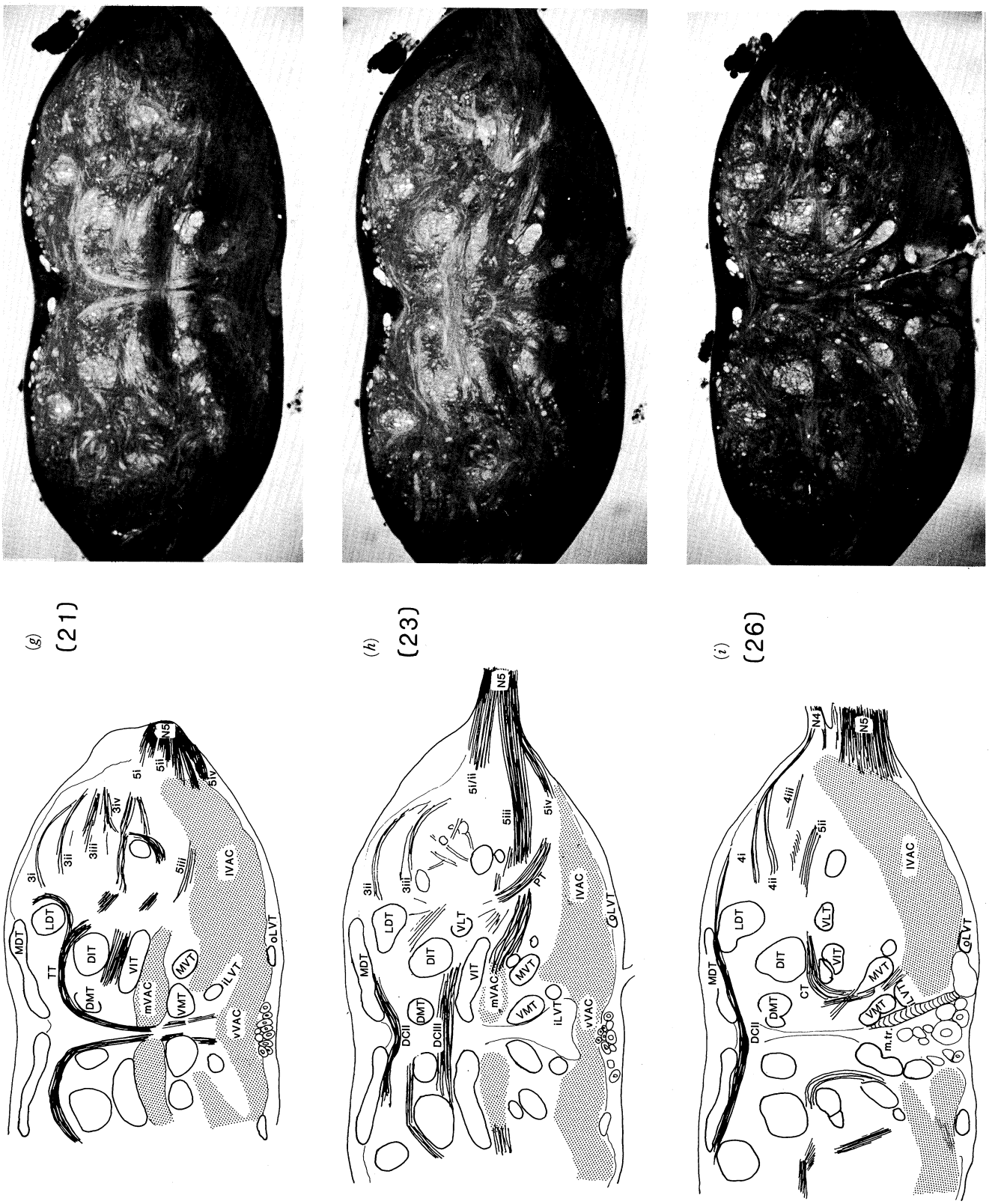


FIGURE 1*g–i*. For description see p. 4.

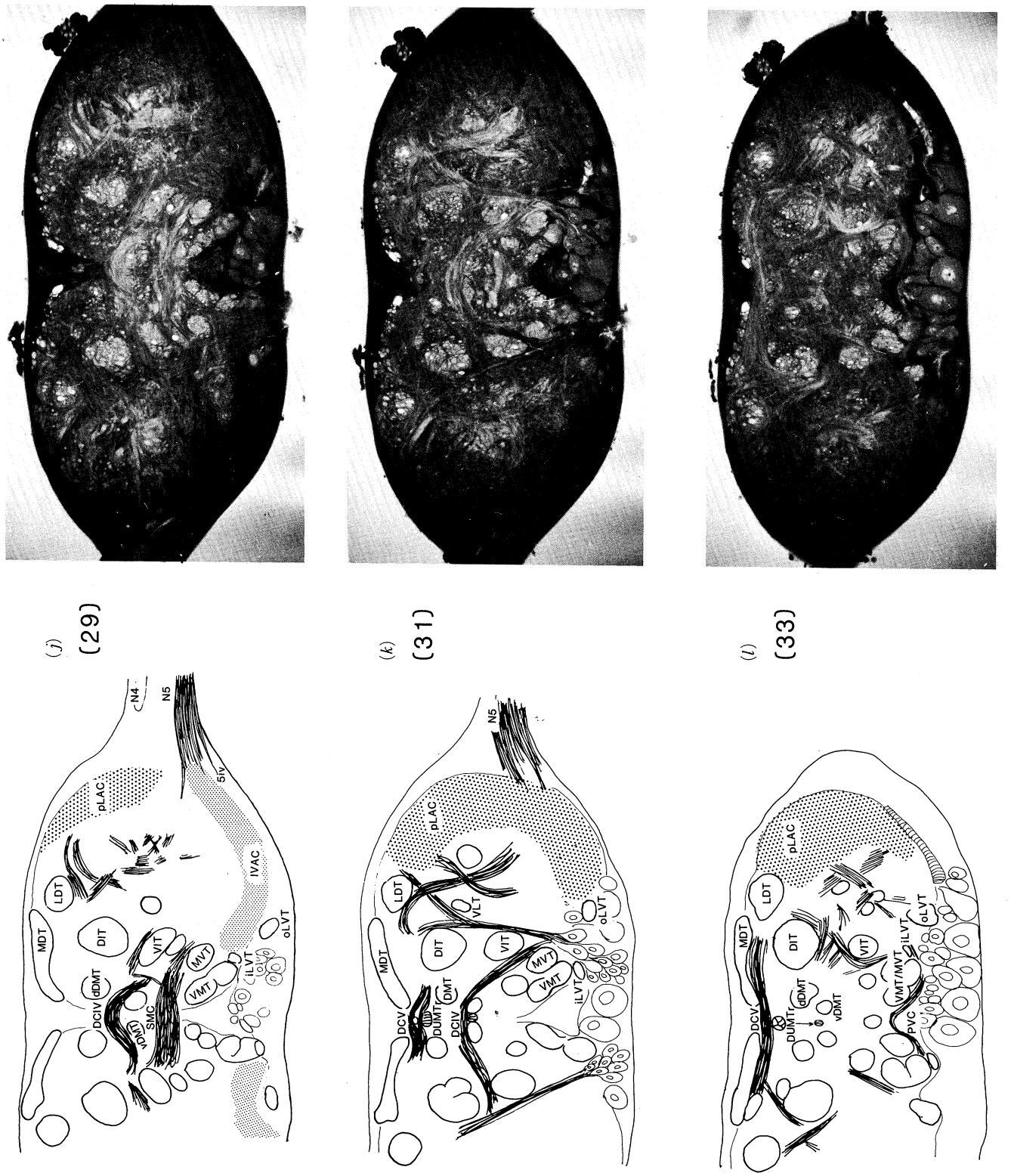
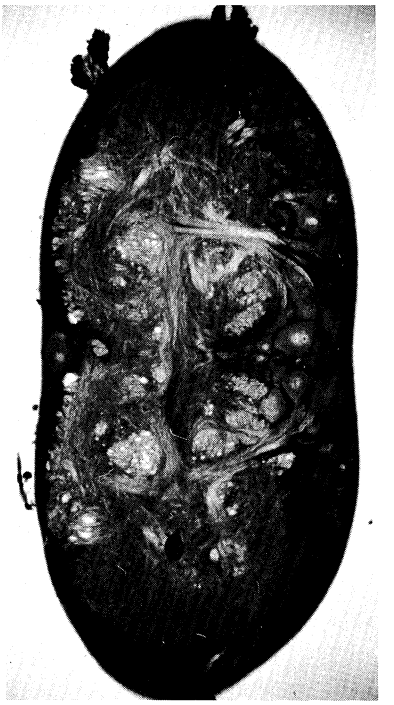


FIGURE 1*j–l*. For description see p. 4.



(*m*) (36)

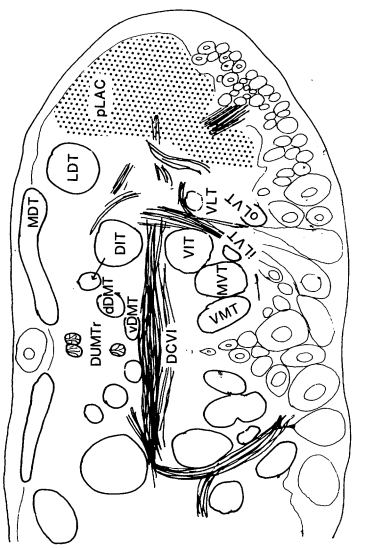


FIGURE 1*m*. For description see p. 4.

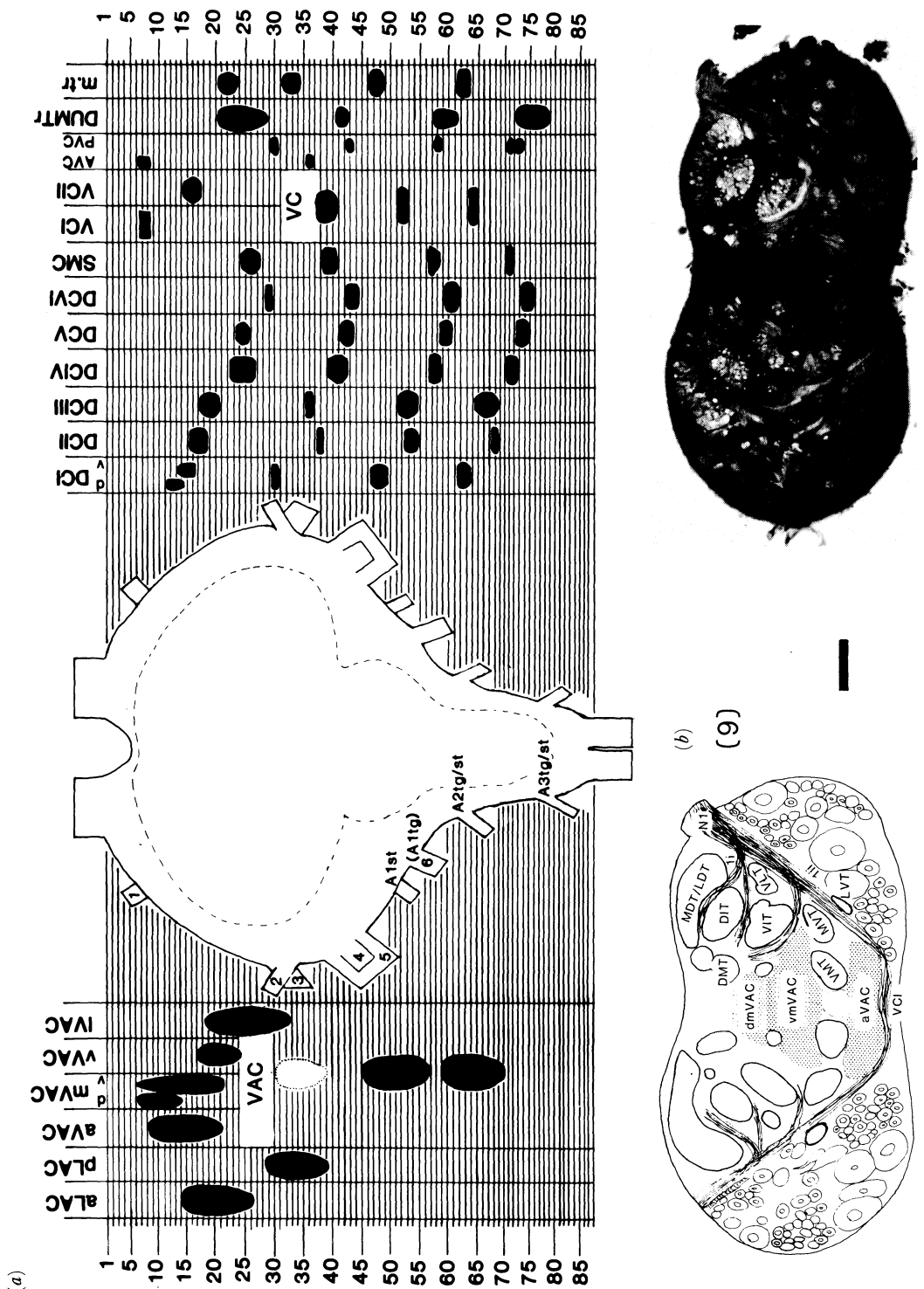


FIGURE 2. (*a*) Ventral view of a metathoracic ganglion cut into 16 µm sections starting with section 1 (first cell bodies visible) and ending with section 88 (last cell bodies visible). Prominent neuropiles, commissures and other structures are indicated as black bars. For white bar surrounded by a dotted line (VAC in the first abdominal neuromere), see text. Thickness of bars gives a relative measure of the size of the structures in the sections. (*b–k*) Selected sections of metathoracic ganglion stained with osmium and ethyl-gallate. Numbers in brackets refer to section numbers in (*a*). Where two numbers are stated the camera lucida drawing (left) is a composite of two sections, whereas the photograph (right) shows only one. Calibration 100 µm; abbreviations: see List of abbreviations used; A1st, A1tg, A2tg/st, A3tg/st refer to the sternal and tergal nerve of the first, second and third fused abdominal neuromere; VC: ventral commissures.

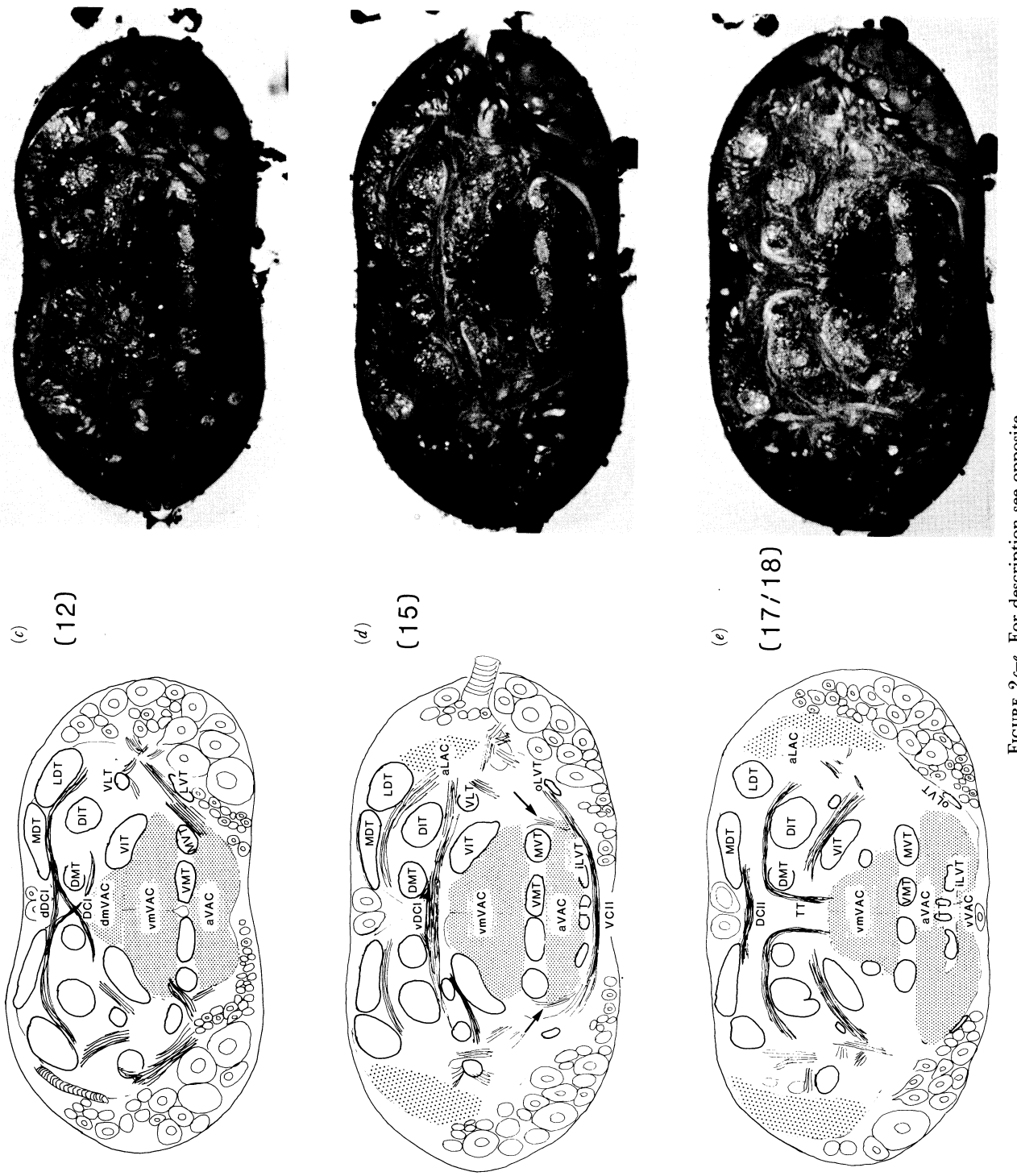


FIGURE 2*c–e*. For description see opposite.

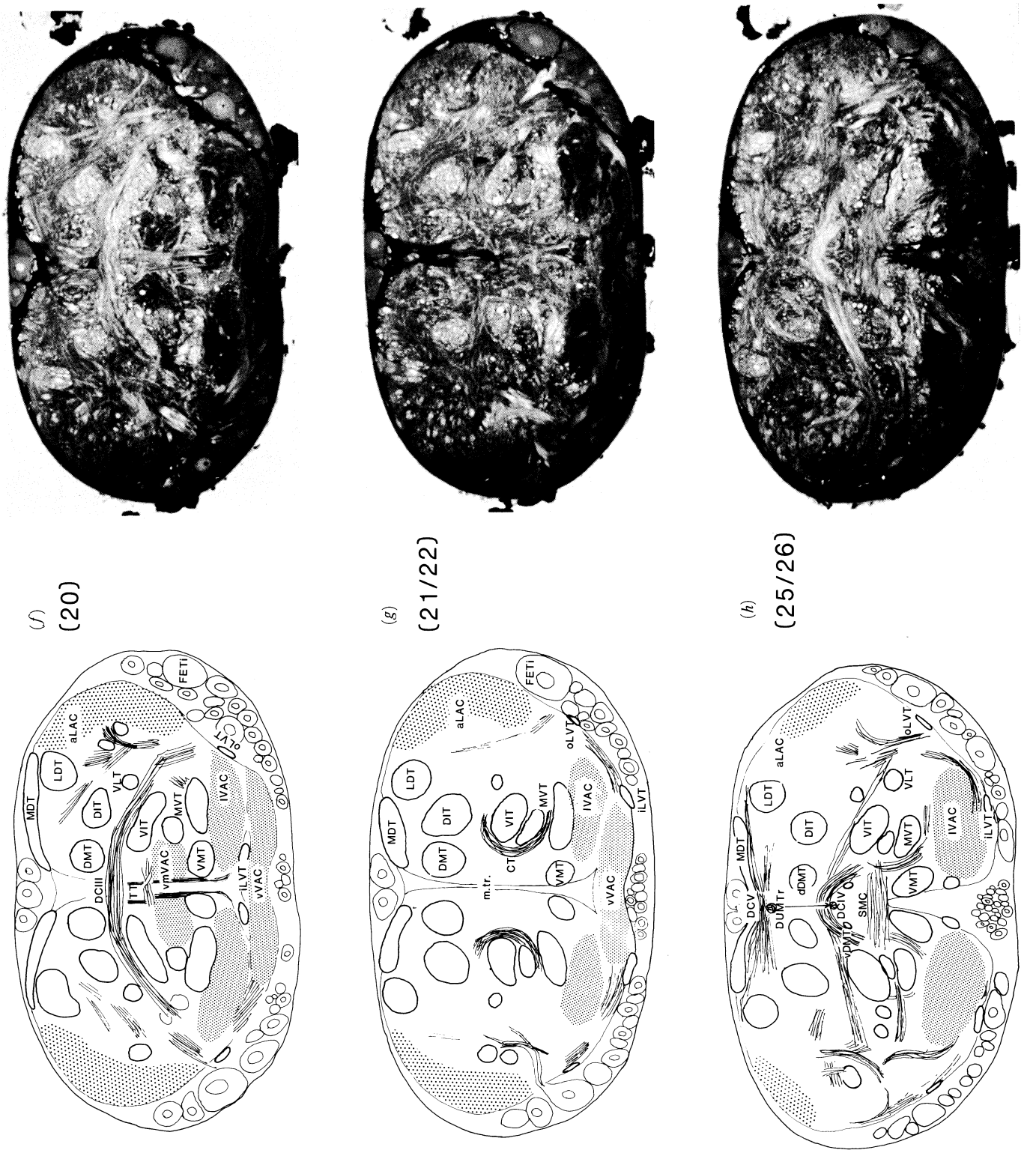


FIGURE 2*f–h*. For description see plate 6.

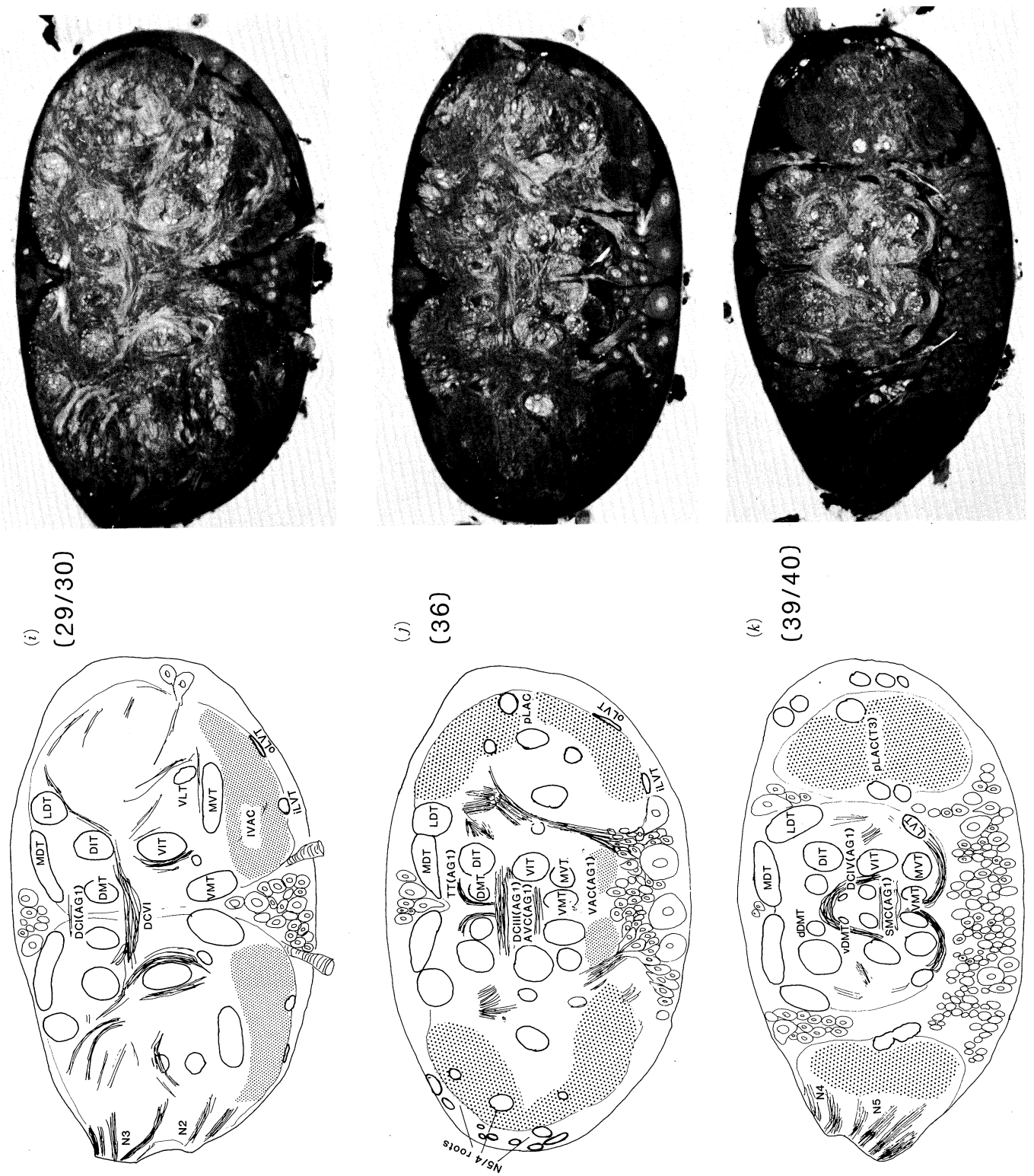


FIGURE 2*i–k*. For description see plate 6.

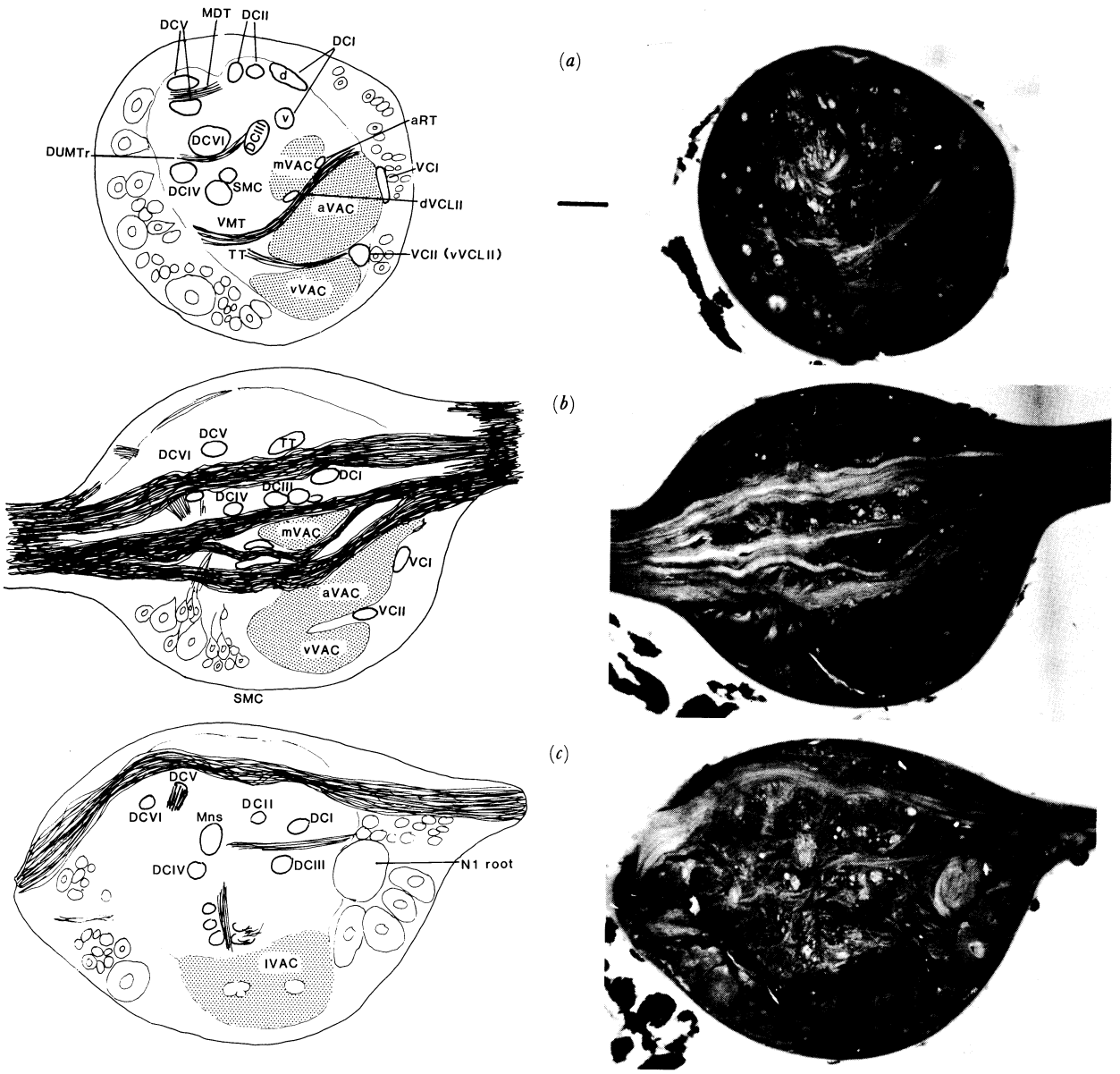


FIGURE 3. Selected sagittal and parasagittal sections (16 μm) through a mesothoracic (*a–c*) and metathoracic (*d*) ganglion, stained with osmium and ethyl-gallate, showing the outline of the ventral neuropiles. Calibration 100 μm.

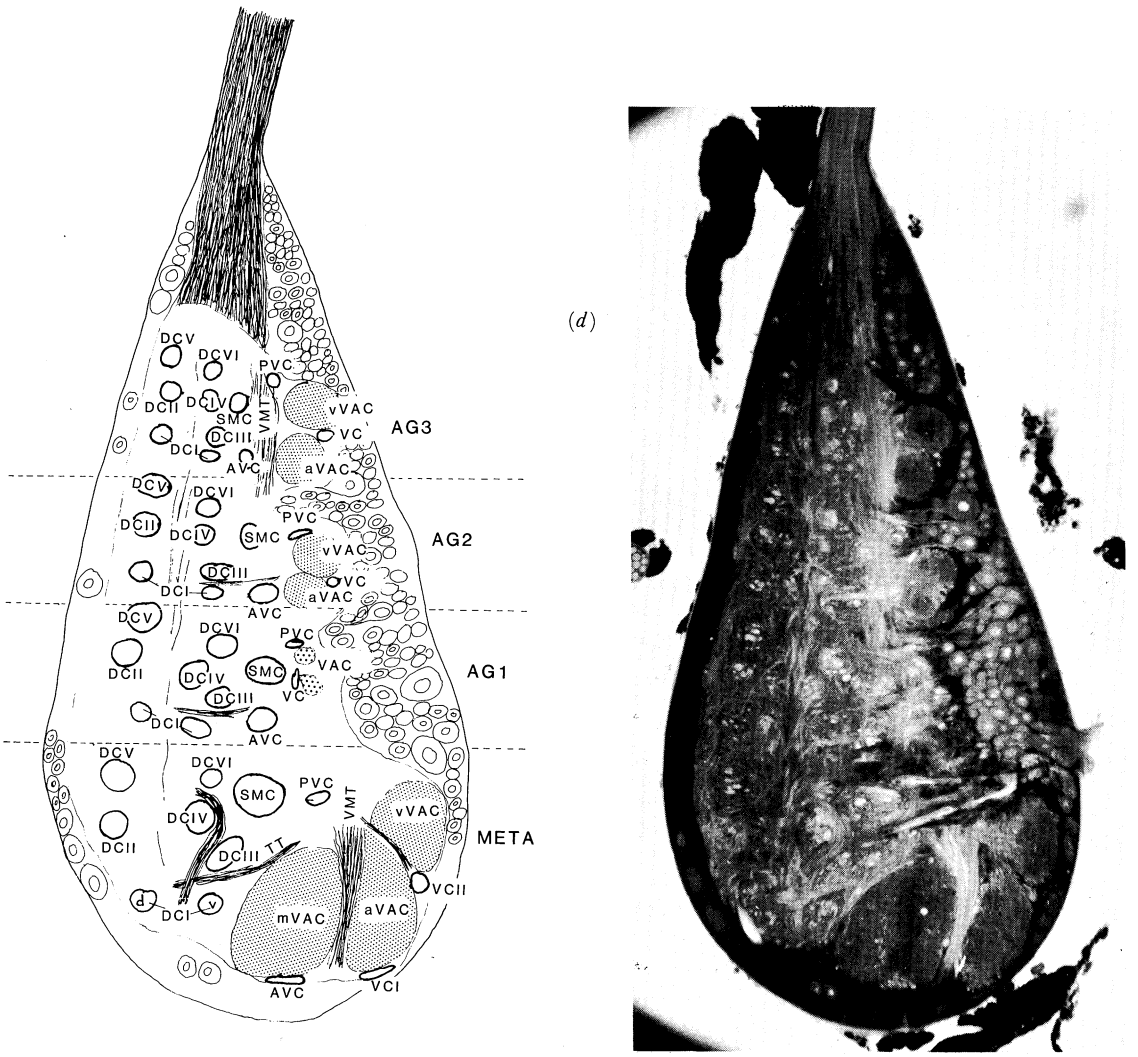


FIGURE 3*d*. For description see opposite.

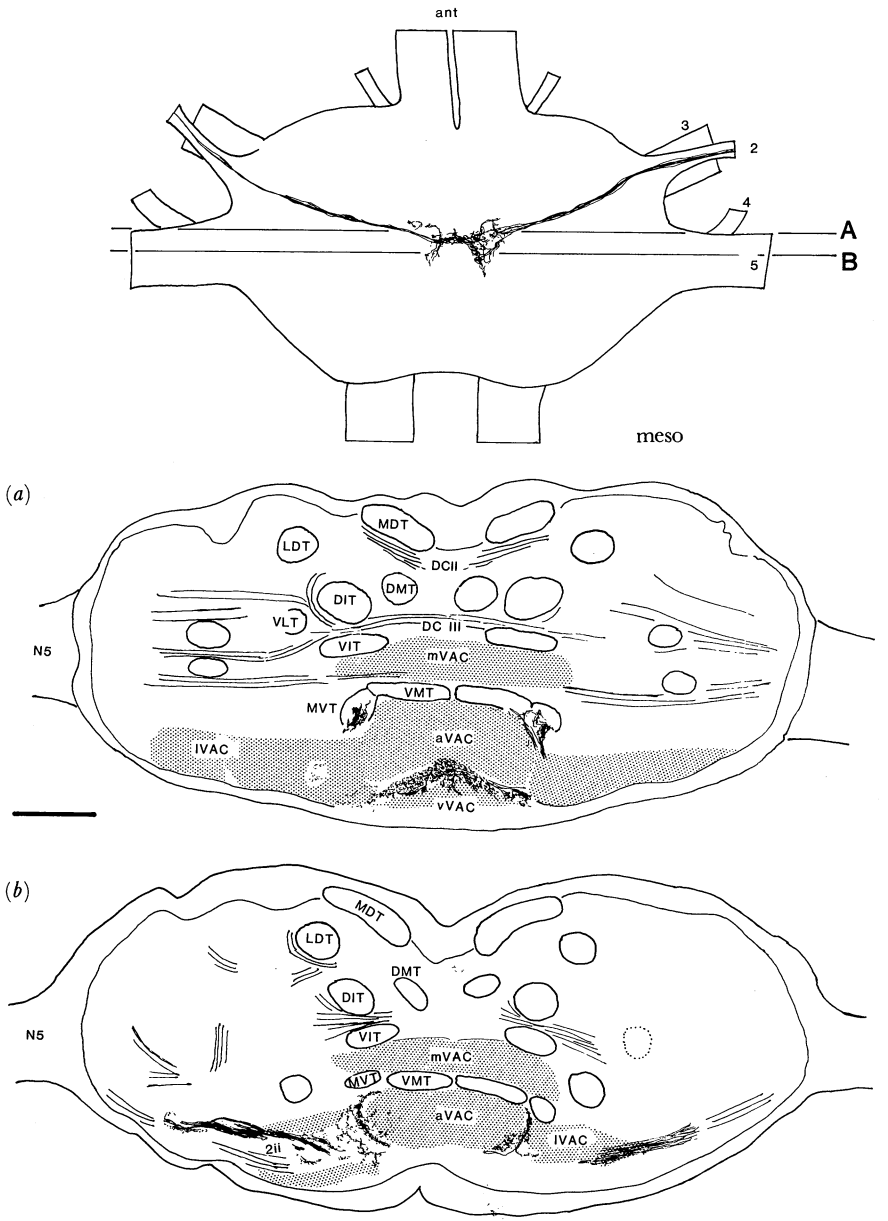


FIGURE 4. (*a–b*) Camera lucida drawings of selected 20 μm sections of a mesothoracic ganglion in which tactile hairs of the mesothoracic sternum were cobalt backfilled. The camera lucida drawing at top shows the central projection pattern of the whole receptor field in a dorsal view with levels of sections indicated. Calibration 100 μm.

develop medially and are uniformly structured neuropiles. The aVAC is situated below the VMT/MVT complex and iVLT and VCII are always ventral to it (figures 1*d* and 2*c*, *d*).

Parts of aVAC are surrounded by the ventral commissural loop II (VCLII, Tyrer & Gregory (1982)), which is a bundle of fibres connecting the commissures dVCLII (dorsal to the VMT/MVT complex) and vVCLII (equivalent to VCII; VCLII marked with an arrow in figure 2*d*). In more posterior sections aVAC is separated medially by the TT (figures 1*f*, *g* and 2*e*, *f*). At this level it merges laterally into the lVAC which is defined as that part of the aVAC that does not extend laterally beyond MVT. The mVAC is situated between VIT and the VMT/MVT complex. In the mesothoracic ganglion its lateral limit extends about 50 μm further than a line drawn through the lateral edges of VIT-MVT (figures 1*e–h*). In the metathoracic ganglion mVAC is comparatively large and is divided into a dorsal part above the level of VIT (dmVAC, figure 2*b–c*), and a ventral part below the level of VIT (vmVAC, figure 2*b–c*). The whole mVAC does not extend laterally beyond VIT. Posteriorly it is divided medially by TT, like aVAC (figure 1*g* and 2*f*), and disappears in more posterior sections.

Tyrer & Gregory (1982) called this neuropile aRT and defined it as an 'anterior extension' of the ring tract, which can only be recognized in horizontal sections. This ring tract is a fibre bundle connecting the anterior dVCLII and the posterior SMC. The neuropilar area surrounded by the ring tract is a true neuropile with a similar fibre texture to aVAC or vVAC. Therefore we use the name medial VAC (mVAC; in Bräunig *et al.* (1981), MVAC).

The vVAC originates more posteriorly than the mVAC and is separated from the more dorsal aVAC by VCII and glial cells. At its dorsal edge lies iLVT and at its ventral edge oLVT (figures 1*e–h* and 2*e–h*). More posteriorly the vVAC is also displaced from the midline by glial and other cells and extends laterally (figures 1*h* and 2*g*). This part of the ventral neuropile, lateral to a vertical line drawn from the lateral edges of DIT–VIT–MVT and from the median edge of LDT is called lVAC (figures 1*e–j* and 2*f*). Johnson & Murphey (1985) named this lVAC and the aVAC 'bristle neuropile'. The lVAC continues posteriorly to the level of nerve 5 in the mesothoracic ganglion (figure 1*j*) and nerve 3 in the metathoracic ganglion (figure 2*i*).

The fused abdominal neuromeres also possess a VAC but in cross sections this is difficult to separate into aVAC and vVAC. The mVAC is either not present or does not possess a similarly fine texture of fibres. In the first abdominal neuromere VAC is very small and does not appear as dense as other neuromeres. This is indicated in figure 2*a* by a white bar surrounded by a dotted line.

The VACs are also revealed in longitudinal sections of an osmium and ethyl-gallate stained meso- (figure 3*a–c*) and metathoracic ganglion (figure 3*d*). The transition between aVAC, vVAC and lVAC is demonstrated in figure 3*a–c*. Figure 3*d* also shows that the VACs of the fused second and third abdominal neuromeres (AG2 and AG3) are also separated into aVAC and vVAC. Again the VAC of the first abdominal neuromere (AG1) is barely visible. That it really exists can be deduced from the central projection pattern of tactile hairs of the first abdominal segment. These projections have arborizations within the first abdominal neuromere in the area indicated in figure 3*d* within VAC.

Dorsal neuropiles

The dorsal neuropiles are not as clearly defined as the ventral ones. They do not appear as densely packed and uniform, resulting in less intensely stained areas (figures 1 and 2). These

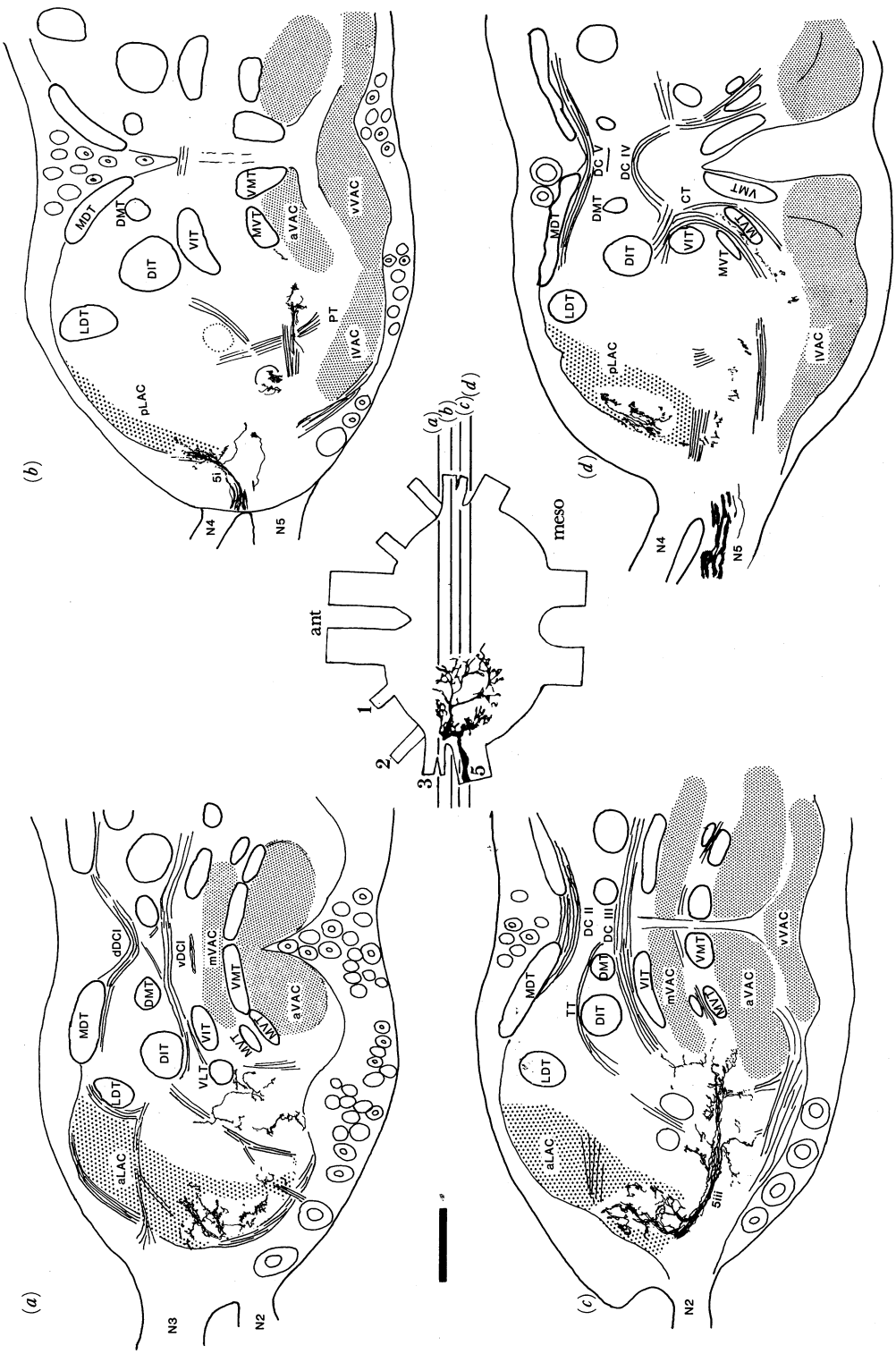


FIGURE 5. (*a–d*) Camera lucida drawings of selected 20 µm sections of a mesothoracic ganglion in which a mesothoracic trochanteral hair plate (trHP1) was stained. Insert shows a camera lucida drawing of the central projection pattern of the whole hair plate together with an indication of the levels of sections. Calibration 100 µm.

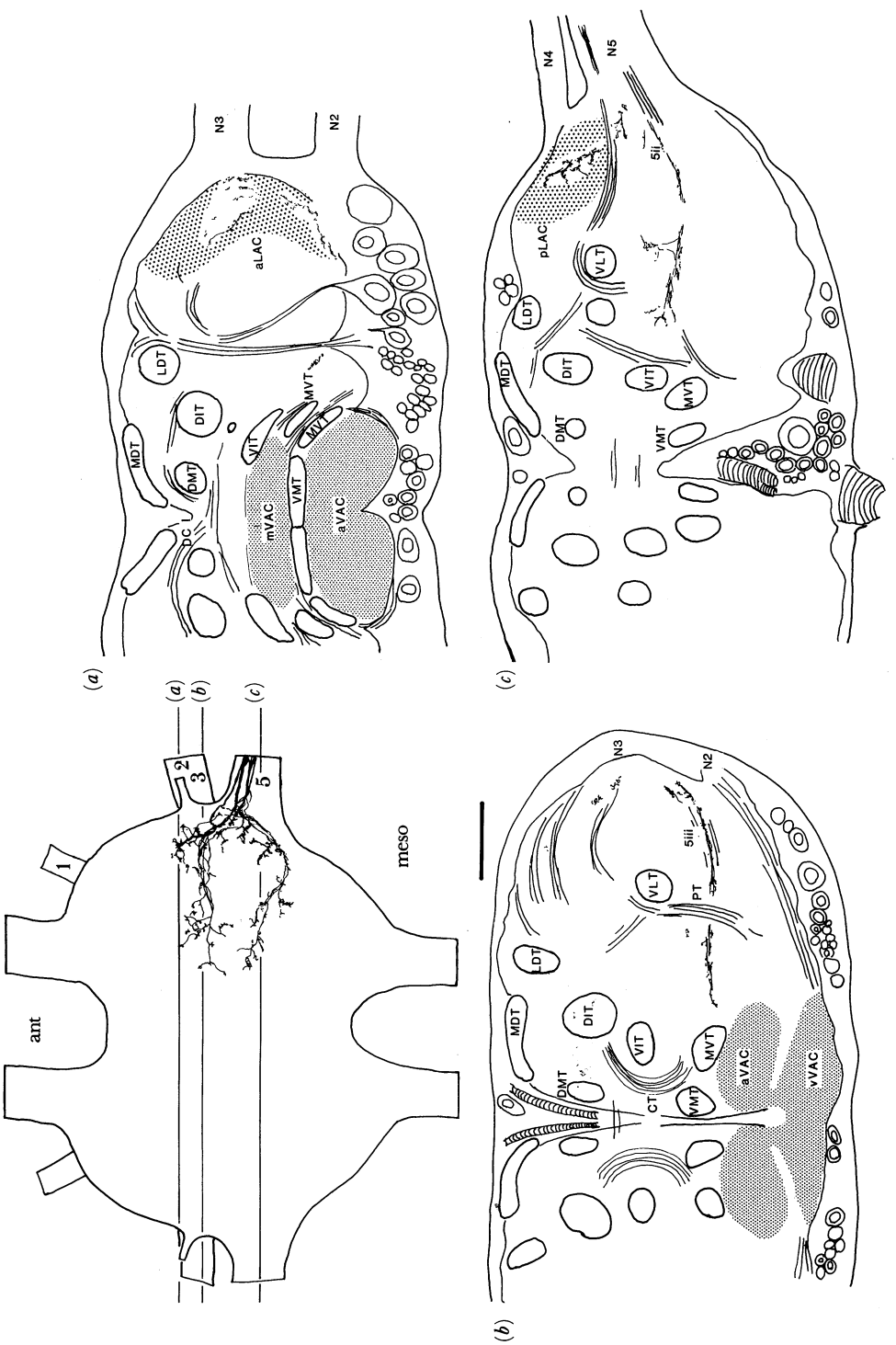


FIGURE 6. (*a–c*) Camera lucida drawings of selected 20 µm sections of a mesothoracic ganglion in which a mesothoracic trochanteral field of campaniform sensilla (trCS3) was stained. Camera lucida drawing at top left shows the central projection pattern of the whole receptor field with an indication of the levels of the sections. Calibration 100 µm.

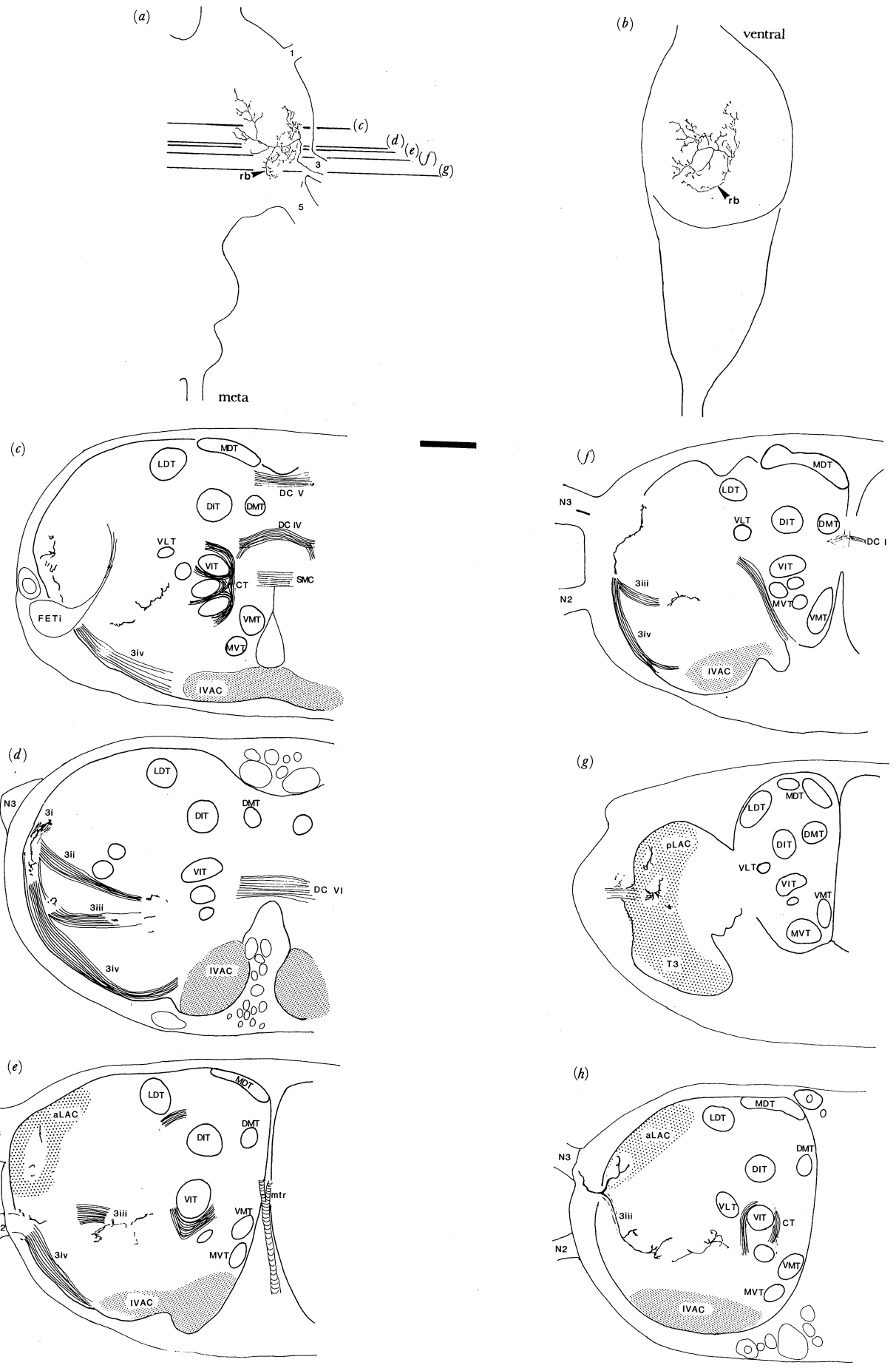


FIGURE 7. For description see opposite.

dorsal neuropiles were called 'sensori-motor-neuropiles' as they consist of a mixture of fibres, already noticed by Binet (1894). In osmium and ethyl-gallate stained sections the most lateral parts are stained with approximately the same intensity as ventral neuropiles suggesting a similar density of fibres. It is in these most lateral areas of the neuropile where axon collaterals of many leg sense organs terminate. To use established terminology and to avoid precipitate functional implications we suggest the neutral name lateral association centre (LAC) for this part of the ganglion. This LAC is divided into an anterior (aLAC, figures 1*c–f* and 2*d–h*) and a posterior part (pLAC, figures 1*j–m* and 2*j*, *k*), by the incoming roots of nerves 3 and 5.

In the meso- and metathoracic ganglion aLAC develops around the roots of nerve 1 and contains the sensory projections from wing sense organs (Altman & Tyrer 1977*a*). It can be most clearly seen in sections anterior to nerve 3. The pLAC starts at about the level of nerves 4 and 5 and is clearly separated from aLAC by the incoming roots of nerve 3. It has transitions to lVAC, from which it can be partly separated by small roots of nerve 5. It is most clearly seen in sections posterior to nerve 5.

Mechanosensory projections

Tactile hairs (H)

All tactile hairs are innervated by a single sensory cell and project into the ventral neuropiles, regardless of their location on the body and the nerve through which their axons enter the ganglion (Pflüger 1980; Pflüger *et al.* 1981). Figure 4 shows the typical projection pattern of mesothoracic basisternal receptors entering the ganglion through the ventral root of nerve 2 (2ii, figure 4*b*). Their axon collaterals terminate in the ventralmost ventral association centre (vVAC) and, characteristically the axons follow the margin of the anterior VAC (aVAC) and terminate in the median ventral tract (MVT, figure 4*a*). A topographical representation of peripheral receptor location has been recognized (Pflüger 1980; Pflüger *et al.* 1981). This somatotopic order has been confirmed and studied in detail for tactile leg hairs by Johnson & Murphey (1985) in the cricket. The result can be summarized as follows.

1. Dorsal receptors, i.e. those on the scutum, enter the ganglion through nerve 1 (root 1ii) and project into the aVAC. Correspondingly tactile hairs of the pronotum terminate within the aVAC (H.-J. Pflüger, unpublished results).

2. Ventral (sternal) receptors enter through nerve 2 (root 2ii) and project into vVAC. A few hairs that are located close to the midline also possess intersegmental projections into the vVAC of the next anterior ganglion (Pflüger 1980; Pflüger *et al.* 1981).

3. Lateral receptors, i.e. those of episternum, epimeron and leg, enter the ganglion through nerves 3, 4 or 5, continue within the most ventral roots and project into the lateral parts of the ventral (vVAC) or into the lateral VAC (lVAC). Within vVAC and lVAC a topographic order can also be found: the most distally located receptors in the periphery (i.e. those from the tibia) terminate most laterally within lVAC. The more proximally located receptors (i.e. those from the coxa) terminate more within the lateral part of vVAC.

FIGURE 7. Camera lucida drawings of a metathoracic ganglion in which a multipolar sensillum of the hind leg (coxotrochanteral muscle receptor organ, cxtrMRO) was cobalt backfilled. (*a*) Dorsal view of the central projection pattern of this cell; arrowhead pointing to the 'recurrent branch' (rb). (*b*) Side view. (*c–g*) Selected 20 μm sections, levels of sections are indicated in (*a*). FETi, fast extensor tibiae motorneuron. (*h*) Camera lucida drawing of a 35 μm-thick section in which the course of the sensory axon could be seen exceptionally well. This section is from a different preparation. Calibration 100 μm.

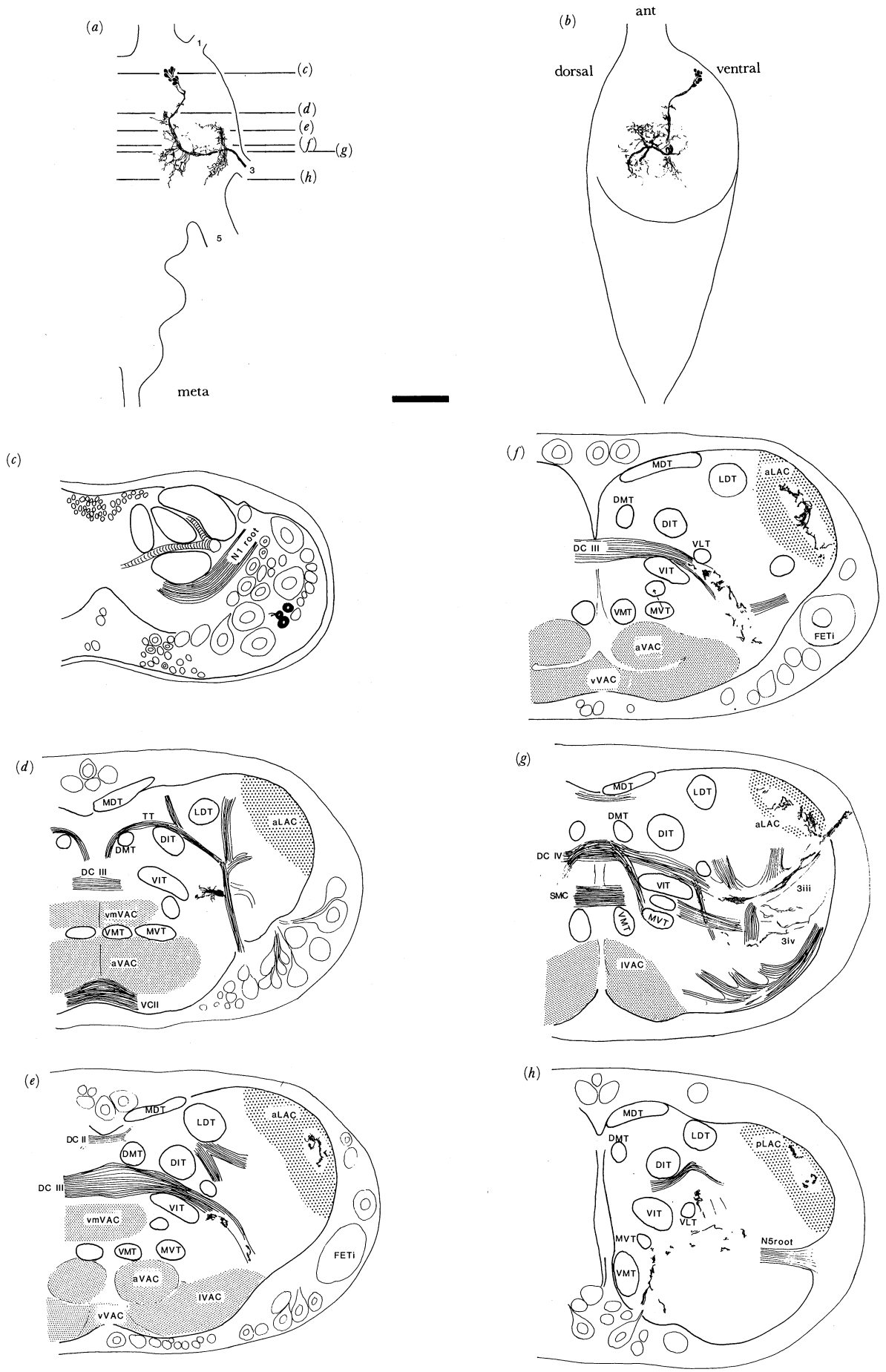


FIGURE 8. For description see opposite.

4. Special sternal hairs, which were first described in crickets by Hustert (1978) and which are also present in locust larvae and adults (H.-J. Pflüger & R. Hustert, unpublished results) are longer than the average and possess intersegmental projections. The axons terminate within vVAC in each ganglion or neuromere they reach.

Hair plates (HP)

Projections from the three hair plates (HP) of each leg differ markedly from those of tactile hairs (figure 5). The afferent fibres of the two coxal HP enter through nerve 3, those of the trochanteral HP through nerve 5 (figure 5*d*). The axons do not approach any of the VAC neuropiles, but immediately after their entrance into the ganglion each axon forms two collaterals, one turning anteriorly (figure 5*b*) and the other posteriorly (figure 5*c*, *d*). Both follow the edge of the neuropile in the most dorsal roots of either N3 (cxHP) or N5 (trHP). These roots probably correspond to roots 3i and 5i of Tyrer & Gregory (1982). The anterior branches extend into the anterior lateral association centre (aLAC, figure 5*a*, *b*). Though some side branches also terminate in rather ventrolateral regions, generally within aLAC, the most ventral continue almost to the edge of aVAC/lVAC. The posterior collaterals extend into pLAC with their terminals nearly reaching as far dorsally as LDT (figure 5*c*, *d*). This applies to all hair plate projections, but those entering through nerve 3 project more anteriorly within aLAC or pLAC compared with those entering through nerve 5. The main axons of HP receptors run either in root 3iii (cxHP) or 5iii (trHP) towards the midline of the ganglion entering the CT (figure 5*d*) and giving off side branches that terminate in the surrounding neuropile with some even reaching the edge of aVAC/lVAC (see figure 5*b*).

Campaniform sensilla (CS)

Campaniform sensilla have a projection pattern resembling that of hair plate receptors. Figure 6 represents the projection pattern of a field of mesothoracic trochanteral CS (trCS3). All axons of leg CS enter the ganglion through nerve 5 and shortly after bifurcate into anterior and posterior branches (figure 6). Collaterals that follow the edge of the neuropile in a dorsal and ventral direction originate from both branches, shortly after the point of bifurcation. Those of the anterior branch terminate in aLAC close to the base of nerves 2 and 3 (figure 6*a*) and those of the posterior one, in pLAC (figure 6*c*). The main anterior branch runs within root 5iii (figure 6*b*) and terminates close to MVT at the bottom of the C-tract. In other CS-projections a medioposterior collateral extends from the anterior branch towards the posterior branch. In femoral CS-projections the anterior branch proceeds dorsally to the level of DMT/DIT.

The posterior branch runs within root 5ii (figure 6*c*) and also terminates close to MVT. From both main branches collaterals arise that terminate in the neuropile surrounding roots 5iii and 5ii and the ventral lateral tract (VLT).

Multipolar sensory cells (MS)

The coxotrochanteral muscle receptor organ (cxtr MRO) consists of a single multipolar sensory cell associated with a receptor muscle (Bräunig 1982*a*; Bräunig *et al.* 1986). The

FIGURE 8. Camera lucida drawings of a metathoracic ganglion in which a subcoxal strand receptor of the hind leg was stained. (*a*) Ventral view of the central projection pattern. (*b*) Side view. (*c–h*) Selected 20 μm sections, levels of sections are indicated in (*a*). Calibration 100 μm.

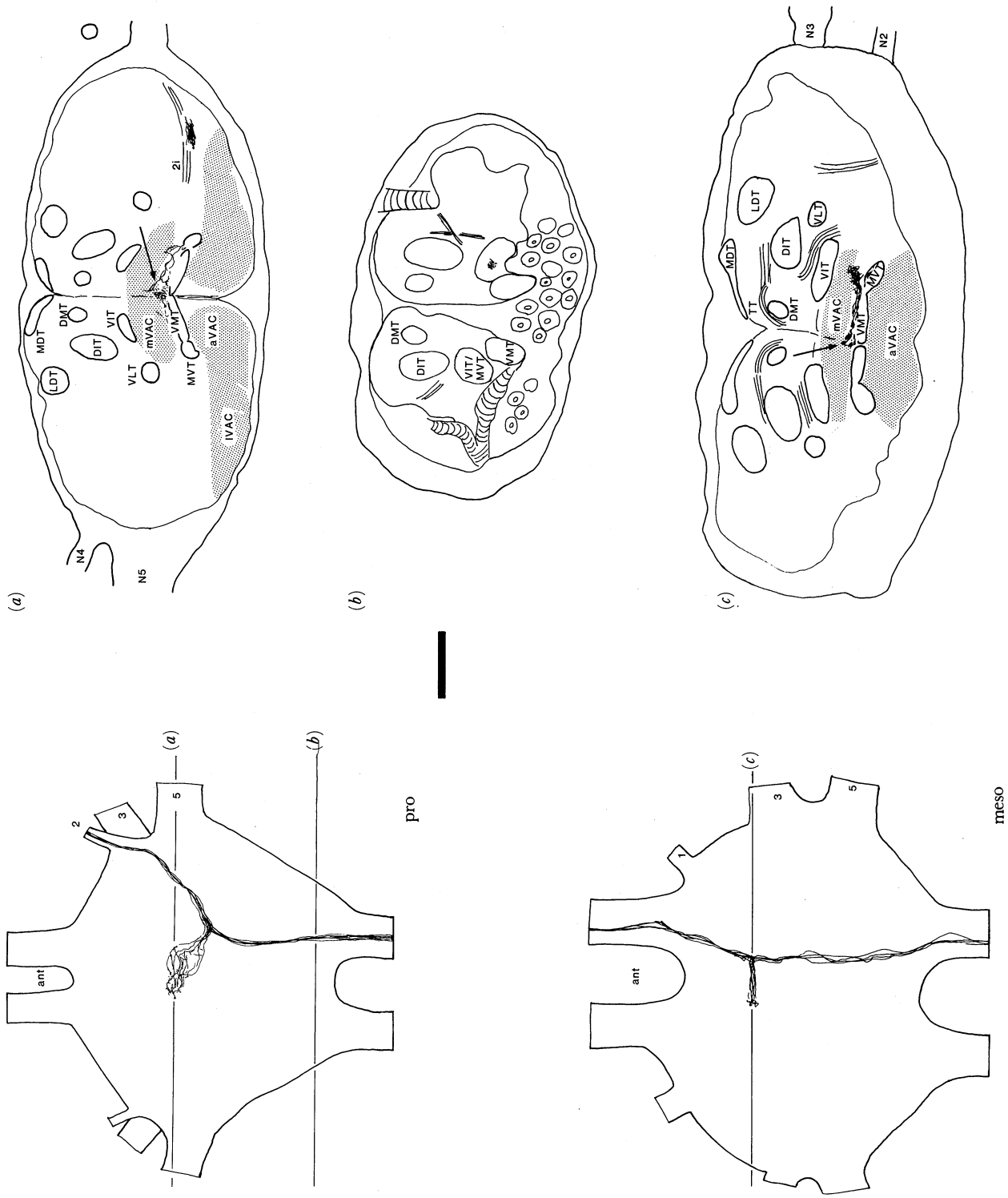


FIGURE 9 (*a–c*). For description see opposite.

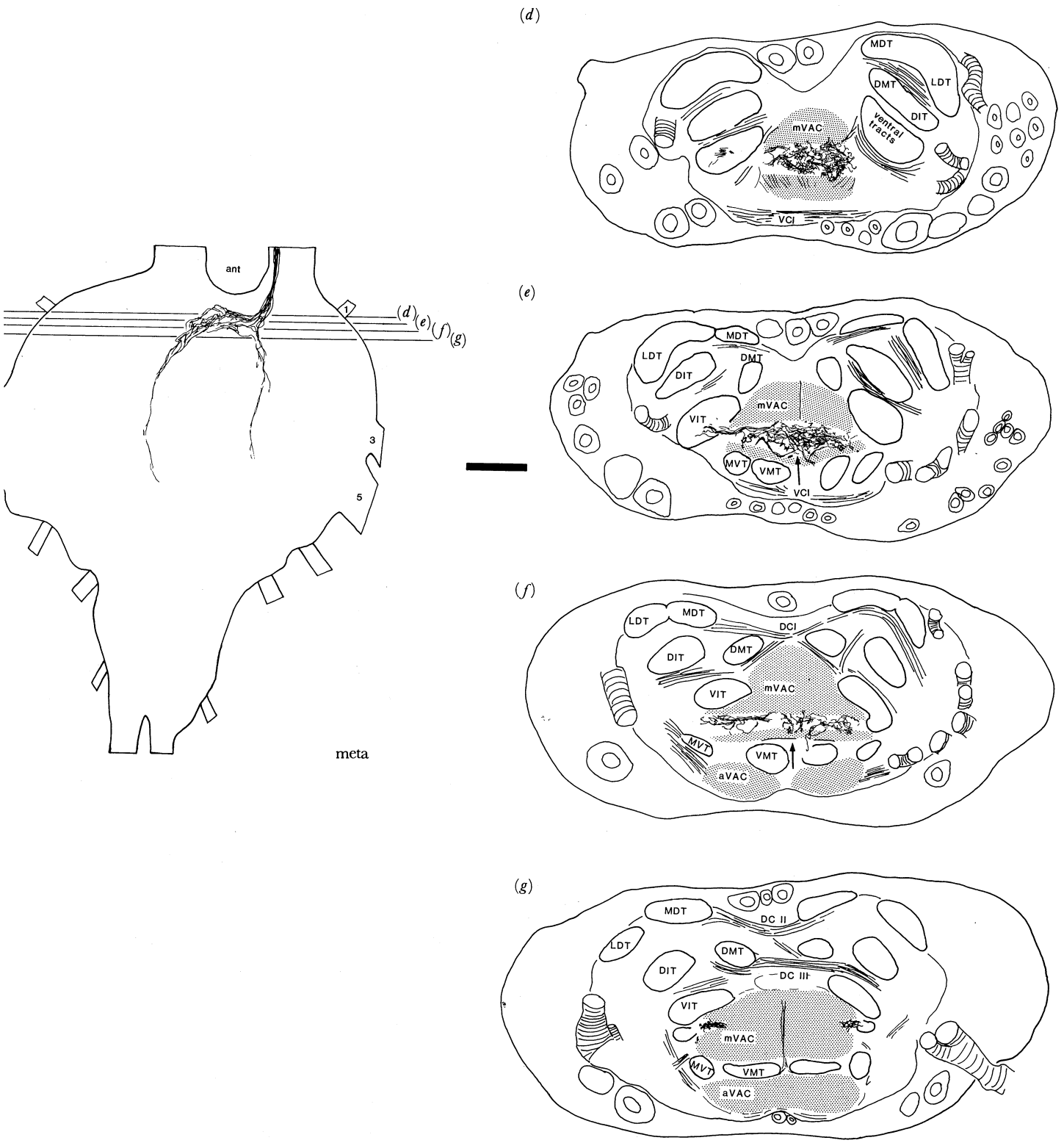


FIGURE 9. Camera lucida drawings of prothoracic (PRO), mesothoracic (MESO) and metathoracic (META) ganglia showing the central projection pattern of a prothoracic anterior chordotonal organ (aCO PRO, drawings on the left). On the right camera lucida drawings of selected 20 μm sections (*a–g*) are shown. Calibration 100 μm.

central projection pattern of the metathoracic sensory neuron is shown in a dorsal view (figure 7*a*) and a side view (figure 7*b*). Its axon enters through nerve 3 and shows collaterals in root 3i (figure 7*d*, *h*) which terminate in the dorsal aLAC, at the edge of the neuropile (figure 7*e*, *h*). The main axon runs within root 3iii (figure 7*d–f*) and bifurcates into an antero-medial and medial branch from which collaterals terminate in a neuropilar area around VIT, VLT and MVT. There is also a prominent recurrent branch (rb) which terminates in the dorsal pLAC (figure 7*g*).

Strand receptors (SR)

The strand receptors are a class of receptor cells with central cell bodies but whose stimulus transducing elements lie in peripheral strands of connective tissue (Bräunig & Hustert 1980; Bräunig 1982*a*, 1985). In figure 8 metathoracic SR-cells associated with the coxotrochanteral strand are shown in a wholemount (ventral view: figure 8*a*, side view: figure 8*b*). Their small ventral cell bodies are clustered among the larger ones of motorneurons in the anterior part of the ganglion (figure 8*c*). The primary neurites run posteriorly, first along a trachea, then joining DCIII (figure 8*d–f*) and root 3iii and 3iv. They give off collaterals which terminate medially in neuropilar areas around DIT, VIT and VLT. Before the primary neurites (axons) leave the ganglion prominent collaterals originate and project into the dorsal aLAC (figure 8*e–g*) and pLAC (figure 8*h*).

Chordotonal organs (CO)

The topography of the chordotonal organ projections has been described by Hustert (1978) and Bräunig *et al.* (1981). Here we describe typical projection patterns of the prothoracic COs.

The anterior (aCO) and ventral CO (vCO) have intersegmental as well as contralateral projections. In contrast, the femoral CO (feCO) has predominantly ipsilateral and intrasegmental projections. Chordotonal organs associated with the subcoxal joint may have features of both types.

Chordotonal organs associated with sternal apodemes, i.e. the apodemal CO (apCO), also project intersegmentally but otherwise are quite different in regard to the ganglionic areas contacted by their fibres.

The aCO of the prothorax inserts proximally on N2 immediately after it has left the ganglion and its strand is attached to a small sclerite in the neck membrane. Its sensory fibres project intersegmentally as far posteriorly as the metathoracic ganglion (figure 9). In the prothoracic ganglion the axons of the receptor cells run towards the midline in an intermediate root of N2 (2i, figure 9*a*). Collaterals terminate within mVAC, just dorsal to the MVT/VMT complex and some can cross to the contralateral side most likely within dVCLII (Tyrer & Gregory 1982) (figure 9*a*, arrow). This CO has no projections into the lateral neuropile (LAC). The main axons enter MVT (figure 9*b*, *c*) and project intersegmentally into the meso- and metathoracic ganglion. In both ganglia collaterals cross the midline again most likely within dVCLII (figure 9*c*, *e*, *f*; arrows) and terminate within mVAC. In the metathoracic ganglion a few ipsi- and contralateral fibres proceed posteriorly along the edge of mVAC (figure 9*g*). The myochordotonal organ (myoCO) shows nearly the same projection pattern within the thoracic ganglia. Its axons also project to the mVAC in all three ganglia where they terminate. Contralateral projections, most likely within dVCLII, are also observed.

The femoral CO has, by contrast, a projection pattern restricted to one segmental hemiganglion. In a pro- and mesothoracic leg this organ lies proximally in the femur and is divided into a proximal and distal scoloparium (Slifer 1935; Burns 1974). The proximal scoloparium consists of more than 300 sensory cells, the distal one of about 40. The functional significance of this division is unknown. The projection pattern shown in figure 10*a*, *b* is from both parts of a prothoracic femoral chordotonal organ. The majority of axons enter the ganglion through root 5iii and run towards the midline of the ganglion (figure 10*c–e*). This densely packed mass of fibres does not allow the course of individual fibres to be traced. However, it is likely that they start branching near VLT and terminate in mVAC.

Another smaller population of fibres runs within root 5iv reaching the lateral edge of aVAC

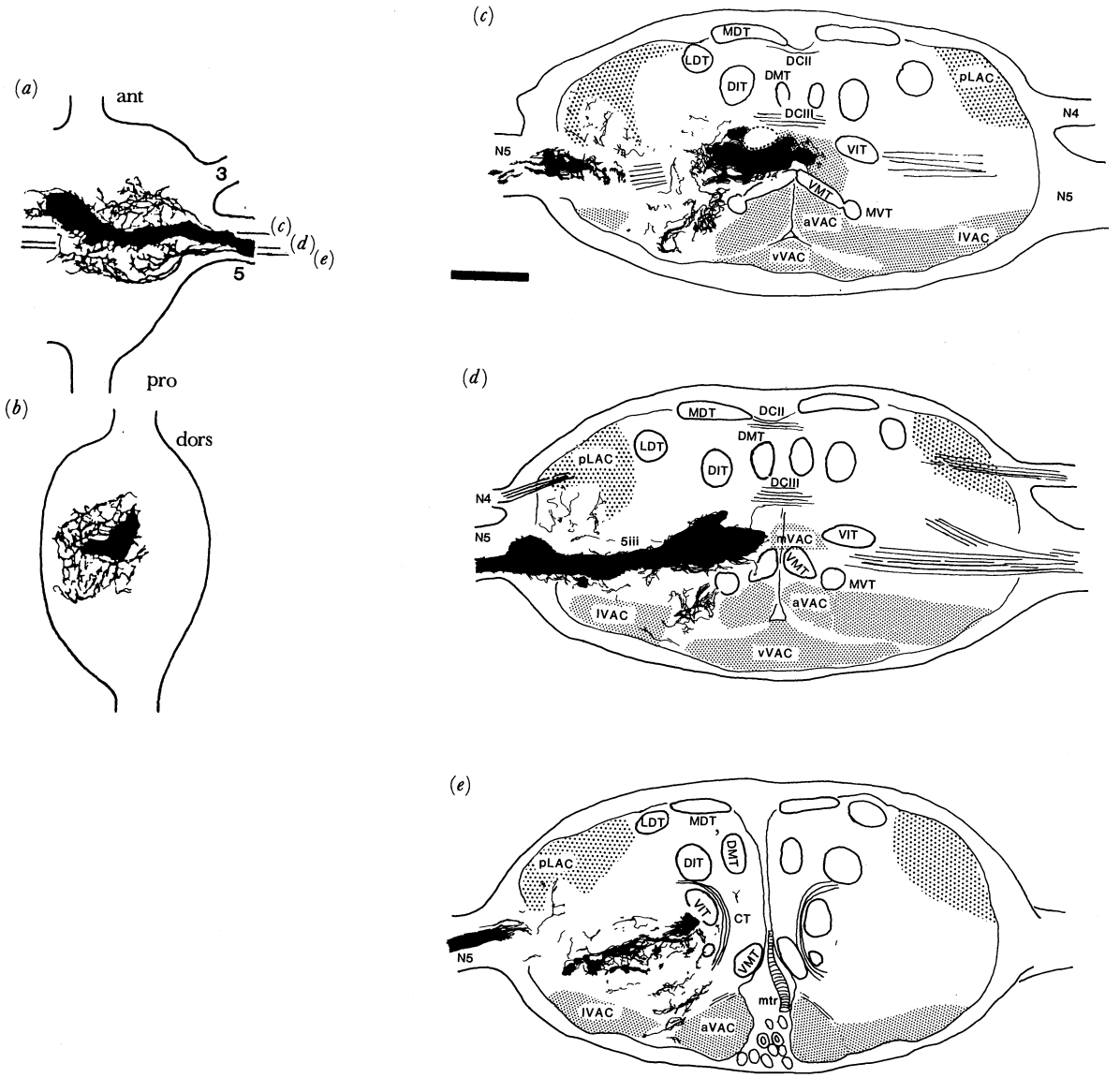


FIGURE 10. Camera lucida drawings of a prothoracic ganglion in which the femoral chordotonal organ of the front leg was stained. (*a*) Dorsal view. (*b*) Side view. (*c–e*) Selected 20 μm sections, levels of sections are indicated in (*a*). Calibration 100 μm.

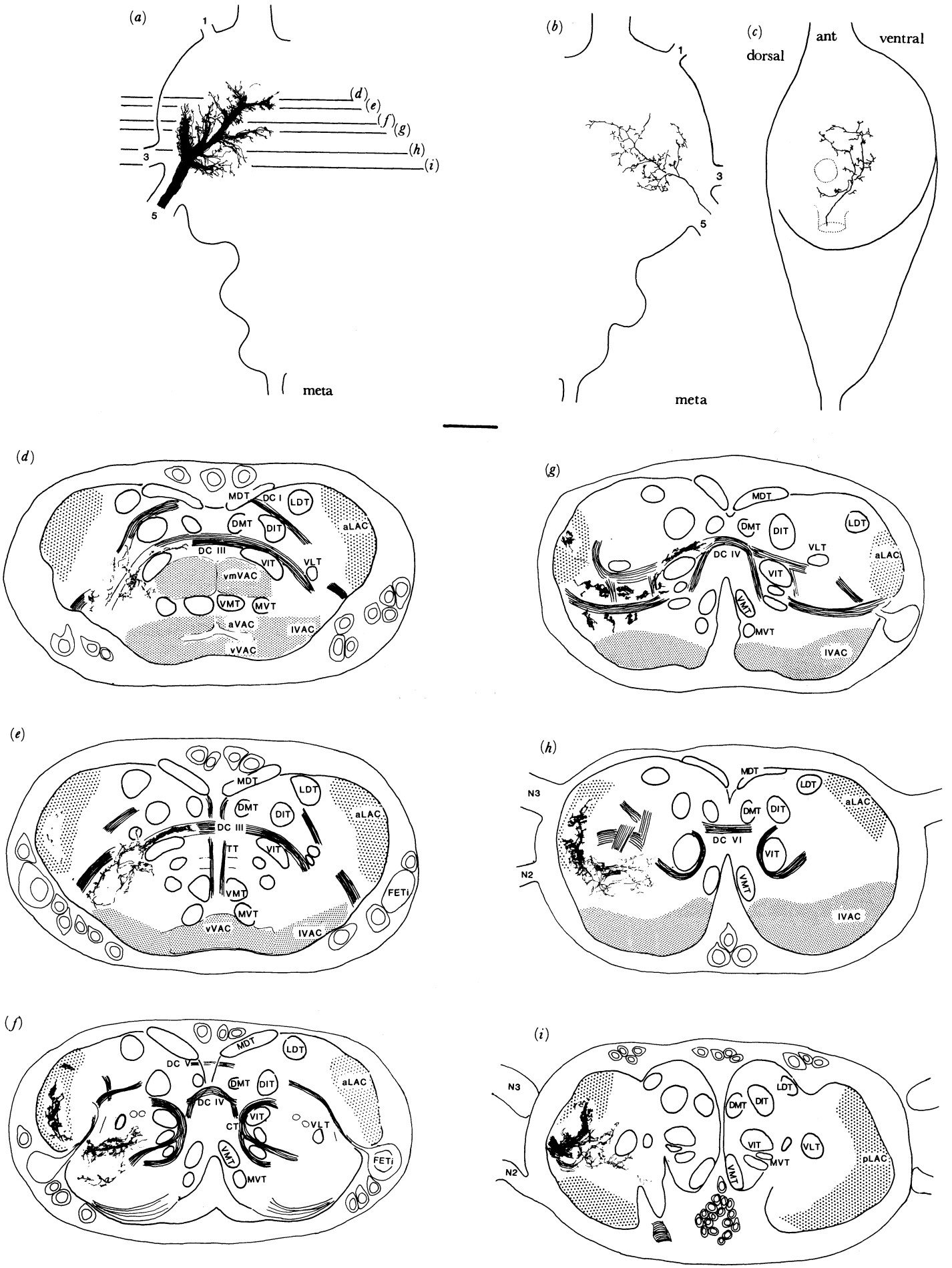


FIGURE 11. For description see opposite.

and terminating within the ventral part of the C-tract (CT), also giving off collaterals into the surrounding neuropile (figure 10*d*, *e*). There are additional projections into pLAC. Projections also reaching lVAC are ambiguous as they could represent tactile hair projections.

In the metathoracic leg, which is modified for jumping, the feCO differs considerably. It is translocated to the distal end of the femur and consists of only one part with about 20–30 sensory cells. We assume that only the distal part has been preserved (Hustert *et al.* 1981). The projection pattern of the whole metathoracic feCO shown in figure 11*a* and in Burrows (1987) supports this view. Obviously missing is the densely stained, plexus-like structure within mVAC (compare with figure 10). Single-fibre stains (dorsal view: figure 11*b*; side view: figure 11*c*) show that individual receptor axons contact all ganglionic regions which the whole population does (see also Burrows 1987). Lateral projections prevail in aLAC and pLAC, some of them terminating dorsally (more dorsal than DCIII). The axons continue in a root of nerve 5 (probably root 5ii or 5iii) towards the midline. They repeatedly give off collaterals into the surrounding neuropile along their path. Two bundles of axon collaterals, an anterior and a posterior bundle, run towards the midline. The anterior bundle passes between VIT, VLT and ventral to DIT, DMT, joining the lateral extension of DCIII wherein they terminate some 50 μm before reaching the midline (figure 11*d*, *e*). The posterior bundle also runs between VIT and DIT/DMT extending into DCIV wherein the fibres also terminate ipsilaterally about 50 μm short of the midline (figure 11*f*, *g*).

The clear division of neuropilar areas in the prothoracic ganglion which receive projections from the femoral CO leads us to the speculation that the two parts of the organ have different projection patterns. The results from staining the metathoracic feCO support our view, that the many fibres terminating within mVAC may be the ones originating from the proximal part of the feCO and that the others are from the distal part.

Chordotonal organs associated with the subcoxal joint typically possess intersegmental projections, collaterals within the dorsal part of aLAC and pLAC, and collaterals crossing the midline (in Hustert (1978), figure 3 and Bräunig *et al.* (1981), figure 4). Their projection patterns can be regarded as a combination of features of the two 'extreme' types (aCO and feCO).

Yet another type of projection pattern is shown by the apodemal CO (apCO). It inserts posteriorly to the sternal apodeme and anteriorly on the ventral surface of the ventral diaphragm (Bräunig *et al.* 1981). Its receptor afferents enter the metathoracic ganglion via N2 (figure 12) and collaterals terminate in the dorsal parts of pLAC (a few anterior branches may also contact aLAC, figure 12*c*). Projections were also found in vVAC with some axon collaterals crossing to the contralateral side through the VCII-commissure (figure 12*a*, *b*), but these could represent hair afferents that were stained accidentally.

Another projection area is more difficult to define: the axon collaterals run in an intermediate root of nerve 2 (2i) to an area dorsal to MVT and ventral to VIT. Side branches terminate in neuropile surrounding VIT and in a median area just posterior to mVAC, just

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FIGURE 11. Camera lucida drawings of a metathoracic ganglion in which the femoral chordotonal organ (feCO) of the hind leg was cobalt backfilled. (*a*) Central projection pattern of the whole chordotonal organ in a dorsal view. (*b*) Central projection pattern of a single sensory fibre from the feCO in a dorsal view. (*c*) The same as in (*b*) but in a side view. (*d–i*) Selected 20 μm sections, levels of sections are indicated in (*a*). Calibration 100 μm.

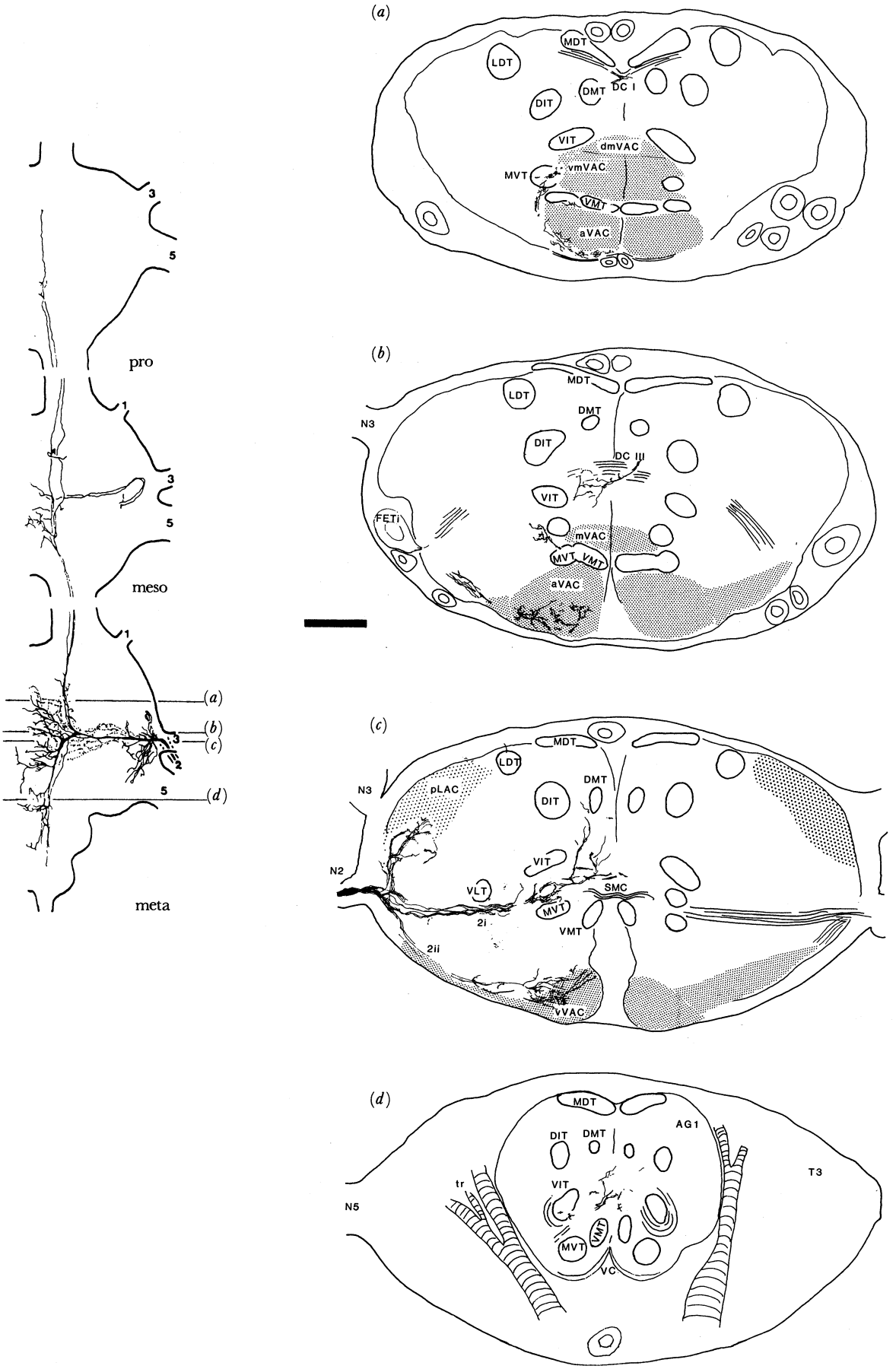

FIGURE 12. (*a–d*) Camera lucida drawing of selected 20 μm sections through a metathoracic ganglion in which the apodemal chordotonal organ of the hind coxa (apCO META) was stained. The drawing on the left shows the central projection pattern of the whole organ within the meta-, meso- and prothoracic ganglia in a dorsal view. The levels of the sections in the metathoracic ganglion are indicated. Calibration 100 μm.

dorsal to the supramedian commissure (SMC, figure 12*c*). The axon collaterals continue dorsally until they terminate ventral to DMT/DIT (figure 12*c*). Axons from this organ also run posteriorly to all three abdominal neuromeres first in MVT then in VIT (figure 12*d*).

The anterior axons stay within MVT (figure 12*a*) and run to the meso- and prothoracic ganglion. In the mesothoracic ganglion collaterals terminate in the neuropile surrounding VIT. Some nearly reach DMT/DIT, others terminate close to MVT and the edge of aVAC. Prominent axon collaterals turn and proceed in an intermediate or ventral root (a root that continues into the CT) terminating in the lateral neuropile (aLAC). In the prothoracic ganglion the axons end near VIT.

The afferent fibres of the homologous prothoracic organ run anteriorly to the suboesophageal and posteriorly to the mesothoracic ganglion. Within the prothoracic ganglion they terminate in areas similar to those described for the metathoracic apCO (Bräunig *et al.* 1981). Again, ventral projections running within root 4iv and terminating within lVAC may be of tactile hair origin. Other axon collaterals enter CT possibly through root 4iii and run dorsally until they reach an area between DIT and DMT. Another area that receives projections is pLAC. The

TABLE 1. THE RESULTS OF THIS PAPER AND OF PREVIOUSLY PUBLISHED LITERATURE ARE SUMMARIZED AND THE PROJECTION AREAS OF VARIOUS SENSE ORGANS INDICATED

(+, The indicated neuropilar region receives many projections; (+), only a few projections terminate in this region or ambiguous, needs further study; −, no projections found; (−), projections found are ambiguous, most likely representing hair afferents.)

receptors and references	mVAC	aVAC	vVAC	lVAC	aLAC	pLAC	others
tactile hairs (H) (Hustert 1978; Tyrer *et al.* 1979; Pflüger 1980; Pflüger *et al.* 1981; Pflüger & Tautz 1982; Elliott 1982; Johnson & Murphey 1985)	−	+	+	+	−	−	−
hair plates (HP): leg (Pflüger *et al.* 1981; this paper)	−	−	−	−	+	+	+
wing (tegula) (Kien & Altman 1979; Bräunig *et al.* 1983)	−	−	−	−	+	+	+
cervical HP (Kien 1980)	−	−	−	−	−	−	+
campaniform sensilla (CS) (Hustert 1978; Hustert *et al.* 1981; this paper)	−	−	−	−	+	+	+
multipolar sensory cells (MS): leg (Bräunig 1982*a*; this paper)	−	−	−	−	+	+	+
wing stretch receptor (Burrows 1975; Altman & Tyrer 1977*a*, *b*)	−	−	−	−	+	−	+
strand receptors (SR) (Bräunig & Hustert 1980; Bräunig 1982*b*; this paper)	−	−	−	−	+	+	+
chordotonal organs (CO) (Hustert 1978; Bräunig *et al.* 1981; this paper)	+	−	−	−	−	−	−
aCO	+	−	−	−	−	−	−
vCO	+	−	−	−	(+)	+	−
myoCO (Bräunig *et al.* 1981)	+	−	−	−	−	−	−
plCO (Hustert 1978)	+	−	−	−	−	−	+
feCO (Pro, Meso)	+	−	−	(−)	−	+	+
feCO (Meta) (Burrows 1986; this paper)	−	−	−	(−)	+	+	+
cCO (Bräunig *et al.* 1981)	(+)	−	−	−	+	+	+
apCO	−	−	(−)	−	−	+	+
wingCO (Tyrer & Altman 1974)	+	−	−	−	(+)	(+)	(+)
tympanal organ (Rehbein 1983; Römer & Marquart 1984)	+	−	−	−	−	−	−
subgenual organ (Grosch *et al.* 1985)	−	−	−	−	+	+	+

axons run anteriorly to the suboesophageal ganglion and posteriorly to the mesothoracic ganglion using first a tract between VIT and MVT before finally joining the MVT/VMT complex.

Summarizing our results and those from the published literature, table 1 shows the contribution of afferent projections to the neuropiles within the thoracic ganglia.

Discussion

Naming of neuropiles

With our increasing knowledge of locust central nervous anatomy we feel that defining structures in an internationally standardized way is now required. One of the main problems in generating such an anatomical atlas is how to name special structures in the ganglion, as each name has its shortcomings. In proposing a general nomenclature for the areas of neuropile within the thoracic ganglion it is important to choose a consistent scheme that will cause minimum confusion with earlier literature and should, therefore, gain general acceptance. We have, therefore, retained the name 'ventral association centre (VAC)', because it has become well established as a morphological term since its introduction by Pipa *et al.* (1959). It should be stressed, however, that 'association' as used here is not equivalent to the areas of the vertebrate cerebral cortex. In our terminology 'association' relates only to connections between pairs of neurons, i.e. between sensory terminals and their postsynaptic neurons. Only a few types of postsynaptic neuron have so far been identified in the VAC, such as local and intersegmental spiking interneurons (Siegler & Burrows 1984; Burrows & Siegler 1984; Murphey *et al.* 1983, 1985; Pflüger 1984; Hustert 1985). We are sure that many more will be identified. Also a specialized motorneuron has been shown to send collaterals into VAC (Bräunig 1982*a*).

The same reasoning applies to the newly defined term 'lateral association centres (LACs)'. In contrast to the VACs, we know already from the published literature that this region contains many fibres from motor- and interneurons (Tyrer & Altman 1974; Altman & Tyrer 1977*a*; Altman 1980; Watson 1984; Watson & Burrows 1981, 1982; Watson *et al.* 1985; Watkins *et al.* 1985; Pflüger *et al.* 1986; Kutsch & Schneider 1987). Correspondingly, all sense organs that make monosynaptic connections to motorneurons possess axon collaterals that run into this area (Burrows 1975; Pearson *et al.* 1976; Burrows 1987).

Ventral association centres

In vertebrates, sensory projections are organized topographically within the central nervous system, and detailed studies show a precise mapping of different sensory modalities. Such topographical rules may also apply for the mechanoreceptive senses in insects. A precise somatotopic mapping of afferent terminals from cercal hairs occurs in the terminal ganglion of crickets (Murphey 1981).

The most clearly structured thoracic neuropiles are the ventral neuropiles, labelled here aVAC, lVAC, mVAC and vVAC. Mechanoreceptive (tactile) hairs terminate within neuropiles aVAC, lVAC or vVAC according to their peripheral location on the segment (Pflüger 1980; Pflüger *et al.* 1981; Johnson & Murphey 1985: 'bristle neuropile') and a somatotopic order was demonstrated (see also Johnson & Murphey 1985). This topographic ordering principle relates to a proximal–distal and anterior–posterior axis on cricket legs. Johnson & Murphey (1985) also postulate a circumferential ordering principle.

This finding of topographical ordering of tactile hairs according to their peripheral location is also supported by staining of hair fields in other insects. Axons of windsensitive head hairs of locusts that have projections to the prothoracic and even mesothoracic ganglion (Tyrer *et al.* 1979) terminate within aVAC. The same is true for tactile hairs of the pronotum (Hustert 1978). Staining of special filiform hairs on the prosternum shows terminals within vVAC (Pflüger & Tautz 1982).

Axons of hairs on cricket wings also terminate within aVAC (Elliott 1983). The term 'hair plates' has been used for these fields, although the hairs are not localized near a joint but on the upper and lower wing surface; also, these wing hairs are considerably longer, 120–250 μm, than those of the leg hair plates (50 μm).

A similarly clear topographical structuring can be found for the medial VAC (mVAC; aRT) (Tyrer & Gregory (1982), and often also referred to as 'acoustic' or 'auditory' neuropile). In locusts the afferent fibres of the tympanal organ in the first abdominal ganglion project into the enormously developed neuropile in the metathoracic ganglion (Rehbein 1973; Rehbein *et al.* 1974; Römer 1983, 1985; Römer & Marquart 1984). Primary afferents also run to the corresponding, but smaller neuropiles of the meso- and prothoracic ganglia. In crickets and tettigoniids, where the tympanal organs are in the front leg, a similarly well-developed neuropile is found in the prothoracic ganglion (Eibl & Huber 1979; Wohlers & Huber 1985; Ball & Field 1981; Oldfield 1982, 1983). There is a tonotopic organization in the arrangement of sensory afferents within this 'auditory neuropile' (Oldfield 1983; Römer 1983, 1985). Our results show that mVAC in the pro- and mesothoracic ganglion also receives inputs from the femoral CO (though only from the proximal scoloparium (H.-J. Pflüger & L. H. Field, unpublished data) and from chordotonal organs associated with the coxa or with the thorax. In the metathoracic ganglion the mVAC receives projections from all COs except the femoral CO of the hind leg. A CO associated with the wing also terminates within mVAC (aRT) (Tyrer & Altman 1974; Tyrer 1983).

If the CO-projections within mVAC are compared with those from tympanic fibres, there is a clear spatial separation of the two receptor types. The COs terminate within the anterior part of mVAC whereas acoustic fibres terminate in the posterior part (H.-J. Pflüger & P. Bräunig, personal observations; H. Römer, personal communication). This is also supported by staining wing CO projections which terminate within mVAC (aRT) (Tyrer & Altman 1974; Tyrer 1983).

Lateral association centres

Another neuropilar area contacted by many sensory receptors is the laterally situated neuropile, here called the anterior and posterior LAC (aLAC and pLAC). These areas do not stain as darkly with osmium and ethyl-gallate as the VACs because they are composed of fibres with more varying diameter, but they can nevertheless be clearly distinguished from surrounding areas and interspersed tracts and nerve roots. Comparing the LACs with the VACs several differences become apparent.

Each of the VACs receives primary afferent terminals from just one class of mechanoreceptor: sensory hairs in the case of aVAC, vVAC and lVAC, scolopidia in the case of mVAC. The LACs, in contrast, receive their inputs from a great variety of mechanoreceptor types: CO, CS, HP, MS and SR. Strikingly, they do not receive any input from tactile hairs.

The topographical order for projections into VACs suggests that aVAC, vVAC and also parts of lVAC contain a highly ordered representation of the body surface, whereas the mVAC

may be regarded as an integration centre for the acoustic and vibrational senses, with their afferent terminals clearly separated according to modalities. Within the acoustic part a tonotopic ordering principle was described by Römer (1983) and Oldfield (1983).

Within the LACs no obvious topographical representation is present, although it has been shown by Zill *et al.* (1980) for CS that the axons of one particular field of receptors fasciculate within the peripheral nerve and a topograpic representation of such axon bundles of different CS fields within that nerve has been described.

The LACs, apart from mechanosensory projections, contain many collaterals of the motorneurons that innervate the muscles moving legs and wings. The VACs do not receive motorneuron branches, with one exception (cxsM-motorneuron, Bräunig 1982*a*).

As the LACs contain many fibres from motorneurons these areas had been defined as the prime sites for direct synaptic contacts of monosynaptic pathways (see Tyrer 1983). Indeed, a few monosynaptic pathways have been identified and all the receptors involved have the common feature of projections into the LACs (wing stretch receptor: Burrows (1975), hair plates: Pearson *et al.* (1976), femoral chordotonal organs: Burrows (1987)). This is in contrast to the aVAC, lVAC and vVAC which were found only to be contacted by interneurons (intersegmental interneurons: Murphey *et al.* 1983, 1985), Pflüger (1984) and Hustert (1985); local interneurons: Burrows & Siegler (1984) and Siegler & Burrows (1984)). The same is probably true for mVAC. The LACs also receive primary afferent projections from other parts of the body than the leg. For example wing hair plates, e.g. the tegula (Kien & Altman 1979; Bräunig *et al.* 1983) possess collaterals that terminate in the dorsal neuropile lateral to MDT, here called aLAC, as well as in the neuropile below and median to MDT and DIT (Tyrer 1983). Although the cervical hair plate (Kien 1980; Bräunig *et al.* 1983) has a very similar intersegmental projection pattern, the axon collaterals into aLAC are not present. Only in the dorsal neuropile surrounding MDT–DIT can branches be found. Also a multipolar sense cell from the wings, the wing stretch receptor, whose projection pattern has been revealed by Burrows (1975) and Altman & Tyrer (1977*a*, *b*) contacts aLAC.

A striking feature common to all mechanoreceptors that send collaterals into the LACs is that none of their other projections terminate in clearly defined neuropile regions. These projections appear to terminate in regions best described as 'lying between the major tracts and commissures' and to which the word 'others' refers in table 1.

In osmium and ethyl-gallate stained material these regions appear as dark halos of varying extent around the through-running fibre bundles, but sometimes it is hard to assess whether these darkly stained regions are mainly of neuronal or also of glial composition. In principle this arrangement suggests that here proprioceptive information may be carried directly to interneurons connecting different regions of a ganglion or different ganglia, or both.

The lateral VAC

The mechanoreceptors that project to well-defined regions of neuropile have been identified.

There is, however, one distinct region of neuropile that, when its size is considered, is only sparsely invaded by mechanoafferent terminal ramifications, the lVAC. Therefore we expect other sensory receptors to terminate here. Indeed we have as yet no information about the central projection pattern of the numerous contact chemoreceptors on the locust body surface. Nearly all attempts to stain them selectively have so far failed, most likely because of the extremely small fibre diameter of their sensory neurons.

Backfills of major peripheral nerves which must also contain the fibres of these contact chemoreceptors did not reveal projections different from the ones described above. In such backfills also lVAC was stained. Two successful selective backfills from coxal contact chemoreceptors (R. Hustert, unpublished results) show projections within lVAC. Therefore we assume that contact chemoreceptors primarily terminate within lVAC.

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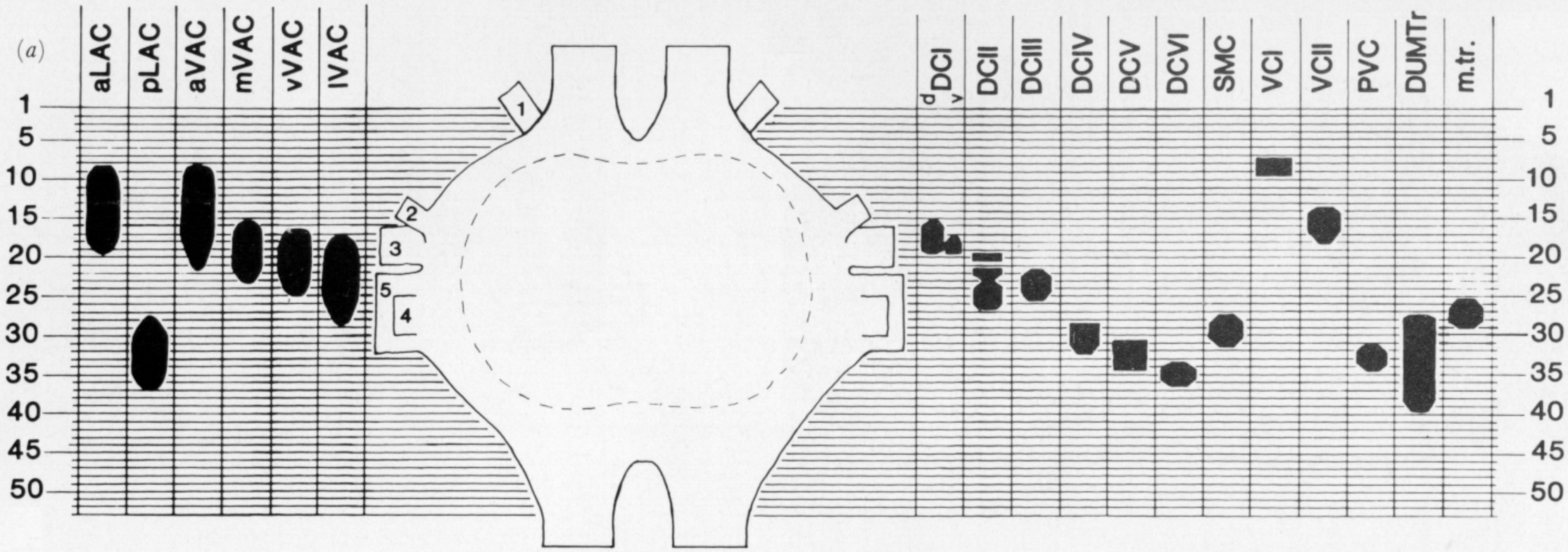
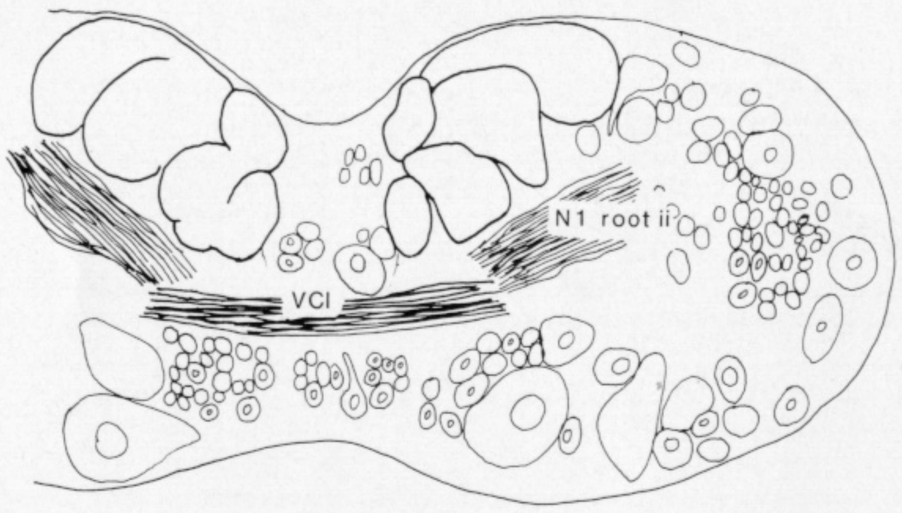
List of abbreviations used

A1–3	abdominal neuromere 1–3	feCO	femoral CO
AG 1–3	abdominal ganglion 1–3 (neuromere)	myoCO	myochordotonal organ
ant	anterior	plCO	pleural CO
AVC	anterior ventral commissure	vCO	ventral CO
CO	chordotonal organ	CS	campaniform sensilla
aCO	anterior CO	trCS	trochanteral field of CS
apCO	apodemal CO	CT	C-tract
cCO	coxal CO	cxsM	coxosutural muscle

LIST OF ABBREVIATIONS USED (*cont.*)

DC I–VI	dorsal commissures I–VI
dDCI	dorsal part of DCI
vDCI	ventral part of DCI
DIT	dorsal intermediate tract
DMT	dorsal median tract
dDMT	dorsal part of DMT
vDMT	ventral part of DMT
dors	dorsal
DUMTr	tract of dorsal unpaired median (DUM) cells
FETi	fast extensor tibiae (motorneuron)
H	tactile hairs
HP	hair plates
cxHP	coxal hair plate
trHP	trochanteral hair plate
LAC	lateral association centre
aLAC	anterior LAC
pLAC	posterior LAC
LDT	lateral dorsal tract
LVT	lateral ventral tract
iLVT	inner LVT
oLVT	outer LVT
MDT	median dorsal tract
MESO	mesothoracic ganglion
META	metathoracic ganglion
Mns	motor neurons
MRO	muscle receptor organ
cxtrMRO	coxotrochanteral MRO
MS	multipolar sensilla
mtr	midline trachea
MVT	median ventral tract
N 1–5	peripheral nerves 1–5, (different roots are indicated i–v)
PRO	prothoracic ganglion
PT	perpendicular tract
PVC	posterior ventral commissure
rb	recurrent branch
RT	ring tract
aRT	anterior part of ring tract
SMC	supra median commissure
st	sternal
SR	strand receptor
T3	thoracic neuromere of the metathoracic ganglion
tg	tergal
TT	T-tract
VAC	ventral association centre
aVAC	anterior VAC
lVAC	lateral VAC
mVAC	medial VAC
dmVAC	dorsal part of mVAC
vmVAC	ventral part of mVAC
vVAC	ventralmost VAC
VC I–II	ventral commissures I–II
VCLII	ventral commissural loop II
dVCLII	dorsal part of VCLII
vVCLII	ventral part of VCLII
VIT	ventral intermediate tract
VLT	ventral lateral tract





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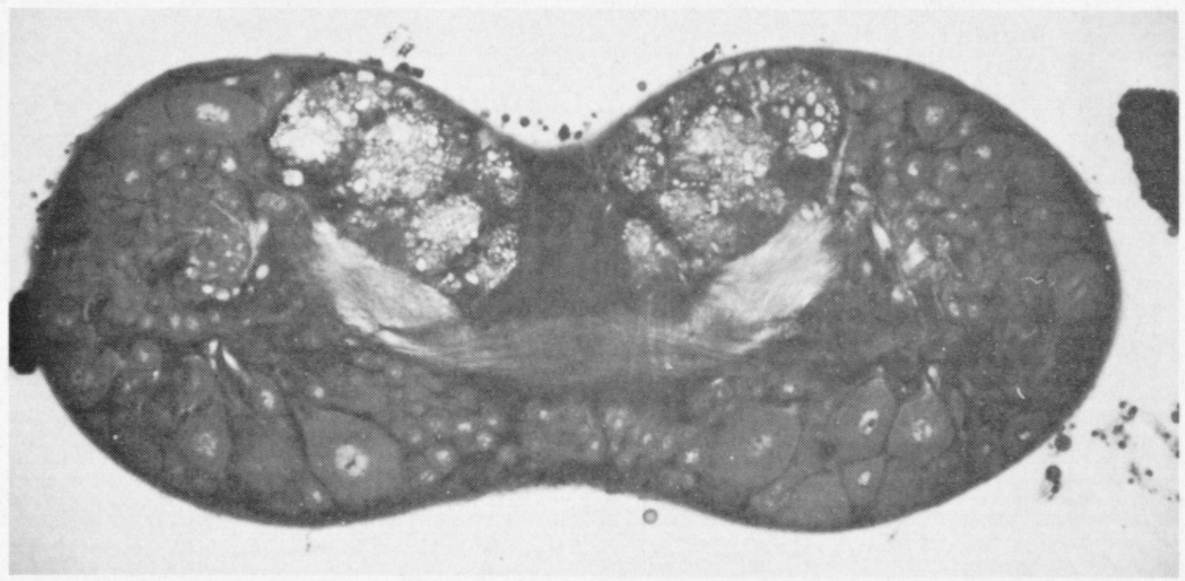
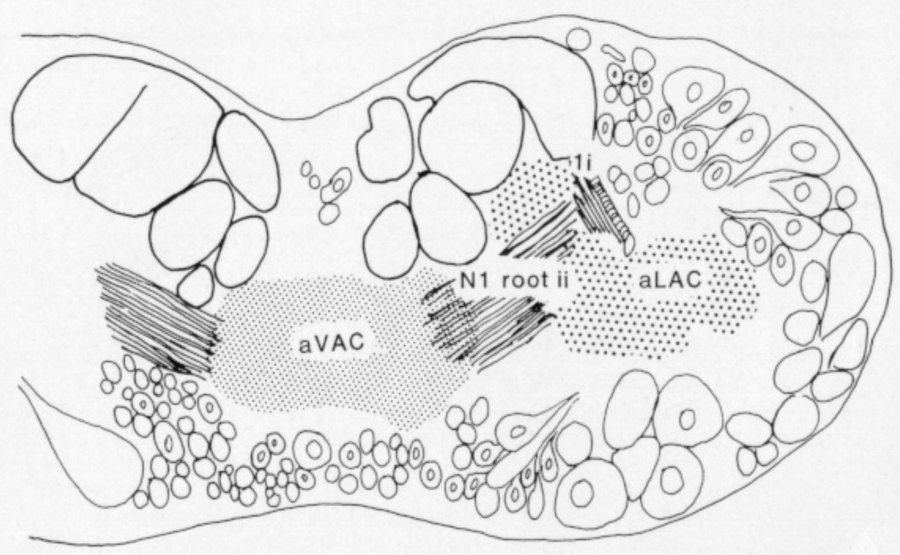
(8)





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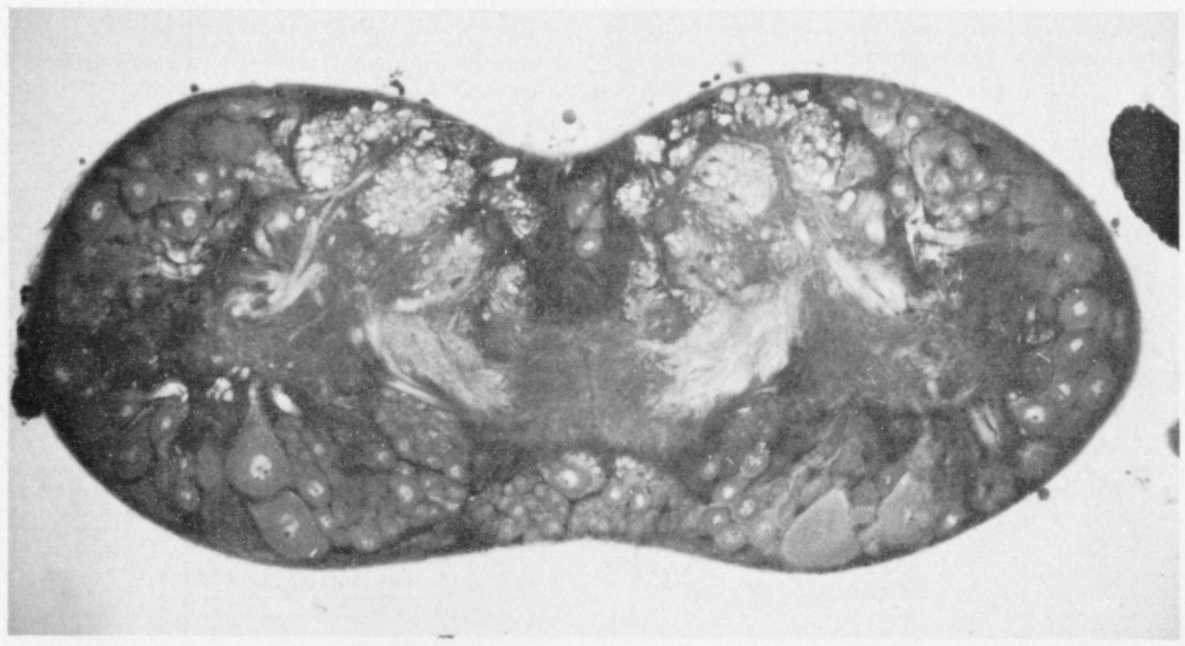

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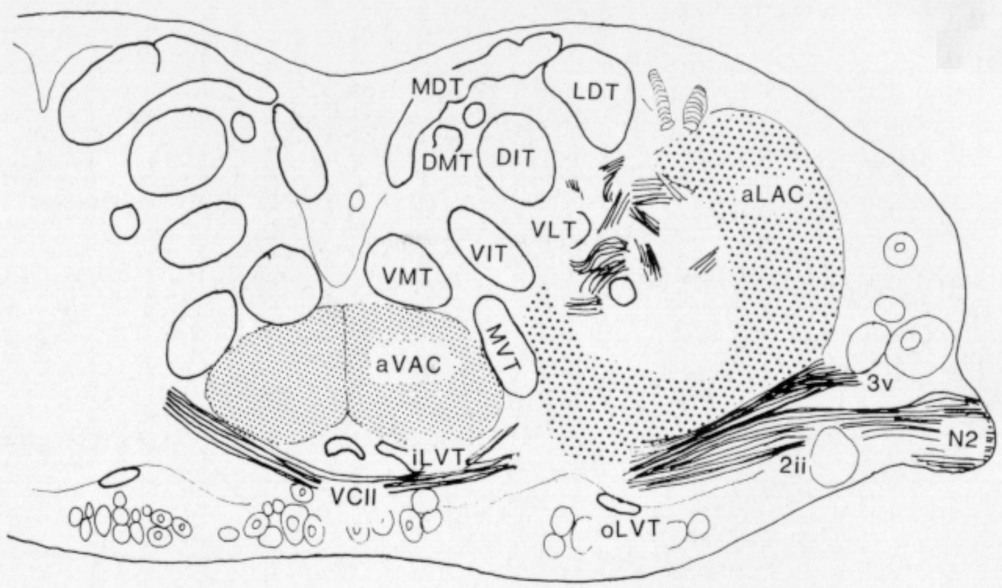

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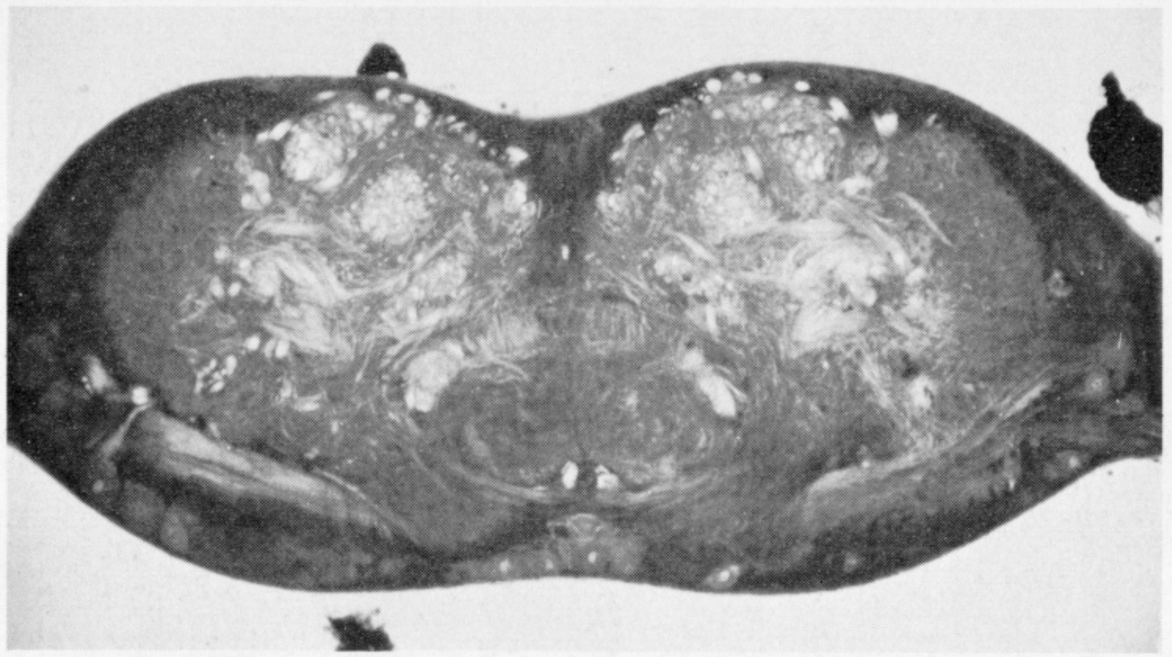
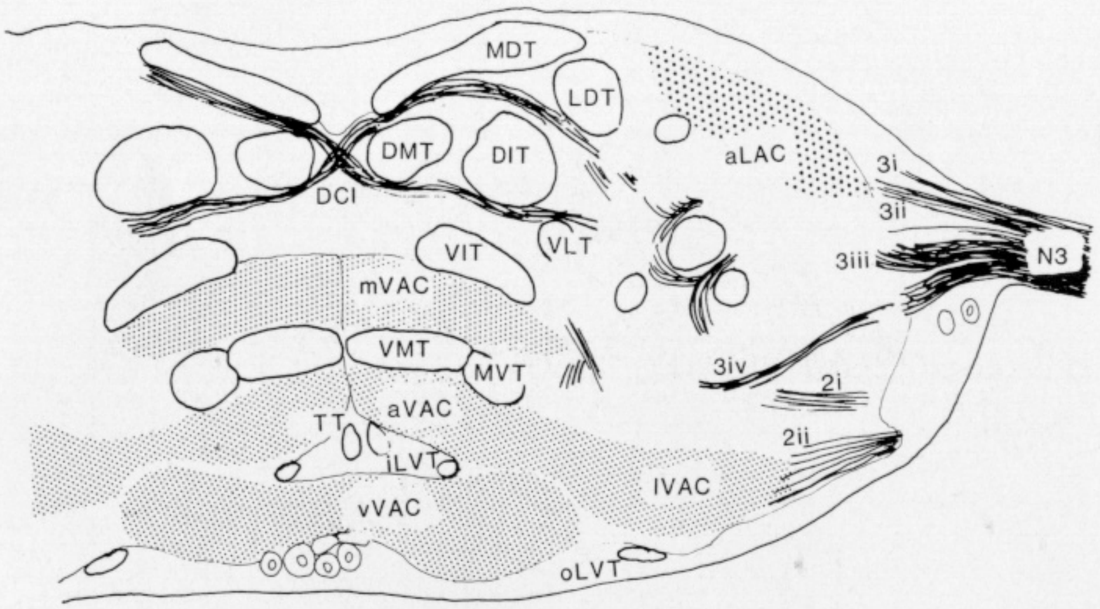
(15)





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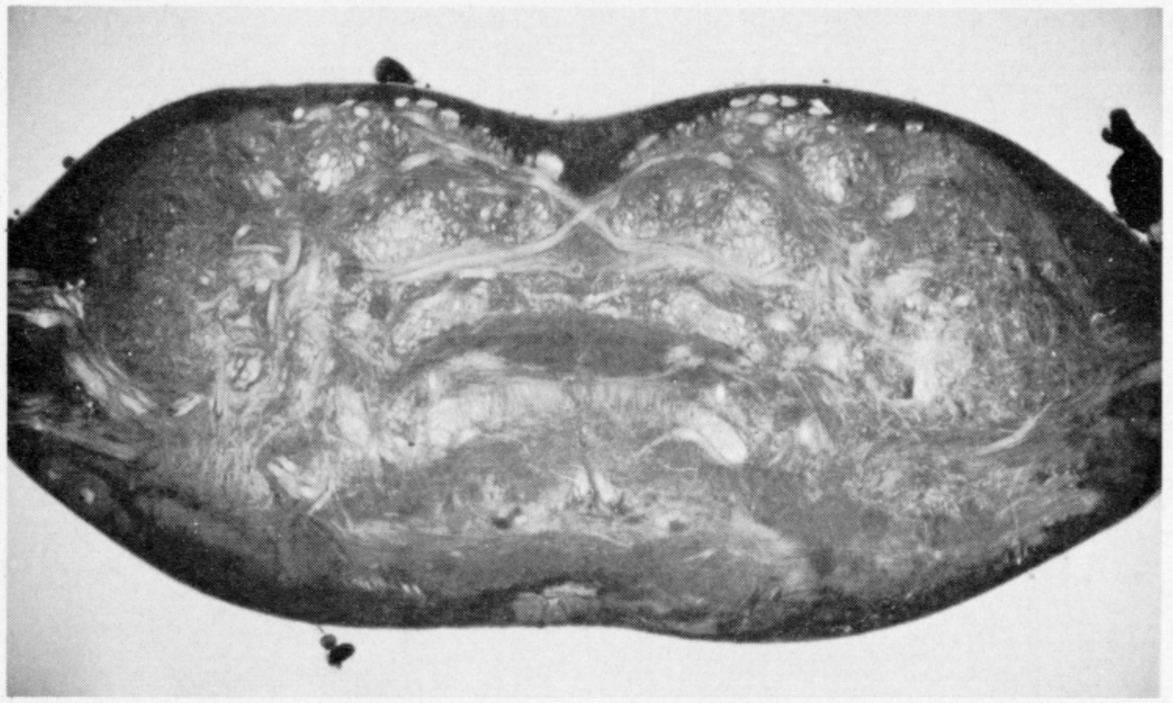

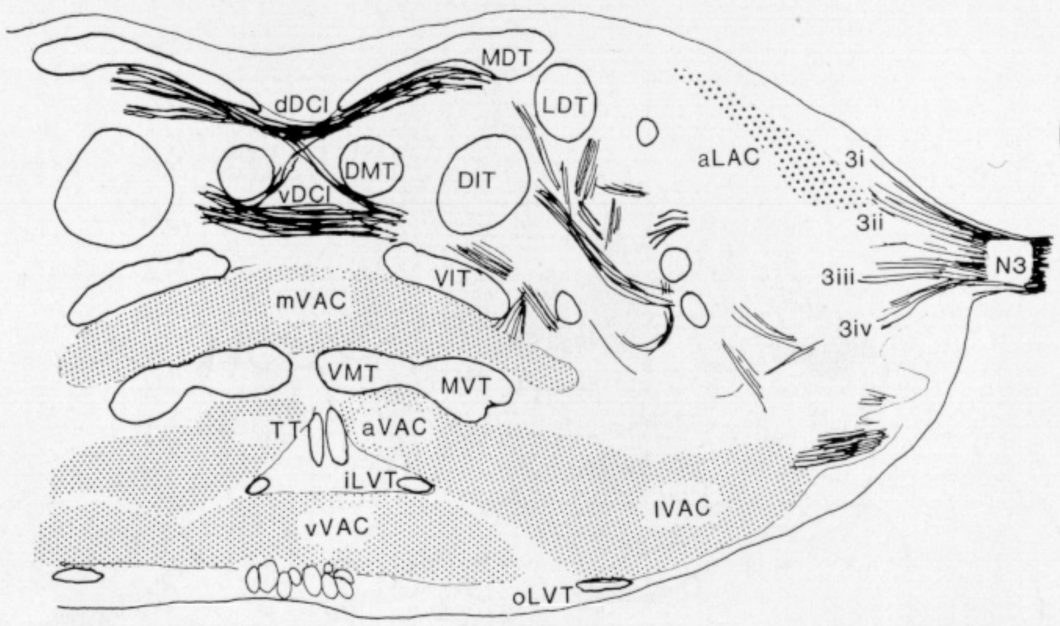

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(19)

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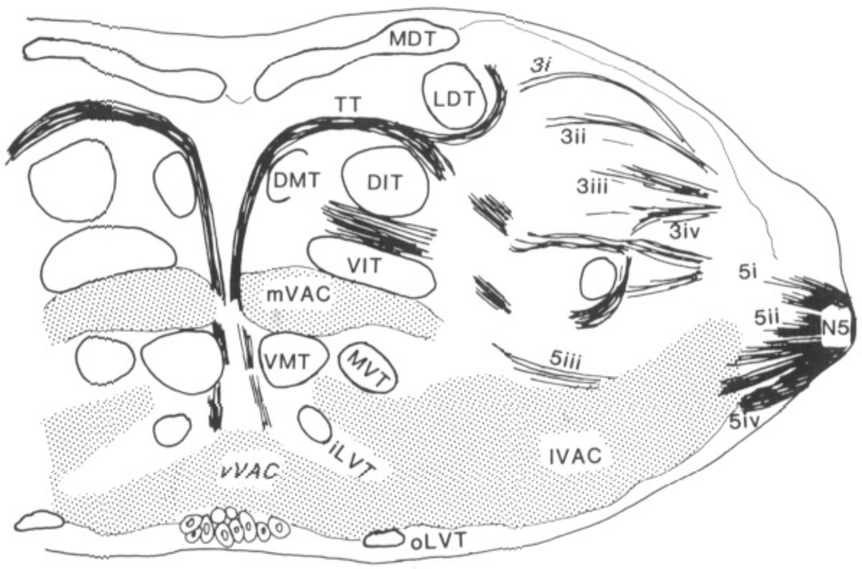

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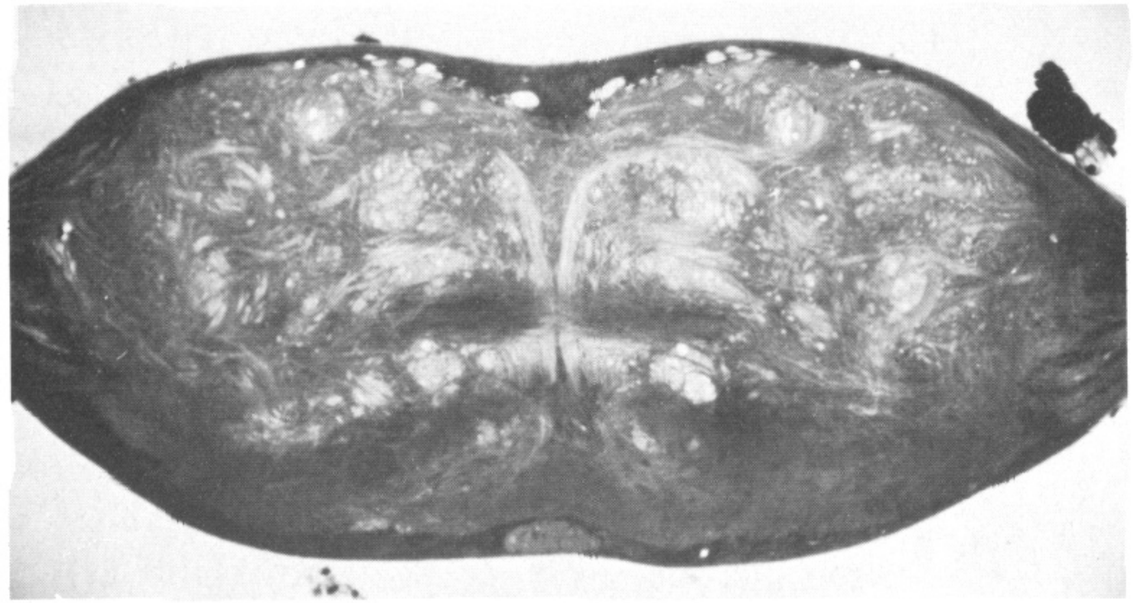

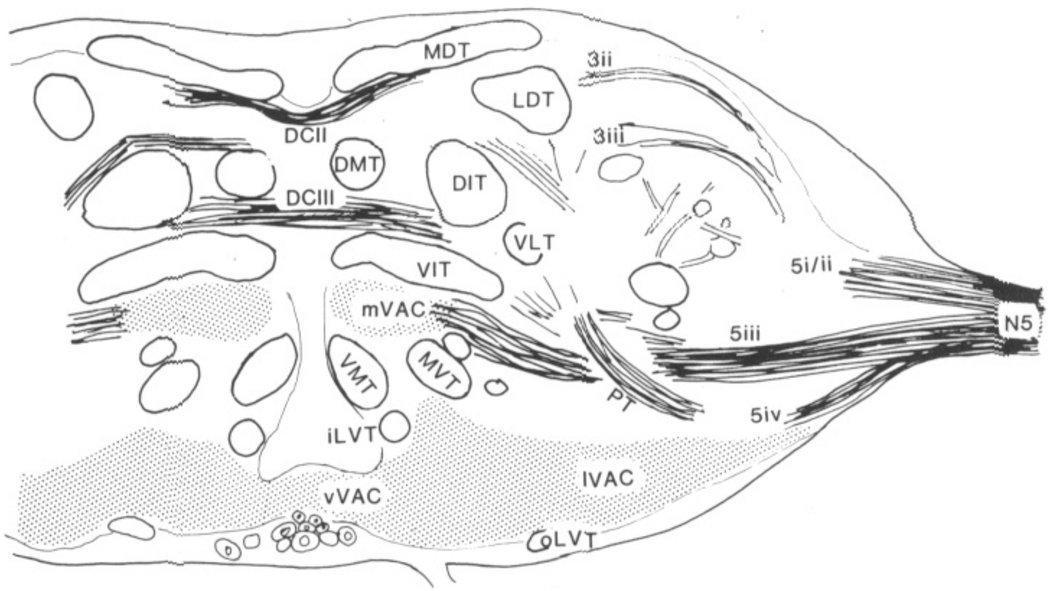

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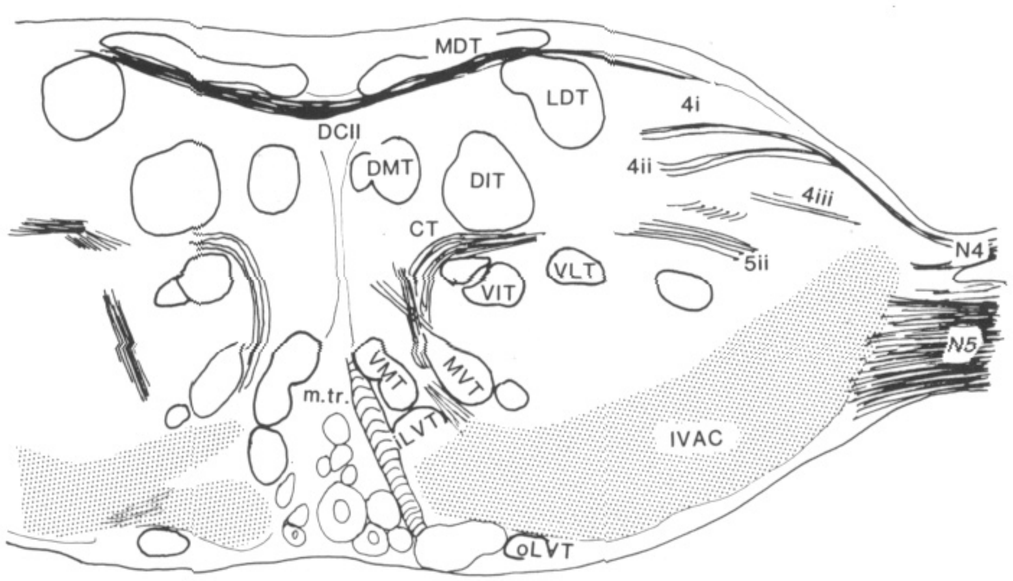

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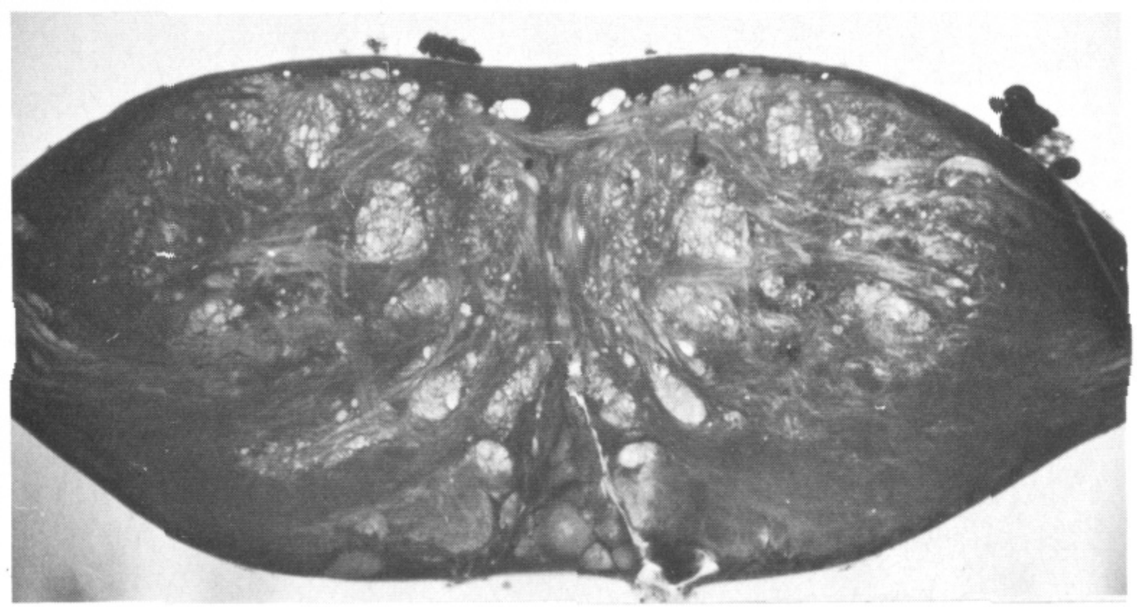

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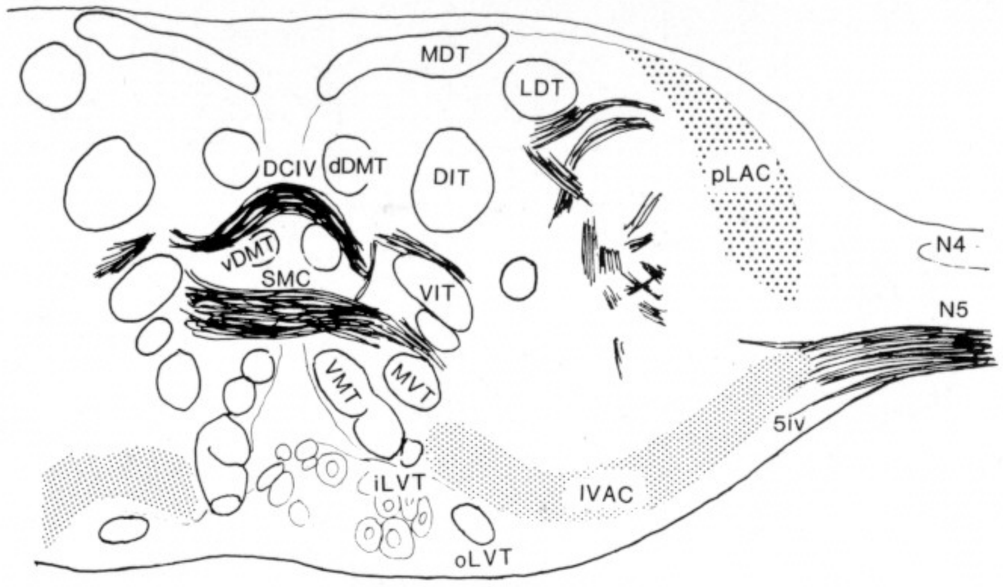

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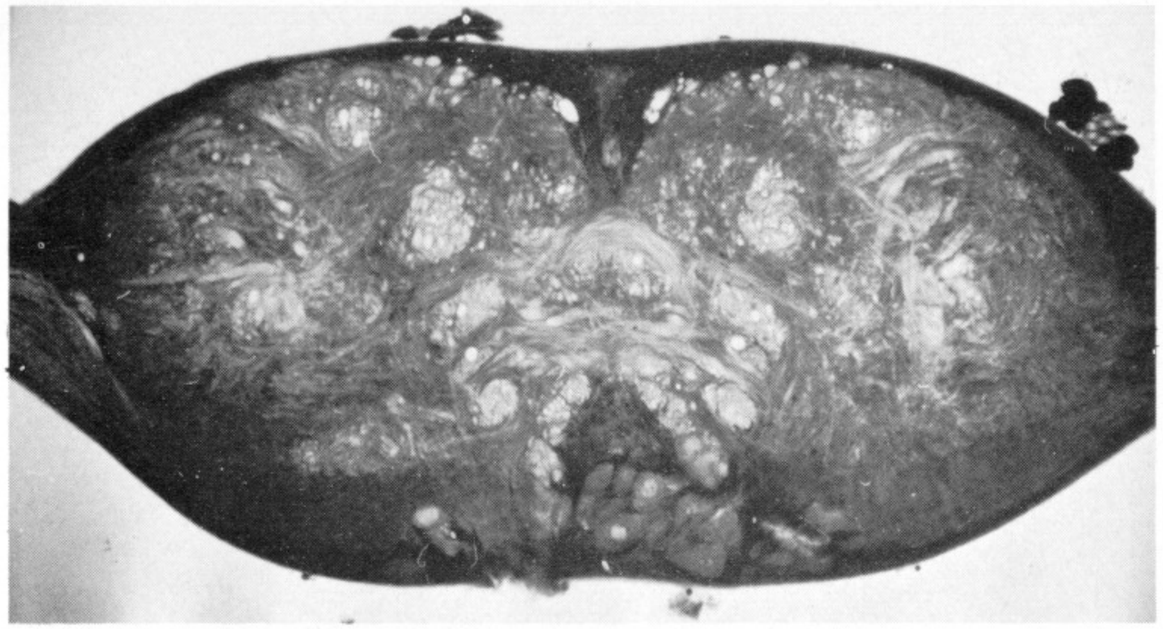

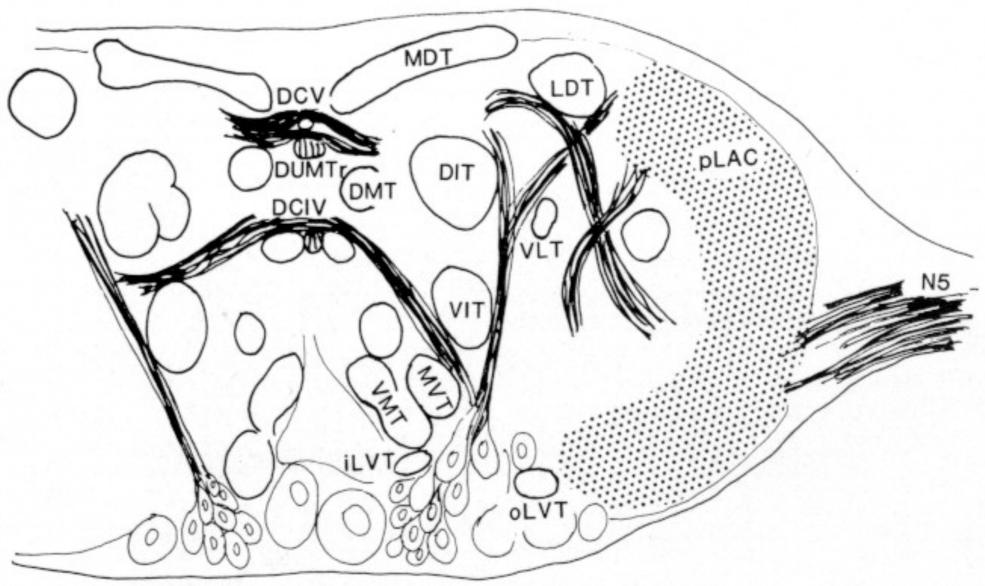

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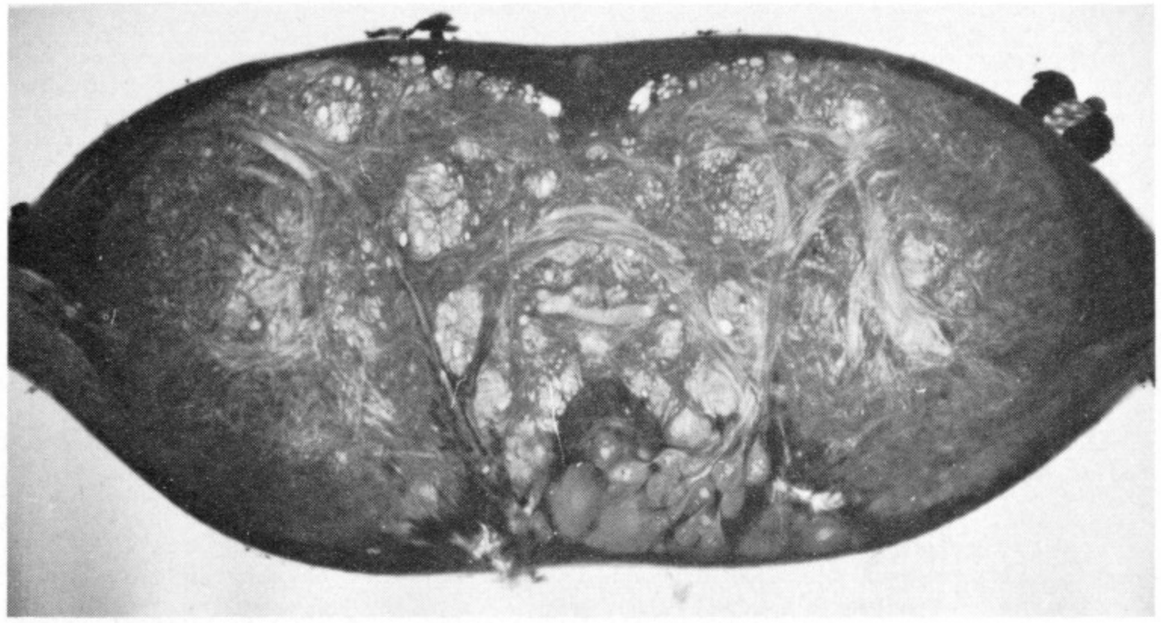

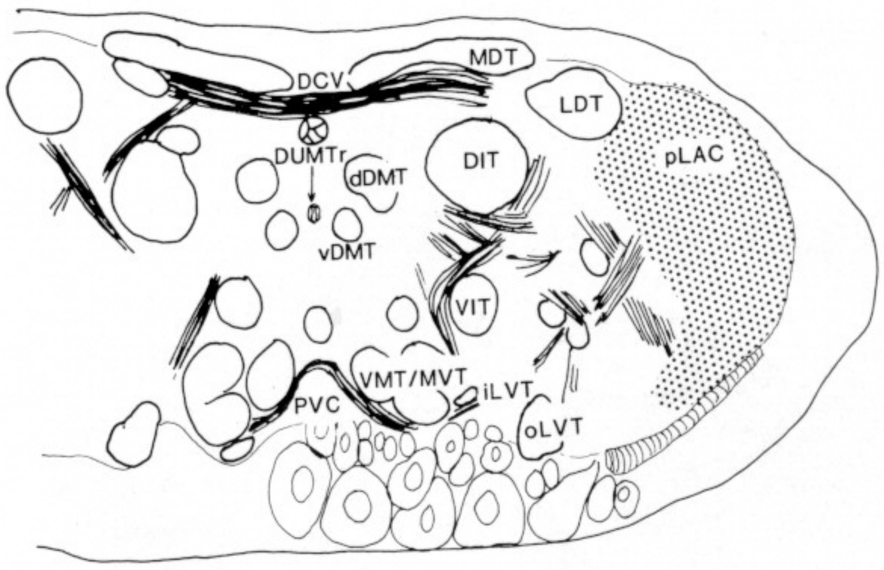

(*l*)

(33)

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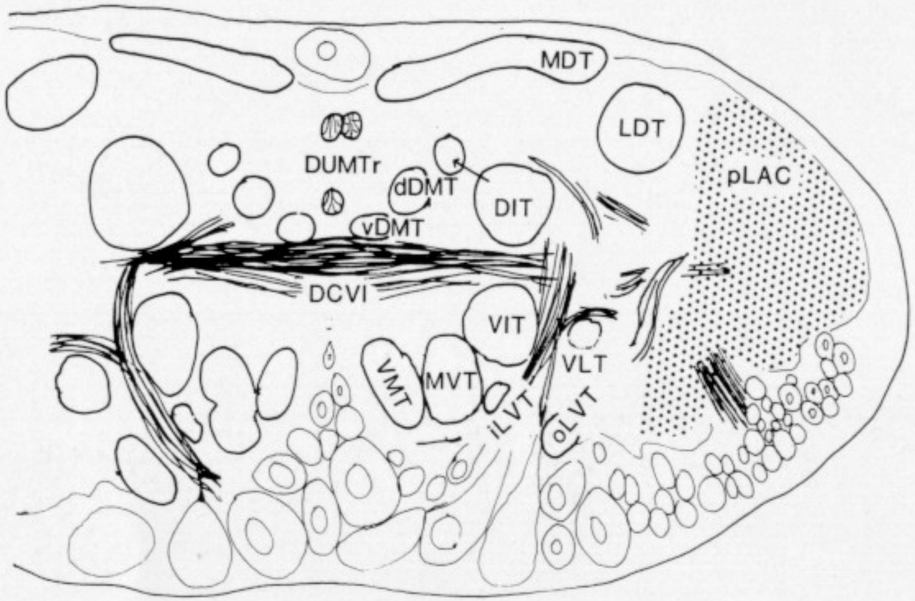

(*m*)

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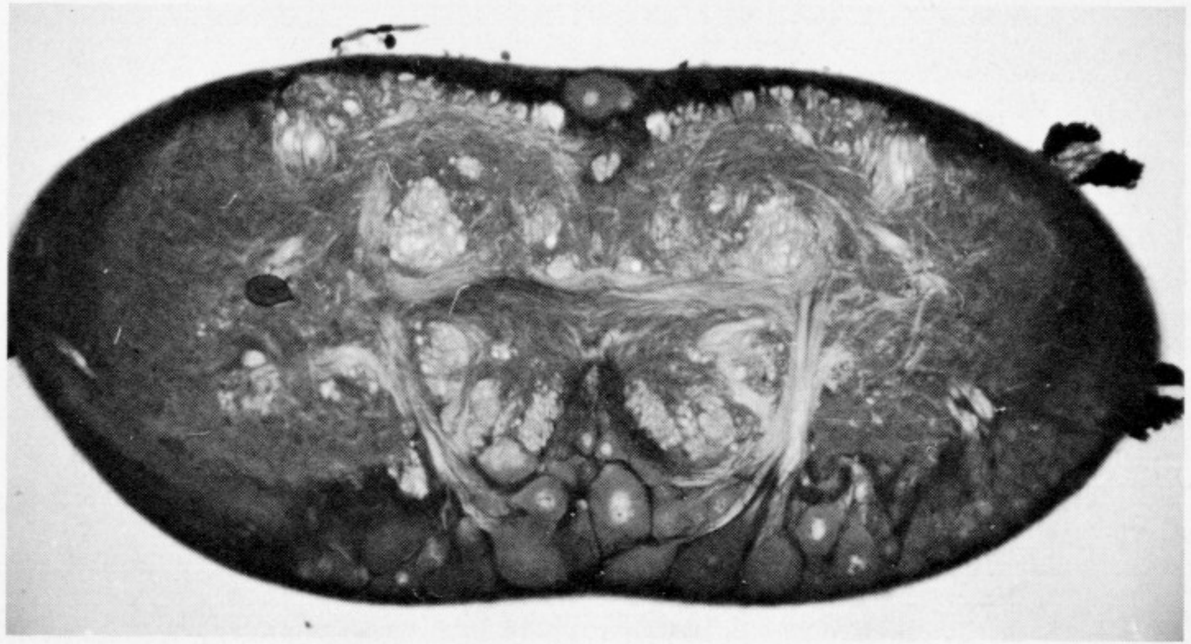

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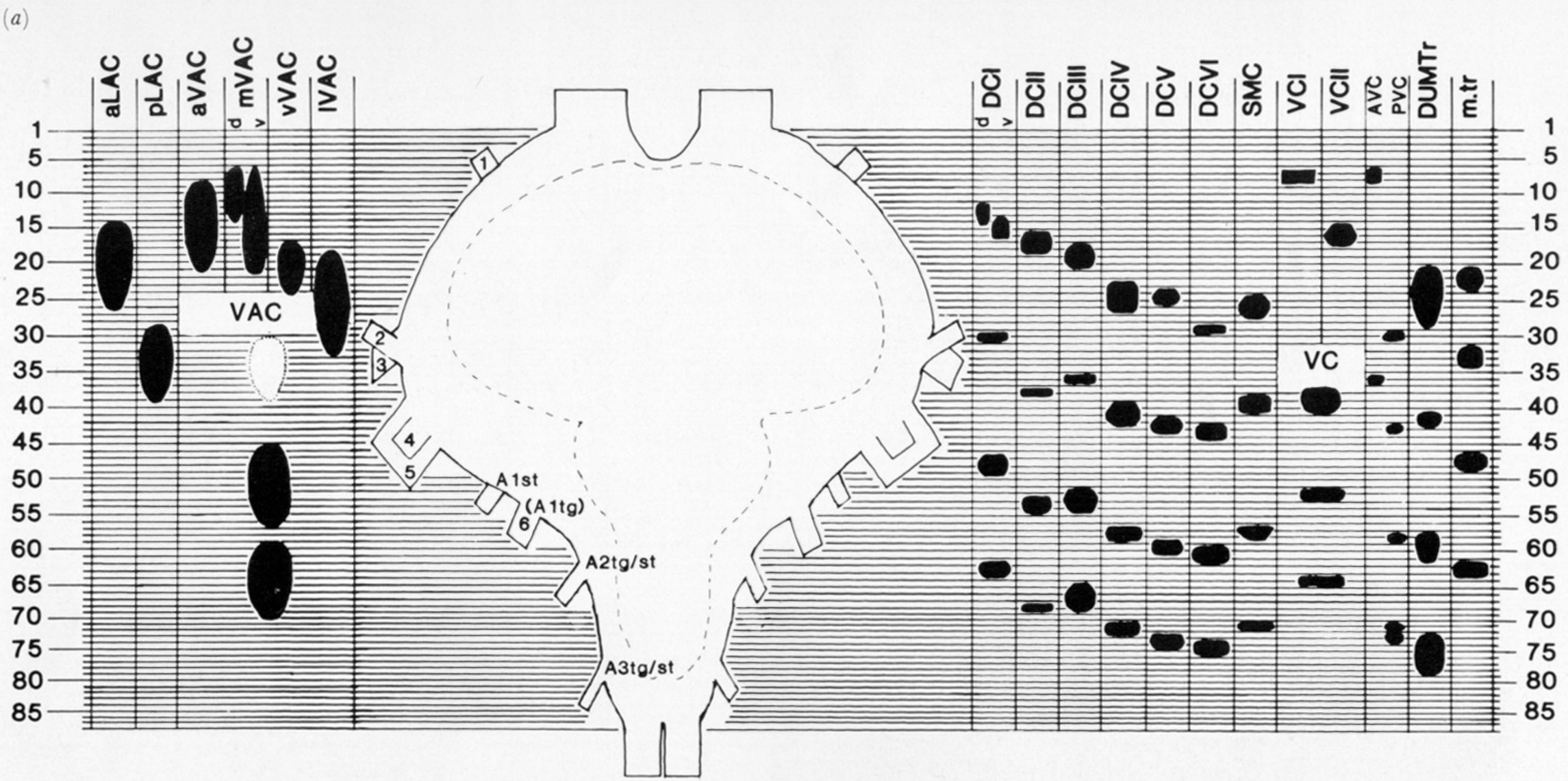

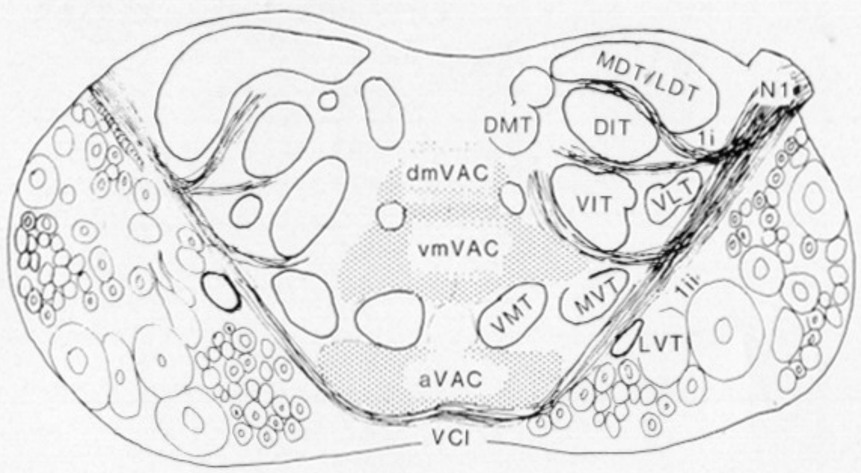

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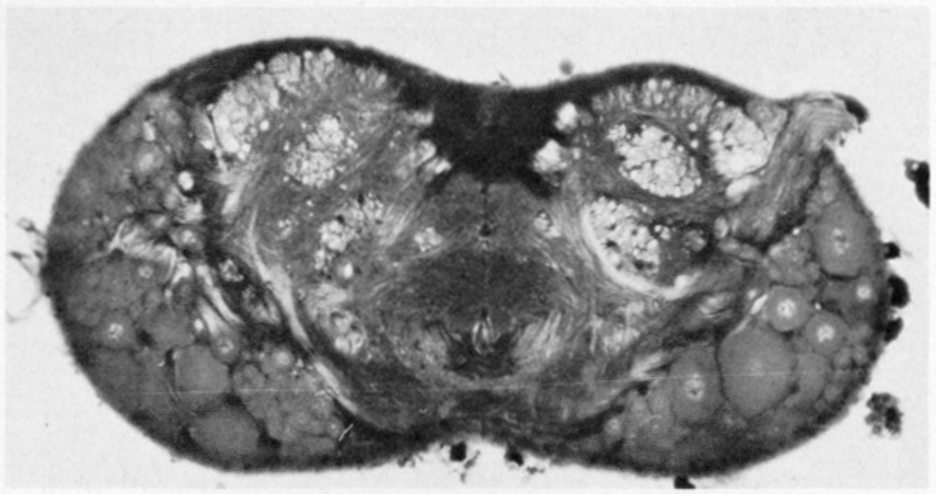
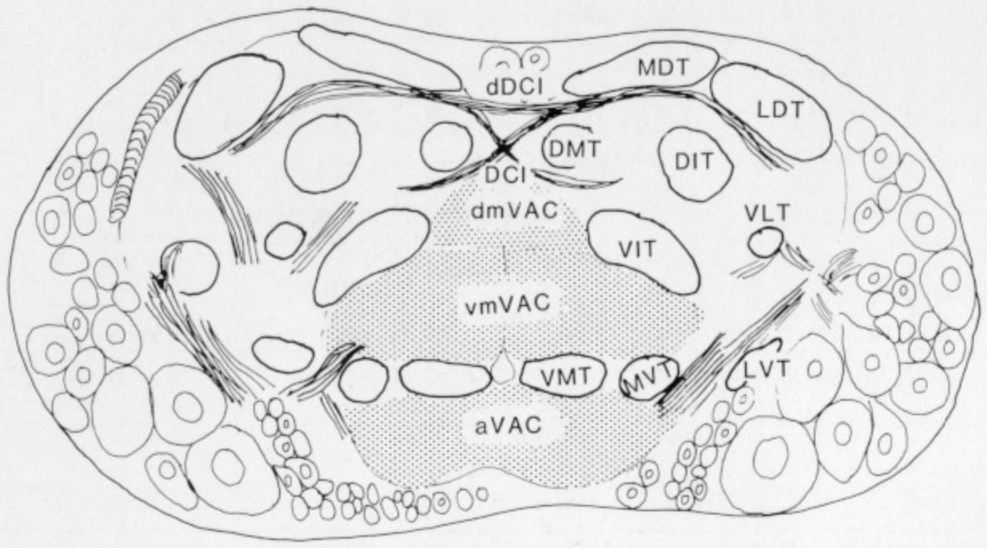
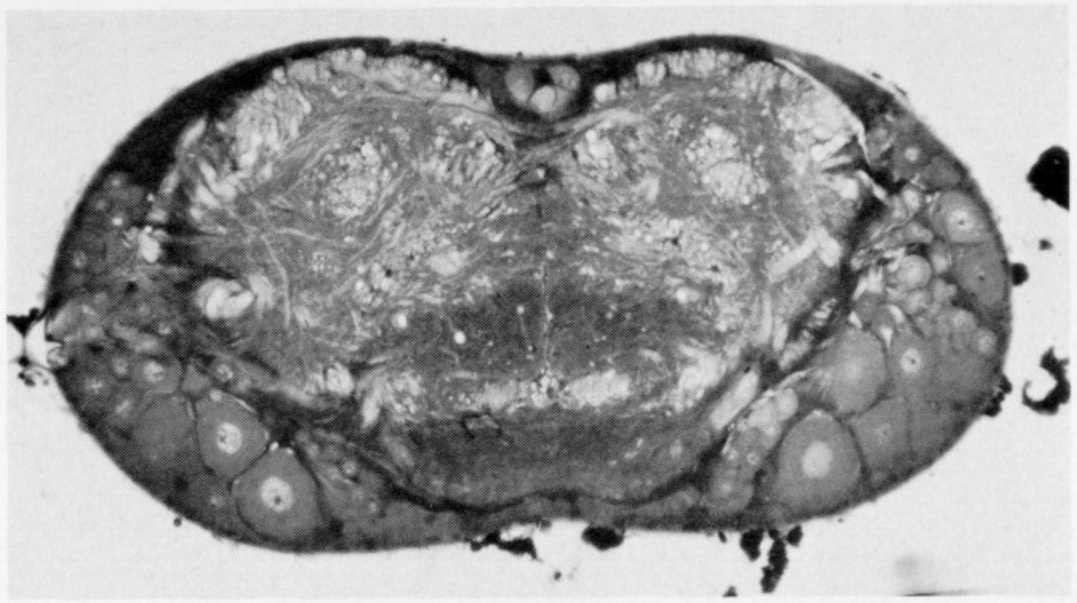


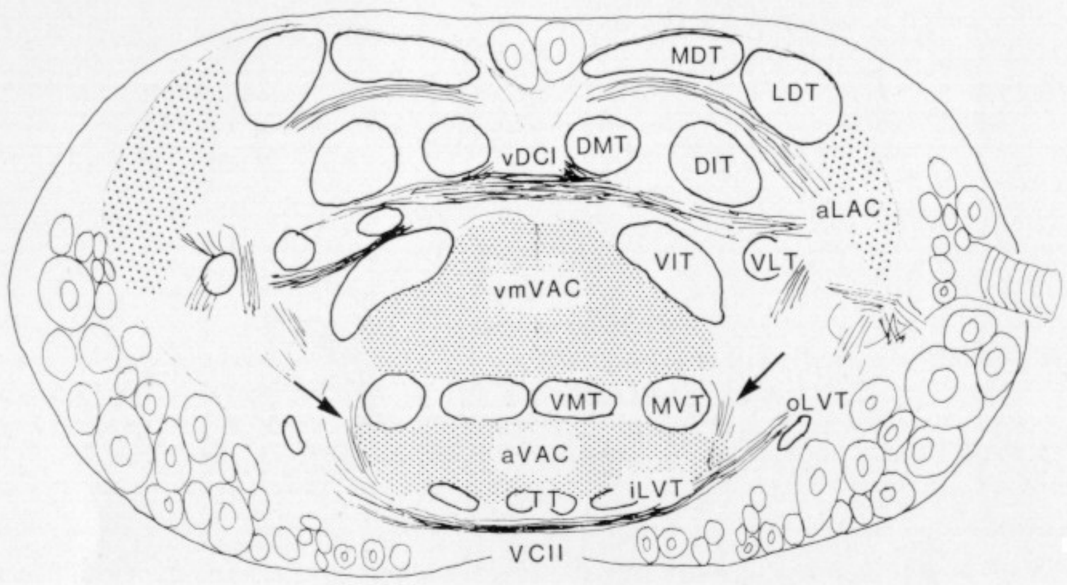
FIGURE 2. (*a*) Ventral view of a metathoracic ganglion cut into 16 μm sections starting with section 1 (first cell bodies visible) and ending with section 88 (last cell bodies visible). Prominent neuropiles, commissures and other structures are indicated as black bars. For white bar surrounded by a dotted line (VAC in the first abdominal neuromere), see text. Thickness of bars gives a relative measure of the size of the structures in the sections. (*b–k*) Selected sections of metathoracic ganglion stained with osmium and ethyl-gallate. Numbers in brackets refer to section numbers in (*a*). Where two numbers are stated the camera lucida drawing (left) is a composite of two sections, whereas the photograph (right) shows only one. Calibration 100 μm; abbreviations: see List of abbreviations used; A1st, A1tg, A2tg/st, A3tg/st refer to the sternal and tergal nerve of the first, second and third fused abdominal neuromere; VC: ventral commissures.



(c)

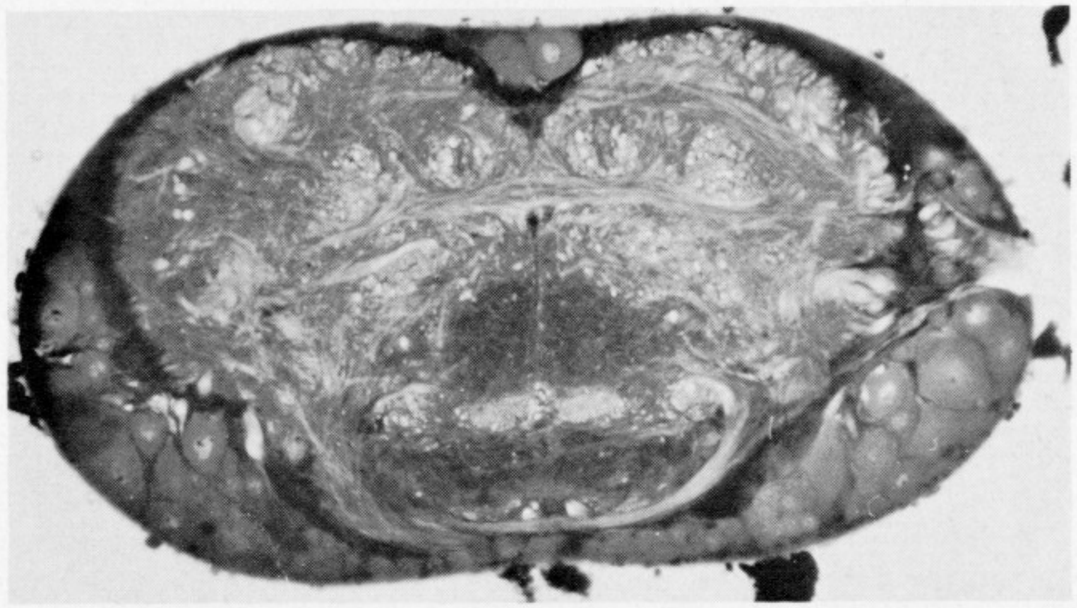
(12)

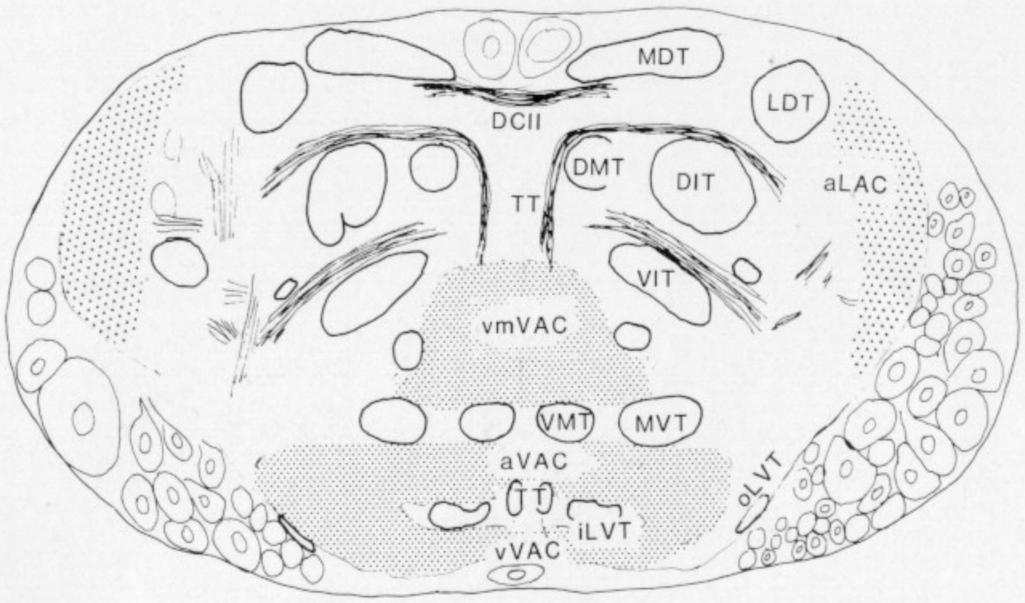




(d)

(15)

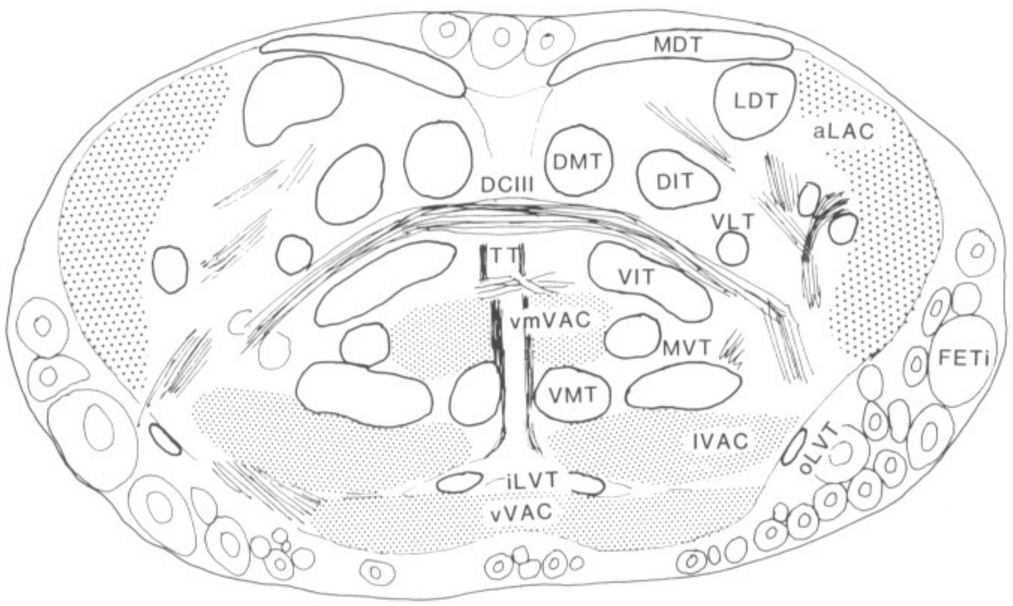




(e)

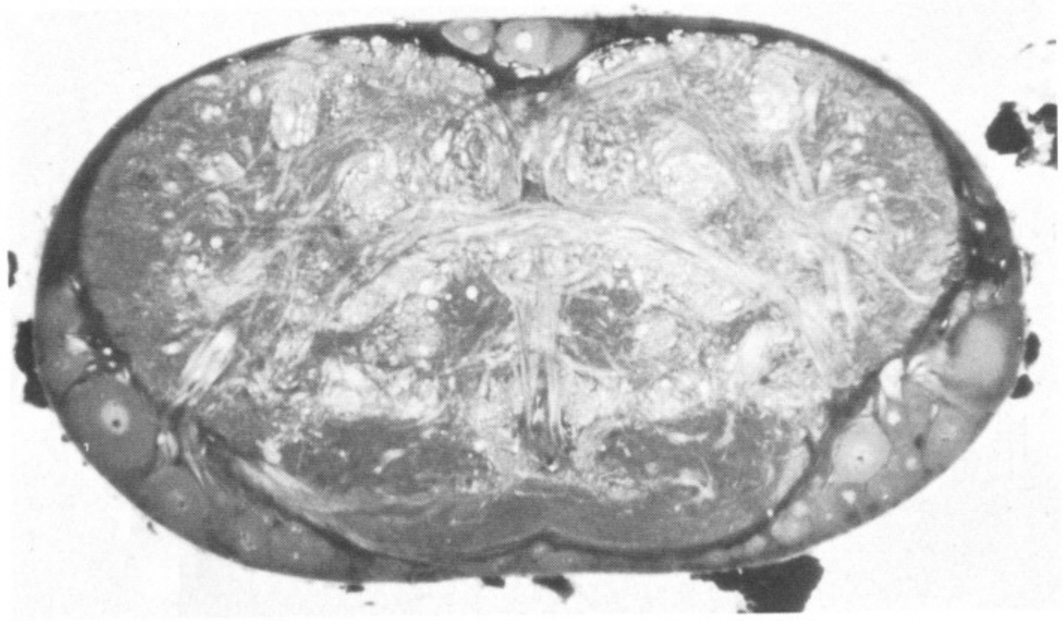
(17/18)

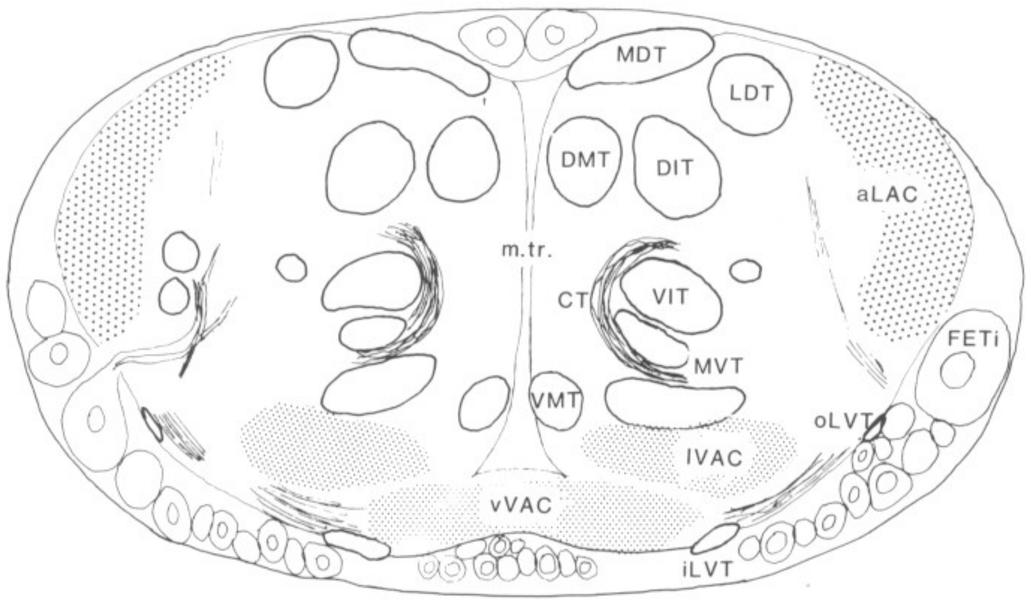
FIGURE 2*c–e*. For description see opposite.



(*f*)

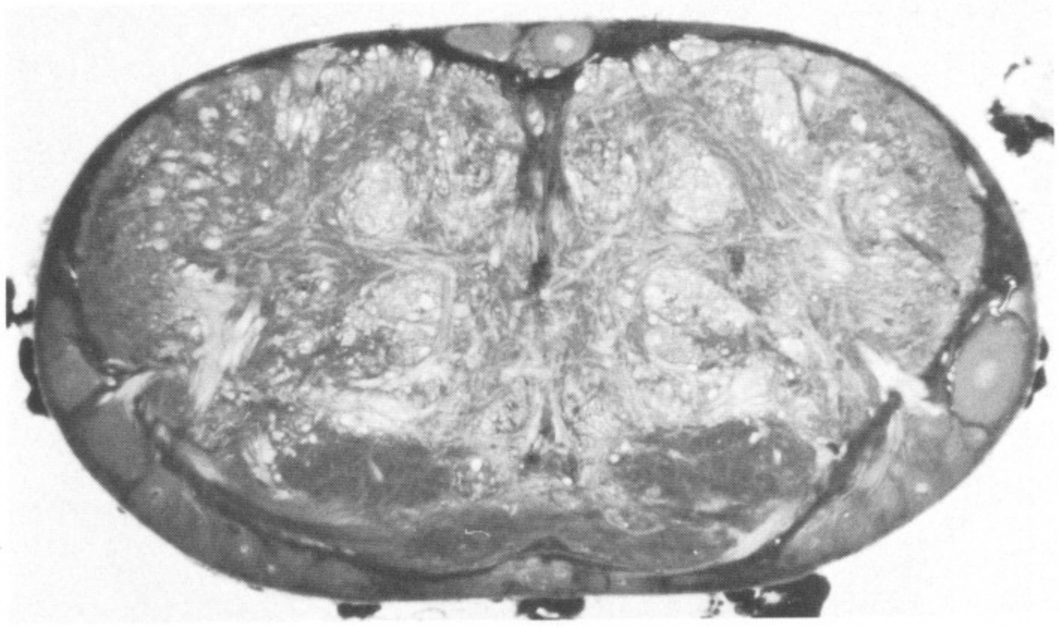
(20)

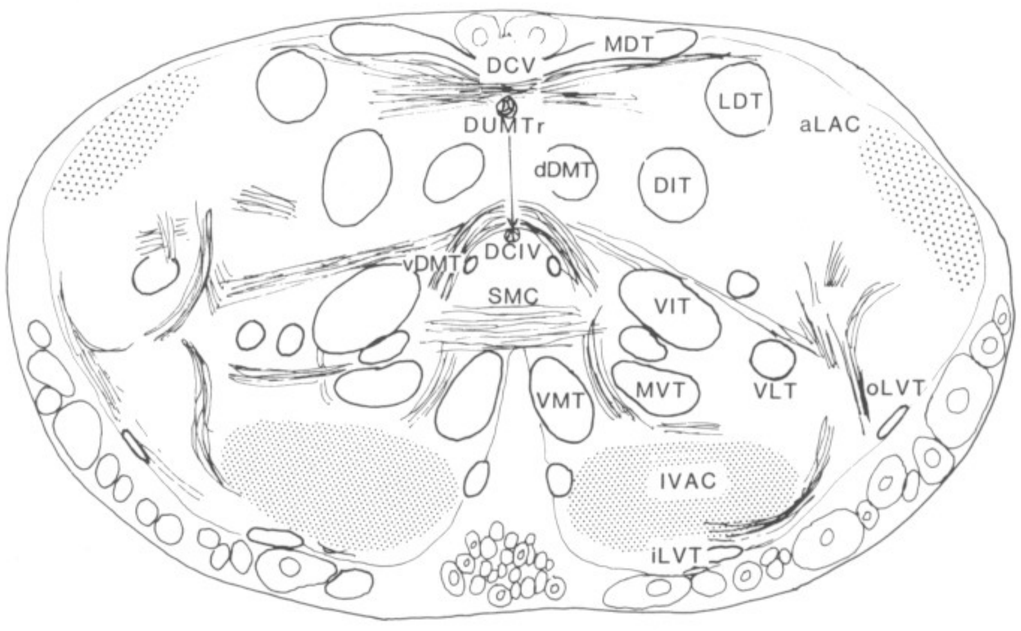




(*g*)

(21/22)

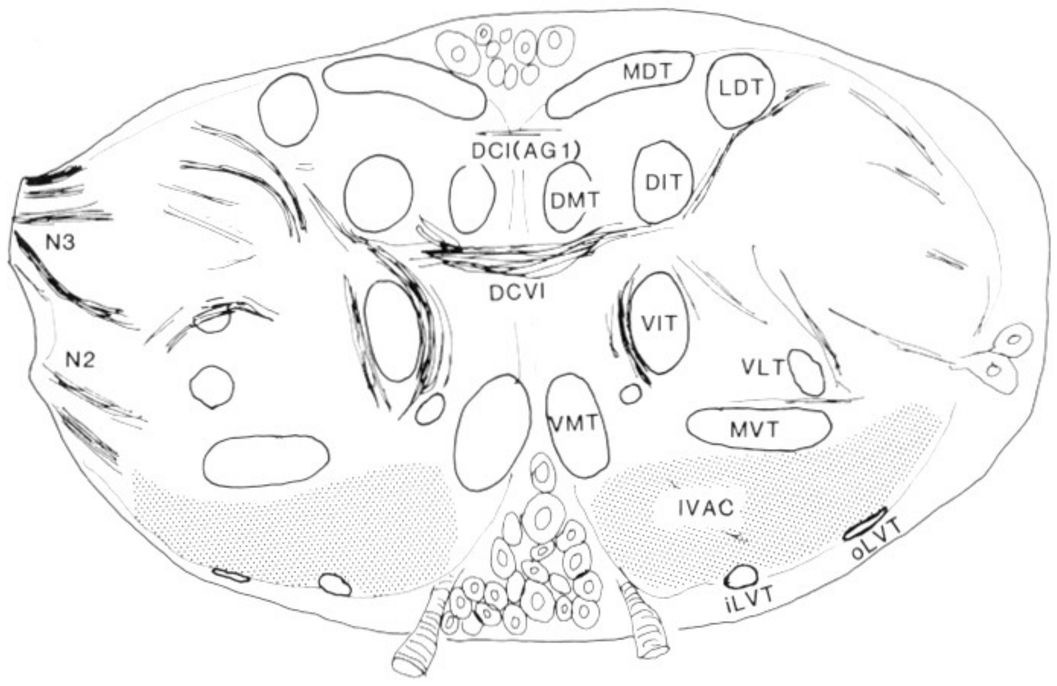




(*h*)

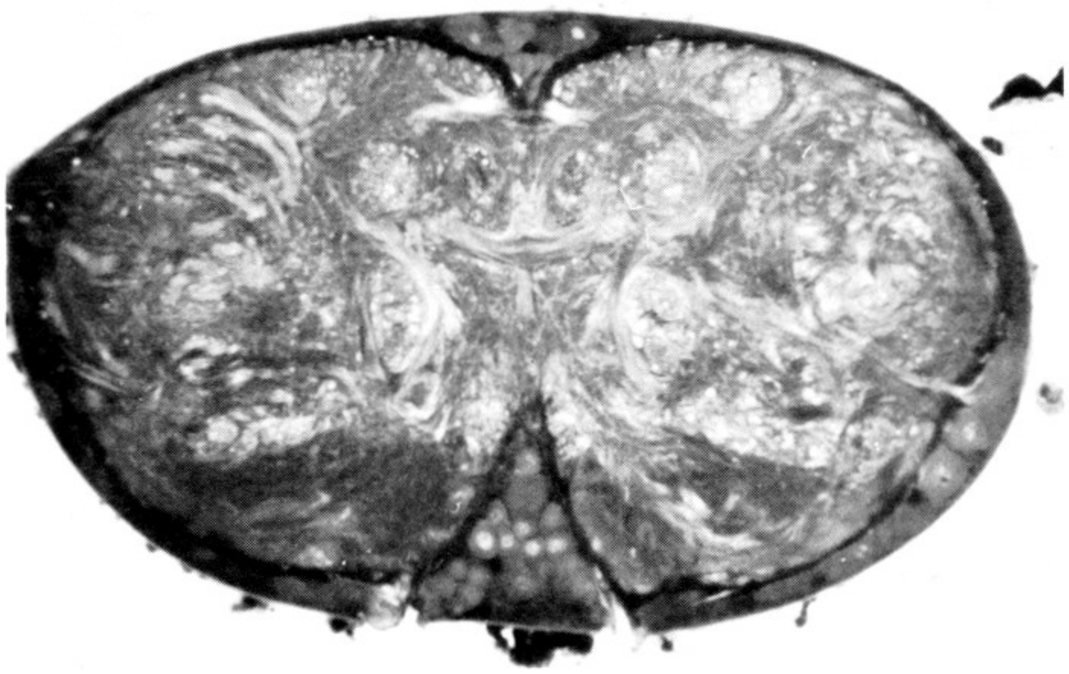
(25/26)

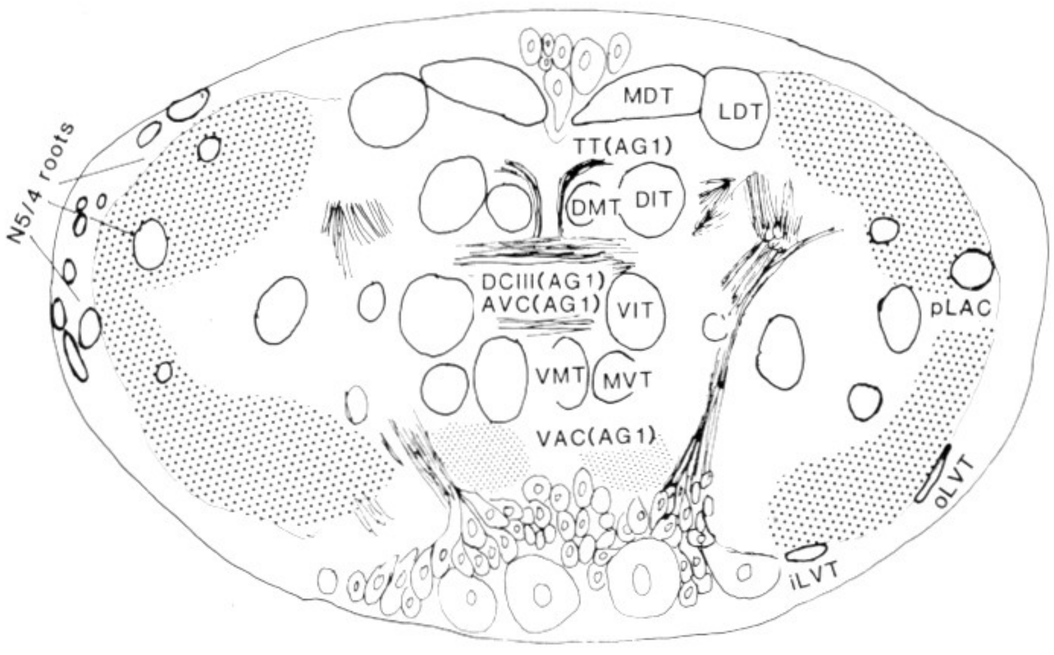
FIGURE 2*f–h*. For description see plate 6.



(*i*)

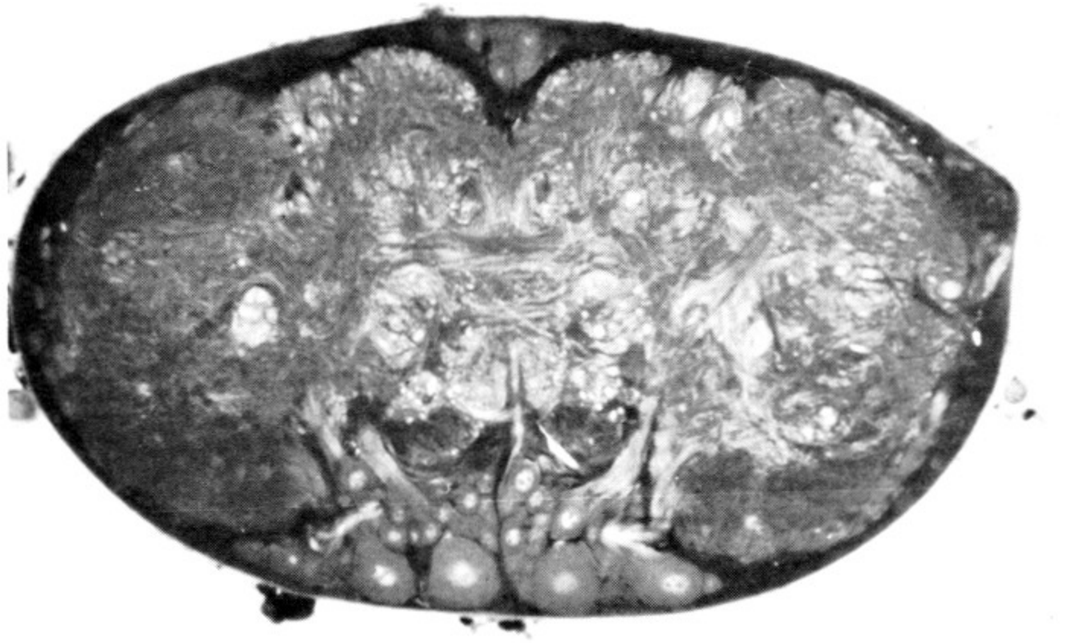
(29/30)

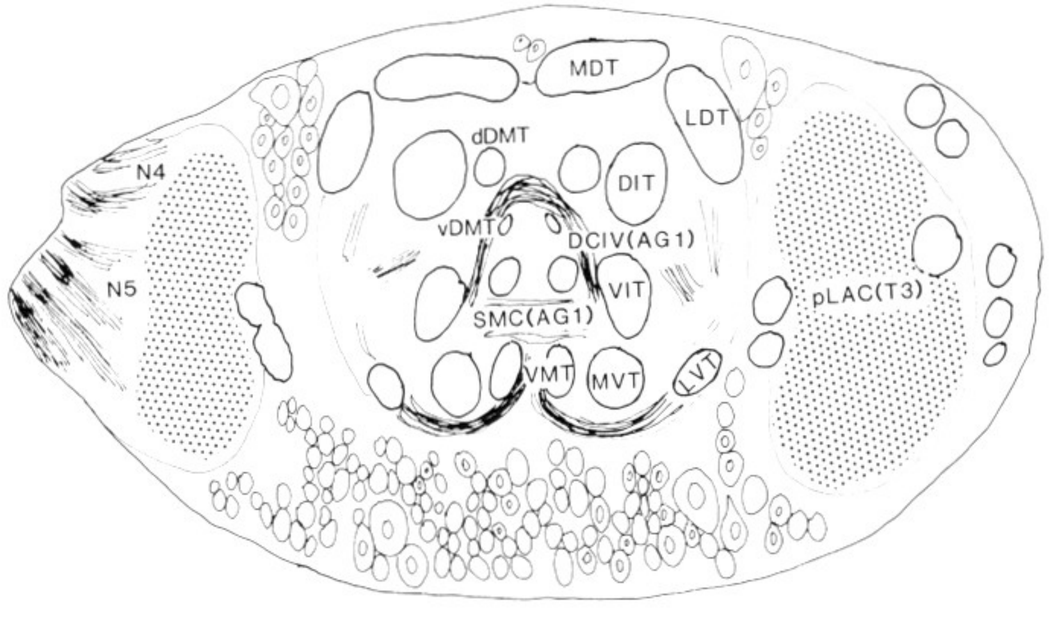




(*j*)

(36)





(*k*)

(39/40)

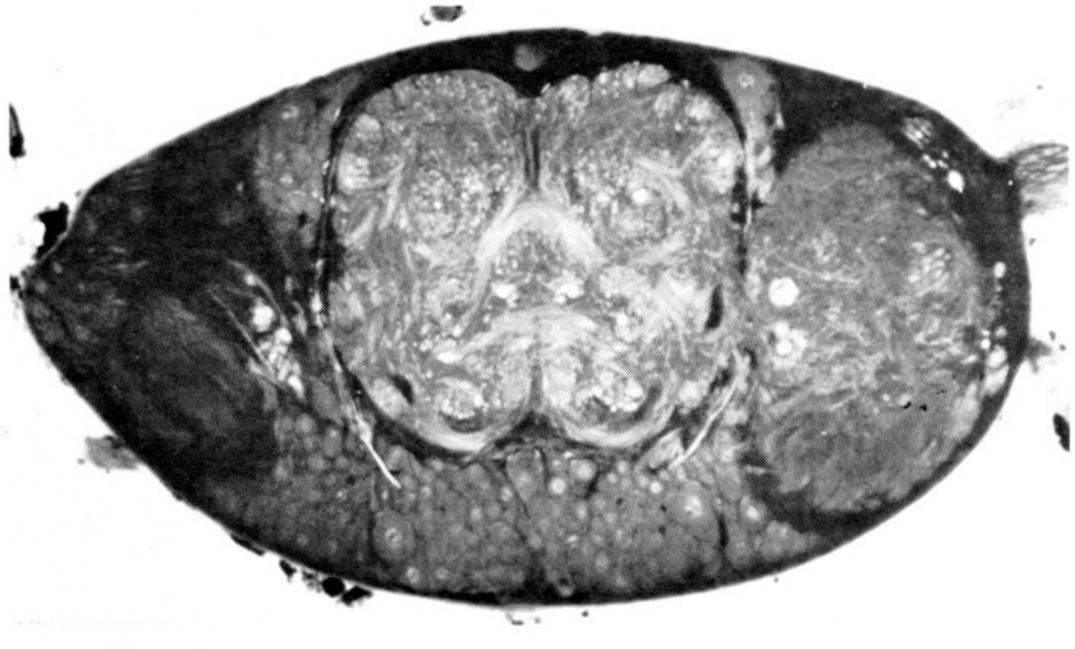
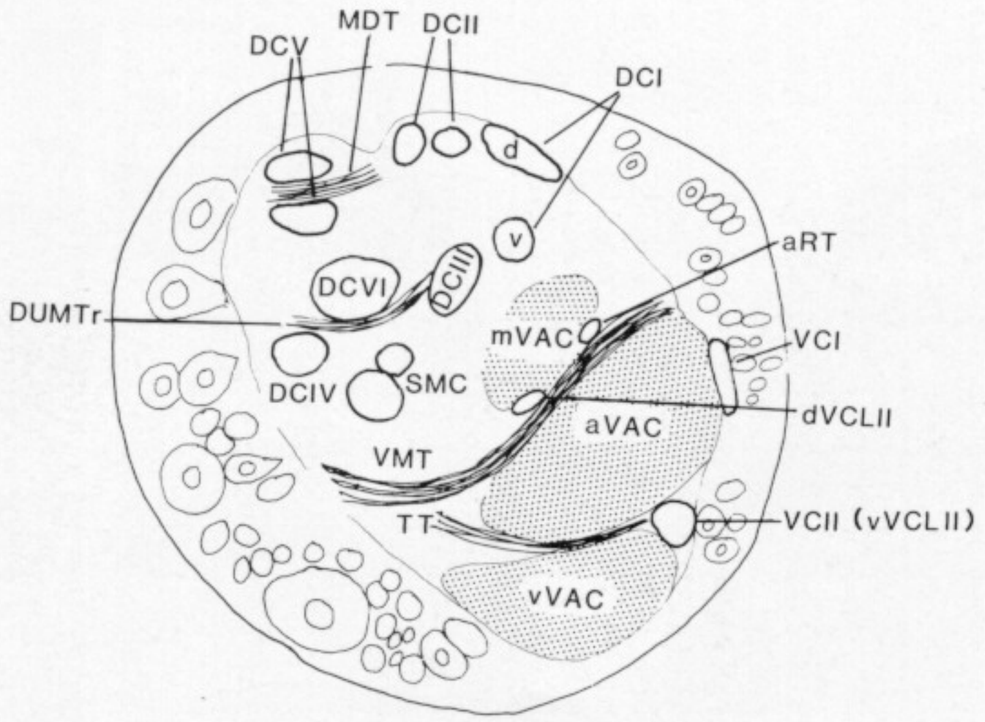
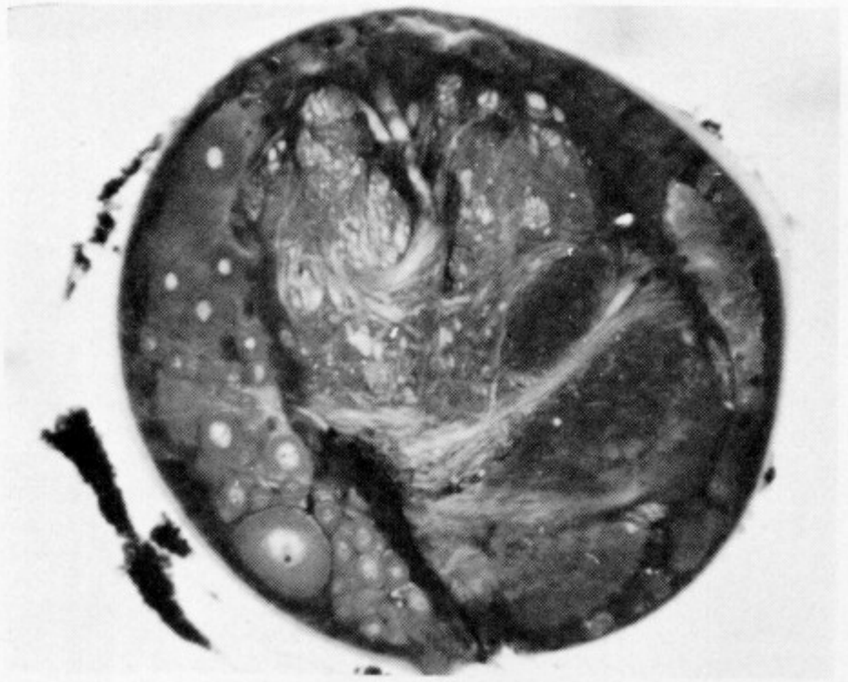
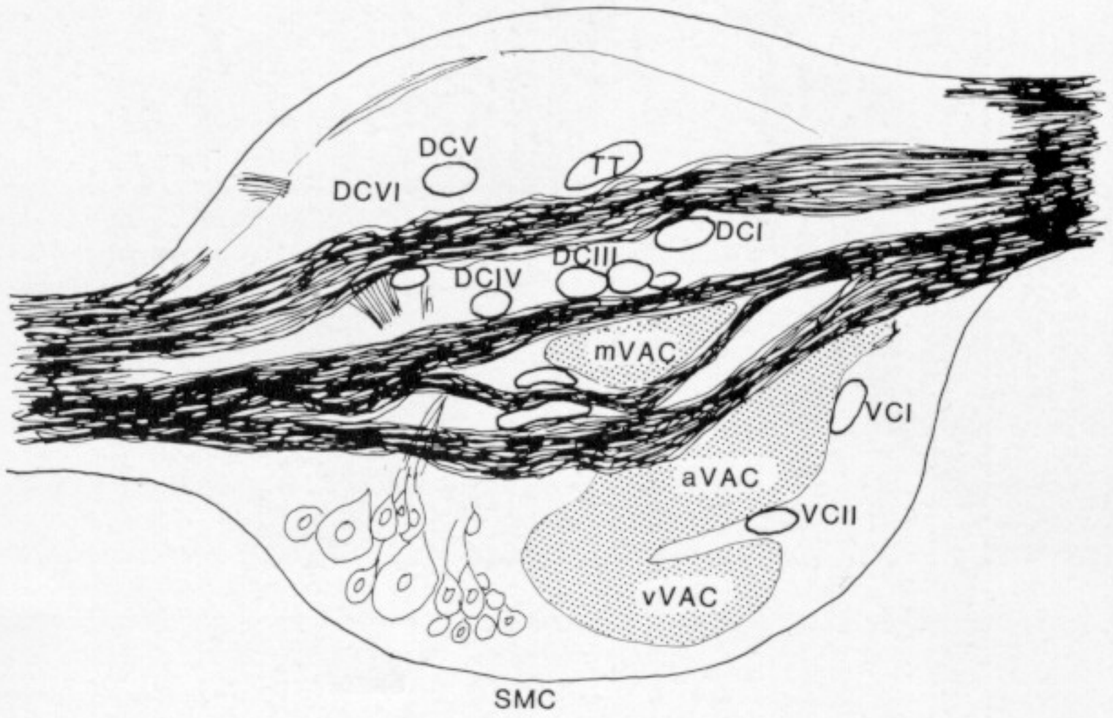


FIGURE 2*i–k*. For description see plate 6.

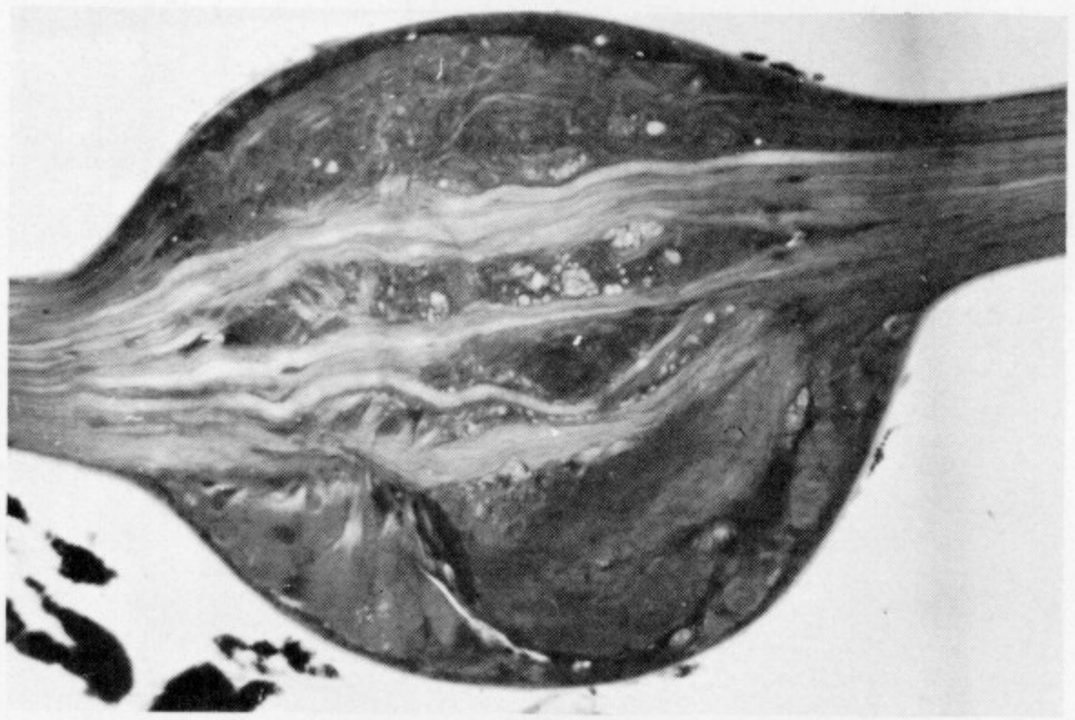


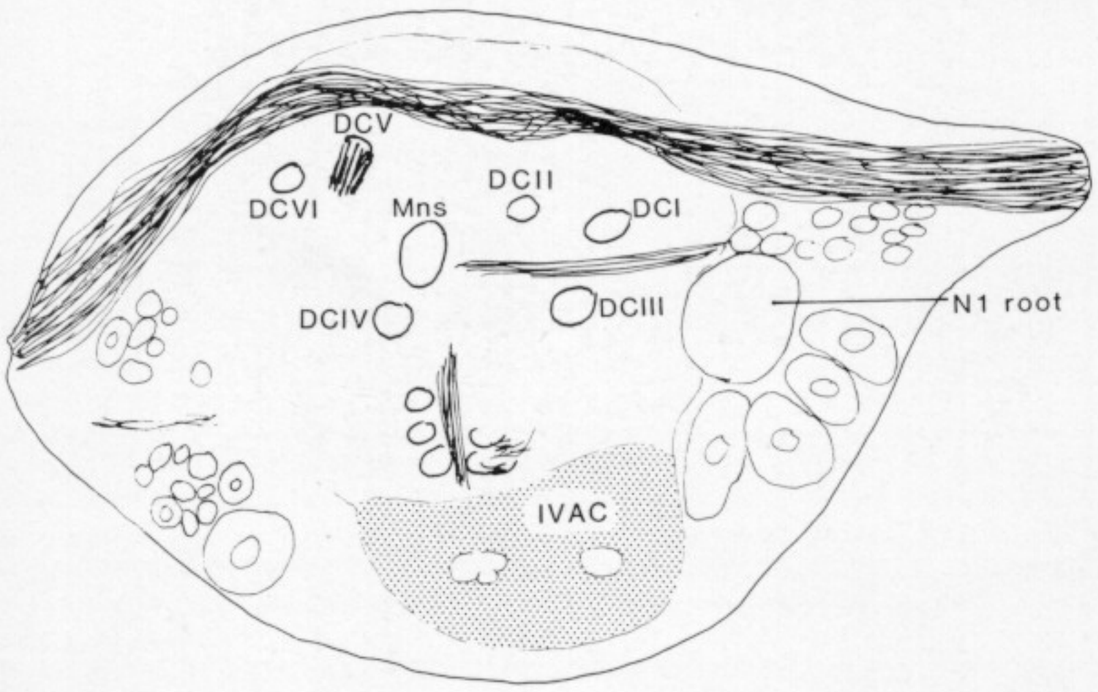
(*a*)





(*b*)





(*c*)

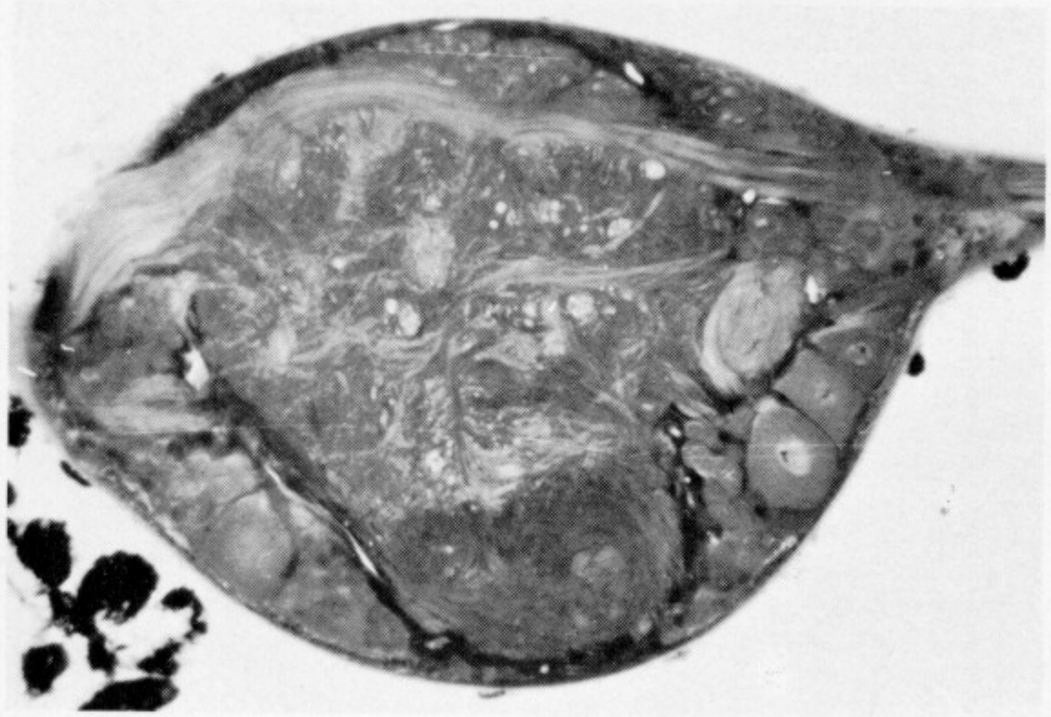
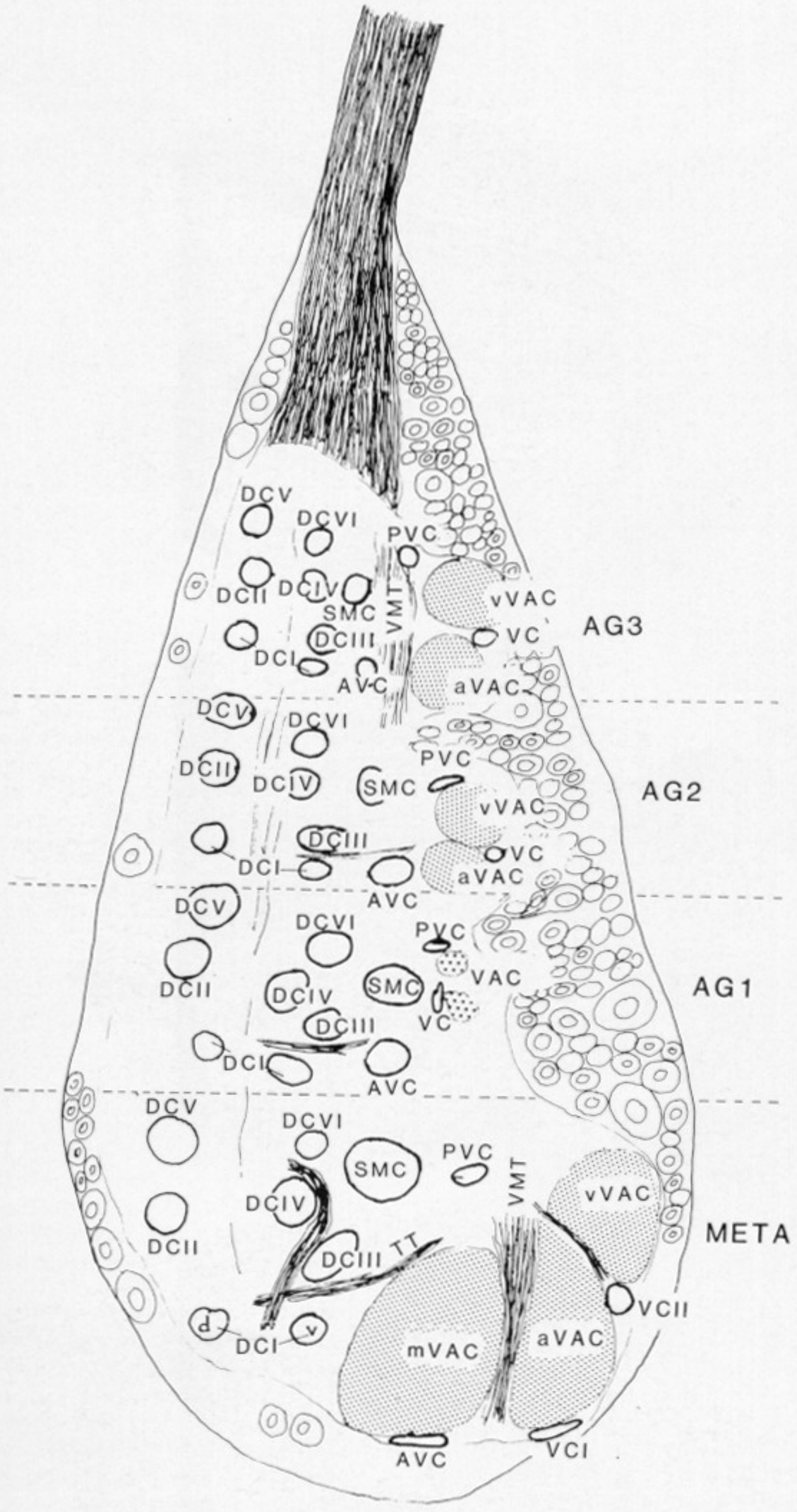


FIGURE 3. Selected sagittal and parasagittal sections (16 μm) through a mesothoracic (*a–c*) and metathoracic (*d*) ganglion, stained with osmium and ethyl-gallate, showing the outline of the ventral neuropiles. Calibration 100 μm.



(*d*)

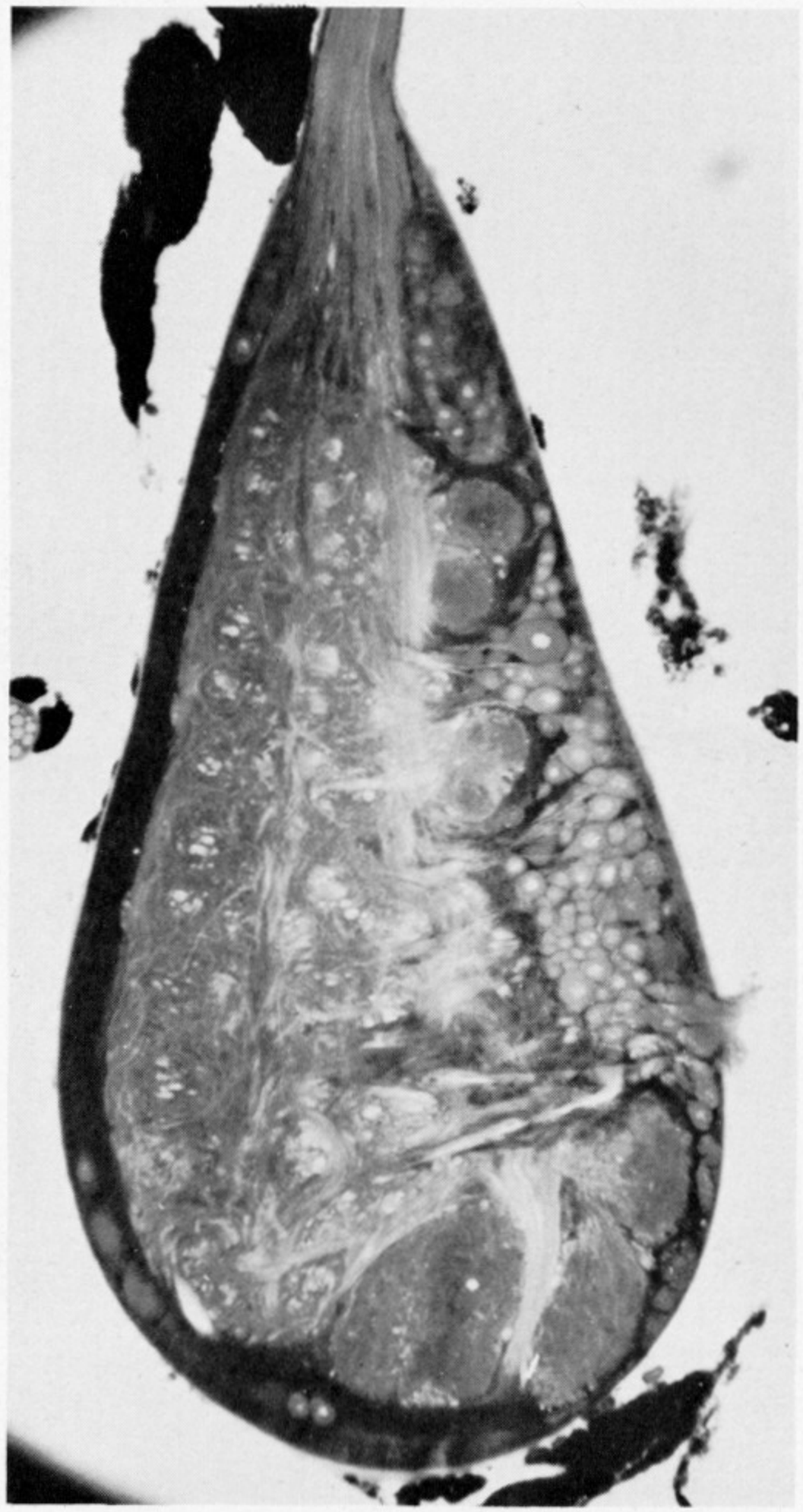


FIGURE 3*d*. For description see opposite.

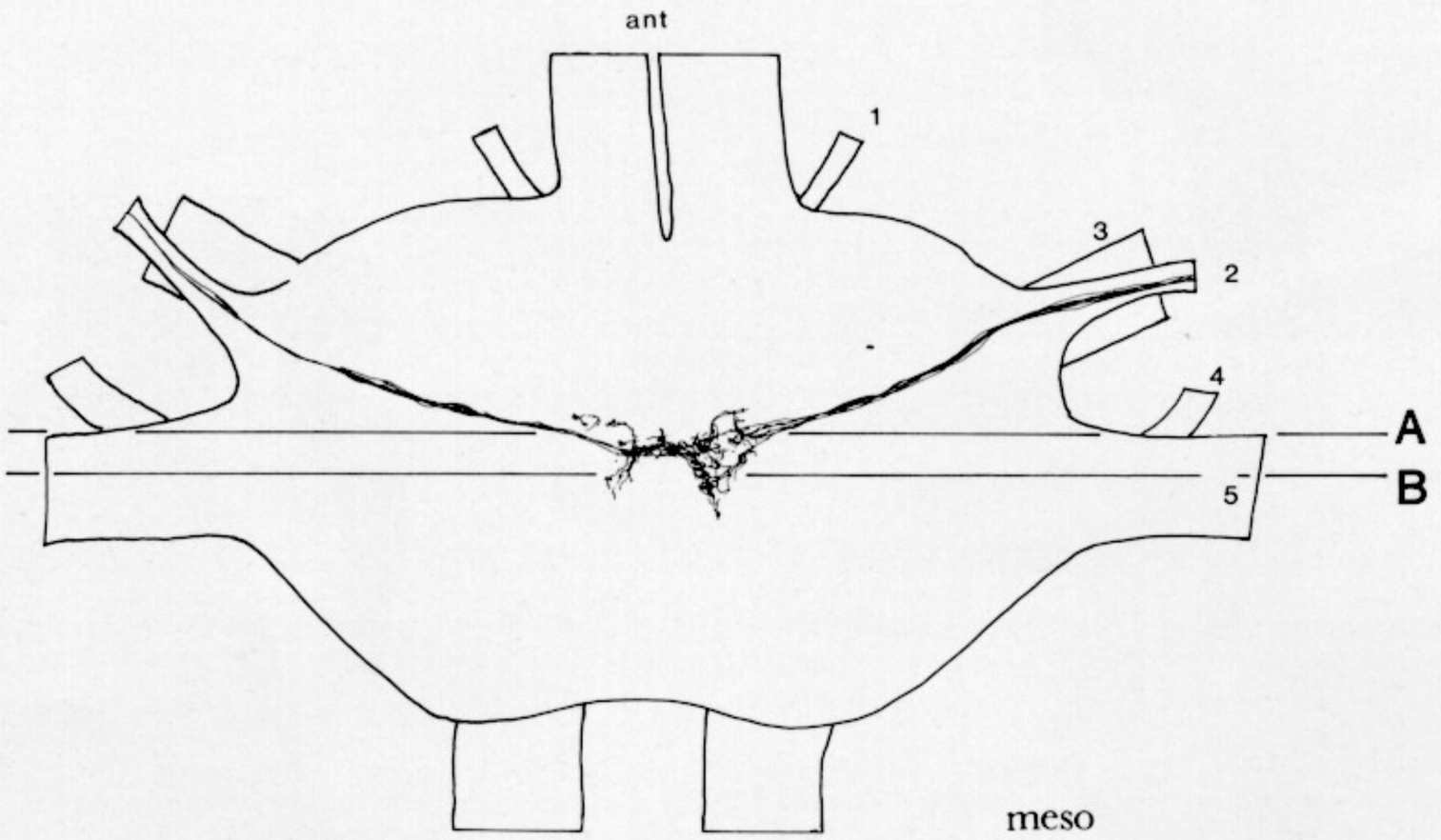


FIGURE 4. (*a–b*) Camera lucida drawings of selected 20 μm sections of a mesothoracic ganglion in which tactile hairs of the mesothoracic sternum were cobalt backfilled. The camera lucida drawing at top shows the central projection pattern of the whole receptor field in a dorsal view with levels of sections indicated. Calibration 100 μm.