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Organization of Motoneurones in the Prothoracic Ganglion of the Cockroach Periplaneta americana (L.)

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ORGANIZATION OF MOTONEURONES IN THE PROTHORACIC GANGLION OF THE COCKROACH *PERIPLANETA AMERICANA* (L.)

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The location within the prothoracic ganglion of neurone somata with axons in identified peripheral nerves is examined by the cobalt iontophoresis technique. Axons are filled with cobalt by diffusion through their cut ends and the cobalt is then precipitated as the black sulphide inside the neurone. It is assumed that neurones with axons in peripheral nerves and somata in central ganglia are either motor or neurosecretory. Fifteen nerves are examined and maps of the location of somata with axons in

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each nerve are presented. The axon distribution in peripheral nerves of three common inhibitory neurones is described. Dendritic morphology of one common inhibitory neurone and two coxal depressor motoneurones is illustrated. It is proposed that some individual neurones can be reliably identified from their soma dimensions and location within the ganglion. The number of motoneurones with somata in the prothoracic ganglion and their homology with cells in the other thoracic ganglia are discussed.

Introduction

The recent development of techniques for selectively marking identified cells in the insect central nervous system has been responsible for a resurgence of interest in combined anatomical and physiological studies.

Cohen & Jacklet (1967) first succeeded in locating the somata of many of the motoneurones in the cockroach metathoracic ganglion and identified them with respect to the major nerve trunk containing their axon. Young (1969) extended these observations to the mesothoracic ganglion and noted many homologies of neuronal organization. Unfortunately the technique of perinuclear RNA aggregation following axotomy (Wigglesworth 1960) which was used by these authors requires that axons be cut very close to the cell body. Consequently this method does not permit motoneurone somata whose axons only diverge in distal nerve branches to be distinguished.

The technique of axonal iontophoresis of Procion Yellow dye (Iles & Mulloney 1971) soon to be superseded by cobalt as the intracellular marker (Pitman, Tweedle & Cohen 1972) has largely confirmed the conclusions drawn from RNA aggregation experiments and extended identification of motoneurones to finer nerve branches. Physiologically identified cells have been located in the metathoracic and mesothoracic ganglia and their morphology examined (Iles 1972*a*, *b*; Young 1973; Pearson & Fourtner 1973).

The best (but technically most difficult) method for identifying physiologically defined neurones is by intracellular injection of a marker from a microelectrode. This method is facilitated by prior mapping of cell body groups by axonal iontophoresis, and is the only one available for use on neurones whose axons cannot be isolated. A few identified motoneurones and interneurones have been demonstrated in cockroach thoracic ganglia by intracellular injection of Procion Yellow or cobalt (Cohen 1970; Crossman, Kerkut, Pitman & Walker 1971; Young 1972; Pearson & Bradley 1972; Tweedle, Pitman & Cohen 1973; Pitman, Tweedle & Cohen 1973; Pearson & Fourtner 1975).

Three aspects of cockroach behaviour involving the thoracic nervous system have been studied. They are walking (see Pearson, Fourtner & Wong 1973), respiration (Farley, Case & Roeder 1967) and flight (Pond 1972). Maps of motoneurones in thoracic ganglia will facilitate physiological analysis of these activities by intracellular recording from the motoneurone somata. The prothoracic ganglion is of particular interest because of the lack of complete homology of the musculature with that of the pterothoracic segments (Carbonell 1947).

In the present study axonal iontophoresis has been used to construct a map of motoneurone somata in this ganglion. Motoneurones in 15 different peripheral nerves and branches have been distinguished. It was not intended to provide a complete description of the morphology of the ganglion as the general disposition of axon tracts within the neuropile and gross features of organization are already available (Pipa, Cook & Richards 1959).

Use has been made of the concept of homology of motoneurones in the different thoracic ganglia. Homology can be invoked where there is close correspondence of: (1) axon diameter and branching in peripheral nerves, (2) synaptic effects on muscles, (3) discharge pattern, and (4) soma position and dendritic branching pattern within the ganglion. In the absence of any information on neuromuscular relations in the prothoracic ganglion criteria 1, 3 and 4 have been utilized. Homology has been retained even where there are slight differences in soma position or central branching.

Materials and methods

Histology

All the material examined was from adult male cockroaches. With the exception of a few experiments designed to check homologies with other segments the prothoracic ganglion was used. The nerves leaving the ganglion were identified from Pipa & Cook (1959).

Axonal iontophoresis of cobalt was performed as follows. The ganglion and nerve of interest were excised from the animal and placed in a small bath of saline (Iles 1972*a*). The bath consisted of two depressions in a block of Perspex which were separated by a narrow (1 mm) gap (see Mulloney 1973). The gap was sealed with Vaseline (petroleum jelly). The nerve was placed across the Vaseline seal and the end was dipped in 140 mM cobaltous chloride solution in the second depression. In a few experiments an electric current of about 1 μA was passed between the cobalt and saline pools, but routinely simple diffusion was found to be adequate to fill axons and their central processes with cobalt. The preparations were kept at 4 °C for 6–14 h. The cobalt was finally precipitated intracellularly with ammonium sulphide (Pitman *et al.* 1972). The ganglia were fixed in 6% glutaraldehyde, dehydrated and cleared in cedarwood oil.

Several ganglia were stained with toluidine blue in order to reveal all the neurone cell bodies (Altman & Bell 1973). This technique was sometimes combined with cobalt filling of motoneurones and found to be very useful for showing the relationships of identified cells with neighbouring somata.

Ganglia were mounted in immersion oil (Carl Zeiss Ltd) and examined with a conventional microscope. Drawings were made either by projecting the image on to paper or from photographs. For study of fine detail a low power oil immersion objective (Watson $\frac{1}{7}$ inch) was invaluable.

Electrophysiology

Extracellular records of nerve activity in peripheral branches were taken with monopolar silver wire electrodes (see Pearson & Iles 1970). Simultaneous recordings from two nerves were frequently made in order to detect branching axons. Nerves were stimulated through bipolar electrodes.

Results

General arrangement of large neurone somata in the prothoracic ganglion

Ganglia stained with toluidine blue revealed that although all the large (diameter > 25 μm) neurone cell bodies were situated peripherally in the ganglion they were not evenly distributed over its surface (figures 1*a*, *b*, plate 1). Discrete groups of somata could be reliably distinguished and are classified in figures 2*a*, *b*. Where homology with the cell body groups identified by Gregory (1974) in the mesothoracic ganglion was clear the same names are used. However, since in the present work somata have been separated only into geographical areas, a less precise

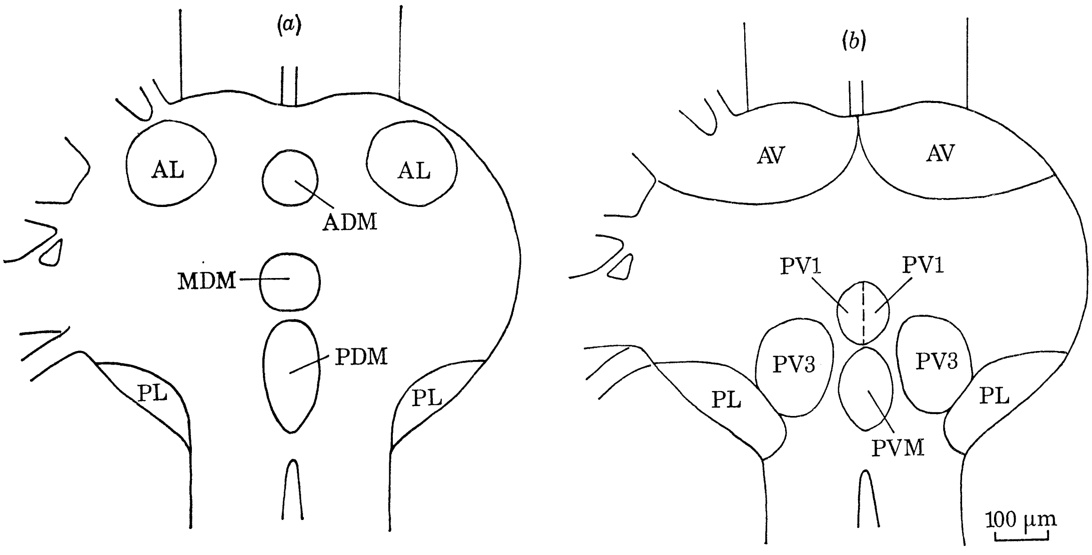

FIGURE 2. Diagram of the location of the major cell body groups in the prothoracic ganglion. (*a*) Dorsal view; (*b*) ventral view. ADM, anterior dorsal median; AL, anterior lateral; AV, anterior ventral; MDM, mid dorsal median; PDM, posterior dorsal median; PL, posterior lateral; PV1, posterior ventral 1; PV3, posterior ventral 3; PVM, posterior ventral median.

classification has been necessary in some parts of the ganglion (anterior lateral and anterior ventral regions).

Location of somata of motoneurones with axons in identified peripheral nerves

Fifteen different peripheral nerves known to contain motor axons (Pipa & Cook 1959) were examined in 300 ganglia by means of the axonal iontophoresis method. The number of motoneurones filled from a single nerve branch was somewhat variable and several preparations of each nerve were made in order to determine the maximum which could be filled. In some nerves sensory axons were filled. It has been assumed that neurones with axons in peripheral nerves and with cell bodies in the central nervous system are either motor or neurosecretory. Soma location was consistent from one preparation to the next except for a few ganglia where there was an obvious loss of organization. In these ganglia cell bodies were extruded into the connectives or nerve trunks. Since this was never observed in ganglia freshly dissected and stained with toluidine blue it was assumed to result from autolysis and to be an artefact. This phenomenon is illustrated by Taylor & Truman (1974, their Figure 5).

In previous work on the cockroach some individual motor neurones were characterized. Pearson & Bergman (1969) described a metathoracic common inhibitory neurone with branches in the major nerve trunks 3–6. This cell has since been given the name D_3 (Pearson & Iles 1971). There is evidence from both the cockroach (Pearson & Fourtner 1973; Pitman *et al.* 1973) and locust (Burrows 1973) that the soma of cell D_3 is located ventrally near the midline. Electrical records made from prothoracic nerves detected a branching neurone with the features of D_3 and thus provisionally established homology.

DESCRIPTION OF PLATE 1

FIGURE 1. Whole mount of prothoracic ganglion stained with toluidine blue. (*a*) Dorsal view; (*b*) ventral view.

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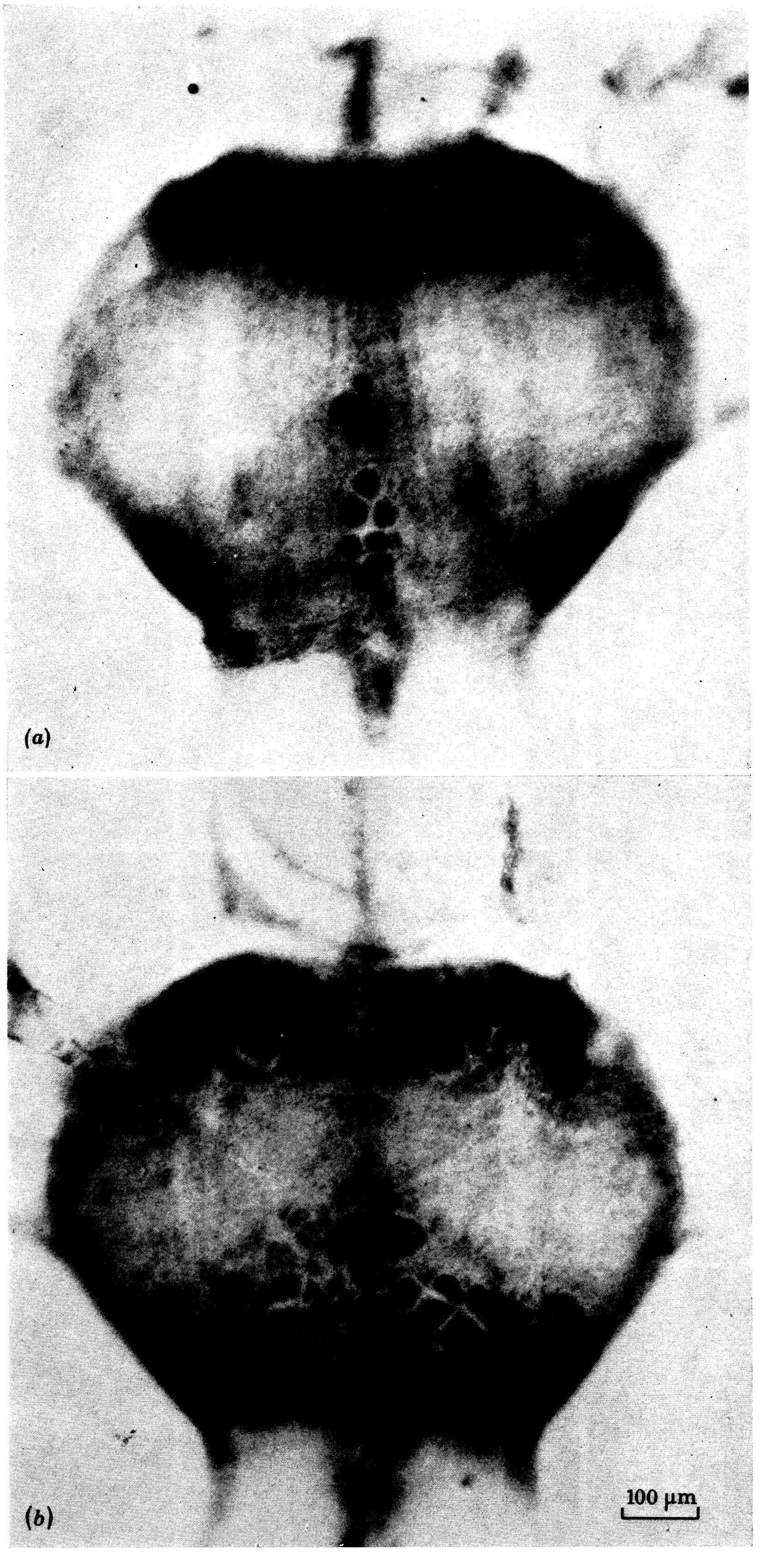

FIGURE 1. For description see opposite.

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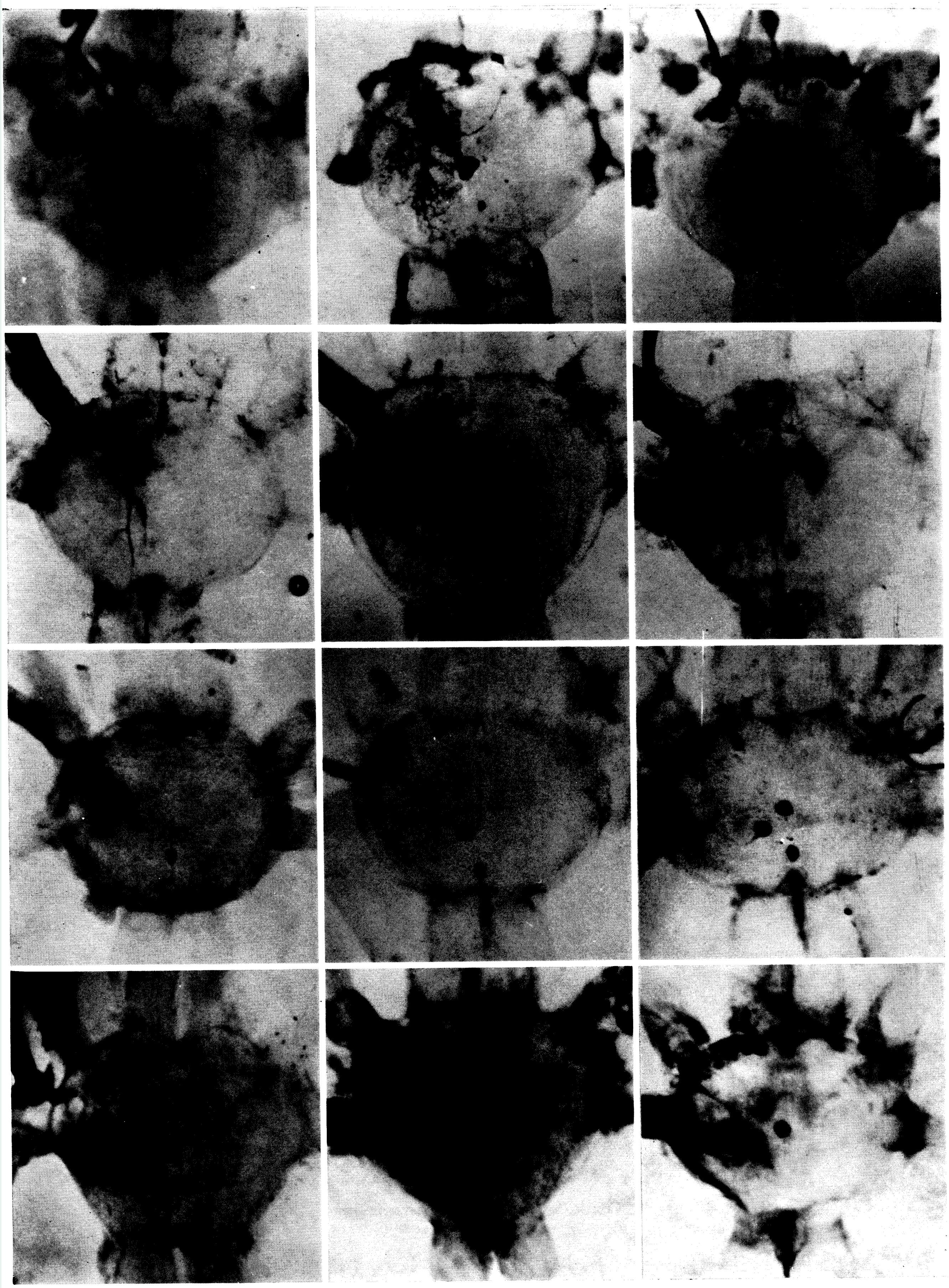

FIGURE 3. (*a*) Photographs of prothoracic ganglia after cobalt iontophoresis through the named nerve branches. The ganglia have been photographed from either the dorsal or ventral surface but all prints have been made such that the filled nerve is to the left. Note that these are typical preparations and reference must be made to table 1 for the maximum number of motoneurones located in each nerve.

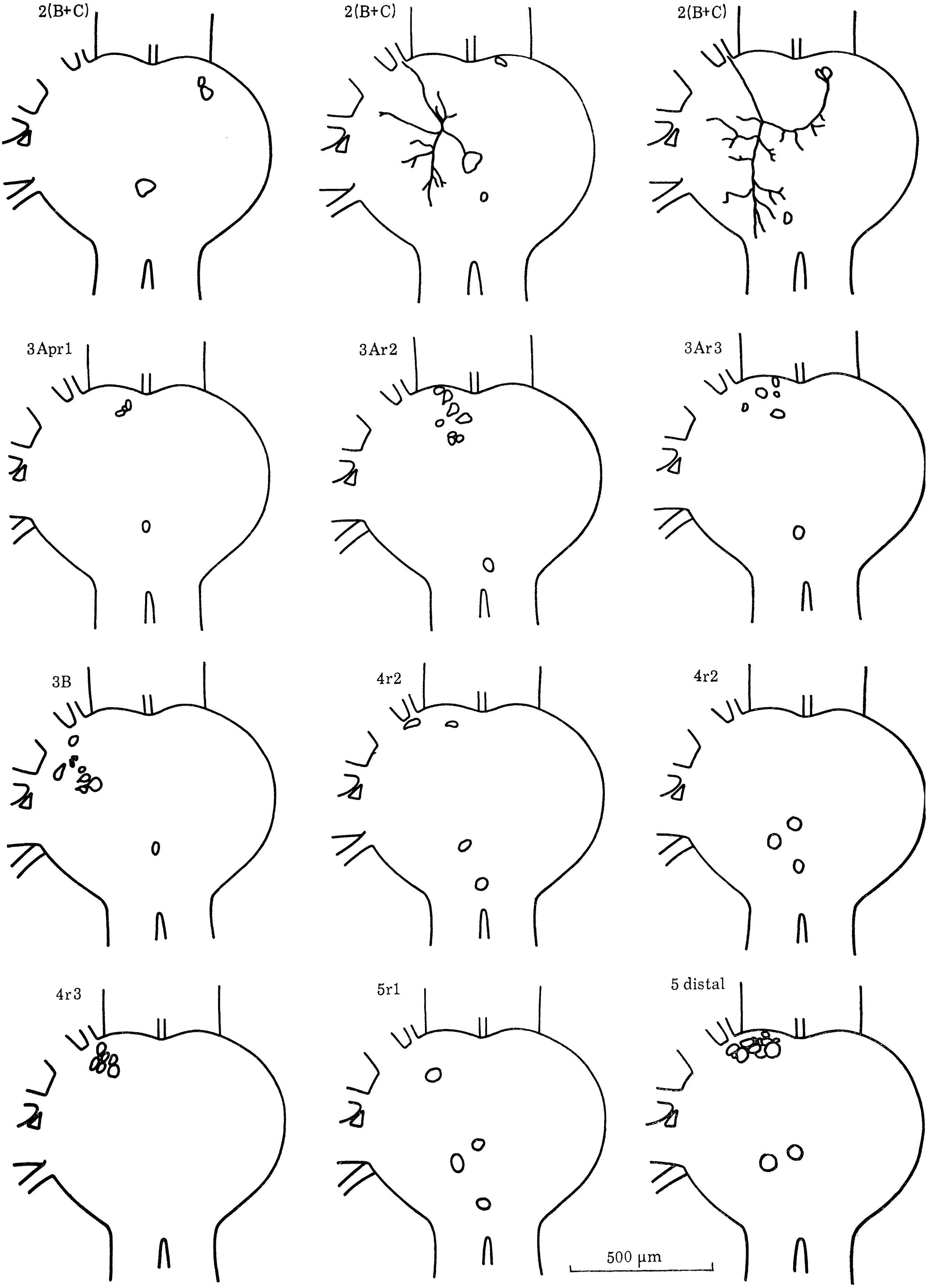

FIGURE 3. (*b*) A diagrammatic interpretation of the ganglia figured in (*a*). The position of motoneurone somata and of the major dendritic branches of some individual cells has been indicated within an averaged outline of the ganglion. Five distal refers to nerve five distal to the trochanter.

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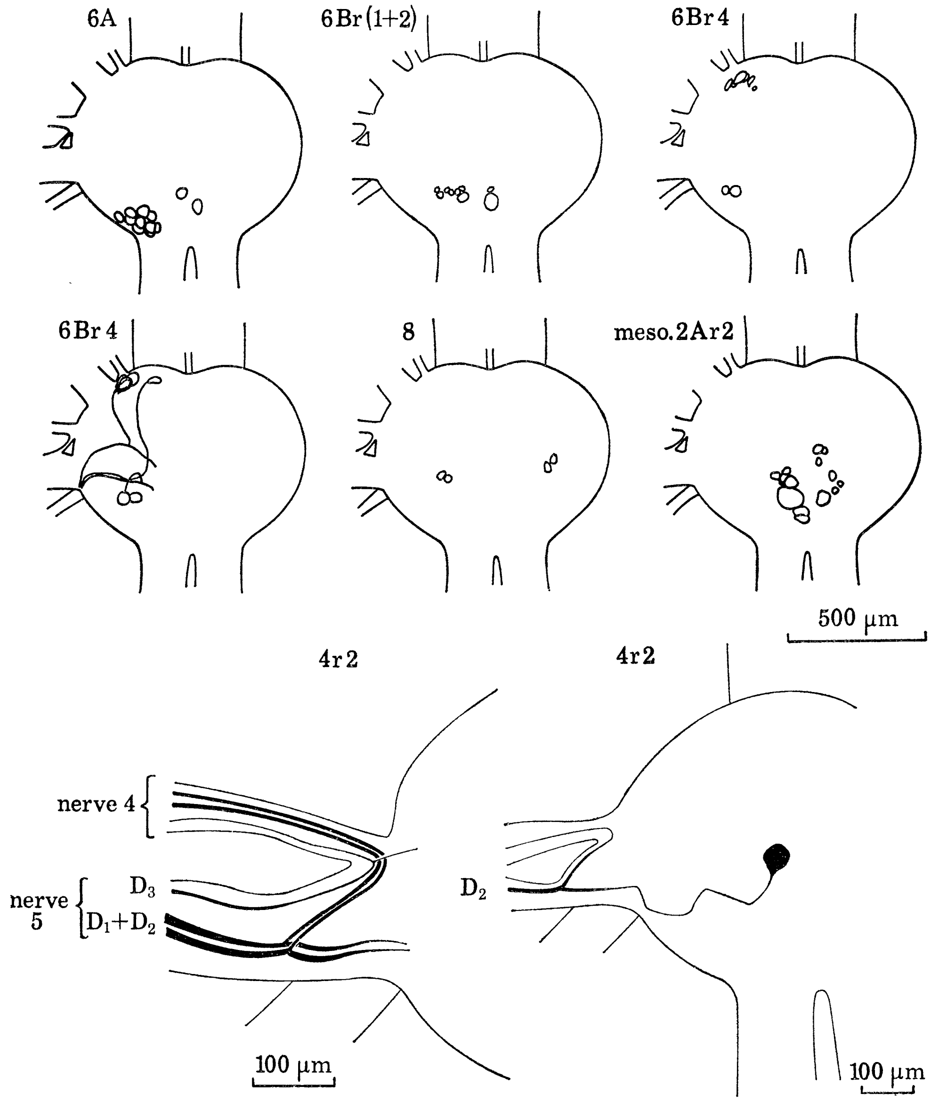

FIGURE 4. (*a*), (*b*). Similar preparations to figure 3. The lower two photographs and diagrams show the branches of axons of the common inhibitory neurones D_1, D_2 and D_3 in the commissure between nerve trunks 4 and 5. Meso. 2Ar2 refers to iontophoresis through mesothoracic nerve 2Ar2 into the prothoracic ganglion.

Four other metathoracic motoneurones have been characterized on the basis of their axon diameter in nerve 5r1, discharge pattern and synaptic relations with muscles (Pearson & Bergman 1969; Pearson & Iles 1970, 1971; Iles & Pearson 1971). These are the fast coxal depressor motoneurone, D_f, the slow coxal depressor motoneurone, D_s, and two further common inhibitory motoneurones D_1 and D_2. Homologues exist in the mesothoracic ganglion (Iles 1972*a*; Young 1972; Gregory 1974). Electrical recording from the prothoracic nerve 5r1 has shown four motoneurones with equivalent axon diameters and discharge patterns. These are regarded as homologues of cells D_f, D_s and D_{1-2} and have been named accordingly.

The location of the somata of motoneurones with axons in various peripheral nerves are illustrated in figure 3 and figure 4, and the full details are summarized in table 1. Nerves 2A, 6Br4, 8 and mesothoracic 2Ar2, require special mention.

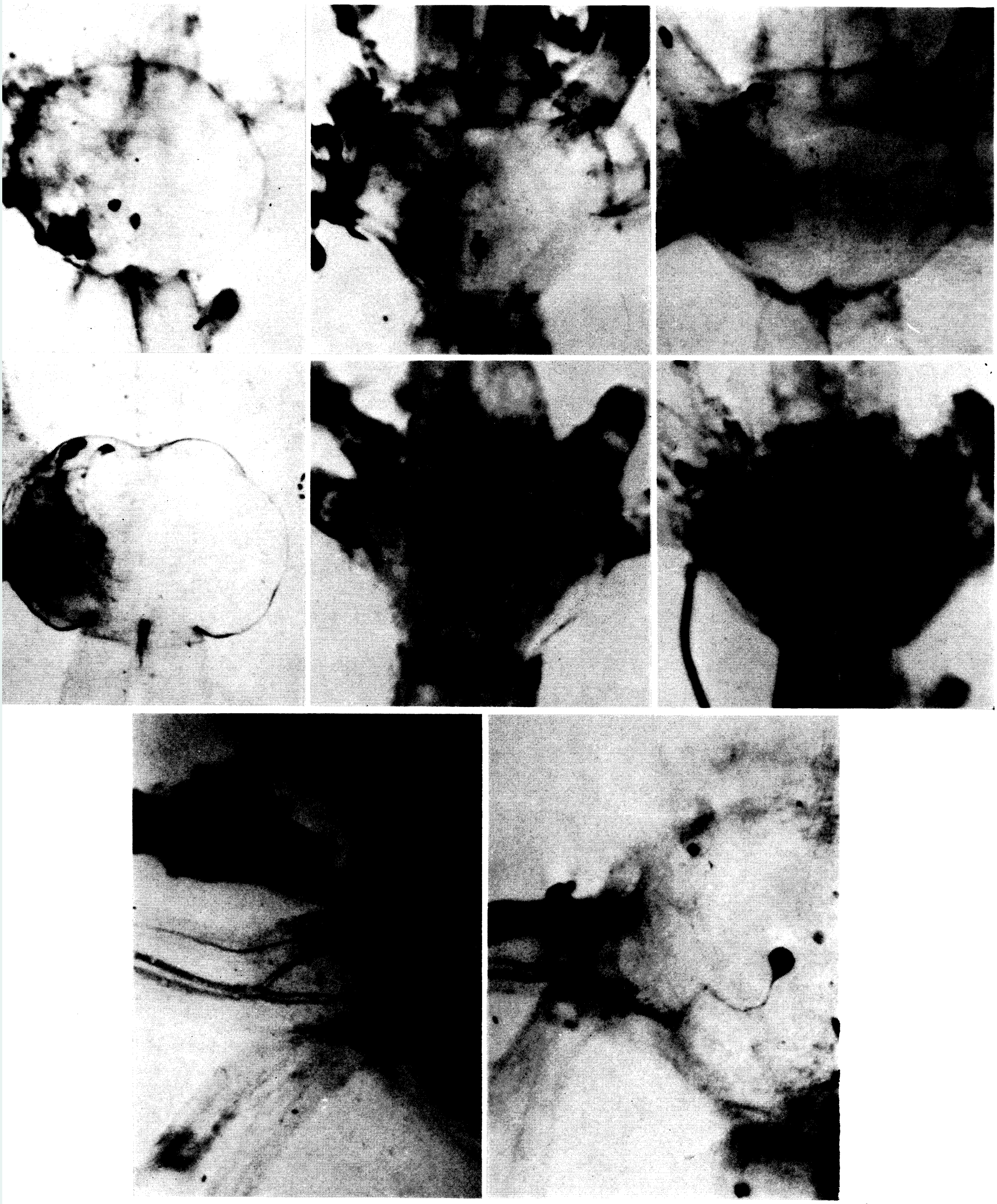

FIGURE 4 (*a*). For description see opposite.

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Prothoracic nerve 2A runs between the prothoracic ganglion and the connective between this and the suboesophageal ganglion. Electrical recording from this nerve in intact animals showed that four units were active. Cutting the connective posterior to the suboesophageal ganglion stopped this activity. No cell bodies were filled in the prothoracic ganglion when cobalt was applied to nerve 2A. The simplest explanation for these results is that motor axons in this nerve have their cell bodies in more anterior ganglia.

Table 1. Location and number of motoneurone somata with axons in identified nerves

nerve	muscles innervated†	location of somata	identified cells	total
2 (B+C)	54, 59–64	AL (2 contralateral) MDM (1), PDM (1)	— —	4
3Apr1	57, 58	AV (4), PVM (1)	D_3	5
3Ar2	56, 65–70, 74, 75	AV (15), PVM (1)	D_3	16
3Ar3	71–73	AV (7), PVM (1)	D_3	8
3B	‡	AV (9), PVM (1)	D_3	10
4r2	83	AL (5), PVM (1), PV1 (1), PV3 (1)	D_1, D_2, D_3	8
4r3	85A–D	AL (6), PVM (1)	D_3	7
5r1	85E–H, 86, 87	AV (1), PL (1), PVM (1) PV (1), PV3 (1)	D_f, D_s, D_3 D_1, D_2	5
5 distal to the trochanter	‡	AV (19), PV1 (1), PV3 (1)	D_1, D_2	21
6A	76–81	PL (14), PVM (1), PV3 (1)	D_3	16
6Br(1+2)	82, 97, 98	PL (6), PVM (1), PV3 (1)	D_3	8
6Br4	88, 89	AV (7), PL (2), PVM (1), PDM (1)	D_3	11
8	107	ventral	—	3
2Ar2 meso-thoracic	107, 110–113	posterior ventral	—	15

† From Carbonell (1947). ‡ Not classified in the prothorax.

Cell bodies with axons in nerve 6Br4 were located in two groups. The anterior group could be subdivided into a lateral cluster of five and two more medial on the basis of axon route in the neuropile (figure 4). These almost certainly correspond to the mesothoracic N6DR1 and N6DR2 axon groups of Gregory (1974).

The positions of cell bodies contributing to nerve 8 were variable. Two pairs were located laterally in the posterior ventral region (figure 4; cf. Lewis, Miller & Mills 1973; Burrows 1974). A third pair of somata were sometimes found in the PV3 groups, each close to (but smaller than) the soma of D_2. Case (1957) describes only two motor axons in the median nerve but G. E. Gregory (private communication) has found four small and four very small axons.

Mesothoracic nerve 2Ar2 leaves the connectives between the prothoracic and mesothoracic ganglia. When cobalt was iontophoresed in this nerve towards the prothoracic ganglion 15 motoneurones with somata located posterior and ventrally were found. Electrical recording confirmed that cell D_3 was *not* included among them. It is not clear what muscles are innervated by this nerve in the periphery but the homologous nerve in the locust innervates dorsal longitudinal muscles (Guthrie 1964; Neville 1963; Bentley 1973; Tyrer & Altman 1974).

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Axon pathways of common inhibitory motoneurones

The present results derived from electrophysiology and anatomy agree with earlier work in the mesothoracic and metathoracic segments showing that one cell sends axon branches into nerve trunks 3–6 inclusive but not trunk 2. All of the branches of nerves 3–6 which were examined contained an axon except nerve 5 distal to the trochanter. All of these nerves were found to include a cell body in the PVM group and it was concluded that a single cell homologous to D_3 of the other thoracic segments was present. Previous electrophysiological work has demonstrated branches in nerves 4r1 (Pearson & Bergman 1969) and 5r3 (Pearson & Iles 1971). In agreement with Pearson & Fourtner (1973) it was found (figure 4) that the axon of D_3 in nerve trunk 5 enters from nerve trunk 4 via a small commissure (see also Gregory 1974; Zilber-Gachelin 1973).

An unexpected finding was that the other common inhibitory neurones of nerve 5r1 (D_1 and D_2) had axon branches in nerve 4r2 (Table 1). These branches left the main axon in nerve trunk 5 and passed through the commissure into nerve 4 (figure 4). This axon branching was confirmed by simultaneously recording from nerves 5r1 and 4r2. The same arrangement was found in the mesothorax and metathorax. Gregory (1974) notes two small axons passing from the distal part of nerve 4 into this commissure in the mesothoracic segment.

Morphology of identified motoneurones

Following cobalt iontophoresis in fine nerve branches containing a small number of axons it was frequently possible to reconstruct the dendritic pattern of single cells. This was done for the identified neurones D_f, D_s and D_3 (figure 5). Comparisons of soma diameter in cobalt filled cells with the unfilled bilateral partner in combined cobalt and toluidine blue preparations suggested that the cobalt technique does not seriously distort the dimensions of filled cells (although the same method using Procion Yellow does produce swelling: Iles & Mulloney, 1971). The major dendritic branches of some unnamed cells are indicated in figures 3 and 4.

Location of identified somata with respect to neighbouring cells

The soma of cell D_f was the most caudal of large somata of the AV group. The soma of cell D_s was the most dorsal large cell body in a posterolateral position.

The largest somata on the posterior ventral surface of the ganglion were usually individually recognizable. Combined toluidine blue staining and cobalt filling of axons in nerve 5r1 (figure 6*a*) showed that the largest soma in the PV1 region corresponds to cell D_1 (following the convention of Pearson & Fourtner 1973); the most anterior and medial large cell in each PV3 group corresponds to cell D_2, and the two largest cell bodies in the PVM group which are usually aligned along a rostrocaudal axis correspond to cell D_3. Similar preparations of mesothoracic nerve 2Ar2 show that the remaining five large somata in each PV3 group have axons in this nerve, as also do the small bilateral pair of cell bodies just lateral to the PVM group (figure 6*b*).

On the dorsal surface of the ganglion a large pair of somata in the MDM region were found to contribute to prothoracic nerve 2 (B+C). A smaller cell body in this area is unusual in that it is unpaired.

Somata in the PDM region are discussed below.

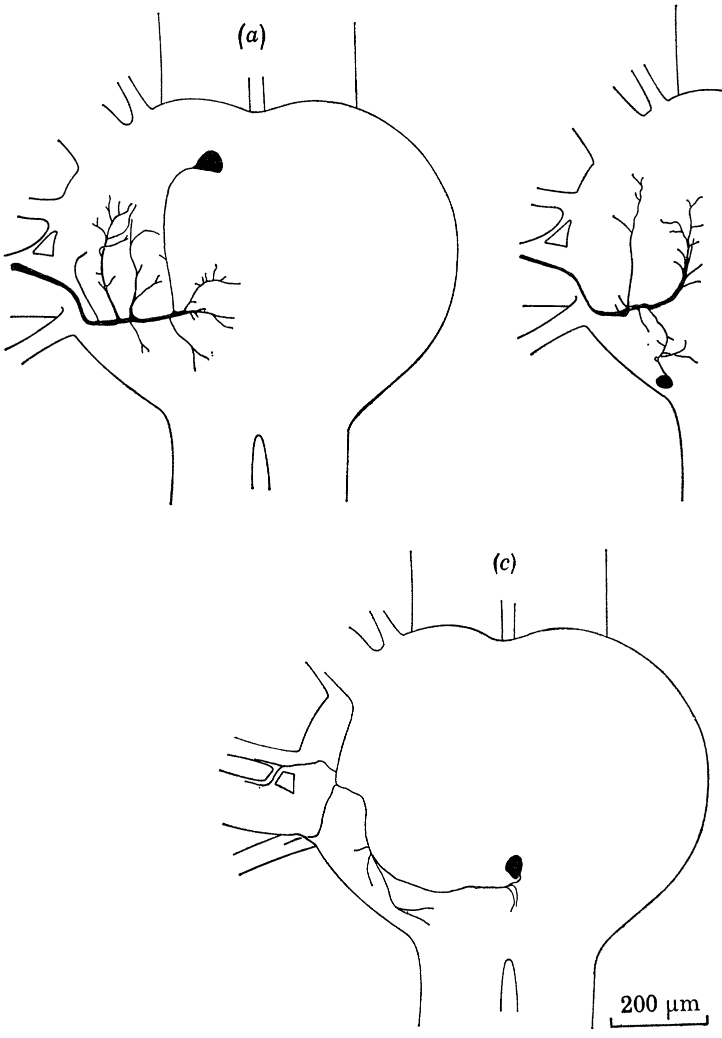

FIGURE 5. Dendritic morphology of identified prothoracic motoneurones, drawn from cobalt preparations. The finest dendritic branches have been omitted. (*a*) Neurone D_f; (*b*) neurone D_s; (*c*) neurone D_3.

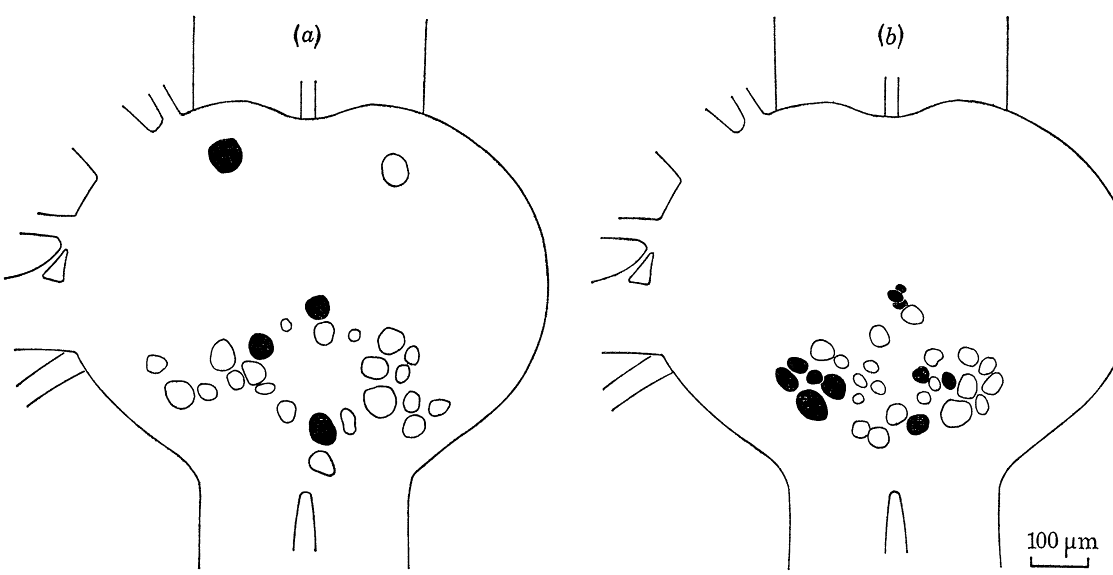

FIGURE 6. The position of large somata on the ventral surface of ganglia stained with toluidine blue in addition to cobalt iontophoresis through nerve 5r1 (*a*) and mesothoracic nerve 2Ar2 (*b*). Cobalt filled somata are drawn solid.

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Discussion

The prothoracic motoneurone soma map

The general arrangement of motoneurone cell bodies (figures 3, 4; table 1) conforms very closely to that described for the metathoracic (Cohen & Jacklet 1967) and mesothoracic segments (Young 1969). The somata of motoneurones with axons in the same nerve trunk tend to be ipsilateral and located together. There are, however, several exceptions. Prothoracic nerve 2 (B + C) contains axons with medial and contralateral somata (cf. Gregory 1974; Cohen & Jacklet 1967 found contralateral somata only in the metathorax). Nerve 6Br4 contains axons from both anterior and posterior lateral cell body groups, as has been observed in the other thoracic ganglia (Iles 1972*a*; Iles & Mulloney 1971; Pearson & Fourtner 1973). The soma of cell D_s of nerve 5r1 is completely isolated from all other nerve 5 somata.

Since prothoracic nerve 3B does not innervate any coxal muscles (unlike in the pterothoracic segments) it would be expected that rather fewer motoneurones would fill from this nerve. Ten motoneurones were found, which is half the number of large axons found in the corresponding mesothoracic nerve (Dresden & Nijenhuis 1958). One conspicuous nerve 3B motoneurone in the metathoracic ganglion (cell 10 of Cohen & Jacklet 1967) has no obvious homologue in the prothorax.

The number of motoneurones in the prothoracic ganglion

The number of cell bodies located when filling the 15 nerves which were examined is given in table 1. Taking into account the fact that the common inhibitory neurones D_{1-3} have axon branches in more than one nerve 122 different *paired* motoneurones were found, providing a total of 244 for the whole ganglion. Two motor nerves which were not examined (4r1, 5r3) would be expected from physiological evidence (Pearson & Bergman 1969; Pearson & Iles 1971) to contribute at least one more cell each giving a total of 248.

In most nerve branches the number of motor axons identified exceeded that given by Dresden & Nijenhuis (1958) from direct counts in the mesothoracic segment. This is unlikely to represent a real difference between the ganglia since Gregory (1974) has shown that the true number of motor axons in mesothoracic nerves is greater. In fact the number of motoneurones detected in the present material is likely to be an underestimate resulting from inconsistent filling of small axons (there is no evidence that cobalt can leak from one axon into another in a peripheral nerve; for example, diffusion filling of nerve 5 distal to the trochanter never produced filling of cells D_f, D_s and D_3, which are found in the more proximal branch 5r1). Previous estimates of the number of motoneurones in thoracic ganglia have been smaller (Cohen & Jacklet 1967; Young 1969). However, as Gregory (1974) has observed this results largely from the assumption by the former authors that all motoneurone somata exceed 20 μm in diameter. Gregory (1974) suggests a total of around 300 motoneurones (including unpaired somata) for the mesothoracic ganglion.

Common inhibitory neurones

The cell bodies with axons in prothoracic nerve 5r1 which were found in the PV1, PV3 and PVM groups are clearly homologous with the three common inhibitory neurones D_{1-3} located by Pearson & Fourtner (1973) and with cells N5R2d, N5R2c and N4R2p described by Gregory (1974). Two unexpected findings deserve further comment. The first was the observation of branches of D_1 and D_2 in nerve 4r2, apparently overlooked by Pearson & Fourtner.

The second was the failure to find branches of cell D_3 distal to the trochanter in nerve 5 by either cobalt iontophoresis or electrical stimulation. Guthrie (1967) showed that stimulation of nerve 3B reduces the tension during slow contractions of the tibial depressor muscle. If this effect is mediated by the common inhibitory neurone D_3 then it must depend upon branches reaching the femur via the anastomoses between nerves 3B or 6Br4 and nerve 5 near the trochanter. The extent of axon branching of the common inhibitory neurone D_3 is illustrated in figure 7.

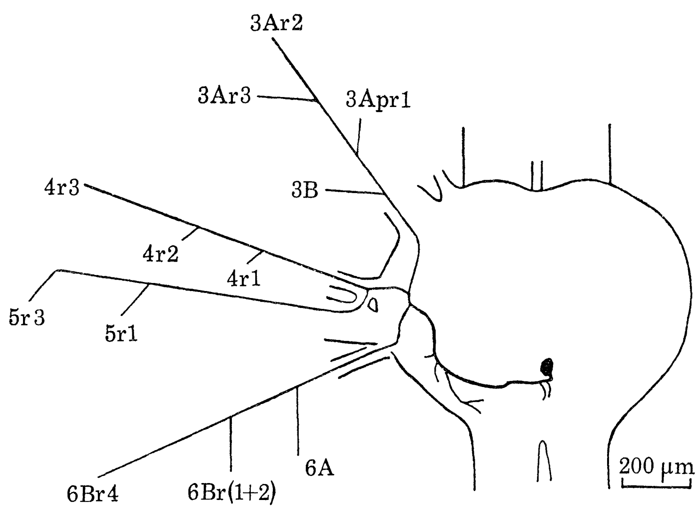

FIGURE 7. Diagram of the axon branches of prothoracic cell D_3. Information from cobalt iontophoresis and electrophysiology has been combined. The peripheral nerve branches containing the axon branches are labelled according to Pipa & Cook (1959).

The cell bodies of the three inhibitory neurones are located on the posterior ventral surface of the ganglion. Miller (1969) has described an inhibitory neurone innervating the first spiracle closer muscle (of *Blaberus discoidalis*) which has its axon in mesothoracic nerve 2Ar2. All of the cell bodies of axons in this nerve are to be found in the posterior ventral region. It can thus be said that all the known inhibitory neurones are located in this region. However, since it is most unlikely that all of the neurones with axons in nerve 2Ar2 are inhibitory it does not follow that *all* posterior ventral cells are inhibitory. Nerves 6Br(1 + 2) and 6A each contain one axon with its soma close to known inhibitory cells (PV3 group). Electrophysiological experiments would be desirable to discover whether further inhibitory neurones do exist in these nerves.

Morphology of identified motoneurones

Reconstructions of the fast coxal depressor motoneurone, D_f of nerve 5r1 in both the metathoracic (Iles 1972*b*; cell 28, Tweedle *et al.* 1973) and mesothoracic (cell N5R2a, Gregory 1974) ganglia are very similar. In the prothoracic ganglion (figure 5*a*), however, the dendritic tree is displaced significantly towards the posterior and the main dendritic branch ('integrating segment') is almost transverse. Nevertheless the soma is in a similar position to its homologues in the other thoracic segments (cell 28, Cohen & Jacklet 1967; cell 30, Young 1969). The general arrangement of ventral cell body, dorsally directed neurite and most dendritic branches in the dorsal neuropile conforms to classical descriptions of insect motoneurones (Hilton 1911; Zawarzin 1924; Pyle 1941; Wigglesworth 1959; Guthrie 1961).

The prothoracic slow coxal depressor neurone, D_s (figure 5*b*), has a dendritic structure very similar to its proposed mesothoracic and metathoracic homologues (cell N5R2b, Gregory 1974; Pearson & Fourtner 1975).

In the present material only the major ganglionic branches of the prothoracic common inhibitory neurone, D_3 could be reconstructed (figure 5*c*), but considerable similarity with the metathoracic homologue (Pitman *et al.* 1973) and mesothoracic cell N4R2p is apparent (Gregory 1974). This neurone has branches leaving the neurite close to the soma. However, since the same is true of cell D_s this cannot be regarded as a unique feature of inhibitory cells. No branches of D_3 which entered the connectives were detected.

The PDM group of neurones

Attention was first drawn to the homologous group of eight cells on the dorsal surface of the metathoracic ganglion by Crossman *et al.* (1971). These authors showed that at least one of these neurones had axons projecting bilaterally in nerve trunks 3–6 and the connectives.

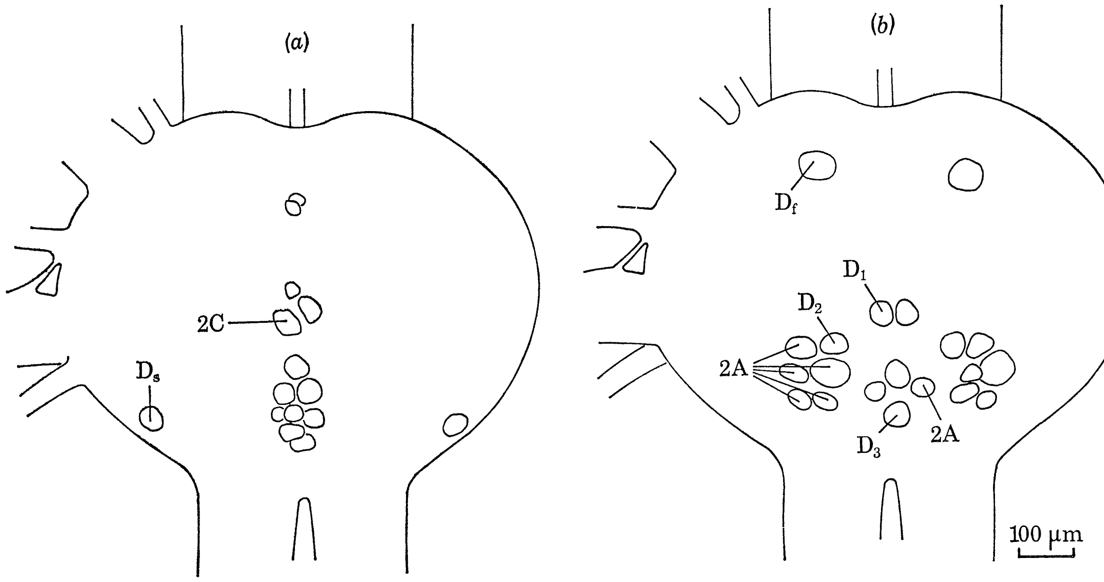

FIGURE 8. The position of some large somata traced from photographs of a prothoracic ganglion stained with toluidine blue. (*a*) Dorsal view; (*b*) ventral view. The most likely identification of cells D_1, D_2, D_3, D_f and D_s has been made. Somata which probably send axons in nerve 2C and mesothoracic nerve 2Ar2 are indicated.

In the present experiments one soma in the PDM group regularly filled with cobalt from prothoracic nerve 2 (B + C). This cell may well have bilateral branches since a small unit in nerve 2 (B + C) was found to follow stimulation of the contralateral nerve. Thus, in the prothoracic ganglion a PDM neurone projects into nerve trunk 2.

In one preparation of prothoracic nerve 6Br4 one PDM soma was filled. Unfortunately insufficient cobalt sulphide precipitated to enable the axon branching pattern to be observed. In the metathoracic segment Pearson & Fourtner (1973) have shown that two small units in nerve 6B4r (axons 1 and 2 of Pearson & Bergman 1969) are from bilaterally projecting neurones.

It is not clear whether *all* the PDM group of cells have axons entering peripheral nerves. Hoyle, Dagan, Moberly & Colquhoun (1974) have proposed that midline dorsal neurones in the locust are neurosecretory cells which innervate fast muscles. Synaptic terminals with dense cored vesicles which may be neurosecretory have been observed on a cockroach fast coxal depressor muscle (Iles 1972*a*).

Cells identifiable by soma position in the ganglion

The pattern of cell bodies visible on the surface of toluidine blue stained ganglia was very consistent from animal to animal. Certain groups such as PDM and MDM were invariably recognizable. Some individual motoneurones were identifiable from their size and position. In figure 8 the larger cell bodies have been traced from a photograph of a toluidine blue preparation and the most probable identification made. Comparison with the map provided for the mesothoracic segment by Young (1973, his Figure 2) suggests the following serial homologies: D_1 – cell 40; D_2 – cell 44; D_3 – cell 41; D_f – cell 30; D_s – cell 56; (cf. Gregory 1974); motoneurones with axons in nerve 2A – cells 45, 46. The ability to recognize some cells or cell groups merely from their position in the ganglion without histological preparation should make possible biochemical analysis (cf. Otsuka, Kravitz & Potter 1967) and study of the behavioural effects of selective ablation.

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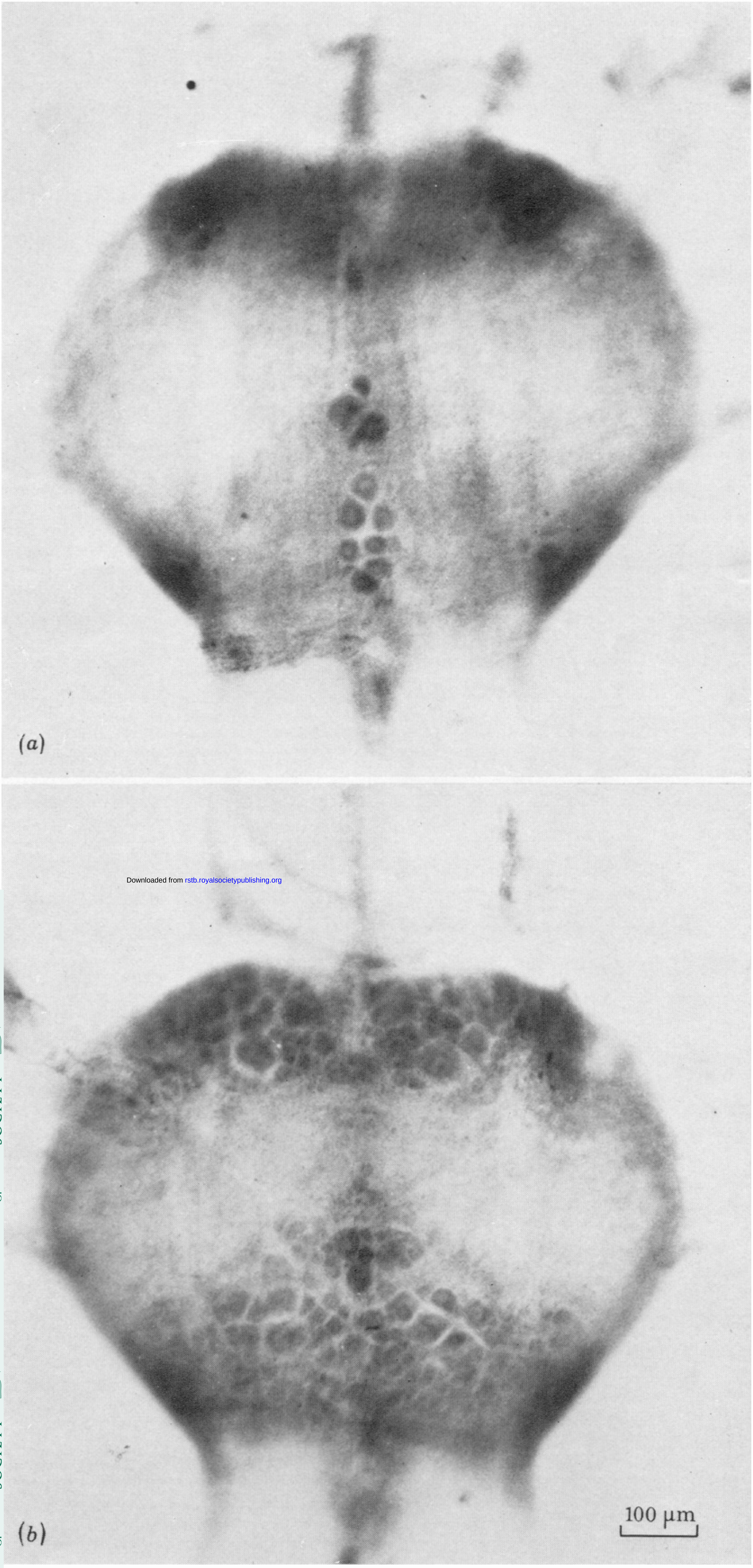

FIGURE 1. For description see opposite.

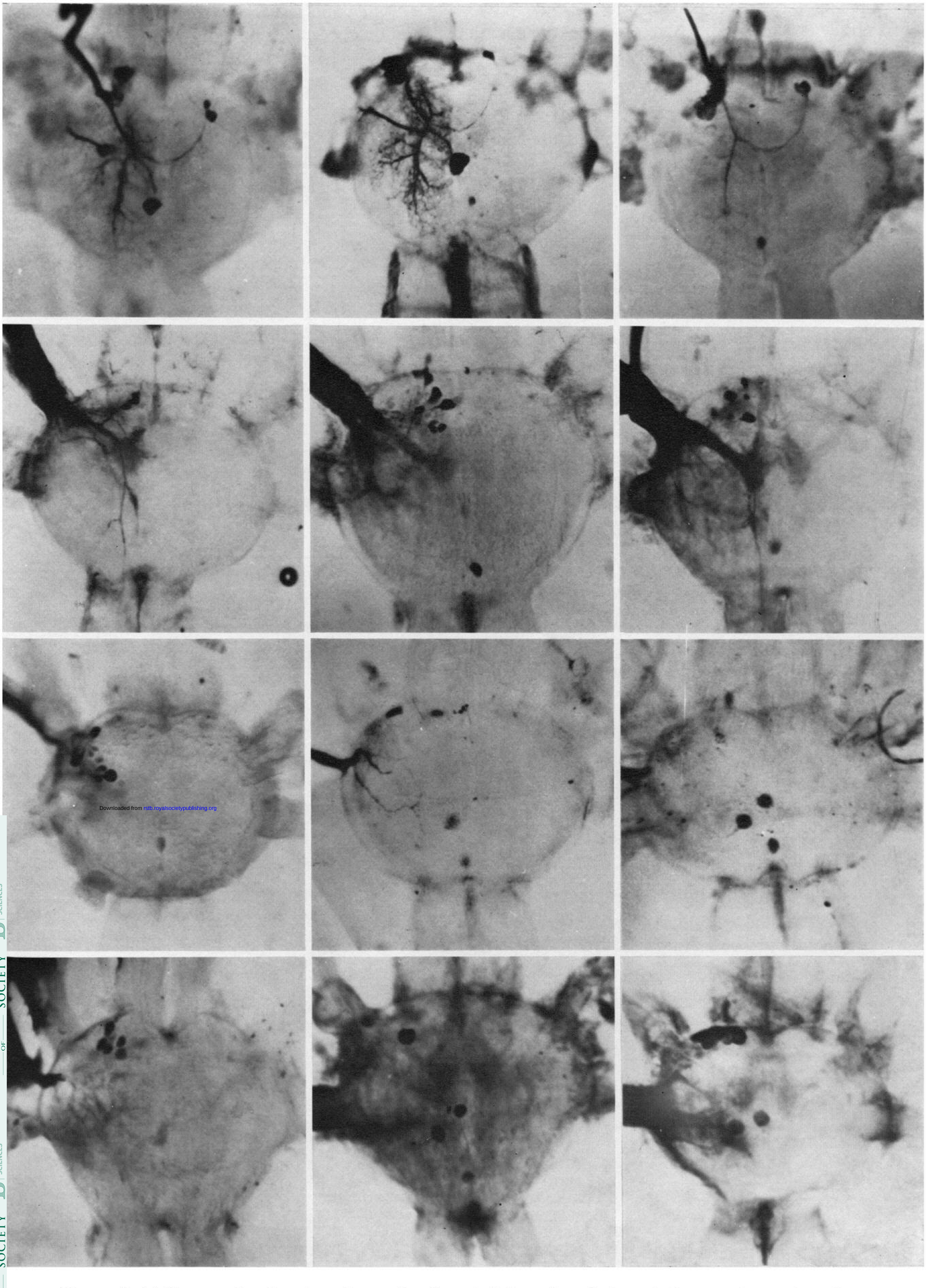

FIGURE 3. (*a*) Photographs of prothoracic ganglia after cobalt iontophoresis through the named nerve branches. The ganglia have been photographed from either the dorsal or ventral surface but all prints have been made such that the filled nerve is to the left. Note that these are typical preparations and reference must be made to table 1 for the maximum number of motoneurones located in each nerve.

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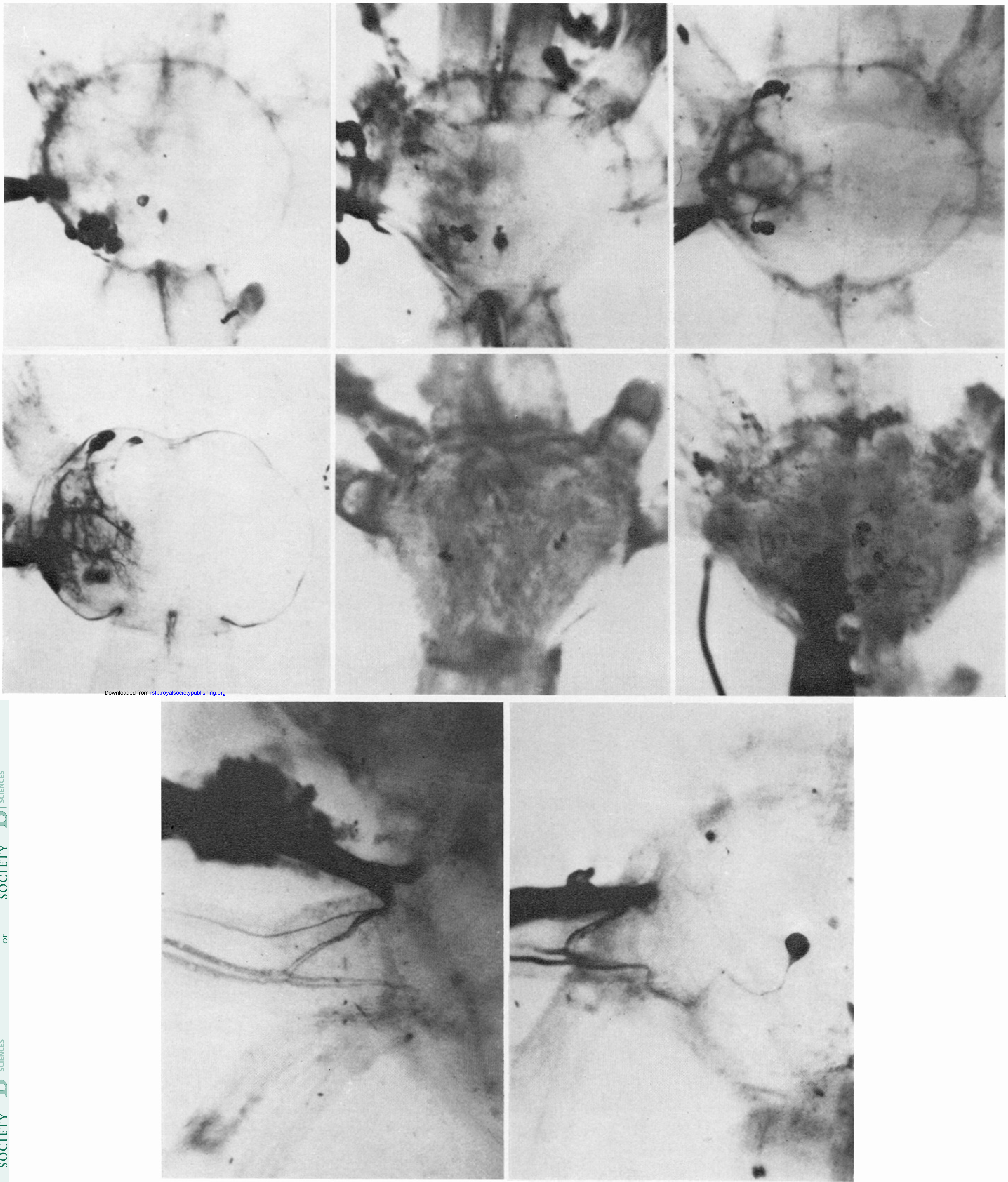

FIGURE 4 (*a*). For description see opposite.

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