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STUDIES ON THE ABDOMINAL GANGLIA OF THE DESERT LOCUST

SCHISTOCERCA GREGARIA (FORSKÄL)

A thesis submitted for the Diploma of Imperial College

by

W.D.Seabrook, M.Sc., (Carleton)

Department of Zoology and Applied Entomology,
Imperial College of Science and Technology,
Sunninghill, Ascot,
Berkshire.

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ABSTRACT

The innervation of a progenital abdominal segment and of the genital and postgenital abdominal segments of Schistocerca gregaria is described in detail and compared with other orders of the Insecta. On the basis of innervation it is concluded that the genital apparatus of the male is derived from the ninth abdominal segment, and that of the female from the eighth and ninth abdominal segments.

Histological studies of the anatomy are carried out on the seventh abdominal ganglion and on the terminal ganglionic mass. The organization of the commissures, longitudinal tracts and groups of neurocytes within the ganglia is described. The terminal ganglionic mass is shown to comprise the fused ganglia of the eighth, ninth, tenth and eleventh abdominal segments and the effects of condensation on the component ganglia are discussed. Seventyfive neurone pathways are traced and described within the seventh abdominal ganglion and one hundred and five within the terminal ganglionic mass.

The abdominal giant fibre system is investigated using histological and electrophysiological techniques. The ventral connectives each contain four giant fibres, unicellular in origin, which pass uninterrupted from the terminal ganglionic mass to the metathoracic ganglion. The giant fibres are shown to synapse ipsilaterally and contralaterally with afferent neurones of the cerebral

nerve, and with afferent neurones of the ninth ventral nerve. Conduction velocities and synaptic delays are determined. The absence of an evasion response upon cercal stimulation is related to the lack of functional synapses with efferent neurones of the metathoracic leg nerve.

Other functional pathways, elucidated by electrophysiological observations, are described including; responses in the contralateral cercal nerve to cercal stimulation, and synchronized efferent potentials in the genital nerves originating from within the terminal ganglionic mass. In addition chemoreceptors are demonstrated on the cercus.

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INTRODUCTION

This investigation is an attempt to integrate anatomical, histological, and electrophysiological studies of the abdominal ganglia of an insect. In recent years considerable attention has been devoted to neurophysiological studies of the insect central nervous system. Unfortunately anatomical literature on the insect nervous system is limited and histological studies in this field can only be described as sparse. Hughes (1965) has pointed out that advances in the functional anatomy of the insect central nervous system may be held up due to the lack of information on the neuronal architecture of the ganglia. This lack of attention may be due to the detailed and time consuming nature of such work.

It is the author's belief that a sound anatomical basis is the essential foundation for histological and electrophysiological investigations of neurone pathways within the central ganglia. Histological studies however can only resolve the pathways to the point of arborization within the neuropile. The actual interneuronal connections cannot be established within this dense felt of fibres using the light microscope. The electron microscope can establish the nature of the actual junction or synapse (Smith, 1965) but it would appear to be an endless task attempting to map a ganglion using this instrument.

The only methods now available to establish the functional neuronal pathways within a ganglion are those of the electrophysiologist.

The results obtained may seem abstract as it is difficult to picture the actual neurones which are being monitored. Using marking methods it is possible however to establish the tip position of very fine microelectrodes (Huber, 1960; Kerkut and Walker, 1962; Thomas and Wilson 1965, 1966). These techniques in conjunction with anatomical and histological studies may, in time, enable us to produce an accurate functional map of the insect central nervous system.

As well as contributing to the primary object of determining some of the neuronal pathways within the terminal ganglionic mass it is hoped that the anatomical studies concerning the innervation of the genitalia may shed some additional light on the segmental origin of these structures.

LITERATURE REVIEW

Anatomy

The literature review concerned with the anatomy of the nervous system will be restricted to those papers which discuss the innervation of the abdomen, its appendages, and its organs. For a broader account of the literature the reader is referred to the papers of Uvarov (1938), Schmitt (1959) and Steinmann (1963).

Ganglionic Composition of the Ventral Nerve Cord.

The ganglionic composition of the ventral nerve cord was investigated by the early insect embryologists. Wheeler (1889) in a paper describing the embryology of Blatta and Doryphora established the presence of eleven abdominal ganglia and located paired commissures within the metathoracic and mesothoracic ganglia. Cholodkovsky (1891) again found eleven abdominal ganglia during the early development of the central nervous system of Blatta germanica. He also pointed out that there was a fusion of abdominal ganglia with the metathoracic ganglion. Heymons (1895) referred to the presence of an eleventh abdominal ganglion in the postembryonic development of Gryllotalpa, Periplaneta and Gryllus.

The embryology of Locusta migratoria has been investigated by Roonwalls (1937). He described the terminal abdominal ganglion as being developed from the fusion of the ganglia of abdominal segments eight to eleven, pointing out that the eleventh abdominal ganglion is

extremely small but definitely present. He also discovered that the first abdominal ganglion is completely fused with the metathoracic ganglion and that the second and third abdominal ganglion became associated with this centre to a lesser extent. The postembryonic development of the metathoracic ganglion of Locusta was described chronologically by Afifi (1958). His findings agree with those of Roonwalls concerning the fusion of this ganglion with the first three abdominal ganglia.

Phylogeny.

Swaine (1921) studying the nervous system of the Stenopsis (Lepidoptera) attempted to base a phylogeny on the degree of separation of the ventral connectives, considering those with widely separated connectives to be primitive and those with little separation to be advanced forms. He also described the origin of the median and lateral nerves (transverse nerves) in several genera of Lepidoptera and one genus of Trichoptera.

Although Swaine made a brief attempt to establish a phylogeny, the work of Nesbitt (1941) put comparative insect neuromorphology on a firm basis. Basing his work on seven families of Orthoptera, one of Isoptera and one of Dermaptera he used the stomatogastric nervous system as a conservative criterion, claiming that the cephalization is a very plastic feature in all orthopteran groups. In a subsequent paper Nesbitt (1958) described the central ganglia of Grylloblatta and on the basis of its nervous system suggested that

it is but distantly related to the Ensifera.

Steinmann (1960a) set out a series of morphometric criteria based on such features as the differential lengths of interganglionic connectives, angular separation of nerve roots, and sizes of the various ganglia. He claimed that these measurements can be used for comparative studies in the Orthoptera and based a phylogeny upon them. Subsequently he published tables of measurements pertinent to the above thesis for Phaneroptera falcata (1960b) and ephippigira iphippiger (1961). In a 1962 paper he discussed the evolution of the insect central nervous system.

Innervation of the Abdominal Segments.

In a very detailed paper Maki (1936) described the musculature and nervous system of the pregenital, genital and postgenital segments of a female Chaulioides formosanus (Neuroptera). Jannone (1940) in a paper on the anatomy and histology of the locust Doclostaurus briefly described the anatomy of the nervous system. Abdominal ganglia one to three are fused with the metathoracic ganglion and the terminal abdominal ganglion is described as consisting of segmental ganglia eight to ten.

Albrecht (1953) published a monograph on the anatomy of the migratory locust Locusta migratoria and later (1958) described the anatomy of the red locust Nomodacris. In both cases treatment of the nervous system was limited.

The innervation of the second and third abdominal segments of the Cecropia larva has been investigated by Libby (1959) and in 1961 he published a study of the abdominal nervous system of the adult male Cecropia, briefly describing the genital innervation. In a series of papers on the comparative anatomy of the abdominal nervous system Schmitt has described the innervation of the pregenital segments of Dissosteira, Acheta, Periplaneta and Diapheromera (1954) Pteronarcys (1963) including the innervation of the male and female genitalia and Ceuthophilus (1964). The innervation of the pregenital abdominal segments of the stonefly Acronyria and of the cicada Tibicen have been described by Knox (1965) and Vasvary (1966).

In a monograph Steinmann (1965) described in detail the central and peripheral nervous system of Acrotylus (Orthoptera) including the innervation of the female genitalia. The female genitalia of Leucophaea has been described by Engelmann (1963).

Considerable attention has been paid to the segmental innervation of the insect heart. Alexandrowicz (1926) showed that the heart of Periplaneta is innervated by a pair of lateral cardiac nerves and by segmental nerves originating in each of the abdominal ganglia. These nerves anastomose with the lateral cardiac nerves and supply fibres to the alary muscles. His student Opoczynska-Sembratowa (1936) found the same arrangement of nerves in Carausius. Kuwana (1932) reported the innervation of the heart in Bombyx to be by a branch of the unpaired ventral nerve (median nerve), he also reported

a branch of this nerve innervating the spiracular muscles. Nyst (1942) discussed the innervation of the heart in Dixippus morosus.

McIndoo's description of the heart of the cockroach (1945) is similar to the previous description of Periplaneta by Alexandrowicz, however in the army worm and silkworm he did not find any innervation of the alary muscles. Johnson (1966) described synapses between the lateral cardiac nerve and the heart of Periplaneta. He also found these nerves to contain neurosecretory granules.

A number of studies have been concerned with the median-transverse nerve complex and its connection with the spiracular muscles. This system was originally referred to as the ventral sympathetic nervous system, a term loosely borrowed from vertebrate studies. The term is currently used by Steinmann (1965).

In one of his remarkable studies of neurone tracts in the dragonfly larva Aeschna, Zawarzin (1924a) described the unpaired ventral nerve. He showed the nerve to contain two sensory and two motor fibres in each of its lateral branches. Nesbitt (1941) claimed that the median nerves in the Orthoptera innervate the spiracular muscles and the tracheal trunks. Ivanova (1956) found that the median nerves in the thorax of Locusta innervate the spiracular muscles, pleurosternal muscles, tympanal muscles and anastomose with the third somatic nerves to innervate the alary muscles. Case (1957) described the median nerve and its lateral branches (transverse nerve) in

the cockroach, Periplaneta and presented experimental evidence for their control of spiracular function. He claimed that sensory neurones in the median nerves arise from mechanoreceptive hairs near the spiracle and that the final pair of median nerves anastomose with the cercal nerves.

The median nerve in the larva and pupae of Cecropia is described as anastomosing with the lateral nerves (Beckel, 1958). In this case the spiracular muscles are innervated by a branch of the lateral nerve (dorsal nerve). In a study of the median nerves of Schistocerca gregaria, Hoyle (1959) found that the lateral branch of the median nerve (transverse nerve) contained a fast and slow motor axon which innervated the spiracular muscle. Schmitt (1959) described the median and transverse nerves in the pregenital abdominal segments of Dissosteira and Diapheromera. In 1965 Schmitt summed up his studies on the median-transverse nerve complex by concluding that it is present in varying form throughout the Insecta and established points of homology which can be recognised in the various orders investigated.

The unpaired ventral nerve (median nerve) in the larva of the blowfly Phormia terrae-novae does not innervate the spiracular musculature (Osborne, 1964), instead it was found to innervate the ventral transverse muscle and the tracheal system. Osborne found each unpaired ventral nerve comprised four neurones. Two neurones branch to each lateral nerve (transverse nerve) and one neurone passes unbranching into each lateral nerve. The transverse nerves of the phasmid Clitumnus have been investigated by Rabbo (1965). She describes a

neurohaemal organ located in these nerves. Brady and Madrell (1967) found organs similar to those of Rabbe associated with the median nerves of Carausius, Schistocerca and Periplaneta.

The abdominal musculature for a number of Orthoptera has been described by Ford (1923), for Dissosteira by Snodgrass (1935) and for Locusta and Nomodacris by Albrecht (1953, 1956).

Histology

As has been previously mentioned the literature pertaining to neurone pathways within the insect central nervous system and the ventral nerve cord in particular is extremely sparse. Early workers concentrated on the structure of the brain and optic lobes. The brain, with the exception of the tritocerebrum, is a pre-oral structure and probably not derived from segmental ganglia of the ventral chain. The tritocerebrum though it is considered to be post-oral and therefore a ganglion of the ventral nerve cord has been highly modified. There is little value considering the structure and tracts of the brain within the context of this thesis. Those interested in this topic may refer to Hanström (1928) for a survey of the structure of the brain of numerous insect orders and a complete bibliography. A more recent bibliography is provided by Bullock and Horridge (1965).

Connections Between the Brain and Lower Centres.

Fibre tracts passing from the brain to the lower centres in the nervous system have been reported by Packard (1887) who found a tract

passing from the commissural lobes (tritocerebrum) to the last abdominal ganglion of the locust Calopterus. Tracts from various centres in the brain to the thoracic and abdominal ganglia have been described by Satija in the Machilidae (1957a), Orthoptera (1957b, 1958a), Odonata (1958b), Hymenoptera (1958c) and Diptera (1958d).

Structure of the Ganglia of the Ventral Cord.

The structure of the suboesophageal ganglion of a trichopteran has been described by Ehnborn (1948). He claimed that the trichopteran nervous system retained the primitive condition and that segmental ganglia comprising this structure are readily discernable. He observed three transverse commissures, and three longitudinal tracts passing through the dorsal surface of the ganglion to lower centres in the ventral cord.

The thoracic ganglia of the ant Telentomyrmex have been briefly described by Brun (1952), he showed a number of longitudinal tracts passing through these ganglia. The structure of the thoracic ganglia of Periplaneta have been studied by Iipa et al. (1959). They reported seven longitudinal tracts which pass through the thoracic and first two abdominal ganglia which are fused with the metathoracic ganglion. Giant axons pass uninterrupted through the thoracic ganglia into the brain.

A number of major tracts in the fused thoracico-abdominal ganglion of Drosophila have been described by Iower (1948). He found the

abdominal ganglia reduced to one centre with no indication of segmentation. There are four fibre tracts from higher centres into the abdominal centre but these are very indistinct. Farson (1960) briefly described the fused thoracic-abdominal neuropile of the Gelastocoris (Heteroptera). She found the opposite sides of the abdominal neuropile separated by a mid line fissure and connected by ten transverse tracts and bridges of neuropile.

Neurone Pathways in the Thoracic and Abdominal Ganglia.

Neurone pathways have been traced in the thoracic and abdominal ganglia by several authors. Hilton (1911) described a number of pathways in the ventral ganglia of the neuropteran Corydalis. He distinguished between sensory, motor and association neurons, and was able to trace a number of axons between ganglia. He found a number of motor neurones entered peripheral nerves on the contralateral side of the ganglia. Undoubtedly the most detailed studies of the neurone pathways in an insect nervous system are those of the abdominal and thoracic ganglia of the Meschna larva, (Zawarzin 1924a, b.). In a paper on the unpaired ventral nerves (1924a) Zawarzin located the two motor cell bodies and traced their axons into the lateral nerves, and their collaterals within the ganglion of origin. He also found two sensory fibres associated with the system. His most extensive work however is a study of the neurone pathways of a thoracic and an abdominal ganglion (1924b). In this paper he described numerous sensory motor and association

neurones in great detail. The only criticism of this work is that he described his neurones on the basis of type (sensory, motor, association) thus the anatomical relationship between the various types of neurones cannot be determined (Bullock and Horridge 1965). This fault is probably due to the capriciousness of the methylene blue staining techniques which he used.

Fyle (1941) described several of neurone pathways within the thoracic ganglia of Ephesia. It is interesting that he does not report any motor neurones that cross the ganglia to innervate muscles on the contralateral side. However Guthrie (1961) in his investigation of the neuronal pathways in the very condensed central-nervous system of Gerris (Heteroptera) found that many of the motor neurones pass to the opposite side of the ganglion prior to entering a peripheral nerve. He also described a majority of the motor cell bodies in the thoracic ganglia as lying in the mid-ventral region and those of the abdominal ganglia as lying in the mid-dorsal region, only a few motor neurones are located on the lateral margins of the ganglia. Mill (1964) described a number of neuronal pathways in the seventh and eighth abdominal ganglia of the nymph of Aeschna. The eighth abdominal represents the fusion of at least two and possibly three segmental ganglia. He found that some of the motor neurones supply nerves on the contralateral side of the ganglion.

Giant Fibres.

The abdominal giant fibre system has been investigated by Tumphrey and Rawdon-Smith (1937), Roeder (1948), Cook (1951, 1952) Fielden (1960) Hughes (1953) and Mill (1964). Using electrophysiological techniques Tumphrey and Rawdon-Smith determined that giant fibres in Periplaneta synapsed with afferent neurones of the cercal nerve. They established the speed of conduction of these fibres as 5 to 6 meters per second and the synaptic delay as approximately 1.0 milliseconds. Roeder found six giant fibres in each abdominal connective of Periplaneta ranging in diameter from 20 to 45 microns. He suspected these of being multicellular in origin, arising from a group of cell bodies close to the cercal nerve. His electrophysiological investigations indicated that six homolateral and three heterolateral giant fibres synapse with efferent neurones of the cercal nerve with a synaptic delay of 1.9 milliseconds. The giant fibres conducted with velocities of 6 meters per second and passed uninterrupted into the metathoracic ganglion. At this level they formed synapses with efferent neurones of the metathoracic leg nerve and with interneurones passing to higher levels in the central nervous system.

Cook (1951) investigated the giant fibres in the abdominal nervous system, of Locusta. He reported four giant neurones in each connective with diameters of 12 to 15 microns. These gave rise to giant potentials when the cercus was stimulated with puffs

of air. These fibres pass without interruption into the metathoracic where they synapse with efferent neurones of the metathoracic leg nerve. Although burst of impulses are recorded from these efferent neurones on stimulation of the cercus no evasion response occurs. The giant fibres of Locusta are reported to have conduction velocities of 3 to 4 meters per second (Cook 1952, Fielden 1960).

Giant fibres in the Odonata have been described in the ventral cord of Anax nymphs by Hughes and in Aeschna nymphs by Mill. In Anax there are two fibres with diameters of 12 to 15 microns. Aeschna has two fibres of 13 to 15 microns although four giant fibres are present in the eighth abdominal ganglion. Giant fibres in the Odonata synapse in each of the abdominal ganglia. Fielden (1960) has studied Anax electrophysiologically and has reported conduction velocity in the giant fibres of 3.5 to 4.5 meters per second and synaptic delays, between these neurones and afferent fibres of the parapneustic nerve, of 2.0 to 4.5 milliseconds.

MATERIALS AND METHODS

The specimens of Schistocerca gregaria used in this study have been obtained from a colony maintained at the Imperial College of Science and Technology Field Station, Silwood Park and from the Anti-Locust Research Centre, London.

Locusts used for morphological studies were prepared in several ways. The gut was removed and they were dissected under 70% alcohol. In some cases a solution of 0.1% methylene blue in locust ringer was injected into the living animal or poured over the exposed nervous systems. After five minutes the locust was washed to remove excess stain and dissected under 70% alcohol. In this case both the nerves and muscles took up the stain, however, the nerves were very obvious against the quantities of fatty tissue invariably present. In an attempt to reduce this fatty tissue locusts were starved for periods of three weeks before use. The reduced methylene blue method of Zacharuk (1963) was used but results were little better than those obtained using the foregoing simple method. In some few cases the locusts were fixed in alcoholic Bouins fixative (Brasil 1904 or Dubosq Brasil of Gray 1954) and dissected under alcohol. This resulted in the nerves taking on a cream colour against the whiter muscles but unfortunately caused the nerves to become brittle making dissection difficult.

Specimens prepared for histological study had the pertinent ganglia dissected out and fixed in either a modified alcoholic Bouins

fixative or veronal buffered osmium tetroxide. It was found that the addition of a few drops of nitric acid to the Bouins fixative resulted in sharper fixation and brighter staining. Tissues were embedded in "Paraplast" using the standard chloroform embedding technique. Serial sections were cut in the frontal, saggital and transverse planes at a thickness of five and ten microns using a "Cambridge rocking" microtome.

Ganglia fixed in the modified Bouins fluid were stained with Harris' haemotoxylin and counterstained using eosin Y in picric acid and alcohol. These sections were used to investigate the glomerular regions within the neuropile and to determine the limits of the segmental areas of neuropile within a ganglionic mass. Ganglia used for tracing neuron tracts were fixed and stained using a modification of Wigglesworth's (1957) osmium ethyl-gallate technique. If this technique is used as published the staining is too intense and sections cut at five microns are unreadable. Good results are obtained by reducing the time in osmium tetroxide to fifteen minutes and the time in ethyl gallate intensifier to twelve hours. The paraffin ribbons were de-waxed in xylene and mounted in Canada balsam, without the addition of ethyl gallate to the mounting medium. Tissues prepared in this manner gave excellent axonal and nuclear detail. The storage properties are good.

Preparations of isolated abdomens were used for studies concerned with the speed of conduction and synaptic relations of the giant fibres at the level of the terminal ganglionic mass. Whole locusts were used for the study of the synapses at the level of the metathoracic ganglion, a section of the dorsal thorax and abdomen being removed in the region of the ganglion. In all instances the gut and ventral diaphragm were dissected from the region under investigation and the ventral nerve cord was split into separate connectives. The preparations were irrigated with locust ringer (Hoyle, 1953).

Both silver/silver chloride and electrolytically tapered tungsten electrodes were used for recording. Silver/silver chloride electrodes were used for electrical stimulation. In order to make maximum use of the micromanipulators paired electrodes were constructed. Two silver wires were inserted into a hypodermic needle (used as a clamp) and a drop of araldite placed 1 cm. from their tips. This was briefly fired over a low flame in order to set the resin. The proximal ends were cut square, fine hooks bent in them and the electrodes chlorided. The hooked tips could then be bent apart to the desired distance for the experiment in hand. The electrodes were inserted into stainless steel sockets permanently mounted in plastic rod electrode holders of a diameter to fit the micromanipulator. Each electrode of this pair was used as a recording electrode; thus one micromanipulator could handle

the recording electrodes for two channels of amplification. Nickle plated insect pins were used as indifferent electrodes. A second useful feature of this electrode configuration was that electrodes could be held steadily, very close together, and moved along the nerve with a fixed distance separating them.

Potentials were amplified using a pair of Tektronix type 122 preamplifiers and displayed on a Tektronix 502-A dual beam oscilloscope. The signals were recorded on a dual track tape recorder and monitored acoustically via the speaker of the tape recorder.

Electrical stimuli were obtained from a square pulse biological stimulator and delivered to the preparation through an isolating transformer. The oscilloscope sweep was triggered by the stimulator which had a built in variable delay.

Electrophysiological and histological investigations have been carried out using male Schistocerca only. The terminology used for the nerves is that of Schmitt (1953). In the morphological diagrams nerves terminating in a muscle have been given the muscle number of Snodgrass (1935), sensory nerves have been indicated with an s.

MORPHOLOGY

The Terminal Ganglionic Mass

The terminal ganglionic mass (Fig. 1, 2) is an ovate structure lying in the eighth abdominal segment. In Schistocerca gregaria it innervates abdominal segments VIII, IX, X and XI; thus comprising the fused ganglia of the last four segments. The structure is therefore referred to as a ganglionic mass (Seabrook and Nesbitt, 1966). The dorsal and ventral surfaces are featureless giving no indication of the position of the component segmental ganglia.

At the anterior surface the ganglionic mass receives the closely appressed ventral connectives (v.c.) and, lying between them the fine median nerve (m.n.). On superficial examination it appears to give rise to four pairs of nerves. The eighth dorsal nerves (8 d.n.) arise from the antero-lateral angles of the ganglionic mass, the eighth ventral nerves (8v.n.) arise close behind and below them. The ninth dorsal nerves (9 d.n.) join the ganglion at the postero-lateral angles and immediately posterad and mesad of these a pair of large nerve trunks arise which supply branches to the ninth abdominal sternum and the tenth and eleventh abdominal terga and sterna.

If however, the surrounding connective tissue is teased away it is found that these nerve trunks contain the separate ninth ventral nerves (9 v.n.) to the ninth sternum, the epiproct nerves (epi. n.) and the cercal nerves (cerc. n.) to the eleventh sternum. In addition the male has a genital nerve (gen. n.) associated

with the ninth segmental ganglion. With the exception of the epiproct nerve and oesophageal nerve which use a short distance posterad of the ganglionic mass the other nerves retain their identity until they enter the ganglionic mass.

The transverse nerve of the eighth abdominal ganglion (8 tv. n.) arises unpaired from the median dorsal surface of the ganglionic mass. In the female a ninth transverse nerve (9 tv. n.) is present which arises, unpaired, immediately posterad of the eighth transverse nerve.

Innervation of the Eighth Abdominal Segment.

The Male (Fig. 3)

Dorsal Nerve.

The eighth dorsal nerve arises on the antero-lateral angle of the ganglionic mass and passes dorso-laterad along the tergum. It innervates the lateral and dorsal muscles; in addition it gives rise to a branch which innervates the sternal muscles of this segment.

A short distance after leaving its ganglion the dorsal nerve gives rise to a ventral branch which divides. The medial branch innervates the median internal ventral muscle (247) and the lateral branch innervates the lateral ventral muscle (248). Close to its origin this nerve gives off in addition an extremely fine branch which passes dorsad to anastomose with the paramedian nerve (pm. n.) supplying fibres to the ventral diaphragm (v. d.).

Continuing laterad the dorsal nerve branches off a major nerve which passes anterad and immediately divides again into anterior and posterior nerves. The anterior nerve passes along the lateral horn of the eighth sternal apodeme and at its tip turns mesad becoming contiguous with the seventh transverse nerve (7 tv.n.). At this point it gives rise to a pair of small nerves. The anterior of the two innervates the first external lateral muscle (251) the posterior member innervates a small bundle of fibres (250x) derived from the internal lateral muscle (Albrocht, 1953). Antero-mesad of this pair of nerves the anterior branch gives off a very small nerve which passes over the apodeme and turns ventrad to anastomose with a branch of the seventh ventral nerve (7 v.n.) close to the point at which this nerve terminates in the external ventral muscle (234) of the seventh abdominal segment.

The aforementioned posterior branch reflexes upon itself and passes ventrad to innervate the spiracular muscles of the eighth abdominal segment. As this nerve passes beneath the dorsal nerve it bifurcates. The lesser dorsal branch innervates the dilator muscle (254), the greater ventral branch innervates the occlusor muscle (255) of the spiracle. The greater branch receives a fine sensory nerve (s) from the hypodermis in the region of the spiracle.

The dorsal nerve passes laterad between the sternal apodemes of the eighth and ninth abdominal segments and receives a substantial sensory nerve. This nerve appears to innervate a large portion of

the eighth pleuron. Close to the point at which this nerve innervates the dorsal nerve a short nerve arises which passes ventrad and divides; both branches extending over the surface of the paradorsal muscle (244).

The dorsal nerve, proceeding dorso-laterally, now becomes closely appressed to the tergal musculature. Some distance further a branch arises which passes posterad; dividing to innervate the two lateral internal dorsal muscles (243a, b). A short distance laterad the next nerve arises and passes antero-laterad receiving sensory fibres (s) from the tergum and supplying a fine nerve to the alary muscles of the heart (al.m.).

The remainder of the eighth dorsal nerve divides serially into three branches innervating the internal dorsal muscles (242a, b, c, d). The nerve innervating 242b gives off a branch which passes postero-mesad to innervate the median external dorsal muscle (245) and receiving sensory fibres (s) from the region of the intersegmental fold.

Ventral Nerve.

The eighth ventral nerve is rather insignificant by comparison with the dorsal nerve. It leaves the ventro-lateral margin of the ganglion, passes ventrad and divides into three branches. The anterior branch is sensory (s) receiving fibres from the anterior region of the eighth abdominal sternum. The median passes laterad bifurcating distally to innervate the internal lateral muscle (250) and the third external lateral muscle (253). A sensory branch (s) from the posterior region of the sternum joins this nerve mesad of

the point of bifurcation. The posterior branch (x) proceeds posterad, without branching, to become contiguous with the transverse nerve of the eighth segment (Fig. 5, 8 tv.n.).

Transverse Nerve.

The eighth transverse nerve in the male is typical of the transverse nerves associated with the pregenital segments (Fig. 10, 7 tv.n.). The superficial difference in the configuration is due to the fusion of the eighth and subsequent abdominal ganglia resulting in a shortening of the nerve.

The nerve arises unpaired from the median postero-dorsal surface of the ganglionic mass, passes posterad a short distance closely appressed to the neurilemma and bifurcates. The nerve now extends laterad passing over the ninth sternal apodeme, and bending ventrad over its tip to become contiguous with a branch of the eighth ventral nerve (8 v.n.). Approximately one third of the distance from the point of bifurcation a very fine nerve is given off which passes dorsad to anastomose with the paramedian nerve (pm.n.). At a varying distance mesad of this point the transverse nerve receives a branch from the ninth dorsal nerve. As the transverse nerve bends ventrad over the tip of the apodeme a short nerve arises which innervates the external lateral muscle (270) of the ninth abdominal segment.

The Female (Fig. 4).

The female eighth abdominal segment is the first of the genital segments. The muscle plan differs considerably from the male,

particularly those muscles associated with the ventral ovipositor valves which have no counterpart in the male (Snodgrass, 1935). The plan of innervation varies accordingly.

Dorsal Nerve.

The eighth dorsal nerve (8 d.n.) is modified to a lesser extent than the ventral nerve. It arises from the antero-lateral angle of the ganglionic mass and proceeds dorso-laterally. The first nerve to emerge is an extremely fine branch passing dorsad to anastomose with the paramedian nerve (pm.n.) innervating the muscles of the ventral diaphragm (v.d.). Immediately distal to this point a ventral nerve is given off which innervates the median internal ventral muscle (247), the lateral ventral muscle (248) is innervated by a branch of the eighth ventral nerve (8 v.n.) in the female.

The dorsal nerve passes unbranching to the mesial face of the lateral apodeme of the ovipositor. A branch arises which passes anterad, and as in the male immediately divides into anterior and posterior nerves. The anterior nerve branches to innervate a bundle of fibres (250x) belonging to the second internal lateral muscle and the first external lateral muscle (251). A very fine nerve arises at the same point as the branch to 251, and turns ventrad over the tip of the eighth abdominal apodeme. This nerve passes within, but does not innervate, the external ventral muscle (234) of the seventh abdominal segment leaving it to anastomose with the ventral

nerve of the seventh abdominal segment (7 v.n.) close to the termination of this nerve in muscle 234. The remainder of the anterior nerve becomes contiguous with the transverse nerve of the seventh ganglion (7 tv. n.). The posterior nerve reflexes upon itself, passes ventrad beneath the lateral apodeme of the ovipositor and its muscles to divide into sensory and motor nerves. The sensory nerve (s) receives fibres from the pleuron in the region of the spiracle. The motor nerve initially sends a branch to the second external lateral muscle (252) and continuing laterad divides, innervating the dilator muscle (254) and occlusor muscle (255) of the spiracle.

The dorsal nerve (8 d.n.) becomes closely appressed to the muscles of the lateral ovipositor apodeme, crawls over its dorsal surface and passes dorso-laterad for some distance without branching.

The pattern of branching now differs considerably from that in the male (Fig. 3). The nerve to the paradorsal muscle which is present in the male is missing. The large sensory branch to the mid-region of the pleuron is also missing, though a lesser sensory nerve is present as will be described subsequently.

A considerable distance distal to the apodeme a branch arises and passes antero-laterad innervating the alary muscles (al. m.) and receiving sensory fibres (s) from the dorsal region of the pleuron. Close by the origin of this branch a nerve is given off which extends antero-mesad along the pleuron to innervate the short protractor muscle of the ovipositor (256). There is no homologous

muscle in the male. This branch receives a small sensory nerve (s) from the mid region of the pleuron. A short nerve now arises from the dorsal nerve (8 d.n.) which passes anterad innervating the fifth bundle of the internal dorsal muscle (242 c) and receiving a sensory nerve (s) from the tergum. Close by the origin of this branch, a pair of nerves arise which pass posterad to innervate the internal dorsal muscles (243 a, b).

The dorsal nerve now divides serially four times sending branches to the remaining bundles of the internal dorsal muscle (242 d, c, b, a). The branch to muscle 242a gives rise to a nerve which passes posteromesad into the intersegmental fold between abdominal segments eight and nine to innervate the median external dorsal muscle (245). It will be noted that in the female muscle 242 divides into five bundles as opposed to four in the male.

Ventral Nerve.

The branching of the eighth ventral nerve (8 v.n.) is barely homologous to the male. This nerve innervates the ventral ovipositor mechanism, the spermathecal duct, and receives sensory fibres from eighth abdominal sternum. Unlike the ventral nerve in the male this is a substantial nerve.

The nerve arises from the lateral face of the ganglion passes ventrad and immediately divides into posterior and ventral nerves. The posterior, greater nerve proceeds unbranching for a considerable distance and gives rise to a mesial branch which becomes distributed

over the muscles of the spermathecal duct (asp.n.). Adjacent to this branch a nerve passes laterad to contribute to the innervation of the depressor muscle of the ventral valvula (272).

The posterior nerve continues without branching until it is about to enter the ventral ovipositor valve. At this point a mesial branch innervates the spermathecal duct in the region of the spermathecal apperture (asp.n.). The nerve continues into the ventral ovipositor valve and divides into mesial and lateral branches which receive sensory fibres from the valve, and a central branch innervating the depressor muscle of the ventral valvula (272). In Dissosteira carolina (Snodgrass, 1935) and Locusta migratoria (Albrecht, 1953) this muscle is considered to belong to the ninth abdominal segment. No details are available as to the innervation of this muscle in these species.

The ventral branch of the eighth sternal nerve (8 s.n.) divides into anterior and posterior nerves. The anterior nerve passes forward; bends back upon itself passing posterad beneath the lateral ovipositor apodeme and its muscles to become distributed over the internal lateral muscle (250). The posterior nerve passes along the eighth sternum for a short distance before innervating the lateral ventral muscle (248). Prior to entering this muscle the nerve receives sensory fibres (s) from the eighth sternum. In the male, muscle 248 is innervated by a branch of the eighth dorsal nerve (Fig. 2, 8 d.n.).

Transverse Nerve.

The transverse nerve of the eighth abdominal ganglion (Figs. 2, 6, 11, 8 tv.n.) in the female differs considerably from that in the male. Unlike the male both halves of this nerve arise separately from the postero-dorsal surface of the terminal ganglionic mass. A fusion of these nerves into a common trunk takes place within the ganglion and may be observed by teasing away the neurilemma (Fig. 2). On emerging from the ganglionic mass the transverse nerve passes antero-laterad enclosing within its sheath the paramedian nerve (pm.n.) with which it makes a connection at the point where the paramedian nerve crosses over it. The nerve now bends postero-laterad to enter the mesial face of the levator muscle of the dorsal ovipositor valve (271) and gives rise to fine anterior and posterior branches to it. On emerging from the lateral face of the muscle at the level of the apodeme the nerve turns ventrad passing beneath muscle 272 (the depressor of the ventral ovipositor valve) to terminate as a sensory nerve in the fold between the sternum and pleuron of the eighth abdominal segment.

Connections between the eighth transverse nerve and the eighth ventral nerve have not been established, nor have connections been established between this nerve and the ninth dorsal nerve as would be expected in a normal segment. The function of this nerve also appears to have been considerably altered. A further discussion will be reserved for a subsequent section dealing with the median-transverse nerve complex.

Innervation of the Ninth Abdominal Segment.

The Male (Fig. 5).

Dorsal Nerve.

The ninth dorsal nerve emerges from the postero-lateral angle of the terminal ganglionic mass immediately anterad of the large posterior nerve trunks. This is a small nerve and its origin is not always apparent. On leaving the ganglion it passes postero-laterad to innervate the muscles of the ninth tergum. In addition this nerve receives sensory fibres from the ninth and tenth terga.

The first branch is the very fine paramedian (pm.n.) nerve which passes anterad to innervate the muscles of the ventral diaphragm (v.d.). The ventral diaphragm in the male of Schistocerca extends across the anterior region of the ninth abdominal segment.

Distal to the paramedian nerve the dorsal nerve gives rise to a substantial branch which passes anterad to anastomose with the eighth transverse nerve (8 tv.n.). The ninth dorsal nerve now divides, into lateral and posterior nerves.

The posterior, sensory nerve redivides into a lesser posterior branch receiving sensory fibres (s) from the ventral region of the pleuron and a greater lateral branch receiving sensory fibres from the dorso-lateral region of the pleuron.

The lateral branch bends dorso-laterad and passes to the tergum where a short branch is given off to the fifth bundle of the median internal dorsal muscle (260 e). The lateral branch now bifurcates,

a lesser anterior branch passing to the alary muscle (al.m.) and receiving sensory fibres (s) from the anterior region of the tergum. The greater branch passes posterad giving off a pair of branches to bundles of the median internal muscle (260 d.c.). At this point a large sensory branch is received from sense organs of the posterior region of the ninth tergum (s) and the tenth tergum (s 10). The remainder of the nerve divides to innervate the two remaining bundles of fibres belonging to the median internal muscle (260 b, a). In the males of Locusta (Albracht, 1953) and Dissosteira (Snodgrass, 1935) this muscle consists of one bundle of fibres only, although in the females there are five bundles as in both sexes of Schistocerca.

Ventral Nerve.

The ninth ventral nerve (Fig. 1, 5, 9 v.n.) is included within large ventral nerve trunks that issue from the postero-lateral angles of the terminal ganglionic mass. If the neurilemma is removed from these trunks it will be found that this nerve originates immediately beneath the ninth dorsal nerve (9 d.n.). It passes posterad in the lateral region of the trunk (Fig. 1), turning ventrad beneath the epiproct nerve (epi.n.), and cercal nerve (cerc.n.) to emerge as the second nerve from the postero-median face of the trunk. This is essentially a sensory nerve, although it does innervate the ventral lateral muscles of the ninth abdominal segment.

On emerging from the trunk the ninth ventral nerve gives rise to a small nerve from its lateral surface which becomes incorporated

within the sheath of the epiproct nerve (epi.n.). It passes with this nerve for some distance. On emerging from the sheath of the epiproct nerve it passes posterad a short distance to innervate the large retractor muscle of the phallus (261). Prior to entering the muscle a very small nerve is given off which proceeds posterad to innervate one of the internal lateral muscles (269). A second branch emerges from the median surface of the ninth ventral nerve, divides giving a small mesial branch to the ventral muscles (265) and a lateral branch which passes beneath the ninth ventral, epiproct, and cercal nerves and comes to lie within the sheath of the ninth dorsal nerve (9 d.n.). It passes a short distance with this nerve, emerges, and turns posterad to innervate the second of the internal lateral muscles (268).

The ninth ventral nerve proceeds posterad and bifurcates into two major branches, the median nerve (9 v.m.n.) which receives sensory fibres (s) from the median ventral region of the ninth abdominal sternum, and the lateral nerve (9 v.l.n.) which receives sensory fibres (s) from the lateral margins of the ninth sternum.

Genital Nerve.

The genital nerve (Fig. 1, 6, gen.n.), present only in the male, is also included among the nerves of the large posterior trunks. It arises on the posterior face of the ganglionic mass immediately beneath the ninth ventral nerve, passes along the mesial face of the trunk and is the first nerve to emerge from the postero-median

surface. This nerve is predominantly a motor nerve, it is a development of the ninth abdominal ganglion, and is responsible for the innervation of the male genitalia.

Upon leaving the trunk the genital nerve gives off a series of very fine fillets to the accessory gland (acc.g.n.) and divides into posterior and lateral nerves. The lateral nerve proceeds for a short distance and branches serially three times. A posterior branch passes to the retractor muscle of the aedeagus (266), a lateral branch innervates the protractor muscle of the aedeagus (267), and a second lateral branch passes to the retractor muscle of the aedeagus (266). The main nerve continues posterad to terminate in the compressor muscle of the ejaculatory sac (284).

The aforementioned posterior nerve redivides into mesial and lateral branches. The lateral branch sends a nerve to the compressor muscle of the ejaculatory sac (284) which also receives a sensory nerve (s) from the sternum. The lateral nerve continues posterad to terminate in the retractor muscle of the aedeagus (266). The mesial branch proceeds posterad bending mesad and giving off a nerve to innervate the muscle of the ejaculatory duct (285). Continuing posterad the mesial branch bifurcates; the lateral branch again dividing to innervate the lateral dilator muscle of the endophallus (281) and the compressor muscle of the endophallus (283). The mesial branch divides to innervate the dorsal dilator muscle of the endophallus (282) and the epiphallic muscle of the aedeagus (278). The

innervation of the muscle of the subventral lobe of the aedeagus was not located.

The transverse nerve of the ninth abdominal segment is not present in the male of S. gregaria.

The Female (Figs. 2, 7, 11).

Dorsal Nerve.

The ninth dorsal nerve arises as in the male, from the posterolateral angle of the terminal ganglionic mass just anterad of the large posterior nerve trunks. It innervates the dorsal muscles of the ninth abdominal segment and contributes to the dorsal ovipositor musculature and rectal musculature. In addition it receives sensory fibres from the ninth abdominal pleuron and tergum.

Immediately upon emerging from the ganglion the ninth dorsal nerve gives rise to the slender paramedian nerve (Fig. 2 pm.n.). This nerve is enclosed within the sheath of the eighth transverse nerve (8 tv.n.). To see its origin one must tease away the neurilemma at the base of the dorsal nerve. The paramedian nerve receives fibres from the eighth transverse nerve and extends forward the entire length of the abdomen to innervate the muscles of the ventral diaphragm (v.d.). In Schistocerca the ventral diaphragm covers only the anterior portion of the terminal ganglionic mass, which lies in the eighth abdominal segment, and extends posterad into the ninth segment as a pair of diaphanous horns terminating close to the origin of the ninth dorsal nerve and apparently adhering to the neurilemma of the ganglionic mass.

The ninth dorsal nerve (Fig. 7, 9d.n.) now passes postero-laterad and gives rise to a broad ventral branch passing beneath the cercal nerve (cerc.n.) to anastomose with the epiproct nerve (epi.n.) within the sheath of the posterior trunk. As this branch enters the trunk a fine nerve emerges from it and passes posterad to innervate the ventral dilator muscle of the rectum (Fig. 7, 264). The dorsal nerve continues postero-laterad and receives a sensory branch (s) which arises on the ventral region of the ninth pleuron, passes beneath the dorsal ovipositor apodeme and muscles, proceeds upwards over its medial face and turns laterad over the surface of the levator muscle of the dorsal valve to join the ninth dorsal nerve. Continuing laterad a nerve arises which extends anterad and divides, both branches innervating the long protractor muscle of the ovipositor (262). Close by the origin of the previous branch a sensory nerve joins the ninth dorsal nerve. This nerve receives sensory fibres from the remainder of the ninth pleuron.

The dorsal nerve now proceeds into the tergum and branches serially four times, the third branch dividing again to innervate the five bundles of the median internal dorsal muscle (260 e, d, c, b, a). In addition a pair of sensory nerves (s) are received from the tergum.

Ventral Nerve.

The ninth ventral nerve (Fig. 2, 9 v.n.) emerges from the ganglion immediately beneath the ninth dorsal nerve and passes ventrad along the lateral margin within the neurilemma of the posterior nerve

trunk turning mesad and passing either between the cercal nerve (cerc.n.) and epiproct nerve (epi.p.) or beneath them both to emerge on the mesial face of the trunk. Upon emerging the ventral nerve passes posterad close to the muscles and apodeme of the dorsal ovipositor valve for a considerable distance, dividing into mesial and lateral branches.

The lateral branch continues posterad supplying a small nerve to innervate the adductor muscle of the ventral valve (273). This nerve gives rise to a very fine branch which passes antero-mesad and divides into a sensory branch (s) and a branch which passes antero-laterad beneath the ninth ventral nerve to contribute to the innervation of the levator muscle of the dorsal ovipositor valve (271). The lateral branch passes posterad entering into, and receiving fibres from, the dorsal ovipositor valve (s 3 v 1). The mesial branch of the ninth ventral nerve passes to the posterior region of the ninth apodeme and turns laterad. At this point a branch arises to innervate the muscle of the intermediate or second ovipositor valve (275). The mesial branch now passes laterad over the levator muscle of the dorsal ovipositor valve giving rise to a posterior branch innervating the adductor muscle of the dorsal valve (274). The mesial nerve then bifurcates, a short posterior branch passing into the dorsal ovipositor valve to innervate the posterior region of the levator muscle of the dorsal ovipositor valve (271) and an anterior branch which extends forward to innervate the retractor muscle of the ovipositor (263).

Transverse Nerve.

The transverse nerve of the ninth abdominal ganglion is present in the female (Fig. 2, 11, 9 tv.n.). It arises as a substantial nerve from the postero-median surface of the ganglionic mass, extends posterad close to the right posterior nerve trunk and bifurcates. A short branch enters the nerve trunk to anastomose with the epiproct nerve of the same side and a long branch crosses to anastomose with the epiproct nerve of the opposite side. No function can be attributed to this nerve at present.

Innervation of the Tenth and Eleventh

Abdominal Segments.

The nerves of the tenth and eleventh abdominal segments are combined into the epiproct nerve (epi.n.), the common dorsal nerve of the two segments, and the cercal nerve (cerc.n.) the common ventral nerve.

The Male (Figs. 1, 8).

Epiproct Nerve.

The epiproct nerves (epi.n.) and cercal nerves (cerc.n.) are contained within the large posterior nerve trunks (Fig. 1). They emerge from the ganglion as a common root and soon separate, the cercal nerve lying mesad of the epiproct nerve. After separation the epiproct nerve turns beneath the cercal nerve coming to lie mesad of it. Only after emerging from the common sheath of the trunk does

the epiproct nerve again turn beneath the cercal nerve coming to lie laterad of it. Continuing posterad the epiproct nerve (Fig. 8, epi.n.) gives rise to a short branch to the ventral dilator muscle of the rectum (264). Distal to this branch a nerve emerges and passes mesad to anastomose with the cercal nerve (cerc.n.). The epiproct nerve then bends posterad and a pair of widely separated branches arise, both pass postero-ventral to the base of the cercus the first to innervate the lateral levator muscle of the cercus (289) and the second to innervate the median levator muscle of the cercus (288). The epiproct nerve passes posterad enters the epiproct and divides. The dorsal branch innervates the dorsal dilator muscle of the anus (295) and receives sensory fibres (s) from the epiproct. The ventral branch divides supplying nerves to the adductor muscle of the cercus (293) and the adductor muscle of the paraproct (294), this nerve receives sensory fibres (s) from the epiproct.

Cercal Nerve.

The cercal nerve (cerc.n.) after separating from the common root with the epiproct nerve continues posterad passing above the epiproct nerve and giving rise to a major branch, the rectal nerve (rect.n.). The rectal nerve proceeds dorsad, a branch emerging which innervates the dorsal dilator muscle of the rectum (286), and bifurcates into cephalad and caudad branches. The cephalad branch becomes distributed among the intrinsic muscles of the rectum (rec.m.). The caudad branch redivides the lateral nerve innervating the lateral

dilator muscle of the rectum (290) and posterior branch innervating the intrinsic muscles of the posterior part of the rectum (rec.m.). Continuing posterad the cercal nerve divides, the dorsal, sensory branch passing posterad and dividing again to receive sensory fibres (s) from the lateral and mesial surfaces of the cercus. The ventral branch passes to the region of the paraproct where it receives a sensory nerve (s) from the paraproct. It then divides one branch innervating the lateral dilator muscle of the anus (296), the other branch passes to the ventral muscle of the paraproct (291) and receives sensory fibres (s) from the paraproct.

The Female: (Fig. 2, 9).

The innervation of the postgenital segments in the female is similar to that of the male, differing only slightly in the pattern of nerve branching and with the addition of the transverse muscle and its innervation which is absent in the male. It is also interesting to note that the cercal nerve-epiproct nerve connection is absent in the female.

Epiproct Nerve.

The two nerves emerge from the ganglionic mass as a common root as in the male. However on separation the cercal nerve is laterad of the epiproct nerve and only becomes mesial to it some distance posterad of the ganglion. As the epiproct nerve separates from the common root it receives a previously mentioned branch of the ninth dorsal nerve which anastomoses with it (Fig. 2). The first branch

or the epiproct nerve is a substantial nerve which passes to the ventral dilator muscle of the rectum (264) which it innervates in co-operation with a branch of the ninth dorsal nerve (Fig. 7, 9 d.n.). It is possible that this branch of the ninth dorsal nerve may contain fibres from the epiproct nerve which have passed via the aforementioned anastomosis to innervate the rectal dilator muscle. Snodgrass (1935) and Albrecht (1953) both consider this to be a muscle of the ninth abdominal segment. We have found no indication of its innervation by the ninth abdominal ganglion in the male, where it is innervated exclusively by a branch of the epiproct nerve (Fig. 8, epi.n.). The epiproct nerve turns laterad and shortly gives rise to a pair of branches to the lateral levator muscle (289) and the median levator muscle (288) of the cercus. Distal to the former nerve a substantial sensory nerve (s) is received from the epiproct. Close to this sensory nerve a short branch passes from the epiproct nerve to the depressor muscle of the cercus (287). The innervation of this muscle was not located in the male. This branch to muscle 287 also receives sensory fibres from the tenth tergum (s 10). The tenth abdominal tergum in the male is innervated by a branch of the ninth dorsal nerve (Fig. 5, s 10). The remainder of the epiproct nerve branches to the usual muscles associated with the epiproct, the adductor muscle of the paraproct (294), the adductor muscle of the cercus (293) and the dorsal dilator muscle of the anus (295).

Cerecal Nerve.

The cerecal nerve (cerc.n.) proceeds posterad from the common root passing laterad of the epiproct nerve. A considerable distance caudad of the ganglion the large rectal nerve (rec.n.) emerges and passes dorsal dividing to innervate the muscles associated with the rectum. The rectal nerve is similar to that in the male except for the nerve to the dorsal dilator muscle of the rectum (286) which emerges close to the posterior ramification of the caudal branch and directly opposite to the branch to the lateral dilator muscle of the rectum (290). The remainder of the caudal branch ramifies to the intrinsic muscles of the rectum. The cephalad branch innervates only the intrinsic muscles of the rectum. Continuing posterad and crossing above the epiproct nerve the cerecal nerve divides into cerecal and paraproct branches. The lateral or cerecal branch gives rise to a branch which turns laterad passing beneath the cerecal nerve to innervate the transverse muscle (292). A small sensory branch (s) is then received from the ventral region of the tenth tergum. The remainder of the cerecal branch proceeds posterad and divides to innervate the lateral and mesial surfaces of the cercus. The mesial or paraproct branch also proceeds posterad and divides. The lateral branch innervates the ventral muscle of the paraproct (291) and receives sensory fibres (s) from the base of the paraproct. The mesial branch enters the paraproct to innervate the lateral dilator muscle of the anus (296) and receives sensory fibres from the paraproct.

Discussion

Terminology

The lack of an accepted standard terminology plagues comparative studies on the segmental innervation of the insects. This point has been taken by Steinmann (1965); he then however proceeds to establish his own terminology which is unrelated to the segmental nature of the nerves. The confusion caused by the use of this system cannot be justified particularly after the work of Schmitt (1954) and his students, who have established a terminology and applied it to several insect orders, (Schmitt 1954, 1959, 1963, 1964; Libby 1959, 1961; Knox 1965, and Vasvary 1966). The terms tergal nerve and sternal nerve applied to the segmental abdominal nerves by Albrecht (1953, 1956) are unfortunately misnomers as the tergal nerve contributes to the innervation of the sternal musculature and the sternal nerve innervates a part of the tergal musculature. We have adopted the terminology of Schmitt (1954) using the terms dorsal and ventral nerve.

Pregenital Segments.

The innervation of the eighth abdominal segment of the male in Schistocerca gregaria is typical of the pregenital abdominal segments, with one exception. The ventral nerve of a typical pregenital segment supplies a branch to the ventral external lateral muscle (Fig. 3, 234). This muscle is absent from the eighth abdominal segment.

Orthoptera.

This general pattern of pregenital abdominal innervation is common to the Orthoptera. In Dissosteira carolina (Schmitt 1954) the innervation of the pregenital segments is similar to Schistocerca, the dorsal nerve supplies a branch to the ventral internal lateral muscle and the ventral internal median muscle. The ventral nerve innervates the ventral external lateral muscle, and the second and third external lateral muscles. In Schistocerca the ventral nerve contributes to the innervation of the second internal lateral muscle instead of the second external lateral muscle as in Dissosteira. The dorsal nerve of Aerotylus (Steinmann 1965) innervates the ventral internal lateral muscle and the external ventral muscle. The ventral nerve innervates the external lateral muscle as in Schistocerca and Dissosteira. In some of the pregenital segments Steinmann finds the sternal nerve receiving sensory branches from the preceding and following sterna, a feature not found in other Acrididae.

In the cricket Acheta the dorsal nerve supplies a branch nerve to the transverse ventral muscle, and to the first and second ventral muscles. The ventral nerve innervates the third lateral muscle.

The dorsal nerve of the tettigoniids Neocnecophaeus and Ceuthophilus (Schmitt 1964) sends a branch to the internal sternal muscle and the transverse sternal muscle. The ventral nerve innervates the secondary tergo-sternal group of muscles in addition to several sternal muscles. The ventral nerve also receives a sensory branch from the tergum.

Other Orders.

It is instructive to consider the pattern of pregenital innervation in other orders of the Insecta. In the plecopteran Icteronarcys the dorsal nerve innervates the segmental musculature. The ventral nerve, although it lies in the region of the sterno-pleural muscle is claimed to be sensory in function (Schmitt 1952). Knox (1965) in a detailed study of the pregenital nervous system and musculature of the abdomen of Acroneuria finds the dorsal nerve supplying fibres to the ventral internal median muscle and the ventral internal lateral muscle. The ventral nerve innervates the external lateral muscle as well as the external median muscle. In this case the sensory nerve supplies only ventral integument.

The dorsal nerve does not supply innervation to the ventral musculature in the phasmid Diapheromera (Schmitt 1954). The innervation of these muscles is by the ventral nerve which also innervates the tergo-sternal muscle. This muscle is considered by Schmitt as homologous to the lateral muscles of the Acrididae. In the same paper Schmitt described the innervation of the intersternal muscle of Periplaneta (Dictyoptera) by a branch of the dorsal nerve. The ventral nerve supplies innervation to the tergo-sternal muscle.

The dorsal nerve of the hemipteran Tibicen supplies the entire segmental musculature, the ventral nerve subserving a sensory function only (Vasvary 1966).

Maki (1936) described the innervation of a pregenital segment of the neuropteran Chauliodes. In this species the dorsal nerve

innervates the first, second and third internal ventral muscle and the second external ventral muscle as well as the usual tergal musculature. The ventral nerve supplies the second paratergal muscle, the external intersegmental muscle, the tergo-sternal muscle and the external tergo-sternal muscle. The pregenital innervation of the caterpillar of the north american silkworm moth Hyalophora has been investigated by Libby (1959). He found the dorsal nerve supplied a branch to the ventral internal median muscle, and to the ventral internal median muscles. The ventral nerve innervated the lateral external muscle and the tergo-sternal muscle.

The innervation of the ventral or sternal muscles by a branch of the dorsal nerve, and of the tergal muscles by a branch of the ventral nerve is widespread throughout the Insecta, being found in orders as widely separated as the Plecoptera and the Lepidoptera. The exceptions to the rule are the Phasmida where there is no apparent innervation of the ventral muscles by the dorsal nerve. In this case the ventral nerve arises as a branch of the dorsal nerve and may carry dorsal fibres to the sternal musculature. The absence of tergal muscle innervation by the ventral nerve in the Hemiptera is not surprising considering the degree of fusion between the abdominal ganglia and the metathoracic ganglion resulting in a highly modified arrangement of segmental nerves.

The innervation of sternal muscles by the first major branch of the dorsal nerve is a very conservative feature of the insect abdominal nervous system. This nerve should therefore prove useful as a point

of homology for comparative studies of the innervation of the insect abdomen. It may also prove useful for homologizing the muscles innervated by this particular nerve complex.

The Transverse Nerve Complex.

Innervation of the Heart and Spiracles.

The alary muscles have been described as being innervated directly by the transverse nerve in Chauliodes (Maki 1936) and in Hyalophora (Libby 1959, 1961). In Periplaneta (Alexandrowicz 1926), Carausius (Opoczynska-Sembratowa 1936), and Acroneuria (Knox 1965) the alary muscles are innervated by a branch of the dorsal nerve.

The innervation of the alary muscles has not been reported in Dissosteira, Acheta (Schmitt 1954) and Noconoccephalus (Schmitt 1964). In this latter group the dorsal nerve anastomoses with the lateral nerve of the heart. Opoczynska-Sembratowa (1936) has shown fibres from the dorsal nerve may pass a short distance with the lateral nerve of the heart before extending over the alary muscles as a very fine net. This situation probably applies in those genera for which no alary innervation is reported.

In Icteronyx the alary innervation in the anterior abdominal segments is by the transverse nerve and in the posterior segments by a branch of the dorsal nerve (Schmitt 1963). Basing his views on this evidence and on the fact that in all the above genera, with the exception of Chauliodes, the transverse nerve anastomoses with the dorsal nerve Schmitt (1965) considered that part of the dorsal nerve

which innervates the alary muscles to be derived from fibres of transverse nerve.

In Schistocerca the alary muscles of the pregenital abdominal segments are innervated by a branch of the dorsal nerve. An unusual feature of the ninth dorsal nerve lends support to Schmitt's hypothesis that the branch of the dorsal nerve to the alary muscles is an extension of the transverse nerve. In the ninth segment of the male the transverse nerve of the eighth ganglion anastomoses with the ninth dorsal nerve in the usual manner, the alary muscles of this segment being innervated by a branch of the dorsal nerve. However in the female there is no anastomosis between the eighth transverse nerve and the ninth dorsal nerve. As a result there is no innervation of the alary muscles although they are present.

In the above mentioned genera the transverse nerve innervates the spiracular muscles with the exception of Pteronarcys in which these muscles are lacking. The innervation of spiracular muscles by the transverse nerve has also been reported in Locusta (Ivanova 1956), Periplaneta (Case 1957), and in Schistocerca (Hoyle 1959).

Anastomoses.

Schmitt (1954) used the transverse nerve complex of Dissosteira to establish six points of anastomosis between the median, transverse, dorsal and ventral nerves. He later (1965) showed them to have widespread significance. They are as follows:

- (a) anastomosis of ventral nerve of preceding segment with dorsal nerve of segment under consideration.
- (b) anastomosis of transverse nerve and ventral nerve of same segment.
- (c) origin of transverse nerve branch to spiracular muscles.
- (d) anastomosis of transverse nerve with paramedian nerve.
- (e) anastomosis of branch of dorsal nerve with paramedian nerve.
- (f) junction of transverse nerve with median nerve.

In both the male and female of Schistocerca the relationship between the dorsal, ventral, and transverse nerves of the seventh and eighth abdominal ganglia is typical of the pregenital abdominal segments (Figs. 10, 11). In the eighth - ninth segmental complex of the male anastomosis "c" is missing. The nerve to the spiracular muscles is absent as there is no ninth abdominal spiracle. In the female anastomoses "a", "b" and "c" are missing. In this instance the transverse nerve terminates as a sensory nerve in the ventral region of the tergum. Case (1957) has shown that sensory neurons included in the transverse nerve of Periplaneta terminate in mechanoreceptive hairs near the spiracles. The sensory termination of the eighth transverse nerve in the female Schistocerca may represent the sense organs of a former spiracle.

The ninth transverse nerve is not present in the male, however this nerve is present in the female and anastomoses with the epiproct nerve; the combined dorsal nerve of the tenth and eleventh abdominal

segments. The last pair of transverse nerves in Periplaneta anastomose with the cercal nerves (Case 1957). Steinmann (1965) has described a caudal sympathetic nerve, arising in a similar manner to the ninth transverse nerve of Schistocerca, but terminating in the ovipositor of Acrotylus. Our investigations indicate that anastomosis "a" is between the dorsal nerve and the transverse nerve of the preceding segment and that anastomosis "b" is between the ventral and transverse nerves of the same segment. This point becomes clear when one considers the anastomosis between the ninth transverse nerve and the epiproct nerve (tenth and eleventh dorsal nerve).

Genitalia.

The innervation of the genitalia has been described by Maki (1936) in the female alder fly Chaulioides, in the male silk moth Hyalophora (Libby 1961), in the female blattid Leucophaea (Engelmann 1963) and in the female Acridid Acrotylus (Steinmann 1965).

Female.

In Schistocerca gregaria the external female genitalia and their muscles are innervated by the eighth and ninth abdominal ganglia. The muscles of the ventral valves are innervated by the eighth dorsal and ventral nerves. In addition the ventral nerve receives sensory fibres from the ventral valves and innervates the spermathecal duct. The ninth ventral nerve supplies sensory and motor innervation to the valves and muscles of the dorsal ovipositor. The dorsal nerve innervates

the protractor muscle of the ovipositor. These findings are in agreement with Engelmann (1963).

Steinmann (1965) claims that the abdomen of the Orthoptera consists of nine segments. It is with this misconception that the problem of interpreting his description of the genital innervation of Acrotylus begins. A second major criticism of Steinmann's work is that he uses his own terminology for the musculature without reference to the established usage of Snodgrass (1935a) although he is familiar with this work. There is some reason to doubt the accuracy of his work. The innervation of second internal lateral muscle and the first external lateral muscle as described in Schistocerca is common to the Orthoptera. In Acrotylus this rather apparent nerve is described as innervating adipose tissue, an unheard of situation. Steinmann's work must be treated with reservation. This is unfortunate as this study offers the most detailed description of genital innervation available.

Steinmann refers to the vagina as innervated by the ganglion of the eighth abdominal segment. If however one considers his unusual segmentation of the orthopteran abdomen it can be established that this is the seventh abdominal ganglion. This would agree with our findings in Schistocerca in which the vagina is innervated by a branch of the seventh ventral nerve, and with Engelmann's study of Leucophaea. The innervation of the external female genitalia in Acrotylus can therefore be attributed to the nerves of the eighth

and ninth abdominal ganglia. As Steinmann's muscle terminology cannot be related to previous descriptions the innervation of the genital musculature cannot be compared in detail.

Male.

The male genitalia is innervated by the genital nerve which is derived from the ninth abdominal ganglion of Schistocerca. The genital nerve may be considered as the motor branch of the ninth ventral nerve. The ninth ventral nerve is essentially sensory with only a few small motor branches arising at its origin.

Libby (1961) briefly described the innervation of the male genitalia of Hylephora. A common nerve arises from the terminal ganglion to supply the ninth, tenth and eleventh segments, it is a branch of this nerve which innervates the genitalia. Steinmann gives no details of the innervation of the male genital musculature. It is interesting to note however that he illustrates five nerve trunks emerging from the terminal ganglion in the female Acrotylus and four in the male. In Schistocerca we find four nerve trunks arising from this ganglionic mass in the female and five in the male.

Segmental Origin.

Snodgrass (1937) and Engelmann (1963) have made use of the innervation of the genitalia as an indication of the segmental origin of these structures. It may be worth considering the implications of the genital innervation in Schistocerca in relation to the segmental

origin of the external genitalia.

In an embryological study of the development of Xiphidium, (Conocephalus) Wheeler (1893) described the male genitalia as being derived from a pair of rudiments on the tenth abdominal somite which migrate forward into the ninth abdominal segment as development continues. Else (1934) found that the male genitalia of Melanopus is derived from the fused rudiments of the ninth sternum and tenth sternal appendages. Roonwall's (1937) working on Locusta agreed with Else that the male genitalia represented a fusion of rudiments derived from the ninth and tenth abdominal segments. Quadri (1940) derived the subgenital plate from the ninth abdominal segment and the penis valves from the tenth segment.

Snodgrass (1935b, 1937, 1957) has rather vacillated in his views on the segmental origin of the male genitalia. In the Principles of Insect Morphology (1935b) he defines them as being derived from the ninth abdominal segment. In his 1937 paper he believes that they have developed from the tenth abdominal segment. He cites the innervation of the male genitalia of the Tettrigoniidae, by a nerve which he interprets as tenth segmental in origin, as evidence. This nerve arises from a common trunk comprising the cercal nerve and the nerve of the tenth segment. An arrangement similar to this is found in Schistocerca, however if the sheath of the common trunk is teased away it is evident that this nerve is not tenth segmental in origin but belongs to the ninth abdominal ganglion.

It is possible that had Snodgrass done this in his studies of the Tettigoniidae the same situation would have been seen to prevail. In a revision of the male genitalia (1957) Snodgrass cites the origin of the genital muscles on the ninth abdominal segment as evidence for a possible ninth segmental origin of the male genitalia. As the genital rudiments lie behind the ninth abdominal segment they appear to be tenth segmental. He therefore points out that the genital musculature could have been derived from the intersegmental musculature of the ninth and tenth segments.

As previously stated the innervation of the male genitalia in Schistocerca is by a ventral nerve of the ninth abdominal ganglion. The cercal nerve which is the combined ventral nerve of the tenth and eleventh segments does not contribute to the innervation of the genitalia. On the basis of segmental innervation the male genitalia of Schistocerca would appear to be derived from the ninth abdominal segment.

It is generally accepted that the anterior or ventral ovipositor valves are derived from the eighth abdominal sternum and that the posterior or dorsal valves are derived from the ninth abdominal sternum. The intermediate valves are considered to be a derivative of the dorsal valves. (Elsø 1934, Snodgrass 1935b, Roonwalls 1937, Quadri 1940, Engelmann 1963). Wheeler (1893) found the ventral and dorsal valves to be derived from the eighth and ninth sterna but

considered the intermediate valves to arise from the tenth sternum. In Schistocerca the eighth ventral nerve innervates the ventral valves and the ninth ventral nerve innervates the dorsal and intermediate valves. Thus the origin of these structures is agreement with the findings of the above authors. On the basis of innervation the intermediate valves are derived from the ninth sternum and not from the tenth as suggested by Wheeler.

Post Genital Segments.

The innervation of the post genital segments is similar in both sexes in Schistocerca. The epiproct nerve represents the combined dorsal nerve of the tenth and eleventh segments and the cercal nerve is the combined ventral nerve of these segments. They arise from the ganglion as a common root. This is similar to the situation in Acrotylus (Steinmann 1965) and Chaulioides (Maki 1937). Engelmann (1963) finds in Leucophaea that cercus and paraprocts are innervated by the eleventh abdominal nerve and that the tenth abdominal nerve innervates the roof of the posterior region of the vagina and the tenth tergum. No such innervation of the vagina was found in Schistocerca.

HISTOLOGY

The Seventh Abdominal Ganglion.

General Structure.

The seventh is the least modified of the abdominal ganglia in the male of Schistocerca gregaria (Fig. 10). It is situated within, and innervates the seventh abdominal segment. The ganglion contributes nothing to the innervation of "special structures" such as the internal or external genital apparatus. It should therefore be considered as the simplest ganglion of the ventral nerve cord.

The ganglion lies in the ventral nerve cord and receives at its anterior and posterior faces the large paired ventral connectives, and between them the unpaired median nerves. The seventh ganglion receives three segmental nerves. The dorsal nerve enters the antero-lateral angle; the ventral nerve is received postero-ventrad of it; and the transverse nerves join the postero-dorsal surface. The peripheral innervation is identical to that of the eighth abdominal ganglion of the male (Fig. 3, 10) which has been described previously.

The ganglionic structure is typical of an insect abdominal ganglion. It comprises a dense central region, the neuropile, covered by a cortex of cell bodies or neurocytes. The entire ganglion is surrounded by the nerve sheath comprising an outer non-cellular neural lamella and its underlying perineurium (Smith and Treherne 1963).

Between the neuropile and the perineurium and completely surrounding the neurocytes are the glial cells (Fig. 12). As in Periplaneta these may be divided into outer (c.g.) and central (c.g.) glial cells (Wigglesworth 1960). These cells appear to have no limiting cell membrane apparently forming a syncytium. The outer glial cells have ovate to spherical nuclei and surround the neurocytes. These are most obvious in the dorsal region of the ganglion where they form a sponge-like reticulum. The central glial cells have sub-oval nuclei, invest the neuropile and appear to send processes into the neuropile with the axons.

The Neuropile.

The neuropile consists of the terminal arborizations of neurones, some of whose cell bodies surround it, and of fine projections from the central layer of glial cells. The neuropile is a very dense tissue and neurones can only be traced within it to the point at which they arborize. Interconnections between individual neurones cannot be established using the light microscope.

The neuropile can be divided into three regions (Fig. 13), a pair of dorsal neuropiles (d.n.p.) and a ventral neuropile (v.n.p.). The dorsal neuropiles are separate through part of their length, however in the region of the ganglion between the dorsal and ventral nerves there is a large bridge of neuropile extending between the two sides (Fig. 14). The ventral neuropile lies in the antero-ventral

region of the ganglion and extends posterad to the region of the ventral nerve (Fig. 15, v.np.). Caudad of this point the ventral neuropile becomes reduced and the remainder merges with the dorsal neuropile. Distributed throughout the neuropiles are glomerulac. These are dark staining regions of irregular shape which represent particularly dense concentrations of terminal arborizations.

The two halves of the neuropile are separated by the mid-ventral fissure which extends dorsad in the extreme posterior region of the ganglion, separating the dorsal neuropiles. The fissure extends anterad into the posterior region of the ventral neuropile where it becomes reduced (Fig. 14, v.f.). This fissure and the transverse commissure are all that remain as evidence of the primitive condition in which the two halves of the ganglion were, it is believed, widely separated. One half was associated with each of the ventral connectives and interconnected by the transverse commissures.

Cell Bodies.

Surrounding the neuropile and external to the inner glial layer are the neurocytes of the neurones comprising the ganglion. These cell bodies are several layers thick on the ventral and ventro-lateral surfaces of the ganglion but are sparse on the dorso-lateral and dorsal surfaces. The mid-dorsal region of the neuropile is bare of neurocytes. Anatomically there are two apparent types of cell bodies: large ovate cells (Iipa et al. 1959) in which the cytoplasm/

nucleus ratio is high, approximately 1.5 and globuli cells (Fipa et al. 1959) in which the cytoplasm/nucleus ratio is low, approximately 1.15 and may approach unity in some cases. The majority of the cell bodies are of the small globuli type. The large ovate cells contain osmophillic granules and may be neurosecretory (Figglesworth 1957). Such cells are usually interneurons of the mid-dorsal and mid-ventral regions although there is at least one of this type of neurone associated with each of the peripheral nerves (cf. Dolphin 1965).

Functionally the neurocytes within the ganglion can be divided into motor and internuncial neurones. The motor neurones (Fig. 13, 14) lie in groups surrounding the bases of the peripheral nerves. A few lie in a small group antero-dorsad of the nerve (d.m.) but the majority lie in a large group ventro-posterad of the nerve extending mesad towards the ventral surface of the ganglion (v.m.). The motor neurones of Schistocerca are defined as those neurocytes located within the ganglion that send axons into the peripheral nerves. Collaterals are given off to the neuropile of the same side or to the contralateral side. In some cases collaterals extend to higher centres in the central nervous system (C.N.S.). There is no evidence of motor neurones extending into peripheral nerves of the contralateral side of the ganglion.

The internuncial or association neurones are those neurones whose axons and collaterals remain with the C.N.S. and synapse with

other neurones but never with an effector organ. They are located mainly on the ventral surface of the ganglion in three major clusters, two lateral groups (Fig. 14, 15, l.v.i.) one on either side of the ganglion, and a median group (Fig. 14, 15, 16, m.v.i.). These groups contain numerous large ovate cells. In addition there is a small group (a.v.i.) on the anterior ventral face of the ganglion. There are two lesser groups of dorsal interneurones (Fig. 15, 16). The anterior group lies close to the origin of the ventral connectives (v.c.). The posterior group extends dorsad from between the ventral connectives and is in closely associated with the median ventral group. A few internuncial neurones are found on the lateral margins of the ganglion.

Commissures.

As has been noted the commissures (transverse tracts) unite the lateral halves of the ganglion. In the seventh abdominal ganglion there are seven well defined commissures (Fig. 15). In addition numerous axons cross the ganglion which are not organised into tracts. The dorsal commissure (d.c.) passes across the dorsal surface of the neuropile in the region between the dorsal and ventral nerves. This commissure contains neurones from, the lateral ventral group of internuncials, the postero-dorsal group of internuncials, and interneurones of the dorso-lateral surface between the seventh dorsal and ventral nerves.

There are four median commissures. The anterior dorsal median commissure (a.d.m.c.) crosses the ganglion in the region of the seventh dorsal nerve. This commissure contains fibres from the second longitudinal tract (Fig. 13, lt. 2); sensory neurones from the seventh dorsal nerve, axons from the median nerve and axons from lateral interneurons lying posterad of the seventh dorsal nerve. The posterior dorsal median commissure (p.d.m.c.) is a small tract passing across the ganglion dorsad of the seventh ventral nerve. It contains fibres from the second and fifth longitudinal tracts (Fig. 13, lt. 2, lt. 5), ascending and descending fibres from the ventral nerve cord, axons from the lateral ventral group of interneurons, and axons from lateral internuncial neurones located between the seventh dorsal and ventral nerves. The anterior ventral median commissure (a.v.m.c.) is the largest of the lateral tracts. It lies beneath the anterior dorsal median commissure and extends posterad close to the region of the seventh ventral nerve. This commissure contains fibres from the second and fifth longitudinal tracts as well as axons from a group of lateral interneurons located between the seventh dorsal and ventral nerves. The posterior ventral median commissure (p.v.m.c.) crosses the ganglion posterad of the seventh ventral nerve. It contains numerous fibres of unknown origin in addition to axons from lateral interneurons located dorsad of the seventh ventral nerve, axons of large ovate interneurons of the postero-dorsal group, and axons of neurones in the median ventral group of internuncials.

The first of the ventral commissures, the anterior ventral commissure, crosses the ventral surface of the ventral neuropile immediately anterad of the seventh dorsal nerve. This tract contains the axons of lateral interneurons lying antero-ventrad and postero-ventrad of the seventh dorsal nerve. The second ventral tract is the posterior ventral commissure (p.v.c.) passing across the posterior region of the ventral neuropile immediately anterad of the seventh ventral nerve. This small commissure contains fibres of unknown origin and from the fourth longitudinal tract (Fig. 13, lt. 4).

Longitudinal Tracts.

The seventh abdominal ganglion contains six longitudinal tracts (Figs. 13, 14, 15, 17). These tracts enter from the ventral connective, pass through the ganglion giving off collaterals and receiving neurones and exit via the ventral connective (v.c.). The first longitudinal tract (lt. 1) passes along the median dorsal surface of each dorsal neuropile bends beneath the dorsal commissure and continues into the ventral connectives. This tract contains the three dorsal giant fibres. It receives axons from cell bodies of the antero-dorsal and postero-dorsal interneurone groups. The postero-dorsal neurones give collaterals to the posterior region of the dorsal neuropile. In addition collaterals are given off from this tract to the ipsilateral dorsal neuropile. The second longitudinal tract (lt. 2) lies along the mesial surface of each dorsal neuropile.

Neurons of this tract give off collaterals which pass via the anterior dorsal median tract to the contralateral dorsal neuropile. The third longitudinal tract (lt. 3) passes through the center of each dorsal neuropile. Neurons of this tract send collaterals to the anterior region of the ipsilateral dorsal neuropile. Neurons enter this tract from cell bodies of the postero-lateral margin of the ganglion, close to the entrance of the ventral connectives.

Two longitudinal tracts lie between the dorsal and ventral neuropiles. The largest of these, the fourth longitudinal tract (lt. 4), passes along the median plane of the ganglion joining with its fellow of the opposite side in the mid region. Collaterals from neurons of this tract pass to the ipsilateral dorsal and ventral neuropiles and to the contralateral ventral neuropile via the anterior ventral median commissure. Descending neurons enter the tract from the antero-ventral group of interneurons. Ascending interneurons join the tract from the median ventral group. The fifth longitudinal tract (l.t.5) passes along the dorsal surface of each ventral neuropile lateral of tract four, beneath the anterior ventral median and above the posterior ventral median commissures. Collaterals are given off to the anterior region of the ventral neuropile. Ascending interneurons enter this tract from cell bodies in the lateral ventral group. The median giant fibre is contained within this tract.

The sixth longitudinal tract (lt. 6) passes along the latero-ventral margin of the ventral neuropile. On entering the neuropile the tract bends ventrad and divides (lt. 6, lt. 6a). Both sections of the tract give off fibres to the ipsilateral ventral neuropile and re-unite dorsad of the posterior ventral commissure entering the ventral connective as a single tract.

Neurone pathways.

The following section is an atlas of those neurones traced within the seventh abdominal ganglion of Schistocerca. It should be realized that this is only a partial list of those neurones which constitute the ganglion. Many axons were observed which could not be traced to a cell body or to the point of arborization within the neuropile. One neurone of each tract will be illustrated and for clarity this will be shown on one side of the ganglion only.

The neurones have been illustrated in the parasagittal, sagittal, transverse and frontal sections. It is hoped this will give some indication of the three dimensional relationships within the ganglion. For this reason neurones have been listed as they appear in these figures and not entirely in natural groupings. (e.g. Neurones of the lateral ventral internuncial group are listed under figures 18, 21 and 22 and not as a single group.)

Figure 18 illustrates those neurones which have been located in a parasagittal section of the ganglion extending from the lateral margin of the neuropile to the mesial face of the ventral connectives.

1. An internuncial neurone with its neurocyte lying in the antero-dorsal group at the point of entry of the ventral connective. The axon passes to the terminal ganglionic mass via longitudinal tract one.
2. An internuncial neurone with its neurocyte located in the postero-dorsal group. Its axon passes to the terminal ganglionic mass. The collateral is distributed in the posterior region of the dorsal neuropile.
3. An internuncial neurone, its cell body located in the lateral-ventral group. The axon passes dorsad and crosses to the contralateral side via the dorsal commissure. Collaterals are distributed in the posterior region of the ipsilateral dorsal neuropile.
4. An internuncial neurone, its neurocyte lying in the same group as three. The axon ascends to higher centres in the C.N.S. via longitudinal tract five. A collateral passes to the mid-region of the ipsilateral dorsal neuropile.
5. An internuncial neurone of the same group. The axon passes dorsad crossing contralaterally via the posterior dorsal median commissure. Collaterals are widely distributed in the posterior and mid regions of the dorsal neuropile.

6. A neurone of longitudinal tract six which passes through the ganglion. Collaterals are widely distributed in the ipsilateral ventral neuropile.
7. A descending neurone of longitudinal tract six (a). This neurone terminates in the ventral neuropile.
8. A descending neurone terminating in the ventral neuropile.
9. A descending neurone terminating in the dorsal neuropile dorsal of the anterior dorsal median commissure.
10. An internuncial neurone the neurocyte located in the lateral-ventral group. Its axon passes to the anterior region of the ganglion and divides terminating in the dorsal and ventral neuropiles.
11. An internuncial neurone with its neurocyte lying in the postero-dorsal group. The axon passes beneath the posterior dorsal median commissure, turns dorsal and crosses contralaterally via the dorsal commissure.
12. An internuncial neurone its cell body located in the postero-dorsal group. The axon passes anterad turning beneath the posterior dorsal median commissure and crossing contralaterally via the posterior ventral median commissure.
13. An ascending neurone of longitudinal tract five. The axon becomes distributed in the anterior region of the dorsal neuropile.

14. An internuncial neurone whose neurocyte is situated in the anterior ventral group. The axon passes postero-dorsad joining longitudinal tract five and descending to the terminal ganglionic mass. Collaterals are given off to the anterior region of the ventral neuropile.
15. An internuncial neurone of the anterior ventral group. The axon passes anterad, reflexing upon itself to enter longitudinal tract five and descending to the terminal ganglionic mass.

Neurons 16 to 25 are illustrated in figure 19. This diagram is a composite of vertical sections through the ganglion in the region between the longitudinal connectives.

16. A neurone of the median nerve descending from higher centres in the C.N.S. The axon passes through the dorsal neuropile, turning ventrad and passing posterad of the anterior ventral median commissure to become distributed in the mid-region of the ventral neuropile (Fig. 20).
17. A neurone of the median nerve descending from higher centres. On entering the neuropile the axon passes ventrad, then turns posterad to enter the anterior dorsal median commissure.
18. A neurone of the median nerve with its neurocyte located in the dorsal region of the antero-ventral group of interneurons. The axon enters the median nerve. Collaterals are given off to the mid-region of the dorsal neuropile.

19. A neurone of the median nerve. The neurocyte is located in the antero-ventral group just ventrad of 18. The axon enters the neuropile, passes above the anterior ventral median commissure and enters the same tract as 16 passing along the dorsal region of the neuropile into the median nerve. Collaterals are given off to the anterior region of the dorsal and ventral neuropiles.
20. An internuncial neurone with its cell body in the antero-ventral group. The axon passes into the mid-region of the dorsal neuropile. A collateral is given off to the anterior region of the ventral neuropile.
21. An internuncial neurone with its neurocyte in the median ventral group of interneurones. The axon passes dorsad to enter the posterior ventral median commissure.
22. An internuncial neurone with its neurocyte located in the posterior region of the mid-ventral group. The axon becomes distributed in the posterior region of the dorsal neuropile.
23. An internuncial neurone of longitudinal tract four. The neurocyte lies in the median ventral group adjacent to 22. The axon passes to higher centres. A collateral is given off to the posterior region of the dorsal neuropile.
24. An internuncial neurone with its neurocyte situated in the median ventral group. The axon arborizes in the anterior region of the dorsal neuropile.

25. An internuncial neurone, its cell body located in the extreme posterior region of the median ventral group. The axon passes unbranching to enter the dorsal commissure.
 26. An internuncial neurone with its neurocyte located in the extreme posterior region of the fused dorso-ventral neuropile.
- Neurons 27 to 39 are illustrated in figure 21. This figure is a composite of cross sections from the anterior margin of the neuropile to a point midway between the seventh dorsal and ventral nerves.
27. A sensory neurone, one of a large tract from the seventh dorsal nerve which enters longitudinal tract one and passes to higher centres in the C.N.S.
 28. A motor neurone its neurocyte lying in the dorsal group of motor cells of the seventh dorsal nerve. The axon enters this nerve. No collaterals could be located.
 29. A motor neurone its neurocyte is one from the large ventral group extending mesad of the seventh dorsal nerve. The axon enters the nerve. A collateral is given off to the ipsilateral ventral neuropile.
 30. A sensory neurone, one of a large tract from the seventh dorsal nerve which becomes distributed throughout the ipsilateral dorsal neuropile.
 31. A sensory neurone from a small tract of the seventh dorsal nerve which passes via the anterior dorsal median commissure to the contralateral dorsal neuropile.

32. An internuncial neurone with its neurocyte lying antero-ventrad of the seventh dorsal nerve. The axon passes ventrad giving a collateral to the ipsilateral ventral neuropile and crossing via the anterior ventral commissure to enter longitudinal tract five of the contralateral side.
33. A neurone of longitudinal tract six which passes dorsad to the ipsilateral dorsal neuropile.
34. An internuncial neurone with its neurocyte situated laterally between the seventh dorsal and ventral nerves. The axon arborizes in the ipsilateral dorsal neuropile. A collateral is given to the ipsilateral ventral neuropile.
35. A neurone of the fourth longitudinal tract. This neurone is one of a substantial tract which extends ventrad and divides sending branches into both sides of the ventral neuropile. There is a possibility that this may represent separate neurones to each side.
36. An internuncial neurone with its neurocyte lying posterad of the seventh dorsal nerve. The axon extends via the anterior ventral median commissure to the contralateral dorsal and ventral neuropiles. Collaterals are given off to the ipsilateral ventral neuropile.
37. An internuncial neurone with its cell body lying dorsad of 36. The axon passes via the dorsal commissure to the contralateral dorsal neuropile. Numerous collaterals are given to the ipsilateral dorsal neuropile.

- 38. A neurone of longitudinal tract five which passes to the contralateral ventral neuropile.
- 39. An internuncial neurone with its neurocyte lying in the anterior region of the lateral ventral group. The axon enters longitudinal tract four. Collaterals are given off to the ipsilateral ventral neuropile.

Figure 22 illustrates neurones 40 to 51 observed in series of cross sections in the region of the ganglion extending from a point anterad of the seventh ventral nerve to the posterior margin of the ganglion.

- 40. An internuncial neurone with its neurocyte located antero-dorsad of the seventh ventral nerve. The axon passes via the dorsal commissure to arborize in the contralateral dorsal neuropile.
- 41. A neurone of longitudinal tract two which passes to the contralateral dorsal neuropile via the posterior dorsal median tract.
- 42. A neurone of longitudinal tract five which passes to the contralateral dorsal neuropile via the posterior dorsal median tract.
- 43. An interneurone with its neurocyte situated mesially in the lateral ventral group. The axon arborizes in the ventral region of the ipsilateral ventral neuropile.
- 44. An internuncial neurone, its cell body located in the posterior region of the lateral ventral group. The axon extends into the first longitudinal tract. Collaterals are given off to the

- ipsilateral ventral neuropile and cross via the dorsal commissure to the contralateral dorsal neuropile.
45. An internuncial neurone its neurocyte located immediately antero-dorsad of the seventh ventral nerve. The axon passes via the posterior ventral median commissure to enter the contralateral longitudinal tract one. Collaterals are given off to the ipsilateral ventral neuropile and to the contralateral dorsal neuropile.
46. A motor neurone with its neurocyte in the large ventral group extending mesad from the seventh ventral nerve. The axon enters this nerve and collaterals are given to the ventral neuropile.
47. A sensory neurone from the seventh ventral nerve which passes beneath the ventral neuropile into the ventral fissure where it becomes distributed in the ipsilateral ventral neuropile.
48. A sensory neurone of the seventh ventral nerve which extends into the ipsilateral ventral neuropile.
49. A motor neurone with its cell body lying in the dorsal group of the seventh ventral nerve. The axon enters this nerve. No collaterals could be located.
50. An internuncial neurone with its neurocyte located anterad of the seventh ventral nerve. The axon passes into the ventral fissure where it arborizes in the ipsilateral ventral neuropile. A collateral passes to the ipsilateral dorsal neuropile.

51. An internuncial neurone with its cell body located in the same group as 50. The axon passes through the ipsilateral ventral neuropile and crosses via the posterior ventral commissure to the contralateral side. It could be traced no further. A collateral is given off to the ipsilateral ventral neuropile.
- Neurons 52 to 76 are illustrated in figure 23. This figure is a composite of frontal sections, dorsal to ventral, through the ganglion.
52. A neurone of the anterior median nerve with its neurocyte located in the antero-ventral group. The axon passes into the median nerve. A collateral extends posterad into the dorsal neuropile and bifurcates, sending branches to each side of the ganglion. Each branch divides again, the anterior fibre arborizing in the dorsal neuropile, the posterior fibre passing to the ventral neuropile.
53. An internuncial neurone of longitudinal tract two passing through the ganglion. Anterior and posterior collaterals are given off which pass via the anterior dorsal median commissure and the posterior ventral median commissure to the contralateral dorsal neuropile.
54. A neurone from higher centres in the C.N.S. terminating in the anterior region of the ipsilateral dorsal neuropile.
55. A neurone from higher centres in the C.N.S. passing to the mid-region of ipsilateral dorsal neuropile.
56. A neurone of longitudinal tract one passing through the ganglion. Collaterals are given off to the anterior and mid-regions of the ipsilateral dorsal neuropile.

57. An ascending neurone from the terminal ganglionic mass passing with longitudinal tract one and crossing to the contralateral dorsal neuropile where it is lost.
58. A descending axon from a higher centre in the C.N.S. which crosses to the posterior region of the contralateral dorsal neuropile via the posterior ventral median commissure.
59. An ascending neurone from the terminal ganglionic mass terminating in the posterior region of the dorsal neuropile and sending a collateral via the posterior ventral median tract to the posterior region of the contralateral dorsal neuropile.
60. An internuncial neurone with its neurocyte located anterad of the seventh dorsal nerve. The axon passes via the anterior ventral median commissure to the ventral region of the contralateral dorsal neuropile.
61. A sensory neurone from the seventh dorsal nerve which ascends the ventral connective to higher centres in the C.N.S. A collateral is given off to the ipsilateral dorsal neuropile.
(Fig. 24.)
62. A neurone ascending from the terminal ganglionic mass sending extensive collaterals throughout the posterior region of the ipsilateral fused dorso-ventral neuropile.
63. An internuncial neurone with its neurocyte located between the seventh dorsal and ventral nerves. The axon branches

extensively throughout the anterior region of the ipsilateral dorsal neuropile and sends a collateral to the posterior region of the ipsilateral ventral neuropile. The neurone crosses via the posterior ventral median commissure to the contralateral side. (Fig. 25.)

64. A motor neurone with its cell body located anterad of the seventh ventral nerve. The axon enters this nerve and the collaterals ascends the ventral nerve cord.
65. A sensory neurone from the seventh ventral nerve which passes to higher centres in the C.N.S. in the same tract as 64, (Fig. 26). A collateral is given off to the posterior region of the ventral neuropile.
66. A motor neurone with its neurocyte located immediately posterad of the seventh ventral nerve. The axon enters this nerve. No collateral was located.
67. A sensory neurone from the seventh ventral nerve which becomes distributed in the fused ipsilateral dorso-ventral neuropile.
- 68, 69. A pair of motor neurones with their neurocytes located antero-ventrad of the seventh ventral nerve. The axons enter the seventh ventral nerve. 68 sends a collateral to the mid-region of the ventral neuropile. 69 sends a collateral to the fused dorso-ventral neuropile.

70. An internuncial neurone with its neurocyte located antero-ventrad of the seventh dorsal nerve. The axon passes anterad of the ventral neuropile and crosses via anterior ventral commissure to arborize in the anterior region of the contralateral ventral commissure.
71. An internuncial neurone with its neurocyte in the same group as 70. The axons ascends to higher centres in the C.N.S. A collateral is given off to the anterior region of the ipsilateral ventral neuropile.
72. An internuncial neurone with its neurocyte lying antero-ventrad of the seventh dorsal nerve. The axon passes via the anterior ventral commissure to become widely distributed throughout the anterior and mid-regions of the contralateral ventral neuropile.
73. An internuncial neurone with its cell body located postero-ventrad of the seventh ventral nerve. The axon descends to the terminal ganglionic mass. A collateral is given off to the posterior region of the fused ipsilateral dorso-ventral neuropile.
74. A motor neurone with its neurocyte located on the postero-median face of the ganglion between the ventral connectives. The axon passes anterad and bifurcates sending a branch into each of the seventh transverse nerves. This neurone is one of a pair (Fig. 27).

75. A sensory neurone from the seventh transverse nerve which becomes distributed in the mid-region of the ipsilateral dorsal neuropile.
76. An ascending neurone of the median nerve which passes to the mid-region of the dorsal neuropile where it can no longer be traced.

The Terminal Ganglionic Mass.

General Structure.

The terminal ganglionic mass has been derived from a fusion of abdominal ganglia eight, nine, ten, and eleven. Superficially it is similar in structure to the seventh abdominal ganglion having a dense central neuropile surrounded by the inner layer of glial cells. These are in turn enclosed on the ventral and lateral surfaces by a cortex of neurocytes whose processes contribute to the matrix of the neuropile. The entire ganglionic mass is ensheathed by the neurilemma and beneath this the outer layer of glial cells.

The Neuropile.

The fusion of the four component ganglia is complete, the only evidence of segmentation is to be found in the indentations of the dorsal and ventral surfaces of the neuropile. This results in the structure having a four lobed appearance in section and in the repetitive arrangement of the neurocyte groups (Fig. 28). This fusion

of the posterior ganglion with the eighth abdominal ganglion has resulted in an extremely dense neuropile which presents considerable difficulty when one attempts to trace individual neurones within it.

Irregularly shaped glomerulae are distributed throughout the fused neuropile. They are frequently associated with those terminal arborizations of the segmental nerves in the ventral neuropile.

The division of the neuropile into dorsal and ventral lobes, as in the seventh abdominal ganglion is apparent only in the extreme anterior region of the eighth abdominal ganglion. A shallow ventral fissure runs the length of the fused neuropile.

Cell Bodies.

The cell bodies (neurocytes) whose processes contribute to the neuropile are several layers thick on the ventral and lateral surfaces. They are sparse on the dorso-lateral surface, the mid-dorsal region being bare.

As in the seventh abdominal ganglion there are two anatomical types of neurocytes. The small globular cells comprise the majority of the motor neurones. The large osmophilic ovate cells are found among the neurocytes of the median and lateral ventral internuncial groups, and those few cells of the dorsal surface. One of these large ovate cells is included among the motor neurones of each of the segmental nerves.

The neurocytes can be divided on a functional basis into motor and internuncial neurones which lie in discrete groups. The motor

neurones are located in dorsal and ventral groups close to the bases of the segmental nerves. A small group of motor neurones lies antero-dorsad of the base of the eighth dorsal nerve (Fig. 29, d.m.), a larger group extends ventro-mesad beneath the neuropile (v.m.). In the case of the eighth ventral nerve (Fig. 30) the dorsal groups of motor neurones (d.m.) is the larger, the ventral group (v.m.) being reduced.

The ninth segmental nerves (Fig. 31. 9d.n., 9v.n.) pass anterad along the lateral margin of the neuropile from the posterior region of the ganglion. The motor neurones are located in a large dorsal group (d.m.) and a lesser ventral group (v.m.) which extend for a considerable distance posterad along the lateral surface of the ganglion. There is no division of neurocytes into discrete groups contributing to the dorsal, ventral and genital nerves, although the neurones of the dorsal nerve lie anterad and those of the genital nerve lie posterad within the group.

As the muscles of the tenth and eleventh segments are reduced in number, so are the motor neurones. These neurones lie in a small dorsal group in the posterior region of the ganglion (Fig. 32, d.m.) and to a lesser extent between the fused epiproct/cercal nerve root and the genital nerve.

The arrangement of internuncial neurone groups (Figs. 30, 31) is similar to that found in the seventh abdominal ganglion. Ganglia eight, nine, and ten each have a large median ventral group of

interneurones (m.v.i.) and a pair of lateral ventral interneurone groups (l.v.i.). In the eleventh ganglion the ventral internuncials are reduced to a single median group. The four median ventral groups of interneurones define the posterior limits of the fused segmental ganglia comprising the terminal ganglionic mass (Fig. 28, 32, m.v.i.).

In addition to the ventral groups there is an anterior dorsal and an anterior ventral group of interneurones (Fig. 32, a.d.i., a.v.i.) located at the anterior surface of the eighth neuropile. Anterad and posterad of the eighth dorsal and ventral nerves there are a few lateral internuncial neurones. Similar neurones have not been located in the posterior region of the ganglionic mass. Four large ovate osmophilic cells are located bilaterally on the dorsal surface of the fused neuropiles. Three of these are interneurones the fourth is a motor neurone of the eighth transverse nerve (Fig. 28, 32, d.e.b.).

Commissures (Fig. 32).

Each of the segmental ganglia comprising the terminal ganglionic mass contains four commissures or transverse tracts. In addition the eighth abdominal ganglion has a fifth commissure, the anterior commissure (8a.c.) located in the extreme anterior region of the neuropile. The broad dorsal commissures (d.c.) cross the dorsal surface of each neuropile. There are two lesser median commissures, the dorsal median commissure (d.m.c.) and the ventral median commissure (v.m.c.) passing across the mid-region of each ganglion. The large ventral commissures pass across the ventral surface of the neuropile.

The eighth dorsal commissure (8d.c.) carries nerve fibres from; the anterior dorsal group of interneurons (a.d.i.), the lateral ventral group of interneurons (8l.v.i.) and one of the large dorsal neurons (d.c.b.). The eighth anterior commissure (8.a.c.) receives neurons from the eighth dorsal nerve, the eighth median ventral group of interneurons (8m.v.i.), the anterior ventral internuncial group (a.v.i.) and lateral interneurons lying anterad of the eighth dorsal nerve. The eighth dorsal median commissure (8d.m.c.) is composed of neurons of the eighth dorsal and ventral nerves and the eighth and ninth median ventral interneurone groups (8m.v.i., 9 m.v.i.). The eighth ventral median commissure (8v.m.c.) comprises fibres from the eighth median ventral group of interneurons (8m.v.i.) and lateral interneurons located anterad and posterad of the eighth dorsal nerve. Fibres of the eighth ventral commissure arise from the eighth dorsal and ventral nerves, motor neurons of the eighth ventral nerve, dorsal cell bodies (d.c.b.) and interneurons from higher centres in the C.N.S.

The ninth dorsal commissure (9d.c.) contains the axons of neurons lying in the ninth lateral ventral group of interneurons and numerous other fibres which could not be traced back to their origin. The ninth dorsal median commissure (9d.m.c.) carries neurons from the ninth dorsal and ventral nerves, the ninth median ventral group of internuncials (9m.v.i.), lateral internuncials lying posterad of the eighth ventral nerve and from longitudinal tract three (Fig. 30, l.t.3). The only neurons which could be identified in the ninth ventral median commissure (9v.m.c.) arose from cell bodies of the ninth median

ventral group of internuncials (9m.v.i.). The ninth ventral commissure (9v.c.) contains fibres from the anterior ventral group of interneurons (a.v.i.) and the collaterals of interneurons from higher centres in the C.N.S.

Very few neurones could be identified in the commissures of the tenth neuropile. The tenth dorsal commissure (10d.c.) splits in two in the mid-region of the ganglion and contains axons from cell bodies located in the lateral ventral group of interneurons (10l.v.i.) and from a large ovate dorsal cell (d.c.b.). The dorsal median commissure (10d.m.c.) receives fibres from the median and lateral ventral groups of internuncial neurones (10m.v.i., 10l.v.i.). A crossover of fibres from the fused epiproct/cercal nerve forms the median ventral commissure (10m.v.c.). The tenth ventral commissure (10v.c.) contains neurones from the anterior ventral group of internuncials (a.v.i.) and internuncials from higher centres in the C.N.S.

Neurones contributing to the eleventh dorsal commissure (11d.c.) and median ventral commissure (11m.v.c.) could not be identified. The eleventh dorsal median commissure (11d.m.c.) contains neurones of the eighth median ventral internuncial group (8m.v.i.). The eleventh ventral commissure (11v.c.) comprises fibres of the anterior ventral group of interneurons (a.v.i.) and from higher centres in the C.N.S. In addition numerous unidentified fibres are present in both of these commissures.

Longitudinal Tracts.

The terminal ganglionic mass contains the same six longitudinal tracts that have been identified in the seventh abdominal ganglion. This identification is based on their similar location within the neuropile. They retain this position only in the anterior region of the ganglionic mass (Fig. 29). As they reach the posterior region of the eighth ganglion their positions begin to alter (Fig. 31). The fourth and fifth longitudinal tracts merge and move into the mid-line of the ganglion. The sixth longitudinal tract (l.t. 6) passes to the lateral margin of the ganglion and enters the eighth ventral nerve.

At the level of the tenth ventral internuncial groups (Fig. 32) the fourth longitudinal tract has become extremely diffuse and fills much of the mid-region of the ganglion. Longitudinal tract three (l.t. 3) has merged with the lateral margin of longitudinal tract one (l.t. 1). Longitudinal tracts one and two (l.t. 1, lt. 2) continue into the eleventh ganglion where they become diffuse.

It is of interest to consider the origin of the longitudinal tracts within the terminal ganglionic mass. Longitudinal tract one arises in the extreme posterior region of the eleventh ganglion from fibres which enter it directly from the fused epiproct/cereal nerve and from the ninth dorsal nerve. This tract also receives neurones from the eighth dorsal nerve and interneurones from the lateral ventral groups of the tenth, ninth and eighth ganglia. It has previously been shown that neurones of the seventh dorsal nerve and interneurones

of the seventh lateral ventral group contribute to this tract. Longitudinal tract two also arises in the posterior region of the ganglionic mass. It receives neurones from the median ventral internuncial groups of ganglia ten and eighth and from the lateral ventral internuncial group of ganglion ten.

As has been noted longitudinal tract three arises in the posterior region of the ninth ganglion as a split from longitudinal tract one. This tract receives fibres from the median ventral interneurone group of ganglion nine and the lateral ventral internuncial groups of ganglia nine and eight. Longitudinal tract four is formed from a merging of ascending sensory neurones of the genital and ninth dorsal and ventral nerves.

Neurones of the fused epiproct/cereal nerve have been shown to enter longitudinal tract one; however a small number of fibres from this nerve also enter longitudinal tract five. This tract receives internuncial neurones from the lateral ventral groups of ganglia ten, nine and eight. Longitudinal tract six arises as a substantial group of fibres from the eighth ventral nerve which pass directly up the ventral connectives to higher centres in the C.N.S. It is worth noting that these "straight through" neurones of the eighth ventral nerve, ninth dorsal and ventral nerves, and genital nerve account for substantial regions within the ipsilateral ventral connective .

Neurone Pathways.

The following is an atlas of those neurones traced within the terminal ganglionic mass of Schistocerca. In the figures one neurone of a pathway will be illustrated and for clarity it will be shown on one side of the ganglion only.

Figures 34 and 38 illustrate those neurones located in a series of vertical sections through the eighth abdominal ganglion.

1. A motor neurone of the eighth transverse nerve. The neurocyte is a large ovate eosinophillic cell located near the mid-dorsal surface of the ganglion. No collateral was located. (Fig. 35.)
2. A sensory neurone of the eighth transverse nerve. The neurone passes along the dorsal surface of the ganglion and enters the posterior region of the eighth neuropile. It arborizes in the postero-median region of the ganglion.
3. An internuncial neurone of the anterior dorsal group, the axon passes up the ventral connective.
4. An interneurone of the same group, the axon passes up the ventral nerve cord, the collateral enters the eighth dorsal commissure.
5. An interneurone, its neurocyte is one of the dorsal cell bodies. The axon arborizes in the postero-median region of the eighth ganglion, a collateral enters the eighth dorsal commissure.
6. An internuncial neurone, its cell body lying on the dorsal surface of the ganglion. The axon passes up the ventral connective to higher centres in the C.N.S. A collateral passes to the antero-dorsal region of the eighth neuropile.

7. An interneurone of the anterior ventral group. The axon passes up the ventral nerve cord.
8. An interneurone of the same group as seven. The axon passes to the antero-dorsal region of the eighth neuropile.
9. A neurone of the eighth median ventral internuncial group. The axon passes to the contralateral side via the eighth ventral median commissure, a collateral is given off to the mid-region of the eighth neuropile.
10. An interneurone of the same group. The axon passes to the contralateral side via the eighth dorsal median commissure. The collateral extends into the mid-region of the ninth neuropile.
11. An interneurone of the same group as nine and ten. The axon passes to the antero-ventral and postero-ventral regions of the ninth neuropile.
12. A neurone of the eighth median ventral group of internuncials. The axon passes to the dorsal region of the eighth neuropile. A collateral extends posterad into the ventral region of the tenth neuropile.
13. An interneurone of the same group as twelve. The axon loops forward into the dorsal region of the ganglionic mass and bends posterad extending to the eleventh neuropile where it crosses to the contralateral side via the eleventh dorsal median commissure. The collateral enters the dorsal region of the eighth neuropile.

14. An internuncial neurone from higher centres in the C.N.S.
The axon arborizes in the mid-ventral region of the eighth neuropile.
15. An internuncial neurone from higher centres in the C.N.S.
The axon terminates in the postero-median region of the eighth ganglion.

The neurones of the ninth abdominal ganglion which have been traced in vertical sections are illustrated in figures 36 and 38.

16. An internuncial neurone of the ninth median ventral group.
The axon passes to the mid-region of the tenth neuropile.
A collateral is given off to the ventral region of the tenth neuropile.
17. An interneurone of the same group as sixteen. The axon passes unbranching to higher centres in the C.N.S. via the ventral connectives.
18. An interneurone of the ninth median ventral group. The axon passes through the dorsal regions of the ninth and tenth neuropiles into the ventral region of the tenth neuropile.
Collaterals are given off to the ventral region of the ninth neuropile and the dorsal region of the eighth neuropile.
19. An interneurone of the ninth median ventral group. The axon crosses to the contralateral side via the ninth dorsal median commissure.

20. A descending interneurone from higher centres in the C.N.S.
The axon bends dorsad of the eighth anterior commissure and continues posterad to arborize in the mid-region of the ninth neuropile.
21. An interneurone from higher centres in the C.N.S. which becomes widely distributed in the mid and dorsal regions of the ninth neuropile.
22. An interneurone with its neurocyte located on the dorsal surface of the ganglion. The axon ascends the C.N.S. via the ipsilateral ventral connective. Collaterals are given off to the mid-regions of the ninth and tenth neuropiles.
23. A neurone from a higher centre in the C.N.S. The axon passes to the ninth ventral neuropile. A collateral is given off to the eighth ventral neuropile.

These neurones traced in vertical sections of the tenth and eleventh abdominal ganglia are illustrated in figures 37 and 38.

24. An internuncial neurone of the tenth median ventral group.
The axon passes to higher centres via the ipsilateral ventral connective. Collaterals are given off to the dorsal regions of the eleventh and ninth neuropiles, and to the mid-region of the eighth neuropile.
25. An interneurone of the tenth lateral ventral group. The axon passes via ipsilateral longitudinal tract one to higher centres in the C.N.S. This neurone is one of the three dorsal giant

fibres (Fig. 49), the other two neurocytes lie adjacent to it and their axons follow the same pathway.

26. A neurone from higher centres in the C.N.S. The axon passes via longitudinal tract five to the mid-region of the eleventh neuropile.
27. A neurone from higher centres in the C.N.S. The axon passes via longitudinal tract one to the ventral region of the eleventh neuropile.
28. An internuncial neurone with its cell body located in the tenth median ventral group. The axon arborizes widely in the ventral region of the tenth neuropile.
29. An interneurone with its neurocyte located in the tenth median ventral group. The axon enters the tenth ventral median commissure.
30. An interneurone its neurocyte lying in the eleventh median ventral group. The axon passes anterad and divides in the posterior region of the ninth neuropile.
31. An interneurone of the same group as thirty. The axon arborizes in the posterior region of the eleventh neuropile.
32. An internuncial neurone. The neurocyte is one of the large ovate dorsal cells. The axon enters the tenth dorsal commissure.
33. A motor neurone with its neurocyte located in a dorsal group at the posterior margin of the eleventh ganglion. The axon enters the fused epiproct/cercal nerve.

Figure 39 illustrates those neurones observed in a series of transverse sections of the terminal ganglionic mass extending from the anterior margin to the level of eighth ventral interneurone groups.

34. A sensory neurone one of a small tract from the eighth dorsal nerve which passes to higher centres in the C.N.S. via ipsilateral longitudinal tract one. (Fig. 40.)
35. A sensory neurone of the eighth dorsal nerve which becomes distributed in the dorsal region of the ipsilateral eighth neuropile.
36. A sensory neurone of the eighth dorsal nerve. The axon passes to the ventral region of the contralateral eighth ventral neuropile via the eighth ventral commissure. A collateral passes via the dorsal median commissure to the contralateral eighth dorsal neuropile (Fig. 41).
37. A sensory neurone of the eighth dorsal nerve which passes to the ventral region of the ipsilateral eighth neuropile.
38. A motor neurone, its axon entering the eighth dorsal nerve. The neurocyte lies in the dorsal group of motor neurones. No collateral was located.
39. As 38 but lying in the ventral group of motor neurocytes.
40. A neurone from the eighth transverse nerve which becomes distributed in the dorsal region of the eighth neuropile.
41. A neurone of longitudinal tract one which passes via the eighth dorsal median commissure to the contralateral eighth dorsal

neuropile. A collateral is given to the ipsilateral eighth dorsal neuropile.

42. An internuncial neurone with its neurocyte located laterally, posterior to the eighth dorsal nerve. The axon becomes distributed in the ventral region of the ipsilateral eighth neuropile.
43. An internuncial neurone with its neurocyte located in the same group as 42. The axon arborizes in the ventral region of the ipsilateral eighth neuropile.
44. An internuncial neurone with its cell body located between the eighth dorsal and ventral nerves. The axon crosses to the dorsal and mid-regions of the contralateral eighth neuropile via the eighth ventral median commissure.
45. An interneurone of the eighth lateral ventral group. The axon enters longitudinal tract five, a collateral arborizes in the ventral region of the ipsilateral eighth neuropile.
46. An interneurone, its cell body located in the eighth lateral ventral group. The axon arborizes in the ipsilateral eighth neuropile.
47. An internuncial neurone of the eighth lateral ventral group. The axon passes dorsad to enter longitudinal tract three. Collaterals cross via the eighth dorsal, and median dorsal commissures, to the dorsal and ventral regions of the contralateral eighth neuropile.

48. An internuncial neurone with its neurocyte located in the eighth lateral ventral group. The axon enters ipsilateral longitudinal tract one. The collateral crosses via the eighth dorsal commissure to the contralateral eighth dorsal neuropile.
49. A neurone of longitudinal tract four which passes ventrad and proceeds along the ventral surface of the ipsilateral eighth neuropile to become distributed in the ventral and mid-region of this neuropile.
50. An interneurone of the eighth median ventral group. (Fig. 42.) The axon passes dorsal to enter ipsilateral longitudinal tract two. The collateral passes to the mid-region of the contralateral eighth neuropile.

Figure 43 illustrates those neurones located in a series of transverse sections extending from a region posterior to the eighth ventral interneurone groups to the posterior region of the ninth ventral interneurone groups.

51. One of a large group of sensory neurones from the eighth ventral nerve which form longitudinal tract six and pass up the ipsilateral connective to higher centres within the C.N.S.
52. A sensory neurone from the eighth ventral nerve which passes antero-dorsad through the ipsilateral neuropile to cross via the eighth dorsal median commissure to the dorsal region of the contralateral eighth neuropile.

53. A sensory neurone of the eighth ventral nerve which divides throughout the ipsilateral eighth ventral neuropile.
54. A sensory neurone of the eighth ventral nerve. This axon passes beneath the ventral surface of the neuropile and extends dorsally into the ventral fissure arborizing in the mid-region of the ipsilateral eighth neuropile.
55. A motor neurone of the eighth ventral nerve, the neurocyte located in the ventral group of cell bodies. Collaterals are given off to the ventral region of the ipsilateral eighth neuropile (Fig. 44).
56. A motor neurone of the eighth ventral nerve the neurocyte lying in the dorsal group of cell bodies. A collateral enters the mid-region of the ipsilateral eighth neuropile.
57. A motor neurone of the eighth ventral nerve, the neurocyte located in the same group as 56. The collateral passes via the eighth ventral commissure to the ventral region of the contralateral eighth neuropile.
58. A sensory neurone of the eighth ventral nerve. The axon passes via the eighth ventral commissure to the mid-region of the contralateral eighth neuropile.
59. An internuncial neurone of the ninth lateral ventral group. The axon passes via the ninth dorsal commissure to the dorsal region of the contralateral ninth neuropile. A collateral is

- given off to the dorsal region of the ipsilateral ninth neuropile.
60. An interneurone with its cell body located in the ninth lateral ventral group. The axon passes dorsad to enter ipsilateral longitudinal tract three. The collateral arborizes in the ninth dorsal neuropile of the same side.
61. An internuncial neurone of the ninth lateral ventral group. The axon enters longitudinal tract one, a collateral passes into the dorsal region of the ipsilateral ninth neuropile.
62. An internuncial neurone of the ninth median ventral group. The axon passes dorsad in the ventral fissure, turning laterad above longitudinal tract four to enter contralateral longitudinal tract three.
63. An interneurone of the ninth median ventral group. The axon enters ipsilateral fused longitudinal tract four/five. The collateral crosses via the ventral median commissure to the ventral region of the contralateral ninth neuropile.
64. An internuncial neurone with its neurocyte located on the dorsal surface of the neuropile. The axon passes into the ventral fissure where it divides a branch going to the ventral region of the ipsilateral and contralateral ninth neuropile.
65. An internuncial neurone with its cell body situated on the dorsal-lateral surface of the neuropile.

The axon passes into ipsilateral longitudinal tract four.

66. An internuncial neurone with its cell body in a lateral group dorsad of the eighth ventral nerve. The axon passes to the antero-ventral region of the contralateral ninth neuropile via the ninth ventral commissure. A collateral is passed to the antero-ventral region of the ipsilateral ninth neuropile.
67. An internuncial neurone with its cell body located in a lateral group, dorsad of the eighth ventral nerve. The axon passes via the ninth dorsal median commissure to the anterior mid-region of the contralateral ninth neuropile. A collateral is given off to the ipsilateral ninth neuropile.

Figure 45 illustrates these neurones located in the region extending posterad from the ninth ventral internuncial neurone groups to the posterior margin of the ganglion.

68. A motor neurone of the genital nerve. The cell body is located laterad of the genital nerve in the dorsal group. The axon curves dorsad of the ninth dorsal nerve passing ventrad to enter the genital nerve.
69. A motor neurone with its neurocyte lying laterad of the ninth ventral nerve. The collateral passes dorsad of the genital nerve to enter the ipsilateral ninth neuropile. This neuropile extends posterad as a pair of horns along the antero-lateral margin of the tenth neuropile.

70. A motor neurone of the ninth dorsal nerve with its neurocyte in the dorsal group. The collateral arborizes in the ventral region of the ipsilateral ninth neuropile.
71. A motor neurone of the ninth ventral nerve with its neurocyte in the dorsal group of cell bodies.
72. A motor neurone of the ninth ventral nerve its cell body in the ventral group. The collateral passes to the ipsilateral ninth ventral neuropile. This neurone may be similar to neurone 69.
73. A neurone of the tenth lateral ventral group. The axon enters the fused epiproct/cercal nerve.
74. An internuncial neurone of the tenth lateral ventral group. The axon passes to ipsilateral longitudinal tract two. Collaterals are widely distributed in the ipsilateral tenth neuropile.
75. An interneurone with its neurocyte lying in the tenth median ventral group. The axon enters contralateral longitudinal tract two. Collaterals are widely dispersed in the ipsilateral tenth neuropile.
76. An interneurone with its cell body located in the tenth lateral ventral group. The axon enters ipsilateral longitudinal tract two. A collateral passes via the tenth dorsal commissure to the dorsal region of the contralateral tenth neuropile.

77. An interneurone of the dorsal surface of the tenth neuropile. The axon enters ipsilateral longitudinal tract one. The collateral passes to the contralateral dorsal region of the tenth neuropile.
78. A neurone of the fused epiproct/cerebral nerve, which terminates in the ipsilateral tenth neuropile.
79. A neurone of the fused epiproct/cerebral nerve which crosses via the tenth ventral median commissure to arborize in the contralateral tenth neuropile.

Figure 46 illustrates those neurones observed in frontal sections through terminal ganglionic mass. Neurones previously described will be omitted, with the exception of sensory neurones from the eighth dorsal and ventral nerves.

80. An internuncial neurone with its neurocyte located in the antero-lateral region of the ganglion. The axon passes up the ventral connectives to higher centres in the C.N.S.
81. An interneurone of the eighth median ventral group. The axon divides, passing to the eighth neuropile of the ipsilateral and contralateral sides.
82. An interneurone of the ninth median ventral group. The axon passes anterad and divides arborizing in the ipsilateral and contralateral eighth neuropiles.
83. An internuncial neurone of the antero-lateral margin of the ganglion. The axon passes posterad sending branches to the

anterior and posterior regions of the contralateral eighth neuropile.

84. A sensory neurone from the eighth ventral nerve which arborizes in the ipsilateral ninth neuropile.
85. A sensory neurone from the eighth ventral nerve which passes to the contralateral eighth neuropile. A collateral is given off to the ipsilateral eighth neuropile.
86. A sensory neurone from the genital nerve which arborizes in the posterior region of the ipsilateral ninth neuropile.
87. A motor neurone of the ninth dorsal nerve the neurocyte located on the lateral margin of the neuropile immediately posterad of the eighth ventral nerve. A collateral passes to higher centres in the C.N.S. via longitudinal tract four.
88. A sensory neurone of the genital nerve which passes anterad into the mid-region of the ipsilateral ninth neuropile.
89. A motor neurone of the ninth dorsal nerve with its neurocyte located on the lateral margin of the ganglion posterad of the eighth ventral nerve. The collateral extends into the mid-region of ipsilateral ninth neuropile.
90. A motor neurone of the ninth sternal nerve with the neurocyte in the same group as eighty-nine. The collateral passes to the mid-region of the ipsilateral ninth neuropile. This neurone may be the same as neurone seventyone (Fig. 45).

91. A sensory neurone of the ninth dorsal nerve arborizing in the anterior region of the ipsilateral ninth neuropile.
92. A sensory neurone of the ninth dorsal nerve which crosses into the anterior region of the contralateral ninth neuropile.
93. A sensory neurone of the ninth ventral nerve which crosses to the mid-region of the contralateral ninth neuropile.
94. A sensory neurone of the ninth ventral nerve which passes into the mid-region of the ipsilateral ninth neuropile.
95. A sensory neurone from the ninth dorsal nerve. This is one of a large tract which passes along the lateral margin of the ninth neuropile, turning mesad to join longitudinal tract four and ascend the C.N.S. Numerous collaterals are given off to the ipsilateral ninth neuropile (Fig. 47).
96. A sensory neurone of the ninth ventral nerve. This is one of a large tract which passes with the tract from the ninth dorsal nerve into the ventral connective ascending to higher centres in the C.N.S. Collaterals are given off to the ipsilateral ninth ventral neuropile. (Fig. 47)
97. A sensory neurone of the genital nerve, one of a large tract which passes through the mid-region of the ninth neuropile forming longitudinal tract four and ascending to higher centres in the C.N.S. via the ipsilateral ventral connective. Collaterals are given off to the ipsilateral ninth neuropile (Fig. 47, 48).

98. A sensory neurone of the fused epiproct/cerecal nerve. This neurone is one of a small tract which passes anterad into the mid-region of the tenth neuropile where it becomes incorporated into longitudinal tract five and passes to higher centres in the C.N.S. (Fig. 47.)
99. A sensory neurone of the fused epiproct/cerecal nerve. This neurone is one of a large group which pass in the same tract with neurone nintyeight to the tenth neuropile where they arborize.
100. A motor neurone of the fused epiproct/cerecal nerve. The neurocyte lies in the extreme postero-median region of the ganglion between the roots of the epiproct/cerecal nerves. The collateral arborizes in the ipsilateral eleventh neuropile.
101. An internuncial neurone with its neurocyte located in the eighth lateral ventral group. The axon passed to the contralateral eleventh neuropile. Collaterals are given off to the contralateral ninth and tenth neuropiles.
102. An internuncial neurone, one of a small tract from higher centres in the C.N.S. which terminates in the ventral region of the contralateral eleventh neuropile. Collaterals are given off to the ventral regions of the contralateral eighth, ninth and tenth neuropiles.

103. A sensory neurone of the fused epiproct/cercal nerve. This neurone arborizes immediately it enters the posterior surface of the eleventh neuropile.
104. A sensory neurone of the fused epiproct/cercal nerve which passes to the contralateral tenth neuropile. This neurone may be one of the same group as neurone seventynine (Fig. 45).
105. A motor neurone of the fused epiproct/cercal nerve. The neurocyte lies in a gap between the bases of the genital nerve and the epiproct/cercal nerve. A collateral is given off to the posterior region of the tenth neuropile.

Giant Fibres

Four neurones in each of the ventral connectives may be considered as abdominal giant fibres (Fig. 49). They have diameters ranging from 12.6 to 14.7 microns (table 1). The largest of the subsidiary fibres in the connectives has a diameter of 8.4 microns, the remainder of the neurones having diameters of 5 microns or less.

The giant fibres are situated in two groups within the connective (Fig. 49); a dorsal group containing three fibres (1, 2, 3) and a single median fibre (4). The fibres of the dorsal group arise from neurocytes located in the tenth lateral group of internuncial neurones (Fig. 37, neurone 25). Each of the fibres in this dorsal group springs from a single large ovate neurocyte. The axon passes dorsad into longitudinal tract one and ascends the nervous system, entering

Table 1. Diameter in microns of giant neurones in the abdominal nerve cord of Schistocerca.

<u>Location in Cord</u>	<u>Fibre</u>			
	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>
Within 8th ganglion	9.5	10.0	8.4	8.4
Between ganglia 8/7	12.8	16.6	14.3	13.2
Within 7th ganglion	9.9	11.2	10.3	8.4
Between ganglia 7/6	11.5	14.7	14.7	12.6
Within 6th ganglion	9.5	10.0	10.5	8.0
Between ganglia 6/5	10.5	10.5	12.1	11.0

the fused abdominal-metathoracic ganglionic mass and passing to the level of the metathoracic ganglion. The median giant fibre extends into the terminal ganglionic mass to the level of the ninth abdominal ganglion where it becomes very attenuated and is lost among numerous large axons from neurocytes of the ninth median ventral group. This fibre also extends the length of the abdominal nervous system, passing through the mid-region of each ganglion and apparently arborizing within the metathoracic ganglion.

As the giant fibres pass through the various abdominal ganglia they become reduced in diameter (table 1). This is particularly true within the terminal abdominal ganglion (Fig. 51) and to a lesser extent within the other abdominal ganglia. The neurones pass without interruption through abdominal ganglia 7 to 1, there is no indication

of any segmental septa nor is there any evidence that neurocytes in these abdominal ganglia contribute to the fibre.

The neurones of the dorsal group have been observed to branch in the anterior region of abdominal ganglia 6 and 7 (Fig. 53, 54). The branches appear as numerous very short projections from the ventral surface of the neurone and arborize immediately within the antero-dorsal region of the ipsilateral neuropile. There is also evidence that giant fibre one gives rise to a collateral which crosses via the dorsal commissure to the contralateral side of the neuropile in the seventh ganglion. Branching of the dorsal giants may occur in the eighth ganglion but the branching is not clear and the author is not certain of its existence. Branching has not been observed in the median giant fibre.

Discussion

Structure of a Segmental Ganglion.

The structure of the seventh abdominal ganglion is typical of those abdominal ganglia which have not undergone fusion due to cephalization. For reasons previously enumerated this ganglion may be considered the least modified of the abdominal ganglia. It will be of value to discuss and review the structure of a simple segmental ganglion prior to discussing the effects of cephalization.

Neuropile.

The neuropile is three lobed, comprising a pair of dorsal lobes and a single ventral lobe. The single ventral lobe has undoubtedly arisen from the fusion of paired ventral lobes derived from opposing halves of the ganglion, one associated with each of the paired ventral nerve cords. The only feature now remaining which bears witness to this primitive separation is the ventral fissure. Posteriorly the ventral neuropile is reduced and the remnants merged with the dorsal neuropile.

Within the neuropile are numerous glomerulae associated with the terminations of segmental sensory fibres. These glomerulae are similar to the ventral association centre in the thoracic ganglia of Periplaneta (Pipa et al, 1959). In Schistocerca sensory neurones arborize in the dorsal and ventral regions of the neuropile and glomerulae are found in both regions

Commissures.

Seven commissures or transverse tracts link the opposite halves of each unfused abdominal ganglion in Schistocerca. They carry sensory and internuncial axons and the collaterals from motor neurones. As the central nervous system is a bilateral structure it would appear that these tracts serve to pass information between opposing halves of the ganglion in order to co-ordinate reactions. Mill (1964) has

described six commissures in a typical single abdominal ganglion of the larva of Aeschna. Ten commissures are present in each thoracic ganglion of Periplaneta and Pipa et al (1959) have noted that these are also present in the first abdominal ganglia which in this genus are fused with the metathoracic ganglion. Those commissures which can be homologized between these species from different orders are listed in table 2.

Table 2. A comparison of the commissures of Schistocerca, Periplaneta (Pipa et al 1959) and Aeschna (Mill 1964) based on location within the abdominal ganglion and on neurone content.

<u>Aeschna</u>	<u>Schistocerca</u>	<u>Periplaneta</u>
anterior dorsal transverse tract	dorsal commissure	dorsal commissure 2
posterior dorsal transverse tract	dorsal commissure	dorsal commissure 5
anterior transverse tract	anterior dorsal median commissure	dorsal commissure 1
subdorsal transverse tract	posterior dorsal median commissure	-
-	anterior ventral median commissure	-
ventral transverse tract	posterior ventral median commissure	supra median commissure
-	anterior ventral commissure	commissural loop 1 commissural loop 2
-	posterior ventral commissure	posterior ventral commissure

Fibres of the central transverse tract of Aeschna cannot be correlated with the commissures found in Schistocerca. There are no ventral tracts comparable to those of Schistocerca to be found in Aeschna. The correlation between the transverse tracts of Periplaneta and Schistocerca is good. Dorsal commissures 3 and 4 in Periplaneta cannot be accounted for; it may be however that these together form a commissure equivalent to the anterior ventral median commissure of Schistocerca.

Longitudinal Tracts.

Seven pairs of longitudinal tracts have been described in the thoracic ganglia of Periplaneta (Ripa et al 1959) which retain their position within the first two abdominal ganglia. With the exception of the ventral tract for which there is no counterpart they can be related to those of Schistocerca on the basis of their location within the ganglion as follows:-

<u>Periplaneta</u>	<u>Schistocerca</u>
dorsal tract	longitudinal tract one
dorsal median tract	longitudinal tract two
dorsal intermediate tract	longitudinal tract three
ventral median tract	longitudinal tract four
ventral intermediate tract	longitudinal tract five
ventral lateral tract	longitudinal tract six
ventral tract	-

Little can be said of the exact homologies of these tracts as we have scant data on their neuronal components.

Cell Bodies.

A regular arrangement of neurone groups within subsequent abdominal ganglia has been reported by Fipa et al (1959) and Mill (1964). This repetative arrangement is evident in the various abdominal ganglia of Schistocerca. Neurones contributing to a particular group of tracts lie within a discrete group.

Mill has identified eleven groups of neurocytes within each abdominal ganglion of Aeschna. Seven groups of cell bodies have been described in each simple ganglion of Schistocerca. In addition small numbers of lateral interneurones are located anterad and posterad of the dorsal nerve. A comparison of the neurone groups in the seventh abdominal ganglion of Aeschna and Schistocerca is given in table 3. It is evident that the major neurone groups of Schistocerca can be correlated with those of Aeschna. However Aeschna lacks the dorsal groups of motor neurones and the anterior groups of interneurones found in Schistocerca. Schistocerca in turn lacks the major interneurone groups E and F found in the dragonfly nymph. Mill has described mid-ventral cell groups as paired extending close to the mid line of the ganglion in Aeschna. In Schistocerca these groups have fused, forming a single median ventral group.

Table 3. A comparison of corresponding neurone groups of the seventh abdominal ganglion of Aeschna and Schistocerca based on location.

Neurone group		Type of Neurone	
<u>Aeschna</u>	<u>Schistocerca</u>	<u>Aeschna</u>	<u>Schistocerca</u>
A1	Dorsal motor 7th dorsal nerve	internuncial*	motor
A2	ventral motor 7th dorsal nerve	motor	motor
B	lateral internuncial	internuncial*	internuncial
C	ventral motor 7 ventral nerve lateral ventral internuncial	internuncial* motor	internuncial motor
D	lateral ventral internuncial	internuncial*	internuncial
E	-	internuncial*	-
F	-	internuncial*	-
L	median ventral internuncial	internuncial*	internuncial
M	median ventral internuncial	internuncial*	internuncial
N	posterior dorsal internuncial	internuncial*	internuncial
F	anterior dorsal internuncial	internuncial*	internuncial
-	dorsal motor 7th ventral nerve	-	motor
-	anterior ventral internuncial	-	internuncial

* function attributed to neurones by present author on grounds used for classification of neurones in Schistocerca.

Cephalization.

There is a tendency in the insects for the central nervous system to become condensed in an anterior direction. In the primitive condition a ganglion was situated in each of the body segments which innervated the segment in which it lay. In the terminal ganglionic mass of Schistocerca we have the opportunity to consider the effects of cephalization on the individual segmental ganglia.

It will be recalled that this ganglionic mass innervates abdominal segments eight, nine, ten and eleven. The structure is located within the eighth abdominal segment, the more posterior ganglia have migrated forward to fuse with the eighth ganglion.

As a reference point for the discussion we will use the structure of the seventh abdominal ganglion which, it will be recalled is considered the least modified of the abdominal ganglia in Schistocerca. The effects of cephalization on the neuropile, commissures and neurone groups will be considered.

Neuropile.

The three lobed condition of the neuropile found in the seventh abdominal ganglion is evident only in the anterior region of the eighth ganglion. At the level of the eighth ventral nerve the neuropile has become a simple fused structure, the division into paired dorsal and single ventral lobes having completely disappeared. The fused condition prevails in the neuropiles of the ninth, tenth and eleventh

ganglia. The ventral fissure extends the full length of the fused neuropiles but is reduced in depth.

The segmental divisions of the fused neuropile are attested to only by the dorsal and ventral notches at the posterior margins of the first three of the component units. A similar condition prevails in the thoracic and suboesophageal neuromeres of Ferris (Guthrie 1961) in this instance however the condensation of the abdominal ganglia has progressed to the point that individual neuromeres appear indivisible. Power (1948) shows no external division of neuromeres within the fused thoracico-abdominal ganglionic mass of Drosophila and divides the neuromeres on the basis of vertical fibre tracts.

There has been a considerable reduction in size of each segmental neuropile comprising the terminal ganglionic mass of Schistocerca. The ninth neuropile is the largest of these units as it extends for some distance posterad along the lateral margins of the tenth neuropile. The tenth and eleventh neuropiles are reduced the eleventh being the smaller. This increase in size may be related to the fact that the ninth ganglion innervates the male genital apparatus. The subsequent reduction of the tenth and eleventh neuropiles may have been affected by the reduced number of muscles and by the reduced size of these abdominal segments.

Commissures.

A considerable reduction in the number of commissures takes place as condensation progresses. As previously noted there are seven

commissures in the seventh abdominal ganglion. The eighth abdominal ganglion represents the least modified of the ganglia within the terminal ganglionic mass. In this ganglion the number of commissures is reduced to five and in subsequent ganglia the number is reduced to four although in the tenth ganglion the dorsal commissure has become divided into two.

This tendency toward the reduction of transverse tracts with ganglionic condensation has been noted in Gerris. Guthrie mentions "several commissures", associated with each thoracic ganglion but only two in each of the more condensed abdominal ganglia. In the fruit fly Drosophila, Power makes no mention of commissures in the extreme condensed abdominal center although these are present in the more diffuse thoracic ganglia.

Cell Bodies.

The retention of a regular array of neurocyte groups is a conservative feature of the nervous system under the stress of condensation in Schistocerca. Power (1948) refers to the regular organization of the abdominal centre of Drosophila noting that the vertical fibre groups are useful references to define the limits of the neuromeres. Guthrie (1961) however, has reported that the organization of individual elements in the abdominal centres is less regular than in the more diffuse higher centres of Gerris. Mill (1964) has observed an increase in the number of neurocyte groups in Aeschna

but does not relate this to the segmental nature of the ganglionic mass.

In the case of Drosophila and Gerris in which a high degree of fusion has taken place among the abdominal ganglia the dorsal surface of the neuropile is covered with neurocytes, many of them being motor neurones. However Mill shows no apparent increase in the area of dorsal neurocytes in the eighth ganglion of Aeschna.

In Schistocerca the regular arrangement of median and lateral ventral interneurone groups within the terminal ganglionic mass is evident. This regular arrangement breaks down only in the eleventh abdominal ganglion which is greatly reduced. In this case the lateral and median ventral interneurone groups have merged into a single unit. The repetitive arrangement of the ventral interneurone groups within the terminal ganglionic mass of Schistocerca allows these neurones to be used to define the posterior limits of the component segmental ganglia. On this basis it can be established that the terminal ganglionic mass has been derived from the fusion of four abdominal ganglia.

Within abdominal ganglia subsequent to the eighth, the anterior dorsal interneurone group may be represented in reduced form as dorsal cell bodies and there is evidence that the antero-ventral group of interneurones may have become incorporated within the median ventral internuncial group.

Accompanying the condensation of the ganglia is a tendency for the ventral groups of motor neurones to become reduced and for the dorsal group to extend onto the dorsal surface of the neuropile. This tendency is apparent in the ninth ganglion of Schistocerca and in the case of the eleventh abdominal ganglion motor neurones are located on the mid-dorsal surface of the neuropile. The motor neurones of the abdominal ganglia of Gerris are located on the dorsal surface of the neuropile.

Neurone Pathways.

It would be a laborious task for the reader, as for the writer if one were to compare in detail the individual neurone pathways of Schistocerca with those described in other genera. The discussion will therefore be limited to the salient points.

Sensory neurones have been reported as passing directly through the ganglion of the segment of origin to higher centres within the C.N.S. in Corydalis (Hilton, 1911) and Aeschna (Zawarzin, 1924; Mill, 1964). Guthrie (1961) found only a few sensory fibres passing to higher centres in Gerris. Contrary to the above Fyle (1941) has not found such fibres in the thoracic ganglia of Ephestia and Hess (1958) using neurone degeneration techniques was unable to find sensory fibres from the cercus of Foriplaneta passing uninterrupted through the last ganglion.

In Schistocerca sensory fibres from the dorsal and ventral segmental nerves of abdominal ganglia six, through eleven have been observed to send neurones via the ipsilateral ventral connective to higher centres in the C.N.S. It has not been established how far these fibres pass within the C.N.S. however those fibres originating in the ninth, tenth and eleventh segmental nerves pass completely through the terminal ganglionic mass. It may be that these fibres ascend at least to the level of the metathoracic ganglion. Sensory fibres of the above type from the seventh dorsal nerve have been observed to give off collaterals to the ipsilateral dorsal neuropile.

Contrary to the views of Guthrie (1961) numerous sensory neurones arborize in the dorsal neuropile although the majority of them enter a glomerular region in the ventral neuropile. Sensory fibres cross to the contralateral side of the ganglion although they have not been seen to enter the contralateral ventral connective.

Motor neurones entering the segmental nerves of the contralateral side have been observed in Corydalis (Hilton, 1911), Aeschna (Zawarzin, 1924b; Mill, 1964) and Gerris (Guthrie, 1961). These neurones enter the ipsilateral segmental nerves only in Ephestia (Fyle, 1941).

The current study on Schistocerca indicates that motor neurones enter segmental nerves of the ipsilateral side only. Large collaterals from some of these have been observed to pass via the ventral commissure to the contralateral side but these fibres have not been observed to enter segmental nerves. The majority of the motor collaterals arborize in the ventral neuropile of the ipsilateral side. It is the

ventral neuropile in which many of the sensory neurones arborize; this leads one to speculate that such an alliance may give rise to numerous segmental reflex arcs.

A summary of the internuncial neurones of Schistocerca may prove of value. Interneurones of the median and lateral ventral groups contribute fibres to the longitudinal tracts. Those of the median ventral group send axons into longitudinal tracts of the contralateral side and give off collaterals to the ipsilateral neuropile of the same ganglion. Interneurones of the lateral ventral group send axons into longitudinal tracts of the ipsilateral side and give off collaterals which arborize in the contralateral neuropile of the same ganglion. The lateral interneurones appear to function as local association neurones within the ganglion of origin.

It is of interest to attempt a correlation of the neurosecretory cell types described by Delphin (1965) in the ventral ganglia of Schistocerca with the neurone cell groups described in this thesis (table 4). The distribution of neurosecretory cells in the seventh abdominal ganglion correlates well with the neurone groups of the seventh abdominal ganglion. Unfortunately the compound nature of the terminal ganglionic mass is not evident in the distribution of the neurosecretory cells. Delphin carried out a number of ligation experiments which indicated that the neurosecretory product is passed

anterad and posterad within the ventral connectives and peripherally within the segmental nerves.

Table 4. Correlation of neurosecretory cells with major neurone groups in the 7th abdominal ganglion and terminal ganglionic mass of Schistocerca.

<u>7th Ganglion</u>		<u>Terminal Ganglionic Mass</u>	
<u>Neurone Group</u>	<u>Cell types</u>	<u>Neurone Group</u>	<u>Cell types</u>
a.d.i.	B ₂	a.d.i.	B ₂ , C
d.m. 7d.m.	C	a.v.i.	C
		d.m. 8d.n.	C
v.m. 7d.n.	C	v.m. 8d.n.	D
d.m. 7v.n.	C	d.m. 8v.n.	C
v.m. 7v.n.	C (D?)	v.m. 8v.n.	C, D
l.v.i.	A ₁ , A ₂ , B ₂ , C	d.c.b.	D
m.v.i.	B ₂ , D	9 ganglion motor neurones	C, D
p.d.i.	B ₂ , C, D	9 l.v.i.	C
		9 m.v.i.	B ₂ , D
		11 m.v.i.	B ₂ , D

A few generalizations can be drawn concerning the cells of origin of the neurosecretory product in these nerves and connectives. The seventh dorsal nerve carries the product from C cells, the seventh ventral nerve carries secretions from C and possibly D. cells.

The eighth dorsal and ventral nerves and the nerves of the ninth ganglion carry the secretions of both C. and D. cells. Neurohaemal organs have been described on the transverse nerves of Schistocerca (Brady and Maddrell, 1967); in the eighth abdominal ganglion this nerve arises from paired neurocytes of the dorsal cell bodies. The product released at this site would be derived from D. cells of this group. It must be pointed out that the above is based on a comparison with published material, to confirm these conclusions and to extend them further would require a comparison of identical sets of serial sections, one set stained for neurosecretory material the other to show the neurone tracts.

Median Nerve.

Zawarzin (1924a) has carried out a detailed study of the median-transverse nerve pathways in a thoracic and an abdominal ganglion of Aeschna. In the thoracic ganglion the median nerve arises from a pair of globular cells in the posterior region between the ventral connectives. In addition this nerve contains two sensory neurones which arborize in the dorsal region of the neuropile. The median nerves of the abdominal ganglia arise from a pair of similar cells. The motor axons pass posterad and divide one entering each ventral connective. They pass via the connective to the next lower ganglion, bend anterad entering the median nerve. Osborne (1964) has shown

the unpaired ventral nerve of Phormia to contain four neurones and Hoyle (1959) has established the presence of a fast and a slow axon in the thoracic median nerves of Schistocerca.

The transverse nerves of the seventh abdominal ganglion of Schistocerca arise from a pair of large ovate neurones placed similarly to those in the thoracic ganglia of Aeschna. Each of these neurones divides sending a branch to each of the paired transverse nerves. An unknown number of sensory neurones arborize in the postero-dorsal neuropile. In the terminal ganglionic mass of the male the transverse nerve arises from a pair of large ovate cells on the dorsal surface at the posterior margin of the eighth abdominal ganglion. In addition several neurones are located between the anterior ventral commissures in the simple ganglia which send axons anterad via the median nerve. Descending fibres from this nerve arborize in the mid-region of the ganglion. The median transverse nerve system in Schistocerca appears somewhat more complex than in Aeschna. The function of the median nerve remains a mystery, one might speculate that it is involved in the co-ordination of the spiracles in adjacent segments. Such an analysis would make an interesting electrophysiological investigation.

Giant Fibres.

Abdominal giant fibres have been described in Periplaneta (Roeder, 1948), Locusta (Cook, 1951), Inax (Hughes, 1953) and Aeschna (Mill, 1964). These fibres synapse caudally with afferent

neurones from the cerci and pass without interruption into the metathoracic ganglion. The giant fibres of Anax and Aeschna synapse in each of the abdominal ganglia. Pipe et al (1959) report certain giant fibres of the ventral group in Periplaneta pass uninterrupted through the thoracic ganglia and may ascend to the brain.

There are six fibres of giant proportions arranged in two groups in the ventral connectives of Periplaneta. These range in diameter from 20 to 45 microns. In Locusta the giants are considerably smaller, there being four neurones with a diameter of 8.9 to 15.2 microns. Two abdominal giant fibres have been described in the ventral connectives of Anax and Aeschna. In Anax they have diameters ranging between 12 and 16 microns and in Aeschna the diameters are from 13 to 15 microns.

The configuration of giant fibres in Schistocerca is reminiscent of the situation in Locusta. There are four fibres with diameters ranging from 12.6 to 14.7 microns. As in Locusta they are arranged in a dorsal group of three fibres and a single median fibre. These fibres extend from the terminal ganglionic mass into the metathoracic ganglia. As they pass through the various abdominal ganglia they become reduced in size as do those of Periplaneta and Locusta. Hess (1958) has pointed out that not only do the fibre diameters become reduced but the fibre sheath similarly becomes thinner within a ganglion.

Roeder has traced the giant fibres of Periplaneta into the posterior region of the sixth abdominal ganglion where they each appear to become associated with groups of neurocytes. He therefore considers these fibres to be multicellular in origin. In Locusta Cook has traced the median fibre to a single neurocyte in the extreme posterior region of the ganglion. Schistocerca offers no evidence to support Roeder's hypothesis that giant fibres represent a syncytium. In this case each of the dorsal group of giant fibres arises from a single neurocyte located in the tenth lateral ventral group of interneurons. The median fibre has been traced to the region of the ninth ventral internuncial groups but has not been followed to its neurocyte.

Giant fibres of the dorsal group have been shown to branch in abdominal ganglia 6, 7 and 8 of Schistocerca. Branching probably occurs also in abdominal ganglia 1 through 5 although this has not been investigated. No branching has been observed in ganglia nine and ten. It has not been possible therefore to establish the synaptic region between these fibres and the cercal afferents. However the dorsal group of giants and the cercal afferents lie side by side in longitudinal tract one and synapses between these neurones of the type described by Young (1939) between second and third order giant neurones of the squid may possibly exist. It is further possible that as the giant fibres become very attenuated at this level in the ganglion the branching has been overlooked.

ELECTROPHYSIOLOGY

Giant Fibres.

It has been shown in Periplaneta (Tumphy and Rawdon-Smith, 1937; Roeder, 1948), Locusta (Cook 1951, 1952; Fielden, 1960), Anax (Fielden, 1960) and Aeschna (Mill, 1963) that stimulation of cercal afferent neurones results in high amplitude and velocity action potentials in neurones of the ventral connective. These neurones are considered to be the giant fibres. The foregoing histological investigations have shown giant fibres to be present in the abdominal connectives of Schistocerca.

Behavioural responses to cercal stimulation have been described in Periplaneta (Roeder, 1948) and in Anax (Hughes, 1953). In the case of Periplaneta the animal runs quickly forward. Cook (1951) does not find this response in Locusta which appears unmoved upon cercal stimulation. A preliminary series of experiments were carried out on Schistocerca to determine if an evasion response could be initiated. Schistocerca in which the compound eyes had been occluded with black paint refused to move when a puff of air from a fine jet was directed at the cerci. Similar results were obtained using decapitated Schistocerca. In control of the ... the slightest movement of the experimenter caused a jump. However if the air jet could be brought unobtrusively within range of the

cercus a puff of air had no apparent effect. It would appear that evasion responses are closely linked to the visual system in Schistocerca.

In view of the anomaly between this behavioural pattern and the presence of giant fibres it was considered of interest to carry out an electrophysiological study of the giant fibre system in this locust.

Stimulation of Cerci.

Isolated abdomens of Schistocerca were used from which the gut and internal genital origins had been removed. When recording electrodes are placed on the cercal nerve and on the ipsilateral ventral connective between the terminal ganglionic mass and the seventh abdominal ganglion and a puff of air is directed at the cercus large amplitude spikes are recorded from the ventral connectives (Fig. 55,a). This response corresponds to the burst of afferent activity in the cercal nerve. In addition to the complex of large spikes there is an increase in the numbers of medium amplitude spikes. The response is recorded approximately 15 to 20 milliseconds after the onset of a natural stimulus.

A similar response is observed when one of the recording electrodes is placed on the contralateral connective at the same level. If one compares the response in the ipsilateral and contralateral connectives (Fig. 55b) it will be observed that the contralateral response is of shorter duration and has fewer fibres responding (on the basis of amplitude). The response in the

contralateral connective appears to be rather labile, not being of a consistent duration relative to the response in the ipsilateral connective. A delay occurs between the onset of the response in the contralateral connective relative to the ipsilateral connective.

Speed of Conduction.

The speed of conduction of these large action potentials has been measured for the ipsilateral and contralateral connectives between the terminal ganglionic mass and the seventh abdominal ganglion. With both recording electrodes placed on the ipsilateral connective approximately one millimeter apart a complex of three or four large spikes is recorded (Fig. 56a). These spikes have velocities ranging from 3.3 to 1.5 meters per second. If measurements are made between each spike of a given complex and the same spike in a complex recorded from a second point further up the connective three different conduction speeds are obtained (table 5). It will be noted that when four spikes are present in a volley that one pair have the same conduction velocity and may well represent repetitive firing of the same neurone.

Although there is a considerable disparity in the velocities of these potentials the variation in any one volley is not great. The overall disparity may be due to raising of the connectives out of the haemolymph and/or saline in order to reduce shunting and to reduce the stimulus artifact. This would

have an adverse effect on the rate of conduction (Hodgson, 1939, cited in Bullock and Horridge, 1965). It was necessary to dry the preparation in the region of the electrodes, particularly the stimulating electrodes or the stimulus artifact completely obscured the volley of potentials.

Table 5. Conduction speeds in meters per second of individual potentials from complex volleys recorded from the ventral connectives on stimulation of the cercal nerve in three different preparations.

<u>Preparation</u>	<u>Ipsilateral connective</u>				<u>Contralateral connective</u>	
	<u>spike in volley</u>				<u>spike in volley</u>	
	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>1</u>	<u>2</u>
a	3.3	3.0	2.3	-	3.0	2.4
b	1.8	2.3	1.8	1.5	4.5	-
c	1.9	2.1	-	-	3.0	-

If the electrodes are now moved to the contralateral connective at the same level and the cercal nerve is stimulated no more than two spikes are recorded (Fig. 56b). They have velocities of 4.5 to 2.4 meters per second.

Electrical stimulation of the epiproct nerve did not result in giant potentials in the ventral nerve cord. The nerve to the paraproct in Schistocerca is too short to be picked up with

stimulating electrodes of the type used. However mechanical stimulation did not result in giant potentials in the connectives.

Roeder (1948) reported a decrease in the velocity of conduction across a ganglion and related this to the reduction in the diameter of the giant fibres as they pass through the ganglion. In the histological studies similar though smaller reduction has been found in the diameter of the giant fibres of Schistocerca as they pass through the seventh abdominal ganglion. If the stimulating electrodes remain on the cercal nerve and recording electrodes are placed on the ipsilateral connective above and below the seventh abdominal ganglion the potentials recorded by the anterior electrode show a substantial shift to the right (Fig. 56c) indicating a decrease in conduction velocity. Three potentials are recorded with velocities of 1.1, 1.2 and .71 meters per second.

Synaptic Delays.

Delay times have been measured for the cercal afferent giant fibre synapse of Periplaneta (Roeder, 1948) Locusta (Fielden, 1960) Anax (Fielden, 1960) and Aeschna (Mill, 1963). As there is a disparity in the velocity of conduction in the ipsilateral and contralateral connectives in Schistocerca it was considered of interest to measure the synaptic delay for both sides of the cord. To measure this feature the stimulating electrodes remain distal on the cercal nerve, recording electrodes are placed at the base of

of the cercal nerve and anterod of the terminal ganglionic mass on the ipsilateral connective (Fig. 56d). Delays measured in this manner range from 2.4 to 3.3 milliseconds. To measure the delay due to the contralateral synapse the anterior electrode was moved to the same level on the contralateral connective (Fig. 56e). Delays at this synapse ranged from 3.5 to 4.3 milliseconds.

In both the above preparations a smooth build up in the amplitude of the pre-synaptic cercal response took place with increased intensity of stimulation prior to a post-synaptic response in the ventral connective. An increase in stimulation frequency at subliminal intensities immediately below threshold level for a post-synaptic response did not result in action potentials in the post-synaptic fibres. No measurements were made on the stability of the synapses under conditions of high frequency stimulation at supra threshold levels. It was observed however that at high frequencies the number of spikes in a complex became fewer as the frequency was increased. Very high frequency stimulation resulted in the disappearance of all giant potentials from both connectives.

Stimulation of the Ninth Sternum.

The ninth sternum of the male Schistocerca has several rows of large hairs along its dorso-lateral margin. These hairs are similar to those found on the cercus and are of the type A or B described by Thomas (1965). This region is innervated by the lateral

branch of the ninth ventral nerve. Mechanical stimulation of these receptors using a single hair resulted in bursts of high amplitude potentials in both the ipsilateral and contralateral ventral connectives (Fig. 57a, b). Stimulation of the dorsal ovipositor valve of the female in a like manner gave similar results (Fig. 57c,d). These potentials are of similar amplitude to those recorded from the connectives while stimulating the cercus and led to a suspicion that sensory neurones of the ninth sternum might also synapse with the abdominal giant fibres. Stimulation of the eighth sternum in the same way resulted in low amplitude volleys in the ventral connectives (Fig. 57e) and ruled out the possibility that afferent neurones of this segment also synapsed with the giant fibres. This was confirmed using electrical stimulation.

Speed of Conduction.

Experiments similar to those using the cercal nerve preparation have been carried out on the ninth ventral nerve to determine the conduction speeds in the post-synaptic interneurones of the ventral cord. It was anticipated that this could give evidence concerning the identity of these neurones and confirm the possibility that they are the same interneurones as those synapsing with the cercal afferents.

In the following experiments stimulating electrodes were placed distally on the lateral branch of the ninth ventral nerve

With both recording electrodes placed on the ipsilateral ventral connective a spike complex as illustrated in figure 58, (a) is obtained. Conduction speeds for giant potentials in the ipsilateral connective range between 1.9 and 1.5 meters per second. If the electrodes are transferred to the contralateral connective a complex of spikes is obtained as in figure 58 (b). In this case the conduction velocities are between 3.8 and 3.0 meters per second. The velocities of individual spikes within these complex volleys is given in table 6. It is apparent that there are three spike velocities on the ipsilateral side and two on the contralateral side, those on the contralateral side having the higher velocities. As in the spike complex obtained on stimulation of the cercal nerve there is a tendency for repetitive discharge in one of the ipsilateral post-synaptic fibres.

Table 6. Conduction speeds in meters per second of individual potentials from complex volleys recorded from the ventral connectives on stimulation of the ninth ventral nerve . . . in three preparations.

<u>Preparation</u>	<u>Ipsilateral connective</u>				<u>Contralateral connective</u>	
	<u>spike in volley</u>				<u>spike in volley</u>	
	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>1</u>	<u>2</u>
a	1.9	1.6	1.5	-	3.0	-
b	1.6	1.2	-	-	3.8	3.3
c	1.5	1.6	1.8	1.5	3.8	3.3

Synaptic Delays.

Synaptic delays have been measured between the ninth ventral afferent neurones and post-synaptic interneurones of the ventral nerve cord. With recording electrodes placed on the 9th ventral nerve and on the ipsilateral ventral connective (Fig. 58c) delays between 2.0 and 2.1 milliseconds have been recorded. If the anterior recording electrode is placed on the contralateral connective (Fig. 58d) the range of delays is from 4.6 to 5.2 milliseconds.

Like the cercal nerve preparation, increase in the amplitude of the compound action potential occurred in the pre-synaptic ninth ventral nerve as the stimulating voltage was increased. Increased frequency of stimulation at intensities immediately below those required to bring about a post-synaptic response in the ventral connectives failed to give such a response. Repetitive stimulation had no effect on the synaptic delay.

Electrical stimulation of the ninth dorsal nerve and of the median branch of the ninth ventral nerve did not result in a "giant" response in the ventral connectives. However in one experiment during which the genital nerve was stimulated electrically a response of giant magnitude was obtained from the combined ventral connectives (Fig. 58e). Conduction speeds measured from this preparation varied from 3.3 to 2.0 meters per second.

Connections Within the Metathoracic Ganglion.

Though giant potentials are recorded from the ventral nerve cord as a result of cercal stimulation Schistocerca does not respond as do Periplaneta and Anax with an evasion response. It was thus pertinent to investigate the synaptic connections between the abdominal giant fibres and subsequent neurones at the level of the metathoracic ganglion. A large nerve innervates the metathoracic leg of the desert locust. Electrodes were placed on the ventral nerve cord below the metathoracic ganglion and on the leg nerve and puffs of air were directed at the cerci. Bursts of potentials corresponding to these puffs were recorded from the ventral nerve cord (Fig. 59a) but no response could be obtained from the leg nerve. The potentials recorded from the leg nerve commencing 1.3 seconds after the onset of the interneuronal volleys were part of a rhythmic activity in the nerve and not related to the cercal stimulation. Cercal stimulation in no way affected this rhythm which built up to a peak over a period of 3.3 seconds and declined. Electrical stimulation of the cercal nerve did not result in activity being recorded from the leg nerve (Fig. 59c).

A complex of small to medium amplitude potentials have been recorded from the connectives between the metathoracic and mesothoracic ganglia as a result of cercal stimulation (Fig. 60). The only potentials recorded at this level have been from the

ipsilateral connectives. There is no apparent activity in the contralateral thoracic connective. A short delay of 1.5 milliseconds occurs between the arrival of the volley in the abdominal connective and the response in the thoracic nerve cord. No spikes of giant amplitude have been recorded from the thoracic connectives in response to cercal stimulation.

Discussion.

Speed of Conduction.

It has been shown (e.g. Nichol and Witteridge, 1955; Bullock and Horridge, 1965) that the speed of transmission in neurones varies directly as the diameter of the axon. Roeder (1948) established the number of active interneurones in the cercal nerve-giant fibre response of Terrestrialis on the basis of spike height. However the base line drift tends to obscure the small amplitude differences which would be expected in Schistocerca where the giant fibres have small differences in diameter. Furthermore the data of Fielden (1963) indicates rapid repetitive firing of an interneurone may possibly result in an apparent small variation in amplitudes from a single fibre. The speed of conduction is therefore considered a better basis on which to determine the number of neurones contributing to a complex volley. The data presented for Schistocerca indicates that there are three neurones active in the ipsilateral

connective and two in the contralateral connective. As these are the largest amplitude, highest velocity potentials to be obtained from the ventral nerve cord they represent action potentials from the giant fibres. It has been pointed out that repetitive firing is a feature of interneurons in the gray fish (Kennedy and Ireston, 1960) and in the dragon fly larva (Fielden, 1963). Repetitive discharges have been recorded from the giant fibres of Schistocerca, it is however not common and is usually from the slowest of the neurones in a given complex.

The conduction velocity for the giant fibres of Schistocerca range between 1.5 and 4.5 meters per second and are slow when compared with those of Periplaneta at 5 to 6 meters per second (Fumphrey and Rowland-Smith, 1937; Poeder, 1948), Locusta at 2 to 4 meters per second (Cook, 1952; Fielden, 1960) and Anax at 3.5 to 4.5 meters per second (Fielden, 1960). The higher conduction velocity in Periplaneta is correlated with the larger fibres. However the giant fibre diameters of Schistocerca are similar to those of Anax and Locusta. In Schistocerca the fastest conduction speeds obtained compare favourably with those reported in the literature and only when the slower replicates are averaged that the giant fibres of Schistocerca appear so efficient. As was previously pointed out this may be due in part to the drying out of the preparations which would have the

effect of reducing the velocity of conduction. It would be of considerable interest to study the diameter of the sheath, for a thin sheath may well have the effect of reducing conduction velocity. Bullock and Horridge (1965) have noticed that the conduction velocity of the giant fibres of the prawn Leander is high (18 - 23 meters per second) and the fibre diameter is relatively low (35 microns). They point out that giant fibres of this crustacean have a sheath that accounts for 10 percent of the fibre diameter. It would be interesting to relate the giant fibre conduction speeds to neurone and sheath diameter in a series of insect preparations.

Conduction velocities of those neurones which make synaptic contact with the ninth ventral nerve are within the range 1.5 to 3.8 meters per second. Again on the basis of conduction rate it is established that three fibres are active in the ipsilateral connective and two in the contralateral connective. As there are only four giant neurones in each connective it may be concluded that these are the same fibres activated by the cercal nerve. Histological observations suggest that the giant fibres activated in this response are those of the dorsal triad, for these have a common margin and lie in the same longitudinal tract as the cercal afferent fibres.

A feature of interneurones is their extensive receptive fields. They act as integrative centers for convergence of many sensory units (Kennedy and Ireston, 1960; Fielden, 1960; Fielden and Hughes, 1962). In addition Fielden (1963) has shown that the majority of

interneurone units in the dragon fly nymph Anax respond to stimuli from more than one segment. It is not surprising therefore that the giant interneurons should be activated by afferent fibres from more than one segment.

Roeder (1948) has shown that there is a decrease in the velocity of giant fibre potentials as they pass through a segmental ganglion. In Schistocerca there is a 55 percent reduction in velocity for a 30 percent reduction in fibre diameter. Such a reduction in the velocities of the potentials may not be entirely correlated with the reduction in the diameter of the giant fibres. If this is the case then a factor other than simple reduction in neurone diameter must be postulated. Hess (1958) has shown not only do the giant fibres decrease in diameter within the ganglion but their sheaths decrease in thickness also. It may be that the decrease in sheath thickness contributed considerably to the decremental conduction within the ganglion.

Synaptic Relationships.

The Terminal Ganglionic Mass.

The smooth buildup of the pre-synaptic compound afferent action potential represents an increase in the number of afferent neurones activated. This and the fact that increased frequency of stimulation

at levels of intensity immediately beneath those necessary to bring about a post-synaptic response, at a lower frequency, did not bring about such a response this would indicate that the synapse is frequency independent and that spatial summation occurs when a suitable number of afferent neurones discharge. Convergence of a number of afferent fibres on a single interneurone resulting in spatial summation appears to be a characteristic of interneurones (Roeder, 1948; Kennedy and Ireston, 1963; Fielden, 1963; Fielden and Hughes, 1962; Mill, 1963).

Synaptic delay times of 1.0 to 1.9 milliseconds have been established for the cercal afferent-giant fibre synapse in Periplaneta, (Fumphrey and Rawdon-Smith, 1937; Roeder, 1948). In Locusta the delay is 2 to 3 milliseconds (Fielden, 1960) and in Anax the delay between parapneustic afferents and giant fibres is 2.0 to 4.5 milliseconds. In Schistocerca the giant fibre-cercal afferent delay time varies between 2.8 and 4.3 milliseconds and the delay between the ninth ventral afferents and the giant fibres between 2.0 and 5.2 milliseconds. In both cases the contralateral delay is substantially longer than the ipsilateral delay. This delay can not be accounted for by the increased transmission distance of the afferent neurones to the contralateral neuropile nor of contralateral giant fibre collaterals into the ipsilateral neuropile. One must either postulate synapses of a different nature on either side of the ganglion or the possibility of a second order inter-

neurone interposed between the afferent neurone and the giant fibre on the contralateral side. This would add only additional synapse to the system and this could be accounted for by the discrepancies in delay between the ipsilateral and contralateral synapses.

The Metathoracic Ganglion.

The escape reaction in Periplaneta is initiated via giant pre-synaptic fibres and post-synaptic motor neurones of the crural nerve. Where as the cercal-giant synapse is stable the giant-leg nerve synapse is easily fatigued (Roeder, 1948). In both Periplaneta and Locusta (Cook, 1951) a puff of air on the cercus results in efferent potentials in the leg nerve. Such a response could not be obtained in Schistocerca nor could the evasion response which is so well known in the cockroach. It is evident that the weak link in this behavioural system is the giant fibre-leg nerve connection and in Schistocerca this is no longer functional. Roeder has shown that this synapse is temporarily summated in Periplaneta and Knight (1965) has pointed out that in Inax motor synapses are frequency dependent. Several hypothesis can be put forward to explain the lack of functional synapse at this level in Schistocerca.

- (a) Repetative firing is not common in the giant interneurones of Schistocerca and a puff of air delivered to the cercus does not result in an extensive burst of giant fibre volleys as it does in the cockroach. It may be that a sufficient

frequency of pre-synaptic volleys is not delivered to the giant-crural synapse.

- (b) The synapse may have become non-functional through the failure of the giant fibre or an interneurone either to produce or to release the synaptic transmitter.
- (c) Glial cells have amoeboid processes that may penetrate the neuropile and completely ensheath the neurone leaving only the areas of synaptic contact bare. It is possible that these giant leg nerve synapses have become non-functional by covering the synaptic regions, although no such case is known.
- (d) Roeder has shown that in Periplaneta the head has a disinhibiting effect on this behavioural pathway. Removal of the head has an inhibiting effect instead of running away from the stimulus the cockroach takes only a few brief steps. In Schistocerca the presence or absence of the head, or any of the anterior ganglion for that matter has an effect on the synapse. It could be that permanent inhibition from neurones of the metathoracic ganglion has taken place.

The first of these possibilities can be readily tested and discarded. An increase in the frequency of electrical stimulation of the giant fibres causes rapid volleys to ascend the cord, no response was obtained from the leg nerve. The second and third of

these suggestions is little more than an exercise in speculation. The evidence of Roeder (1948) lends support to the fourth view that the giant-crural synapses are permanently inhibited.

Only a small response is found in the thoracic connectives in reply to the ascending giant fibre volley in the abdominal connectives. It is evident that those giant fibres which are active in the cercal-giant response terminate in the metathoracic ganglion and do not pass uninterrupted to higher centres in the C.N.S. The delay across the metathoracic ganglion is brief in comparison with the afferent-giant fibre synapses, being 1.5 milliseconds. This figure however is fairly high when compared with Leriplaneta (0.15 to 0.5 milliseconds).

Evolution of Giant Fibres.

Hughes (1965) has speculated on the evolution of giant fibres, deriving a hypothetical ancestral type. This neurone would be capable of conduction in both directions and would make synaptic contact with afferent and efferent neurones in each segment. The histological and electrophysiological data derived for Schistocerca lend support to Hughes' hypothesis. In Schistocerca the giant fibres branch in the abdominal ganglia and further, they synapse with afferent neurones in at least two abdominal segments. A multi-segmental afferent supply has not previously been described for giant fibres.

Frosser (1961) has suggested that giant fibres have evolved independently many times in the arthropods. However if one compares the giant fibre systems of Anax, Periplaneta, Locusta and Schistocerca, they can be arranged in an evolutionary series. In Anax the giant fibres have effective efferent synapses in each abdominal and thoracic ganglion, an evasion response is present. In Periplaneta this has been reduced to efferent connections in the metathoracic ganglion only, the evasion response is present. In Locusta the same case exists as in Periplaneta except that the giant fibres are reduced in diameter and no evasion response occurs.

In Schistocerca the number and size of the giant fibre is similar to Locusta however no evasion response occurs and the giant-leg nerve synapse is no longer functional.

Cook (1951) has rightly pointed out that it is not surprising that an evasion response does not occur in Locusta considering the small size of the cerci and the fact that they are covered by wings. It might be further noted that a gregarious way of life would be incompatible with a cercal evasion response. It would be of considerable interest to study the physiology of the giant fibre system of Schistocerca throughout the ontogeny of the individual particularly the response at the metathoracic ganglion.

Occasional Observations.

The following section comprises a series of unrelated observations obtained during the foregoing study. They are not conclusive in themselves but may be taken as indications of functional pathways, the details of which leave considerable scope for further study.

Mechanical stimulation of the cercus brings about an efferent response in the contralateral cercal nerve which corresponds to the afferent volleys in the ipsilateral cercal nerve (Fig. 61). These efferent volleys do not always occur following an afferent burst, nor does their duration correspond to the length of the afferent volley. This indicates a rather labile synaptic function. A similar pathway has been reported from the uropod nerves of the cray fish (Hielden, 1960) and from the fifth roots (paraprost nerves) of Aeschna (Mill, 1963).

Stimulation of the mechanoreceptive hairs on the dorso-lateral margin of the ninth sternum results in a low frequency burst of efferent potentials, apparently from a single neurone of the eighth dorsal nerve (Fig. 62). This indicates a pathway between mechanoreceptors associated with the lateral branch of the ninth ventral nerve and efferent neurones of the eighth dorsal nerve. The data gives no indication whether the efferent synapse is with afferent ninth ventral fibres which have been shown histologically to pass

through the eighth ganglion or with an interneurone.

A similar pathway is observed on stimulation of the cercus (Fig. 63). High frequency bursts are recorded from the eighth dorsal nerve upon stimulation of the cercus. Potentials in these volleys are of two amplitudes and do not always occur on cercal stimulation, nor was this pathway apparent in all animals tested. There is a labile synapse in the system.

Lateral bending of the cercus results in a low frequency efferent volley in the eighth dorsal nerve (Fig. 64) which corresponded to the period of the stimulus and ceased on cessation of the stimulus. The sense organs responsible for such stimuli have not been located, they may be stretch receptors located in the cercal muscles or possibly campaniform organs which have been shown to be present on the cercus (Thomas, 1965).

Mechanical stimulation of the paraproccts results in a burst of low frequency, low amplitude potentials in the contralateral ventral nerve of the sixth abdominal segment (Fig. 65). A similar response is not obtained in the ipsilateral sixth ventral nerve. The synaptic pathways in this response are not clear. There are four possible pathways on the basis of our histological data.

1. Afferent fibres synapsing with contralateral interneurons whose collaterals extend into the ipsilateral ventral

neuropile. These interneurons would then synapse with efferents of the sixth ventral nerve.

2. Afferent fibres synapsing with ipsilateral interneurons and these in turn with collaterals of the motor neurons which pass to the contralateral side.
3. Afferent fibres passing directly up the ventral connective and synapsing with contralateral collaterals of the sixth ventral nerve.
4. Afferent fibres passing to the contralateral half of the terminal ganglionic mass and synapsing with interneurons which would in turn synapse with efferent fibres in the sixth abdominal ganglion.

This problem could be resolved by a sequential cutting of the ventral connectives to determine the connective which is functional in this pathway and by the application of a synaptic block (e.g. nicotine) to the terminal ganglionic mass to establish whether or not synaptic contact takes place at this level.

The behavioural significance of such a pathway is apparent. Contractions of muscles on the contralateral side only would cause the animal to bend the posterior region of the abdomen away from the noxious stimulus.

Stimulation of the seventh tergum causes potentials to be picked up by electrodes placed on the ventral connective below the

seventh abdominal ganglion (Fig. 66). Though these could conceivably represent descending sensory neurones (they have not been located histologically) it is probable that they represent interneurons. The problem could be resolved through the use of electrical stimulation and/or a synaptic block.

In one particular preparation a locust was observed extending and withdrawing the aedaeagus. Section of the ventral nerve cord immediately anterad of the terminal ganglionic mass had no effect on this activity.

Electrodes were placed on both genital nerves and the neural nature of this activity was recorded (Fig. 67). In the "relaxed" state there is a constant barrage of low amplitude potentials with the slow repetitive firing of a high amplitude neurone. The latter potential probably represents a motor neurone maintaining a state of tonus in the muscle involved. With the extension of the aedaeagus there is an increase in the frequency of firing in all neurones particularly in the ones responsible for the high amplitude potentials. As extension continues the large potentials fall into synchrony between nerves and with time these break up into short high frequency bursts in exact synchrony each separated by a pair of medium amplitude spikes. Each of these bursts lasts approximately .07 of a second and is separated by an interval of .05 of a second during which the two lesser neurones continue firing. It may be

postulated that these are sensory neurones giving information on the degree of extension. The occurrence of discrete bundles of large amplitude signals only occurs during maximum extension. These may represent motor neurones maintaining maximum contraction of the muscles and thus of the aedeagus. Upon cessation of these large potentials the aedeagus retracts into the genital pouch. The fact that this rigid synchrony between nerves is maintained in the absence of higher centers would indicate the presence of a timing device in the terminal ganglionic mass.

Fopov (1958) has shown that female locusts are sensible to sodium chloride solutions. He determined that Schistocerca females would not oviposit in soils containing 25 grams per litre sodium chloride in water.

The cercus of a male Schistocerca was stimulated with a small drop of saturated sodium chloride solution. A very high frequency burst of impulses is obtained from the cercal nerve (Fig. 68, lower record) lasting approximately 3 seconds. At this point the sense organs become adapted although the saline solution is still present. These afferent neurones synapse with interneurons of the ventral connectives (upper record). This synapse is labile and adapts rapidly, the volley is in the ventral cord lasting .07 of a second and consists of only nine spikes of two sizes. A like stimulus applied to the ninth sternum of the male gave no response in the ninth sternal nerve.

The cerci of the male Schistocerca bear chemoreceptors
sensitive to concentrated sodium chloride solutions. Thomas (1965)
however has been unable to locate anatomically any chemoreceptors,
unique to the posterior segments of the female Schistocerca
which might be salt sensitive.

SUMMARY

The terminal ganglionic mass situated in the eighth abdominal segment of Schistocerca gregaria innervates abdominal segments eight, nine, ten and eleven. A summary of the detailed segmental innervation is given in table 7.

Table 7. A summary of the innervation of the eighth, ninth, tenth and eleventh abdominal segments of Schistocerca.

<u>8th. dorsal nerve (male)</u>		
<u>branch</u>	<u>muscle innervated</u>	<u>other function</u>
1	v.d., 247, 248	anastomose pm.n.
2a	254, 255	s-ventral tergum
b	250x, 251	anastomose 7 v.n. main branch is contiguous with 7 tv.n.
3	-	s tergum
4	244	-
5	243a, b,	-
6	alary	s-tergum
7	242c, d,	-
8	242b, 245	s-intersegmental fold and tergum
9	242a	-

8th. dorsal nerve (female)

<u>branch</u>	<u>muscle innervated</u>	<u>other function</u>
1	v.d.	anastomose pm.n.
2	247	
3a	252, 254, 255	s-ventral tergum
b	250x, 251	anastomose 7 v.n; main branch contiguous with 7 tv.n.
4	clary	s-tergum
5	242c	-
6	243b	-
7	243a	-
8	242c	-
9	242b	-
10	242a, 245	-

8th. ventral nerve (male)

<u>branch</u>	<u>muscle</u>	<u>other function</u>
1	-	anastomose-8 tv.n.
2	-	s-sternum
3	250, 253	s-sternum

8th. ventral nerve (female)

<u>branch</u>	<u>muscle</u>	<u>other function</u>
1	250, 248	s-sternum
2a	-	spermathecal duct
b	272	-
c	-	spermathecal apperature

<u>branch</u>	<u>muscle</u>	<u>other function</u>
d, e	-	s-ventral ovipositor valve
f	272	-

8th. transverse nerve (male)

<u>branch</u>	<u>muscle</u>	<u>other function</u>
1	-	anastomose-pm.n.
2	-	anastomose-9d.n.
3	270	-

8th. transverse nerve (female)

<u>branch</u>	<u>muscle</u>	<u>other function</u>
1	-	anastomose-pm.n.
2	271	-
3	-	s-tergum

9th. dorsal nerve (male)

<u>branch</u>	<u>muscle</u>	<u>other function</u>
1	v.d.	pm.n.
2	-	anastomose 8 tv.n.
3a	alary	s-tergum
b	260a-c	s-9 tergum, 10 tergum

9th. dorsal nerve (female)

<u>branch</u>	<u>muscle</u>	<u>other function</u>
1	v.d.	pm.n.
2a	264	-
b	-	anastomose epi.n.

<u>branch</u>	<u>muscle</u>	<u>other function</u>
3	262	-
4	-	s-tergum
5	260 a-e	s-tergum

9th. ventral nerve (male)

<u>branch</u>	<u>muscle</u>	<u>other function</u>
1	261	-
2	265, 268	-
3	-	s-lateral sternum
4	-	s-ventral sternum

genital nerve (male only)

<u>branch</u>	<u>muscle</u>	<u>other function</u>
1	-	accessory gland
2	266, 267, 284	-
3	266, 284	s.
4	285	-
5	281, 283	-
6	278, 282	-

9th. ventral nerve (female)

<u>branch</u>	<u>muscle</u>	<u>other function</u>
1a	273, 271	s.
b	-	s-dorsal valve
2	275	-
3	274	-
4	271, 263	-

Epiproct nerve (male)

<u>branch</u>	<u>muscle</u>	<u>other function</u>
1	264	-
2	-	anastomose-cerc.n.
3	289	-
4	288	-
5	295	s-epiproct
6	293, 294	s-epiproct

Epiproct nerve (female)

<u>branch</u>	<u>muscle</u>	<u>other function</u>
1	264	-
2	289	-
3	288	-
4	-	s-epiproct
5	287, 294, 293, 295	s-10 tergum

Cercal nerve (male)

<u>branch</u>	<u>muscle</u>	<u>other function</u>
1	286, 290, rectal muscles	s?
2	291, 296	s-paraproct
3	-	anastomose-epi.n.
4	-	s-cercus

Cercal nerve (female)

<u>branch</u>	<u>muscle</u>	<u>other function</u>
1	286,290,rectal muscles	s?
2	296,291	s-para root
3	292	-
4	-	s-cercus

Comparison with other orders of the Insecta has shown that the innervation of some of the ventral musculature by the first branch of the dorsal nerve is a conservative feature of the insect nervous system. The transverse nerve of the abdominal segments of Schistocerca is unique among all species studied so far.

It arises independently from the ganglion anterior to the segment which it innervates and not as a branch of the median nerve or of the dorsal nerve. The only parallel is found in the thoracic segments of certain species.

The genitalia are innervated in the male by a nerve of the ninth abdominal ganglion, the genital nerve, and in the female by the eighth and ninth ventral nerves. Using innervation as evidence it is concluded that the male genitalia are derived from the ninth abdominal segment. The ventral ovipositor valves in the female are derived from the eighth abdominal segment and the dorsal and intermediate ovipositor valves are derived from the ninth abdominal segment.

Histological studies of the simple seventh abdominal ganglion reveal a three lobed neuropile containing seven transverse commissures and six longitudinal tracts. The neuronal composition of these tracts has been studied. There are six groups of inter-nuncial cell bodies. The anterior dorsal, anterior ventral, and posterior dorsal groups all contributing descending fibres to the connectives. The lateral ventral group supplies ascending fibres to the ipsilateral connective and local association neurones within the ganglion. The median ventral group gives fibres to the contralateral connective via longitudinal tract four. Motor neurones are located in a dorsal and ventral group at the base of each segmental nerve. Their axons enter the ipsilateral segmental nerves. Sensory neurones arborize in the ipsilateral and contralateral sides of the ganglion and also ascend the ipsilateral ventral connective. Seventyfive neurone pathways have been traced within the seventh abdominal ganglion.

Sections of the terminal ganglionic mass reveal a neuropile comprising four fused units corresponding to the eighth, ninth, tenth and eleventh abdominal ganglia which have condensed to form the ganglionic mass. Segmentally arranged groups of median ventral and lateral ventral interneurones further show the segmental nature of this structure.

Condensation of these ganglia has resulted in a reduction in the number of transverse tracts, the eighth ganglion retaining

five of the original seven and each subsequent ganglion retaining four. The same six longitudinal tracts that are found in the seventh abdominal ganglion can be identified in the terminal ganglionic mass. The anterior dorsal and ventral interneurone groups are present in the eighth ganglion but in the subsequent ganglia they are reduced and have become incorporated into the remaining neurone groups. The median ventral and lateral ventral groups of interneurons are present in the eighth, ninth and tenth ganglia but become reduced to a single ventral group in the eleventh ganglion. There is a reduction in the number of lateral interneurons coincident with the degree of condensation.

The motor neurones of the eighth abdominal ganglion retain the same positions as those in the seventh ganglion. In the ninth ganglion the ventral group becomes reduced and the dorsal group extends toward the dorsal surface of the neuropile. With the increased condensation in the tenth and eleventh ganglia the motor neurones become distributed over the dorsal surface of the neuropile.

One hundred and five neurones, many representative of tracts, have been traced within the terminal ganglionic mass. The distribution of neurones of the genital nerve reinforces the opinion that this nerve is ninth segmental in origin and that the male genitalia are derived from the ninth abdominal segment.

There are four giant fibres in each abdominal connective of Schistocerca. Each fibre of the dorsal triad has been shown to

originate from a single neurocyte in the tenth lateral ventral group of interneurons. These fibres pass without interruption into the metathoracic ganglion although their diameter becomes reduced as they pass through the various abdominal ganglia. Short branches are given off to the dorsal neuropile of the abdominal ganglia and certain of these branches pass via the dorsal commissure to the contralateral side of the ganglion.

Electrophysiological studies have indicated that there are three giant fibres activated in the ipsilateral connective and two in the contralateral connective when the cercus is mechanically stimulated. The identification of individual fibres in a complex volley has been on the basis of velocity rather than on spike amplitude. Conduction speeds in these fibres range from 1.5 to 4.5 meters per second. Synaptic delays at the cercal-ipsilateral giant synapse are between 2.4 and 3.3 milliseconds and at the contralateral synapse between 3.5 and 4.2 milliseconds. A second order interneurone is postulated between the cercal afferent fibres and the contralateral giant fibres. There is a considerable reduction in velocity as the potentials pass through the seventh abdominal ganglion. This decrease cannot be accounted for on the basis of reduced neurone diameter alone and may be related to a reduction in sheath thickness within the ganglion.

Afferent neurones of the lateral branch of the ninth sternal nerve have been shown to synapse with the giant fibres.

This conclusion is based on the similarities of conduction velocity and amplitude of potentials when compared to the volleys recorded upon cercal nerve stimulation.

Though the giant fibres respond to cercal and ninth sternal stimulation there is no evasion response in Schistocerca. This lack of response is correlated with the absence of functional synapses between the giant fibres and the efferent neurones of the metathoracic leg nerve. The giant fibres activated by cercal stimulation terminate within the metathoracic ganglion. Only low amplitude potentials in the thoracic connectives above this ganglion can be correlated with the abdominal giant fibre volleys.

An evolutionary sequence towards loss of function in giant fibres has been suggested which is illustrated by Anax, Periplaneta, Locusta and Schistocerca.

Other electrophysiological data concerning functional pathways in the abdominal nervous system of Schistocerca are reported; including the following observations. Synaptic connections exist between the ipsilateral and contralateral cercal nerves. A synchronizing mechanism exists within the terminal ganglionic mass for correlating discharges in the genital nerves. Receptors sensitive to aqueous sodium chloride solutions have been shown experimentally to be present on the cercus. These afferent neurones synapse with interneurones of the ipsilateral ventral connective.

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FIGURES

Abbreviations used in Figures

a, b, c, d, e, f, - points of anastomosis
a.c. - anterior commissure
a.d.i. - anterior dorsal group of interneurones
a.d.m.c. - anterior dorsal median commissure
al.m. 9 alary muscle
a.v.i. - anterior ventral group of interneurones
asp.n. - nerve of the spermathecal apperature
a.v.i. - anterior ventral group of interneurones
a.v.m.c. - anterior ventral median commissure
c.g. - central glial cells
cerc.n. - cercal nerve
d.c. - dorsal commissure
d.c.b. - dorsal cell bodies
d.m. - dorsal group of motor neurones
d.m.c. - dorsal median commissure
d.n. - dorsal nerve (preceeded by number of ganglion of origin)
d.np. - dorsal neuropile
epi.n. - epiproct nerve
gen.n. - genital nerve
l.t. - longitudinal tract (followed by number)
l.v.i. - lateral ventral group of interneurones
m.n. - median nerve
m.v.i. - median ventral group of interneurones

np. - neuropile

o.g. - outer glial cells

p.d.i. - posterior dorsal group of interneurons

p.d.m.c. - posterior dorsal median commissure

pm.n. - paramedian nerve

p.v.m.c. - posterior ventral median commissure

rec.m. - rectal muscles

rec.n. - rectal nerve

s - sensory branch nerve

tv.n. - transverse nerve (preceded by number of ganglion of origin)

v.c. - ventral connective

v.c. - ventral commissure (preceded by number of segment)

v.d. - ventral diaphragm

v.f. - ventral fissure

v.m. - ventral group of motor neurons

v.m.c. - ventral median commissure

v.n. - ventral nerve (preceded by number of ganglion of origin)

v.np. - ventral neuropile

9 v.l.n. - ninth ventral lateral nerve

9 v.m.n. - ninth ventral median nerve

Muscle Enumeration (Snodgrass 1935)

<u>Number</u>	<u>Muscle</u>
234	external ventral
242 (a-c)	median internal dorsal
243 (a. b.)	lateral internal dorsal
244	paradorsal
245	median external dorsal
247	median internal ventral
248	lateral ventral
250x	first internal lateral
250	second internal lateral
251	first external lateral
252	second external lateral
253	third external lateral
254	dilator of spiracle
255	occlusor of spiracle
260 (a-c)	median internal dorsal
261	retractor of phallus
262	long protractor of ovipositor
263	retractor of ovipositor
264	ventral dilator of rectum
265	ventral muscles
266	retractor of aedeagus
267	protractor of aedeagus
268	internal lateral
269	internal lateral

<u>Number</u>	<u>Muscle</u>
270	external lateral
271	levator of dorsal valve
272	depressor of ventral valve
273	adductor of ventral valve
274	adductor of dorsal valves
275	muscle of intermediate valves
278	epiphalic muscle of aedeagus
281	lateral dilator of endophallus
282	dorsal dilator of endophallus
283	compressor of endophallus
284	compressor of ejaculatory sac
285	muscles of ejaculatory duct
286	dorsal dilator of rectum
287	depressor of cercus
288	median levator of cercus
289	lateral levator of cercus
290	lateral dilator of rectum
291	ventral muscle of paraproct
292	transverse muscle
293	adductor of cercus
294	adductor of paraproct
295	dorsal dilator of anus
296	ventral dilator of anus

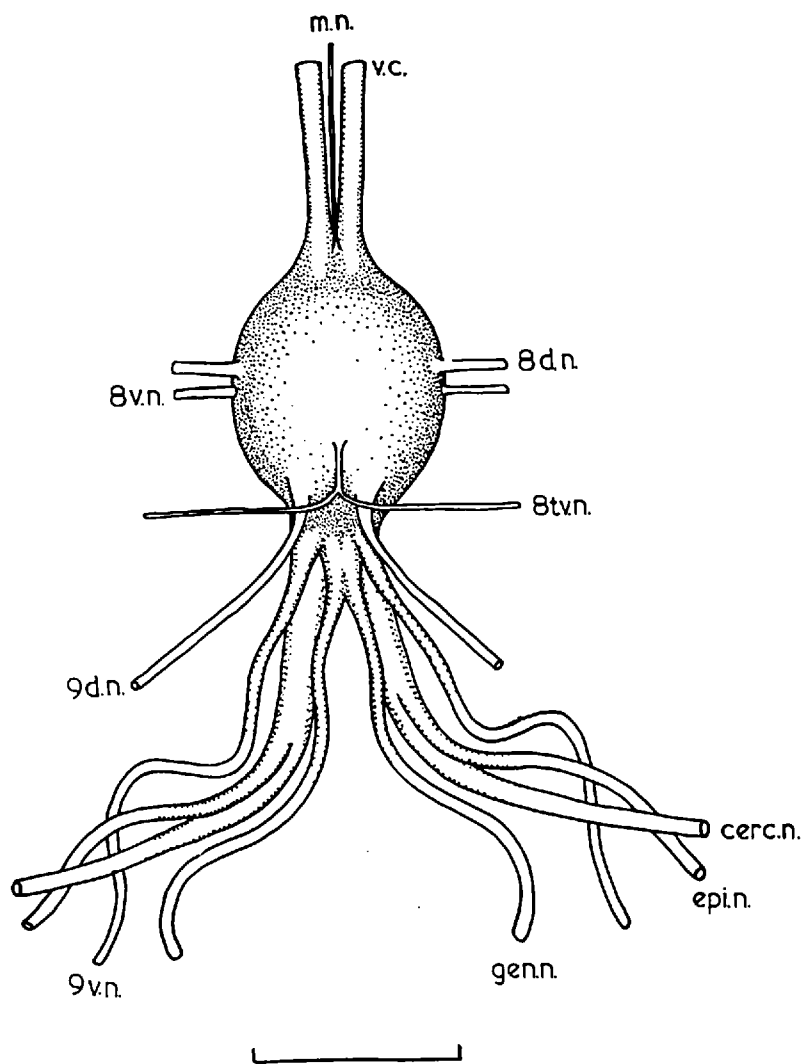


Fig. 1. Terminal ganglionic mass (male). Scale 0.8 mm.

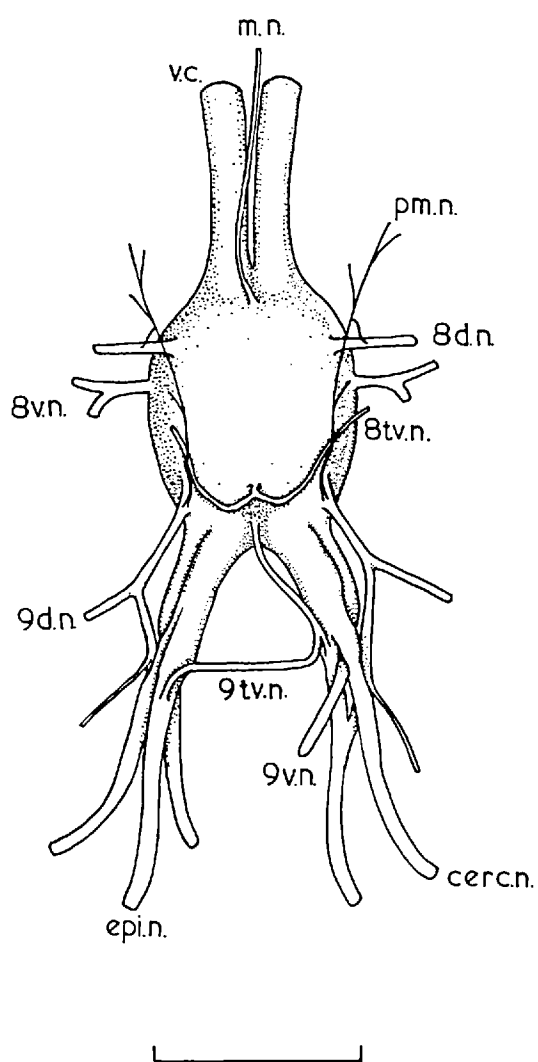


Fig. 2. Terminal ganglionic mass (female). Scale 0.8 mm.

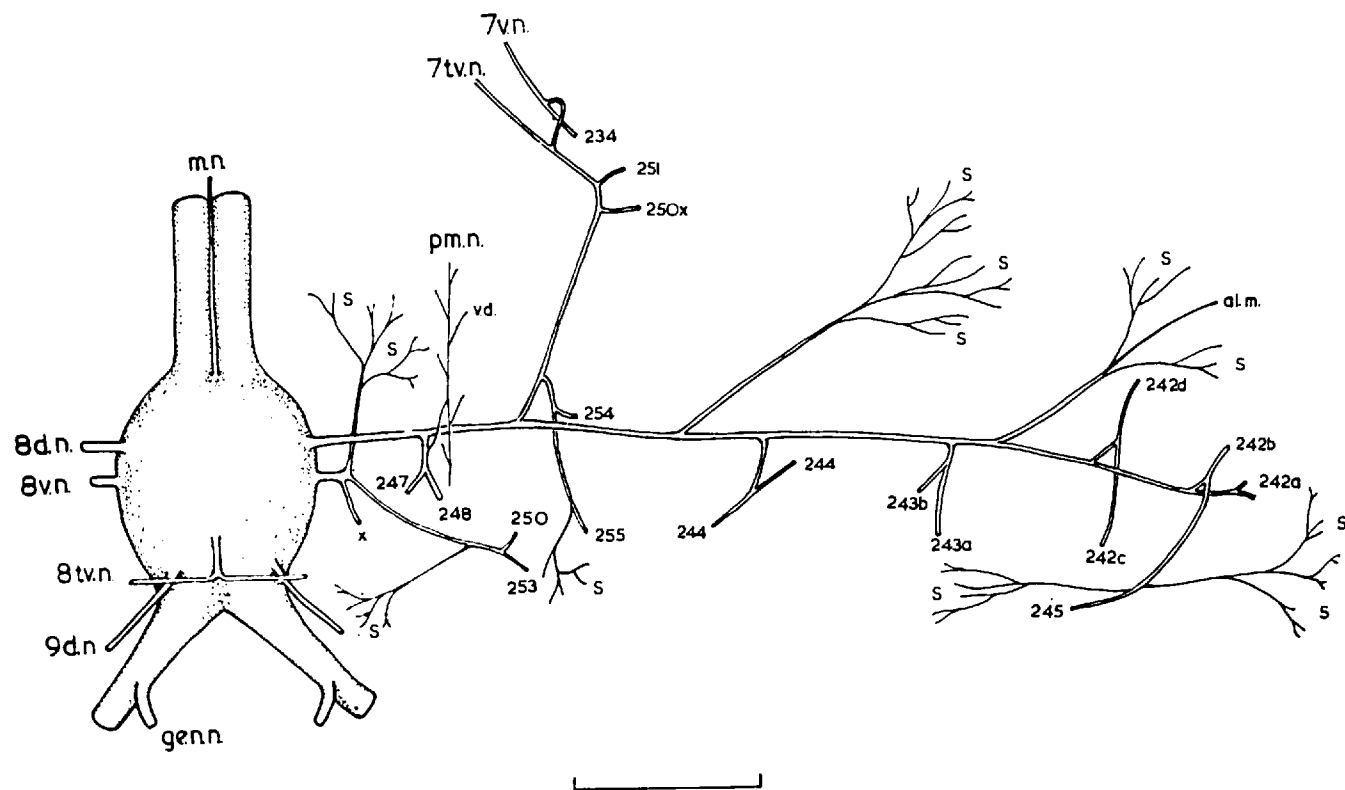


Fig. 3. Innervation of the eighth abdominal segment (male). Scale 0.8 mm.

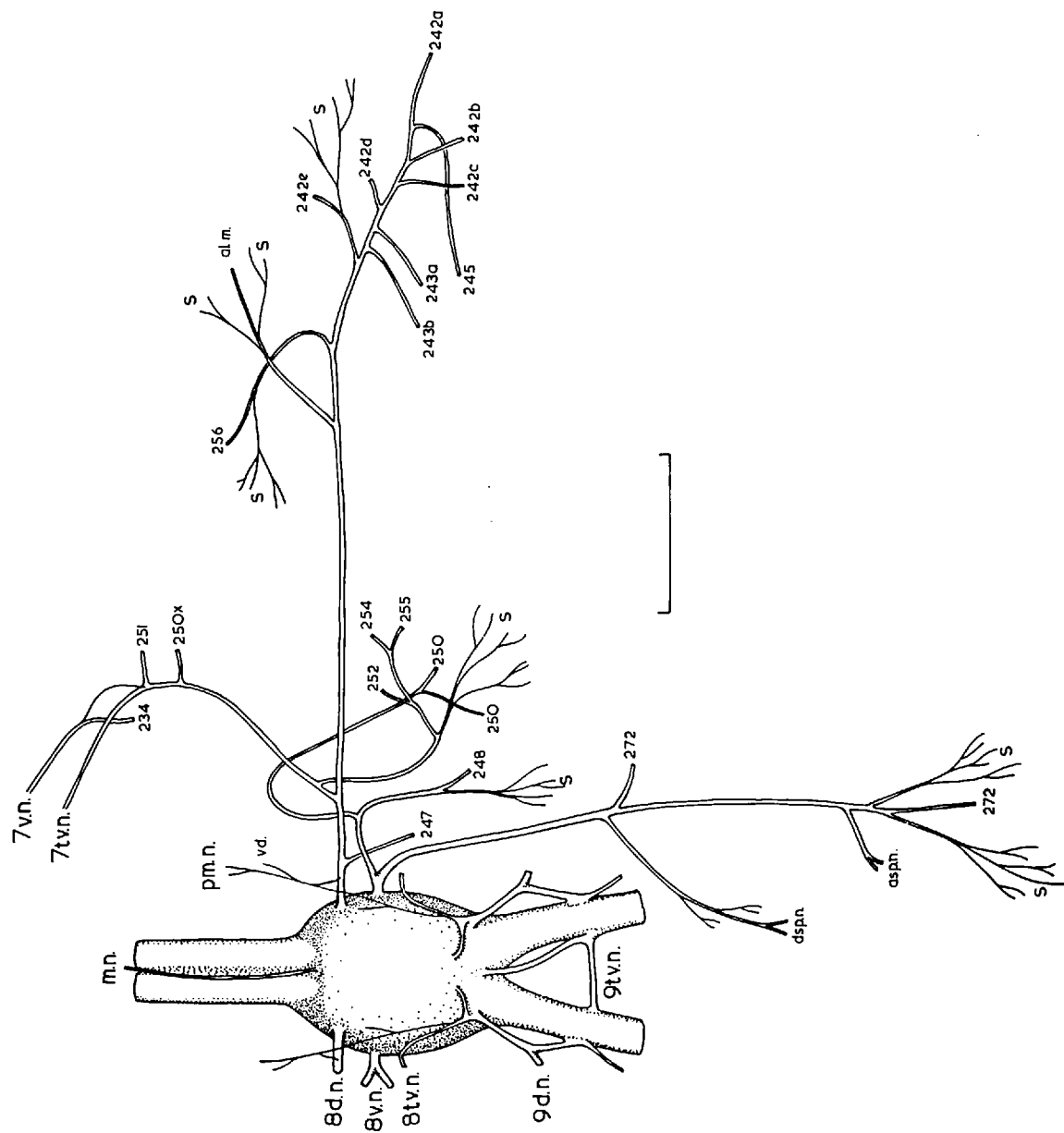


Fig. 4. Innervation of the eighth abdominal segment including the ventral ovipositor valve (female). Scale 0.8 mm.

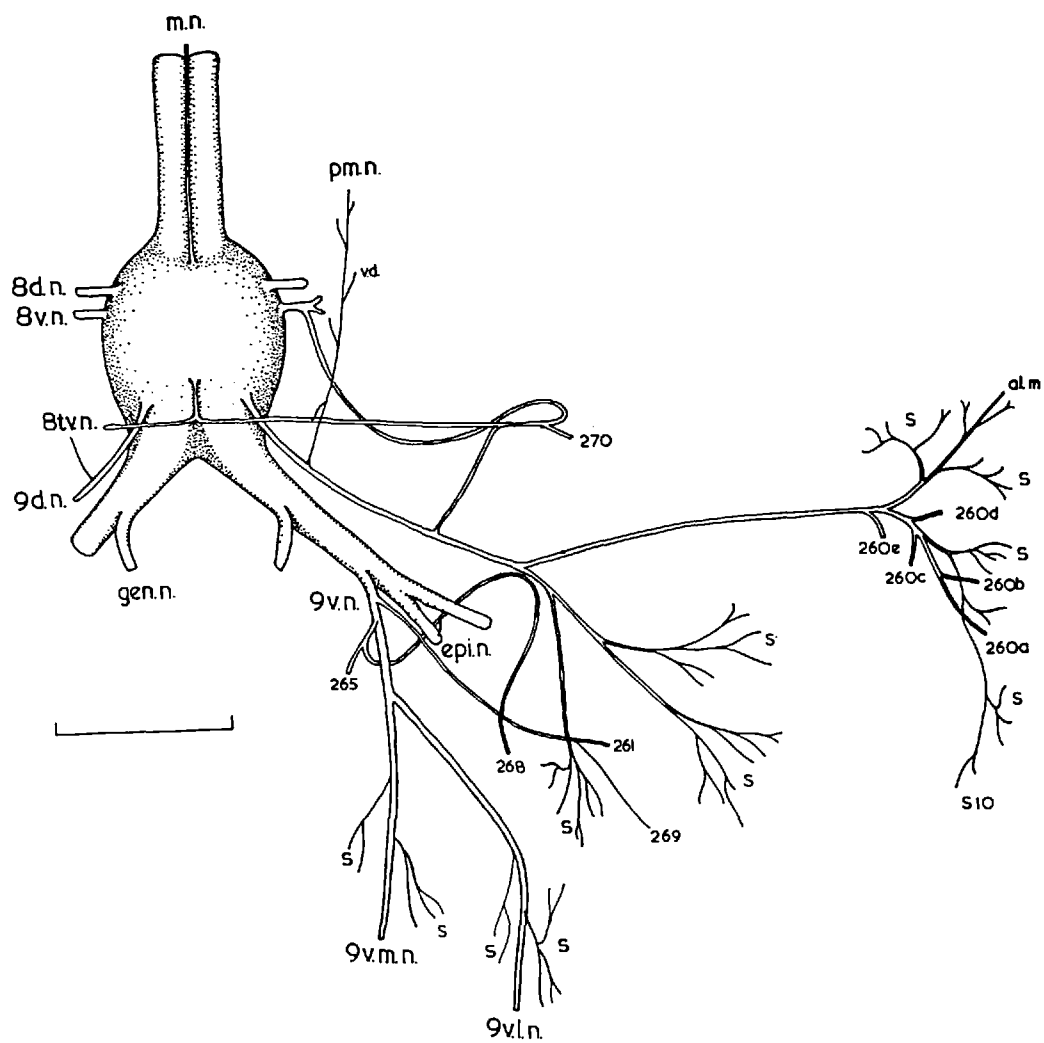


Fig. 5. Innervation of the ninth abdominal segment.

Scale 0.8 mm.

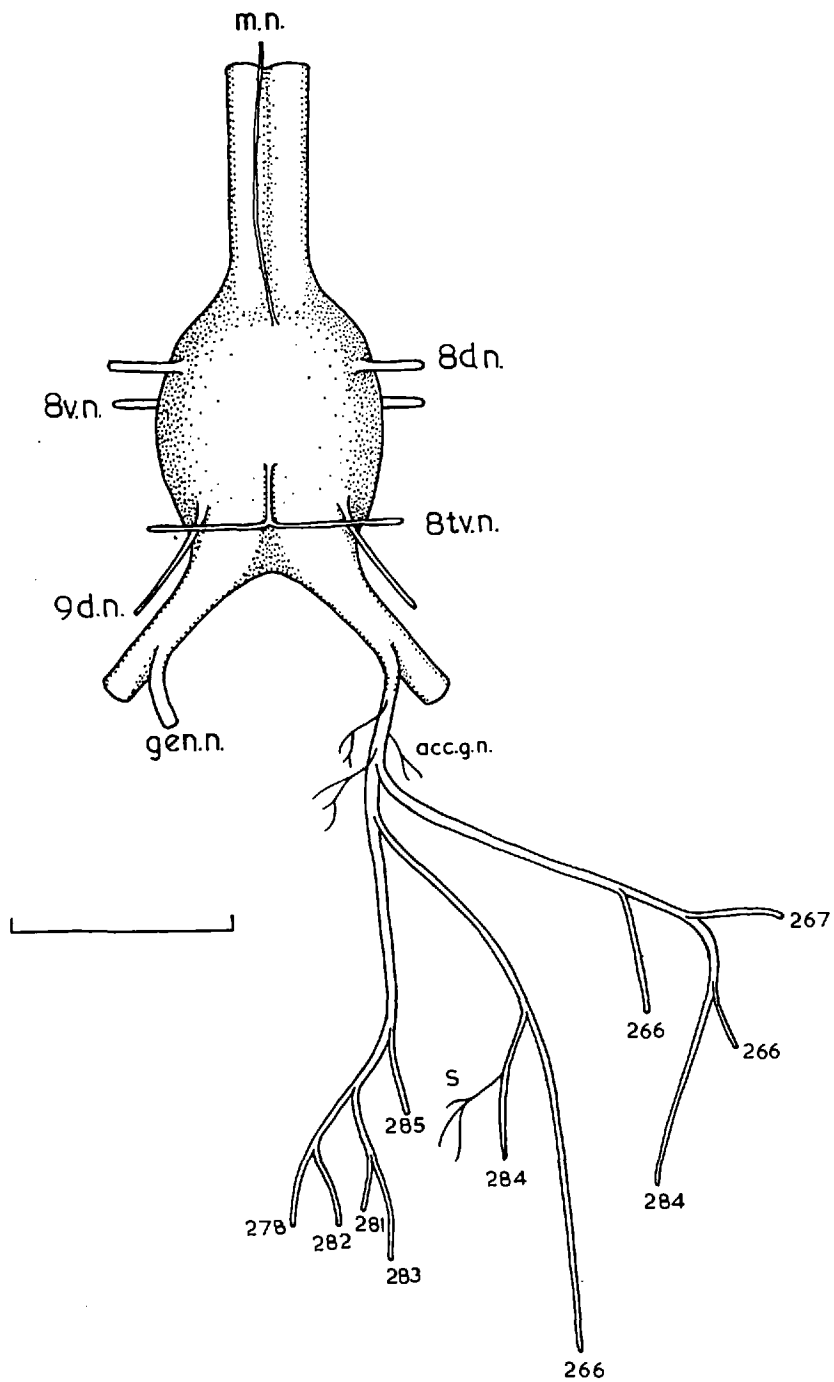


Fig. 6. Innervation of male genitalia. Scale 0.8 mm.

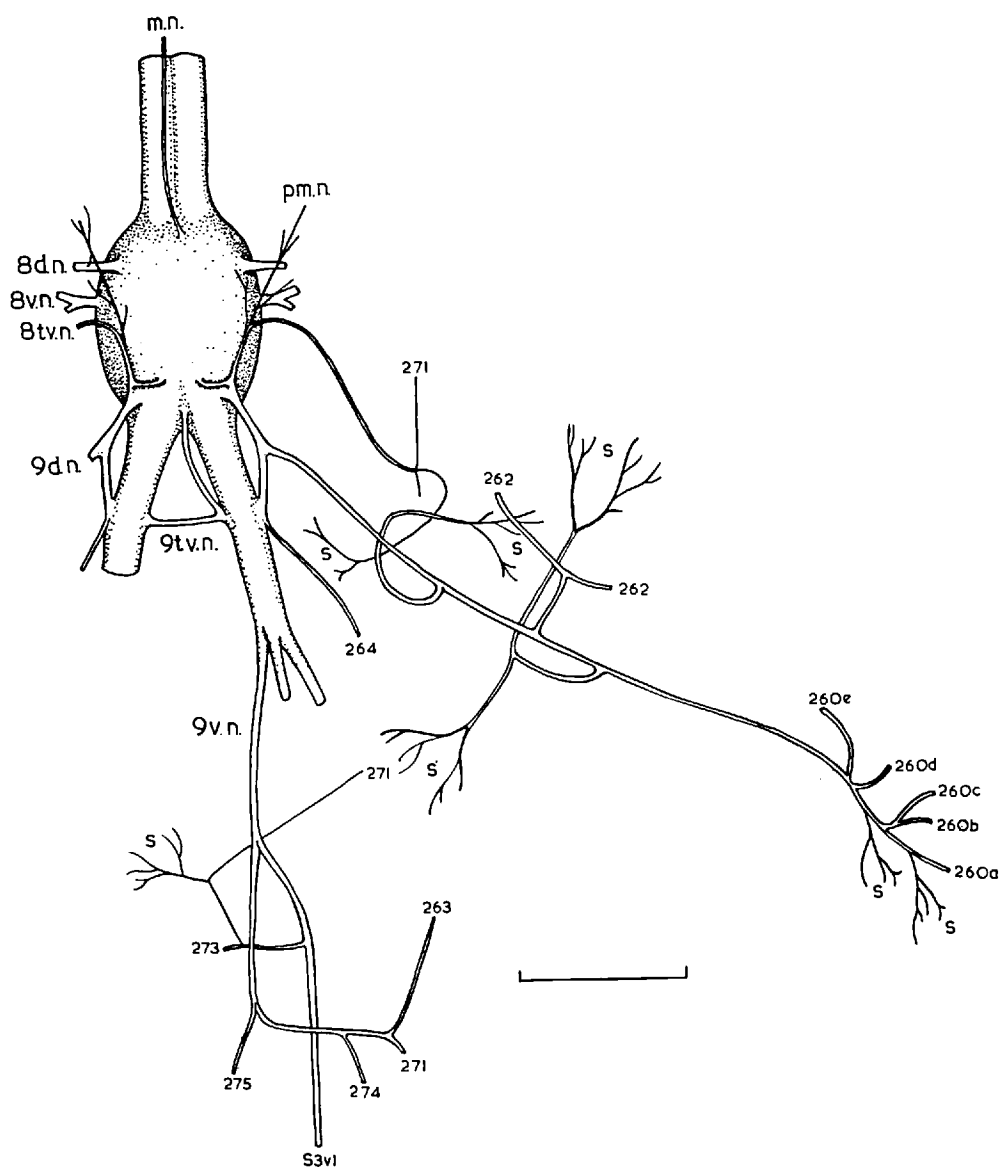


Fig. 7. Innervation of the ninth abdominal segment including the dorsal and intermediated ovipositor valves (female).
Scale 0.8 mm.

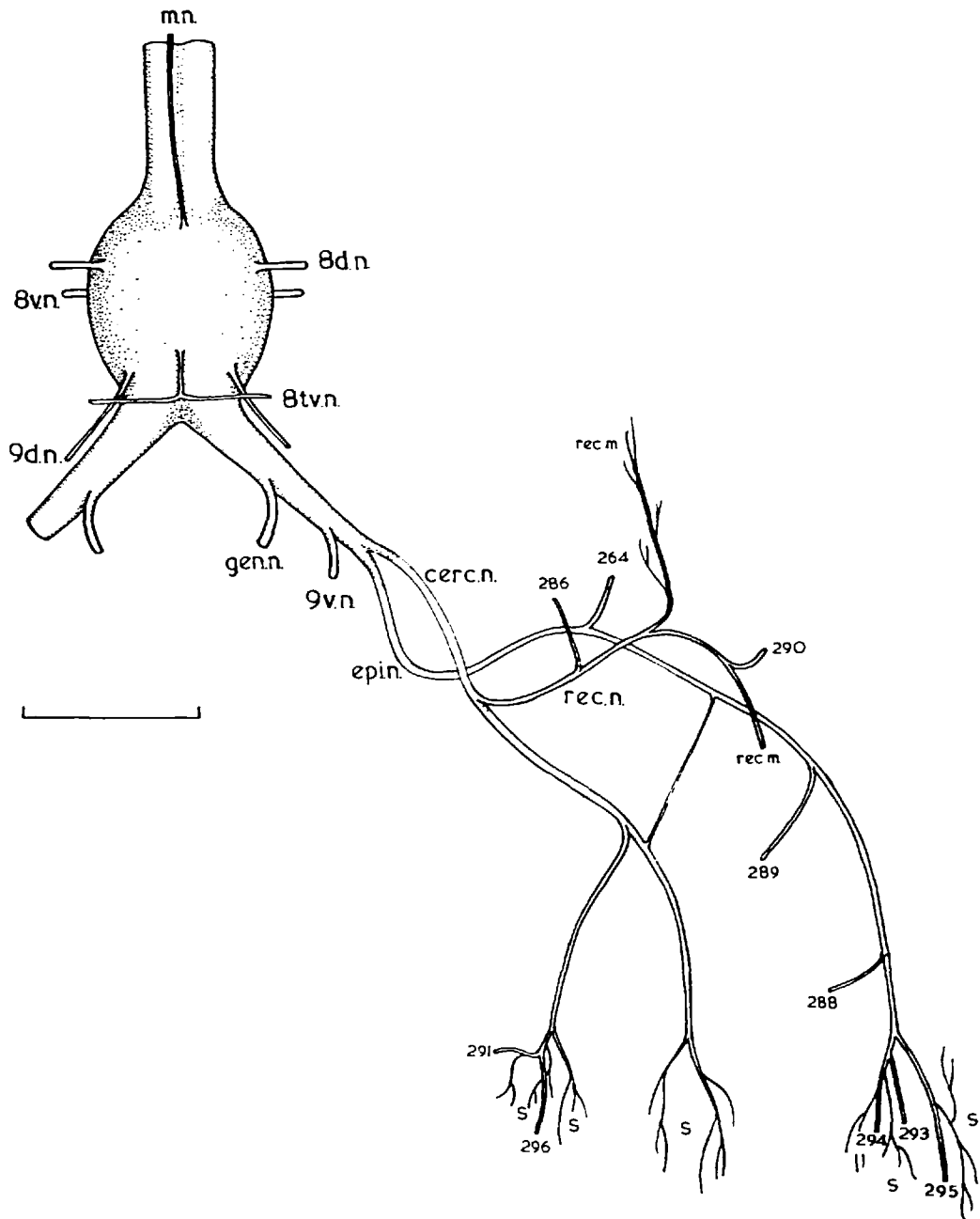


Fig.3. Innervation of the tenth and eleventh abdominal segments (male). Scale 0.8 mm.

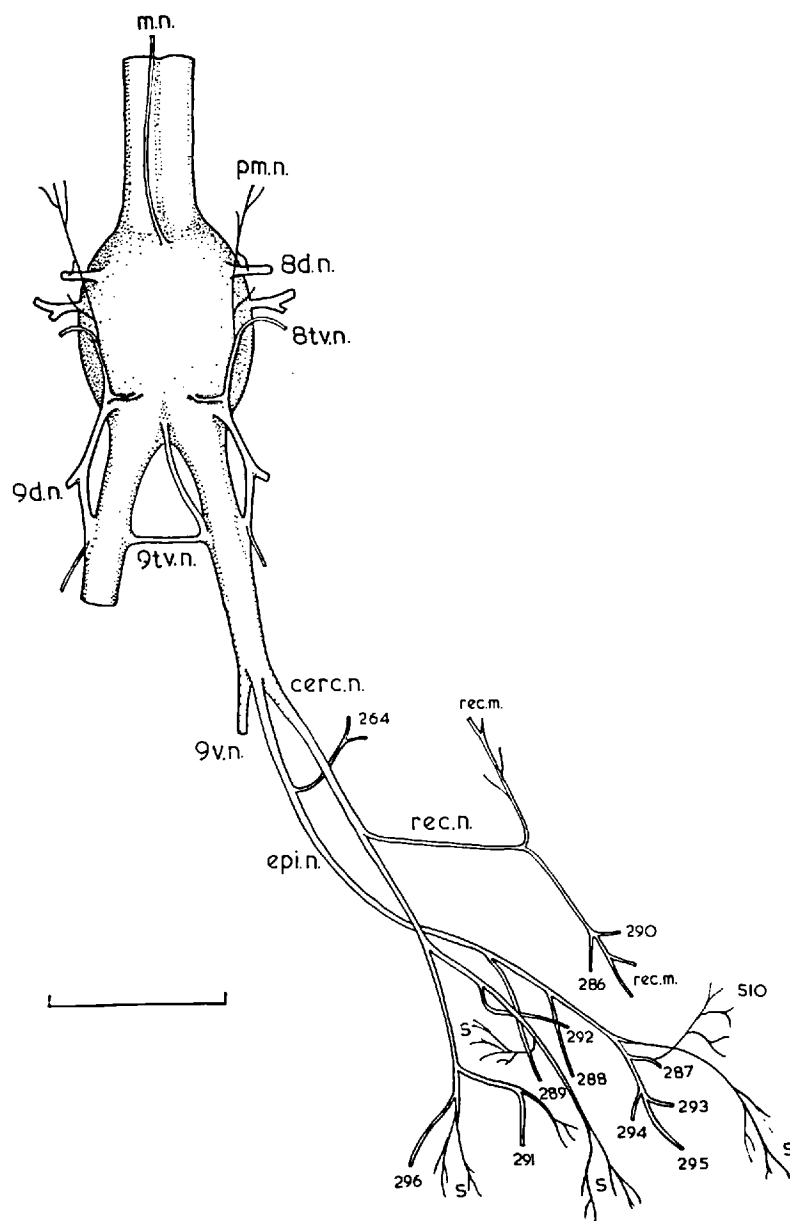


Fig. 9. Innervation of the tenth and eleventh abdominal segments (female). Scale 0.8 mm.

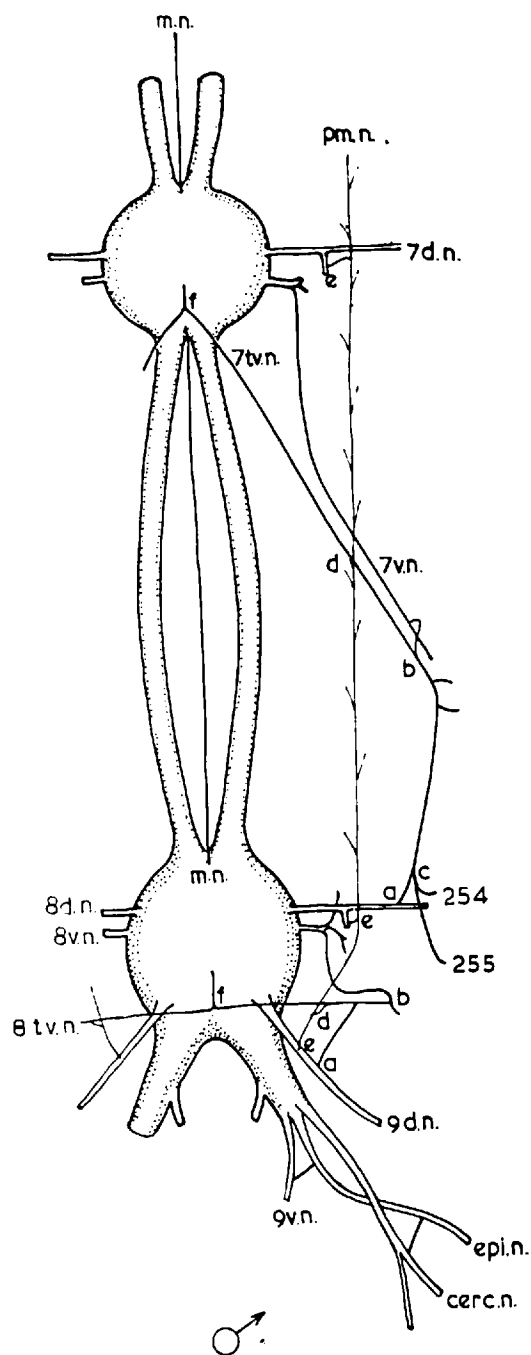
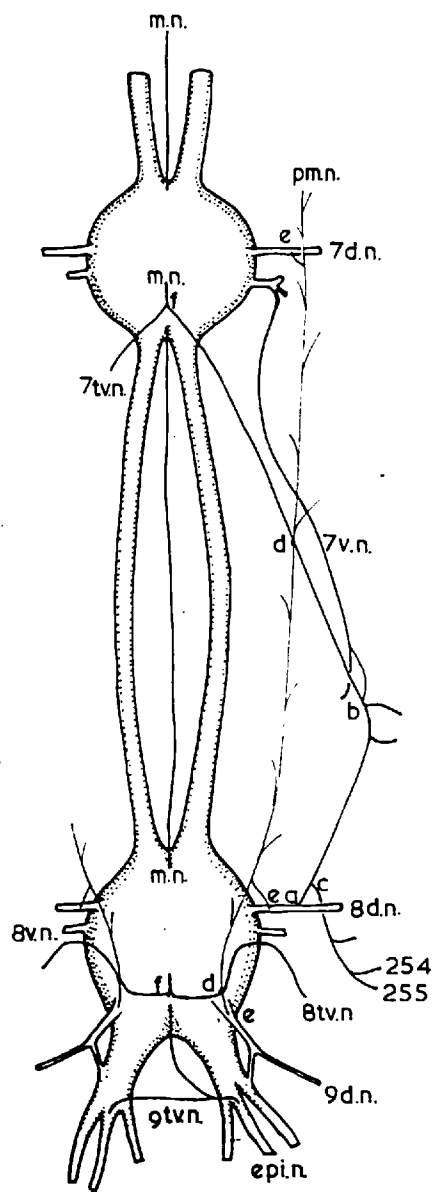


Fig. 10. The median nerve - transverse nerve complex of the seventh abdominal ganglion and the terminal ganglionic mass (male).



♀

Fig. 11. The median nerve - transverse nerve complex of the seventh abdominal ganglion and the terminal ganglionic mass (female).

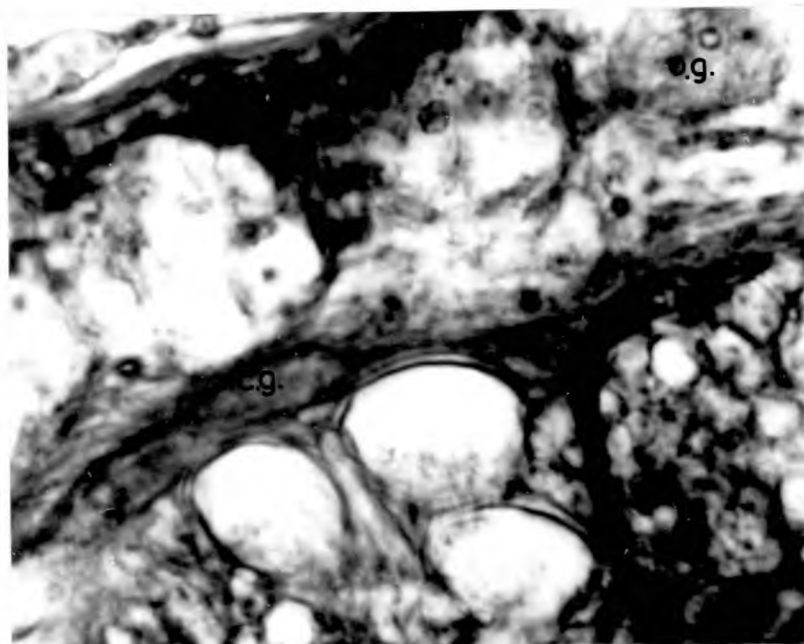


Fig. 12. Transverse section through dorsal region of the seventh abdominal ganglion showing outer glial cells (o.g.) and central glial cells (c.g.) (x2300).

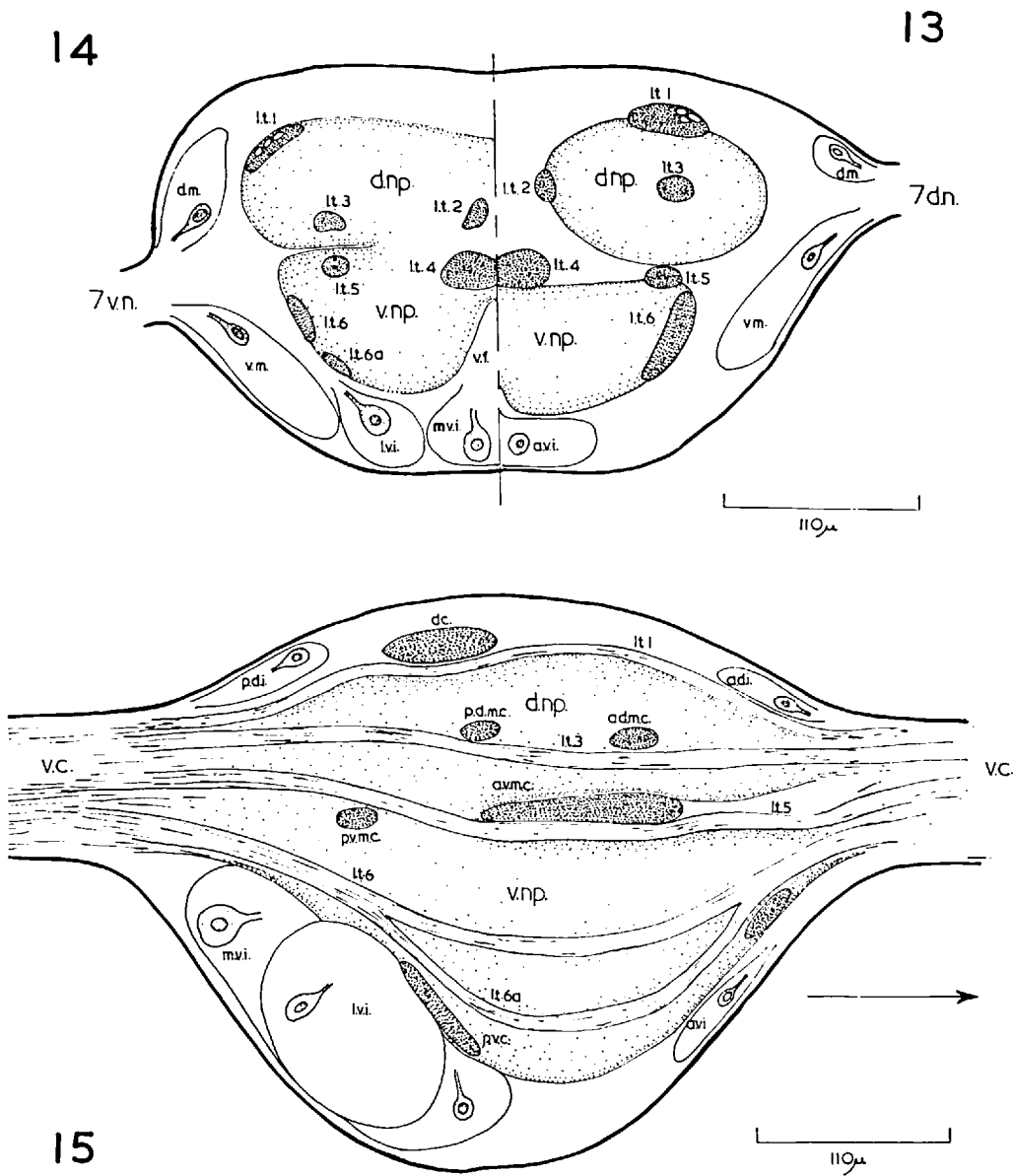


Fig. 13. Transverse section of seventh abdominal ganglion at the level of the seventh dorsal nerve, showing lobes of neuropile.

Fig. 14. As in figure 13, at level of seventh ventral nerve.

Fig. 15. Vertical section of seventh abdominal ganglion showing lobes of neuropile, commissures, longitudinal tracts and groups of neurocytes (arrow points anterad).

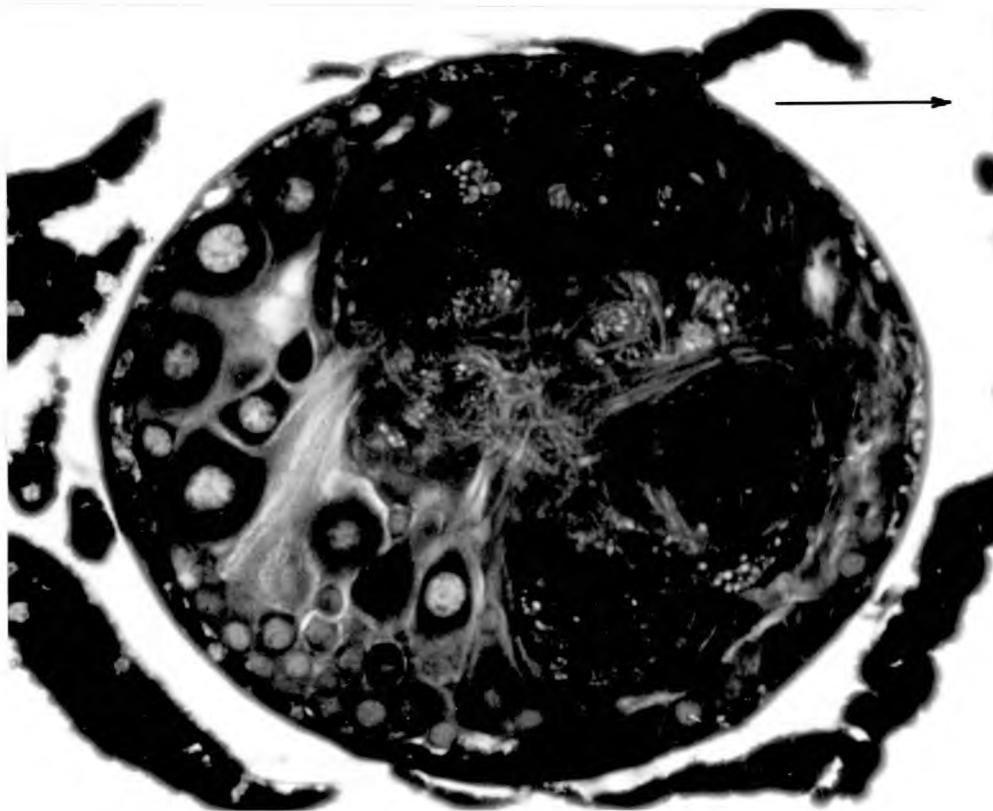


Fig. 16. Median ventral internuncial neurone group of the seventh abdominal ganglion. (Sagittal section x240, arrow points anterad.)

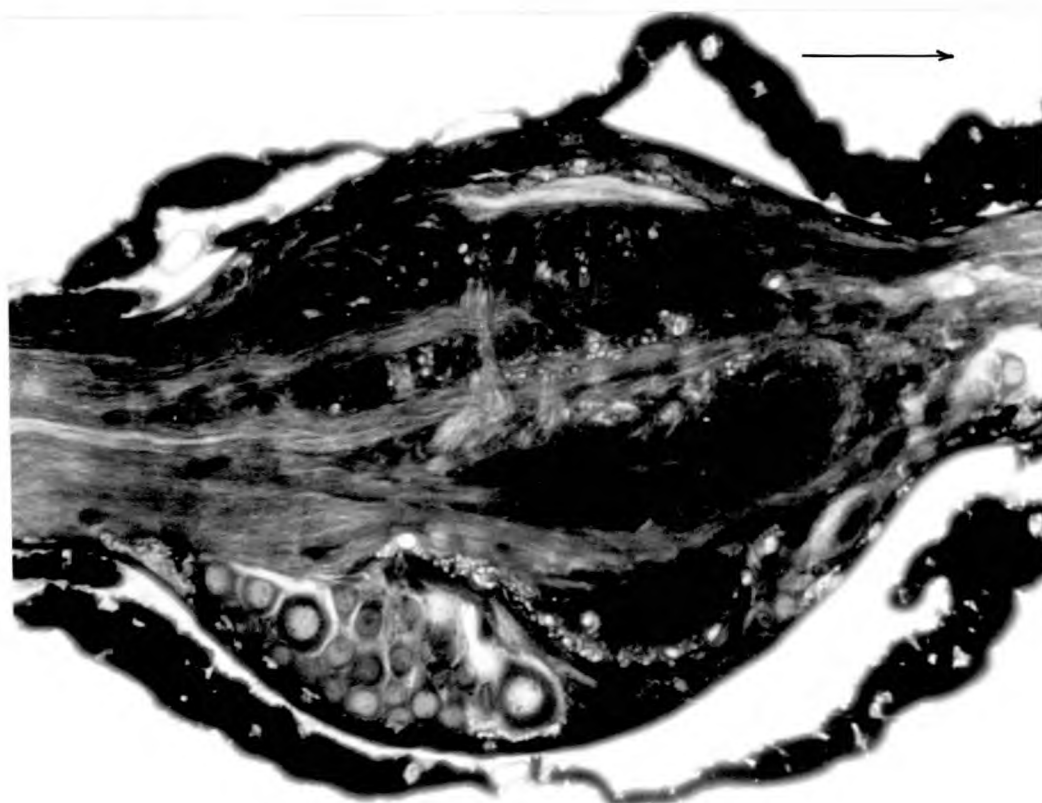


Fig. 17. Longitudinal tracts passing through the seventh abdominal ganglion. (Vertical section x230, arrow points anterad.)

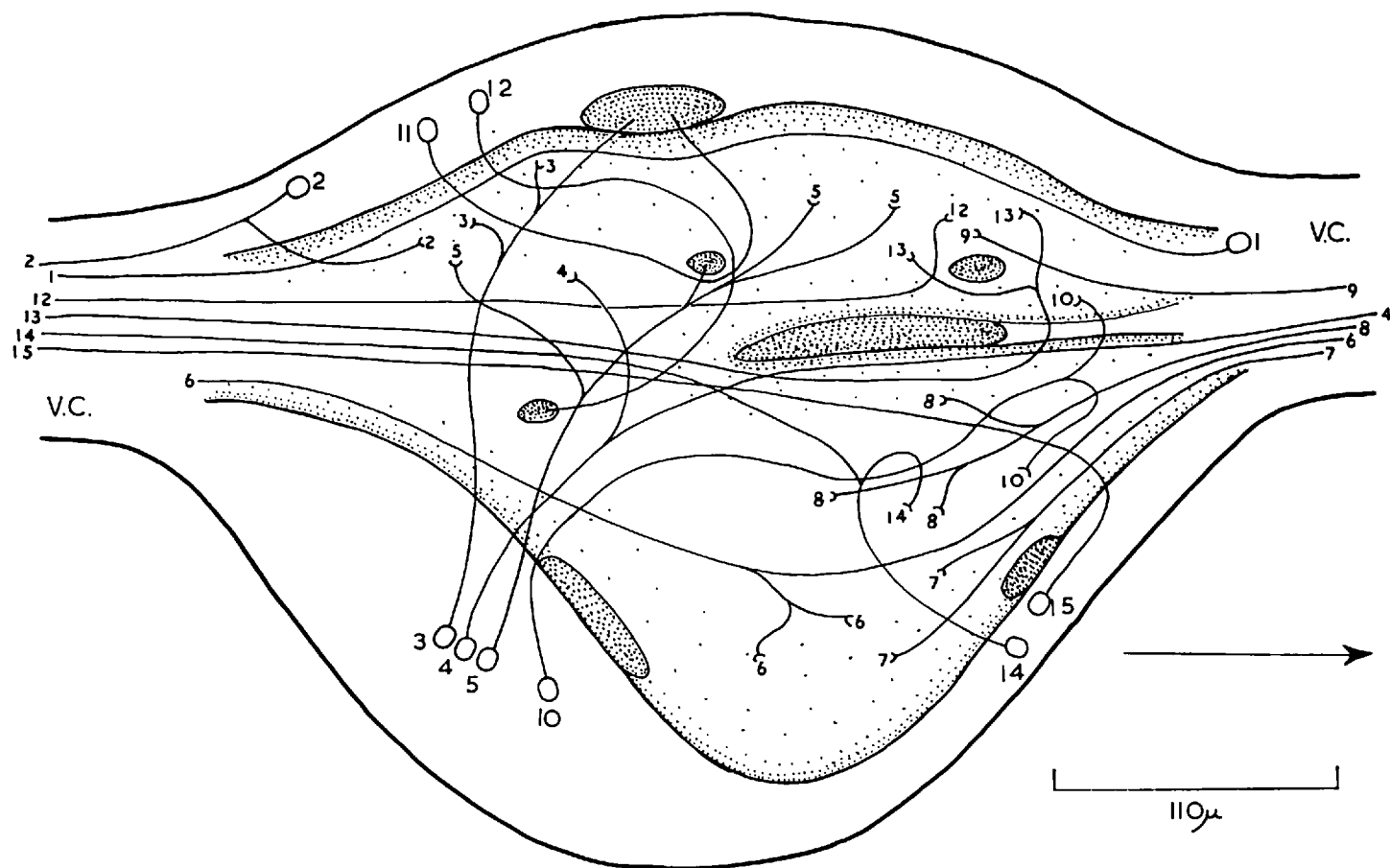


Fig. 18. Neurones of the seventh abdominal ganglion compiled from a series of vertical sections extending from the margin to the level of the lateral ventral group of interneurones (arrow points anterad).

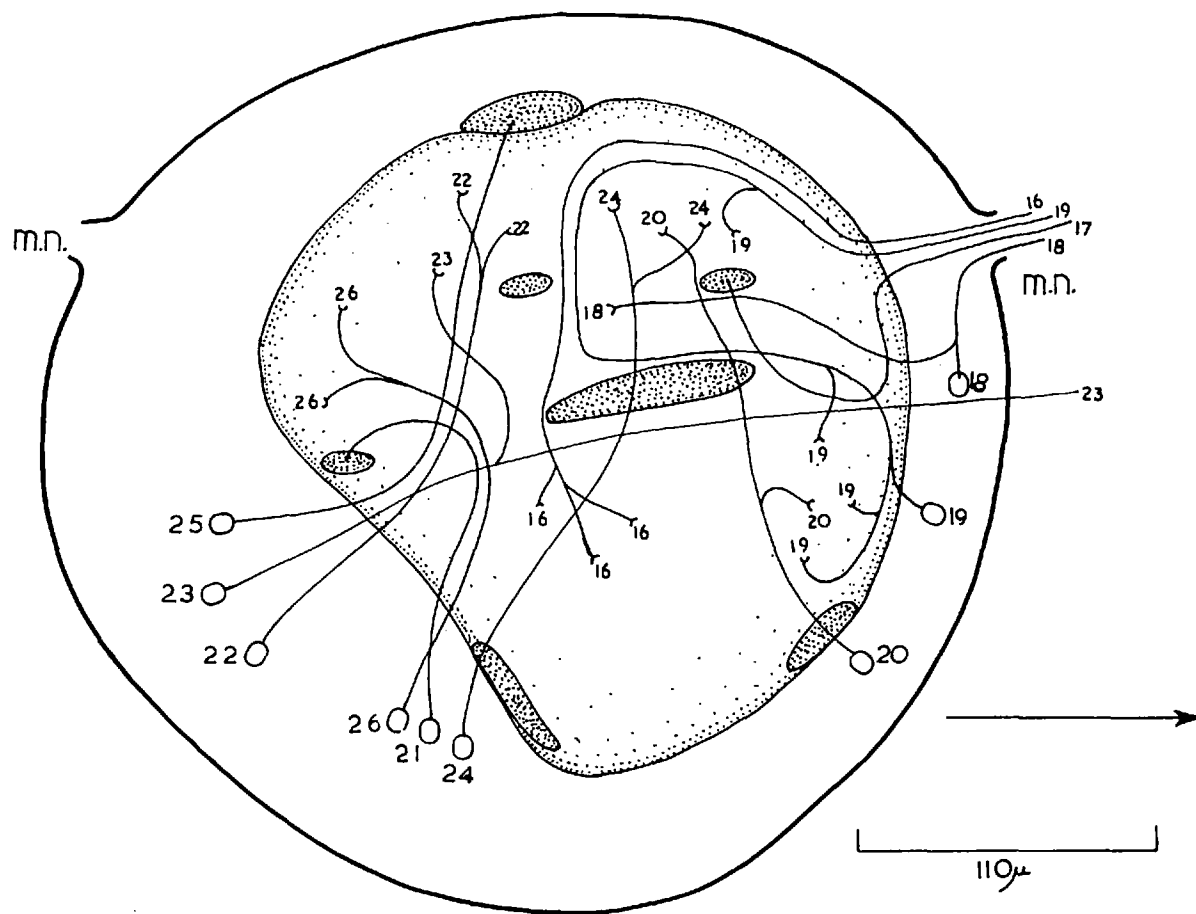


Fig. 19. Neurones of the seventh abdominal ganglion compiled from a series of vertical sections in the region of the median ventral group of interneurones (arrow points anterad).

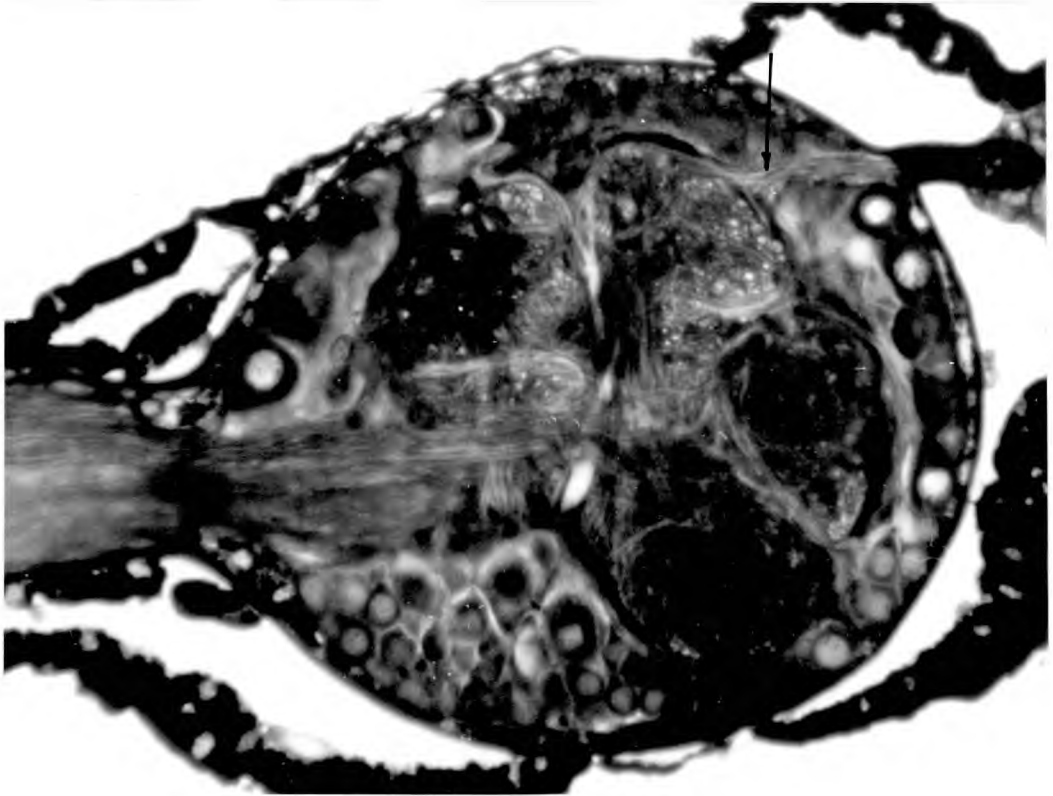


Fig. 20. Sagittal section through the seventh abdominal ganglion showing the distribution of fibres of the median nerve (arrow) (x220).

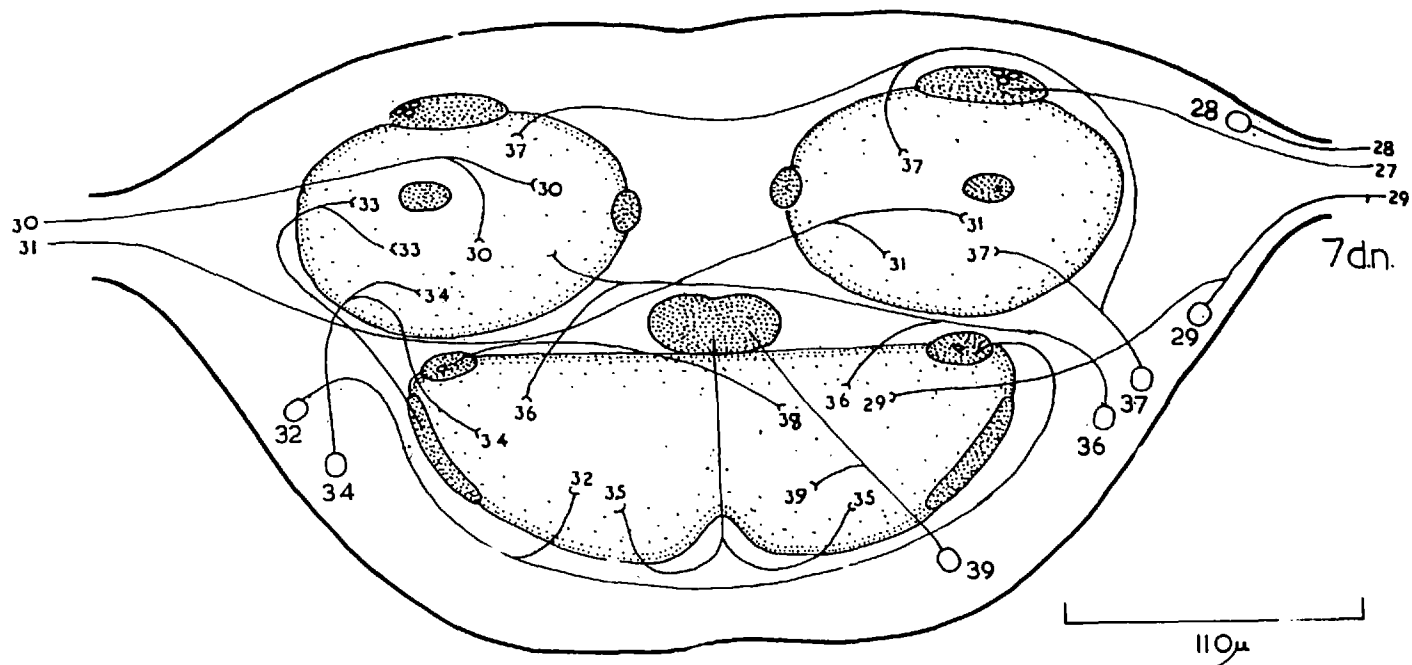


Fig. 21. Neurones of the seventh abdominal ganglion compiled from a series of transverse sections extending from the anterior margin to the level of the seventh dorsal nerve.

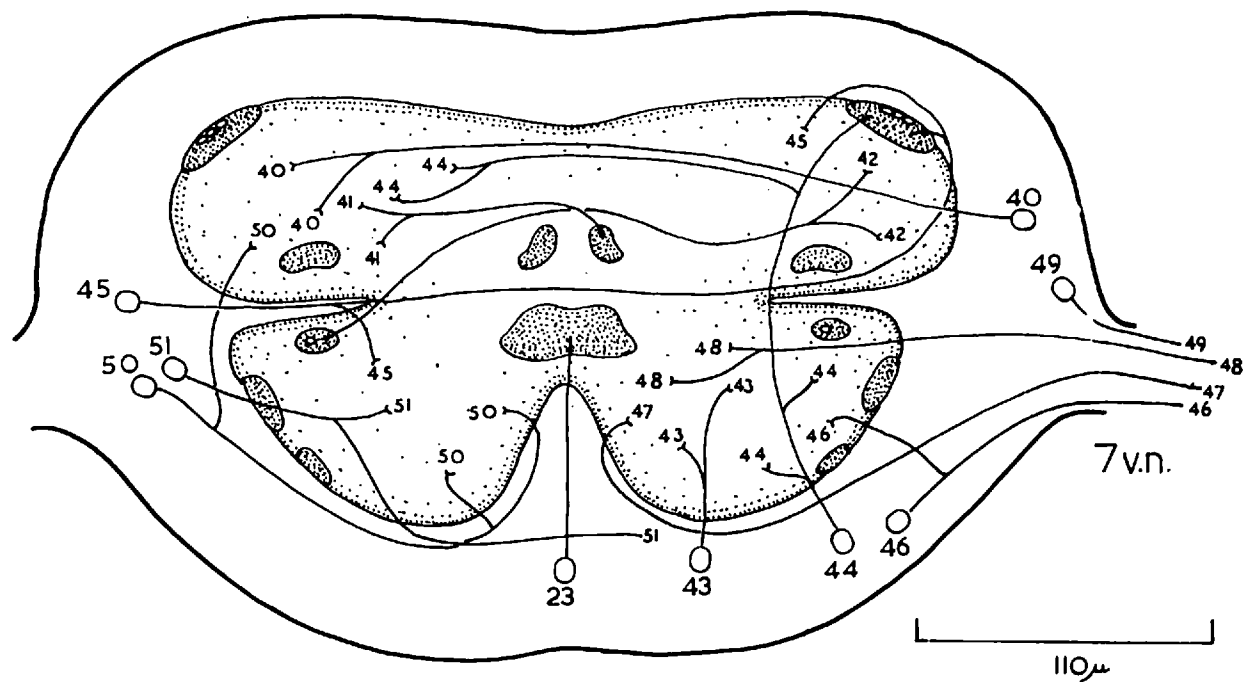


Fig. 22. Neurones of the seventh abdominal ganglion compiled from a series of transverse sections extending posterad from the level of the seventh ventral nerve.

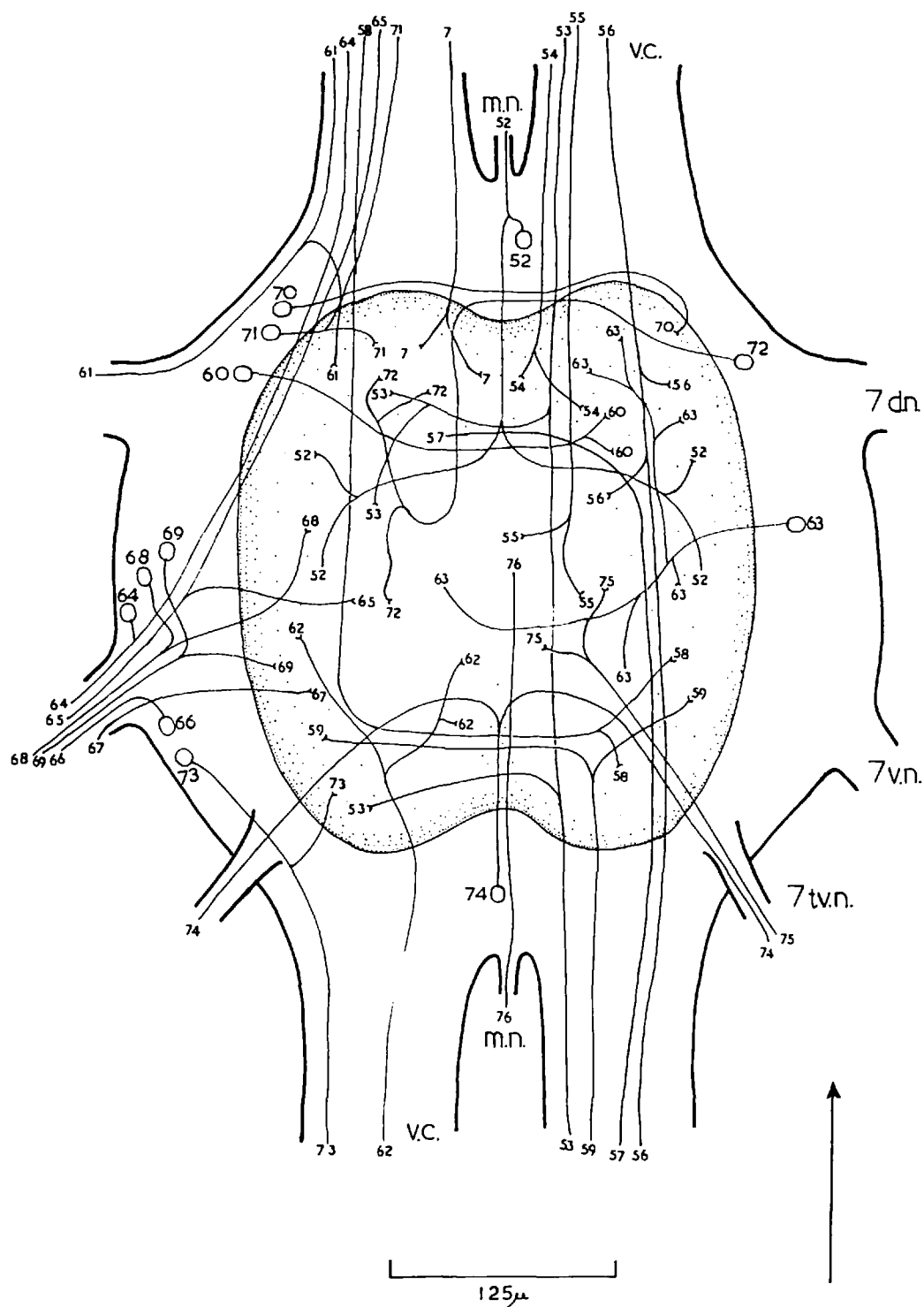


Fig. 23. Neurones of the seventh abdominal ganglion compiled from a series of frontal sections. (Arrow points anterad.)

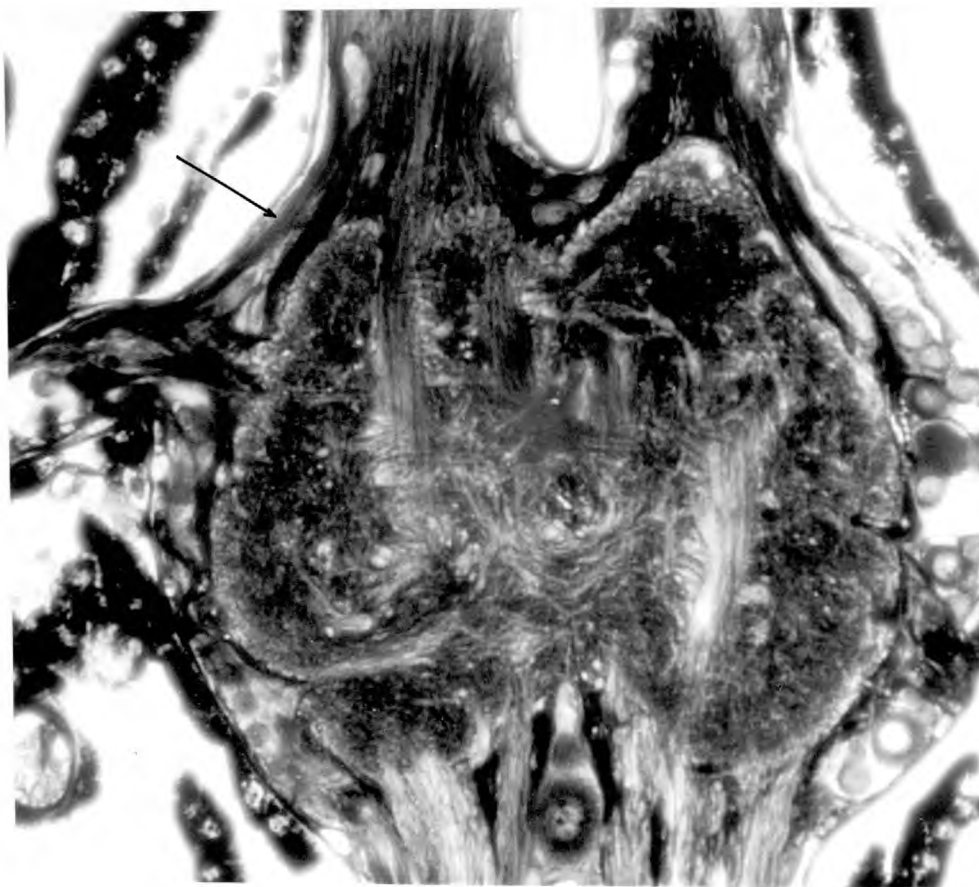


Fig. 24. Fibres of the seventh dorsal nerve (arrow) entering the ipsilateral ventral connective to pass to higher centres in the central nervous system. (Frontal section x250.)

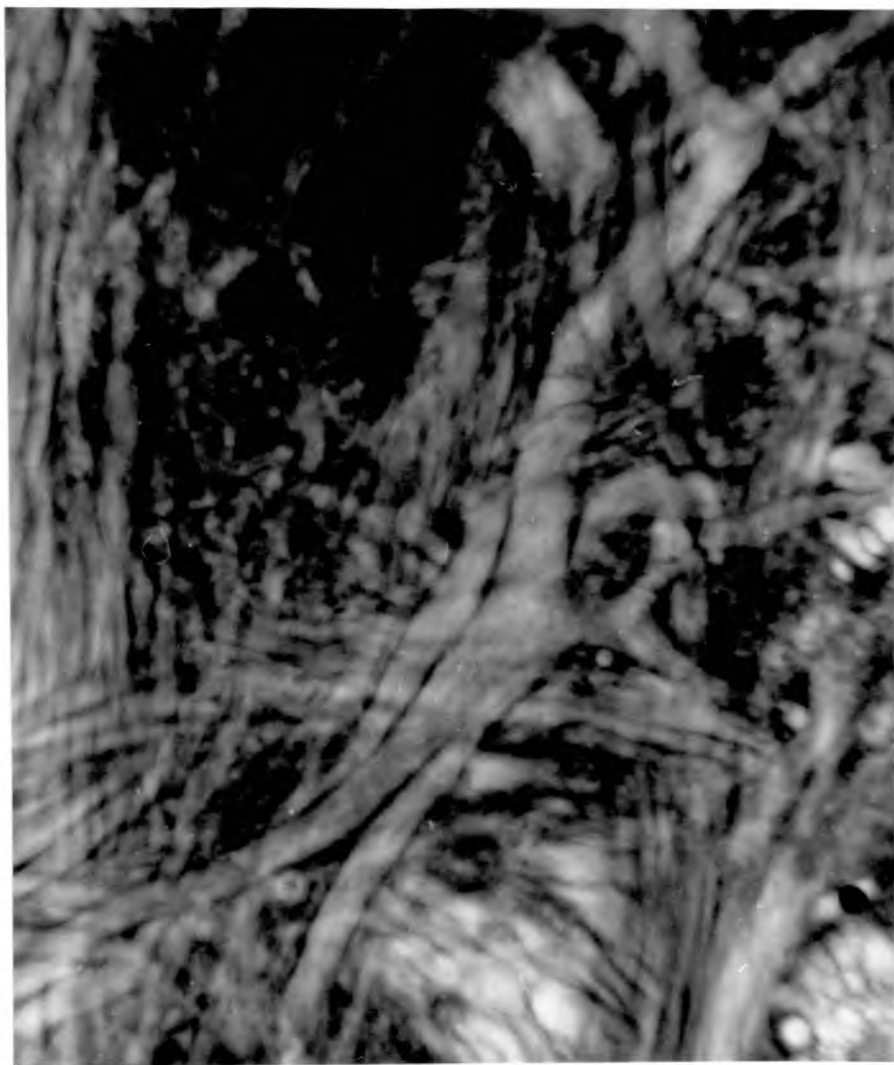


Fig. 25. Large axon branching in the dorsal neuropile of seventh abdominal ganglion. (Frontal section x720.)

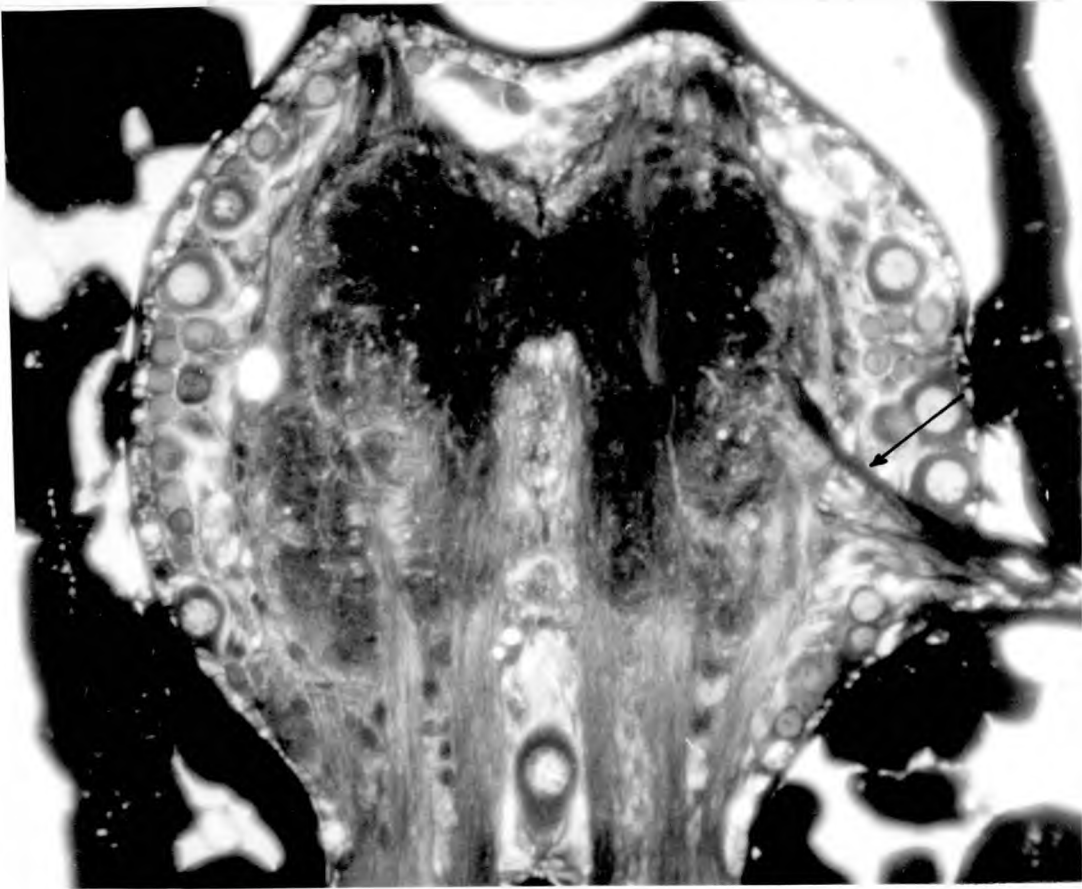


Fig. 26. Fibres of the seventh ventral nerve (arrow) passing through the seventh abdominal ganglion to enter the ipsilateral ventral connective and pass to higher centers in the central nervous system. (Frontal section x 250.)

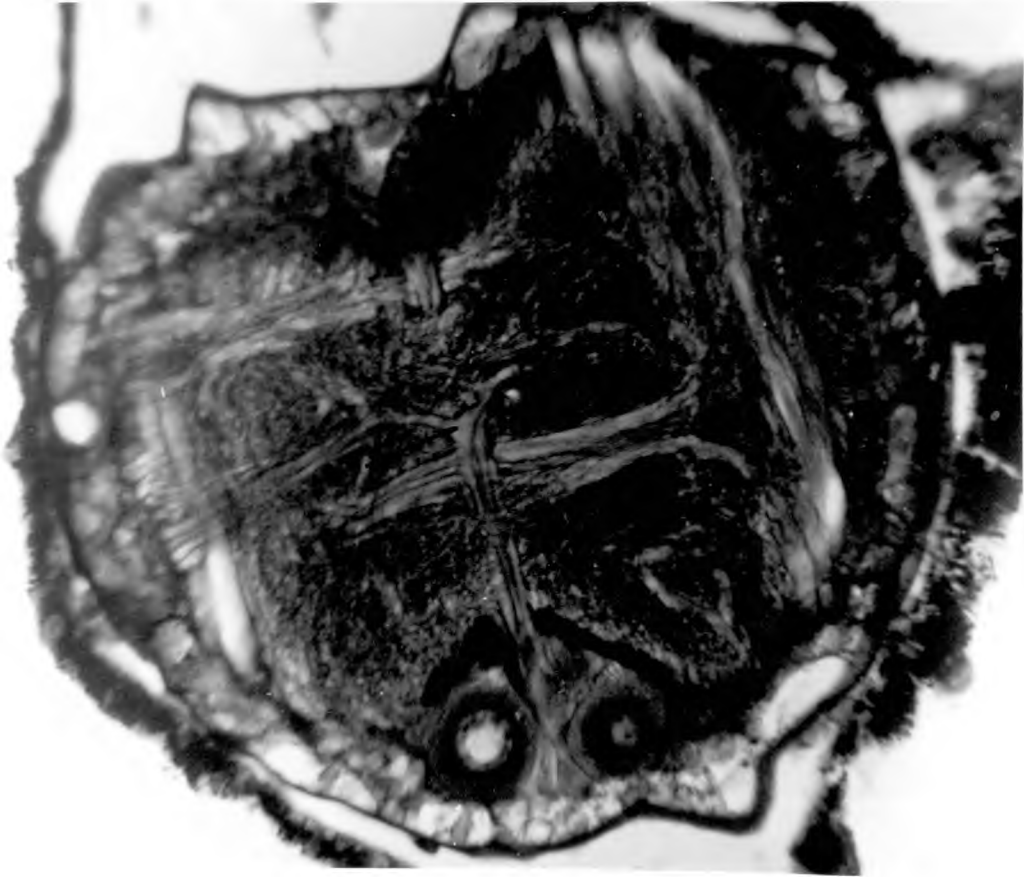


Fig. 27. Motor neurones of the seventh transverse nerve bifurcating (arrow) in the dorsal neuropile of the seventh abdominal ganglion. (Frontal section x280.)

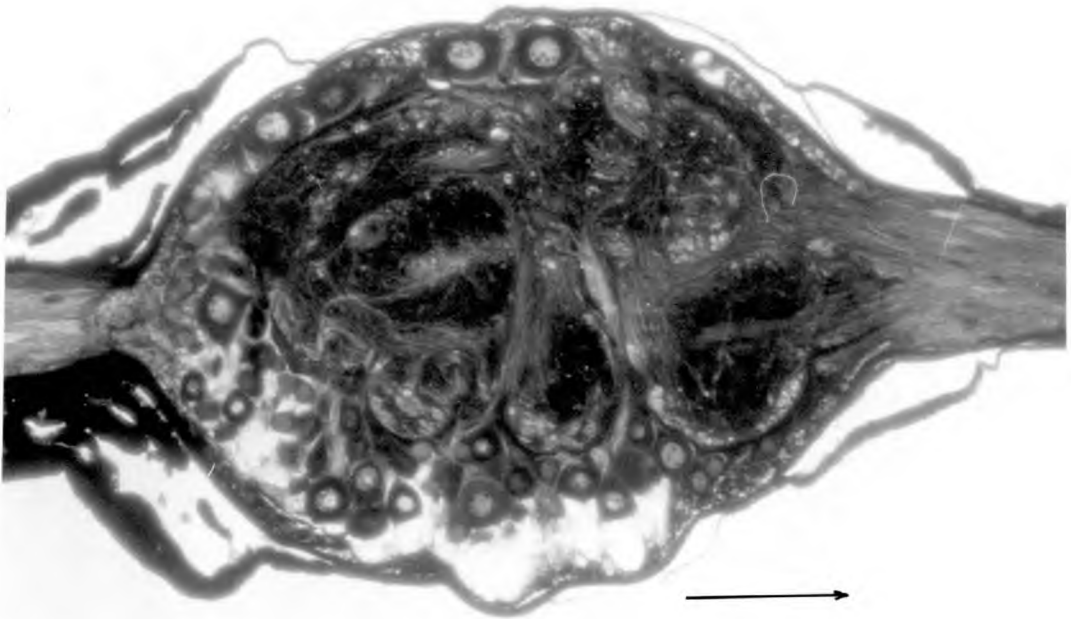
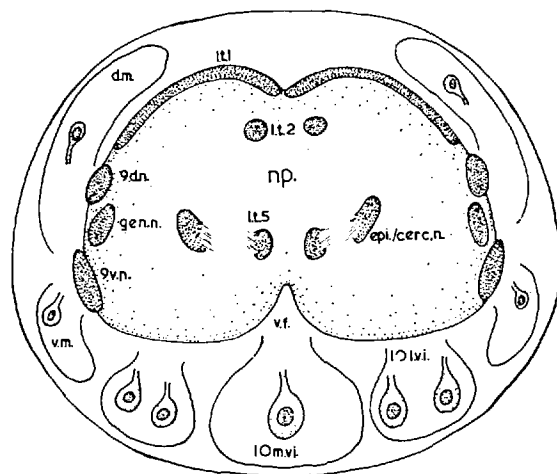
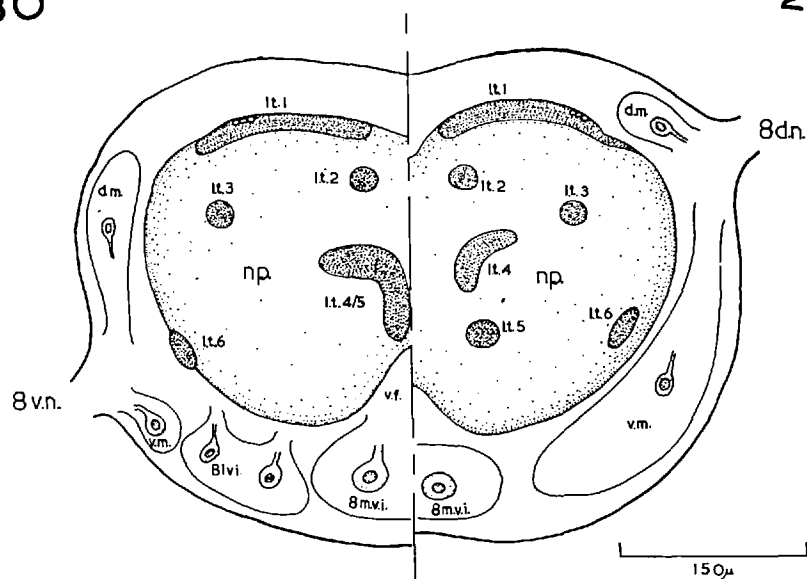


Fig. 28. Vertical section through the terminal ganglionic mass showing major groups of ventral internuncial neurones. The four cell groups indicate the ganglia that fused to form the terminal ganglionic mass (arrow points anterad) (xl60).

30

29



31

Transverse sections of terminal ganglionic mass showing longitudinal tracts and groups of neurocytes.

Fig. 29. At the level of the eighth dorsal nerve.

Fig. 30. At the level of the eighth ventral nerve.

Fig. 31. At the level of the ventral interneurone groups of tenth abdominal ganglion.

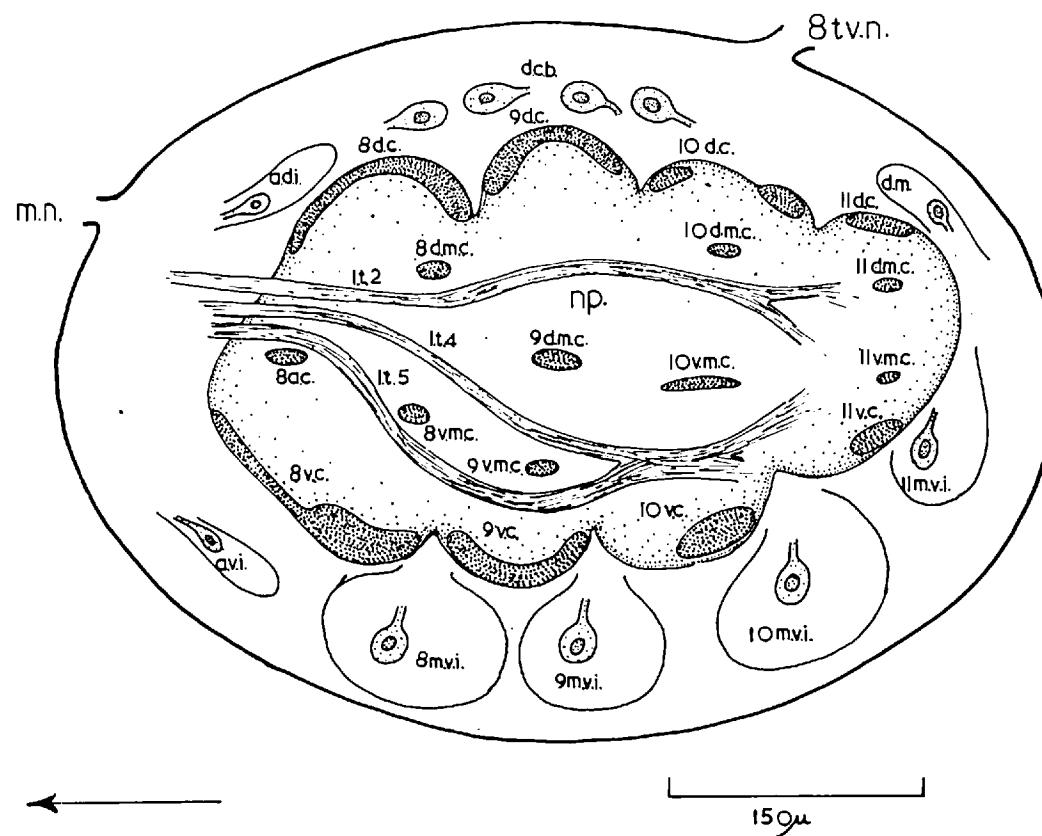


Fig. 32. Saggital section of terminal ganglionic mass showing neuropile, commissures, longitudinal tracts and groups of neurocytes (arrow points anterad).



Fig. 33. Longitudinal fibre tracts entering the terminal ganglionic mass. (Vertical section x170.)

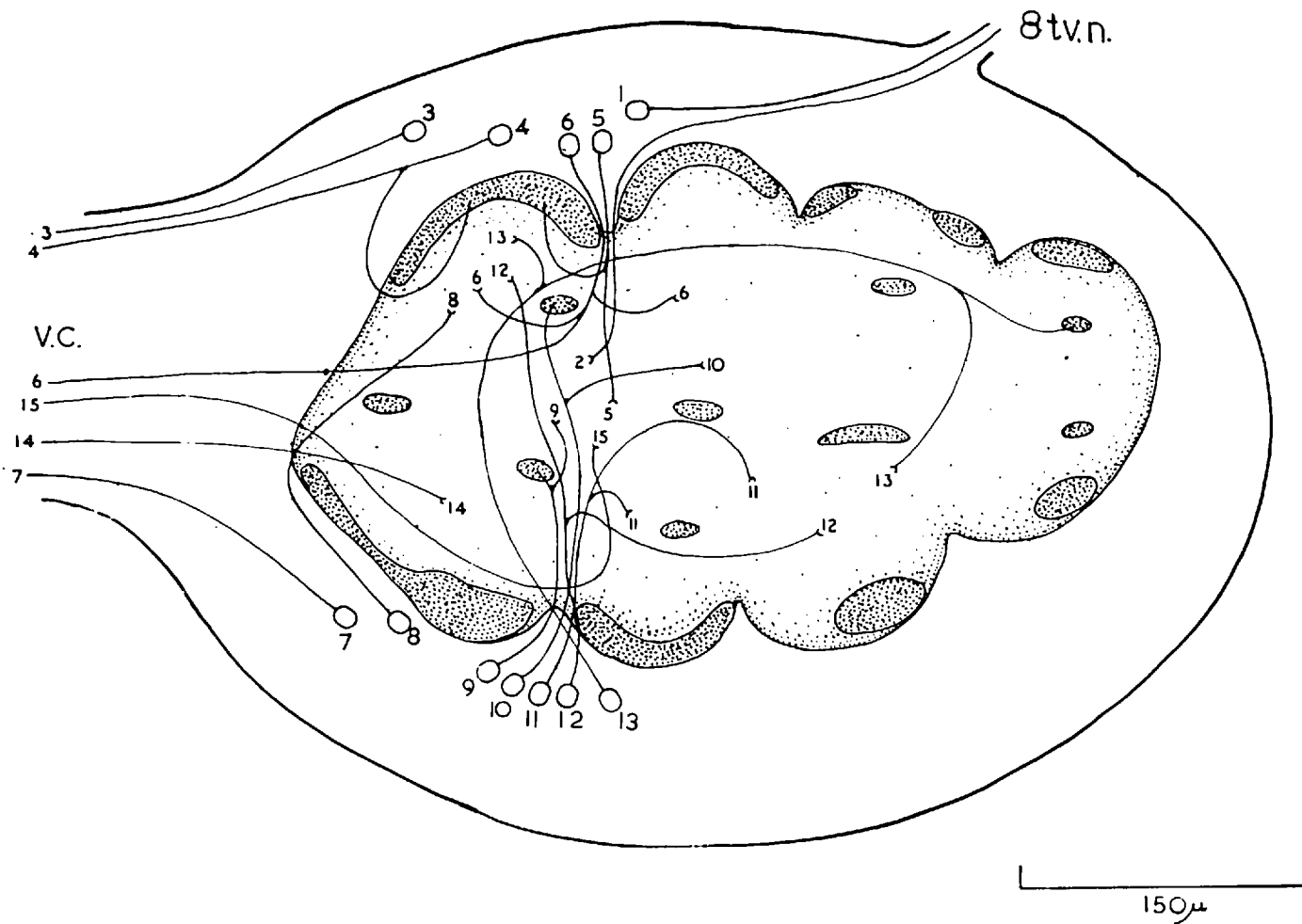


Fig. 34. Neurones of the eighth abdominal ganglion compiled from a series of vertical sections of the terminal ganglionic mass.

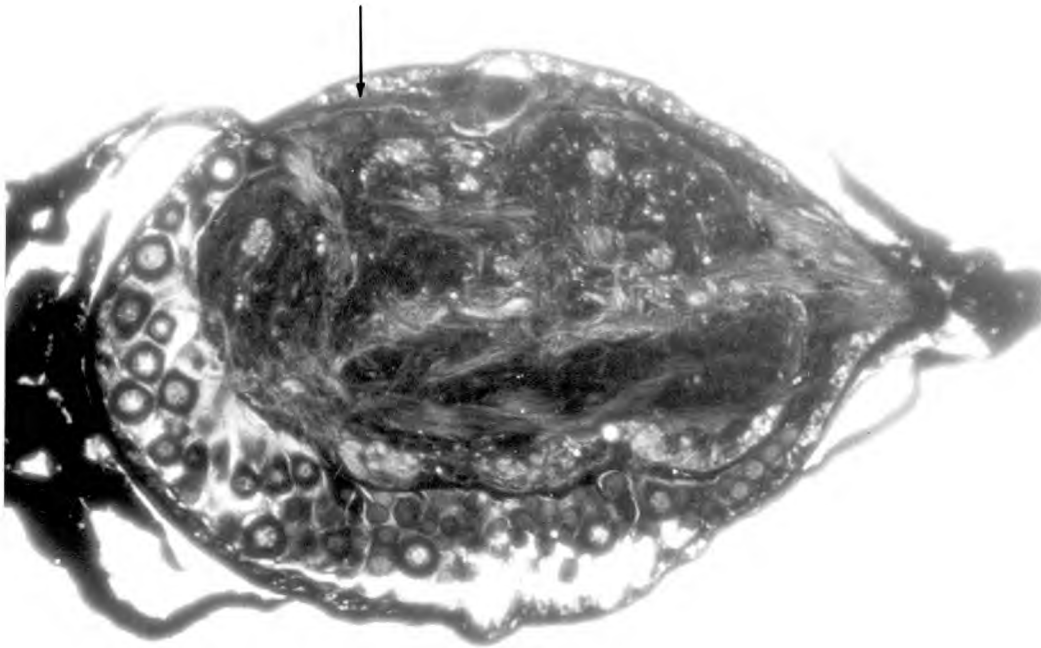


Fig. 35. Vertical section through the terminal ganglionic mass showing origin of the eighth transverse nerve (arrow) (x160).

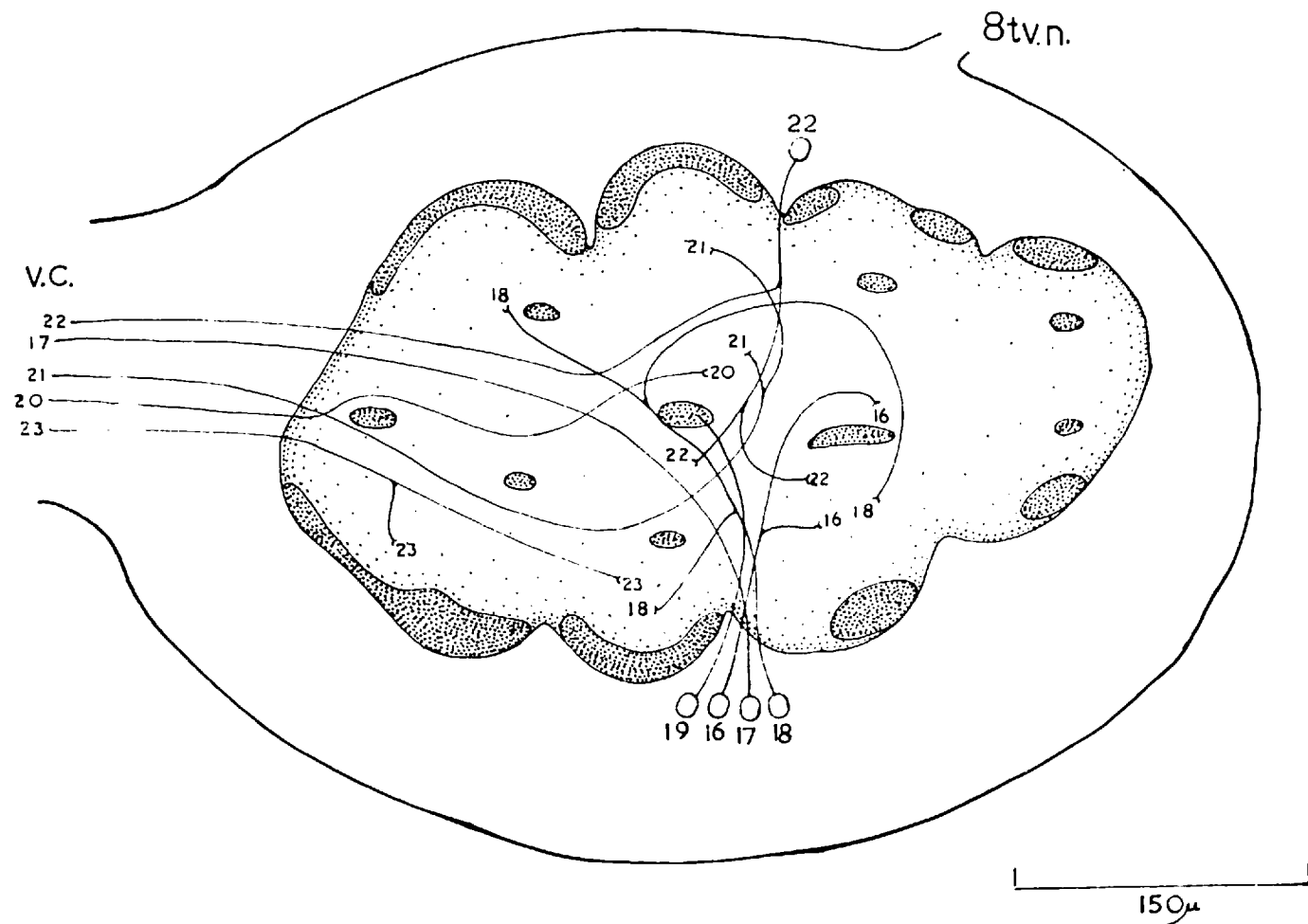


Fig. 36. Neurones of the ninth abdominal ganglion compiled from a series of vertical sections of the terminal ganglionic mass.

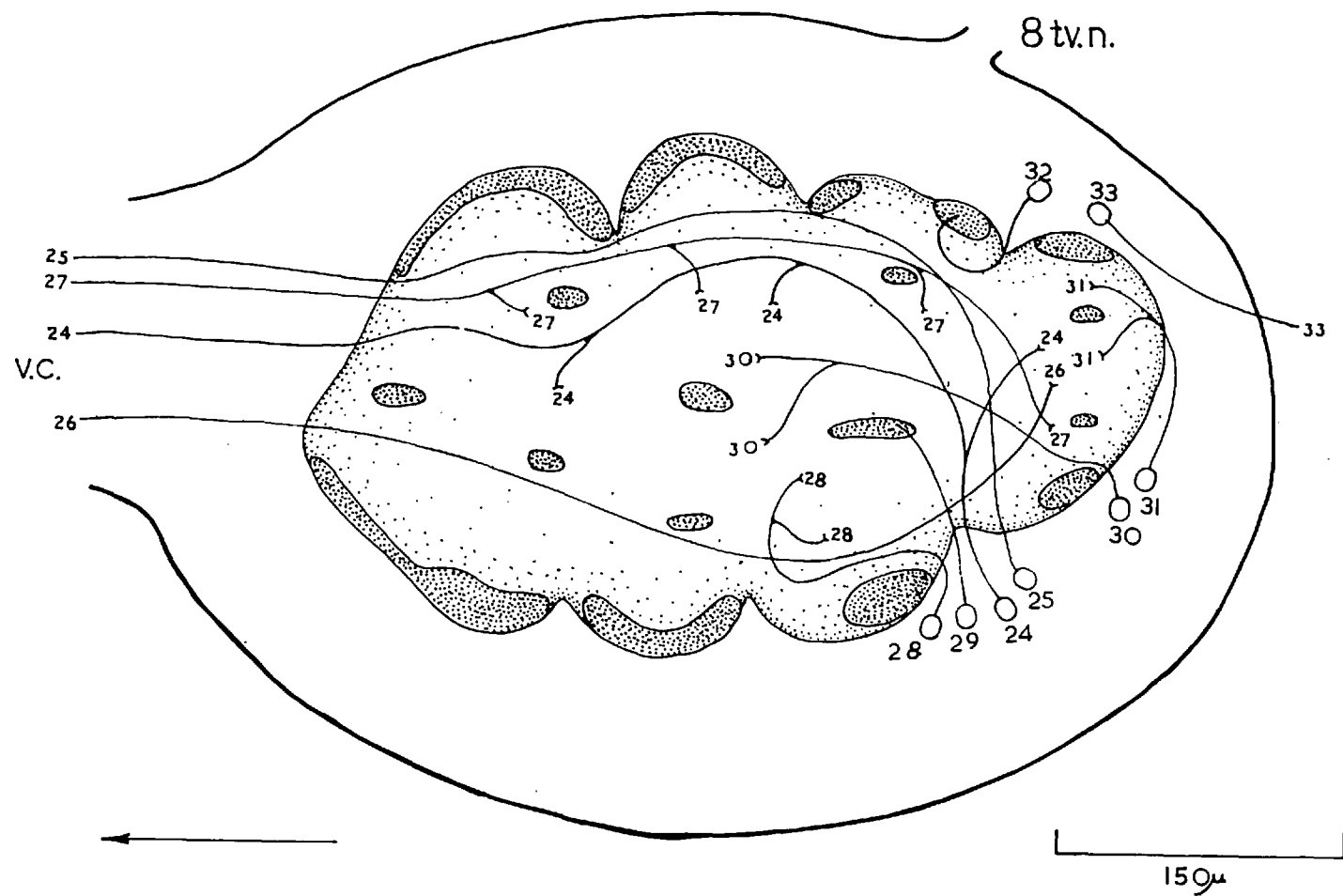


Fig. 37. Neurones of the tenth and eleventh abdominal ganglia compiled from a series of vertical sections of the terminal ganglionic mass. (Arrow points anterad.)

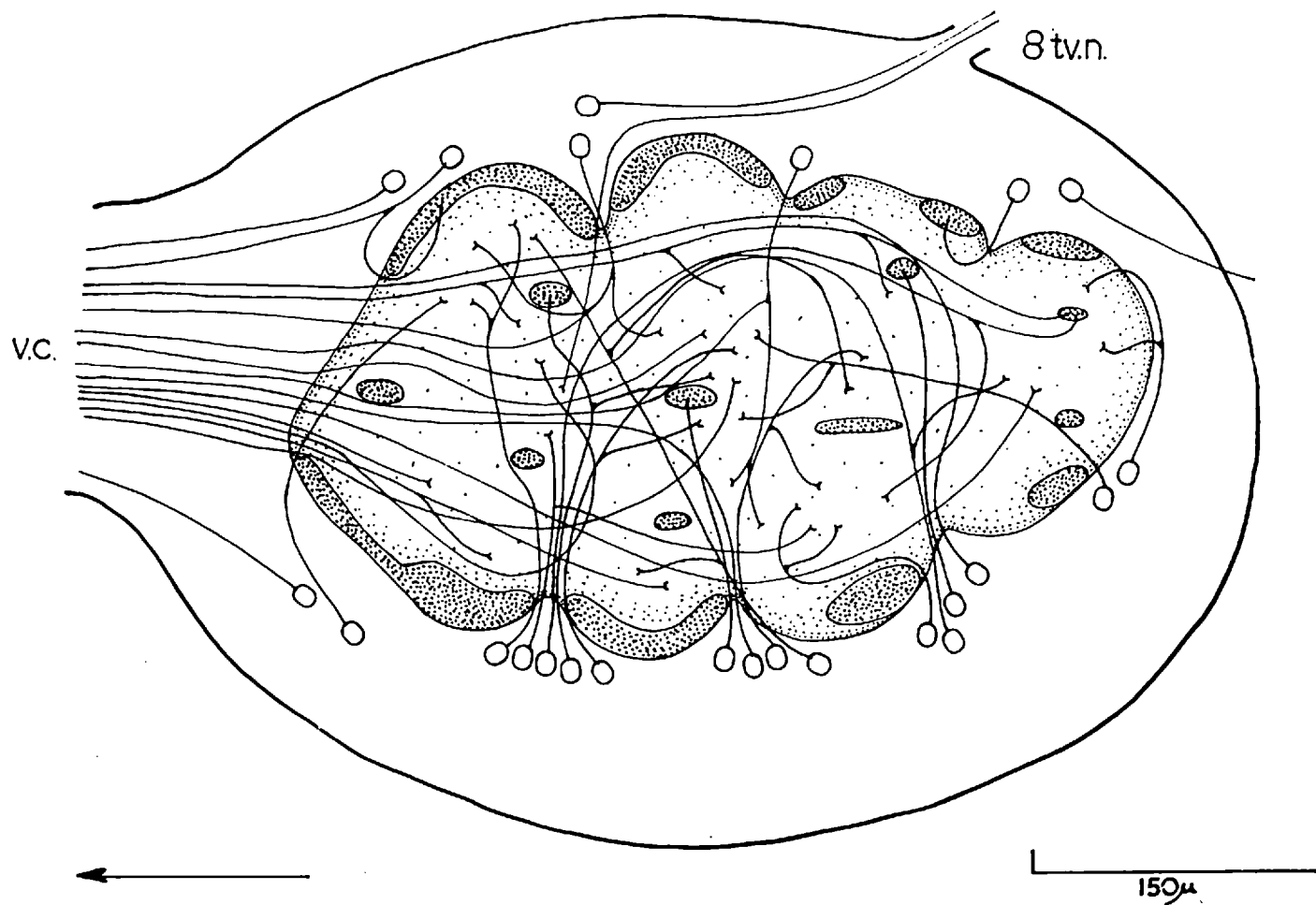


Fig. 38. Composite figure of terminal ganglionic mass showing those neurones illustrated in figures 34, 36 and 37. Neurone numbers omitted for clarity. (Arrow points anterad.)

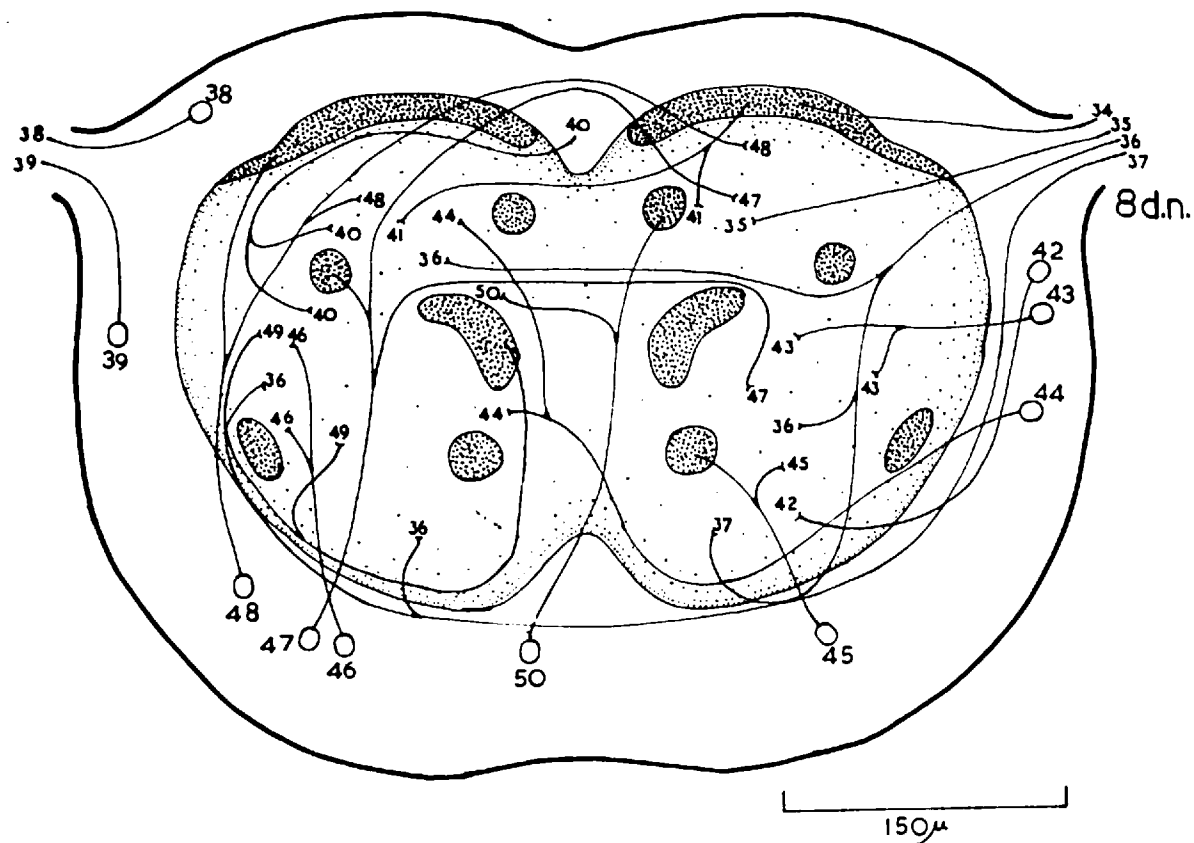


Fig. 39. Neurones of the terminal ganglionic mass compiled from a series of transverse sections extending from the anterior margin of the ganglionic mass to the level of the eighth ventral interneurone groups.

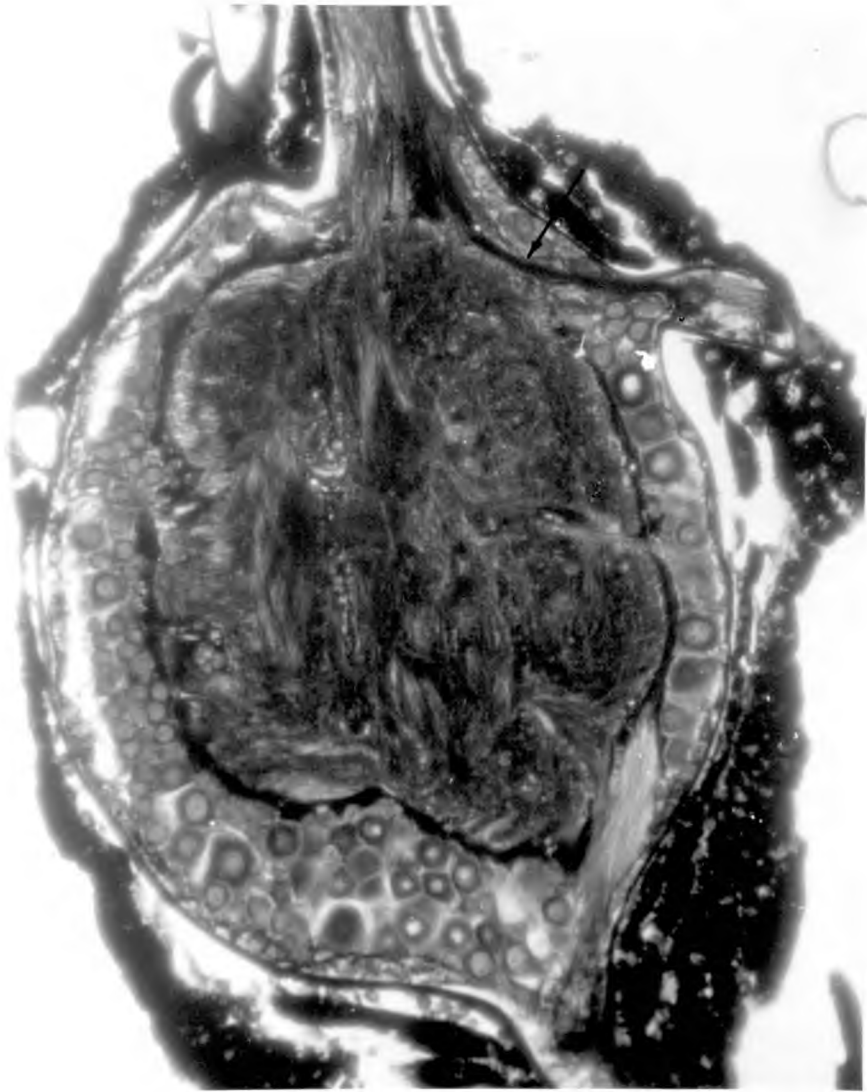


Fig. 40. **Fibros** of the eighth dorsal nerve (arrow) entering the ipsilateral ventral connective to pass to higher centers in the central nervous system. (Frontal section xl85).

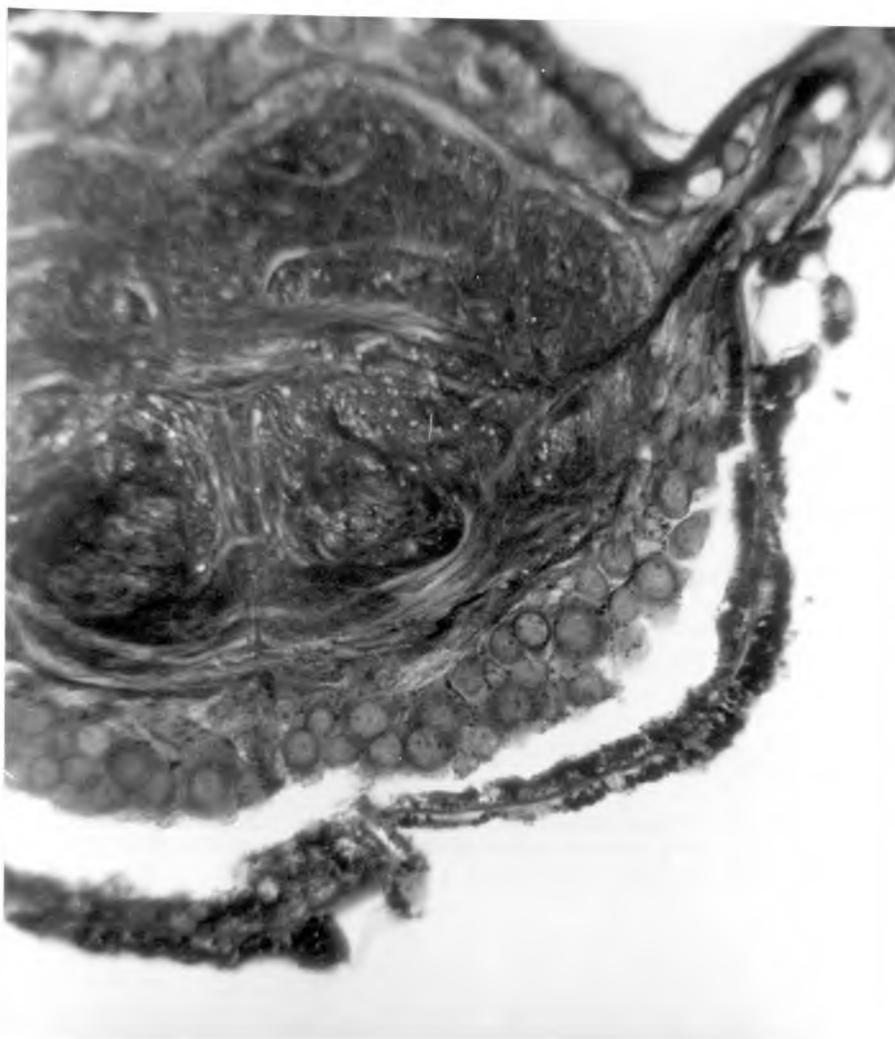


Fig. 41. Sensory neurones of the eighth dorsal nerve entering the eighth abdominal ganglion. (Transverse section x260).

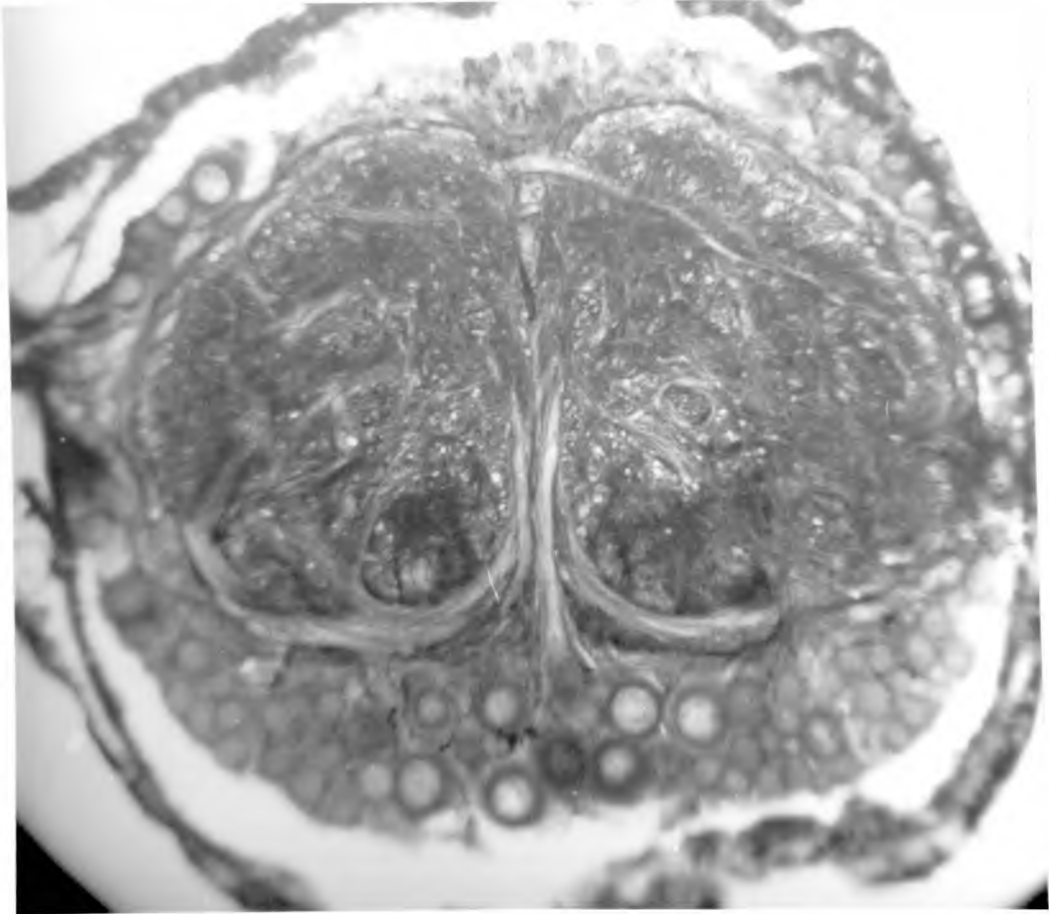


Fig. 42. Transverse section through the terminal ganglionic mass in the region of the ninth median ventral group of interneurons. (x240)

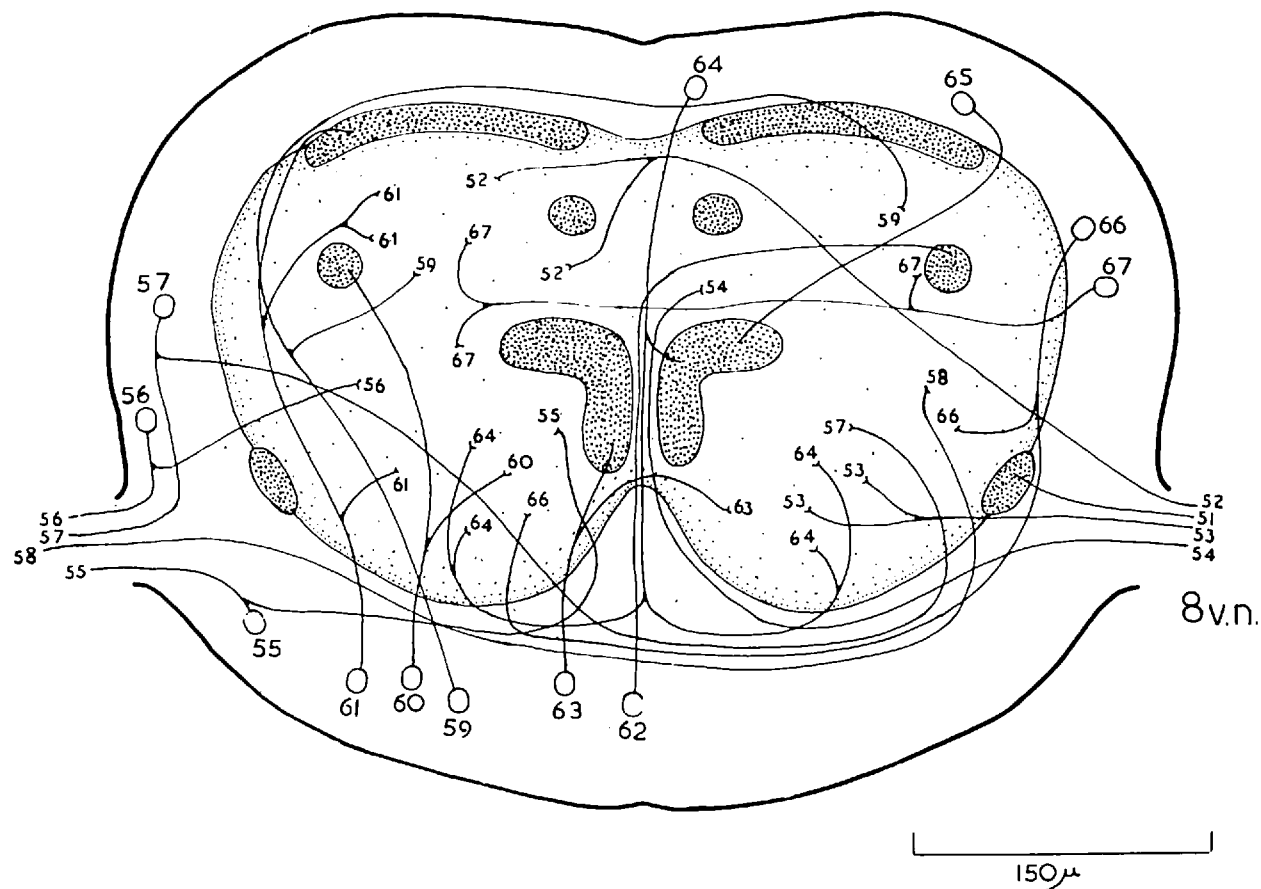


Fig. 43. Neurones of the terminal ganglionic mass compiled from a series of transverse sections extending from the eighth ventral groups of interneurons to the ninth ventral groups of interneurons.

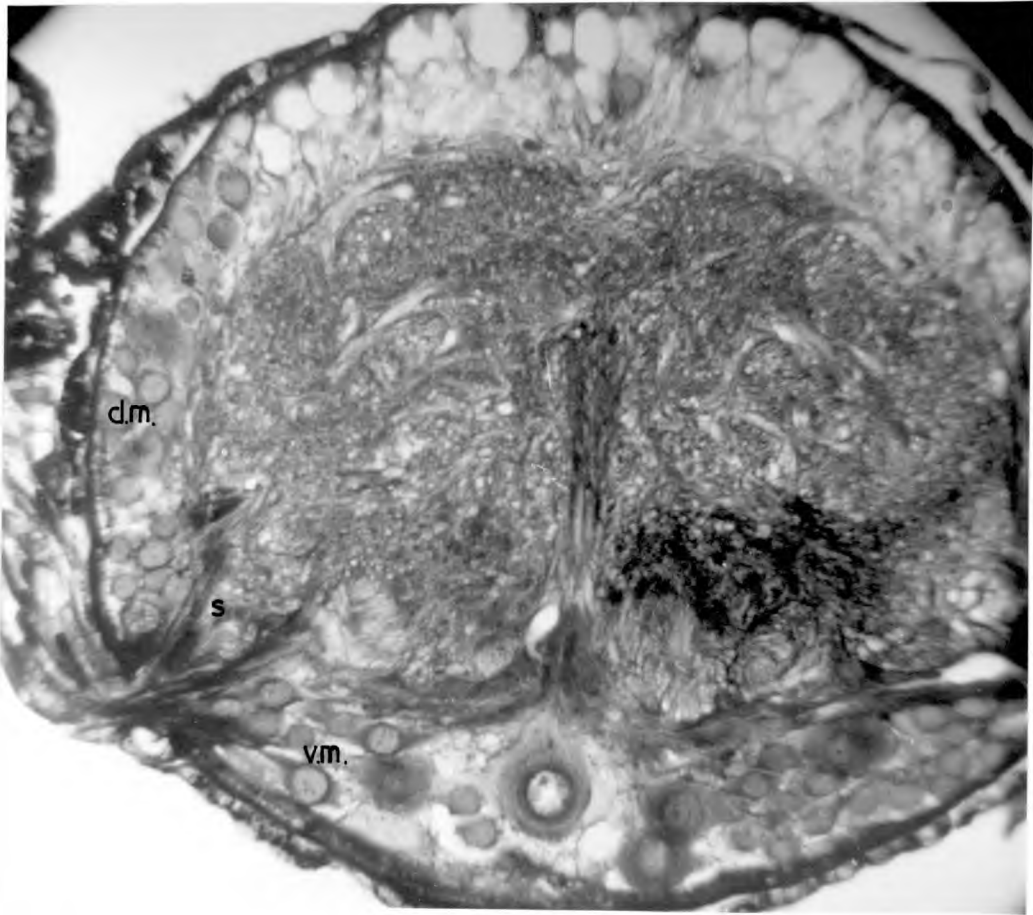


Fig. 44. Sensory neurones (s) of the eighth ventral nerve entering the eighth abdominal ganglion. Motor neurones of the ventral group (v.m.) enter the segmental nerve. (Transverse section x260.)

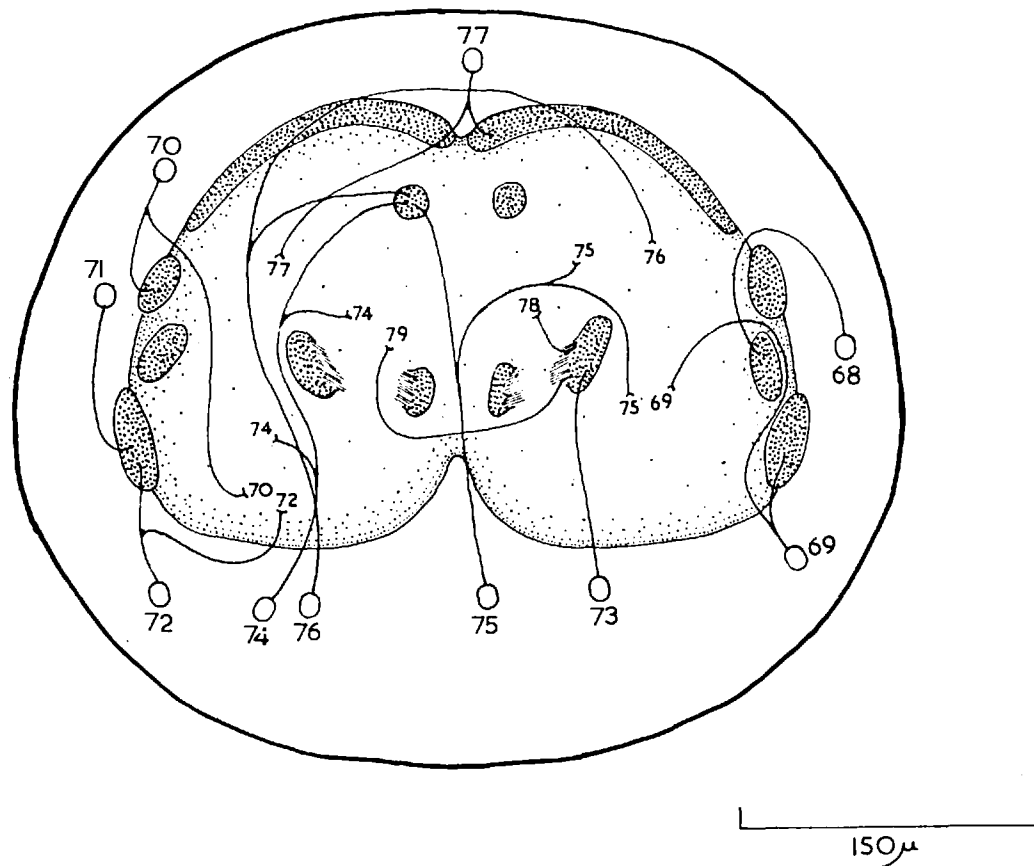


Fig. 45. Neurones of the terminal ganglionic mass compiled from a series of transverse sections extending from the level of the ninth ventral groups of interneurones to the tenth ventral group of interneurones.

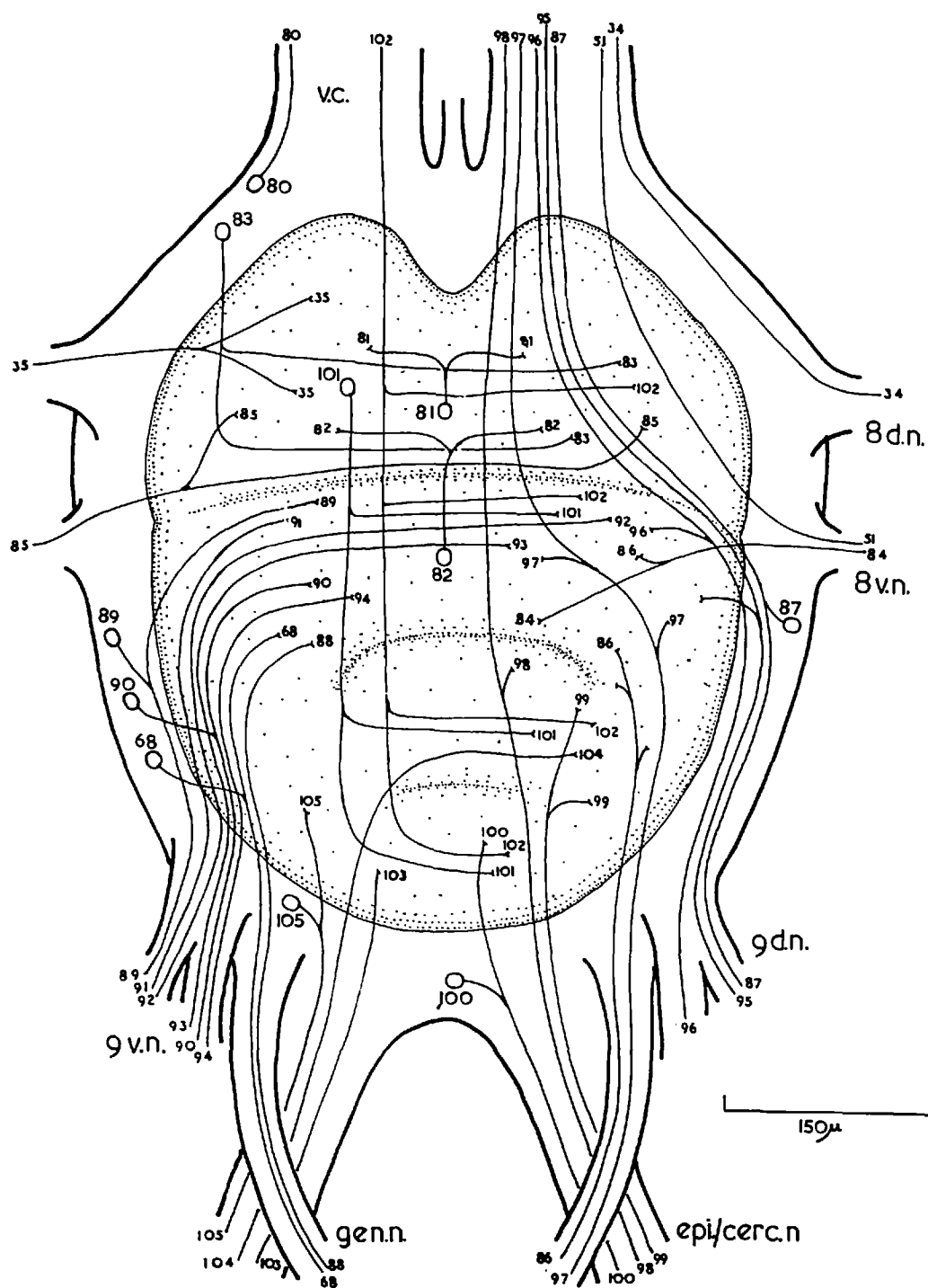


Fig. 46. Neurones of the terminal ganglionic mass compiled from a series of frontal sections.

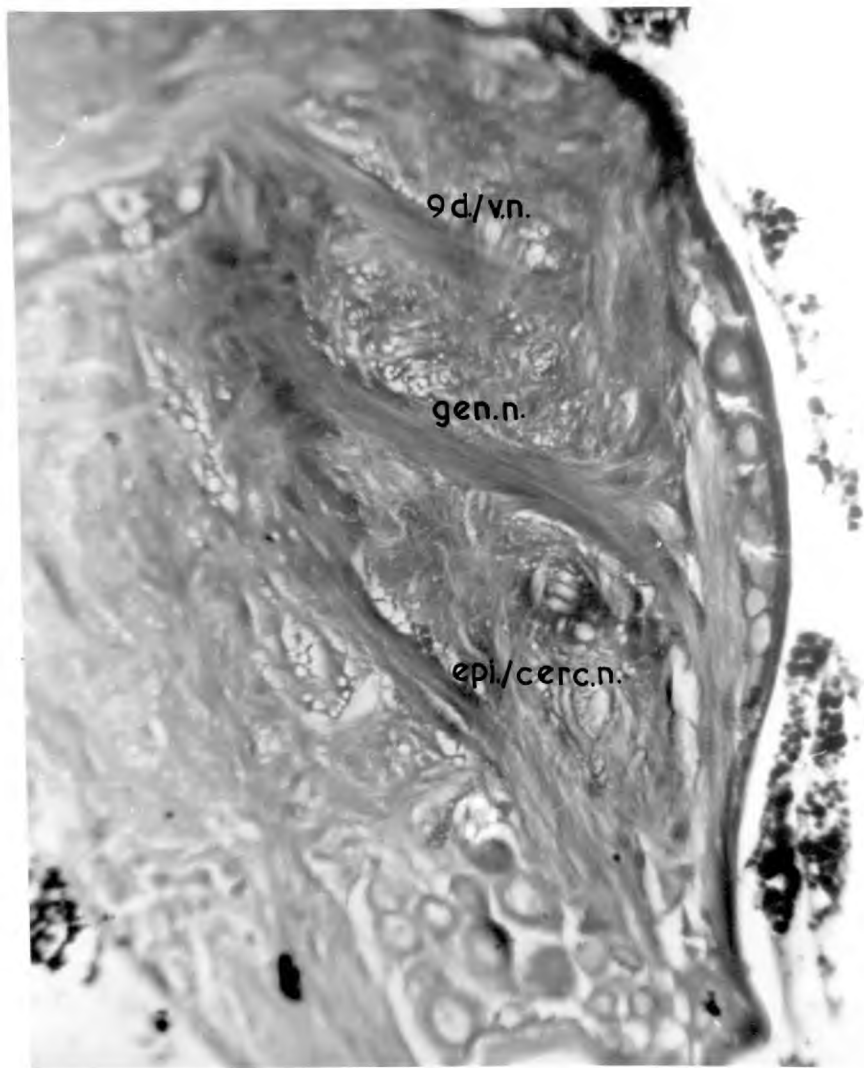


Fig. 47. Fibres of the fused epiroot/cerc ⁷ nerve, genital nerve, and the fused ninth dorsal/ventral nerve passing through the terminal ganglionic mass to enter the ipsilateral ventral connective. (Frontal section x260.)

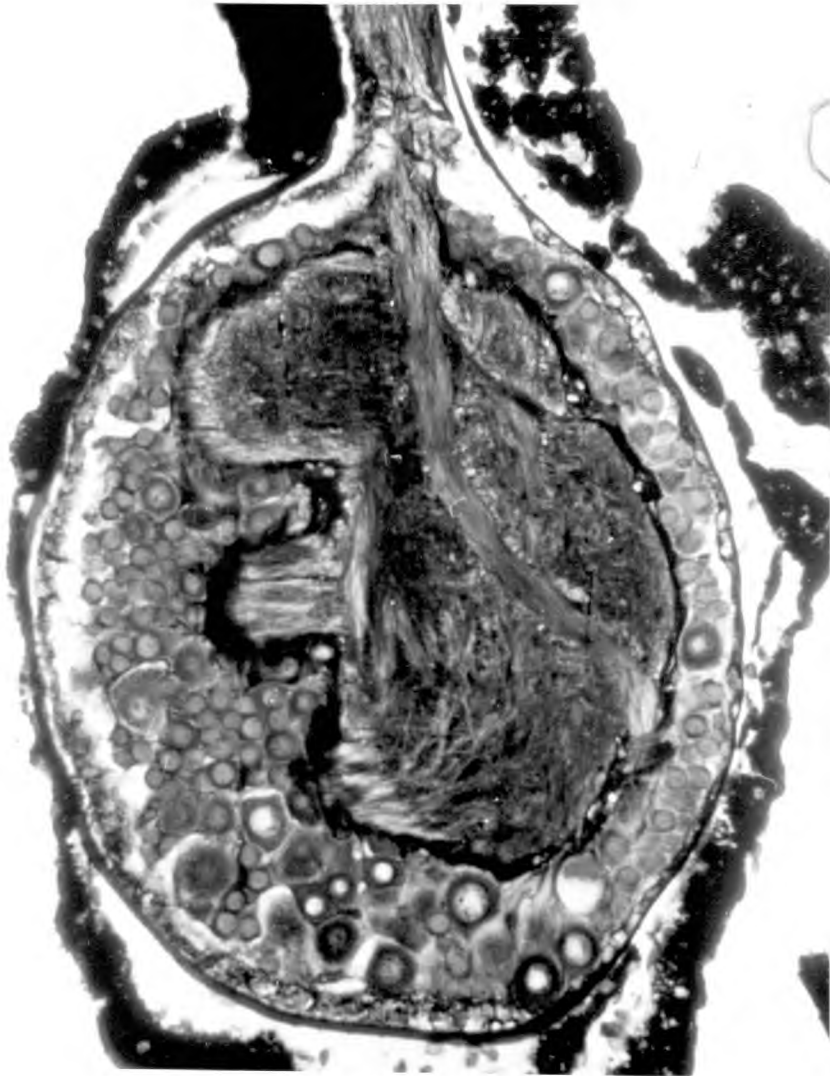


Fig. 48. Fibres of the genital nerve passing through the terminal ganglionic mass and entering the ipsilateral ventral connective. (Frontal section xl80.)

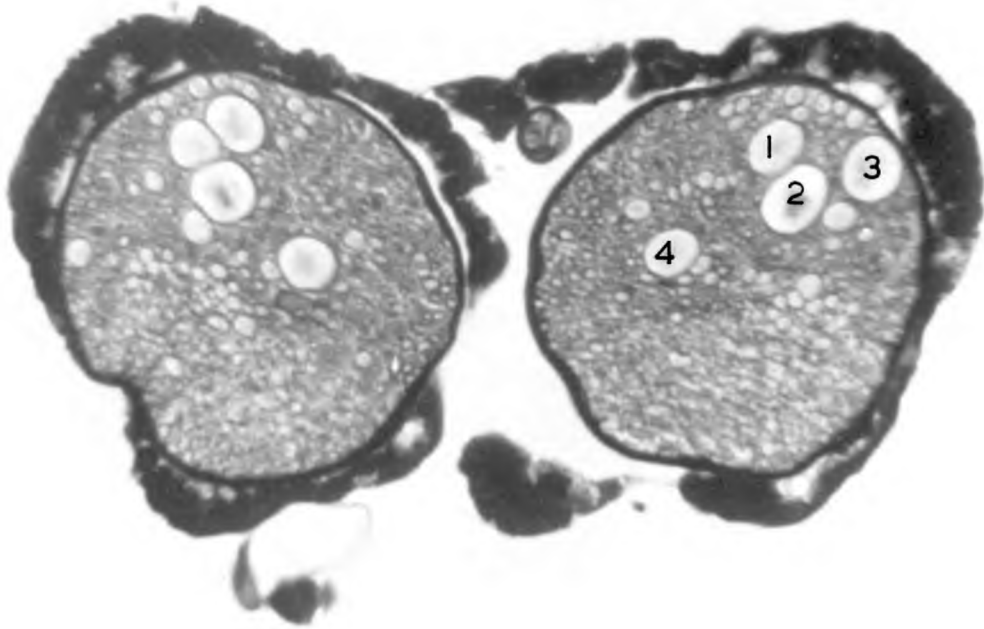


Fig. 49. Transverse section through the ventral nerve cord between the seventh abdominal ganglion and the terminal ganglionic mass showing giant fibres. (x535)

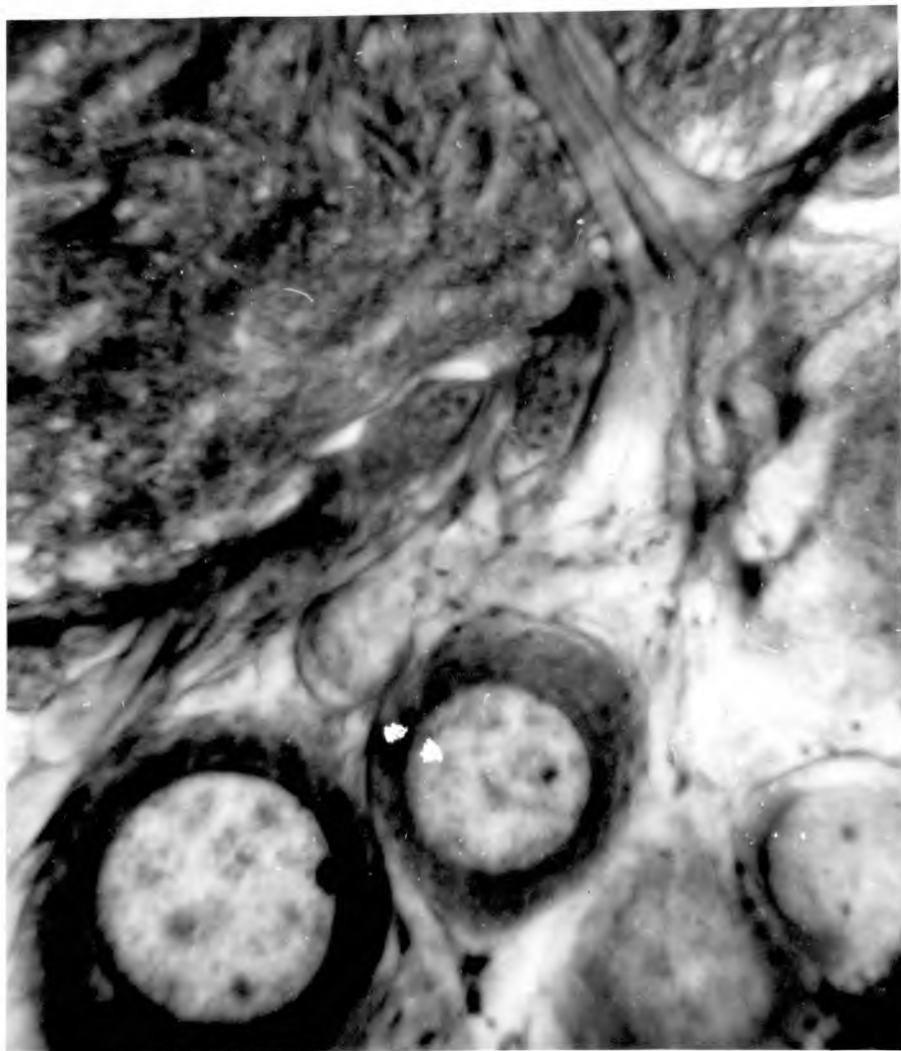


Fig. 50. Nerve cell bodies of the dorsal group of giant fibres located in the tentorial lateral ventral group of internuncial neurones (x2300).



Fig. 51. Vertical section of the terminal ganglionic mass showing reduction in the diameter of a giant fibre (arrow) as it enters the dorsal region of the neuropile (xl30).

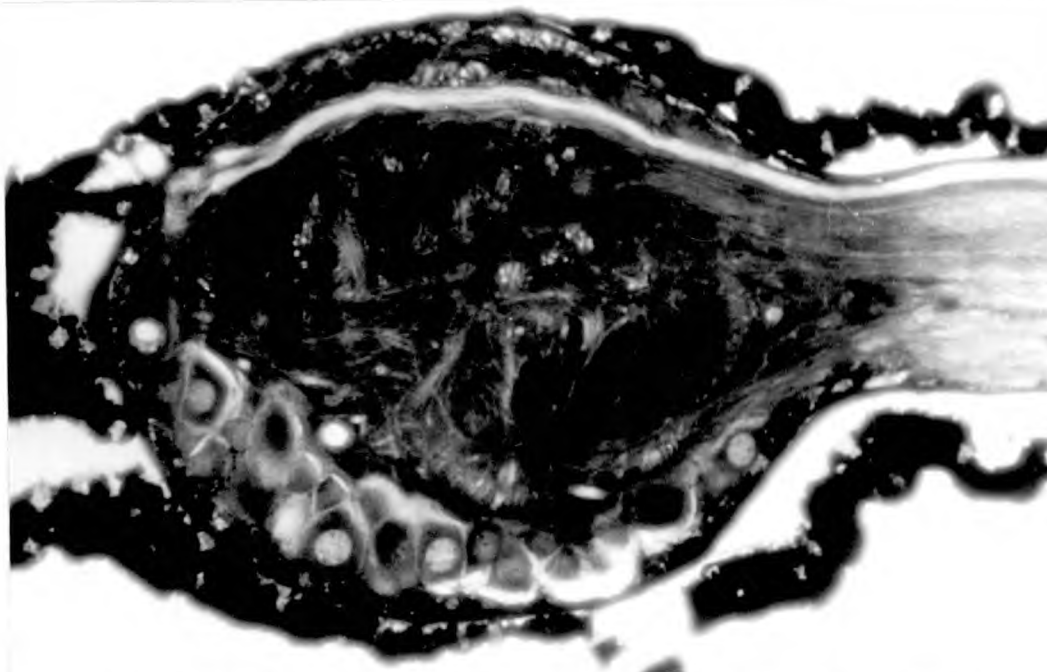


Fig. 52. Giant fibre passing uninterrupted through the dorsal neuropile of the seventh abdominal ganglion.
(Vertical section x230.)

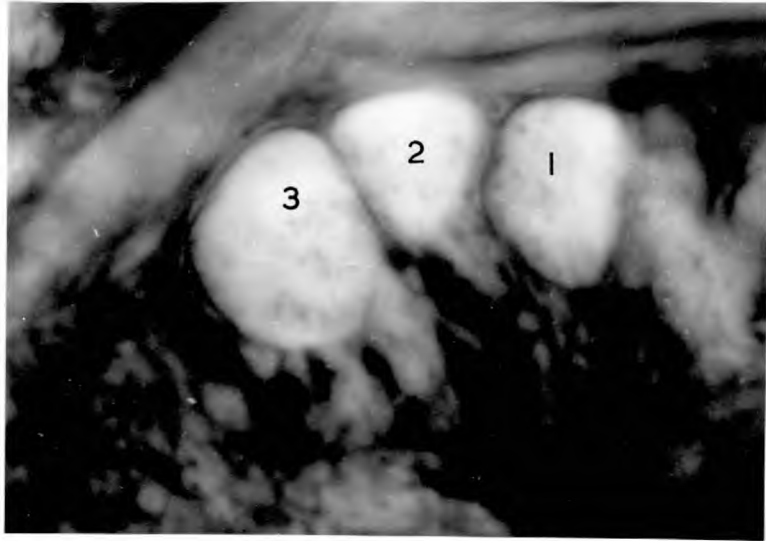


Fig. 53. Branching of giant fibres within the dorsal neuropile of the seventh abdominal ganglion. (Transverse section x2300)

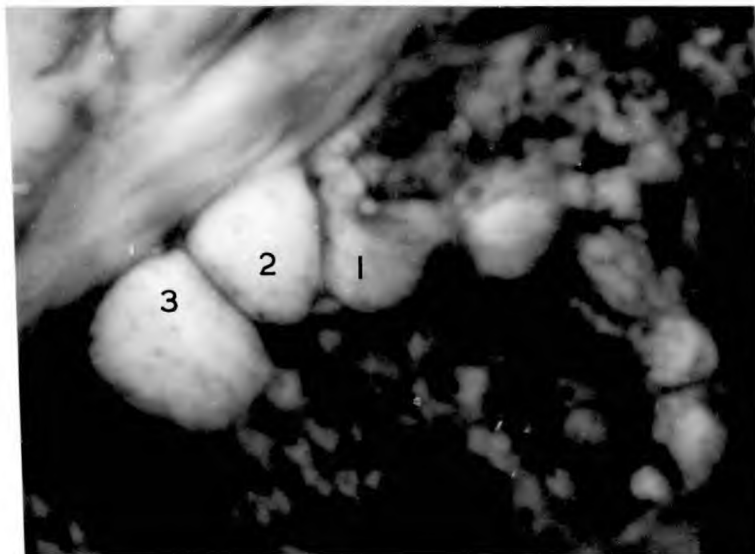


Fig. 54. Branching of a giant fibre in the dorsal neuropile of the seventh abdominal ganglion. Fibre 1 sends a collateral into the dorsal commissure. (Transverse section x2300.)

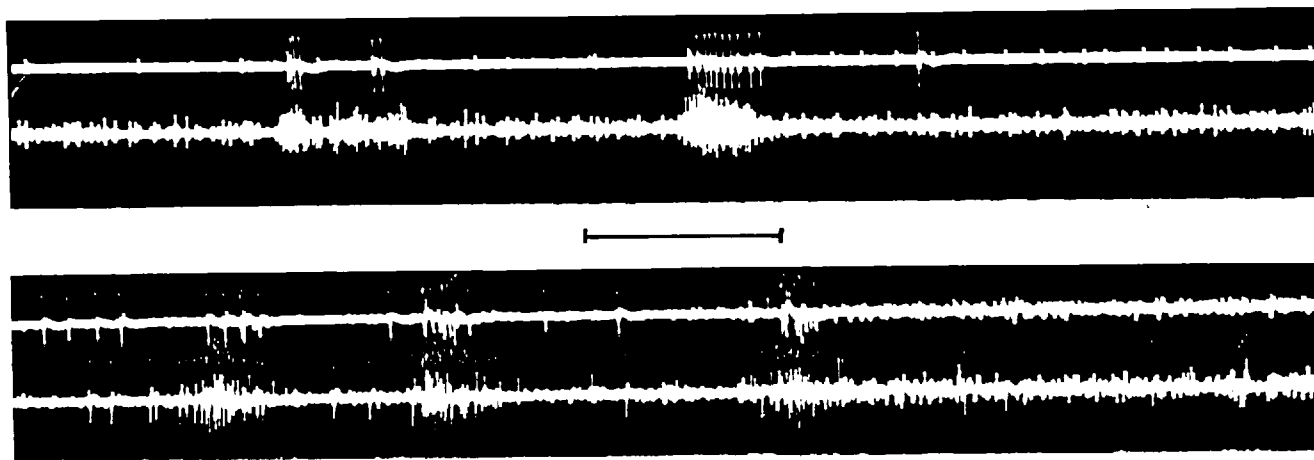


Fig. 55. Stimulation of cercus with a puff of air.

(a) Upper trace - ipsilateral ventral connective between the terminal ganglionic mass and the seventh abdominal ganglion. Lower trace - ipsilateral cercal nerve.

(b) Upper trace - contralateral ventral connective between the terminal ganglionic mass and the seventh abdominal ganglion. Lower trace - ipsilateral ventral connective at the same level. (Scale = 0.4 seconds.)

Fig. 56. Electrical stimulation of cercal nerve.

- (a) Speed of conduction in ipsilateral ventral connective between terminal ganglionic mass and seventh abdominal ganglion.
- (b) As in (a) but in contralateral connective.
- (c) Speed of conduction across the seventh abdominal ganglion, ipsilateral connective.
- (d) Synaptic delay between cercal afferent fibres (lower trace) and ipsilateral post-synaptic fibres (upper trace).
- (e) Synaptic delay between cercal afferent fibres (lower trace) and contralateral post-synaptic fibres (upper trace).
- (f) Plan of electrode positions used in the above experiments.

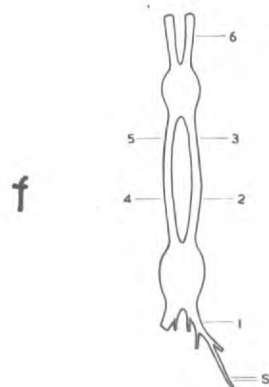
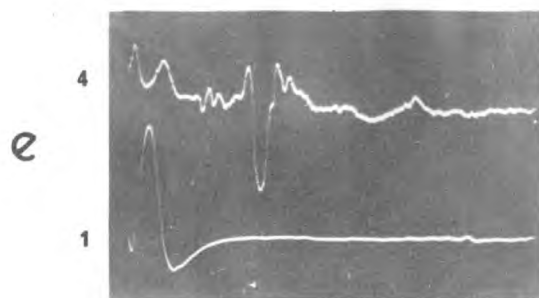
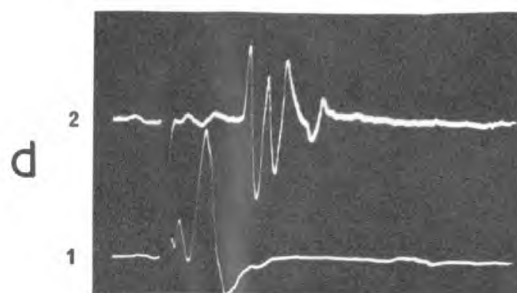
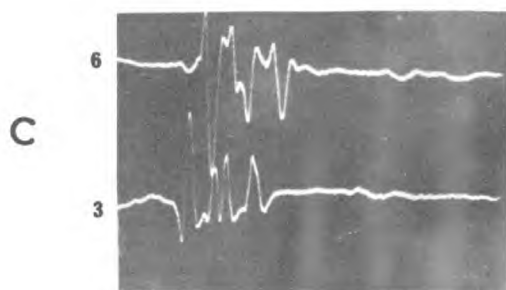
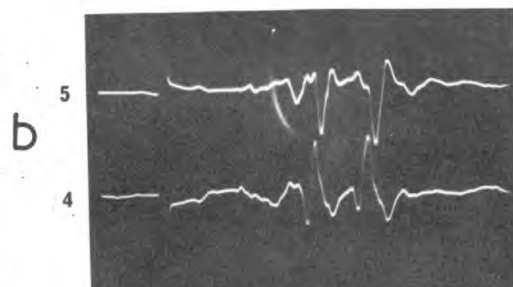
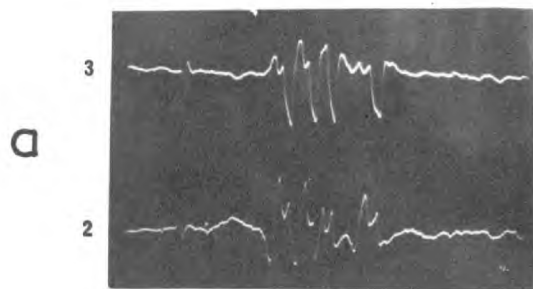
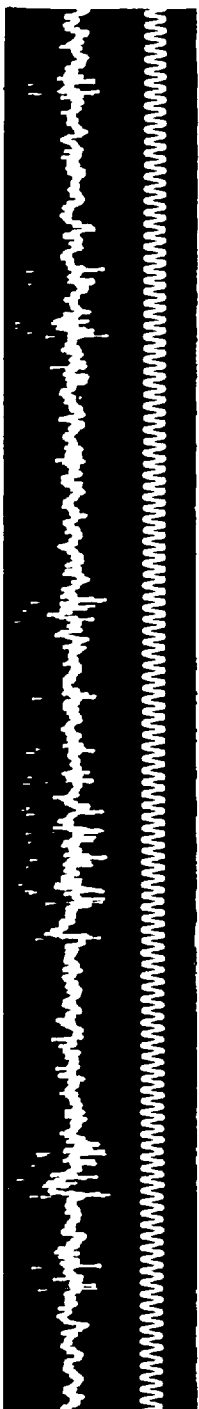
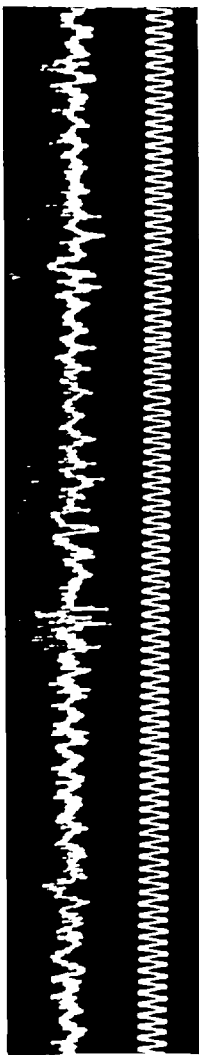


Fig. 57. Mechanical stimulation of the ninth and eighth abdominal segments.

- (a) Stimulation of row of hairs on dorso-lateral margin of the ninth sternum (male). Recording from ipsilateral ventral connective between terminal ganglionic mass and seventh abdominal ganglion (wave form 100 cycles per second).
- (b) As (a) but recording from contralateral ventral connective (wave form 100 cycles per second).
- (c) Stimulating dorsal ovipositor valve with small brush recording from ipsilateral ventral connective between terminal ganglionic mass and the seventh abdominal ganglion (wave form 100 cycles per second).
- (d) As (c) but recording from contralateral ventral connective (wave form 100 cycles per second).
- (e) Stimulation of eighth sternum (male). Upper trace ventral connectives between terminal ganglionic mass and seventh abdominal ganglion, lower trace eighth ventral nerve (2.5" = 1 second).



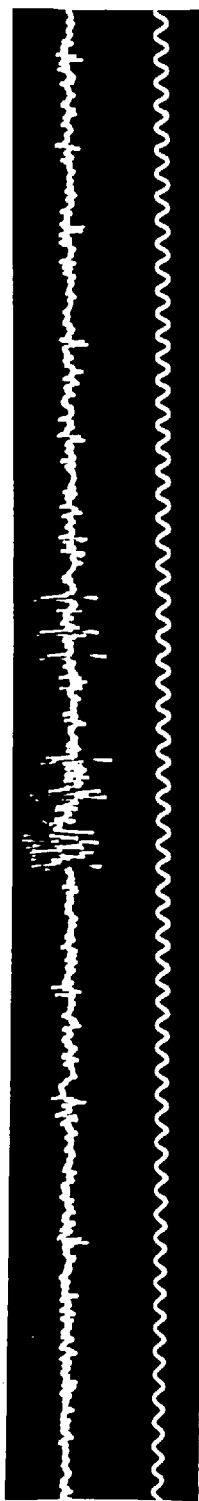
a



b



c



d



e

Fig. 58. Electrical stimulation of lateral branch of ninth ventral nerve.

- (a) Speed of conduction of post-synaptic fibre in ipsilateral connective.
- (b) As in (a) but in contralateral connective.
- (c) Synaptic delay between afferent fibres of the ninth ventral nerve (lower trace) and ipsilateral post-synaptic fibres (upper trace).
- (d) Synaptic delay between afferent fibres of the ninth ventral nerve (lower trace) and contralateral post-synaptic fibres (upper trace).
- (e) Electrical stimulation of genital nerve recording from both ventral connectives between terminal ganglionic mass and seventh abdominal ganglion.
- (f) Plan of electrode positions used in the above experiments.

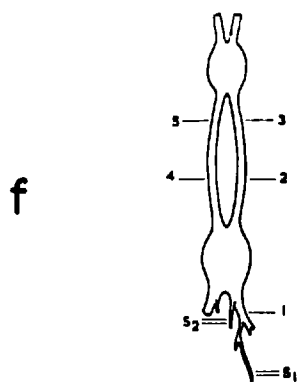
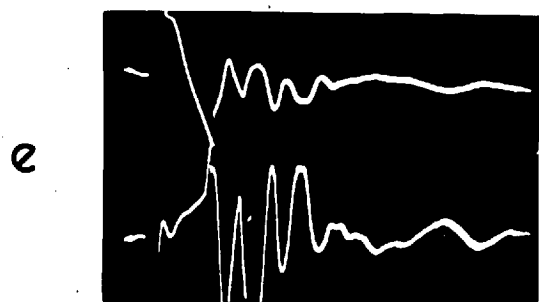
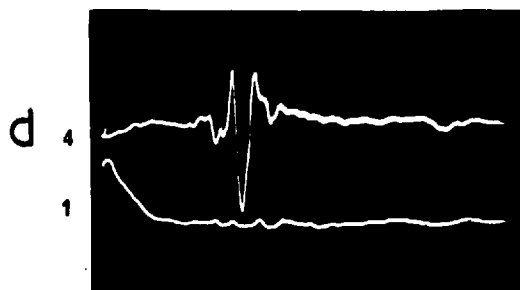
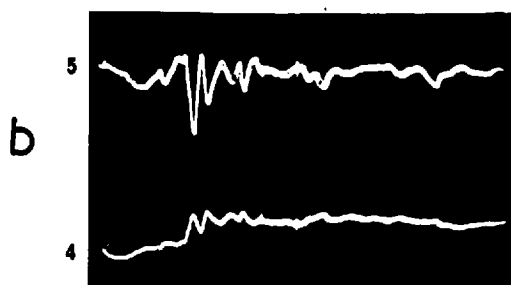


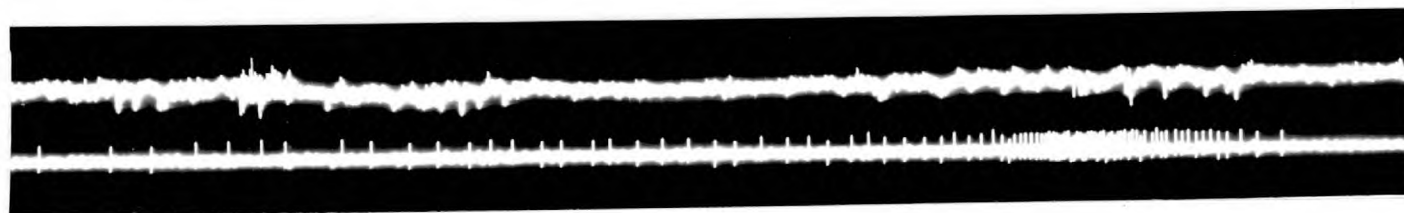
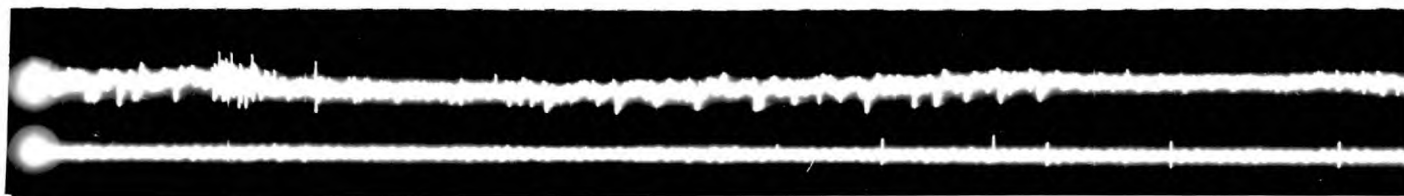
Fig. 59. The effect of cercal stimulation on efferent neurones of the metathoracic leg nerve.

(a) Puff of air on cercus, upper trace - ventral nerve cord below metathoracic ganglion, lower trace - ipsilateral metathoracic leg nerve (scale = 1 second).

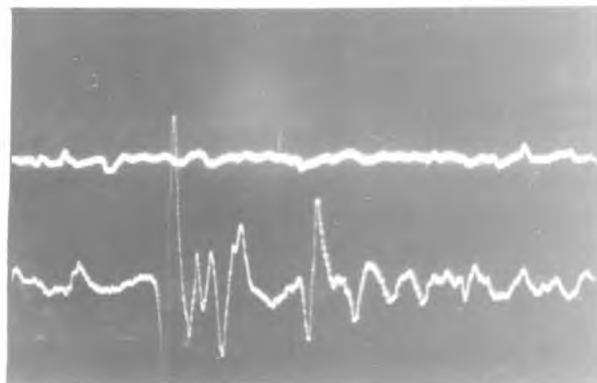
(b) Electrical stimulation of cercal nerve, upper trace - metathoracic leg nerve, lower trace - ventral nerve cord below metathoracic ganglion
(Total trace 20 milliseconds.)

Fig. 60. Electrical stimulation of cercal nerve, upper trace - ipsilateral thoracic nerve cord between metathoracic and mesothoracic ganglia, lower trace - ipsilateral ventral connective below metathoracic ganglion . (Total trace 20 milliseconds.)

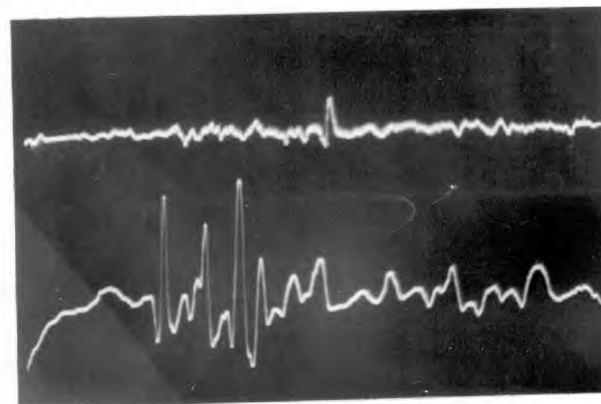
59A



59B



60



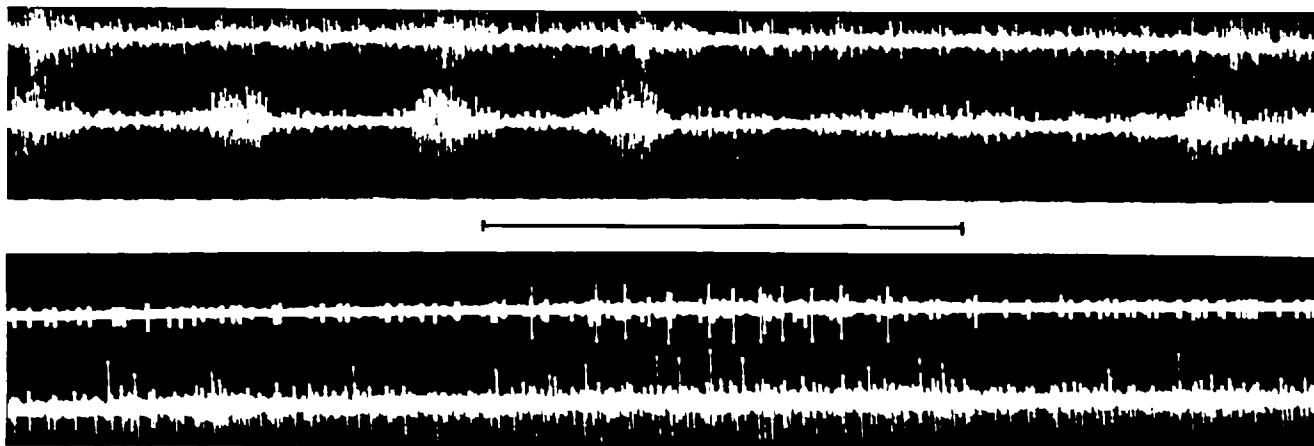


Fig. 61. Response in contralateral cercal nerve to stimulation of cercus with a fine brush, upper trace - contralateral cercal nerve, lower trace - ipsilateral cercal nerve (scale = 1 second).

Fig. 62. Response in ventral connective (lower trace) and the eighth dorsal nerve (upper trace) to stimulation of the ninth sternum (scale = 1 second).

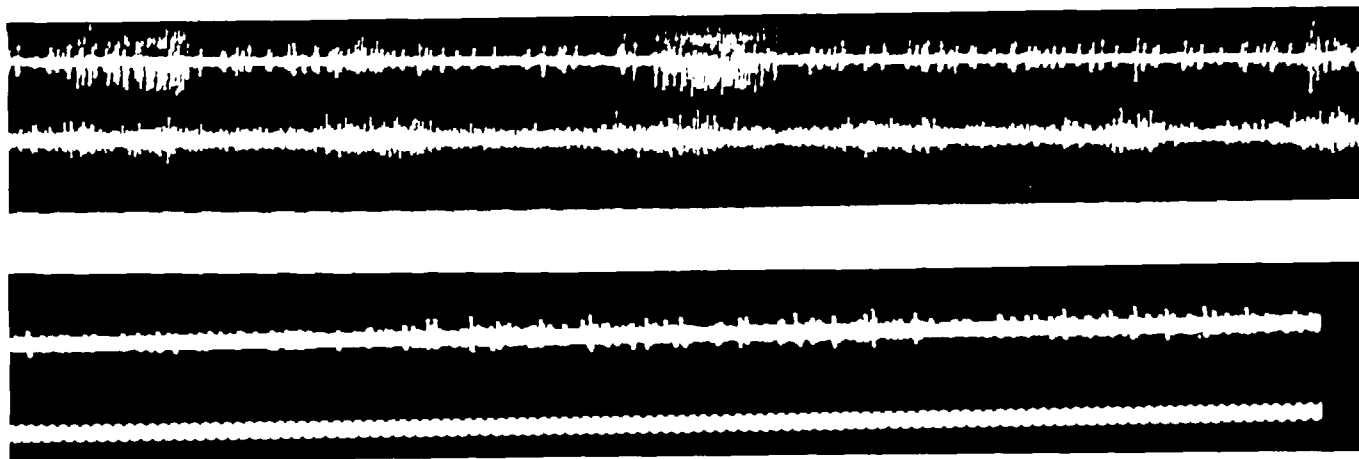


Fig. 63. Response in the ipsilateral eighth dorsal nerve (upper trace) and the ipsilateral cercal nerve (lower trace) to stimulation of the cercus. (2.5" = 1 second.)

Fig. 64. Response in the ipsilateral eighth dorsal nerve to the lateral bending of the cercus (wave form 50 cycles per second).

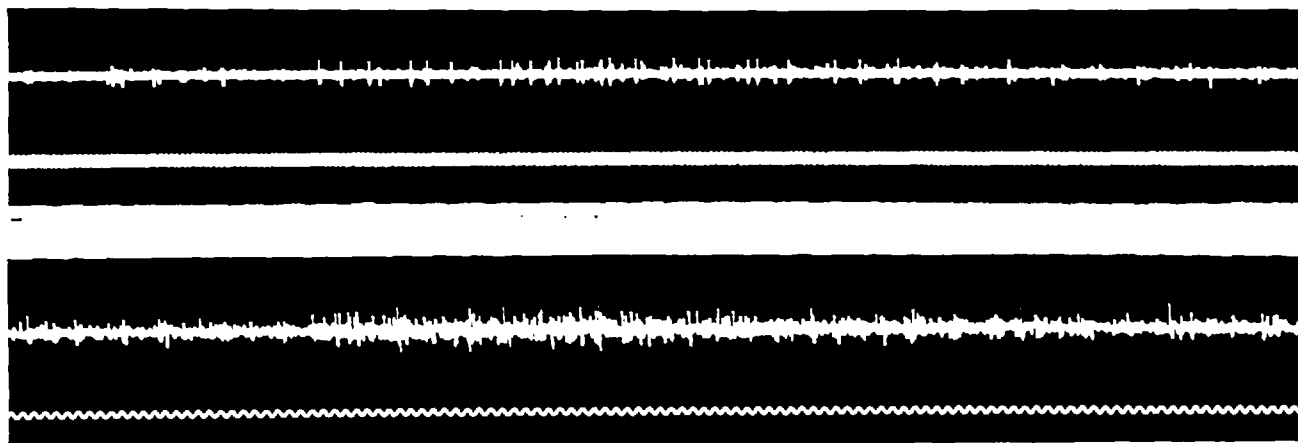


Fig. 65. Response in the contralateral ~~sixth~~ ventral nerve to stimulation of the paraproct with a needle (wave form 100 cycles per second).

Fig. 66. Response in the ventral connective below the seventh abdominal ganglion to stimulation of the seventh sternum with a brush (wave form 100 cycles per second).

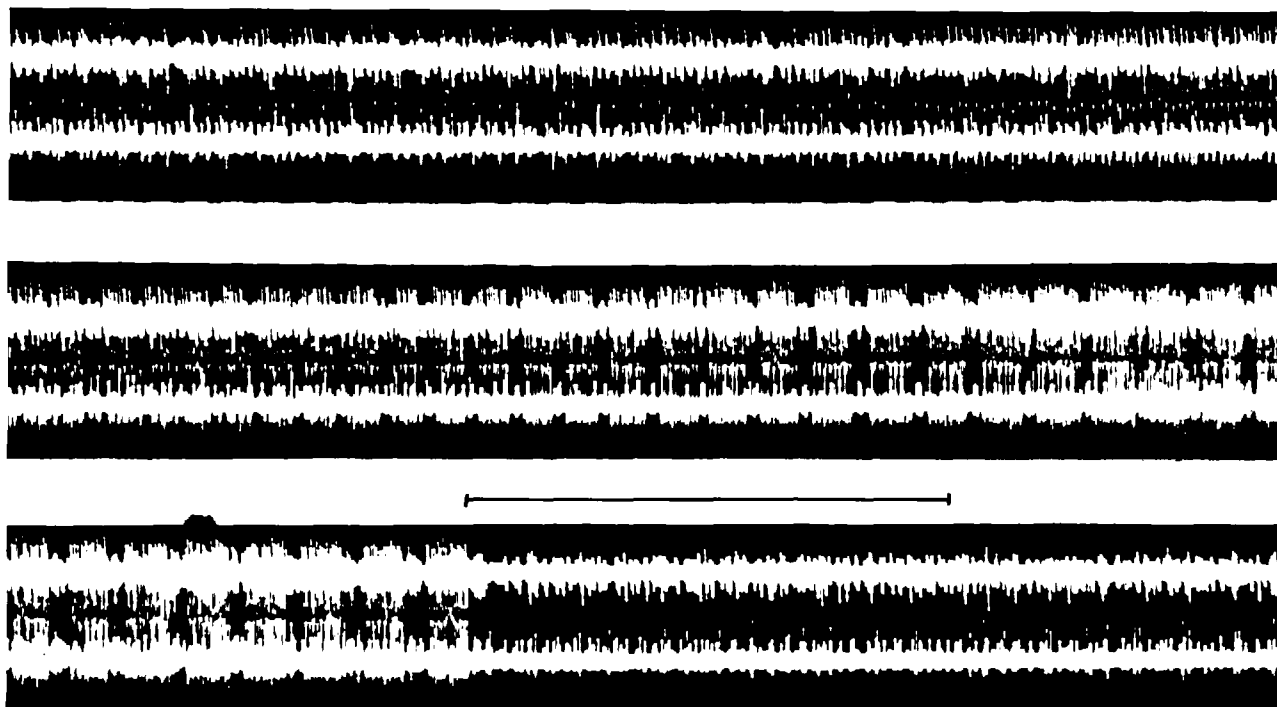


Fig. 67. Synchronized rhythmic activity in the paired genital nerves. Ventral nerve cord severed anterad of the terminal ganglionic mass. (Scale = 1 second.)

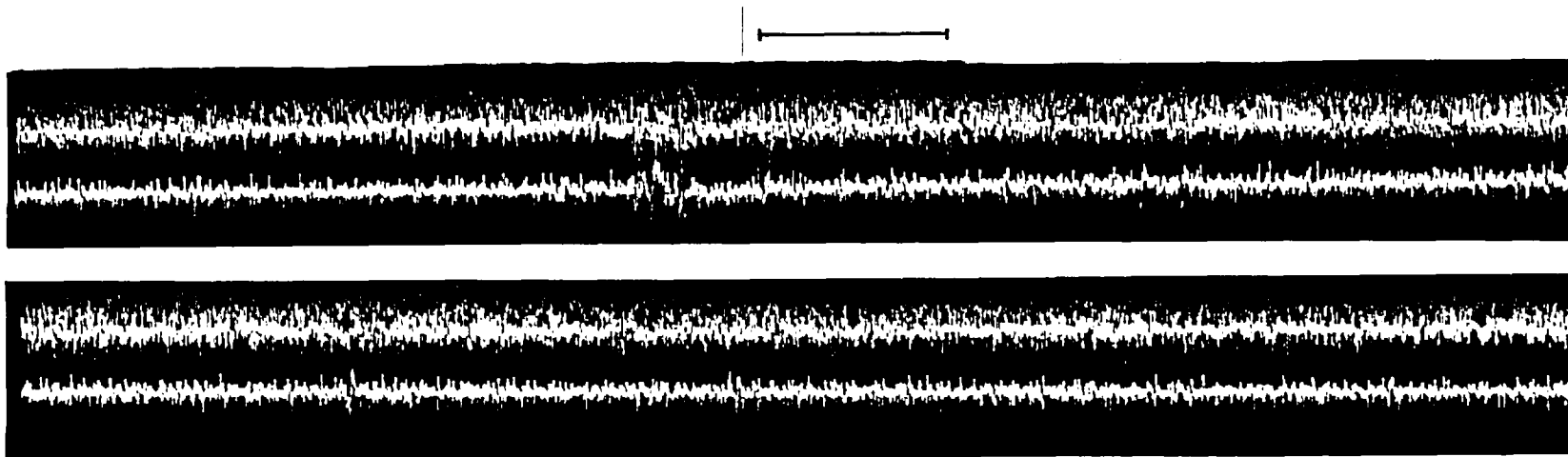


Fig. 68. Stimulation of the cercus with a saturated aqueous solution of sodium chloride, upper trace - cercal nerve, lower trace - ipsilateral ventral connective between terminal ganglionic mass and seventh abdominal ganglion (scale = 0.1 seconds).

THE MORPHOLOGY AND STRUCTURE OF THE BRAIN OF ORCONECTES VIRILIS (HAGEN) (CRUSTACEA, DECAPODA)

W. D. SEABROOK¹ AND H. H. J. NESBITT

Department of Biology, Carleton University, Ottawa, Canada

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Abstract

The morphology and histological structure of the supraoesophageal ganglionic mass are reported. The accessory nerve supplying motor fibers to the muscles of the eyestalk, antennules, and antennae, and sensory fibers to the antennules and antennae, is described for the first time. It is suggested that the term optic lobes be applied to those structures previously described as the optic nerves in the stalked-eyed Crustacea. It is further suggested that the term ganglionic mass be applied to compound ganglia such as the arthropod brain.

Sixty-one conducting elements are traced and illustrated.

This work substantiates the view that the protocerebrum and deutocerebrum have an ancient and close relationship. Both are considered to be preoral. The tritocerebrum was recently acquired by the supraoesophageal ganglionic mass and is postoral in origin.

Introduction

The literature on the morphology of the nervous system of the Decapoda is extremely sparse. Audouin and Milne-Edwards (1828), in one of the earliest papers, gave the gross details of the central nervous system of *Homarus*. Later, Bouvier (1889) made a comparative study of the nervous system of the Macrura, Anomura, and Brachyura. The definitive morphological work on the crayfish nervous system is that of Kiem (1915), who delineated this system in great detail in *Astacus fluviatilis*, the European river crayfish.

Heath (1941) described the nervous system of *Pungetia producta*. His description of the brain of *Pungetia* agreed with the findings of Kiem except for the innervation of the green gland. Henry (1948) worked on the brain of *Palaemon paucidens*. Her findings substantiated those of Heath regarding the innervation of the green gland and with this exception corroborated the work of Kiem. George *et al.* (1955) investigated the central nervous system of *Panuliris polyphagus* in one of a series of papers on the morphology of this species. Unfortunately their work was not sufficiently detailed to be of much value.

An extensive survey of the literature on the histological structure of the crustacean nervous system was published by Hanström in 1928 and again in

¹Present address: Department of Zoology and Applied Entomology, Imperial College of Science and Technology, London S.W.7, England.

1947. The reader is referred to these articles for a complete bibliography. In the latter of these papers, Hanström described the structure of the decapod protocerebrum, deutocerebrum, and tritocerebrum. Particular emphasis was placed on the *X* organ and the sinus gland, and a few of the major neuron tracts were described.

Of particular interest is the work of Walker (1935), who described the nervous system of *Oniscus* (Isopoda) and traced 66 neuron tracts within this system.

Methods and Materials

The specimens of *Orconectes virilis* used in this study were obtained from a supplier who collected them in the Toronto, Ontario, area. They were prepared for dissection by being anesthetized in a bath of ice and water and killed in 70% ethanol. Such treatment resulted in the nerves taking on a cream color; the muscles remained white.

Specimens for histological study were fixed in alcoholic Bouin's (Brasil 1904 or Dubosq Brasil of Gray 1954). They were embedded in "Tissuemat" (50–54 °C) by means of the chloroform technique. Sections were stained in Harris' haematoxylin and counterstained with eosin *Y* in picric acid and alcohol. Bretschneider 1914 stain (Gray 1954) for insect brains was also used. This stain gave excellent nuclear detail, but the definition of the neuron tracts was not as good as that given by the haematoxylin and eosin method.

The terminology used is an Anglicized version of the Latin used by Kiem (1915) and Hanström (1947). The names of the muscles are those of Schmidt (1915).

Morphology

The supraoesophageal ganglionic mass (Fig. 1) is a subovate structure, approximately twice as wide as long, reflected upwards at an angle of 45° to the remainder of the central nervous system. The dorsal surface is featureless, giving no indication of the position of the ganglia within; the ventral surface (Fig. 2), on the other hand, displays the two hemispheres of the deutocerebral ganglia in the anterolateral quadrant.

At the anterior angles on the dorsal surface, two stout optic lobes (*o.l.*) proceed in an anterolateral direction into the eyestalk, where they bulge distally in the region of the optic ganglia. These lobes do not give off any nerves to the muscle of the eyestalk.

The morphological papers cited refer to "optic nerves" arising from the dorsolateral angles of the supraoesophageal ganglion. In this paper these are called the "optic lobes", this terminology being in agreement with the views of Walker (1935). The optic nerves are those nerves connecting the outermost optic ganglion, the *lamina ganglionaris*, to the retinal elements of the eye (Hanström 1947). Kiem (1915) referred to the small swellings on the supraoesophageal ganglion at the base of the "optic nerves" as the optic lobes. It is suggested that the term "optic lobes" be applied only to those structures previously referred to by other authors as the optic nerves in the stalked-eyed Crustacea and that the term "optic nerves" be reserved for those nerves connecting the *lamina ganglionaris* to the ommatidia of the eye.

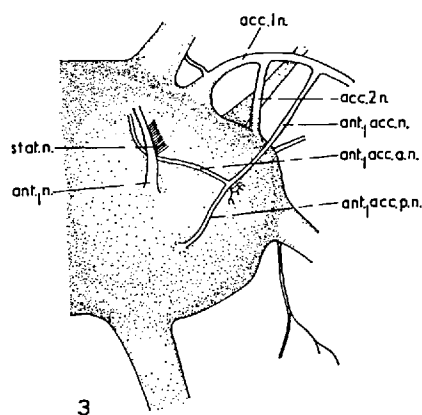
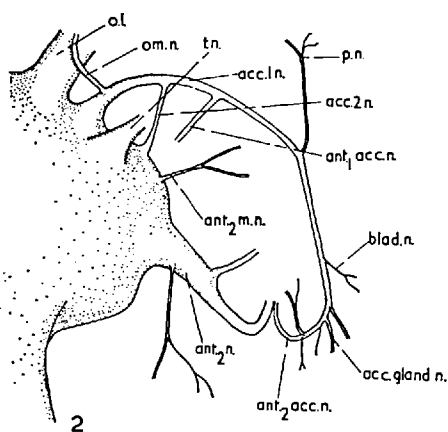
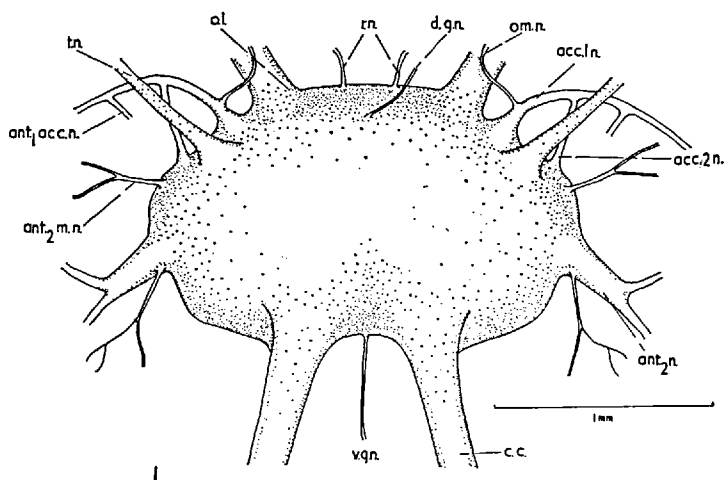


FIG. 1. Dorsal view of supraoesophageal ganglionic mass.

FIG. 2. Dorsal view of right side of the supraoesophageal ganglionic mass, showing detail of the accessory nerve.

FIG. 3. Ventral view of left side of the supraoesophageal ganglionic mass, showing detail of the accessory and the antennular nerve.

Mesad of the optic lobes, a pair of nerves arise from the anterodorsal face of the supraoesophageal ganglionic mass. These rostral nerves (*r.n.*) (Fig. 1) proceed anterodorsally to innervate the muscles of the rostrum.

Just laterad of the base of the optic lobe on each side, the first root of the accessory nerve (Figs. 1 and 3, *acc.1 n.*) emerges from the supraoesophageal ganglion. This is a small flat nerve which anastomoses with the second root (*acc.2 n.*) originating just posterad of it, beneath the tegumentary nerve. Immediately after emerging from the cerebral ganglion, the first root gives off a branch, the oculomotor nerve (*om.n.*), to innervate the muscles of the

eyestalk. The oculomotor nerve, lying in a depression between the optic lobe and the abductor of the eyestalk, becomes closely appressed to the optic lobe. The oculomotor nerve divides into a branch to the abductor muscle and into another that in turn divides into a branch to the connective tissue of the eyestalk and a second one to the *retractor lateralis* muscle of the eyestalk. The first root of the accessory nerve turns caudad shortly after emerging from the supraoesophageal ganglion and the second root joins the first at this time. A short distance posterior to the fusion of the second root, a branch arises to the antennule. This nerve, the accessory nerve of the antennule (*ant.₁ acc. n.*), will be discussed in detail when the innervation of the antennule is considered. Posterior to the origin of the accessory nerve of the antennule, a branch, the proventicular nerve (*p.n.*), arises. This nerve is immediately reflexed forward, dividing at its distal end. The greater branch innervates the muscles of the proventiculus; the lesser goes to the hypodermis in this region of the head. Several small nerves, given off at the junction of the accessory nerve and the proventicular nerve, innervate the hypodermis and connective tissue of that region.

The accessory nerve continues posteriorly, giving off a small branch, the bladder nerve (*blad. n.*), to the bladder of the green gland. Continuing caudad, the accessory nerve divides into three branches: proximal, median, and distal. The accessory nerve of the antenna (*ant.₂ acc. n.*) is the distal branch and the largest of the three nerves. It contributes to the innervation of the antenna and will be discussed in the section on the innervation of this appendage. The proximal branch innervates the remotor muscle of the antenna. The median branch innervates the green gland (*acc. gland n.*).

A nerve similar to the accessory nerve has not been mentioned in the literature. Kiem (1915) and Stoll (1925) described the oculomotor nerve of *Astacus fluviatilis*, which innervates the muscles of the eyestalk. Heath 1941, Henry 1947, and George *et al.* 1955 described an oculomotor or similar nerve to the muscles of the eyestalk. In no case is this nerve associated with a complex to the other head appendages.

Immediately caudad of the origin of the accessory nerve and dorsad of its second root, the tegumentary nerve (Fig. 2, *t.n.*) arises from the dorsal face of the cerebral ganglion.

This nerve is as described by Kiem (1915), with one exception. He described it as innervating the bladder of the green gland; no evidence of this was found in *Orconectes virilis*.

The antennular nerves (Fig. 2, *ant.₁ n.*) arise from the deutocerebral hemispheres on the anteroventral face of the supraoesophageal ganglionic mass and proceed anteriorly into the antennules. Shortly after leaving the cerebral ganglion, the antennular nerve gives off numerous, short, fine fillets (*stat. n.*) to the statocyst organ, which is located on the upper surface of the first segment of the antennule in this species. It consists of a shallow pit, its open face surrounded by a fringe of bristles which enclose the statolith. The antennular nerve continues into the flagellum of the antennule. It was seen to give branches to the leathery chitin of the intersegmental joints.

Associated with the antennular nerve in the innervation of the antennule is the accessory nerve of the antennule (*ant.₁ acc. n.*). The origin of this nerve

was discussed above in the section on the accessory nerve. As the accessory nerve of the first antenna proceeds ventrally from its origin on the accessory nerve, it divides into an anterior and a posterior branch. The anterior branch (*ant.₁ acc. a.n.*) becomes closely appressed to the antennular nerve and proceeds into the antennule, giving off branches to the intrinsic musculature of this appendage and to the connective tissue and hypodermis of the antennule. The posterior branch (*ant.₁ acc. p.n.*) joins the anteroventral face of the brain near the midline and posterior to the origin of the antennular nerves.

Kiem (1915) referred to a single nerve innervating the antennule. Henry (1948) described a double innervation of the first antennae of *Palaemon*, and implied that such double innervation of the head appendages is a feature of the decapods. George *et al.* (1955) referred to the "antennular nerves", and the "antennular elevatory-abductor nerves" arising separately from the cerebral ganglion in *Panuliris*. Heath (1941) made no mention of a second innervation of the antennules in the kelp crab.

Returning to the posterodorsal surface of the supraoesophageal ganglion (Fig. 3), there is a pair of small nerves, the antennary motor nerves (*ant.₂ m.n.*), issuing from its lateral face just posterior to the origin of the tegumentary nerve. Each nerve of the pair divides. The anterior branch innervates the muscles depressor *c* and promotor II (Schmidt 1915) of the antennae and the posterior branch innervates muscle depressor *b* (Schmidt 1915) of the antennae. Kiem (1915) made no mention of such a nerve in *Astacus fluviatilis*, nor do any of the other authors cited.

The antennary nerves (Figs. 1 and 4, *ant.₂ n.*) are second in size only to the optic lobes. They emerge from the posterolateral angles of the supraoesophageal ganglion. Each nerve has one major division into a lesser, anterior branch to the exopodite (*ant.₂ exo n.*), and a greater, slightly posterior branch to the endopodite (*ant.₂ endo n.*). Both these branches become closely associated with the branches of the accessory nerve. On leaving the cerebral ganglion, the antennary nerve gives off a small nerve from its dorsal surface. This nerve (*ant.₂ n.₁*) divides. The smaller branch anastomoses with a branch of the

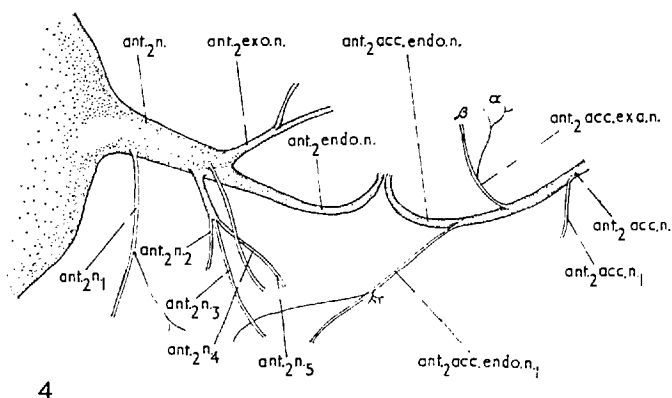


FIG. 4. Dorsal view of a portion of the supraoesophageal ganglionic mass, showing detail of the innervation of the antennae.

accessory nerve (*acc. gland n.*) and together they innervate the green gland. The larger branch divides again, supplying, on the one hand, the compressor muscle of the basipodite of the antennae and, on the other, the levator muscle of the antennae. This innervation of the green gland is in general agreement with the work of Heath (1941) and Henry (1948), although they mention only one nerve, this arising from the antennary nerve. Kiem (1915) claimed that the innervation of the green gland was from the mandibular ganglion. Distally, from its posterior face, the antennary nerve gives off a branch. This branch divides almost immediately into distal, medial, and proximal branches. The proximal branch (*ant.₂ n.₂*) innervates muscle *b* (Schmidt 1915) of the meropodite. The median branch (*ant.₂ n.₃*) proceeds posteroventrally, becoming closely appressed to a branch of the accessory nerve (*ant.₂ acc. endo. n.₁*). Together they innervate the region of the nephropore at the base of the antenna. The distal branch (*ant.₂ n.₄*) innervates the abductor muscle of the exopodite.

Close to the origin of the aforementioned nerve trunk from the dorsal surface of the antennary nerve, a nerve (*ant.₂ n.₅*) is given off which proceeds caudad, crossing above the previous nerve and entering the *musculus abductor exopoditis* (Schmidt 1915).

The previously mentioned nerves (*ant.₂ n.₂, 3, 4, 5*) are invariably present. The sequence of origin and position along the antennary nerve displays great variation, often differing on the left and right sides of the same animal.

Distal to the point of origin of the previous nerves, the antennary nerve divides into the aforementioned branches to the exopodite (*ant.₂ exo n.*) and endopodite (*ant.₂ endo n.*). The lesser of the two branches proceeds to the exopodite, giving off a nerve to muscle *a* (Schmidt 1915) of the meropodite. The greater branch becomes very closely applied to the accessory nerve. In some places they appear to anastomose. These nerves enter the endopodite and its flagellum.

Closely associated with the innervation of the antenna is the antennary branch of the accessory nerve (Figs. 2 and 4, *ant.₂ acc. n.*). The origin of this branch of the accessory nerve has been discussed in a previous paragraph. As the accessory nerve of the antenna proceeds medially, a small nerve (*ant.₂ acc. n.₁*) arising from its posterior surface innervates the connective tissue in the region of the levator muscle and may have a very tenuous connection with this muscle. On the anterior surface of the antennal accessory nerve, almost opposite the origin of the previous nerve, a larger nerve emerges (*ant.₂ acc. exo. n.*), the accessory nerve to the exopodite of the antenna. This nerve divides, one branch (α) innervating the connective tissue and hypodermis of the exopodite, and the second branch (β) innervating the muscles of the exopodite. There is some variation in the form of this nerve. The α and β branches may in some cases arise separately from the antennal accessory nerve, rather than as described.

The main trunk of the accessory nerve of the antenna now becomes the endopodite branch of the accessory nerve of the antenna (*ant.₂ acc. endo. n.*). This nerve gives off a small nerve (*ant.₂ acc. endo.₁ n.*) which proceeds posteroventrally, anastomosing with a branch of the antennal nerve (*ant.₂ n.₃*), to innervate the region of the nephropore. The endopodite branch of the accessory

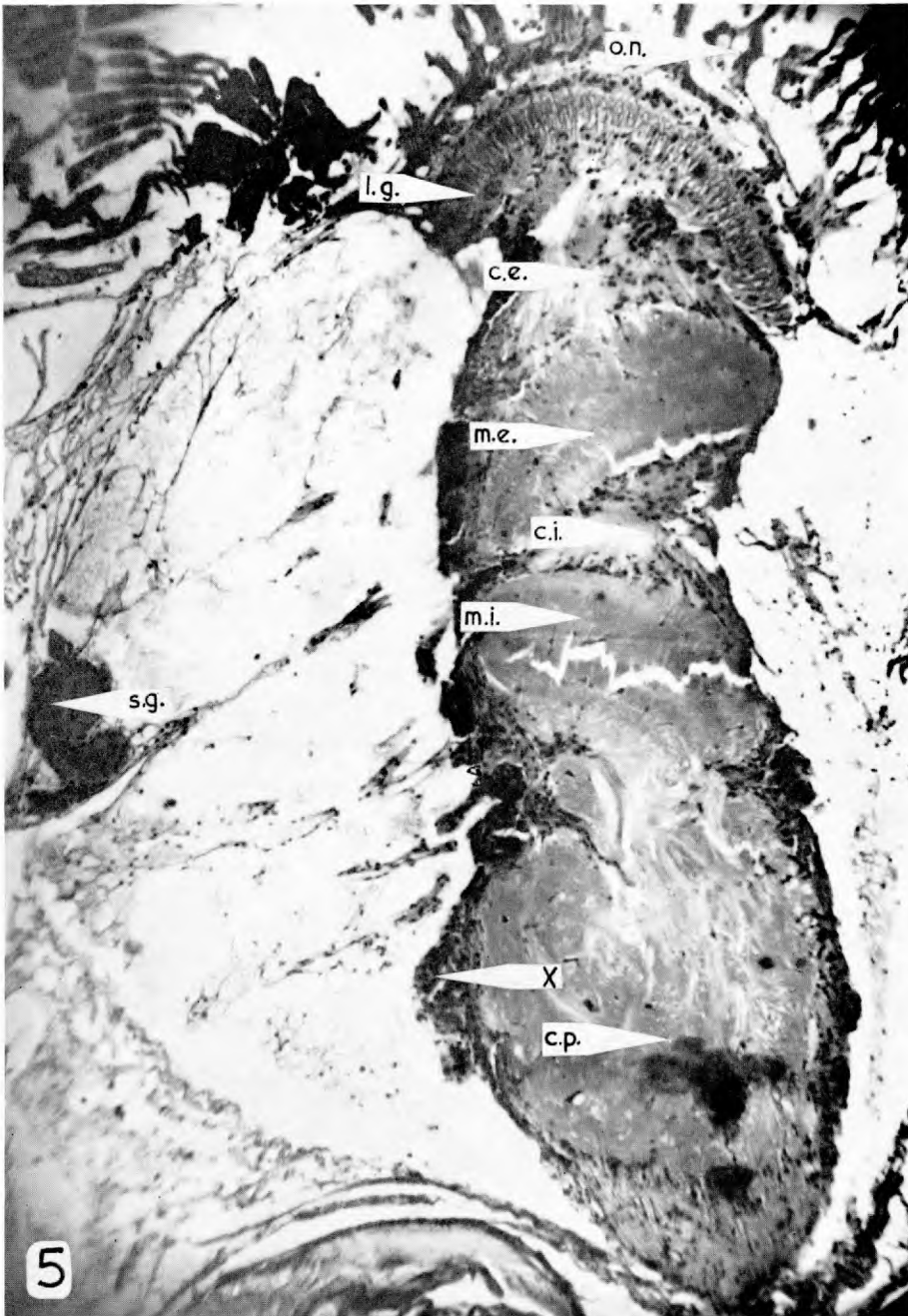


FIG. 5. Ganglia of the optic lobe. $\times 24$.

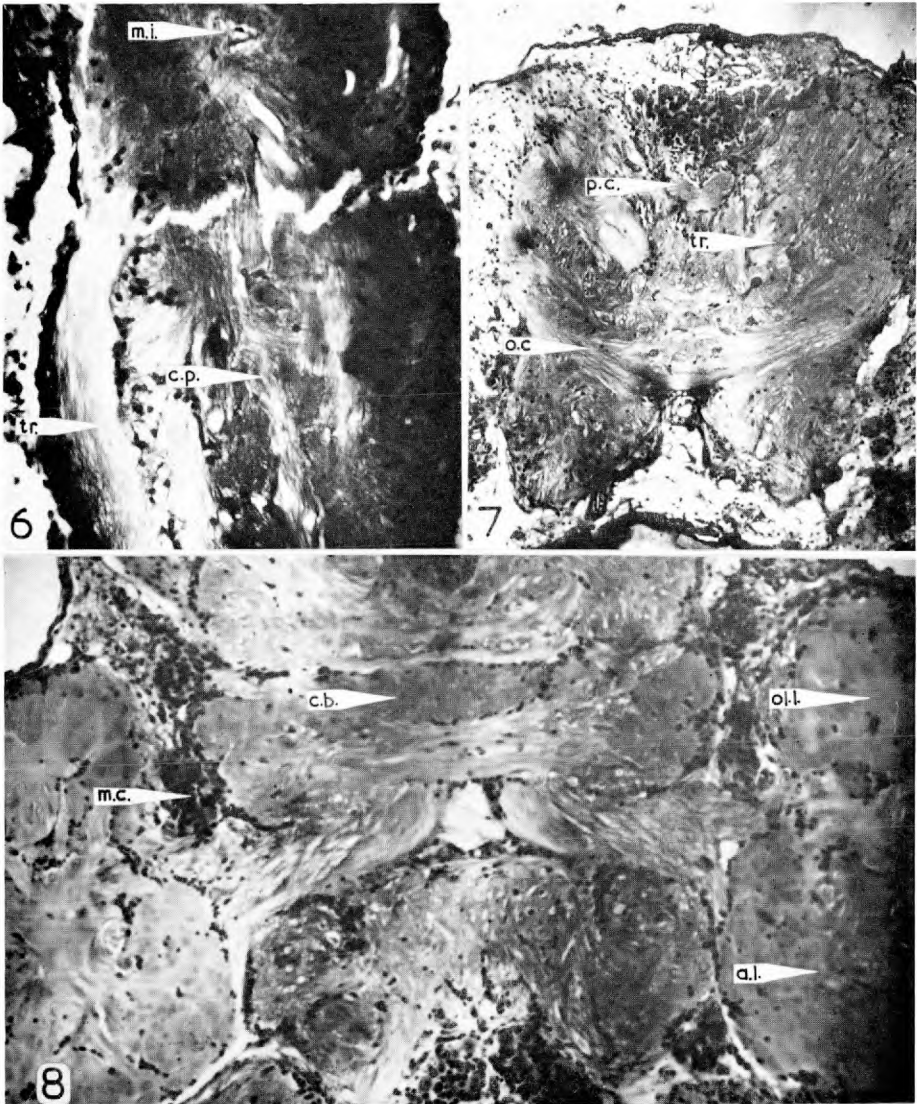


FIG. 6. *Corpora pedunculata*. $\times 100$.

FIG. 7. Frontal section through the supraoesophageal ganglionic mass. $\times 24$.

FIG. 8. Frontal section through the supraoesophageal ganglionic mass. $\times 24$.

nerve turns anterad, becoming very closely associated with the endopodite branch of the antennary nerve, and enters the endopodite of the antenna. The accessory nerve, which is the finer of the two entering the endopodite, gives off branches to the extensor and flexor muscles of the endopodite.

Histological investigations indicate that the antennary and accessory nerves are both sensory and motor in function.

A double innervation of the antenna by the antennal nerve and by a branch of the accessory nerve is similar to that found in the eyestalk and the antennules. The remarks made, in the discussion of the antennules, regarding the findings of the other authors apply in this case. It is interesting to note that the double innervation of the antennae in *Palaemon* (Henry 1948) is effected by a branch of the antennary nerve and not by the supraoesophageal ganglion independently or by a branch of the accessory nerve.

In addition to the innervation of the head appendages, there are two unpaired gastric nerves arising from the supraoesophageal ganglionic mass (Fig. 1). These are the dorsal unpaired gastric nerve (*d.g.n.*) and the ventral unpaired gastric nerve (*v.g.n.*). The dorsal nerve arises in the midline of the dorsal surface of the brain, approximately between the optic lobes. It proceeds dorsally for a short distance and joins with the inferior stomatogastric nerve at the frontal ganglion. The ventral unpaired gastric nerve arises from the posterior face of the brain, between the circumoesophageal commissures. This nerve proceeds posteriorly to become associated with the stomatogastric nervous system. Henry (1948) described a pair of frenal nerves arising just posterior to the antennary nerves in *Palaemon* and connecting with the stomatogastric system. No trace of these nerves was found in *Orconectes*.

Histology

Orconectes belongs to the stalked-eyed Crustacea. In this group, the optic ganglia (Fig. 5), which made up the bulk of the protocerebrum, have migrated into the eyestalks. The brain of *Orconectes* is reminiscent of that which Hanström (1947) referred to as the *Carcinus*-type brain.

The *lamina ganglionaris*, the first of the optic ganglia, lies immediately beneath the compound eye and receives the optic nerves. This is a cup-shaped ganglion which in section appears crescentic (Fig. 5, *l.g.*). This mass of neuropil has a very diffuse structure and the optic nerves can be traced into its body. The sensory cell bodies associated with this ganglion are located at the base of the retinal elements. The internuncial neurons whose axons comprise the *chiasma externum* (*c.e.*) connect this neuropil with the *medulla externa* (*m.e.*) immediately below it. The *medulla externa* (Fig. 5, *m.e.*) has a slightly crescentic form and lies at an angle to the *lamina ganglionaris*. The latter is a very dense neuropil and individual axons cannot be traced within it. It has a stratified appearance caused by dense and less dense layers of tissue. This mass of neuropil receives axons from the large group of cell bodies which surround the *chiasma externum* as well as from cells lying on the median surface of the neuropil itself. These are internuncial neurons having connections with the *lamina ganglionaris* and with the next two lower centers, the *medulla interna* (*m.i.*) and the *corpora pedunculata* (*c.p.*). Hanström (1947) illustrated direct axonal connections between the *medulla externa* and lower centers in

the supraoesophageal ganglion. A careful search failed to indicate connections to or from such centers in *Orconectes virilis*. The *medulla externa* is connected with the *medulla interna* by the *chiasma internum* (*c.i.*), a crossing of ascending and descending internuncial neurons.

The third of the optic ganglia is the *medulla interna* (Fig. 5, *m.i.*), which has a spherical form, and in *O. virilis* is very closely associated with the *corpora pedunculata*, which lies below it. This mass of neuropil, like the *medulla externa*, is very dense and shows a stratified structure. It receives axons from cell bodies on its medial surface and from cell bodies lying on the surface of the *corpora pedunculata*. Internuncial neurons connect this ganglion with the *medulla externa* and *corpora pedunculata*. A descending tract was located running from this mass of neuropil, continuing through the *corpora pedunculata* to lower centers in the supraoesophageal ganglionic mass, and giving off collaterals to the *medulla interna* and the *corpora pedunculata*.

The largest of the neuropilar bodies located in the eyestalk is the *corpora pedunculata* (Fig. 5, *c.p.*). It is a dense spherical ganglion which does not show the stratification typical of the *medulla externa* and *medulla interna*. In *Orconectes*, the *X* organ (Fig. 5, *X*) has been located on the lateral surface of the *corpora pedunculata*. It takes the form of a papilla consisting of large globular cells. These are in contrast to most of the nerve cell bodies of the eyestalk, which are small cells having a very large nucleus relative to the size of the cell, and little cytoplasm.

The sinus gland (Fig. 5, *s.g.*) located laterad of the *medulla interna* at the surface of the eyestalk appears on superficial observation to be derived from the neurilemma, as indicated by Hanström (1947). Under careful observation, however, it may be noted that the tips of the axons associated with this organ become expanded and themselves form the sinus gland. This is in agreement with the observations of Bliss and Welsh (1952). In addition to the innervation of the sinus gland by the cells of the *X* organ, strong tracts are present from cells associated with the *lamina ganglioraris*, *medulla externa*, and *medulla interna*. The *corpora pedunculata* is connected with the deutocerebrum by the *tractus olfactorio-globularis* (Fig. 6, *t.r.*), in which are ascending and descending neurons. It would appear, therefore, that the *corpora pedunculata* is an association center combining optic and olfactory stimuli rather than being strictly an optic ganglion. In addition to the *tractus olfactorio-globularis*, numerous neurons of the *corpora pedunculata* descend into the lower centers of the supraoesophageal ganglionic mass and tracts from these lower centers terminate in the *corpora pedunculata*. There is also a large group of neurons of this neuropil which form an optic commissure (Fig. 7, *o.c.*) passing to the opposite optic lobe and terminating in the *corpora pedunculata* of that side. These commissural axons and the previously mentioned ascending and descending axons, as well as the axons of the *tractus olfactorio-globularis*, comprise the optic tract (*o.t.*).

Anterad and dorsad of the optic commissure lies the *pons cerebri* (Fig. 7, *p.c.*). This small neuropil consists of a pair of glomeruli which lie at an angle to the horizontal and point in a slightly posterior direction. At the posterior end they meet in the midline of the supraoesophageal ganglionic mass.

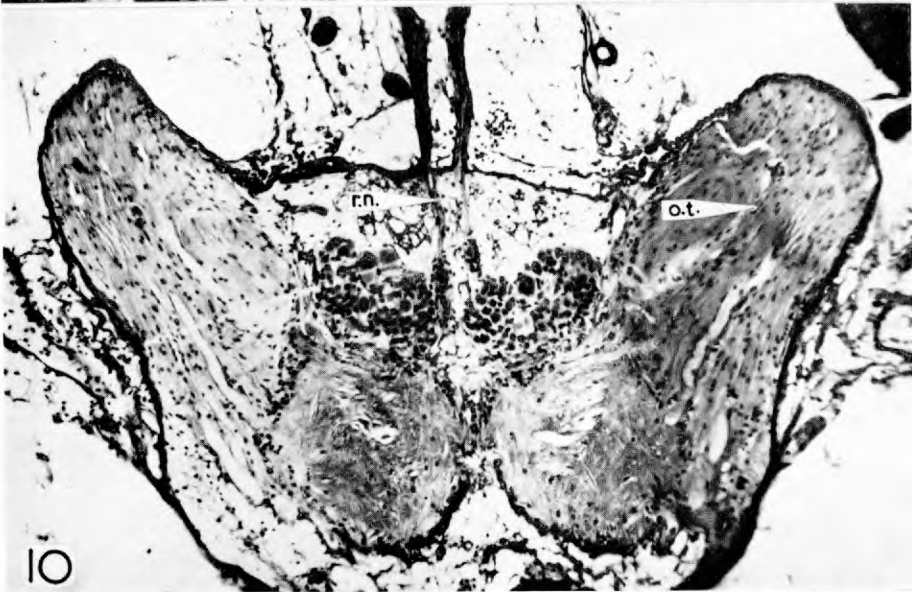
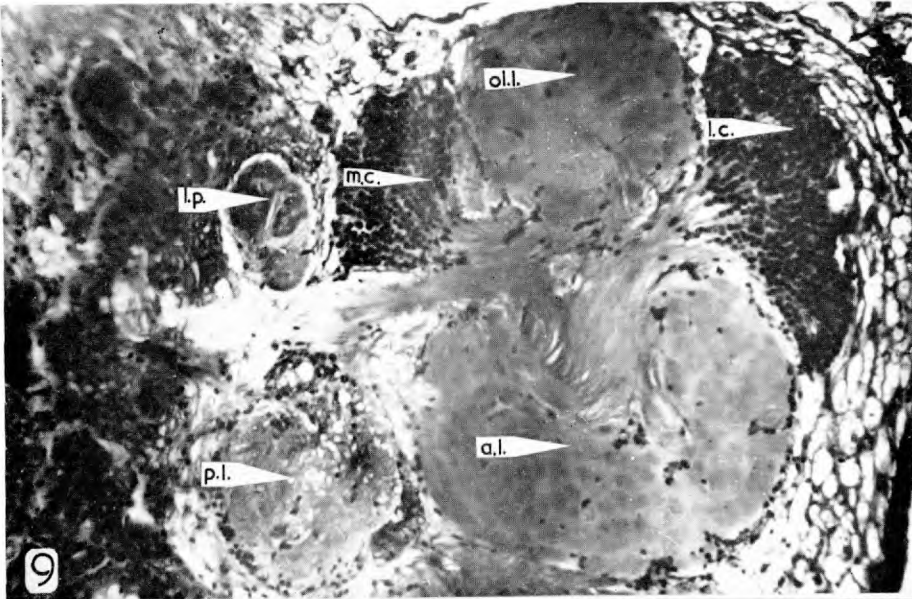
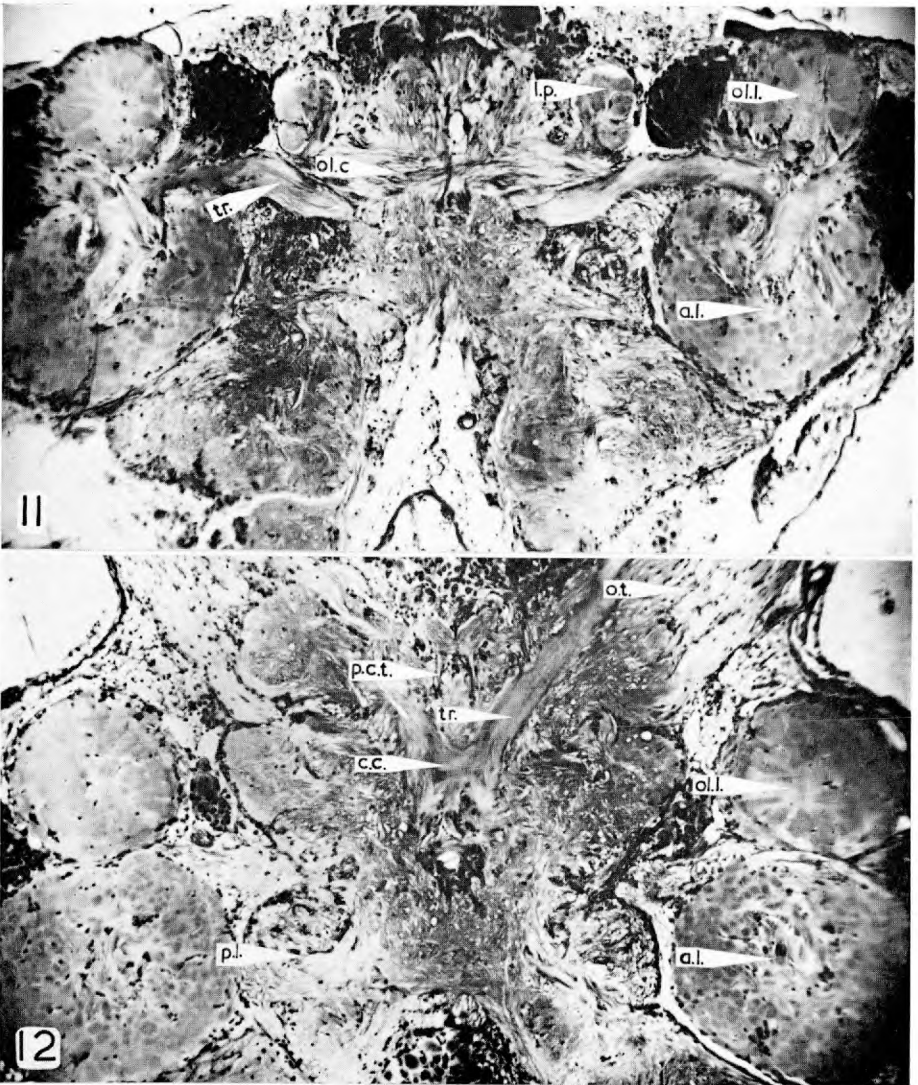


FIG. 9. Frontal section through the deutocerebrum. $\times 100$.
FIG. 10. Origin of the rostral nerves. $\times 24$.



FIGS. 11 and 12. Frontal sections through the supraoesophageal ganglionic mass.
 ×24.

Posterad and ventrad of the *pons cerebri* but anterad of the optic commissure, the central body (Fig. 8, *c.b.*) may be found. This is a large, oval, non-glomerular neuropil. A pair of distinct nerve tracts connect the *pons cerebri* with this structure.

The last of the masses of neuropil to be associated with the protocerebrum in *Orconectes* is the *lobus paracentralis* (Fig. 9, *l.p.*). These paired areas of neuropil lying medial of the large deutocerebral lobes have a glomerular structure. They each receive a nerve tract (*tr.l.p.*) from the large group of cell bodies that cover the anterodorsal face of the supraoesophageal ganglionic mass in the region lying between the optic lobes. This nucleus also gives rise to a pair of rostral nerves (Fig. 10, *r.n.*). These are the motor neurons which innervate the muscles of the rostrum; the collaterals of these neurons end in the central body. Cells of this nucleus also send a group of motor fibers laterally into the first root of the accessory nerve.

Hanström (1947) stated that in *Astacus*, the *corpus hemiellipsoidale* is poorly developed. This was found to be the case in *Orconectes*. A very loose mass of synaptic tissue was located in the dorsolateral region of the brain, at the base of the optic lobes. This tissue had the appearance of a loose neuropil in some sections, and is considered to be analogous with the *corpus hemiellipsoidale*.

The deutocerebrum (Figs. 9 and 11) contributes to, and receives axons from, the nerve of the antennule and the accessory nerve. In *Orconectes* it comprises three lobes, the olfactory (*ol.l.*), accessory (*a.l.*), and parolfactory (*p.l.*) lobes. The definitions of the lobes are those given by Hanström in his 1947 paper.

The olfactory lobe lies at the anterior angle of the supraoesophageal ganglionic mass just posterad and ventrad of the optic lobe. It is intermediate in size between the large accessory lobe and the smaller parolfactory lobe. It shows a very well-developed glomerular structure. The glomeruli are wedge-shaped and extend inwards from the periphery of the lobe. They represent very dense areas within the neuropil tissues and stain more intensely than do the surrounding tissues. The olfactory lobe receives the lateral branch of the antennular nerve and a sensory tract from the second root of the accessory nerve.

The accessory lobe (*a.l.*) is well developed in *O. virilis* and is the largest of the three deutocerebral lobes. This lobe lies posterad and slightly dorsad of the olfactory lobe. It also has a glomerular structure. The glomeruli in this case are small round areas randomly distributed throughout the mass of neuropil. A sensory tract from the second root of the accessory nerve enters the upper surface of this lobe.

The olfactory and accessory lobes receive processes from two groups of cell bodies, one lying laterad of the lobes (*l.c.*) and the other lying mesad of the lobes (*m.c.*). These groups of cell bodies consist of internuncial neurons, and motor neurons to the muscles of the antennule via the accessory nerve. A group of motor neurons proceed from the lateral nuclei into the second root of the accessory nerve, their collaterals entering the accessory lobe of the deutocerebrum. A large motor tract proceeds from the medial group of cells, giving collaterals to the olfactory lobe and entering the second root of the accessory nerve.

From the ventral surface of the lateral group of cell bodies, a group of motor neurons enter the posterior branch of the accessory nerve of the first antenna. The collaterals of these neurons enter the accessory lobe. In addition, there is a group of sensory axons from this posterior branch which become distributed in the ventral region of the neuropil of the accessory lobe.

The lateral group of cell bodies is composed of cells having large, dark staining nuclei and relatively little cytoplasm. The same type of cells is found on the surface of the medial group of cell bodies. In the center of this group, however, are cells which have the form of neurosecretory cells. A complete discussion of the neurosecretory system in the brain of *Orconectes virilis* has been undertaken by Durand (1956).

The last of the deutocerebral neuropils is the parolfactory lobe (*p.l.*). This is located mesad of the large accessory lobe. In *O. virilis* it is small, feebly developed, and composed of loose non-glomerular tissue. This lobe is supplied with a large group of sensory fibers from the medial branch of the antennular nerve. A small group of nerve cell bodies lying between the accessory lobe and the parolfactory lobe, near the ventral surface of the ganglionic mass, supply internuncial neurons connecting the two lobes. A second small group of cell bodies lying mesad of the parolfactory lobe send axons into this lobe (Fig. 19). Both groups contain cells which show the form of neurosecretory cells.

As previously mentioned, the *tractus olfactorio-globularis* (Figs. 11 and 12, *t.r.*) has connections in the deutocerebrum. Descending fibers originating in the *corpora pedunculata* and *medulla interna* become distributed in both the olfactory and accessory lobes. Ascending fibers arise from cell bodies in the lateral group (*l.c.*) and proceed medially, giving a few collaterals to the olfactory lobe and many to the accessory lobe. This large tract continues medially to the central chiasma (*c.c.*), which lies directly above the central body. A number of the fibers cross at this point. From the chiasma, two arms proceed anterolaterally into the optic lobes, terminating in the *corpora pedunculata* and *medulla interna*.

The large olfactory commissure (Fig. 13, *ol. c.*) connects accessory lobes of the opposite sides. This is a large, loose tract which crosses the supraoesophageal ganglionic mass directly ventrad of the *tractus olfactorio-globularis*. The neurons contributing to this tract lie in the lateral nuclei (*l.c.*), giving off collaterals to the accessory lobe. The axons of these neurons terminate in the accessory lobe of the opposite side. Axons were observed to pass from the *lobus paracentralis* by way of the olfactory commissure to the accessory lobe. The cell bodies of these axons were not located. The presence of this commissure within the supraoesophageal ganglionic mass is evidence in favor of the preoral origin of the deutocerebrum. The exceedingly well-developed *tractus olfactorio-globularis* would also indicate an ancient and close connection between the protocerebrum and the deutocerebrum. Such an intimate connection does not exist between the tritocerebrum and the higher centers in the supraoesophageal ganglion.

The tritocerebral lobe (Fig. 14, *t.*) lies immediately posterad of the accessory lobe of the deutocerebrum. This is a rod-shaped mass of neuropil, not very dense, showing no glomerular structure. It receives sensory axons from the antennary nerve. These are distributed over the lateral and posterior surface of the tritocerebral neuropil. Ascending tracts passing up through the

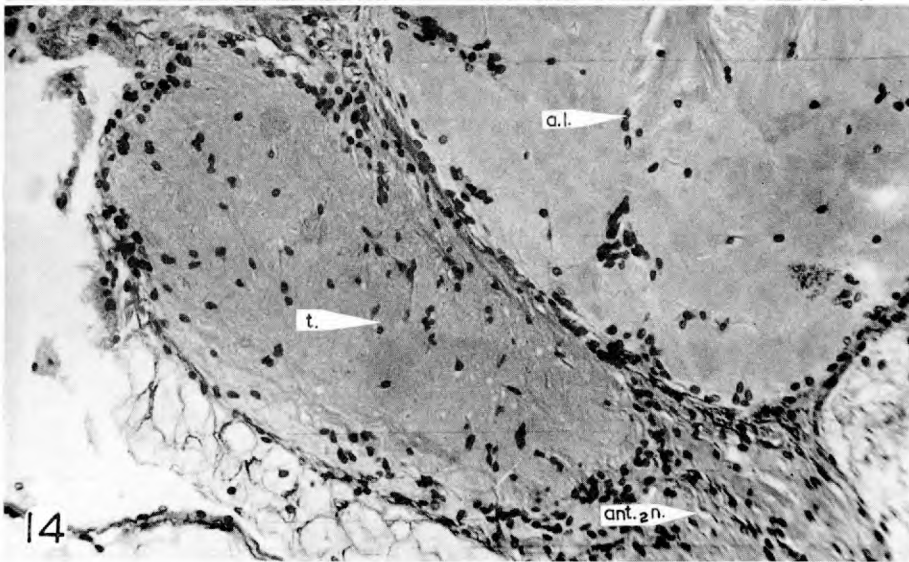
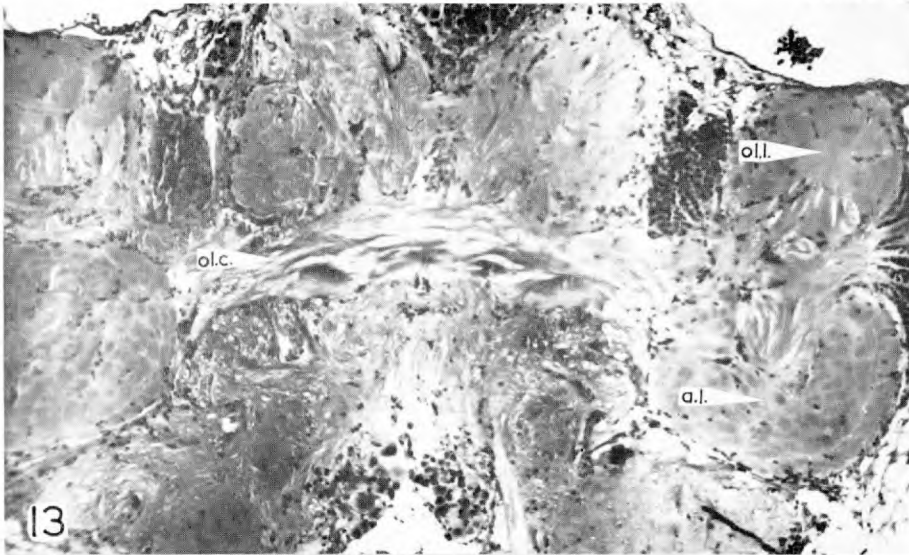


FIG. 13. Frontal section through the supraoesophageal ganglionic mass. $\times 24$.
FIG. 14. Tritocerebrum. $\times 100$.

circumoesophageal commissures from lower centers enter the dorsal surface of this mass of neuropil. The motor tracts to the muscles of the antenna arise in a group of cell bodies lying on the dorsal surface of the anteromedial angle of this lobe. The axons of these cells pass along the anterior face of the lobe and into the antennary nerve. The collaterals are distributed in the tritocerebral neuropil. A group of internuncial neurons have their neurocytes in a large group lying between the right and left tritocerebral lobes in the midline of the ganglionic mass. These cells have their axons and collaterals distributed in the posteromedian angle of the tritocerebral neuropil and in a small mass of neuropil lying mesad of the tritocerebral lobes.

Hanström (1947) referred to a tegumentary neuropil associated with the main tritocerebral neuropil. In *O. virilis*, this tegumentary lobe (*t.l.*) is poorly developed. It receives a group of sensory axons from the tegumentary nerve (*t.n.*). This nerve enters the supraoesophageal ganglion at the anterolateral angle and passes dorsad of the deutocerebral lobes. Before entering the tegumentary neuropil, the nerve divides, one large group of fibers turning anterad to become distributed among the loose fibers in the central region of the ganglionic mass, the other or posterior group entering the tegumentary neuropil.

The antennary motor nerves, the unpaired inferior oesophageal nerve, and the dorsal unpaired gastric nerve are also associated with the tritocerebral ganglion. The antennary motor nerves enter the lateral face of the ganglionic mass, turn posteriorly, and pass between the accessory lobe of the deutocerebrum and the tritocerebral neuropil. These nerves arise in the same group of cell bodies as do the aforementioned motor fibers to the antenna. The collaterals enter the tritocerebral neuropil. The unpaired inferior oesophageal nerve takes its origin in the previously described group of cell bodies which supply internuncial neurons to the tritocerebral and tegumentary neuropils. The collaterals of these neurons are distributed in the tritocerebral lobe. Hanström (1947) affirmed that the fibers of the dorsal unpaired gastric nerve arise from cell bodies in the tritocerebrum. The writer, however, was unable to follow these fibers through the central portion of the ganglionic mass.

Associated with the motor neurons of tritocerebral origin, a tract of motor fibers of deutocerebral origin enters the antennary nerve. These fibers have their origin in the posterior portions of the lateral group of deutocerebral nerve cell bodies. The collaterals of these neurons enter the accessory lobe of the deutocerebrum.

There are no major connections between the higher centers and the tritocerebral ganglion, such as the *tractus olfactorio-globularis*. There is no preoral tritocerebral commissure such as the preoral optic and olfactory commissures. The tritocerebral commissure is referred to as the stomadeal commissure and is postoral. This would lend evidence to the belief that the protocerebrum and deutocerebrum are preoral ganglia and that the tritocerebrum is a postoral ganglion which has recently migrated forward to join the supraoesophageal ganglionic mass.

The Conducting Elements

The following section will consist of a list of those neurons which have been traced within the supraoesophageal ganglionic mass of *Orconectes virilis*. The list will be broken into three divisions: neurons having their neurocytes and

collaterals associated with the protocerebrum, the deutocerebrum, and the tritocerebrum. It will be evident that this is only a partial list of the neurons in this ganglionic mass; numerous axons and small tracts were observed for which no neurocyte or insertion into a mass of neuropil could be found. Only one neuron of each tract will be illustrated. The neurons are illustrated in Figs. 15, 16, and 17.

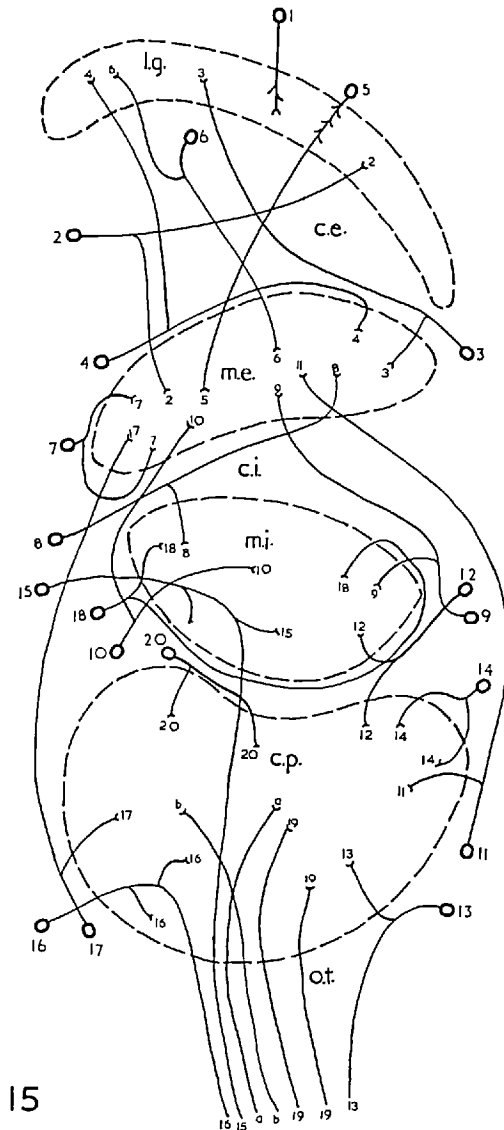


FIG. 15. Neurons of the optic lobe.

Protocerebrum

Neurons 1 to 20 are illustrated in Fig. 15.

1. A sensory neuron with its neurocyte lying at the base of the retinal elements, the axon terminating in the *lamina ganglionaris*.
2. An internuncial neuron with its neurocyte lying in the median group of cell bodies surrounding the *chiasma externum*, its axon terminating in the lateral half of the *lamina ganglionaris*. The collateral enters the *medulla externa*.
3. An internuncial neuron with its cell body lying on the lateral surface of the *medulla externa*. The axon enters the *lamina ganglionaris*; the collateral is distributed in the *medulla externa*.
4. An internuncial neuron with its cell body lying on the medial side of the *chiasma externum*. The axon crosses to, and enters, the lateral surface of the *medulla externa*. The collateral enters the medial surface of the *lamina ganglionaris*.
5. An internuncial neuron with its cell body on the anterior surface of the *lamina ganglionaris*. The axon proceeds through the *lamina ganglionaris*, contributing collaterals to this neuropil and entering the *medulla externa*.
6. An internuncial neuron with the neurocyte lying beneath the *lamina ganglionaris*, the collateral entering this ganglion and the axon entering the *medulla externa*. The axons and collaterals of neurons 2 to 6 comprise the *chiasma externum*. Neurons of type 2 are the largest group of neurons associated with this chiasma.
7. An internuncial neuron with its cell body lying on the medial surface of the *medulla externa*; the axon and collateral both enter this mass of neuropil.
8. An internuncial neuron with its neurocyte on the median surface of the *medulla externa*, the axon entering this ganglion and the collateral distributed in the *medulla interna*.
9. An internuncial neuron with its cell body situated on the lateral surface of the *medulla interna*, the axon entering the *medulla externa* and the collateral entering the *medulla interna*.
10. An internuncial neuron with its cell body lying on the median surface of the *corpora pedunculata*, the axon entering the *medulla externa* and the collateral entering the *medulla interna*.
11. An internuncial neuron with its cell body lying on the lateral surface of the *corpora pedunculata*, the collateral entering this mass of neuropil. The axon passes along the lateral margin of this ganglion and the *medulla interna*, to enter the posterior margin of the *medulla externa*. Neurocytes 8 to 11 contribute collaterals and axons which comprise the *chiasma internum*.
12. A small internuncial neuron gives branches to the *medulla interna* and *corpora pedunculata*.
13. An internuncial neuron with its cell body lying on the lateral surface of the *corpora pedunculata*. The collateral enters this neuropil. The axon descends to lower centers.

14. Small internuncial neurons on the lateral surface of the *corpora pedunculata*. The collaterals and axons both enter this ganglion.
15. An internuncial neuron contributing to the *tractus olfactorio-globularis*. The neurocyte lies on the medial surface of the *medulla interna*. An axon is given off which passes through this mass of neuropil and the *corpora pedunculata*, terminating in the deutocerebrum. This neuron represents the principal descending pathway of the *tractus olfactorio-globularis*.
16. An internuncial neuron contributing to the optic commissure. The neurocyte lies on the medial surface of the *corpora pedunculata*. The axon passes through this lobe, giving off collaterals to it, and terminates in the *corpora pedunculata* of the opposite eyestalk.
17. An internuncial neuron, the neurocyte lying on the lower medial surface of the *corpora pedunculata*. The axon given off by this cell passes along the medial surface of this lobe and the *medulla interna*, to enter the *medulla externa*. The collateral enters the *corpora pedunculata*.
18. An internuncial neuron with the neurocyte located on the medial ventral surface of the *medulla interna*. It gives off an axon which passes along the posterior surface of the *medulla interna* and enters the lateral surface of this lobe. The collateral enters the median face of the *medulla interna*.

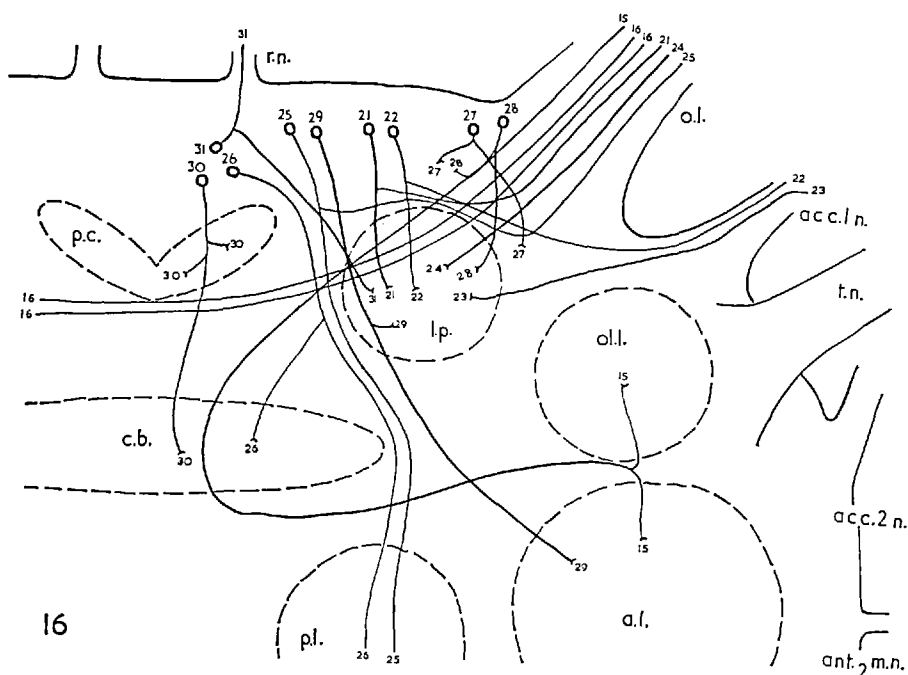


FIG. 16. Neurons of the protocerebrum, except those of the optic lobe.

19. These axons represent numerous ascending tracts from lower centers, which terminate in the *corpora pedunculata*. These could not be traced to their neurocytes.
20. A small internuncial neuron lying on the anteromedian surface of the *corpora pedunculata*, giving off an axon and collateral to this immediate region.

Neurons 1 to 20 are those which have their origin in the eyestalk of *Orconectes*; *a* and *b* are the terminations of ascending tracts from lower centers.

- (a) An ascending neuron within the *tractus olfactorio-globularis*, arising in the lateral nuclei of the deutocerebrum and terminating in the *corpora pedunculata*.
- (b) A terminating axon of the optic commissure, the neurocyte of which is located on the medial surface of the *corpora pedunculata* of the opposite eyestalk.

Neurons 21 to 31 are illustrated in Fig. 16.

21. An internuncial neuron having its cell body lying on the anterodorsal face of the supraoesophageal ganglionic mass. The collateral enters the *lobus paracentralis* and the axon terminates in the *corpora pedunculata* of the eyestalk.
22. A motor neuron having its neurocyte situated on the anterodorsal face of the brain, adjacent to neurocyte 21. The axon enters the first root of the accessory nerve; the collateral enters the *lobus paracentralis*.
23. A sensory neuron from the accessory nerve via the first root. This axon enters the *lobus paracentralis*.
24. An internuncial neuron, the neurocyte of which is located in one of the eyestalk ganglia. The axon is distributed in the *lobus paracentralis*.
25. An internuncial neuron located in the midregion of the anterodorsal group of cell bodies. The axon of this neurocyte proceeds posteroventrally into the circumoesophageal commissure of the same side and thus into lower centers in the nervous system. In the figure, this axon appears to pass through the parolfactory lobe; in reality, it passes dorsad of it. The collateral of neurocyte 25 enters the eyestalk.
26. An internuncial neuron, the neurocyte lying adjacent to neurocyte 25. The collateral is distributed in the central body. The axon follows the same path as does the axon of neuron 25 and together they form a substantial descending tract to lower centers in the nervous system.
27. An internuncial neuron with its neurocyte located in the anterodorsal nucleus, at the base of the optic lobes. The axon and collateral become distributed in a loose mass of neuropil at the base of these lobes. This neuropil tissue has previously been described as being analogous to the *corpus hemiellipsoidale*.
28. An internuncial neuron with its cell body located in the same nucleus as is that of neuron 27. The collateral enters the structure analogous to the *corpus hemiellipsoidale*. The axon proceeds posteriorly, entering *lobus paracentralis*.
29. An internuncial neuron with its cell body located in the midregion of the group of cell bodies on the anterodorsal face of the supraoesophageal

ganglionic mass. The collateral enters the *lobus paracentralis*. The axon proceeds by way of the olfactory commissure to the accessory lobe of the deutocerebrum.

30. An internuncial neuron with its neurocyte lying in the middorsal region of the anterodorsal group of cell bodies. The axon terminates in the central body; collaterals are given off to the *pons cerebri*.
31. A motor neuron exciting the rostral muscles. The neurocyte lies in the middorsal region of the anterodorsal group of cell bodies. The axon forms the rostral nerve; the collateral enters the *lobus paracentralis*.

The axons of neurons 15 and 16 are illustrated. The neurocytes of these neurons lie within the optic lobe. It will be noted that axon 15 is illustrated as having connections with both the accessory and olfactory lobes of the deutocerebrum. This axon contributes to the *tractus olfactorio-globularis*, which has descending connections with the deutocerebrum in both the accessory and olfactory lobes. The tract is too dense to sort out the individual axons connecting with these lobes; thus for clarity, it has been illustrated as a single tract with connections to both lobes. Axon 16 of the optic commissure is being included to illustrate the location of this major tract within the protocerebrum.

Neurons 1 to 31 comprise those investigated which originate within the protocerebrum of *Orconectes virilis*.

Deutocerebrum

The neurons of this section are illustrated in Fig. 17.

32. A motor neuron with the neurocyte lying on the dorsal surface of the medial group of deutocerebral cell bodies. The axon proceeds around the anterior face of the olfactory lobe, gives a collateral to this lobe, and enters the second root of the accessory nerve.
33. A sensory neuron from the second root of the accessory nerve, with its axon passing around the anterior surface of the olfactory lobe and along the medial surface of the accessory lobe, and terminating in the tegumentary lobe of the tritocerebrum. During its passage the axon gives off branches to the olfactory lobe and the accessory lobe. The heaviest innervation is to the accessory lobe.
34. A motor neuron having its neurocyte in the lateral group of deutocerebral cell bodies. The axon enters the second root of the accessory nerve, giving off a collateral to the accessory lobe.
35. A sensory axon coming from the second root of the accessory nerve. This axon enters the accessory lobe of the deutocerebrum.
36. A motor neuron with its cell body located at the ventral surface of the lateral group of cell bodies. The collateral enters the accessory lobe. The axon proceeds into the posterior branch of the accessory nerve of the antennule which leaves the anteroventral face of the supraoesophageal ganglion.
37. A sensory neuron emerging from the posterior branch of the accessory nerve of the antennule and entering the ventral surface of the accessory lobe of the deutocerebrum.

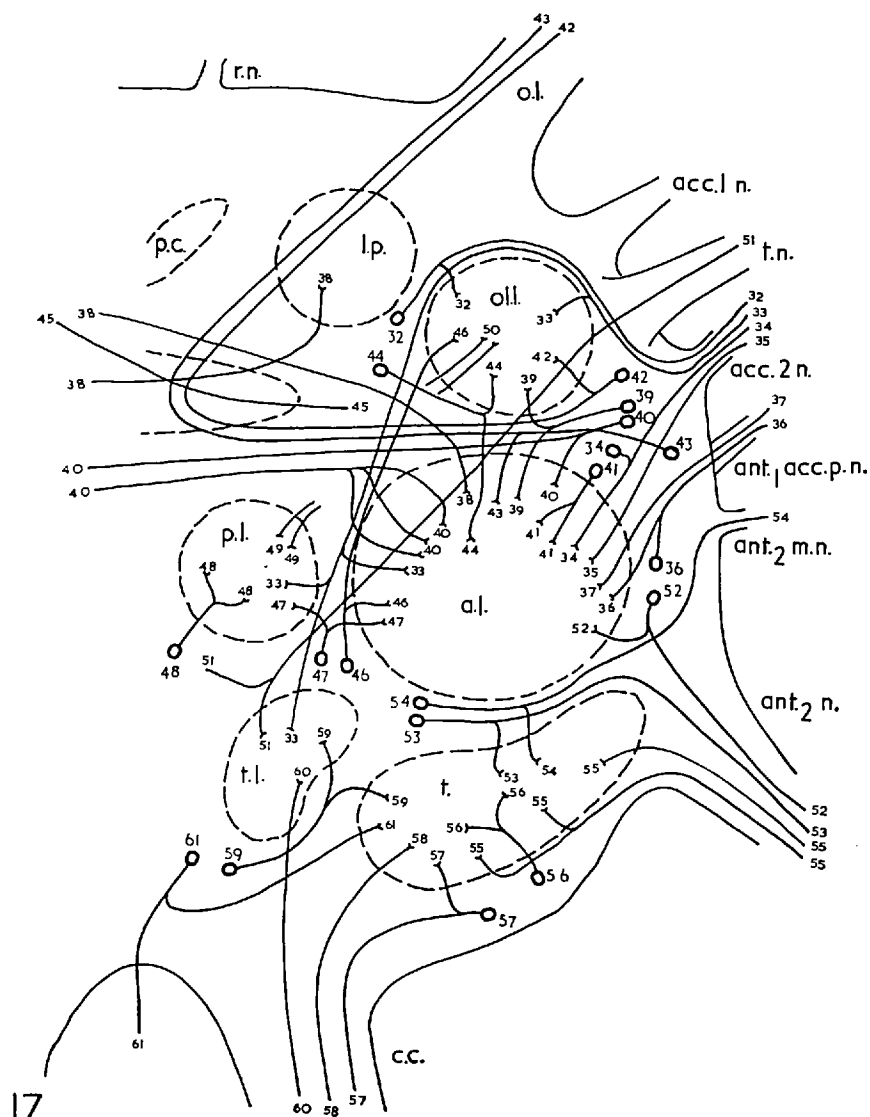


FIG. 17. Neurons of the deutocerebrum and the tritocerebrum.

38. Internuncial neurons connecting the *lobus paracentralis* with the accessory lobe of the deutocerebrum of the opposite side. These neurons cross the supraoesophageal ganglionic mass within the olfactory commissure. The neurocytes belonging to these axons have not been located.
39. An internuncial neuron with its cell body located within the lateral nucleus of the deutocerebrum. The axon enters the accessory lobe and the collateral enters the olfactory lobe.

40. Internuncial neurons of the olfactory commissure, with their cell bodies lying in the lateral nucleus. The axons pass between the olfactory and accessory lobes, then bridge the supraoesophageal ganglionic mass to enter the accessory lobe of the opposite side. The collaterals enter the accessory lobe. This is a very broad, loose tract. Axons from this tract are distributed over the entire medial surface of the accessory lobe.
41. An internuncial neuron with its neurocyte located in the lateral nucleus. The axon and collateral are both distributed in the accessory lobe.
42. An internuncial neuron of the *tractus olfactorio-globularis*. The neurocyte lies in the lateral nucleus. The axon proceeds medially to the central chiasma, where it turns anteriorly, proceeding into the optic lobe. The collaterals enter the olfactory lobe.
43. An internuncial neuron of the *tractus olfactorio-globularis*, having its cell body located in the lateral nucleus. The axon contributes to this tract in the same manner as does that of neuron 41. The collateral enters the accessory lobe.
44. An internuncial neuron with its neurocyte located in the medial nucleus of the deutocerebrum. The axon enters the olfactory lobe and the collateral enters the accessory lobe.
45. An internuncial axon belonging to the *tractus olfactorio-globularis*. Several axons of this tract are seen to cross in the central chiasma. However, they could not be traced to their neurocytes owing to the density of this tract. After crossing, they proceed into the optic lobe of the opposite side.
46. An internuncial neuron having its cell body located in a small nucleus lying between the accessory lobe and parolfactory lobe. The axon passes between these two lobes and enters the median surface of the olfactory lobe. The collateral enters the accessory lobe.
47. An internuncial neuron located in the same small group of cell bodies as is neuron 45. The axon enters the accessory lobe and the collateral enters the parolfactory lobe.
48. An internuncial neuron with its cell body lying in a very small nucleus on the ventral surface of the supraoesophageal ganglionic mass, mesad of the parolfactory lobe. The axon and collateral both enter this lobe.
49. A sensory neuron from the medial branch of the antennular nerve, entering the anteroventral face of the parolfactory lobe.
50. A sensory neuron from the lateral branch of the antennular nerve, entering the posteroventral face of the olfactory lobe.

Neurons 32 to 50 are those neurons investigated which comprise the deutocerebrum of *O. virilis*.

Tritocerebrum

The neurons associated with the tritocerebrum are illustrated in Fig. 17.

51. A sensory neuron from the tegumentary nerve. The axon passes dorsad of the accessory lobe, then proceeds ventrally to enter the tegumentary mass of neuropil. A group of fibers associated with this nerve turn anterad just before entering the tegumentary lobe and become distributed in the loose tissue of the central area of the brain.

52. A motor neuron representing a most interesting tract; it is deutocerebral in origin, for its neurocyte lies in the lateral nucleus of the deutocerebrum and the collateral enters the accessory lobe. The axon, however, passes posteriorly to enter the antennary nerve.
53. A motor neuron whose neurocyte is located in a small group of cell bodies lying in the area bounded by the accessory lobe of the deutocerebrum and the tegumentary and tritocerebral lobes of the tritocerebrum. The axon passes between the accessory and tritocerebral lobes to enter the antennary nerve. The collateral enters the tritocerebral lobe.
54. A motor neuron with its cell body lying adjacent to neurocyte 52. The axon passes between the accessory and tritocerebral lobes, then proceeds anteroventrally to enter the antennary motor nerve. The collateral enters the tritocerebral lobe.
55. A sensory neuron arising from the antennary nerve and entering the lateral and posterior surfaces of the tritocerebral lobe.
56. An internuncial neuron with its neurocyte lying in a small nucleus posterodorsad of the tritocerebral lobe. The axon and collateral are both distributed in the tritocerebral lobe.
57. An internuncial neuron with its neurocyte located in the same nucleus as that of neuron 55. The axon proceeds posteromedially into the circumoesophageal commissure of the same side, and thus into lower centers in the nervous system. The collateral enters the tritocerebral lobe.
58. A neuron from lower centers in the nervous system, entering the postero-medial face of the tritocerebral lobe.
59. An internuncial neuron with its neurocyte located on the ventral surface of the supraoesophageal ganglionic mass, mesad of the tegumentary lobe. The axon enters the tritocerebral lobe and the collateral enters the tegumentary lobe.
60. An ascending axon from lower centers in the nervous system, arising from the circumoesophageal commissure and entering the tegumentary lobe.
61. A neuron having its cell body in the same nucleus as is that of neuron 58. The axon contributes to the ventral gastric nerve. The collateral enters the tritocerebral lobe.

Neurons 51 to 61 are those neurons investigated which comprise the tritocerebrum.

Summary and Conclusions

The supraoesophageal ganglionic mass is typical, in most respects, of the decapod Crustacea. The outstanding difference in *Orconectes virilis* is the presence in this species of an accessory nerve complex. This nerve arises from the brain at three points: the first root at the base of the optic lobe, the second root just posterad of the tegumentary nerve, and the posterior branch posterolaterad of the antennular nerves. This is a mixed sensory and motor nerve innervating the muscles of the eye, the muscles of the antennule, and, in part, the muscles of the antenna. The first root receives motor fibers from the protocerebrum and supplies a sensory tract to the *lobus paracentralis*. The second

root receives motor fibers from the lateral and medial groups of deutocerebral cell bodies and sends sensory fibers to the olfactory lobe and accessory lobe of the deutocerebrum and to the tegumentary lobe of the tritocerebrum. The posterior branch receives motor neurons from the ventral surface of the lateral nucleus and gives a sensory tract to the ventral surface of the accessory lobe. This nerve complex has not previously been described in the literature.

It is suggested that the so-called 'optic' nerves of the stalked-eyed Crustacea be termed optic lobes and that the term optic nerves be reserved for those tiny fillets connecting the *lamina ganglionaris* to the retinal elements.

The X organ has been located on the medial surface of the *corpora pedunculata*. In addition, neurosecretory cells, having axons terminating in the sinus gland, are associated with each of the optic ganglia, the *lamina ganglionaris*, *medulla externa*, and *medulla interna*.

The descending pathways within the *tractus olfactorio-globularis* are found to originate in the *medulla interna*, rather than in the *corpora pedunculata*, as described by Hanström (1947). The ascending fibers from the deutocerebrum, however, were found to terminate in the *corpora pedunculata*. Contrary to Hanström (1947), no ascending connections from the lower parts of the brain could be found to centers higher than the *corpora pedunculata*.

The following masses of neuropil are located within the protocerebrum of *O. virilis*: the *lamina ganglionaris*, *medulla externa*, *medulla interna*, *corpora pedunculata*, *pons cerebri*, central body, and *lobus paracentralis*. A loose area of synaptic tissue considered to be analogous to the *corpus hemiellipsoidale* is present. Neurocytes associated with the protocerebrum innervate the rostral muscles via the rostral nerve and the eyestalk muscles via the oculomotor nerve.

The deutocerebrum is composed of three lobes: the olfactory lobe, the very well-developed accessory lobe, and the feebly developed parolfactory lobe. The olfactory and accessory lobes may be recognized by their distinctive glomeruli. The deutocerebrum is the origin of the very well-developed *tractus olfactorio-globularis* connecting the deutocerebrum and protocerebrum. A large olfactory commissure connects the accessory lobes of the opposite sides. The antennular nerve terminating in the olfactory and parolfactory lobes contains only sensory fibers. All motor nerves to the antennules pass by way of the accessory nerve. The presence of a very well-developed *tractus olfactorio-globularis* would attest to the ancient and close connection of the protocerebrum and the deutocerebrum. Well-developed preoral optic and olfactory commissures would suggest that these ganglia are preoral in origin, contrary to the views of Henry (1948) and Ferris (1950).

There is a very interesting connection between the accessory lobe of the deutocerebrum and the antenna. Motor neurons arise in the lateral nucleus, giving collaterals to the accessory lobe, and proceed to enter the antenna of the same side.

The tritocerebrum is composed of a large tritocerebral lobe and a lesser tegumentary lobe. This ganglion supplies motor neurons to the muscles of the antenna via the antennary nerve and the antennary motor nerve which originates anterad of the antennary nerve. Sensory axons from the antennary nerve enter the tritocerebral lobe. The tegumentary nerve, situated at the anterior angles of the supraoesophageal ganglionic mass, supplies sensory

fibers to the tegumentary lobe from the hypodermis of the head capsule. Axons from lower centers, arising by way of the circumoesophageal connectives, enter both these lobes. Descending fibers arise in the tritocerebrum and enter the circumoesophageal connectives. The unpaired inferior oesophageal nerve arises from neurocytes associated with the tritocerebral lobe. Motor fibers to the muscles of the antenna are also supplied by the accessory nerve. The data is in agreement with the work of Heath (1941) and Henry (1948), regarding the innervation of the green gland by a branch of the antennal nerve, and is contrary to that of Kiem (1915). In addition, the green gland in *O. virilis* is innervated by the accessory nerve.

There are no large tracts connecting the tritocerebrum to the higher centers such as the *tractus olfactorio-globularis*. This would lead one to believe that this ganglion is a recent acquisition by the supraoesophageal ganglionic mass.

It is suggested that the term ganglionic mass be used to designate compound ganglia such as the supraoesophageal and suboesophageal ganglionic masses. At present, a degree of confusion exists in the use of the term ganglion, as it is also used for the single segmental ganglion. It is suggested that the term ganglion be reserved for those structures innervating a single segment.

Sixty neuronal pathways within the supraoesophageal ganglion are described and illustrated.

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ABBREVIATIONS USED IN FIGURES

<i>acc.1 n.</i>	first root of the accessory nerve	<i>ant.2 n.4</i>	nerve of the adductor muscle of the exopodite of the antenna
<i>acc.2 n.</i>	second root of the accessory nerve	<i>ant.2 n.5</i>	nerve of the <i>musculus abductor exopoditis</i> of the antenna
<i>a.l.</i>	accessory lobe	<i>c.b.</i>	central body
<i>ant.1 n.</i>	nerve of antennule	<i>c.c.</i>	central chiasma
<i>ant.1 acc. n.</i>	accessory nerve of the antennule	<i>c.e.</i>	<i>chiasma externum</i>
<i>ant.1 acc. a.n.</i>	anterior branch of the accessory nerve of the antennule	<i>c.i.</i>	<i>chiasma internum</i>
<i>ant.1 acc. p.n.</i>	posterior branch of the accessory nerve of the antennule	<i>c.c. (Figs. 1, 17)</i>	circumoesophageal commissure
<i>ant.2 acc. n.</i>	accessory nerve of the antenna	<i>c.p.</i>	<i>corpora pedunculata</i>
<i>ant.2 acc. endo. n.</i>	accessory nerve of the endopodite of the antenna	<i>d.g.n.</i>	unpaired dorsal gastric nerve
<i>ant.2 acc. endo. n.1</i>	a branch of the endopodite branch of the accessory nerve of the antenna, innervating the region of the nephropore	<i>l.c.</i>	lateral nucleus of deutocerebrum
<i>ant.2 acc. exo. n.</i>	accessory nerve of the exopodite of the antenna	<i>l.g.</i>	<i>lamina ganglionaris</i>
<i>ant.2 acc. n.1</i>	a branch of the accessory nerve of the antenna to the hypodermis	<i>l.p.</i>	<i>lobus paracentralis</i>
<i>ant.2 endo. n.</i>	nerve of the endopodite of the antenna	<i>m.c.</i>	medial nucleus of deutocerebrum
<i>ant.2 exo. n.</i>	nerve of the exopodite of the antenna	<i>m.e.</i>	<i>medulla externa</i>
<i>ant.2 m.n.</i>	motor nerve of antenna	<i>m.i.</i>	<i>medulla interna</i>
<i>ant.2 n.</i>	nerve of the antenna	<i>o.c.</i>	optic commissure
<i>ant.2 n.1</i>	nerve of the compressor muscle of the basipodite of the antenna and of the levator muscle of the same appendage; a branch is given off to the green gland	<i>o.l.</i>	optic lobe
<i>ant.2 n.2</i>	nerve of muscle <i>b</i> of the meropodite of the antenna	<i>ol. c.</i>	olfactory commissure
<i>ant.2 n.3</i>	nerve to the region of the nephropore	<i>ol. l.</i>	olfactory lobe
		<i>om. n.</i>	occulomotor nerve
		<i>o.n.</i>	optic nerve
		<i>o.t.</i>	optic tract
		<i>p.c.</i>	<i>pons cerebri</i>
		<i>p.c.l.</i>	nerve tracts connecting <i>pons cerebri</i> and central body
		<i>p.l.</i>	parolfactory lobe
		<i>r.n.</i>	rostral nerve
		<i>s.g.</i>	sinus gland
		<i>stat. n.</i>	nerve of the statocyst organ
		<i>t.</i>	tritocerebral lobe
		<i>t.l.</i>	tegumentary lobe
		<i>tr.</i>	<i>tractus olfactorio-globularis</i>
		<i>v.g.n.</i>	unpaired ventral gastric nerve
		<i>X.</i>	<i>X</i> organ