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The Anatomy of the Nervous System in the Genus Gerris (Hemiptera-Heteroptera)

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THE ANATOMY OF THE NERVOUS SYSTEM IN THE GENUS *GERRIS* (HEMIPTERA-HETEROPTERA)

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[Plate 8]

CONTENTS

The most successful methods used in this study were Palmgren's silver-on-the-slide technique, the rapid silver nitrate method of Golgi, and a method that has seldom been applied to insect material, the Golgi–Cox mercuric chloride method. A way of preparing sections of adult hardened insects by infiltrating with wax prior to softening with chlorinated acetic acid and nitric acid was also employed.

The nervous system of *Gerris* shows a high degree of condensation in that all the segmental neuromeres are fused. This characteristic of the nervous system may be associated with the disposition of the one hundred and twenty-two pairs of muscles.

The nerves of the head are specialized in association with the complex mouthparts. There are distinct stylet and labral ganglia, and peripheral interconnexions between some of the nerves.

The posterior labral nerve was traced to the principal salivary gland. The reticulum described by Baptist (1941) as of a nervous nature was shown to consist of fine muscle fibres: the much finer nerve fibres were also stained in silver preparations.

The many separate nerves of the prothorax reflect the unspecialized nature of this segment as compared with the meso- and metathorax in which most of the fibres are gathered into a few nerve trunks. The coalesced neuromeres of the abdominal region give rise to a pair of posterior nerve trunks connected with small ganglia or lateral bodies lying near the spiracles. These ganglia appear similar to the structures described by Landois & Thelen (1867), as controlling spiracular movements in *Cossus*.

Rough estimates of the number of cells in different parts of the nervous system were correlated with the percentage success of staining methods, and specialization of the neuromeres.

The form and arrangement of neurones within the optic and protocerebral centres of *Gerris* conforms for the most part to the patterns worked out in other insects, though there do not seem to be as many different types of internuncial neurone in the optic lobes of *Gerris* as exist in *Apis* or

Calliphora (Cajal & Sanchez 1915). The corpora pedunculata are connected through a dorsal glomerulus with the deutocerebrum, the glomerulus having the form of a loose meshwork of fine fibres rather than of a distinct calyx.

The deutocerebrum is indistinctly divided into anterior and posterior glomeruli, as described in *Apis* by Sanchez (1936). The form and size of the elements composing the somewhat enigmatic posterior glomerulus in *Gerris* supports the view that this is a motor centre.

The close association between the maxillary and mandibular nerves is to some extent reflected in the internal organization of these neuromeres. Separate ventral areas could be distinguished, but ganglionic boundaries were indistinct. The large labral centre shows many of the features of a trunk ganglion.

The pattern of neurones in the thoracic and abdominal centres could be compared in detail with the pattern described by Zawarzin (1924) in the larva of *Aeschna*. There are three unusually large internuncials with processes in this region, and cell bodies in the protocerebrum and suboesophageal centres. It is suggested that they form part of a dual physiological system controlling the motor centres of the thorax (Roeder 1953).

The mesothoracic centre was made a special object of study as representative of the thoracic neuromeres. The fibre tracts are clearly marked and can be seen to correspond to functional regions within the centre.

The alary nervous system of the mesothorax was investigated in some detail in both winged and wingless forms of *Gerris*. In the flying forms dorsal and ventral tracts can be distinguished, associated with motor and sensory regions of the mesothoracic neuropile respectively. In forms without wing muscles or fully developed wings the dorsal tract is absent or vestigial and the ventral tract is clearly reduced.

The abdominal neuromeres are very closely compacted so that they tend to lose their identity. The ventral longitudinal tracts are unusually well developed and this may be correlated with the importance of the sensory areas.

INTRODUCTION

The purpose of this paper is to describe the detailed anatomy of the nervous system in a group of surface-skating hemipterans belonging to the genus *Gerris*, with the main emphasis on the commonest species, *Gerris lacustris* L. These insects are to be found, often in abundance, skating on the surface of still and flowing waters, and feeding on other insects which have become trapped in the surface film. From the neurological standpoint their main interest lies in their exhibition of an extremely condensed condition of the central nervous system (see figure 1), specializations of the peripheral nervous system, and a polymorphism of the flight apparatus.

Most of the detailed work on insect neurology (that is to say work dealing with neurone patterns) has dealt with the more simply organized insect nervous systems (*Aeschna*, Zawarzin 1924; *Locusta*, Cook 1951; *Periplaneta*, see Roeder 1953), or with a small part of the central nervous system, in particular the optic lobes (*Apis*, Kenyon 1896; *Aeschna*, Zawarzin 1914; *Calliphora*, Cajal & Sanchez 1915; various Heteroptera, Pflügfelder 1937). An attempt has been made in this study to give a comprehensive yet detailed account of the nervous system of these structurally very specialized insects.

The descriptions in this paper are divided into three parts. The first part deals with the general form of the body with a detailed list of the muscles. The second section covers the topography of the nervous system, and the third division contains detailed information relating to individual neurones. Clearly, both the gross and fine structure of a nervous system must be dependent on the nature of the motor and sensory fields with which it is associated, and for this reason some inventory of the other organs of *Gerris* has been included.

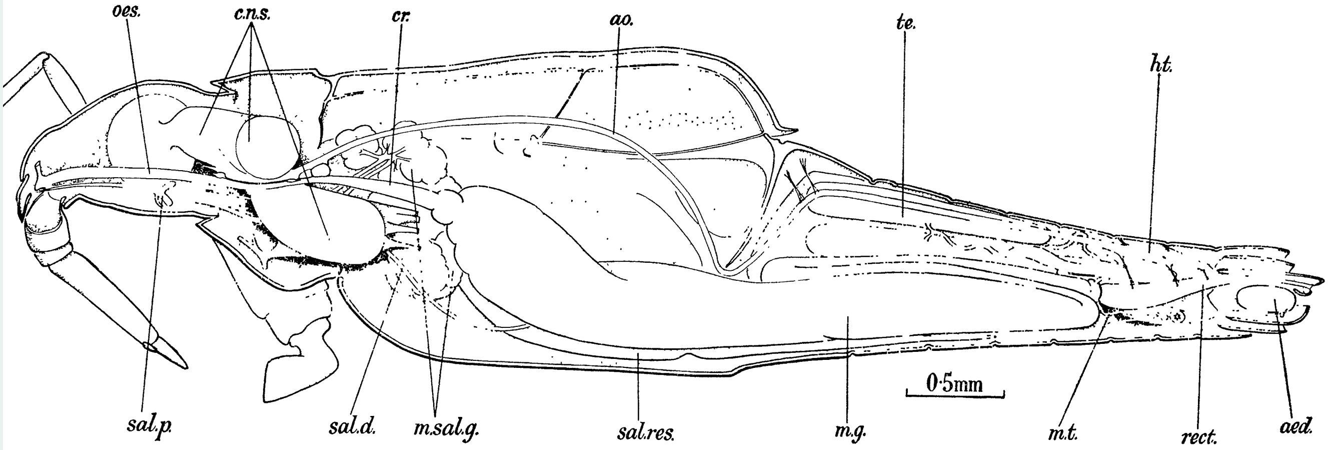


Figure 1. The right half of a male gerrid dissected to show the position of the central nervous system relative to the viscera.

aed. aedeagus; *ao.* aorta; *c.n.s.* central nervous system; *cr.* crop; *ht.* heart; *m.g.* midgut; *m.sal.g.* main salivary gland; *m.t.* Malpighian tube; *oes.* oesophagus; *rect.* rectum; *sal.d.* salivary duct; *sal.p.* salivary pump; *sal.res.* salivary reservoir; *te.* testis.

Material and methods

The descriptions of the *Gerris* nervous system were based on dissections and prepared slides of the winged form or macropter of *Gerris lacustris* L. Small numbers of *Gerris odontogaster* Zett., *Gerris gibbifer* Schum., and *Gerris asper* Fieb. were used as sources of additional material. No significant differences between the nervous systems of the winged forms of these four species were found. Each figure and textual description of a neuromere or major anatomical region has been reconstructed from a series of slides and dissections, with the exception of figure 20 which was drawn directly from a single preparation. The figures showing individual neurones were compiled from between five and thirty preparations, the form of the individual elements being treated semi-diagrammatically. In the topographical sections, nerve trunks have been described as innervating certain muscles when they can be clearly seen to send branches which end on the surface of the muscles. It has been assumed that these branches contain motor nerve fibres since there seems to be little evidence for the presence of proprioceptors in insect skeletal muscles.

The histological methods employed were as follows: For general anatomy, Duboscq–Brasil was the most used fixative and gave good results, though prolonged exposure produced overhardening of the tissues; for studies on the nervous system the fixative was first heated to 70 °C to ensure rapid penetration and localization of stainable substances. The most consistently successful stain combinations were: Heidenhain's iron haematoxylin and orange G; and Ehrlich's haematoxylin and light green.

Sectioning adult gerrids was at first a considerable problem as the cuticle is thick and well sclerotized ten days after metamorphosis. Before this time the cuticle is soft and easily cut, but the muscles are not fully enlarged, and the innervation of the integument is incomplete.

In order to study the internal anatomy of the fully developed adult, the insects were fixed and hardened in Duboscq–Brasil and embedded in a hard wax—58 °C m.p. paraffin plus 10% Ceresin—for a short period at reduced pressure. They were then rinsed rapidly in warm xylol to remove the wax from the integument and passed into Gurr's freshly prepared 'Diaphanol' (chlorinated acetic acid plus nitric acid) until soft. The insects were then brought back into xylol and the insulating wax replaced by fresh wax at reduced pressure, care being taken not to overharden the specimens.

Specimens prepared by this method sectioned easily and the tissues, having been protected from the softening reagent, would take up most stains including silver nitrate.

Although this method was successful, it should be stated that several other methods were applied both to *Gerris* and other fully hardened adult insects, and it was clear that, while many insects can be sectioned by avoiding the hardening of the cuticle caused by dehydration and high temperature embedding, using the following methods: (i) a butyl alcohol series (Smith 1940), (ii) embedding in low viscosity nitrocellulose, (iii) double embedding, or using a hard low melting-point wax such as Steedman's ester wax or Waterman's wax, the fully hardened adults of many Coleoptera, Heteroptera and Hymenoptera cannot be prepared even as thick sections by these methods alone, but must be softened by some such method as the Diaphanol method described here.

Metal impregnation methods were used extensively for studying the detailed anatomy of the nervous system. Of the 'silver-on-the-slide' methods, those of Holmes (1947) and Romanes (1950) were found less satisfactory than that of Palmgren (1948), which gave some excellent results. For cell bodies alone, Einarson's gallocyanin and Ehrlich's haematoxylin gave good results.

The rapid Golgi silver-bichromate process occasionally gave good results (5% success) but the Golgi–Cox mercury-bichromate method gave a much higher percentage of successful preparations (50 to 70% success) and was much simpler to perform. However, the silver process gave a much finer and clearer deposit than even the best mercury preparations. I am indebted to the Anatomy Department of University College London for the method of developing Golgi–Cox material. After cutting, the sections were brought into 5% potassium sulphite to which a few drops of 5% oxalic acid had been added. Thorough washing in distilled water was followed by dehydration in equal parts of absolute alcohol and chloroform; the sections being cleared in terpineol and mounted in dammar xylol.

Methylene blue was found to penetrate the c.n.s. very imperfectly although peripheral nerves were often stained.

In order to study the early development of the nervous system, eggs between two and ten days old were sectioned and stained by the methods already described. Metallic impregnation gave only poor results, and routine staining combinations were the most useful. Untreated eggs were sectioned as well as those from which the chorion had been removed. Methyl benzoate and clove oil double embedding had no advantage over wax embedding as described for the adults.

The muscles

The gross morphology of the nervous system of *Gerris* must be determined, at least in part, by the layout of the muscles and skeleton, and the position of the major sense organs. While the relationship of the larger nerves to the muscles need not be as critical as the relationship of these muscles to the parts of the skeleton they move, there are considerations of space and economy of materials that will relate nerve and muscle topography. The size and distribution of the muscles may be associated with the remarkable condensation of the *Gerris* central nervous system. For this reason, and because it is difficult to describe the position of nerve trunks without reference to the musculature, a brief survey of the muscles is included in this paper.

In his paper on the skeleto-muscular system of Heteroptera Larsen (1945) gives a brief mention to the thoracic muscles of *Gerris rufoscutellatus* Lat., but otherwise there is little work on this topic.

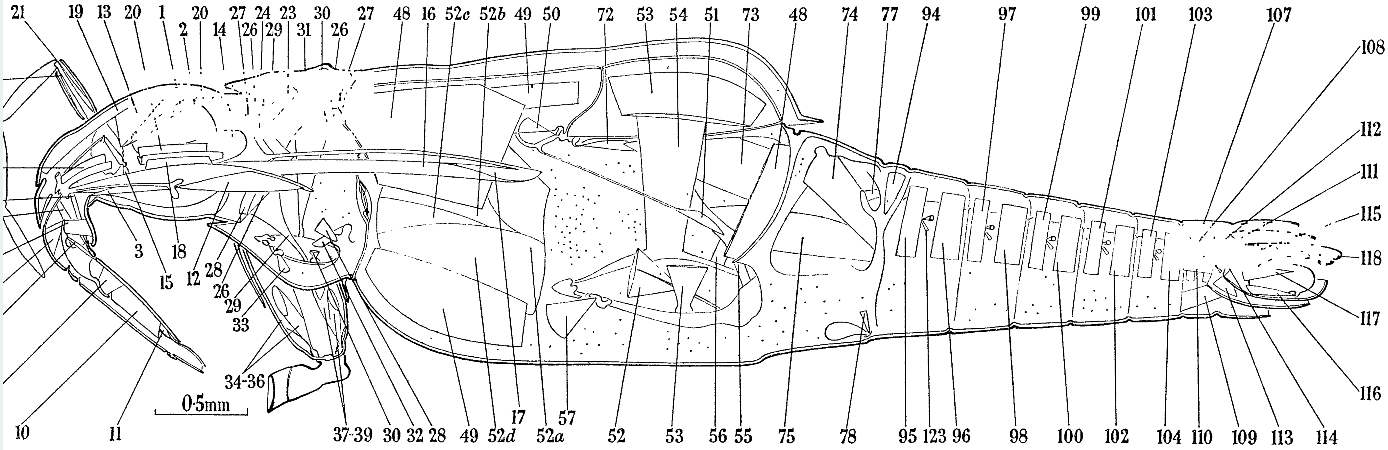


FIGURE 2. The right half of a male gerrid dissected to show the skeletal muscles 1 to 118 and 123.

For this study the arrangement, numbers and sizes of the different muscles in *Gerris lacustris* L., were examined. One hundred and twenty-nine distinct pairs of skeletal muscles could be distinguished (see figure 2), and in addition the non-skeletal muscular plexi of the gut, heart, and salivary glands. A fuller account of the muscles will be published elsewhere.

The head contains twenty-two pairs of muscles; nine of these associated with the large and complex labium typical of Hemiptera, and five pairs attached to the other mouthparts. There are four pairs of antennal muscles, and the remaining four pairs of muscles operate the cibarial and salivary pumps. Most of the head muscles are small, consisting of less than a dozen fibres, but the pump muscles and the retractor of the mandible are larger.

The segments of the thorax all bear a pair of limbs of the same general form, and each of these limbs contains fourteen muscles. The mesothoracic legs are a good deal larger than the limbs of other segments. In the prothorax it is possible to distinguish five pairs of extrinsic leg muscles, and six pairs of muscles responsible for head movements. Most of these muscles are of about the same size, but in the mesothorax there are a few very large muscles (100 to 200 fibres), and a number of much smaller muscles. The large muscles are: the indirect muscles of flight (two pairs), the trochanteral abductors (muscle 52 in figure 2), and the rotators of the coxae (muscles 53 and 54). The development of the indirect flight muscles varies, and as they are supplied by a few axons only, they must be considered apart from the rest of the musculature. *m.* 52 is the largest muscle in the body (one muscle was found to contain two hundred and twenty fibres), and supplies a large part of the energy required to drive the skater over the surface of the water. The small muscles comprise three pairs of direct wing muscles, and three pairs of coxal muscles.

The metathoracic muscles are basically similar to those of the preceding segment but in association with the reduced nature of the metathorax they are much smaller in size.

The abdomen as in most specialized insects contains a small number of ventilating muscles in the pregonadial region, and a much more complex musculature in the gonadial part (in *Gerris* segments 7 to 9); none of these muscles is of large size.

Taking into account the minute spiracular muscles there are twenty-two muscles in the head, seventy-four pairs of muscles in the thorax including the legs (in each segment 27, 26 and 21 pairs respectively), and thirty-three pairs of muscles in the abdomen, nine of them spiracular.

As there is a certain constancy in the size of muscle fibres, the number of fibres in a muscle give some indication of its size, and this will reflect on the amount of axon material associated with it, whether in the form of few or many units. The following figures represent the numbers of muscle fibres in the largest muscles (single) in different regions of the body of one specimen of *Gerris lacustris* L. The numbers of muscle fibres in transverse sections were counted with the aid of a squared eyepiece. These are the largest numbers of fibres counted in transverse sections: Head, salivary pump retractor *m.* 12, 19 fibres; mandibular retractor *m.* 14, 20 fibres. Thorax, prothoracic trochanteral muscle *m.* 29, 37 fibres; mesothoracic trochanteral muscle *m.* 52, 207 fibres; metathoracic trochanteral muscle *m.* 73, 63 fibres. The abdominal muscles included in this series of sections were not cut sufficiently transversely for them to give much information, but the abdominal ventilators appeared to contain at least twenty fibres. A number of less completely sectioned insects were examined and these gave fibre counts similar to those described for the same muscles, thus *m.* 52 showed a range from 190 to 220 fibres in five individuals.

A further consideration of the relationships between nerve and muscle topography is embodied in the Discussion.

Description of plate 8

Figure 22. Parasagittal section of the whole central nervous system. Compare in detail with figure 4, in text.

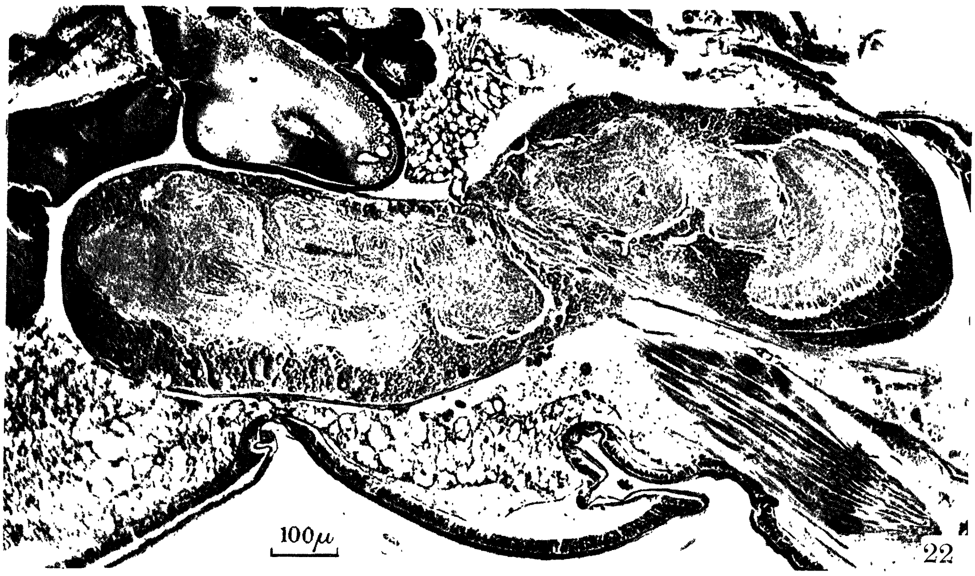
Figure 23. Horizontal longitudinal section through the protocerebrum. Branching fibres from the protocerebral lobes to the central body can be seen (examine *p.i.* 1, figure 11).

Figure 24. Vertical longitudinal section through an optic lobe showing fibres in the medullae, especially the large radiating fibre of the medulla interna—optic internuncial 7 (*o.i.* 7 in figure 11).

Figure 25. Transverse section of the mesothoracic neuromere showing the dorsal alary tract (*d.al.t.*) and the ventral alary tract (*v.al.t.*) see figure 14. Note also parts of the giant fibre—*g.i.* 4.

Figure 26. Vertical longitudinal section of the thoracic neuromeres to show the large fibre, *g.i.* 4 (see also figure 15). Note the ventral limbs.

Figure 27. Vertical longitudinal section of the posterior region of the central nervous system to show the large glomeruli of the abdominal centre and the longitudinal fibre tracts (*gl.* and *l.t.*).



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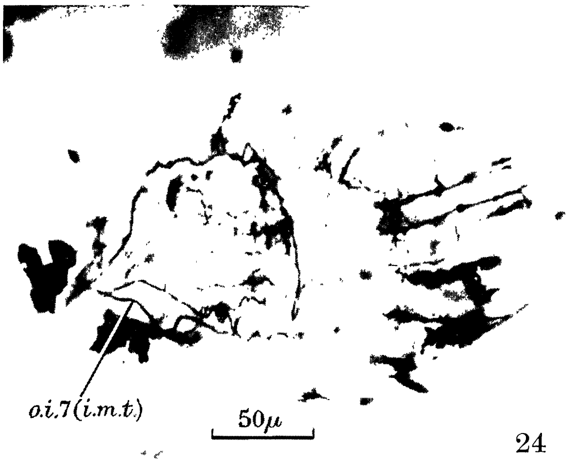

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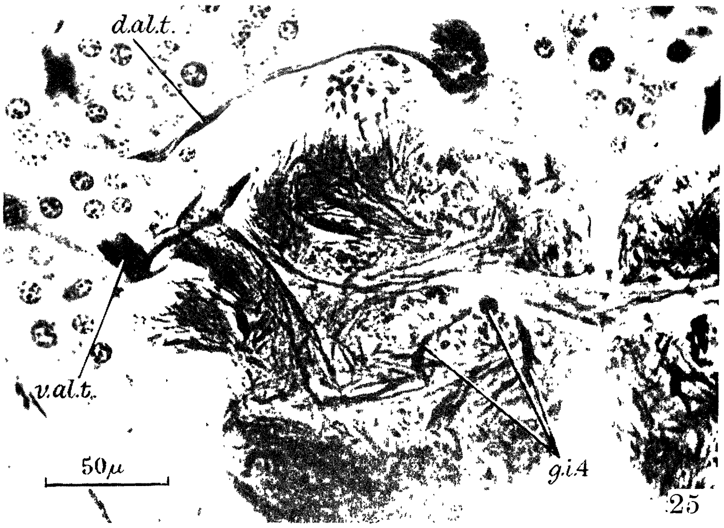

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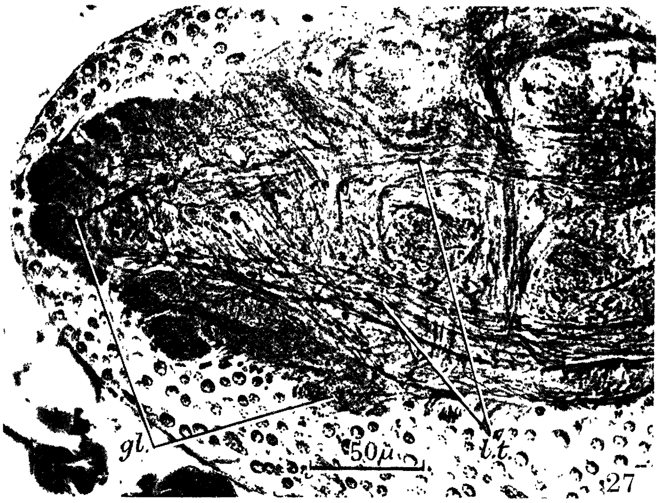

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(*Facing p.* 70)

The topography of the nervous system

The most striking characteristic of the *Gerris* nervous system is its high degree of condensation (figures 1 and 4, and figure 22, plate 8). There is evidence to suggest that the primitive number of segments in insects is twenty-one, although the twelfth abdominal neuromere appears to be lacking even in the embryos of modern forms (Johannson & Butt 1941). Adult insects possess supra- and suboesophageal centres within the head capsule, each formed of three neuromeres; and a posterior ganglionic chain modified by fusion of the abdominal elements. Eight abdominal centres are found in adult Thysanura and the larvae of certain Lepidoptera, but this is exceptional, and most adult pterygotes exhibit less than nine post-cephalic ganglia. Varying degrees of fusion occur but only within the higher Diptera (Schizophora) and the specialized families of Hemiptera, the Cicadidae and the Gerridae, do all the neuromeres merge.

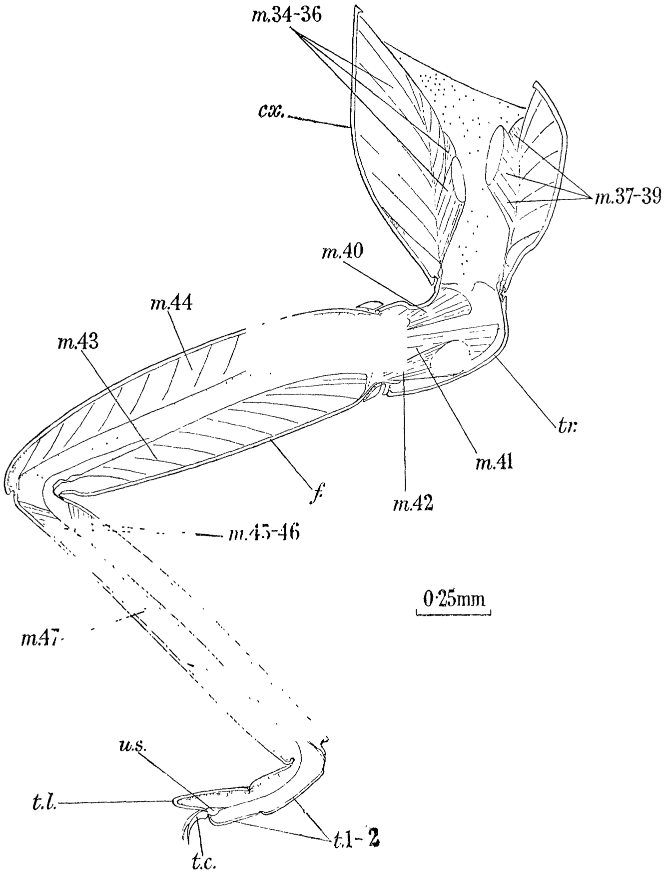

Figure 3. The right prothoracic leg viewed from the midline and dissected to show skeletal muscles 34 to 47.

cx. coxa; *f.* femur; *t.* 1–2. tarsal segments 1–2; *t.c.* tarsal claw; *t.l.* tarsal lobe; *ti.* tibia; *tr.* trochanter; *u.s.* unguitractor sclerite; *u.t.* unguitractor tendon.

Johansson (1957) points out that the neuromeres of first instar larvae of *Oncopeltus* exhibit a similar degree of condensation.

In *Gerris*, the ventral ganglia are coalesced, while the connectives between the supra- and suboesophageal centres are very short, the tritocerebrum being broadly contiguous with the gnathal centres. The central nervous system therefore appears externally as a single undivided organ only pierced by a narrow foramen containing the oesophagus and aorta.

While none of the internuncial fibres can be more than 1 mm long, some of the motor axons to the abdominal muscles are 4 to 5 mm in length. Defined as the ratio of the longest motor to the longest internuncial axon, the nervous system of *Gerris* shows the highest degree of centralization, for even in the higher Diptera and the Homoptera in which a considerable degree of ganglionic fusion occurs, the cervical connectives remain elongated in association with a mobile head.

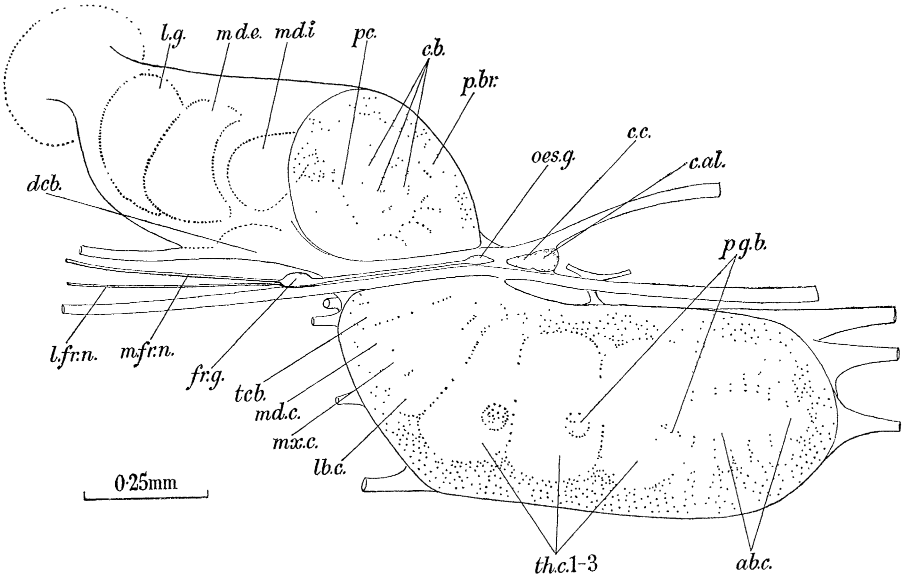

FIGURE 4. The central nervous system cut sagittally to show the position of the neuromeral fibre masses and the retrocerebral system.

ab.c. abdominal centre; *c.al.* corpora allata; *c.b.* central body; *c.c.* corpora cardiaca; *dcb.* deutocerebrum; *fr.g.* frontal ganglion; *lb.c.* labral centre; *l.fr.n.* lateral frontal nerve; *l.g.* lamina ganglionaris; *md.c.* mandibular centre; *md.e.* medulla externa; *md.i.* medulla interna; *m.fr.n.* median frontal nerve; *mx.c.* maxillary centre; *oes.g.* oesophageal ganglion; *pc.* protocerebrum; *p.br.* protocerebral bridge; *pg.b.* postglomerular bridge; *tcb.* tritocerebrum; *th.c.* 1–3, thoracic centres one to three.

In the 3-day *Gerris* embryo, nine preabdominal neuromeres are distinct, but only five could be made out in the abdominal region. In the adult, the ganglionic fibre masses are larger and better defined, and six transverse commissural tracts are visible in the post-thoracic region, and as there are six pairs of innervated spiracular muscles in the abdomen, they probably correspond to six abdominal ganglia. From an examination of the numbers and sizes of the muscles supplied by these centres it seems likely that they are derived from abdominal segments 1 plus 2, 3, 4, 5, 6, 7 plus 8 plus 9 plus 10. These fifteen neuromeres will be described, first, as regards their nerves and peripheral connexions, and secondly, from the point of view of their detailed internal structure.

The nerves of the head

The complex nature of the mouthparts and their musculature in *Gerris* is associated with a complex innervation. Not only are there many nerve trunks, but there are also interconnexions between nerves from different centres, a feature that may reflect the elaborate nature of hemipteran feeding (Pesson 1943). The connexions between the gnathal nerves and the anterior visceral nervous system appear to subserve co-ordination between gut and mouthparts. The formation of peripheral rather than central connexions between neuromeres is a common feature of many nervous systems and may be the result of a direct growth response from superficial cell bodies.

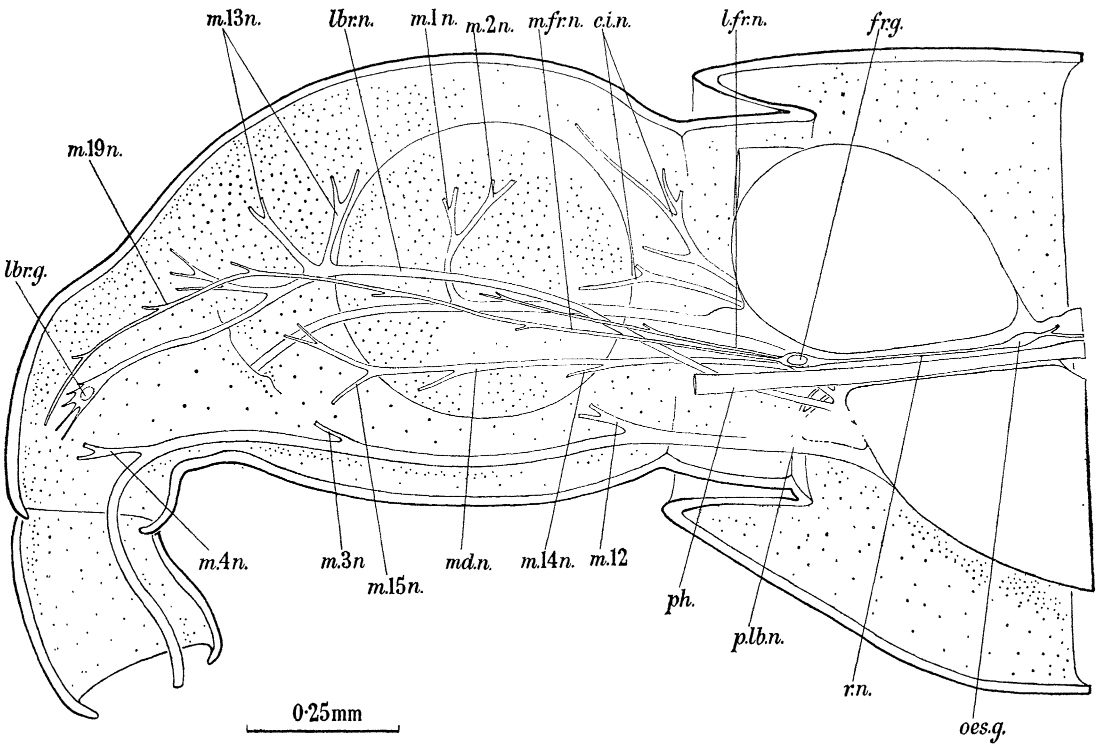

FIGURE 5. Parasagittal sections of the head showing the main nerve trunks innervating the left half of the head. The optic lobe of the left side has been cut away to show the cephalic integumentary nerves.

c.i.n. cephalic integumentary nerve; *fr.g.* frontal ganglion; *lbr.g.* labral ganglion; *lbr.n.* labral nerve; *l.fr.n.* lateral frontal nerve; *md.n.* mandibular nerve; *m.fr.n.* median frontal nerve; *m.n.* nerve to muscle; *oes.g.* oesophageal ganglion; *ph.* pharynx; *p.lb.n.* posterior labral nerve; *r.n.* recurrent nerve.

In the following description the nerves of each segment are grouped under the heading of their segmental neuromere. The descriptions are intended primarily as a guide to the figures.

(*a*) *Supraoesophageal centres*

(i) *Protocerebrum* (see figures 4, 5 and 6)

This neuromere (figure 4, *pc.*) is intimately associated with optic fibres from the eyes, and to a lesser extent with a number of fine sensory nerves from the integument of the head. The largest of these integumentary elements (*c.i.n.*, figures 5 and 6) is associated with the mouthpart nervous system, but although many fibres may have terminals within the mouthpart ganglia, detailed study indicates the protocerebral identity of some of them. Dorsal to the stylet ganglion (figure 6, *st.g.*) the protocerebral trunk (figure 6, *c.i.n.*)

gives off a posterior nerve (*p.p.n.*), which appears to have a connexion with the retrocerebral complex. This may correspond to the integumentary–cardiac body connexion found in *Icerya* (Pesson 1943).

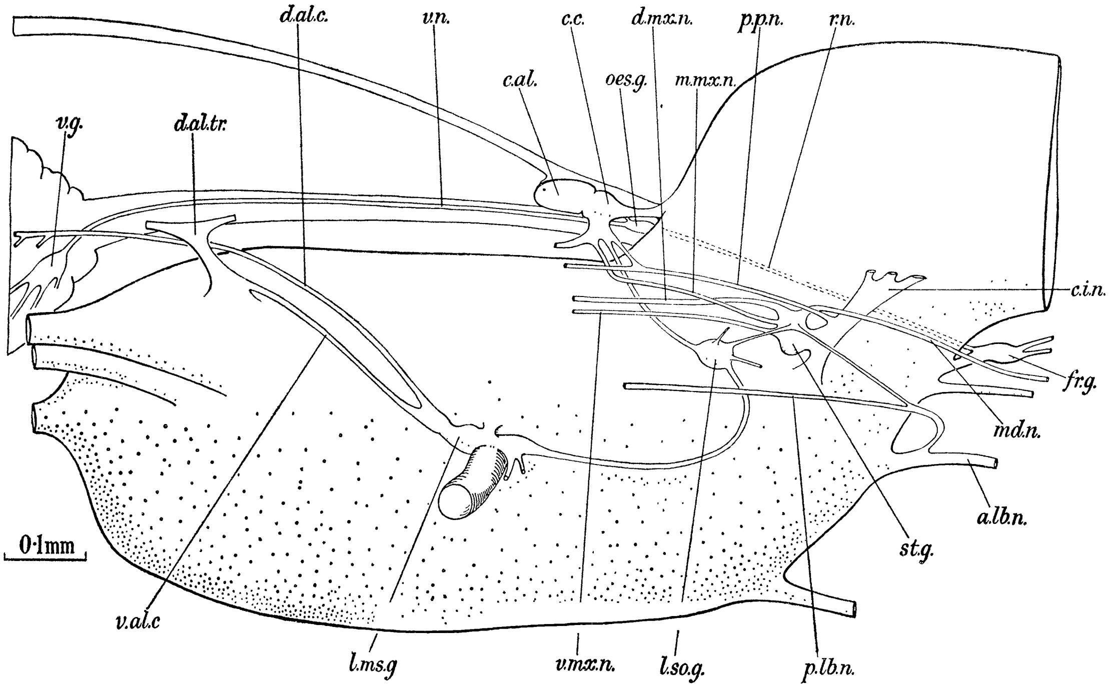

FIGURE 6. The central nervous system viewed from the right side to show the retrocerebral system and part of the stylet nervous system.

a.lb.n. anterior labral nerve; *c.al.* corpora allata; *c.c.* corpora cardiaca; *c.i.n.* cephalic integumentary nerve; *d.al.c.* dorsal alary connective; *d.al.tr.* dorsal alary trunk; *d.mx.n.* dorsal maxillary nerve; *fr.g.* frontal ganglion; *l.ms.g.* lateral mesothoracic ganglion; *l.so.g.* lateral suboesophageal ganglion; *md.n.* mandibular nerve; *m.mx.n.* median maxillary nerve; *oes.g.* oesophageal ganglion; *p.lb.n.* posterior labral nerve; *p.p.n.* posterior protocerebral nerve; *r.n.* recurrent nerve; *st.g.* stylet ganglion; *v.al.c.* ventral alary connective; *v.g.* ventricular ganglion; *v.mx.n.* ventral maxillary nerve; *v.n.* ventricular nerve.

(ii) *Deutocerebrum* (figures 4 and 5)

This centre (figure 4, *dcb*) is largely composed of antennal nerve connexions. The antennal nerve is present as a large single trunk running anteriorly on either side of the cibarium. It gives off two branches (figure 5, *m.* 1 *n.* and *m.* 2 *n.*) within the head, to the extrinsic antennal muscles *m.* 1 and *m.* 2, and a slender sensory branch (not shown) to the articular membrane between the head and the antenna. Within each antenna, it innervates the small intrinsic antennal muscles *m.* 20 and *m.* 21. The rest of the innervation is sensory, a disproportionately large number of fibres being associated with the last antennal segment.

(iii) *Tritocerebrum* (figures 4, 5 and 6)

The tritocerebrum (*tcb.* figure 4) is readily identifiable, but its boundaries are less distinct in *Gerris* than in other insects, associated with its fusion with the gnathal centres. The nerves of the tritocerebrum are mainly associated with the muscle and sense organs of the anterior region of the gut, supplying the muscles of the pump apparatus directly (figure 5, *m.* 13 *n.*) or directly via the frontal ganglion (figure 5, *m.* 19 *n.*). Many of the sensory fibres appear to be associated with paired labral ganglia (figure 5, *lbr.g.*), some being integumentary in origin, while others appear to originate from the food meatus itself although these do not seem to form a distinct sense organ as in some Homoptera (*Icerya* Pesson 1943). In weevils (Dönges on *Cionus* 1954), there is no distinct labral ganglion.

(*b*) *Suboesophageal centres* (figures 4, 5 and 6)

This centre is formed by the intimate fusion of three gnathal neuromeres (*mx.c.*, *md.c.*, and *lb.c.*, figure 4) early in development with the result that the components are difficult to identify in the adult. The labial centre (*lb.c.*) appears the most distinct in sections, due to its greater bulk and to the anteriorward orientation of its nerves. The maxillary and mandibular centres (*mx.c.* and *md.c.*) have a common lateral nerve trunk and ganglion so that for the purposes of topographical description they are best regarded as a single unit. The fusion of mouthpart nerves also occurs in the weevil *Cionus* (Dönges 1954) but a ganglion is absent.

(i) *The maxillary and mandibular centres*

The common stylet nerve trunk enlarges to form a stylet ganglion (figure 6, *st.g.*) near its junction with the protocerebral nerve. This striking structure appears to be absent in the less specialized *Oncopeltus* (Johansson 1957).

The stylet ganglion has two kinds of connexions; nerves to the stylets and their muscles, and connexions with other parts of the nervous system whose functional significance is less obvious. The stylet nerves comprise a mandibular nerve (figure 6, *md.n.*) to the mandibular stylet sac and two muscles (*m.* 14 *n.* and *m.* 15 *n.* in figure 5), and two maxillary nerves. The larger maxillary nerve (figure 6, *d.mx.n.*) appears to innervate the stylet sac, but this branch was difficult to trace in detail. The other connexions of the stylet ganglion are with the corpora cardiaca (figure 6, *m.mx.n.*), the labial nerve and a small lateral oesophageal ganglion (*l.so.g.*). The first of these connectives may carry fibres to the oesophageal ganglion and mediate co-ordination between gut muscles and stylets. A similar connexion occurs in both *Cionus* (Dönges 1954) and *Naucoris* (Cazal 1948). The labial connective may be part of a system controlling serial feeding. The connective with the lateral oesophageal ganglion would seem to have at least two possible functions. This ganglion appears to receive a few fibres from the spiracle and may be analogous with the abdominal spiracular ganglia. Alternatively, it is possible that there are connexions between the stylet centres and the wing muscle nerves through the lateral mesothoracic ganglia (*l.ms.g.*, figure 6). Dissections show that the long maxillary stylets could obstruct the indirect wing muscles when the insect is flying so that the development of a system regulating the position of the thoracic mouthparts in flight would be understandable.

(ii) *Labial centre*

This gnathal centre has three main connexions, by far the largest being with the labium and salivary syringe. In the Hemiptera, the labium is a large and complex organ, providing and directing the muscular force for stylet insertion. Associated with it is a salivary pump apparatus and salivary glands. All these structures receive nerve fibres from a large anterior nerve trunk which divides into anterior (*a.lb.n.*, figure 6) and posterior (*p.lb.n.*, figures 5 and 6) rami soon after leaving the central nervous system. The anterior nerve innervates the labial muscles (*m.* 3 to *m.* 11) and the large muscles of the salivary pump (*m.* 12), while the posterior nerve passes back to the salivary gland. Baptist (1941) showed that the fine fibrous reticulum investing the racemose principal gland took up methylene blue very readily, and concluded from this that the reticulum was in the nature of a nerve plexus. A similar picture was obtained in the present study, but the stained structures were much more irregular than are nerve fibres, and no nerve trunk to the hypocerebral ganglion, as described by Baptist, could be traced. Silver preparations, however, demonstrated that the greater part of the reticulum consisted of radiating muscle fibres with conspicuous light and dark bands, and in some sections, a nerve derived from the retrocerebral system can be seen crossing the surface of the gland.

The third connexion of the labial centre is with the lateral suboesophageal ganglion by a fine nerve strand (shown in figure 6) the possible function of which has been discussed in association with the maxillary and mandibular centres.

The anterior visceral nervous system

(Retrocerebral system, figures 4, 5 and 6)

As in *Rhodnius* (Wigglesworth 1950), the retrocerebral glands are intimately connected. The glands and nerves of this region have been described in more detail by Cazal (1948) in *Naucoris*, and by Johansson (1957) in *Oncopeltus*. The system in *Gerris* resembles more closely that of *Oncopeltus* than the more diffuse system found in *Naucoris*.

In front of the oesophageal foramen, the frontal ganglion (*fr.g.*) is present as a slightly thickened medial structure connected to the tritocerebral lobes postero-ventrally by a frontal bridge of fibres. A median frontal nerve (*m.fr.n.*) runs antero-dorsally between the postclypeal muscles to which it gives a number of fine branches, and then runs forward to innervate the anteclypeal muscles. Paired lateral frontal nerves (*l.fr.n.*), finer than the median nerve, run to the outer face of the postclypeal muscles. A recurrent oesophageal nerve (*r.n.*) unites the frontal ganglion with a median oesophageal ganglion (*oes.g.*). From the oesophageal ganglion, lateral connexions pass to the corpora cardiaca and paired nerves (figure 6, *v.n.*) run posteriorly to the ventral side of the oesophageal valve where ventricular ganglia (*v.g.*, figure 6) are situated.

The corpora cardiaca (*c.c.*) are divided into two parts by a slight constriction as in *Naucoris* (Cazal 1948). There is a lateral ganglionic portion receiving nerves from the lateral suboesophageal ganglion (*l.so.g.*), the stylet ganglion (*st.g.*) and possibly also from the cephalic integumentary nerve (*c.i.n.*, figure 6). Also visible in some sections are paired nerves running posteriorly (figure 4), possibly homologous with the prothoracic nerves of *Cicada* (Cazal 1948). The more internally-lying parts of the corpus cardiacus on each side are united posteriorly and to the single corpus allatum, and anteriorly to the oesophageal ganglion. There are also paired connectives to the supraoesophageal centre which appear to separate internally into three tracts, two of which run to the pars intercerebralis, as in other bugs (Pflügfelder 1937; Cazal 1948). Lateral cardiac nerves are visible in the anterior region of the aorta, but their connexions with cardiac bodies are obscure. Unlike *Naucoris*, there is no fibroglial lamella.

It is difficult to rationalize the connexions between the corpora cardiaca and the mouth-part nerves unless it is assumed that fibres pass through the corpora cardiaca from the oesophageal ganglion, which may well be the case.

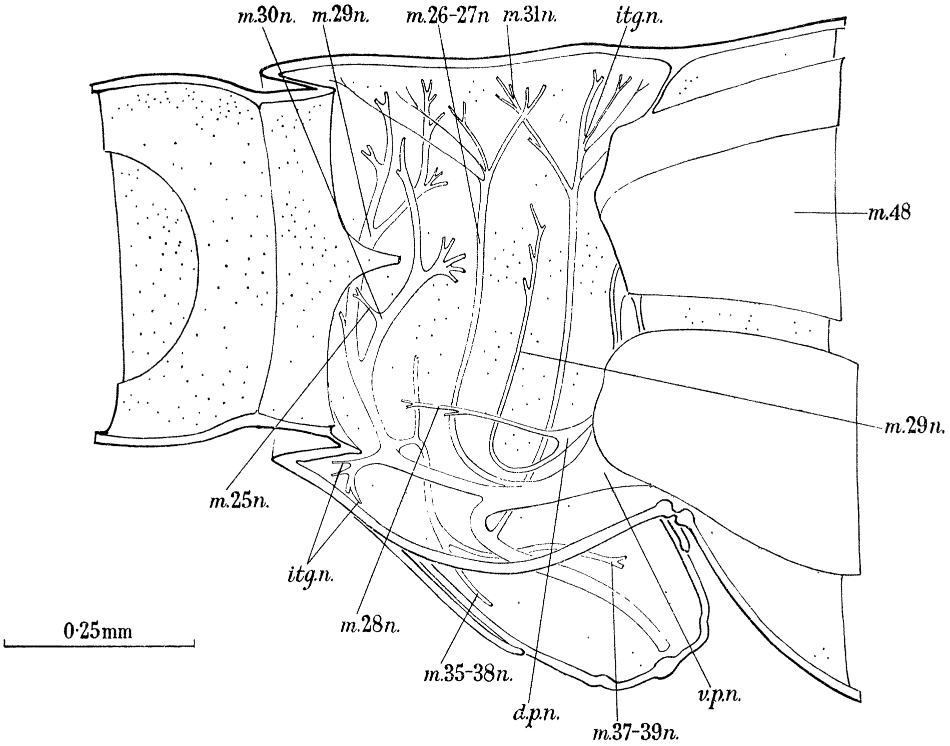

FIGURE 7. The nerves of the left side of the prothorax. The central nervous system has been cut through in the midline, and the gnathal and supraoesophageal neuromeres have been removed.

d.p.n. dorsal prothoracic nerve; *itg.n.* integumentary nerve; *m.n.* nerve to muscle; *v.p.n.* ventral prothoracic nerve.

Prothoracic centre

The pattern of the prothoracic nerves reflects the unspecialized nature of this segment, in that the major roots soon divide into many branches rather than maintaining their individuality for a large part of their length as do the mesothoracic nerves. This is, in part, associated with the small distance separating the prothoracic centre (figure 4, *th.c.* 1) from the organs it innervates. There are two major roots: a small dorsal root (figure 7, *d.p.n.*), and a much larger ventral root (*v.p.n.*). The former expands into a ganglionic enlargement before dividing to innervate muscles 29 and 28 (*m.* 28 *n.*, *m.* 29 *n.*). The larger nerve divides several times, forming branches to the extrinsic leg muscles (*m.* 29 to *m.* 33), and to the muscles responsible for intersegmental movements (*m.* 23 to *m.* 28). Several sensory nerves were traced, most of them associated with the integument of the tergal and sternal areas (figure 7, *itg.n.*). The large trochanteral abductor of the prothorax (figure 2, *m.* 29), appears to receive fibres through both dorsal and ventral roots, suggesting that there may be some functional differentiation within the muscle, a suggestion that is strengthened by the clearly segmented appearance of the muscle. The ventral trunk continues into the leg, innervating muscles *m.* 34 to *m.* 47 and receiving large numbers of sensory fibres from the limb surface.

Mesothoracic centre (figures 4, 8 and 9)

The large and specialized mesothorax of *Gerris* has a well-developed mesothoracic centre (*th.c.* 2, figure 4) in the central nervous system and a complex system of nerves. There are four main roots or groups of nerves arising from this centre. (*a*) Large mixed median nerves. These supply the leg muscles and integumentary sense organs of the limb. (*b*) Dorsal alary trunk. This nerve innervates the longitudinal indirect flight muscles and a basal wing muscle, and also receives a number of sensory fibres from the pleural areas and the forewing. (*c*) Ventro-lateral ganglion and nerves. These delicate structures appear to supply the vertical flight muscles. (*d*) Ventral nerves. A variable number of fine sensory nerves enter the mesothoracic centre ventrally from the sternal area.

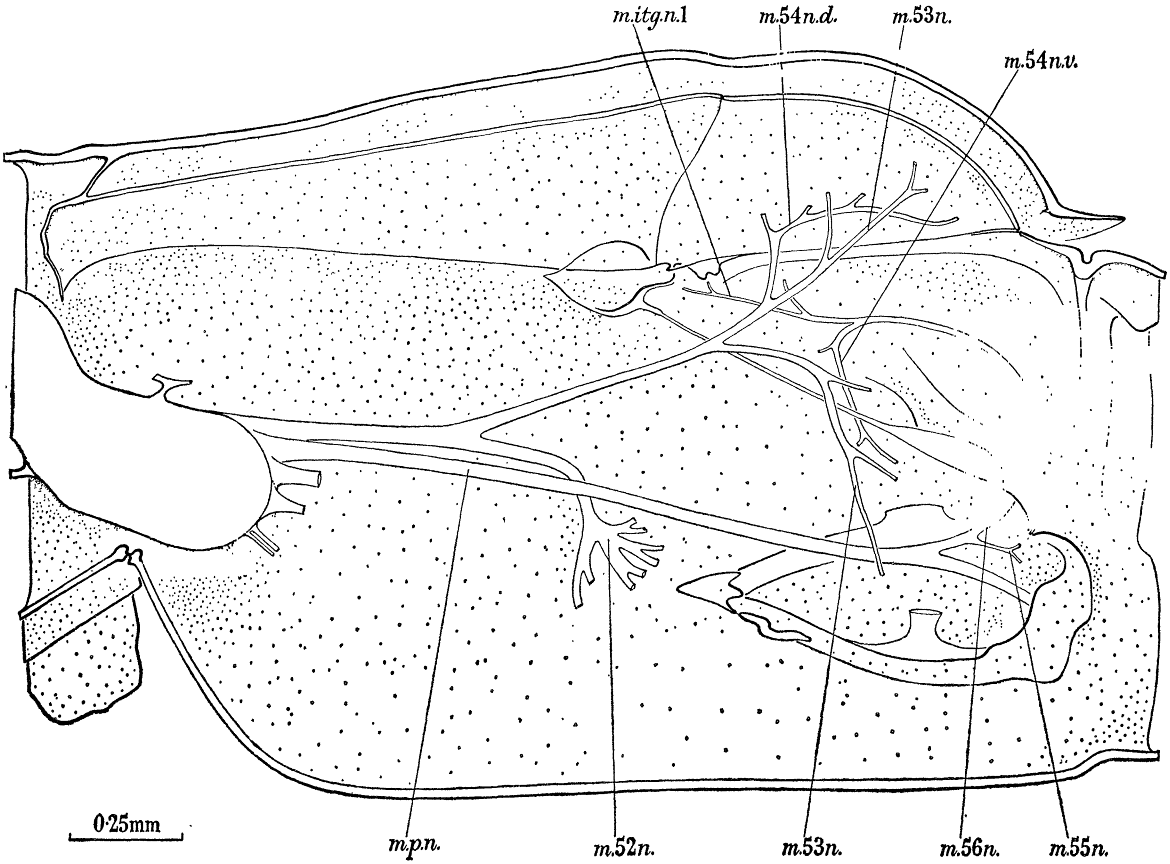

FIGURE 8. The nerves of the left side of the mesothorax (i). The major nerve trunks of the leg muscles.

m.itg.n. mesothoracic integumentary nerve; *m.n.* nerve to muscle; *m.*54*n.d.* nerve to the dorsal part of muscle 54; *m.*54*n.v.* nerve to the ventral part of muscle 54; *m.p.n.* mesothoracic podial nerve.

(*a*) *Median nerves* (figure 8)

Almost all the large tubular muscles of the mesothorax and limb are supplied by these nerves, and many of the sense cells contribute fibres to them. The main outflow is through a median dorsal root that soon divides into a ramus with branches (figure 8, *m.* 52 *n.*, *m.* 53 *n.* and *m.* 54 *n.d.*) to the large muscles—*m.* 52, *m.* 53 and *m.* 54, and a more ventral nerve (*m.p.n.*) the greater part of which enters the limb. Small dorsal rami from this podial nerve supply the small muscles *m.* 55 and *m.* 56 (*m.* 55 *n.*, *m.* 56 *n.*) and the ventral part of the coxal rotator *m.* 53 (*m.* 54 *n.v.*); in addition it receives numerous sensory branches from the integument (*m.itg.n.* 1). The trochanteral muscles antagonistic to *m.* 52 are supplied by a separate nerve (figure 9, *m.* 58 to *m.* 60 *n.*), which also gives off a short branch (*m.* 57 *n.*) to the trochantinal muscle *m.* 57.

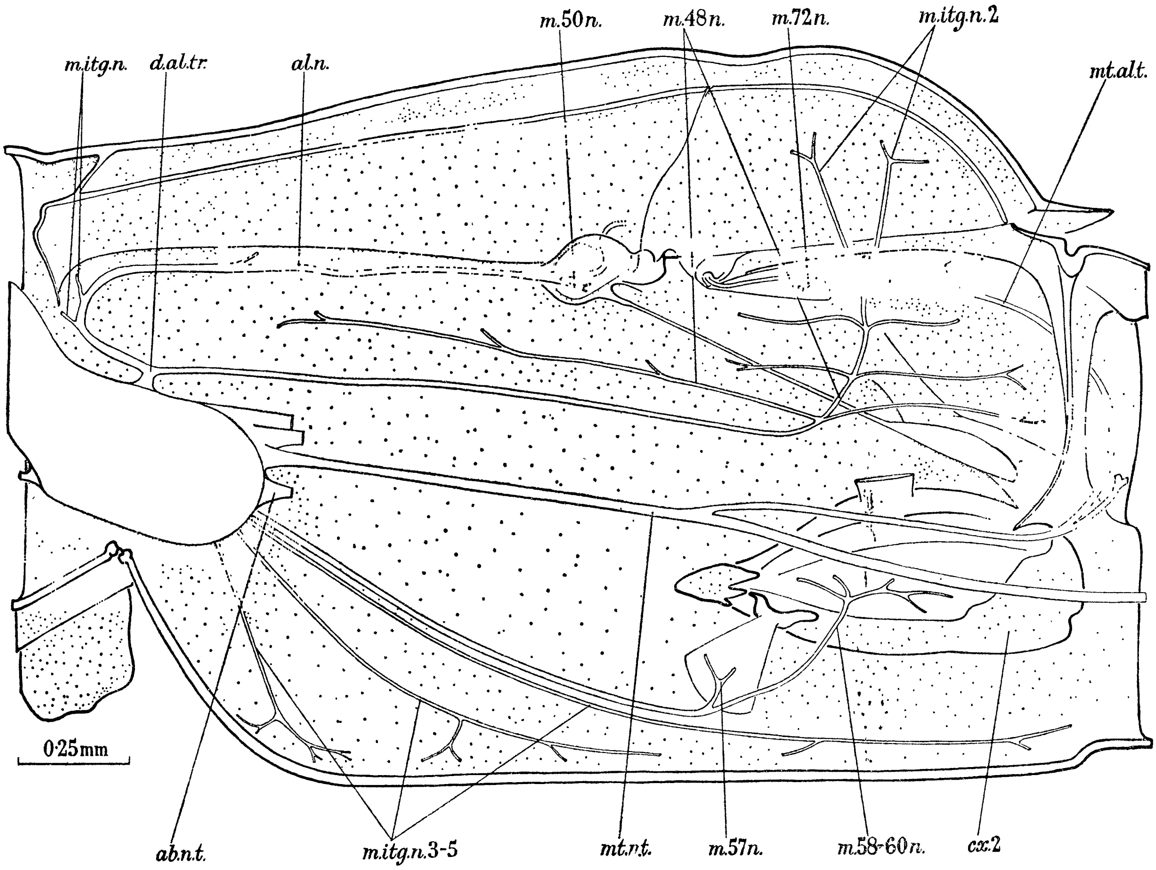

FIGURE 9. The nerves of the left side of the mesothorax (ii). The nerves to the forewing, wing muscles, and minor nerve trunks to the leg muscles.

ab.n.t. abdominal nerve trunk; *al.n.* alary nerve; *cx.* 2, mesothoracic coxa; *d.al.tr.* dorsal alary trunk; *m.itg.n.* mesothoracic integumentary nerve; *m.n.* nerve to muscle; *mt.al.t.* metathoracic alary trunk; *mt.n.t.* metathoracic nerve trunk.

(*b*) *Dorsal alary trunk* (figure 9 *d.al.tr.*)

The detailed structure and variation of the nerves of the alary apparatus is described at greater length under the heading of detailed anatomy (see p. 94). This topographical description applies to the macropterous or fully winged forms of *Gerris*.

The dorsal nerve divides into two rami. The anterior ramus (figure 9, *al.n.*) innervates the anterior basal wing muscle *m.* 50 (*m.* 50 *n.*) and the forewing, while the more slender posterior ramus innervates the longitudinal indirect wing muscles (*m.* 48 *n.* in figure 9) and receives a number of sensory fibres from the overlying tergum (*m.itg.n.* 2). The relative independence of the dorsal alary trunk seems to be a feature of many insect nervous systems associated at least in part with the centro-dorsal position of the longitudinal muscles. In *Drosophila* (Hertweck 1931), and *Oncopeltus* (Johansson 1957), the dorsal nerve has much the same connexions, although the detailed pattern of innervation is more complex as there are several pairs of indirect muscles.

(*c*) *Ventro-lateral ganglion* (figure 6, *l.ms.g.*)

It has not been possible to work out the connexions in this region in detail, as they are very fine and apparently rather variable. The ganglion, which is connected to the central nervous system by a short strand, appears to have the following connexions: (i) an anterior connective with the lateral suboesophageal ganglion (*l.so.g.*), (ii) a postero-dorsal nerve (*v.al.c.*) to the base of the dorsal alary nerve, and (iii) a nerve (*d.al.c.*) passing above (ii) and over the dorsal root. This nerve appears to innervate the vertical indirect flight muscles, but great difficulty was experienced in following it to the muscle. If these muscles receive their motor axons by this pathway, it is easy to see some co-ordinating function for nerve (ii)—the postero-dorsal nerve.

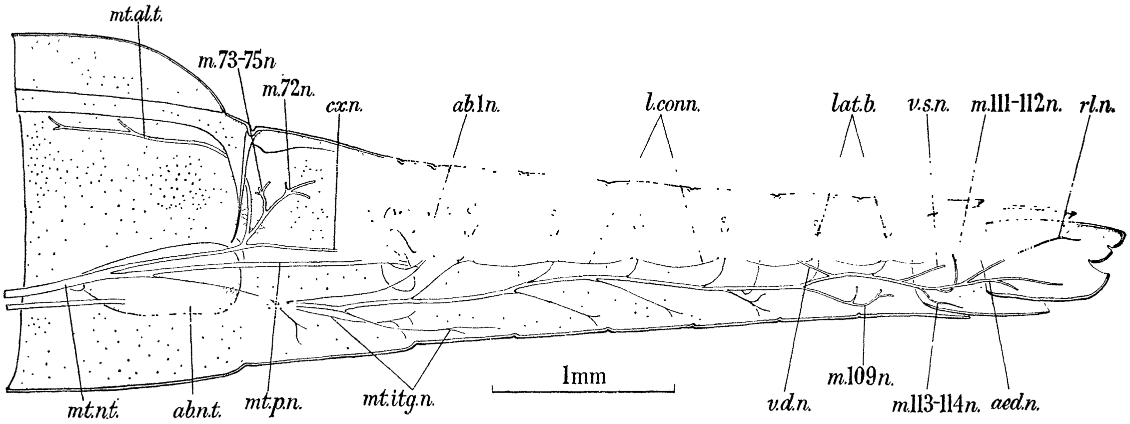

FIGURE 10. The nerves of the left side of the metathorax and abdomen.

ab.n.t. abdominal nerve trunk; *ab.*1*n.* nerve to first abdominal segment; *aed.n.* aedeagal nerve; *cx.n.* coxal nerve; *lat.b.* lateral body; *l.conn.* lateral connective; *m.n.* nerve to muscle; *mt.al.t.* metathoracic alary trunk; *mt.itg.n.* metathoracic integumentary nerve; *mt.n.t.* metathoracic nerve trunk; *mt.p.n.* metathoracic podial nerve; *rl.n.* rectal nerve; *v.d.n.* nerve to vas deferens; *v.s.n.* nerve to vesicula seminalis.

(*d*) *Ventral nerves* (figure 9, *m.itg.n.* 3–5)

There are usually three pairs of these purely sensory nerves collecting fibres from the ventral and lateral areas of the mesothorax. Their isolation from the motor nerves is probably dependent on the lateral and dorsal position of the muscles.

The metathoracic centre (figures 4, 9 and 10)

Detailed studies indicate that although the metathoracic centre is smaller than the mesothoracic centre, it has a generally similar fibre pattern. The smaller size is accounted for by there being fewer sensory fibres, and by the smaller diameter of the motor axons. The connexion between segment and neuromere is by a single pair of nerves (figures 9 and 10, *mt.n.t.*). These nerves divide near the anterior margin of the metathoracic segment into a ventral sensory ramus (figure 10, *mt.itg.n.*) a lateral podial nerve (*mt.p.n.*) and a dorsal nerve. The latter innervates the extrinsic leg muscles (figure 10, *m.* 73 to 75 *n.*) and the external coxal muscles (*cx.n.*), while a recurrent branch passes anteriorly (*mt.al.t.*) innervating the posterior basal wing muscle (*m.* 72 *n.*) and the wing. There is a small, peripheral connexion between the abdominal and the metathoracic nerves, that appears as the continuation of the lateral abdominal connective. This may perform the function of linking the abdominal spiracles with those lying more anteriorly.

Abdominal centres (figure 10)

The abdominal centres form a comparatively small part of the central nervous system. However, the separate fibre masses of each segment can be discerned in lateral horizontal sections (shown in figure 4). A single posterior nerve trunk (figures 9 and 10, *ab.n.t.*) leaves the central nervous system from this centre and runs ventro-laterally to the gut. On entering the abdominal region, it gives off a slender connective which joins a small posterior trunk from the large metathoracic podial nerve, to form the nerve to the 1st tergum (figure 10, *ab.* 1 *n.*) already mentioned. In abdominal segments 2 to 5 the distribution of the nerve trunks conforms to a typical pattern. The sternal areas receive a nerve arising from the main trunk towards the middle of the preceding segment. Laterally, a fine nerve runs to a thickened strand which appears to contain a single large cell body, called here the lateral body (*lat.b.*). The lateral bodies of each segment are inter-connected by a longitudinal cord (*l.conn.*). Each lateral body extends dorsally, then divides into lateral nerves to the tergo-sternal muscles and a single median nerve that supplies the spiracular occlusor muscle, and then passes dorsally as a sensory nerve to the tergum. This terminal branch may have connexions with the heart as in the roach (Alexandrowicz 1926).

Although the median abdominal tract is visible in both adult and embryo, the spiracular fibres cannot easily be traced to it owing to the inclusion of all abdominal fibres in a single pair of nerves, as occurs in other advanced groups (Escherich 1902 on *Lucilia*).

The lateral body appears similar to the small spiracular ganglion, responsible for peripheral control of spiracular movements in *Cossus* (Landois & Thelen 1867) although its most direct connexions are with the tergo-sternal muscles and the longitudinal cords suggest co-ordination of rhythmic processes such as ventilation.

In segment 6, the main abdominal nerve trunk on either side gives rise to a testicular branch (*v.d.n.*) running anteriorly along the vas deferens. Farther posteriorly, another nerve with gonadial connexions is visible (*v.s.n.*) contributing some fibres to the vesicula seminalis; within the 8th segment, nerves supplying the muscles *m.* 111 to *m.* 114 can be observed (*m.* 111 *n.* to *m.* 114 *n.*) and beyond them, the nerve divides into dorsal and ventral rami. The dorsal ramus (*rl.n.*) innervates the rectum and the 10th segment, while the ventral branch (*aed.n.*) supplies the aedeagal muscles of segment 9.

The histology of the nervous system

In order to study the fine structure of the nervous system, it was necessary to employ the metal impregnation techniques outlined under the section on methods. These techniques often gave good results with either cells or fibres, but rarely stained elements in their entirety due in part to the slight affinity for stains of the delicate polar filament or cell process (‘Zellfortsatz’ of Zawarzin 1924). For this reason, some of the fibres figured in the illustrations are shown without cell bodies.

The neuromeres lying behind the protocerebrum have been given the fullest treatment in these descriptions, because they appear to be more affected by condensation than do the optic lobes and protocerebrum. In addition, the latter regions have been extensively investigated by other anatomists on different insects, while the former, though more accessible for physiological analysis, have received much less attention.

Cell numbers

It is possible to make a rough estimate of the numbers of internuncial and motor elements in different parts of the nervous system by the following simple method. The volume of the cell body layer concerned is estimated as the product of the area of a complete series of sections through the region, measured in μ^2 with a calibrated squared eyepiece, and the thickness of the sections in μ. It is then necessary to make several assumptions, these are that the cell bodies occupy the cell body layer almost completely, that they are perfect spheres, and that large regions of the central nervous system have cell bodies of the same size. Certain parts of the nervous system appear to conform closely to the above conditions. The small cell bodies in the optic lobes are perfect spheres indented slightly where they are in contact with each other. They are closely packed with interstices hardly visible, and their diameters vary little about $5\,\mu$. The larger cells of the rest of the nervous system on the other hand do not conform so well to these conditions, being altogether more varied as would be expected on a functional basis. It is necessary for purposes of comparison to find the commonest cell diameter in this region, and this was found to be $10\,\mu$. The cell volumes derived from these diameters can then be divided into the estimated volume of the cell layer for the appropriate part of the nervous system to give the number of cells. By this method the number of cells in the paired optic lobes together was estimated as 370,000, and those in the rest of the central nervous system as 50,000 cells. Allowing a possible margin of error of as much as 10 % on either side for these estimates, one may still infer that there are several times as many cells in the optic lobes as in the whole of the rest of the central nervous system.

The relatively great number of cells in the optic lobes may be correlated with the importance of vision in the life of *Gerris*, the representation in the lobes of a large visual field, and the considerable success of capricious histological methods when applied to these structures.

It would be of interest to compare the number of elements in the ventral centres of *Gerris* with the number of elements in discrete ganglia.

The supraoesophageal centre

The arrangement of cells and fibres within the cerebral ganglion or brain of insects has been studied by several workers, notably Kenyon (1896), Zawarzin (1914) Cajal & Sanchez (1915) and most comprehensively by Hanström (1928). Pflügfelder (1937) has described the detailed structure of the brain of several species of Hemiptera with special emphasis on *Pyrrhocoris apterus*.

(i) *The optic lobes* (figure 11)

The optic lobes of insects are of particular interest. No other part of the central nervous system has attracted so much detailed attention (most of the work cited above is largely devoted to the description of these organs). As already pointed out, the optic lobes of *Gerris* contain seven times as many elements as the rest of the nervous system, and it is probably for this reason that partial impregnation methods, such as the Golgi method, frequently give such good results. Furthermore, the glomeruli are discrete and the connexions between them simply orientated. The typically laminated structure of the optic glomeruli may be compared with the cerebral cortex and corpora quadrigemina of vertebrates.

The three optic glomeruli of *Gerris* are, in general, similar to those of the other insects in which these structures have been described; they differ mainly in points of detail.

Most of the elements connecting the lamina ganglionaris with the medulla externa in other insects appear to be uniramous elements with cell bodies lying external or lateral to the lamina (*o.i.* 1 and 2). A few biramous elements with cell bodies lying between these glomeruli have been figured (Cajal & Sanchez 1915), but they were not described by Pflügfelder (1937) in any of the Hemiptera he studied. In *Gerris* they appear to be abundant (figure 11, *o.i.* 3), and may outnumber the former type of element.

The long axon elements of the lamina are of particular interest for the following reason. It is apparent that the nearer the glomerulus is to the protocerebrum, the larger are the number of cells with longitudinal fibres to the protocerebrum and the smaller the number of cells with connexions only in glomeruli. Thus the lamina ganglionaris is largely composed of the second type of element, and it is seldom that elements of the first type can be demonstrated. Pflügfelder (1937) figures the anterior terminal of such an element, but does not show the cell body or posterior ramus. However, the element was clearly displayed (*o.i.* 4) in several preparations of the brain of *Gerris*.

The longitudinal elements in the medulla externa are of varied form (*o.i.* 5 and 6), corresponding to optic internuncials 1 and 2. Long axon cells are represented by many larger elements (*o.i.* 7 and 8) having connexions through the tractus opticus posterior of Pflügfelder with the posterior part of the protocerebral lobes. Elements resembling optic internuncial 3 are present (*o.i.* 9), others with a striking longitudinal ramus (*o.i.* 10), and cells having some of the characteristics of both these types (*o.i.* 5). Purely local elements are also present (*o.i.* 11).

A striking feature of the medulla externa is the presence of large transverse neuroglial elements with ramifying longitudinal branches (*o.n.* 1). The internal medulla appears to differ from that of *Aeschna*, *Calliphora* or *Apis* in being markedly less complex in the arrangement of its fibres. The bifurcated terminals seem to be absent, and indeed, the form of this glomerulus as shown by Pflügfelder is much like that of the external medulla. There are many longitudinal fibres with protocerebral terminals in this glomerulus and they form at least three distinct tracts. Pflügfelder was able to work out the arrangement of the fibres within these tracts in *Pyrrhocoris*. Although a detailed comparison of *Gerris* and *Pyrrhocoris* was not possible, similar elements could be traced. The posterior optic tract (*p.o.t.*) was distinct as far as the protocerebral bridge and seems to contribute fibres to this glomerulus and the protocerebral lobe of the opposite side. The inferior median tract (*i.m.t.*) has central body connexions, while the superior median tract (*s.m.t.*) may be represented by the element illustrated (figure 11). The optic tubercle is shown in detail by Pflügfelder, but only a single element could be identified in this region in *Gerris* (*a.o.t.*).

As far as it is possible to make a comparison with *Aeschna* and *Calliphora*, it appears that, in the larger optic centres of these insects, the elements are probably more numerous and diverse than in *Gerris*.

Autrum (1958) has shown that there is an association in *Calliphora* and probably also in *Apis* between a diphasic resting potential of the retina, high frequency flicker perception, and the presence of certain neurones in the lamina ganglionaris with centrifugal axons. The eyes of endopterygotes, on the other hand, seem to be characterized by a monophasic resting potential and low frequency flicker perception. As a possible correlation, the laminae ganglionares of *Aeschna* (Zawarzin 1914) and *Gerris* do not appear to possess these centrifugal neurones.

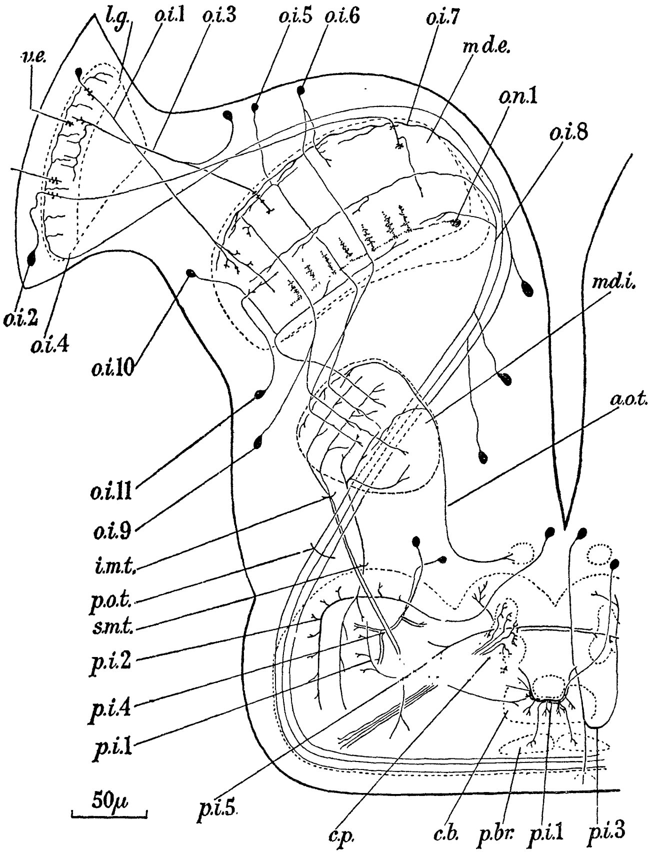

FIGURE 11. Semi-diagrammatic representation of the nerve cells and fibres of the protocerebrum and optic lobes as seen in horizontal sections.

a.o.t. anterior optic tract; *c.b.* central body; *c.p.* corpora pedunculata; *i.m.t.* inferior median optic tract; *l.g.* lamina ganglionaris; *md.e.* medulla externa; *md.i.* medulla interna; *o.i.* optic internuncials; *o.n.* optic neuroglial element; *p.br.* protocerebral bridge; *p.i.* protocerebral internuncial; *p.o.t.* posterior optic tract; *r.e.* retinal element; *s.m.t.* superior median optic tract.

(ii) *The protocerebrum* (figures 4, 11 and 12)

This region of the central nervous system is very closely compacted and, for this reason, difficult to describe systematically. Careful examination of almost any of the major glomeruli reveals numerous tracts connecting it with many of the other regions of the protocerebrum. This account will be limited to the most striking features of the gerrid protocerebrum.

The protocerebral bridge (*p.br.*) is well developed and appears to have some connexions with the posterior optic tract (*p.o.t.*) although they were never impregnated very clearly and have therefore not been figured. Fibres connecting the bridge with the central body were evident (figure 11, *p.i.* 1). The globuli cells described by Hanström (1928) were either absent or indistinctly differentiated from other cells.

The central body consists of four glomeruli, the largest of them having the form of a calyx and enclosing the rest. It receives large fibres from the thoracico-abdominal centres (figure 15, *g.i.* 2), the optic lobes (figure 11, *i.m.t.*) and the protocerebral lobes (figure 11, *o.i.* 1 and figure 23, plate 8). It also has slender connexions with the ventral bodies ('Nebenlappen' of Hanström) and the corpora pedunculata (not figured). Connexions with the pars intercerebralis (Pflügfelder 1937) were not evident. The central body in *Gerris* is probably concerned with opto-motor mixing, and, since several large-diameter fibres have terminals here, may involve rapid withdrawal reactions.

The corpora pedunculata (figure 11) as shown by Pflügfelder in *Syromastes* does not form a dorsal calyx or calyces of the hymenopteran type, but consists of a dorsal glomerulus receiving fibres from a nest of globuli cells and an ascending tract from the antennal centre (figure 12, *d.d.t.*). The corpora pedunculata have, in addition, a number of fine connexions with the protocerebral lobes and the central body as in *Pyrrhocoris* (Pflügfelder 1937).

The latero-dorsal areas, the protocerebral lobes, are large and indistinctly subdivided. They consist of both fibres and terminals ('Punktsubstanz' of Zawarzin 1924) rather loosely aggregated about the smaller glomeruli. The protocerebral lobes receive many large fibres from the ventral centres (*p.i.* 3), and from the optic lobes, and finer fibres from the central body and corpora pedunculata. Much of the area consists of large internuncials with cell bodies lying in the anterior region of the protocerebrum. A few long axon intercentral elements are connected with this region of the brain (figure 15), but none of them resemble the giant protocerebral cell figured by Sanchez (1940) in *Apis*. Elements of smaller size, however, resembling the L-shaped neurone of Sanchez (1940) can be seen clearly (figure 11, *p.i.* 2). Many of these elements have processes running in a circular fashion in the antero-dorsal region of the lobes to form a laminated zone (*p.i.* 2 and *p.i.* 4). Other elements form transverse commissures (*p.i.* 5) connecting the two sides of the protocerebrum. The great variety of form and size of the elements composing this part of the nervous system suggest that it may be the site of circuits mediating the more complex and variable actions.

(iii) *Deutocerebrum* (figure 12)

This centre is largely associated with the antennae. As demonstrated by Sanchez (1936) in *Apis*, there may be two separate glomeruli present; an anterior sensory glomerulus (bulbe olfactoire), and a posterior motor glomerulus (centre antennomoteur). These centres have been shown to occur in some Heteroptera by Pflügfelder (1937). In *Gerris*, the sensory centre (*d.s.c.*) is clearly visible, and Golgi preparations demonstrate fine afferent fibres (*d.s.* 1) entering the centre and arborizing within the spherical subglomeruli. The subglomeruli are largely formed by the terminals of small (*d.i.* 1) and large (*d.i.* 2) internuncials. A conspicuous tract (*d.d.t.*) is associated with the deutocerebrum anteriorly, connecting the antennal centre with the dorsal glomerulus of the corpus pedunculatus on each side. This tract was described by Pflügfelder (1937), although he did not demonstrate its detailed structure. Golgi preparations of this tract in *Gerris* impregnated few whole elements, but suggested that its main components were internuncials arborizing in the posterior region of the sensory centre. In *Gerris* the motor centre (*d.m.c.*) takes the form of a diffuse fibre mass lying closely adjacent to the sensory centre. The two centres are connected by a smaller number of short (*d.i.* 4) and long (*d.i.* 3) axon internuncials, the latter contributing to the dorsal motor tract (*d.m.t.*) A transverse commissural tract (*t.d.c.*) links the two sides of the deutocerebrum, but its component fibres could not be traced in detail. Some of the thick fibres entering the motor centre have the appearance of motor elements (*d.m.e.* 1) with branches in one of the motor tracts; others, however, arborize near the sensory centre and have connexions with strikingly shaped internuncials with long dorsal and ventral rami (*d.i.* 5), forming parts of the dorsal (*d.m.t.*) and ventral (*v.d.c.*) tracts of the motor centre. Although the motor centre of the deutocerebrum has been described in some detail in *Apis* (Sanchez 1936) and more recently in *Drosophila* by Maxwell-Power (1946—no Golgi preparations), little is known about its function. That

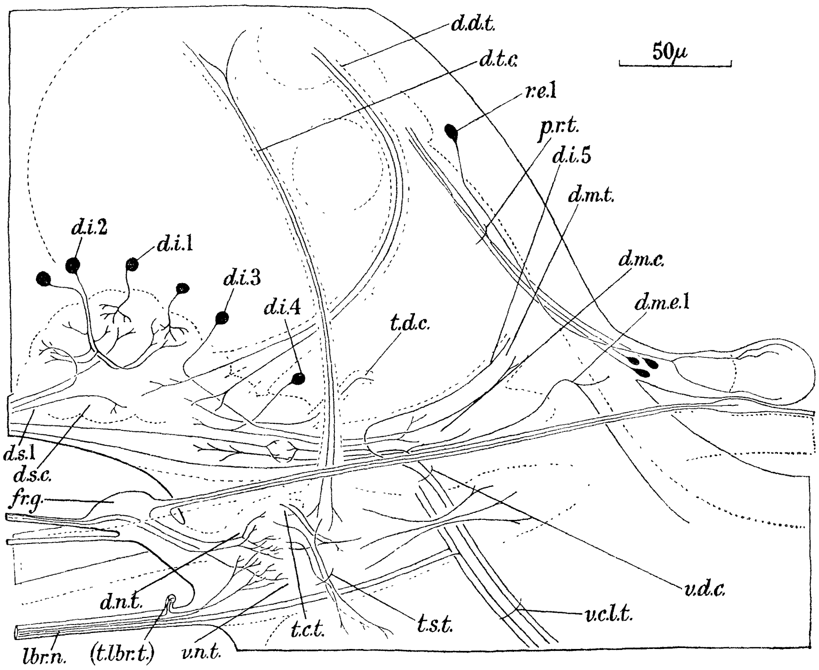

FIGURE 12. Semi-diagrammatic representation of the nerve cells and fibres of the deutocerebrum and tritocerebrum as seen in vertical longitudinal sections.

d.d.t. dorsal deutocerebral tract; *d.i.* deutocerebral internuncial; *d.m.c.* deutocerebral motor centre; *d.m.e.* 1, deutocerebral motor element; *d.m.t.* deutocerebral motor tract; *d.n.t.* dorsal neuropile of tritocerebrum; *d.s.* sensory element of deutocerebrum; *d.s.c.* sensory centre of deutocerebrum; *d.t.c.* dorsal commissure of the tritocerebrum; *fr.g.* frontal ganglion; *lbr.n.* labral nerve; *p.r.t.* posterior retrocerebral tract; *r.e.* retrocerebral element; *t.c.t.* transverse commissure of tritocerebrum; *t.d.c.* transverse deutocerebral commissure; *t.lbr.t.* transverse labral tract; *t.s.t.* tritocerebral sensory tract; *v.c.l.t.* ventro-central longitudinal tract; *v.d.c.* ventral deutocerebral commissure; *v.n.t.* ventral neuropile of tritocerebrum.

this complex centre has some other function beside the innervation of the small antennal muscles (two pairs in *Drosophila*, Miller 1950; four pairs in *Gerris*) seems very probable.

(iv) *Tritocerebrum* (figure 12)

This part of the central nervous system, like the suboesophageal centre, has been very little investigated. This small centre has its main external connexions with the muscles and sense organs of the clypeal region, and can be divided into a dorsal region (*d.n.t.*) connected with the frontal ganglion (*fr.g.*) and a ventral region (*v.n.t.*) associated with the labral nerve (*lbr.n.*). The dorsal neuropile is largely composed of some twenty fibres with anterior connexions with the frontal ganglion and bridge. In addition, there are fibre tracts between the dorsal neuropile and the protocerebral lobes (*d.t.c.*), the suboesophageal centres (*t.s.t.*), the labral nerve (*lbr.n.*), and the dorsal neuropile of the opposite side (*t.c.t.*). The protocerebral tracts are of some interest as they terminate in the region of the pars intercerebralis and may have connexions with the neurosecretory cells there. The suboesophageal connective consists of a few fine fibres that pass laterally to the main ventral neuropile of the mandibular centre. They may pass to other parts of the suboesophageal ganglion but could not be traced beyond the mandibular centre. Because of the posterior position of the tritocerebrum in *Gerris*, the transverse commissure is a short horizontal tract, rather than a posteriorly running loop as in other insects. Some of its fibres are of large diameter (more than 1μ). The labral nerves (*lbr.n.*) lie below the frontal bridge and each contains about twenty fibres, four or five of these being of large size. Before the fibres penetrate the cell body layer, there is an exchange of some four fibres through a transverse tract (*t.lbr.t.*) forming a distinct nerve crossing the oesophageal foramen. Within the tritocerebrum, the labral fibres run beneath the dorsal neuropile for a short distance before many of them pass up into it, while three or four of the largest run postero-dorsally to the ventro-central longitudinal tract (*v.c.l.t.*) where they join large fibres of this tract.

Retrocerebral system (figure 12)

The many nerve connectives of the retrocerebral glands described in the section on topographical anatomy could not be identified in most of the Golgi preparations. In one or two preparations, however, cell bodies could be seen lying in the region of the posterior root (nerf paracardiaque externe of Cazal 1948). A single element was traced to the corpora allata (*r.e.* 1), while a number of other elements with cell bodies apparently lying in the corpora cardiaca sent fibres into the dorsal region of the protocerebrum (*p.r.t.*). Pflügfelder (1937) described some of the large cells of the pars intercerebralis with fibres in the anterior or internal root. Parts of similar elements were observed during this study.

Suboesophageal ganglion (figure 13)

The suboesophageal ganglion is described very briefly in *Apis* (ventrocerebron) by Sanchez (1941) and mentioned by Maxwell-Power in *Drosophila* (1950), but has otherwise received no detailed attention.

The suboesophageal neuromeres are so closely integrated in *Gerris* that only in sections passing through certain parts of the central nervous system can they be distinguished. The position of the transverse tracts is the most reliable guide to their orientation, but the main fibre mass is essentially continuous, and it is difficult to decide the precise termination of the elements within it. Viewed as a whole, the stylet centres are notably smaller than the labial centre (*lb.c.*), which is clearly associated with the size and importance of the labium and hypopharyngeal region, including as it does ten pairs of skeletal muscles, a network of visceral muscles, and a large number of internal and external sense organs. The small size of the dorsal region of these neuromeres, as compared with the thoracic centres, is partly associated with the dorso-ventral flexure of the central nervous system in the suboesophageal region.

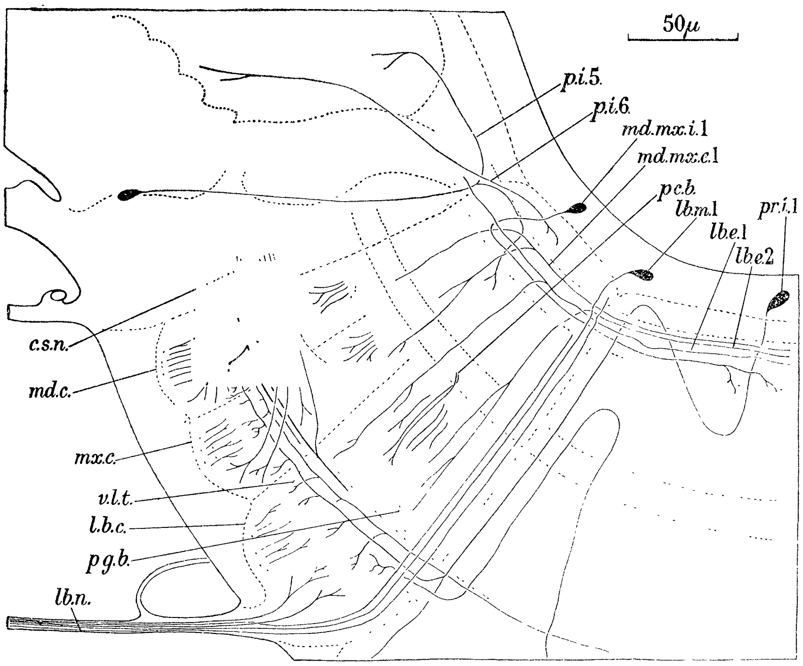

FIGURE 13. Semi-diagrammatic representation of the nerve cells and fibres of the maxillary, mandibular and labial centres seen in vertical longitudinal sections.

c.s.n. common stylet nerve; *lb.c.* labial centre; *lb.e.* labial element; *lb.m.* labial motor element; *lb.n.* labial nerve; *md.c.* mandibular centre; *md.mx.e.* element common to mandibular and maxillary centres; *md.mx.i.* internuncials of mandibular and maxillary centres; *md.mx.i.* internuncials of mandibular and maxillary centres; *mx.c.* maxillary centre; *pc.b.* precentral bridge; *pg.b.* postglomerular bridge; *p.i.* protocerebral internuncial; *pr.i.* prothoracic internuncial; *v.l.t.* ventral longitudinal tract.

The mandibular centre (figure 13, *md.c.*) has its main external connexion through a common stylet nerve (*c.s.n.*) with the stylet ganglion, from which a mandibular nerve runs anteriorly to innervate three muscles and a small, mainly internal, sensory field. Some eight fibres of varying diameters (0·25 to 1·0 μ) form the root of the nerve and most of these arborize within the main ventral neuropile. Ventral transverse commissures are well developed and contain a few fibres of large diameter. A few large fibres enter the ventral neuropile from the ventral longitudinal tract (*v.l.t.*). The dorsal region above these longitudinal tracts is small, consisting of large intercentral tracts and weakly developed transverse commissures.

The fibre pattern of the maxillary centre closely resembles that of the mandibular neuromere. It differs from the latter mainly in its smaller transverse commissures, and in that a striking feature of the maxillary nerve root is its reception of two or more fibres from the ventral longitudinal tract. These latter elements probably have cell bodies in the protocerebral or thoracic region of the central nervous system, but they could not be traced out in detail. A certain proportion of the fine fibres in the stylet nerve root form part of the integumentary nerve trunk to the head (figures 5 and 6, *c.i.n.*) but they could not be followed out in the central nervous system. Some of them may belong to the supra-oesophageal neuromeres, although there are many integumentary fibres in the deutocerebral and tritocerebral nerves.

The labial centres exhibit a number of marked similarities with the thoracic centres both in size and detailed structure, despite manifest differences in the motor and sensory fields. There is a small precentral bridge of fibres (figures 13 and 14, *pc.b.*) a postglomerular bridge (*pg.b.*) and vertical tracts linking dorsal and ventral neuropiles, as in the thoracic centres. Furthermore, a bundle of some five or six fibres (*lb.m.* 1) from the labial nerve root pass to a small dorsal neuropile, as do many of the motor fibres within the thoracic centres. The dorsal region of the gnathal centres, especially of the anterior ones, forms a zone of interwoven fibres of an intersegmental rather than intrasegmental nature. Long-fibred elements in the dorsal longitudinal tract have terminals in the maxillary, mandibular (*md.mx.e.* 1) and labial (*lb.e.* 1 and *lb.e.* 2) centres, while other elements connect the dorsal region with the protocerebral lobes (*p.i.* 5 and *p.i.* 6). A few complete intersegmental elements with fibres in the prothoracic and the gnathal centres could be traced (*md.mx.i.* 1, and *pr.i.* 1).

The absence of a well-developed dorsal motor neuropile in the stylet centres may be associated with the development of a lateral stylet ganglion (figure 6, *st.g.*), and also with the fusion of the neuromeres.

Thoracic centres

The three thoracic centres are approximately equal in size and exhibit general similarity in the internal arrangement of the nerve fibres, and for this reason only one of them, the mesothoracic ganglion, will be described in detail. This is the largest thoracic centre and contains the main connexions of the alary nerves. The most important contributions towards an understanding of the anatomy of the thoracic and abdominal ganglia of insects are those of Zawarzin (1924) and Maxwell-Power (1948), while Smith's recent work (1957) on the polychaete nervous system has a bearing on arthropod studies.

Mesothoracic centre (figures 14 to 17, figure 27, plate 8)

In order to describe the complex aggregation of fibres that constitute the adult neuromere with any clarity, it is necessary to proceed from a very general description to a more detailed one of individual elements. The whole neuromere has a somewhat cubical form produced laterally and posteriorly into lobes from which the large posterior nerve trunks arise. If a transverse section is made across the middle of the centre, various features of its internal organization are visible (shown in figure 14). The cell bodies form a continuous layer of nearly equal thickness round the fibres and in this respect *Gerris* differs from a polychaete (Smith 1957), or the *Aeschna* larva (Zawarzin 1924) in which they lie laterally and ventrally. The neuropile forms lateral (*l.gl.*) and ventral glomeruli (*v.gl.*), and longitudinal (*d.c.l.t.*, *d.l.l.t.*, *v.c.l.t.*, *v.l.t.*) and transverse (*d.t.t.*, *c.t.t.*, *v.t.t.*) tracts. In addition to the dorsal and ventral longitudinal tracts of the polychaete and *Aeschna*, in *Gerris* there are numerous other tracts lying between them, and there are several transverse tracts. The multiplicity of both intercentral and intracentral commissures presumably reflects a high degree of integration of function.

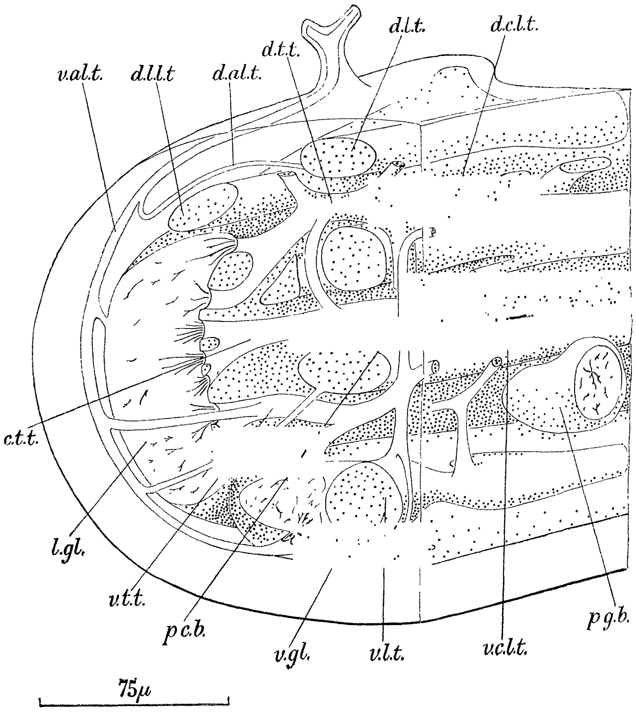

FIGURE 14. Diagram of the main fibre masses of the mesothoracic neuromere. Oblique antero-median view of the right half of the neuromere.

c.t.t. central transverse tract; *d.al.t.* dorsal alary tract; *d.c.l.t.* dorso-central longitudinal tract; *d.l.l.t.* dorso-lateral longitudinal tract; *d.l.t.* dorsal longitudinal tract; *d.t.t.* dorsal transverse tract; *l.gl.* lateral glomerulus; *pc.b.* precentral bridge; *pg.b.* postglomerular bridge; *v.al.t.* ventral alary tract; *v.c.l.t.* ventro-central longitudinal tract; *v.gl.* ventral glomerulus; *v.l.t.* ventral longitudinal tract; *v.t.t.* ventral transverse tract.

Two other structures lying near the anterior and posterior extremities of the centre deserve mention as they are of great utility as landmarks. These are firstly a hoop-like tract of fibres—the precentral bridge (figure 14, *pc.b.*), and a transverse zone of complex terminals—the postglomerular bridge (*pg.b.*). A structure similar to the postglomerular bridge is figured by Zawarzin as a posterior part of his Marksubstanz. It must be emphasized that this plan of tracts is a very general one and does not take account of small bundles of fibres pursuing an independent course. The nerve trunks of this centre (see section on topography) consist of: a number of connexions with the lateral mesothoracic ganglion (figure 6), possibly a part of the alary nervous system; a dorsal alary trunk (figure 6, *d.al.tr.*; figure 25, plate 8) containing six identifiable motor elements and fifty or more sensory fibres; and the large posterior nerve trunks (figures 8 and 9) supplying the muscles and sense organs of the mesothorax and limb. It is this latter nerve trunk and its internal connexions which will be described first. Sections through the base of the posterior nerve trunk reveal many axons of differing diameters. Those of the central and dorsal regions of the nerve can be distinguished clearly, and range from 0·2 to 4·0 μ in diameter. There appear to be between 110 and 120 of these fibres. Occupying the ventral region of the nerve are a number of fibre bundles so closely packed together that individual fibres cannot be discerned, though the number of elements probably lies between 50 and 100. Golgi preparations show them to be sensory fibres.

(i) *Internuncial elements* (figures 12, 14 and 15)

The mesothoracic centre contains numerous intrinsic internuncials, but also receives processes from large elements whose cell bodies lie in another neuromere. These large intercentral elements (figure 15) are of particular interest, as they may be studied with greater facility in *Gerris* than in other insects, due to the compact nature of the nervous system. In more diffuse nervous systems, these elements are so long as to be most difficult to prepare or describe; here, they may be seen in a single slice through the central nervous system. The longest intercentral internuncials observed were two fibres with cell bodies in the intercerebral region of the protocerebrum (*g.i.* 1 and *g.i.* 2). These had collaterals in the anterior and lateral regions of the protocerebral lobes, and posterior fibres running in the dorsal or dorso-lateral tracts. In one of them (*g.i.* 1), this posterior fibre definitely extends into the abdominal region, but in the other this is difficult to ascertain. These elements have numerous collaterals in the protocerebrum and might be stimulated through a variety of pathways. They possess anterior connexions similar to those of elements demonstrated in the brain of *Periplaneta* by Hanström (1928). In several preparations, an element was partially impregnated that appears to run from the medulla externa of the optic lobes to the ventral centres. Taking their origin in the suboesophageal centres are two elements (*g.i.* 3 and *g.i.* 4) running in the ventro-central longitudinal tracts with arborizations, in the postcentral glomeruli. One of these (*g.i.* 4, figures 15 and 20; figure 26, plate), could be followed out in considerable detail and both were striking features of silver-on-the-slide preparations. Even so, it is doubtful whether all their branches were observed. The postglomerular bridge (*pg.b.*) to which they contribute many arborizations, receives terminals from sensory elements, from internuncials in the lateral and ventral glomerular regions, and from numerous motor cells. They are, as it were, the central bodies of the thoracic neuromeres. Element *g.i.* 4 is similar in some respects to the large element figured by Zawarzin in the zone of ventral commissures of *Aeschna*. Pompilian (1899), Bodenheimer (1924, cited in Wigglesworth 1950) and others have demonstrated the inhibitory effect of the supraoesophageal ganglion on locomotory reflexes, while von Buddenbrock (1921, cited in Wigglesworth 1950) and Roeder (1937) have shown that the suboesophageal centres may exert an excitatory influence on these reflexes. The latter author is of the opinion that only pathways affecting tonus may be direct from supraoesophageal to thoracic ganglia, the inhibition of locomotor reflexes being exercised indirectly through the suboesophageal ganglion. The distribution of these large internuncials (*g.i.* 1 to 4) suggest direct dual control of locomotor action.

The smaller internuncials may be divided into those forming part of the inner apparatus (figure 17*B*), and those lying nearer the centre and not strikingly associated together (figure 18*B*). Zawarzin described a lateral group of internuncials forming a coil-like mesh of fibres as the 'innerapparat' of the 'grundneuropil'. A structure very like this and occupying the same lateral part of the ganglion was observed in *Gerris* (figure 17*B*, *i.a.*). In most preparations, it was difficult to distinguish the individual fibres throughout their length, but there were at least three cell bodies associated with them. The position of this structure suggests some function not involving the more complex integrated centres lying internal to it. The more centrally situated internuncials are of diverse form. Some of these elements (figure 18*B*, *m.i.* 7, *m.i.* 8, and *m.i.* 11) can be seen to form a well defined tract even in Golgi preparations as do the cells of the 'innerapparat' of Zawarzin (1924). The cell bodies and fibres lie in the midline and may form part of the middle strand ('mittelstrang' of Zawarzin 1924). This median strand or nerve appears only in development and in some insects has connexions with the spiracles (in *Malacosoma*, Snodgrass 1935) or the heart (*Bombyx*, Kuwana 1932). Several small fine-fibred internuncials (*m.i.* 2 and *m.i.* 4) appear to contribute arborizations to the ventral glomerulus. Many of the remaining intercentral internuncials have vertical rami that appear to connect the dorsal and ventral regions of the centre (*m.i.* 3, *m.i.* 6 and *m.i.* 10). As was pointed out earlier, the numerous dorsal motor cells have few ventrally running processes so that any integration between dorsal and ventral regions is likely to be performed by internuncials. In addition, there are a number of intercentral internuncials (*m.i.* 1 and *m.i.* 5) for the most part limited to the ventral centres.

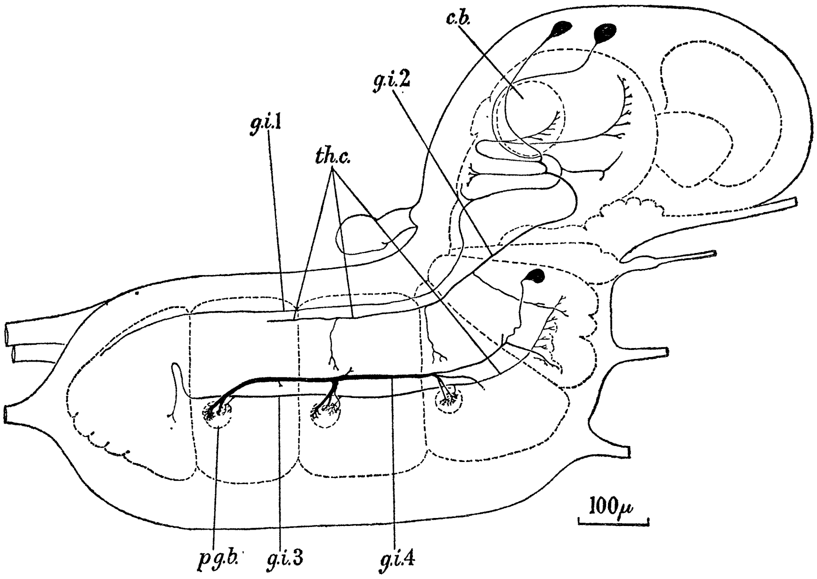

FIGURE 15. Semi-diagrammatic representation of the central nervous system to show the position of the largest internuncial elements.

c.b. central body; *g.i.* giant internuncial; *pg.b.* postglomerular bridge; *th.c.* thoracic centre.

(ii) *Sensory elements* (figure 16)

These appear in Golgi preparations as fine, frequently varicose, fibres entering the centre in the ventral region of the nerve root. A few fibres (*m.s.e.* 1) pass to the lateral glomerular region, but the majority pass to the ventral glomerulus, where they arborize in a complex manner. Some fibres have rami passing forwards in the ventral longitudinal tract (*m.s.e.* 2) or transversely in the centre, but these are rare, probably correlated with the great development of motor and internuncial commissures. In both partial and total impregnations, the sensory fibres appear to become very closely compacted within the nerve trunk and it is possible that some kind of fusion occurs. In polychaetes, many of the sensory fibres have dorsal connexions within the central nervous system (Smith 1957), but this does not seem to occur in insects, though some of the fibres in *Gerris* begin to break up into fine terminals before descending to the ventral glomerulus.

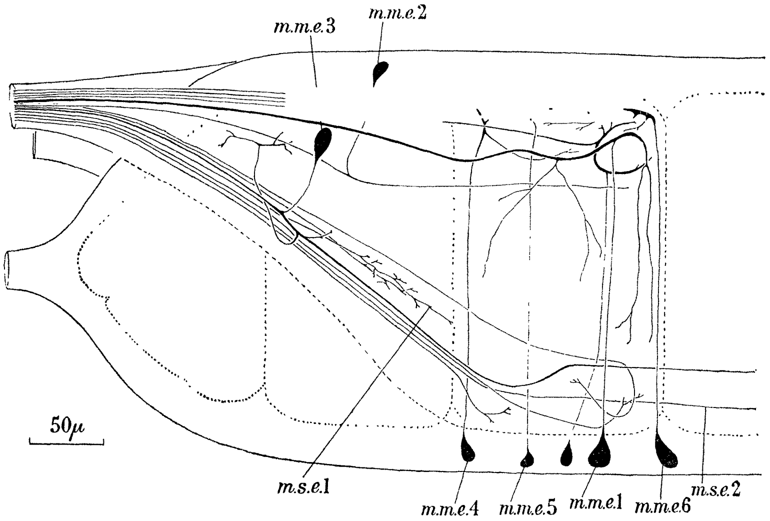

FIGURE 16. Semi-diagrammatic representation of the motor cells and sensory fibres of the mesothoracic centre as seen in vertical longitudinal sections.

m.m.e. mesothoracic motor element; *m.s.e.* mesothoracic sensory element.

(iii) *Motor elements* (figure 16)

The motor-cell bodies lie for the most part in the ventral region of the centre, their cell processes (Zellfortsätze) passing dorsally into the upper region of the lateral glomerulus. Here they branch extensively, some of these branches entering the transverse or longitudinal tracts, while their axons run out in the dorsal part of the posterior nerve trunk. Some of these elements (*m.m.e.* 1) have ventrally running processes that terminate in the vicinity of the sensory endings. This kind of motor neurone was described by Zawarzin in *Aeschna*. In addition, there are a small number of dorsal fibres with dorsal cell bodies (*m.m.e.* 2) possibly associated with the development of the dorsal cell body layer and consequent on the shortening of the interganglionic connectives. There are also a number of motor fibres (*m.m.e.* 3) with lateral or ventral cell bodies and few collaterals, that enter the ventral longitudinal tracts. Longitudinal processes of dorsal fibres seldom extend far anteriorly in the dorsal tracts, but the ventral fibres of motor elements may attain the prothoracic centre.

A large axon, probably part of the large motor cell figured (*m.m.e.* 1) can be seen in silver-on-the-slide preparations of the nerve trunk to the skating muscle *m.* 52. The fibre appears to break up on the surface of the muscle when traced through a series of sections. The many complex processes of this large motor cell within the mesothoracic centre would suggest that it played an important part in the function of this segment of the thorax.

Many of the other motor cells (*m.m.e.* 4 and 6) show certain resemblances to cells figured by Zawarzin (1924) in *Aeschna*, but it is impossible to follow these in detail, due to differences between the orientation of the preparations figured by Zawarzin as compared with those figured in this paper. This difference in orientation is determined by the depressed form of the ganglia in *Aeschna*, and the ovoid form of the central nervous system in *Gerris*.

The alary nervous system (figures 14; figure 25, plate 8)

The nervous system in the winged form of *Gerris* consists of three groups of elements: (i) sensory fibres from the sensillae of the wing surface and its articulation with the thorax, (ii) motor elements innervating the small direct wing muscles and (iii) motor elements innervating the large indirect wing muscles. The mesothorax is the motorium of the insect both on water and in the air and contains all the elements listed above. The metathorax contains small direct wing muscles and a sparsely innervated membranous hindwing. The fibres associated with these structures appear to run in the common metathoracic nerve and could not be dissociated from other fibres in the central nervous system. The mesothoracic structures could be worked out in more detail.

It is important to realize that the fibres of the alary apparatus are closely associated with parts of the nervous system that are developmentally older. Most of the nerve trunks that carry alary fibres in the adult winged form could be discerned in the young nymphs, and one of them, the posterior dorsal nerve, in the eight-day embryo. At this early stage, these nerve trunks appear to be wholly sensory, collecting axons from the dorsal and lateral areas of the mesothorax. With the formation of wing buds and wing muscles in the later nymphal instars, the dorsal nerve roots acquire sensory and motor elements. The ventral alary tract may arise *de novo*, as it appears to consist of one or two motor fibres only, and was not observed in young animals. The course of the fibres entering the central nervous system from the dorsal alary trunk could be traced in some detail (figure 25, plate 8 and figure 14). There are at least five thick fibres (*d.al.t.*) with processes in the dorsal longitudinal tract, and many finer fibres that pass ventrally (*v.al.t.*) terminating at various levels, though the largest number pass to the ventral longitudinal tract (*v.l.t.*) and ventral sensory glomerulus (*v.gl.*). If the thicker fibres are motor, then it is difficult to account for all of them. Preparations of the wing muscles indicate that they are probably innervated by single fibres, or alternatively, by two or more motor fibres with separate motor fields as in *Telea* (Nuesch 1954). In some preparations, the anterior dorsal nerve can be seen to give off branches to the spiracle, and although these could not be traced in detail, it is possible that the pro-mesothoracic spiracle, which has two muscles, receives motor fibres from the alary trunk. The course of the motor fibres supplying the vertical wing muscles was again impossible to elucidate completely, although it seems probable that these fibres do contribute to the dorsal motor tract within the central nervous system. An examination was made of the following gerrids with reduced wings and lacking wing muscles: brachypterous *Gerris lacustris*, micropterous *Gerris odontogaster* and apterous *Gerris najas*. In these insects, the dorsal tract was either absent or represented by one or two fibres, whilst the ventral tract was much less reduced in size, the greatest reduction occurring in *Gerris najas*. This result supports Binet's conclusions (Binet 1894) with regard to carabid beetles. The arrangement of the alary nerves as a whole differs from that found in *Diptera* (Hertweck

1931) or *Orthoptera* (Ewer 1954) mainly in the simplification of the nerve trunks. The relative independence of the dorsal alary nerves seems to be a feature of most insect nervous systems and is probably dependent on the centro-dorsal position of the longitudinal muscles.

The prothoracic and metathoracic centres

Both these centres show considerable resemblances to the mesothoracic centre. The prothoracic centre, however, has a somewhat different orientation consequent on the ventral and anterior position of the main nerve trunk. This appears to affect the position and form of the motor elements rather than that of the internuncials, which are much the same. The metathoracic centre is slightly smaller than the mesothoracic but there appeared to be no major differences in the arrangement of the neurones.

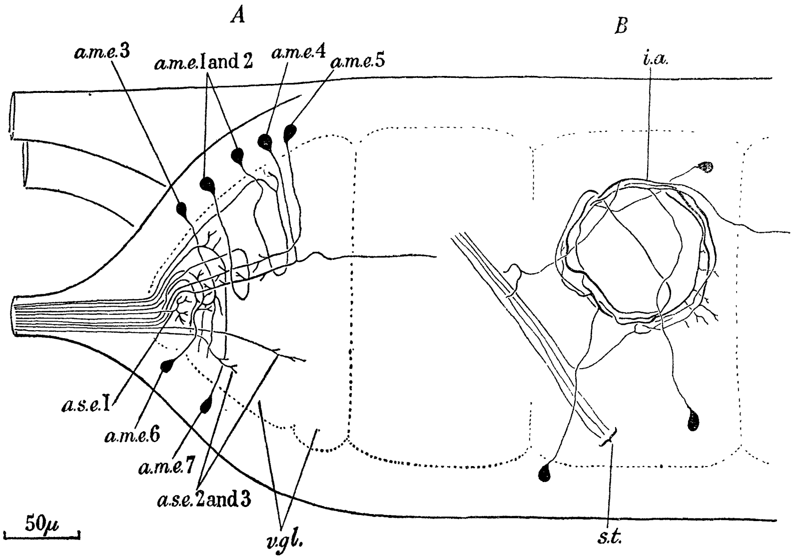

FIGURE 17. Semi-diagrammatic representations of *A*, the motor cells and sensory fibres of the abdominal central nervous system, and *B* the inner apparatus of the mesothoracic centre.

a.m.e. abdominal motor element; *a.s.e.* abdominal sensory element; *i.a.* inner apparatus; *s.t.* sensory tract; *v.gl.* ventral glomerulus.

Abdominal centres (figures 17, 18, 19; figure 27, plate 8)

The abdominal neuromeres are closely compacted, forming a cone-shaped body, the apex of which gives rise to the paired nerves. Internally, the abdominal centres exhibit some of the simplicity shown by Zawarzin (1924) in *Aeschna*. Longitudinal tracts are weakly developed, there being only ventral (*v.l.t.*) and dorso-central (*dc.l.t.*) tracts clearly visible in transverse section (figure 19). In addition, each neuromere possesses bundles of transverse fine fibres (*d.t.t.* and *c.t.t.*). One of the most striking features of the abdominal nervous system is the abundance of vertical fibres. Many of these are cell body processes rather than axons or collaterals (figure 18, *a.i.* 15, 16, 17 and 18). A ventral glomerular region (figure 17*A*, *v.gl.*) is well developed and in addition there is a posterior glomerulus (figure 18*A*, *p.gl.*) at the posterior extremity of the abdominal region (figure 27, plate 8). The greater part of the abdominal region is formed by fibres and terminals mingled together ('Punktsubstanz', Zawarzin 1924). Totally impregnated transverse sections through the base of the abdominal nerves (see figure 19) demonstrate the presence of dorsal (*d.a.t.*) lateral (*l.a.t.*) and ventral (*v.a.t.*) groups of fibres. The dorsal and ventral groups each consist of five fibre bundles, the former being fewer and coarser than the latter. These evidently correspond to motor sensory roots, but the lateral fibres do not enter the nervous system in the same segmental manner. At the base of the abdominal nerve, the lateral group appears to consist of five fibres of relatively large diameter, four of which enter the abdominal mass anteriorly while the fifth divides into several branches entering the neuropile posteriorly. It seems possible that these lateral fibres are connected to the heart, gut or spiracular ganglia.

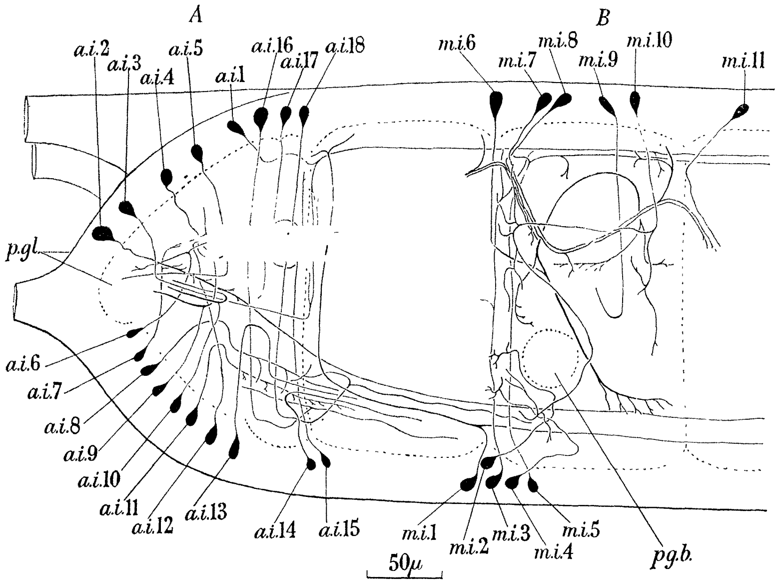

FIGURE 18. Semi-diagrammatic representation of the internuncial elements of *A*, the abdominal centres, and *B* the mesothoracic centres as seen in ventral longitudinal sections.

a.i. abdominal internuncial; *m.i.* mesothoracic internuncial; *pg.b.* postglomerular bridge; *p.gl.* posterior glomerulus.

(i) *Sensory elements* (figure 17*A*)

As with the thoracic centres, these elements were not well impregnated by the Golgi–Cox technique, although Golgi silver nitrate preparations gave better results. The posterior glomerulus (*p.gl.*, figure 18) receives a number of sensory fibres that terminate in dense arborizations (see *a.s.e.* 1, figure 17, but note that this is a simplified representation of this fibre). The form and position of the posterior glomerulus suggest that the great development of the sensory neuropile here is associated with abundant sensillae present on the 8th, 9th and 10th segments. The more anterior parts of the sensory neuropile form a ventral glomerulus (*v.gl.*) which is expanded near the border of the metathoracic centre. A few fine fibres with simple endings could be traced within the ventral glomerulus (*a.s.e.* 2 and 3).

(ii) *Motor elements* (figure 17*A*)

These elements are noticeably simpler in form than those of the thoracic centres, having short collaterals with few branches. They originate from both ventral and dorsal cell bodies in association with the complete cell body layer. Many of the elements (*a.m.e.* 1

and 2) appear to cross over to the opposite side of the abdominal mass before passing out in the dorsal tracts. As in the thoracic centres, only a few elements (*a.m.e.* 3) have collaterals entering the sensory neuropile. The majority of motor cells originate dorsally, but a few possess ventral cell bodies (*a.m.e.* 6 and *a.m.e.* 7). This preponderance of dorsal motor cell bodies over ventral may be dependent on the extreme condensation of this region; indeed, the coiled form of some of the dorsal fibres (*a.m.e.* 1 and 2) suggests that their growth pathways may have undergone considerable changes. Some of the motor cells run in the dorso-central longitudinal tract (*a.m.e.* 4 and 5).

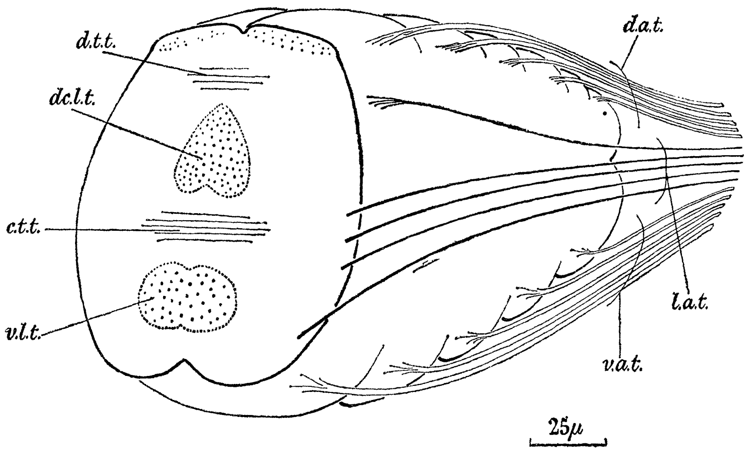

FIGURE 19. Diagram of the abdominal central nervous system viewed obliquely from an antero-lateral position.

d.a.t. dorsal abdominal tract; *dc.l.t.* dorso-central longitudinal tract; *d.t.t.* dorsal transverse tract; *c.t.t.* central transverse tract; *l.a.t.* lateral abdominal tract; *v.a.t.* ventral abdominal tract; *v.l.t.* ventral longitudinal tract.

(iii) *Internuncials* (figure 18*A*)

Some eighteen different forms of internuncial were observed in Golgi preparations of the abdominal centres. Most of these elements could be classified as contributors to (i) the ventral longitudinal tract (abdominal internuncials 8, 11, 13, 14, 16, 18 and part of 2), (ii) the dorso-central longitudinal tract (abdominal internuncials 4, 6 and 12), or (iii) the weakly developed transverse tracts (*a.i.* 10, 15 and 17). In addition, there are a few median longitudinal fibres (*a.i.* 3 and 5). The dorsal longitudinal tract appears to be a purely thoracic tract and the only abdominal cell body observed with processes at this level contributed to the thoracic neuropile (*a.i.* 1). Most of the elements forming the ventral longitudinal tract did not extend anteriorly beyond the metathoracic centre, but a large element (*a.i.* 2) lying above the main bundle of fibres traversed all the thoracic neuromeres. This distinctive neurone appeared in several preparations and probably possesses an important integrating function with regard to the abdominal centres and the rest of the nervous system. In addition to the internuncials described, a few elements with vertically orientated processes were observed (*a.i.* 7 and 9). Internuncials with obvious similarities to the median internuncials of the thorax were not found (figure 18*B* *m.i.* 7, 8 and 11), though one of the dorsal abdominal neurones (*a.i.* 4) exhibited a certain general resemblance.

As a whole, the pattern of individual elements within the abdominal central nervous system is much less orderly than within the thoracic neuromeres. But ganglionic fusion has probably led to changes in the pattern of neurones found in this region, so that detailed comparisons with the thoracic centres are not possible.

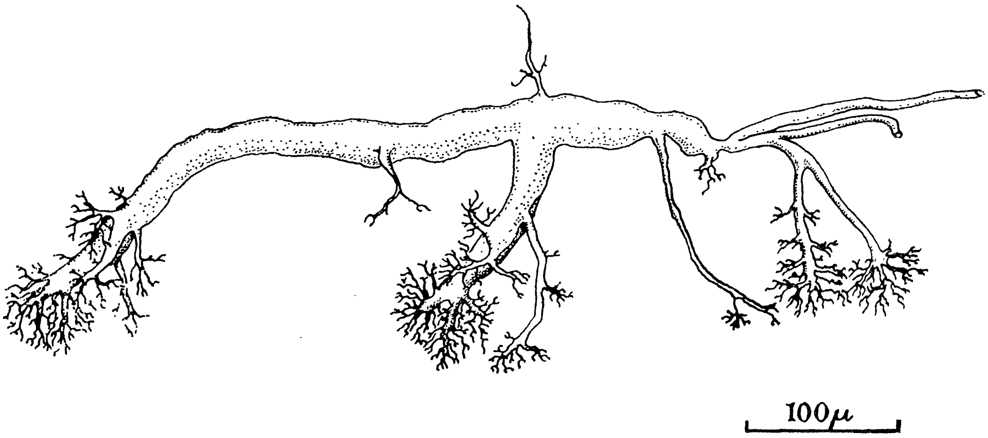

Figure 20. The fourth giant internuncial (*g.i.* 4) as it appears in a preparation of the central nervous system made by the Golgi–Cox technique. The element is viewed from the midline.

Discussion

The detailed observations on the anatomy of *Gerris* recorded in the present paper raise certain problems which require wider comparisons than are appropriate to the descriptive sections. These problems include the functions of the optic lobes, the generalized structure of the ventral ganglia, the nature of the sensory neurones, and the probable factors underlying condensation of the nervous system in arthropods.

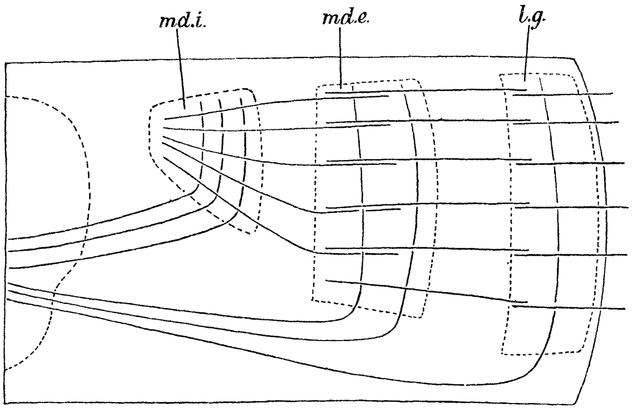

Figure 21. Greatly simplified diagram of the optic lobe of an insect to show the main longitudinal and transverse elements.

l.g. lamina ganglionaris; *md.e.* medulla externa; *md.i.* medulla interna.

Although comparatively little is known of the functions of the intricate meshwork of fibres that compose the optic lobes, and it would be dangerous to make any detailed inferences from their structure, the complex arrangements of the elements can be reduced to a simple plan as shown in figure 21. If only the commonest and largest elements are considered, those that are a feature of the optic lobes of such diverse forms as *Aeschna*, *Gerris* and *Calliphora*, and each optic lobe is thought of as a cylinder one end of which is the retina, then the elements can be described as of two main types. First, longitudinal interglomerular elements with at least some correspondence in number and orientation to the retinal elements, and secondly, fewer and larger elements with terminals distributed transversely over a large part of each glomerulus and with fibres passing back to the protocerebrum. In *Gerris*, the former are represented in figure 11 by optic internuncials 1, 2, 5, 6 and 9, and the latter by optic internuncials 4, *o.i.* 7 and the inferior and superior median optic tracts (*i.m.t* and *s.m.t.*). The first group of localized elements with a point-to-point correspondence to the retinal cells could be responsible for pattern perception, which would therefore be especially associated with the optic glomeruli, while the second group of elements with widely distributed processes might take part in perception of a more general nature such as luminosity and movement perception.

From the studies of Smith (1957, on nereid polychaetes), Zawarzin (1924, on the *Aeschna* larva), Maxwell-Power (1948, on *Drosophila*), and the present one on *Gerris*, a number of comparisons between the ventral ganglia of annelids and arthropods can be made. In the ventral ganglia of the *Aeschna* larva, Zawarzin was able to discern a fundamental plan of simple design. The cell body layer occupying the lateral and ventral regions of the ganglion, surrounded a neuropile, the dorsal, central and ventral regions of which corresponded largely to zones in which motor, internuncial and sensory fibres respectively were the dominant elements. The nerves would be divided into dorsal motor and ventral sensory regions, and the motor elements tended to have longitudinal collaterals in the dorsal longitudinal tracts; the axons passing out of the ganglion on the same side as that on which the cell bodies were situated. The main features of this plan are to be seen in the nervous systems of *Gerris* and to a lesser extent *Drosophila* (Maxwell-Power 1948), despite the extension of the cell body layer to the dorsal region of the ganglia. It might be thought that this plan would be displayed in even greater clarity in the nervous system of the polychaete (Smith 1957). Such is not the case, for in certain respects, notably the varied nature of the sensory fibre pattern, and the crossing over of motor elements, the polychaete pattern conforms less to Zawarzin's plan than does that of *Gerris* or *Drosophila*. Instead, the polychaete nervous system shows many insectan features, whilst suggesting a derivation from a more diffuse type. The localization of function may be an important aspect of the evolution of the central nervous system in invertebrates.

One of the most interesting points raised by the work of Smith (1957) on the polychaete nervous system relates to the central representation of peripheral sensory cells. Although the peripheral nervous system of *Gerris* proved itself somewhat refractory to staining methods, an estimate of the number of sensory fibres in the main mesothoracic nerve trunk could be made (less than 100), and compared with the numbers of trichoid sensillae in the area innervated (about 1000). A similar discrepancy between numbers of sensillae and of sensory fibres was noted in recent studies on cockroach nerves (unpublished). Either only a small proportion of the trichoid processes have sense cells or there are long and short axon elements as in polychaetes. The latter system provides a proportional representation within the central nervous system of a large sensory field.

The fourth topic to be discussed is that of condensation. The *Gerris* nervous system shows a high degree of condensation when compared with those of most mandibulate arthropods.

The Chelicerata, on the other hand, are characterized as a group by the highly centralized nature of the nervous system, even in the supposedly primitive forms. It is possible then to suggest several factors that may underlie this condition based on a study of arthropods varying in this respect. (1) Changes in the numbers and position of sense organs and muscles, due particularly to the hypertrophy or reduction of certain regions of the body. (2) Specializations of the central nervous system leading to greater functional integration and involving the longitudinal intercentral commissures. (3) Changes leading to neurone economy dependent on the functional transference of elements from small centres to larger and more complex centres. This factor might be important in small nervous systems. All these factors are certain to be closely integrated and their separation merely a means of theoretical simplification.

The migratory locust (Albrecht 1956) possesses a large complex abdomen, and a head and thorax of slightly greater specialization. In *Drosophila* (Miller 1950), the thorax is fused to form a single unit for the highly developed flight apparatus; the abdomen is mobile but reduced by segmental fusion as compared with that of the locust. In *Gerris*, the thorax is again extremely specialized in association with both skating and flying modes of locomotion, but in addition the abdomen forms a narrow rigid unit.

The numbers of muscles and separate ganglia (in brackets) in the different tagmata are listed below:

	head		thorax	abdomen
Locusta	45 (2)		95 (3)	156 (5)
Drosophila	20 (2)		77 (1)	56 (—)
Gerris	22 - - - - -	(1) - - - - -	74	33 (—)

The figures given represent pairs of distinct muscles, but do not give account of the size of the muscles. The effect of size may be important. The large wing muscles of insects receive few axons, but in *Gerris* the large skating muscles (*m.* 52, *m.* 53 and *m.* 54) were certainly associated with large nerve fibres (figure 16, *m.m.e.*1.) in the nervous system. The layout of sense organs is much more difficult to analyze. The head, in most insects, is much the richest sensory field and from studies on the flight mechanism (Pringle 1957) it seems probable that the thorax contains a larger number of sensillae for its size than does the abdomen. Since only a proportion of the unicellular sensillae are probably represented in the central nervous system as pointed out above, a census would be difficult to achieve.

In the three genera under consideration, there appears to be some correlation between the number of free ganglia and the arrangement of muscles and sense organs. The difference in the degree of condensation between *Drosophila* and *Gerris* is greater than would appear from the figures given above. In *Drosophila*, the neuromeres are clearly visible in the thoracic nervous system and well separated from the head centres, while in *Gerris* total fusion has occurred. Functional specialization may be associated with the fusion of neuromeres controlling a single or serial function, and their enlargement, through increase in number or complexity of the components. The longitudinal commissural tracts are large and well marked in the *Gerris* nervous system, and, as has been demonstrated histologically, they contain large internuncials linking the thoracic neuromeres. The shorter the longitudinal tracts, the shorter are the integrating pathways between segments.

In addition, it can be pointed out that the more nearly the form of the nervous system resembles a sphere, the greater will be the number of central connexions possible with a fixed number of centripetally directed axons of approximately the same form. The end-organ specialization that would require such integration can be seen in the mouthpart and skating apparatus of *Gerris*.

The third factor put forward, that of neurone economy, is suggested by the presence of single large elements in the nervous system of *Gerris* and *Drosophila* (Maxwell-Power 1948) which may correspond to chains of elements found in the cockroach (Roeder 1953). In a centralized nervous system, further complexity within a localized region might be achieved by the enlargement of one pair of fibres in connexion with a function *A*, previously controlled by a series. The redundant *A* fibres may then be used for a function *B* with no increase in cell number. The abdominal internuncials 1 and 2 (see figure 17) may be an example of elements with a changed function. In very small nervous systems, the small distances involved may allow a good functional coverage with few elements.

It would be exceeding the aim of this section to speculate on the mechanism of condensation, but one point is worth making. In the arthropod embryo, the neuromeres arise early in development and in close contiguity, the cell body layer being at first continuous (Johannson & Butt 1941). The later increase in size of the embryo is accompanied by separation of the neuromeres, and the extended growth of the longitudinal elements. Condensation therefore must involve the survival of this feature of the embryonic nervous system, which accommodates to the increasing size of the body by peripheral rather than central fibre growth.

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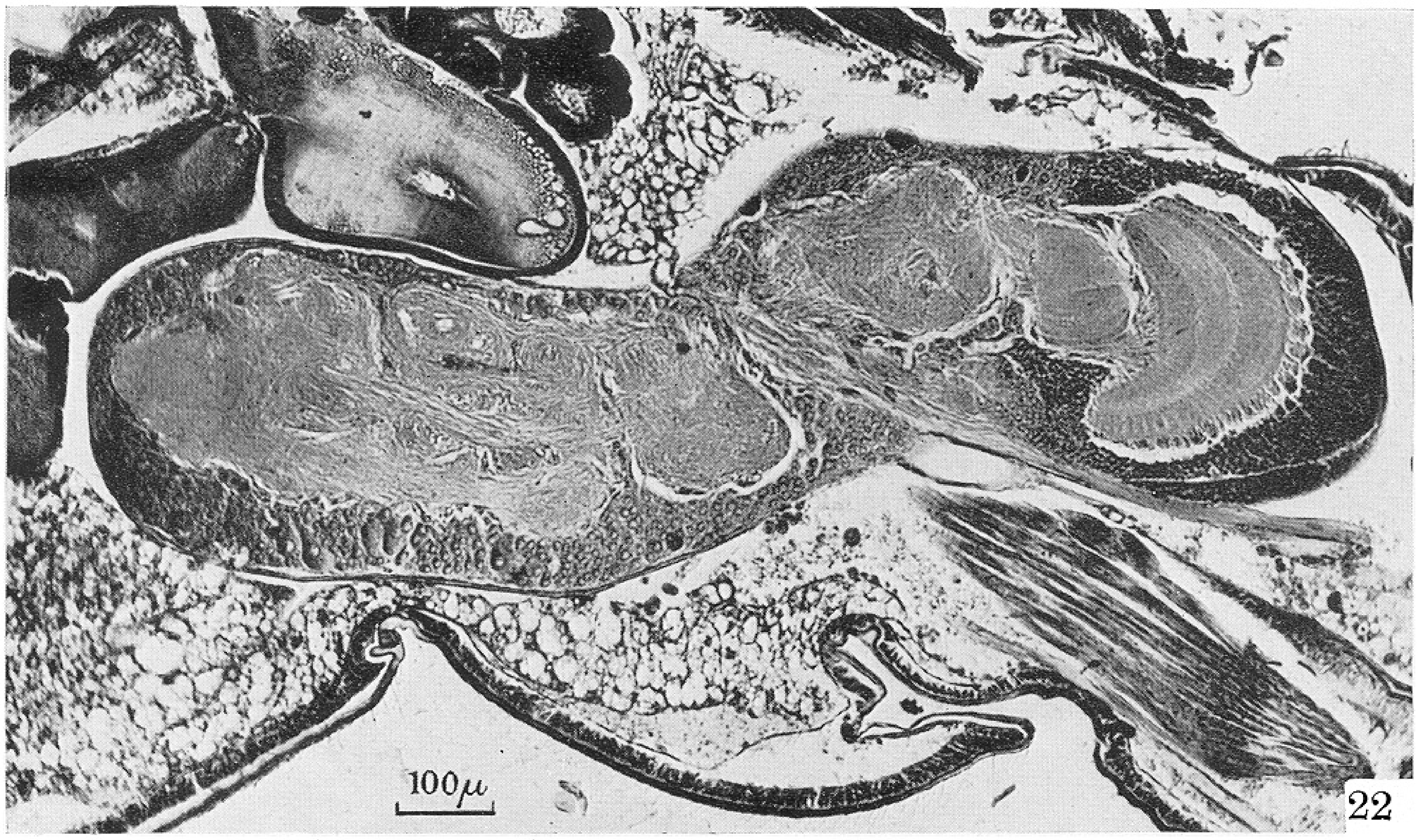

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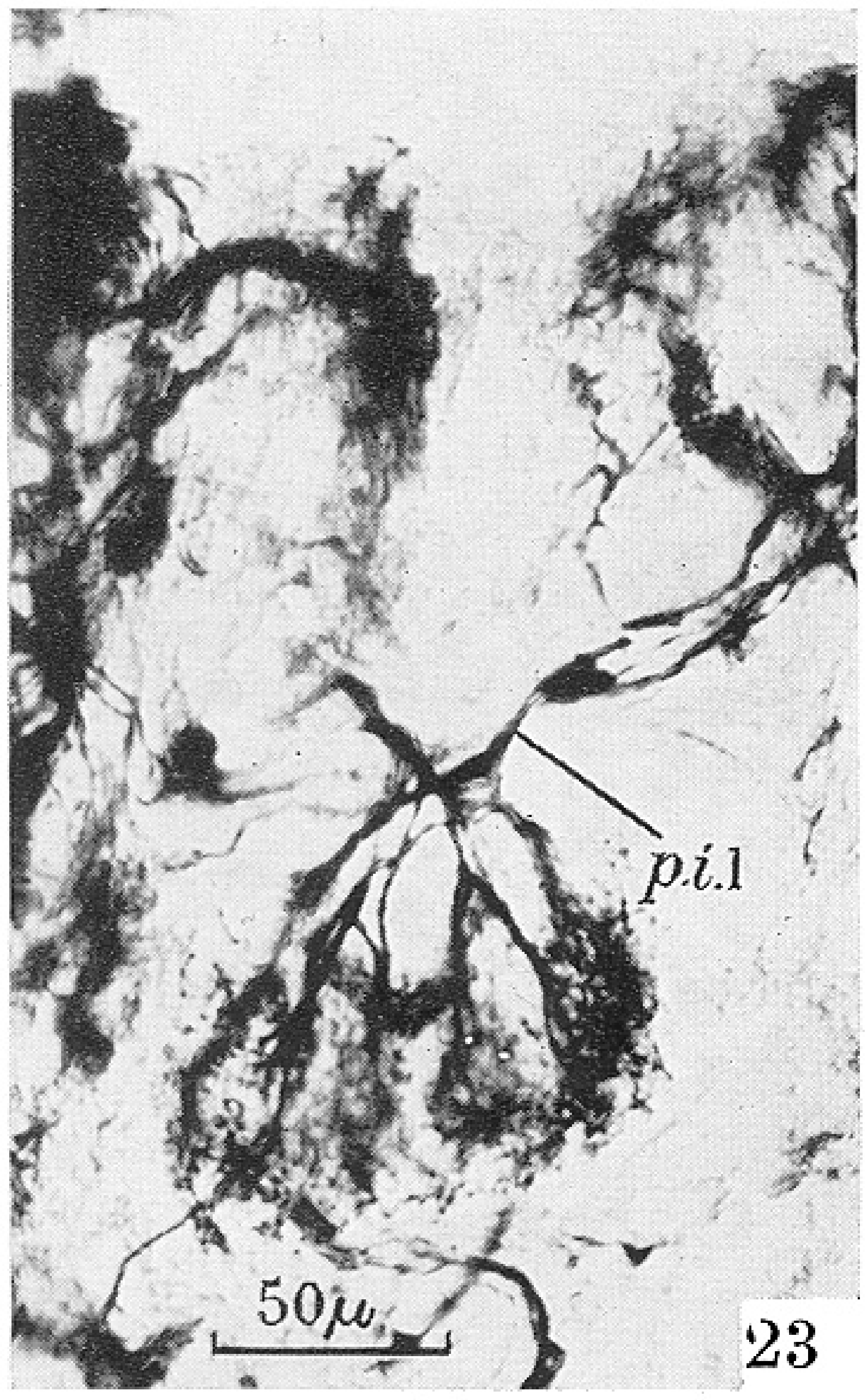

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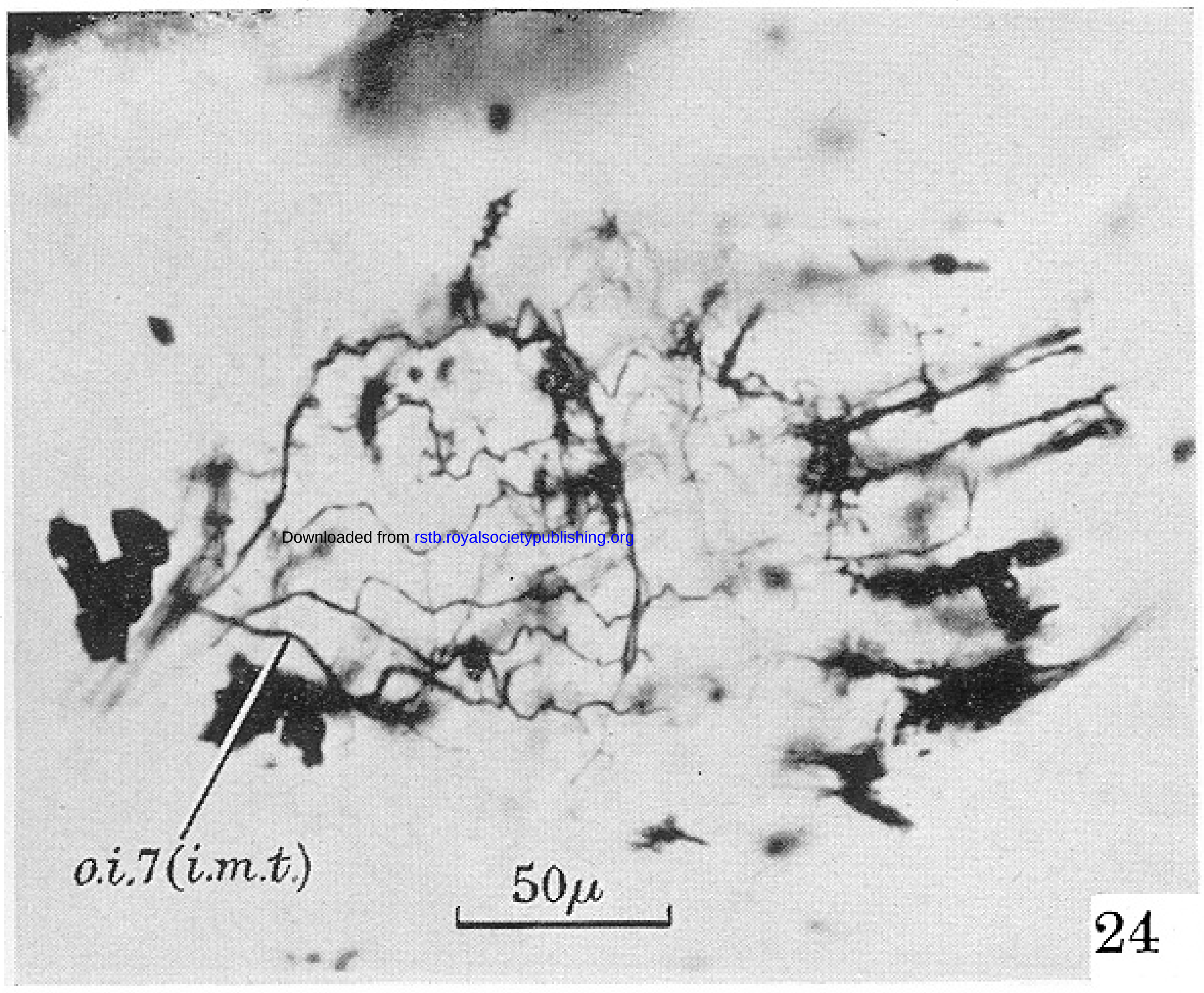

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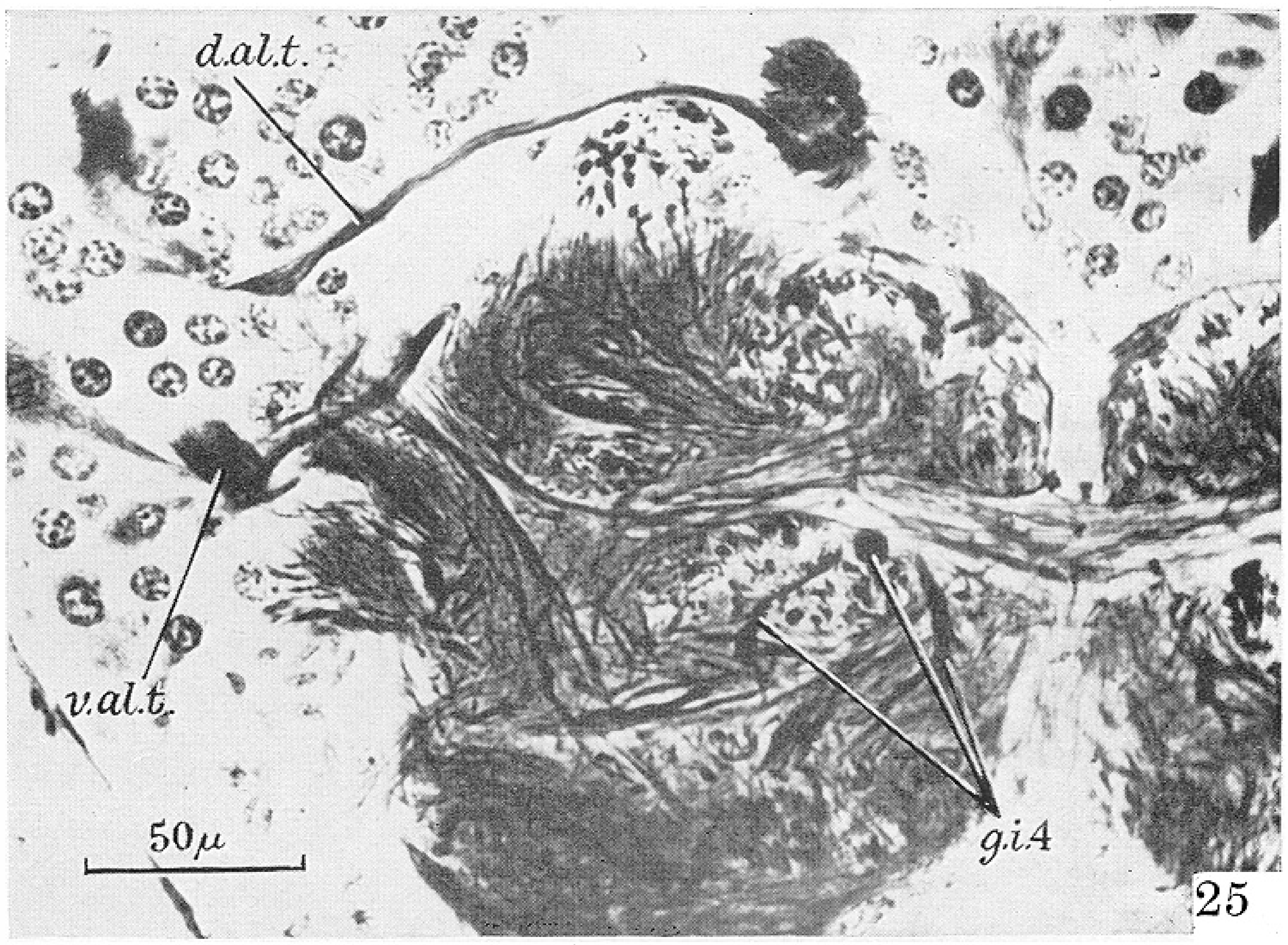

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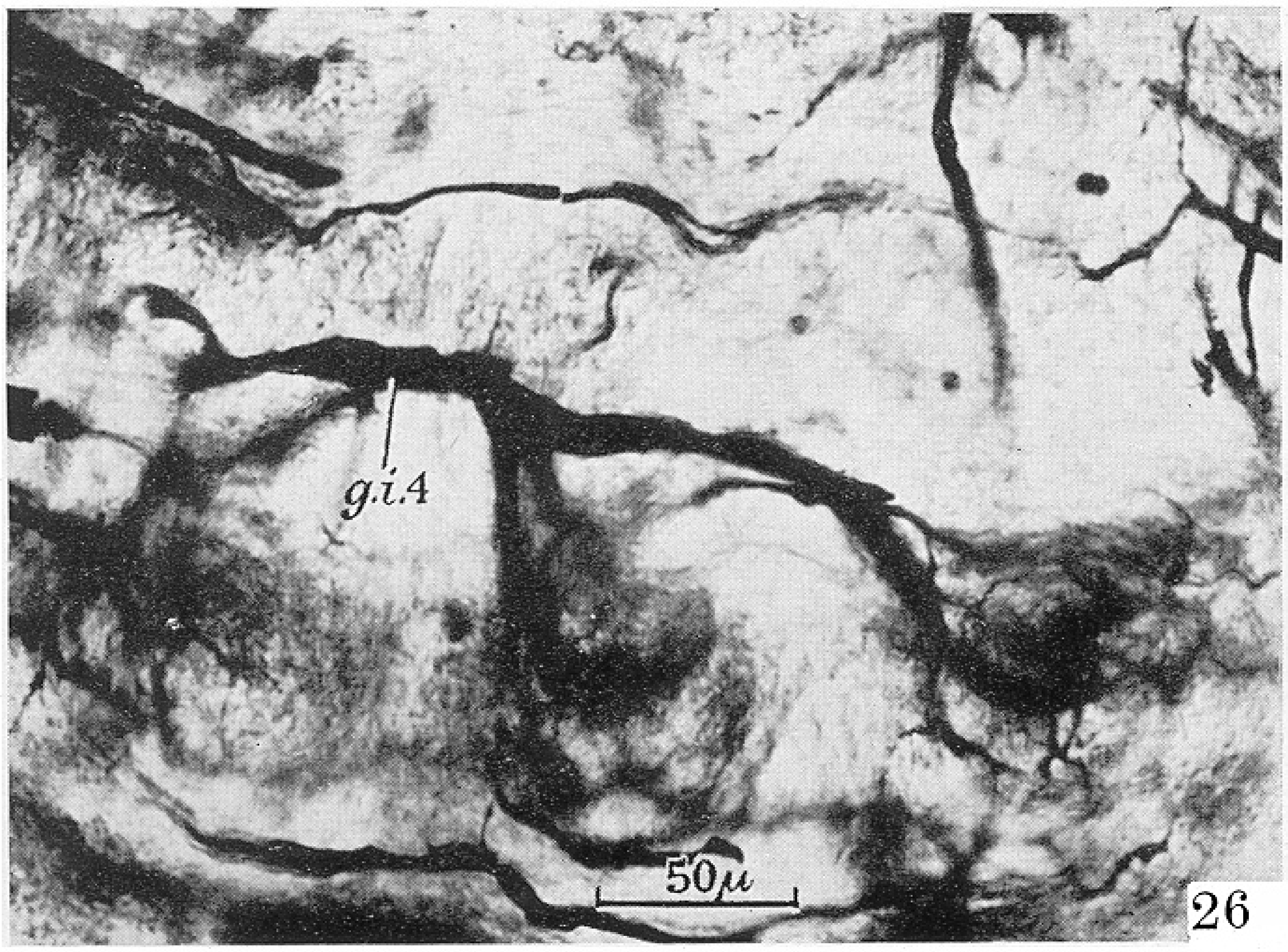

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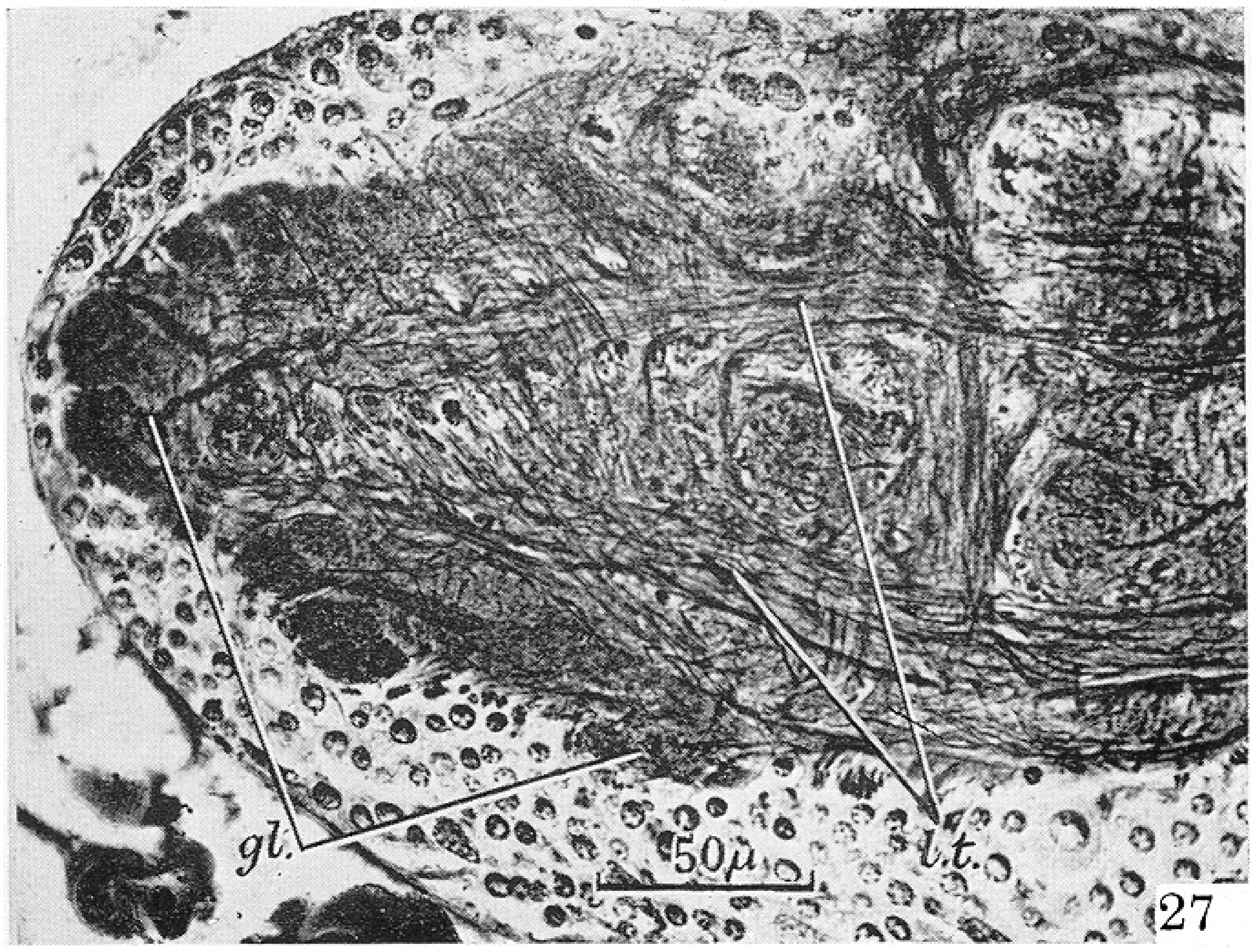

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