The Fine Structure of Nerve Cells and Fibers, Neuroglia, and Sheaths of the Ganglion Chain in the Cockroach (*Periplaneta americana*)

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Plates 364 to 375

(Received for publication, April 28, 1958)

ABSTRACT

The abdominal nerve cord of *Periplaneta americana* was studied utilizing light and electron microscopes. In the nerve cells, delicate granules, similar to those probably responsible for cytoplasmic basophilia, are evenly distributed in "dark" cells and clumped in "light" cells. Neuroglial cells are stained metachromatically by cresyl violet. The neuroglial cells have many processes which ramify extensively and are enmeshed to form overlapping layers. These imbricated processes ensheath the nerve cells; the inner layer of the sheath penetrates into the neuron and is responsible for the appearance of the trophospongium of Holmgren. Nerve fibers are embedded within glial cells and surrounded by extensions of the plasma membrane similar to mesaxons. Depending on their size, two or several nerve fibers may share a single glial cell. Nerve fibers near their terminations on other nerve fibers contain particles and numerous, large mitochondria. The ganglion is ensheathed by a thick feltwork of connective tissue and perilemmal cells. The abdominal connective has a thinner connective tissue sheath which is without perilemmal cells. The nerve fibers and sheaths in the connective become thinner as they pass through ganglia.

The present investigation is an attempt to correlate cytological and neurohistological observations of the nervous system of insects by studying with the light and electron microscopes the third thoracic and sixth abdominal ganglia and other abdominal ganglia and connectives of the nerve cord in the cockroach. Beams, Sedar, and Evans (2) have made some early observations with the electron microscope on the ganglion chain of the grasshopper. The electron microscope affords the opportunity of visualizing all of the elements, neural and glial, in one preparation. Some considerations of the structure and relations of the various organelles in insect nerve cells and neuroglia will be presented, as well as the relations of the cell types and their processes to each other.

Material and Methods

For light microscopy, an individual ganglion or the entire ganglionic chain of the cockroach (*Periplaneta americana*), from the sixth abdominal to the third thoracic ganglion, was exposed by a dorsal approach and Bodian's (80 per cent alcohol, 90 ml.; 5 ml. formaldehyde; 5 ml. glacial acetic acid) or Bouin's fluid poured on it. The chain or ganglion was removed, allowed to fix for 1 to 2 hours, dehydrated and cleared rapidly, and embedded in paraffin. Sections, 10 μ to 15 μ in thickness, were stained by cresyl violet or by Bodian's protargol method. Fixation in Bodian's fluid and a double impregnation in 2 per cent protargol with about 10 grams of copper per 100 ml. of solution, according to the modification of Power (19), yielded the best results for silver staining.

For electron microscopy, the third thoracic or the sixth abdominal ganglion or a short length of the abdominal nerve cord containing ganglia was removed and placed for 30 to 45 minutes in Dalton's fixative (Dalton and Felix, 5), a solution containing 1 per cent osmium tetroxide, 1 per cent potassium dichromate at a pH of 7.2–7.6, and 0.85 per cent sodium chloride. The tissues were then rinsed in distilled water, dehydrated, and embedded in a partially polymerized mixture of one part methyl- to six parts butyl-methacrylate. After infiltration, the plastic was polymerized at 45°C. with benzoyl peroxide as the catalyst. Ultrathin cross- and longitudinal sections were cut with a Servall Porter-Blum microtome. The sections, mounted on copper mesh grids coated with a film of collodion, were examined in an RCA-EMU 2E electron microscope. Negatives were exposed at a magnification of 1000 to 8000 diameters and photographically enlarged. Thicker sections (1 μ to 5 μ) were also made and examined with the phase contrast microscope to provide orientation.

RESULTS

The Architecture of the Insect Ganglion

A typical roach ganglion in cross-section exhibits a cortical portion containing nerve cells, and a large medullary area containing nerve fibers coursing in all directions (Figs. 1 *A* and *C*). The abdominal ganglia have two prominent groups of large fibers, dorsal and ventral, in each lateral half. Some of these fibers are said to arise in the sixth abdominal ganglion and to ascend and end in the third thoracic ganglion (Pumphrey and Rawdon-Smith, 20; Roeder, 22).

Nerve Cells

Most of the nerve cells are uni- or bipolar (Fig. 1 *A*) and vary greatly in size. Two distinct cell types are found. In one, the cytoplasm is dense in electron micrographs; clear spaces between the cytological elements are small and infrequent (Fig. 2). The contrasting cell type is less dense in electron micrographs, and clear spaces between the cytological elements are relatively large and frequently encountered (Fig. 2). These two cell variants may be encountered side by side. The clear spaces in the cells are possibly produced by distortions during fixation. If so, the two cell types may be said to react differently to the fixative. In any event, the two cell types differ in the appearance of their organelles.

The nerve cell nuclei have large clumps of chromatin and exhibit prominent nucleoli after staining with cresyl violet (Figs. 1 *D* and *F*). Nuclei are impregnated heavily by protargol and frequently the karyoplasm is concentrated on one side of the nucleus (Fig. 1 *A*), probably as a result of distortion during fixation. In electron micrographs, the nuclei exhibit evenly distributed granules. The nucleolus occurs as a very dark area in the nucleus (Fig. 2). The appearance of the nucleus aids in distinguishing nerve cells from other kinds of cells in the ganglion.

The limiting membrane of the nerve cell is rough edged and frequently is invaginated for a considerable distance into the cell's cytoplasm. In some nerve cells, the invaginations are very marked.

Neurofibrils appear as elongated threads in silver preparations of perikarya examined with the light microscope. As in the nerve cells of other animals (Hess, 9), no structures have been seen in electron micrographs of cockroach nerve cell cytoplasm which can be correlated with the structure of neurofibrils as seen in the light microscope.

Nerve cells are basophilic and their cytoplasm stains deeply with cresyl violet (Fig. 1 *D*). After cresyl violet or protargol procedures, the cytoplasm frequently appears vacuolated (Figs. 1 *B* and *F*). As an index of the possible protein content of the vacuoles, a mercuric bromphenol blue stain, thought to be specific for proteins (Mazia, Brewer, and Alfert, 16), was used. The vacuoles remained unstained. The cresyl violet–stained portions of the neuron cytoplasm do not reveal any conspicuous clumps of basophilic material; hence, chromophil substance, occurring as discrete Nissl bodies, is not apparent.

All of the cockroach nerve cells examined with the electron microscope exhibit microgranules scattered throughout their cytoplasm. These granules are similar in size and appearance to those described by Palade (17) and hence probably represent the structures called ribonucleoprotein particles (or ergastoplasmic granules by other authors). Their distribution is such that they may well be responsible for the basophilia of the cockroach neuron. It is in the disposition of these granules that the nerve cell types differ. The "dark" cell has granules dispersed almost evenly throughout its cytoplasm; the "light" cell contains the granules in small aggregations or clumps (Fig. 2). No membrane-bound tubules of endoplasmic reticulum or ergastoplasm have been seen in association with these granules. The granules have no preferred orientation in the cell, but are apparently distributed randomly except for their disposition in clumps as noted above. It is probably because of this prevailing randomness that no definitive Nissl bodies can be seen in the roach neuron.

Dense elongated bodies with smooth margins are seen in the cytoplasm of nerve cells (Fig. 2). In their interiors, double-membraned folds occur. These bodies are identifiable as mitochondria and are similar in structure to the mitochondria of vertebrate nerve cells (Hess, 9). They are distributed at random in the cytoplasm.

A complex structure, consisting of flattened sacs surrounded by small vesicles, is frequently encountered in the cytoplasm (Fig. 4). This structure resembles that described as the Golgi apparatus in vertebrate spinal ganglia (Hess, 9) and other cells (Dalton and Felix, 5). The Golgi apparatus shows no special relation to the mitochondria or to the invaginated nerve cell membrane.

Frequently seen in the cytoplasm are dense droplets, larger than the mitochondria, more irregular in outline, and showing no organized internal structure (Fig. 2). These droplets are presumably of a lipide nature and are apparently the lipochondria or lipide bodies seen in invertebrate neurons. They bear no constant relationship to the mitochondria or to the Golgi apparatus and are disposed randomly in the cell.

Both types of nerve cell, "light" and "dark," contain these bodies. However, they are far more numerous in the dark cell type (Fig. 2). Thus, the high density of the dark cell type is probably due partly to the high incidence of lipochondria as well as to the distribution of the small granules discussed above.

In the cytoplasm and most frequently near the plasma membrane, a structure is seen, moderately dense in the electron micrograph, enclosed in a membrane, and containing small vesicles and mitochondria (Figs. 2 and 4). As will be explained below, this structure represents a process from a neuroglial cell which penetrates the neuron. In some sections, such as that illustrated in Fig. 4, the process lies in a plane different from that of the section and therefore appears to be isolated from the neuroglial cell.

Neuroglia

Other cells besides the nerve cells are found in insect ganglia. Since they are not nerve cells and since they occur between and among the nerve cells and fibers, they are probably comparable to neuroglia and will be considered as such in this paper.

Preparations stained with cresyl violet exhibit at least four types of nuclei in and around the ganglia (Fig. 1 *B*). Some nuclei are dark and elongated and usually rest on the sheath of the ganglion (Fig. 1 *B*, *1*). Another nuclear type occurs inside and contiguous to the homogeneous layer of the ganglion sheath (Fig. 1 *B*, *2*). These nuclei are dark, but clumps of chromatin can be seen. They are not so elongated or so flattened as the aforementioned nuclei. This nuclear type belongs to the perilemmal cell to be defined below. The third type of nucleus is larger than the other two and is relatively lightly stained (Fig. 1 *B*, *3*). Large clumps of chromatin are present which frequently rest on the nuclear membrane. In some instances they appear to radiate from the nuclear membrane yielding a spoke wheel effect. In some nuclei, an especially conspicuous clump of chromatin occurs, which may be the nucleolus. This nucleus belongs to a neuroglial cell. The nucleus of the nerve cell is the largest type seen (Figs. 1 *B*, *4*; *D* and *F*). Although lightly staining, it contains clumps of chromatin, which are more granular than those of the neuroglial cells and which do not usually accumulate on the nuclear membrane. Its nucleolus is extremely prominent and appears as a large round densely stained mass (Figs. 1 *D* and *F*).

After cresyl violet, most elements stain with a violet color. However, an apparently fibrous network, accumulated most conspicuously in the area of junction between cortical nerve cells and medullary fibers, stains metachromatically an intense pink color (Fig. 1 *C*). These strands of cytoplasm enclose the neuroglial cell nuclei (Figs. 1 *E* and *G*). Cell borders are difficult to define so that the pink cytoplasm appears as a reticulated net. This pink staining cytoplasm is apparently that of the neuroglial cells. Scharrer (25) used Bismarck brown, a basic dye, to stain the neuroglia, and illustrated this tissue also at the junction of collections of cell bodies and bundles of fibers in the cerebral ganglion of the cockroach. As will be described below, the apparently fibrous network of these glial cells is revealed in electron micrographs to be composed of interwoven processes of cytoplasm.

Although the nuclei of neuroglial cells occur most frequently at the junction of nerve cell bodies and fibrous bundles, many of them are located in the interior of the ganglion, frequently in the midline (Fig. 1 *C*). It is difficult to see any cytoplasm surrounding these nuclei in the interior of the ganglion, but structurally, they are entirely similar to the clusters of nuclei surrounded by pink cytoplasm at the area of cell body–fiber junction.

In thin sections examined with the electron microscope the neuroglial cell nucleus contains dense accumulations of granules apposed to the nuclear membrane (Fig. 6). It is easily differentiated from the homogeneously granular nerve cell nucleus in electron micrographs. The cytoplasm of the glial cells contains small granules, mitochondria, and flattened vesicles similar to those of the Golgi apparatus described elsewhere. The cytoplasm in the area surrounding the nucleus is very limited in amount, but the glial cells have many processes which ramify extensively (Fig. 6). The processes and their associated plasma membranes are oriented to form a series of two to twenty overlapping layers running in the same direction. The processes of the glial cell ensheath the nerve cells and fibers; this relation will be described in more detail below. Also prominent in the neuroglial cell cytoplasm are vesicles, small round bodies with relatively clear centers and dense borders. There is evidence that at least some of these vesicles are the infoldings of the cell membrane cut in cross-section. The membranes do not form complete layers, but are interrupted, indicating that perhaps they are changing direction. At times, an interrupted portion of the membrane seemingly ends as a vesicle, indicating that the membrane courses longitudinally, changes direction, and is then seen cut in cross-section. Wherever imbricated layers of membrane are seen, circular contours are disposed between them. However, in some parts of neuroglial cells, the vesicles appear too numerous to be accounted for as cross-sections of membranes. The membranes are very complex and in oblique sections, their ramifications are extremely elaborate.

Also seen in the ganglion in the extracellular spaces are granular areas, apparently not cytoplasmic, containing a few dense thin rods with no detectable internal structure (Fig. 12). Tracheoles, ensheathed by cells, can often be seen in these areas.

The Relation of Neuroglia and Nerve Cells

The processes of the neuroglial cells described above form around the nerve cells a thin sheath consisting of several overlapping layers (Figs. 2 to 4, 6). These processes, although commonly interrupted, are occasionally continuous for long distances around the surface of the neuron. Thus, the nerve cells are ensheathed by neuroglial cells.

The inner layer of glial cytoplasm frequently penetrates into the neuron cytoplasm and causes an invagination of the neural plasma membrane (Figs. 2 to 4). Strictly speaking, the glial cytoplasm is not admixed with the neuronal cytoplasm but is always separated from it by two membranes, the plasma membrane of the glial cell and that of the nerve cell. In some sections, the origin of the glial cell cytoplasm is not seen and the piece of glial cell appears as an inclusion within the neuron (Figs. 2 and 4). The glial processes pushing into the neuron, in some sections, appear numerous and elaborate (Fig. 3). The glial process which penetrates the neuron contains mitochondria and vesicles (Figs. 3 and 4). Its mitochondria are frequently smaller than those in other parts of the glial cell. The vesicles in the evaginated glial process frequently are larger and exhibit clearer centers than are those in other portions of the glial cell. Holmgren (12) found that definite prolongations of the cells surrounding invertebrate neurons penetrate into the neuronal cytoplasm and form networks of canaliculi. He believed (13) that the canaliculi or the trophospongium serve as nutritive passages into the cell and are responsible for the appearance of the Golgi apparatus in cells. Beams and King (1) rejected these suggestions in a study of the nerve cells of the grasshopper. They believed that the intracellular trabeculae are fibrous structures. It can now be seen that the glial processes are not strictly intracellular and are not fibrous, but are cytoplasmic. The evaginations of the glial cytoplasm pushing into the neuronal cytoplasm, but separated from it by plasma membranes, are thus probably responsible for the appearance of the trophospongium of Holmgren as seen in the light microscope. As Beams and King (1) contended, there is no morphological connection between these cell processes and the Golgi apparatus.

Nerve Fibers in Ganglia

The nerve fibers in the ganglion are similar in structure to those described in insect peripheral nerves (Fig. 7) (Hess, 11). The fibers frequently contain granules which, in some sections, appear to be tubular or vesicular with a clear center and a more dense border. Dense bodies with an internal structure typical of mitochondria occur frequently in the axoplasm. The sheaths of the nerve fiber will be reserved for later discussion. The nerve fibers vary in diameter from less than 1 μ to more than 10 μ.

The Relation of Glial Cells and Nerve Fibers in Ganglia

The relation of nerve fibers and neuroglial cells is rather difficult to elucidate because of the extensive and complex ramifications of the processes of the neuroglial cell. The impression is certainly gained that the nerve fibers are ensheathed by neuroglial cells. In some instances, the nerve fiber rests in an indentation of the glial cell nucleus (Fig. 10), and separated from the nuclear material by the limiting plasma and nuclear membranes. Around some fibers, many imbricated processes are apposed. The largest fibers appear to be solitary. Medium sized fibers are usually gathered into groups of two or three (Fig. 7), whereas eight to ten of the smallest fibers are enclosed as a fascicle by the glial cell sheath. Most of the larger nerve fibers are clearly surrounded by a triple membrane, one belonging to the axon, the other two to the glial cell (Fig. 7). The fibers probably are not entirely enclosed by the glial cell, since a connection to the exterior through apposed glial plasma membranes is frequently demonstrable (Fig. 7). This arrangement is similar to that exhibited by the mesaxons of vertebrate nerve fibers (Gasser, 8; Hess, 10). Frequently, the nerve fibers fill the glial cells so completely that little glial cell cytoplasm can be detected (Fig. 7). Nevertheless, although scant in amount, there is nothing to indicate that the cytoplasm of glial cells surrounding nerve fibers is different from that ensheathing nerve cells.

The Relation of Nerve Fibers in Ganglia to Each Other—the Synapse

"The anatomy of synapses in the cockroach or any other insect has not been described in any detail" (Roeder, 23). However, Leghissa (15), using methylene blue or silver impregnation, described "some terminal little buttons . . . , which find their place upon the cellular body and dendrites" and also occur on nerve fibers in the ganglion chain of the stick insect *Carausius morosus*.

In a cross-section of the medullary portion of the ganglion, many fibers are cut in cross-section and some are sectioned longitudinally. Contiguous to many of these fibers are oblique or cross-sections of structures bounded by membranes and containing particles and mitochondria (Figs. 11 and 16). The particles are sometimes distributed evenly throughout these structures, or are concentrated on one side, or are restricted to processes bulging from one of these structures. In those structures in which the particles are located eccentrically and not evenly disposed, the portion devoid of particles is similar in appearance to a nerve fiber (Figs. 11, 16, 17, 20, and 21). It thus appears that these particle-containing structures are continuous with nerve fibers. Further evidence that they are not neuroglial is provided by the fact that their particles are more numerous than are those of neuroglial cells. Moreover, these neural particles are either smaller or larger and denser in appearance than are any comparable inclusions observed in neuroglia. In synapses on mammalian nerve cells (Palay, 18), on earthworm fibers (De Robertis and Bennett, 6), frog cells (De Robertis and Bennett, 6), and in invertebrate axo-axonic synapses (Robertson, 21), microvesicles have been described. It is entirely probable that these roach nerve fibers represent the portions of the fiber at or near the synapse.

Vesicles occur in the presynaptic part of the axo-axonic or axo-somatic synapses of the earthworm and frog (De Robertis and Bennett, 6) and mammal (Palay, 18), but are located in the postsynaptic portion of the axo-axonic synapse of the squid and crayfish (Robertson, 21). It is probable that the particles described here are presynaptic since the structures containing them are relatively numerous and their size is small compared to those of the other nerve fibers. It thus appears that most of these particle-filled processes are the smaller branches of parent fibers which are approaching their termination.

A further point to be mentioned is that the particles extend throughout the region where the nerve fibers approach their terminations. Thus, not all particle-filled fibers make direct contact with others. Rather, the presence of particles can indicate the approach to a synapse as well as the terminal part of the nerve fiber itself. This point of view is strengthened by the occasional appearance of fibers containing particles restricted to one side or disposed in varicosities. These appearances probably represent oblique sections through two regions of the same nerve fiber—a portion of the fiber which does not have particles and part of the fiber that is nearing its ending and has particles.

The place where two nerve fibers are close together, with one having particles and the other devoid of them, is not necessarily the exact site of synaptic contact since the presynaptic fiber may approach closely to another fiber for a short or long distance but make synaptic contact only at one point. Thus, one cannot be sure that the exact point of synapse is being observed or that one is at the site of the pre- and postsynaptic membranes of the nerve fibers. Nevertheless, in all places of very closely apposed nerve fibers, one with and the other without particles, there appear to be no extensive modifications of the structure of the axoplasm of the usually larger fiber devoid of particles and presumably postsynaptic. In some locations, there are indications of oriented rows of small structures along the postsynaptic membrane (Figs. 19 and 23), but no outstanding collection of particles has been seen nor are there any striking structural modifications of the presumably post-synaptic nerve fiber comparable to that seen in the particle-containing presynaptic axoplasm.

Leghissa (15) has described silver-stained preparations of insect nerve fibers sectioned longitudinally which exhibit a series of terminal buttons lined up equidistantly along the length of the nerve fiber. Such an arrangement has also been seen in electron micrographs. An occasional longitudinally sectioned fiber has exhibited a series of small nerve fibers containing particles lined up along its length and pushing into it (Fig. 23). This is not necessarily the only arrangement of synaptic contact between nerve fibers and, indeed, there are instances where one nerve fiber appears to push into another and neither contains any particles like those described above (Fig. 18).

Insect nerve endings probably occur, at least most frequently, on other nerve fibers, rather than on nerve cell bodies. Leghissa (15) described terminal buttons on the nerve cells of the stick insect. Particle-filled nerve fibers have not been seen apposed to the nerve cell bodies in the cockroach. In support of the contention that these particle-filled fibers represent neural terminations, it may be remarked that small fibers and apparent endings as revealed in silver-impregnated sections are restricted to the fibers and are not seen contiguous to the nerve cells in the roach ganglion.

There are at least three kinds of particles: the smallest, usually about 300 A to 500 A, called granules; the next in size, usually about 1000 A to 1500 A, denoted as vesicles; and the largest, designated as droplets and ranging from about 1200 A to 2500 A and above in size. The granules are the most frequently encountered as well as the smallest (Figs. 11, 16, and 17). In some instances, the granules appear to be microvesicular and seem to have dense borders and lighter interiors. The least frequently occurring particle, but the next in size to that of the granules, is the vesicle (Fig. 19). The vesicle has a dense border and a relatively light interior. There are indications of structure within the vesicle, but its nature has not yet been fully determined. Granules are always found scattered among the vesicles in the same nerve fiber. Other nerve fibers in ganglia contain droplets (Figs. 11, 20, and 21). The droplets are homogeneous and very dense and often give the general impression of being about the same size in an individual nerve fiber. They vary greatly in size from one nerve fiber to the other. Granules in the same nerve fiber or in neighboring fibers are always seen in association with the droplets.

The mitochondria in the synaptic area appear to be larger and more numerous than in nerve fibers in other locations (Figs. 11, 16, 17, 19, and 23). The mitochondria located near the synapse, both in fibers with and without particles, appear to have a characteristic structure. A hole is frequently seen in the center of the mitochondrion and the internal folds seem to form a spiral around this center (Figs. 17, 19). As would be expected from such a spiral organization, other mitochondria, depending on the plane of section, exhibit parallel internal folds lined up either transversely or longitudinally along the long axis of the mitochondrion (Figs. 17 and 19). The large size of the mitochondria in synaptic areas frequently causes them to be excluded from the small particle-filled terminal nerve fibers.

The mitochondria in nerve fibers in other locations, such as in peripheral nerves in the cercus, also have hollow centers (Fig. 22) and an apparent spiral organization (Fig. 22, inset). The spiral organization in synaptic areas is especially striking because of the large size of the mitochondria.

The structure of the synaptic regions in the insect thus conforms to that of other forms (see Fernández-Morán, 7) and contains an accumulation of large mitochondria and an extensive number of synaptic particles. The large number of the particles and their variety of form in the cockroach makes this a very favorable animal for normal and experimental studies of the structure of the synapse.

The exact significance of the particles in axons at and near their terminations remains to be determined. The particles at the synapse have been considered as containing small units of a chemical transmitter, or precursors of this transmitter, which are discharged at the synapse (see Fernández-Morán, 7). This idea is compatible with a quantum concept of neuromuscular transmission advanced by del Castillo and Katz (3), whereby the discharge of acetylcholine, spontaneously or in response to an impulse, occurs in "quantal," *i.e.* multi-molecular units. The recent report of Colhoun (4) appears to lend support to these suggestions. Acetylcholine in the thoracic nerve cord of the cockroach can be released by both osmotic pressure and mechanical disruption more easily than in mammals. This supports the hypothesis that acetylcholine is not in chemical combination but is located within "structural compartments." These structural compartments may well be the particles described at and near the synapse in the present investigation. The relative ease with which acetylcholine can be released in insects compared to mammals might also be correlated with the relatively greater number and size of these particles as described here in the cockroach compared to the synaptic vesicles of other forms. If the particles at and near the synapse are associated with a chemical transmitter, then the different kinds of particle found here in the cockroach might indicate different kinds of chemical transmitters or different functional states of formation and discharge of a chemical transmitter. It is also possible that different kinds of particle are related to the nerve fibers from a certain source.

Roeder (23), in a discussion of the nature of synaptic transmission in invertebrates, states that "there are indications of gradual transition of axonic into synaptic transmission." Thus, synapses vary from "axon-like," which are scarcely affected by the chemical environment and in which current flow is the dominant factor, through various types of junction in which chemical control plays a progressively larger part, to the other extreme of labile synapses, which are greatly influenced by the chemical environment and in which the electrical factor is negligible, such as in neurosecretion. "Within a single reflex system, there may be several types of synapse" (Roeder, 23). The three kinds of particles found in axons near and at their terminations in the present investigation may illustrate this discussion with the granules perhaps representing the axon-like synapses, the larger vesicles representative of a synapse more influenced by the chemical surroundings, and the largest droplets illustrative of a phenomenon like neurosecretion, with all three kinds of particles in the same reflex system.

Further evidence of the significance of the particles in axons at and near their terminations can perhaps be supplied by degeneration and stimulation experiments which are in progress.

Trachea and Tracheoles in Ganglia

It is not intended here to consider the structure of tracheae or tracheoles in detail. They can easily be identified in the electron microscope by their dense (cuticle) linings. Tracheoles can sometimes be seen within cells the nuclei of which are similar to those of neuroglia but the cytoplasm, although containing both vesicles and membranes, is less complex. In cells enveloping tracheoles, dense droplets, apparently lipide in nature, are found. Rarely myelin figures, consisting of overlapping evenly spaced lamellae, are also seen. These elements are apparently those which have been called tracheal end cells. Their cytoplasm is frequently attenuated so that the tracheoles do not appear as if they are included in a cell; however, at least the plasma membrane of this cell can be seen in electron micrographs to enclose the tracheole.

Tracheoles have been said to occur intracellularly in nerve cells (Ross and Tassell, 24). Delicate tracheoles have been observed, in this study, located between nerve fibers and near nerve cells, but none have been seen penetrating the nervous elements.

The Sheath of the Ganglion

Scharrer (25) called the sheath of the cockroach cerebral ganglion the "perilemma" and divided it into two parts: an inner cellular "perineurium" and an outer homogeneous "neural lamella." Hoyle (14), in the peripheral nerve trunk of the locust, restricted the term "perilemma" to the inner cellular layer and retained the term "neural lamella" for the homogeneous part of the sheath. Electron microscopic investigation of the peripheral nerve trunk of the cockroach has revealed that the inner cellular layer of the sheath is made up of Schwann cells and the outer homogeneous layer consists of fibers resembling collagen (Hess, 11).

The confusion in terminology, especially concerning the word "perilemma," has resulted from the assumption that the nerve trunks and ganglia of insects are ensheathed in an entirely similar manner. As will be seen below, this is not so. The following terminology for the sheaths of ganglia will be used in the present study: the neural lamella will refer to the homogeneous layer seen in the light microscope, whereas the perilemma will denote the inner cellular layer next to the neural lamella. The term "perineurium," used by Scharrer (25) to signify a cellular layer, has been discarded since this word denotes a connective tissue layer in the nerves of other animals.

Sections through the sheath of the ganglion reveal a dense feltwork of connective tissue layers, each one oriented in general in a different direction (Figs. 13 and 14). The sheath of the ganglion is thicker and more complex than that of the peripheral nerve trunk (Hess, 11). The outermost layer of the sheath is thin and, in the electron microscope, appears to be finely granular or homogeneous in appearance. Inside this thin layer, collagen fibers occur. They are striated in a manner analogous to that of vertebrate collagen (Fig. 14). The collagen fibers of the sheath occur roughly in three layers (Figs. 13 and 14). Next to the thin relatively structureless layer in a cross-section of a ganglion, the connective tissue fibers are cut predominantly in cross-section. Proceeding centrally, the next layer of fibers is sectioned longitudinally or obliquely. Still further toward the interior, cross-sections of collagen again predominate, although in this inner layer several thin bundles course longitudinally and obliquely. Thus, a meshwork of collagen contributes predominantly to the composition of the neural lamella. The fibers resembling collagen may be chitin or lipoprotein derivatives of the cells in the sheath. The connective tissue layer may be the fused basement membranes of several ensheathing cell types. A sharp line divides this connective tissue layer from the inner cellular layer. This is the basement membrane of the cellular layer.

Inside the basement membrane, a cellular layer is seen (Figs. 13, 15). In cross-sections of the ganglia the nuclei are usually round in outline. Clumps of chromatin are disposed throughout the nucleus and along the nuclear membrane. These nuclei are the rounded, darkly stained nuclei described with the light microscope (Fig. 1 *B*, *2*). The cytoplasm is light. Narrow short tubules occur in the cytoplasm and small vesicles with dark borders and clear centers, some of which may be cross-sections of these tubules, are also found. The cells are roughly cuboidal and the cytoplasm can be seen clearly surrounding the nucleus. The outstanding structural characteristic of this cell is its mitochondria (Figs. 13 and 15). These are relatively large, dense, and with clearly defined numerous internal folds. These cells have characteristics different from those of neuroglia. Their plasma membranes do not ramify to form layers as do those of glial cells; their vesicles are larger and not so numerous; their cytoplasm is seen readily and its limits more easily defined; and their mitochondria are conspicuously different from those of the cells called neuroglia. It is suggested that these cells compose the perilemma or cellular layer of the sheath of the ganglion. However, these cells do not extend into the peripheral nerve trunks and are not seen there (Hess, 11). The cells occupying a similar position next to the connective tissue layer in peripheral nerves are Schwann cells (Hess, 11). The cells under discussion are restricted to the ganglia. The Schwann cells, wrapping around the fibers of peripheral nerves, are similar to the neuroglial cells, ensheathing the nerve cells and fibers of the ganglion. The perilemmal cells appear to be more closely related to the connective tissue sheath of the ganglion than to the neural elements. Indeed, in places where the sheath artificially has been pulled away from the remainder of the ganglion during preparation of the tissue, the perilemmal cells adhere to the connective tissue layers. A cellular layer was also seen with the light microscope to accompany the connective tissue layer in places of artificial rupture of sheath and neural tissue (Twarog and Roeder, 26).

Thus, the peripheral nerve has a connective tissue layer and a Schwann cell layer; while the ganglion has a thicker connective tissue layer, a perilemmal cellular layer, and neuroglial cells, the latter being similar in morphological disposition to Schwann cells.

Abdominal Connective

Roeder (22) has pointed out that the long ascending nerve fibers become thinner as they pass through each abdominal ganglion or enter the third thoracic ganglion and enlarge as they enter the abdominal connective. Not only do the nerve fibers become attentuated, but the sheaths around them, although continuous, also become thinner (Figs. 8 and 9). Thus, the decrease in fiber diameter as nerve fibers enter ganglia from the connectives is due to two factors: thinning of both the nerve fiber itself and of its sheath.

Since the perilemmal cells do not extend into the peripheral nerves, it is necessary to see whether they occur throughout the length of the ganglion chain or are restricted only to the level of the ganglia.

Sections of an abdominal connective reveal that the perilemmal cells do not form a distinct or conspicuous layer (Fig. 5). The appearance of the nerve fibers and their sheaths and the organization of the connective resemble those in a peripheral nerve more than those of a ganglion. The term "neuroglial cells" will still be used since the cells ensheathing the nerve fibers in the connective are in the ganglion chain. However, the structure and disposition of the sheath cells in the connective are entirely like those of the Schwann cells in insect peripheral nerves (Hess, 11).

Neuroglial cell nuclei are found under the connective tissue layer (Fig. 5) and in the interior of the connective. The cytoplasm of the neuroglial cell has processes covered by plasma membranes which interweave and pass into the interior of the connective in thin extensions of the cell and which ensheath the nerve fibers (Fig. 5). They thus resemble the disposition of Schwann cells in peripheral nerves.

The connective tissue layer of the connective is relatively thin, and, in cross-sections, its fibers are oriented both transversely and longitudinally (Fig. 5). The sheath of the connective is somewhat thicker than, but resembles that of peripheral nerves more than it does the thick, layered meshwork of connective tissue fibers characteristic of the ganglion sheath.

Both the third thoracic and sixth abdominal ganglia have a distinct and conspicuous layer of perilemmal cells. It thus appears that these cells form a separate cellular layer only at the level of the ganglia throughout the abdominal cord. Similarly, both ganglia studied have thick complexly layered connective tissue sheaths, which also appear to be limited to the ganglia. As described above, the perilemmal cells have a more intimate relation to the connective tissue sheath than to the neural elements of the ganglia. Since both thick meshworks of collagen and perilemmal cells occur at the same level, it seems that the cells might be responsible in some way for the development and maintenance of the complex connective tissue sheath of the ganglia. Only developmental and experimental studies can offer definitive proof for this suggestion.

SUMMARY

The third thoracic and sixth abdominal ganglia and the abdominal connective of the cockroach (*Periplaneta americana*) were studied in the light and the electron microscopes.

Nerve cells have lightly stained nuclei and prominent nucleoli. In electron micrographs, a Golgi apparatus and mitochondria are revealed, whereas no structures resembling neurofibrils have been seen. Nissl bodies are not prominent. In electron micrographs, microgranules are present which probably represent the basophilic component of neurons. These granules differ in their distribution: in some cells they are evenly distributed ("dark" cells), whereas others exhibit them in clumps ("light" cells). The dark cells have many more lipochondria, or droplets of lipide, than do the light cells.

Neuroglial cells are stained metachromatically an intense pink color by cresyl violet. They occur as an apparent network of cells and processes, which is displayed best at the junction of the cortical cellular portion and medullary fibrous area of the ganglion. In electron micrographs, neuroglial cells have many processes covered by plasma membranes which ramify extensively and are oriented to form a series of two to twenty overlapping layers. These overlapping processes of the glial cell ensheath the nerve cell. The inner layer of this neuroglial sheath commonly penetrates into the neuron cytoplasm and causes an invagination of the neural cellular membrane. This disposition is probably responsible for the appearance of the trophospongium of Holmgren. Nerve fibers are also ensheathed by glial cells. Depending on size, two or several nerve fibers can share a single glial cell. The nerve fibers are surrounded by extensions of the plasma membrane similar to mesaxons.

Nerve fibers near their termination contain particles of various size and density. Mitochondria are large and numerous in these synaptic areas. Nerve fibers appear to end on other fibers, rather than on nerve cells.

Tracheoles in the ganglia are ensheathed by their own cells, are never located strictly within nerve cells or fibers, and usually course through extracellular spaces.

With the light microscope, the sheath of the ganglion consists of a homogeneous neural lamella and a cellular perilemma. With the electron microscope, cross-sections of the neural lamella consist of a thick feltwork of connective tissue with two layers of predominantly cross-sections of fibers separated by a layer of longitudinally sectioned fibers. The perilemma consists of cuboidal cells whose mitochondria are very prominent and are a distinctive structural characteristic.

The abdominal connective lacks a distinct and conspicuous perilemmal cellular layer and its neural lamella is reduced in thickness and in complexity. The nerve fibers in the connective are larger in diameter and their sheaths are thicker than are the same fibers passing through the ganglion. The sheath structure and the organization of the ganglia, the abdominal connective, and the peripheral nerve trunk are compared.

The author wishes to thank Miss Sonia Michelson for her invaluable aid in all phases of this research involving the electron microscope, and Mrs. Dorothy Goldstein and Mr. James T. Elliott for their help with paraffin sections and staining.

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Explanation of Plates

PLATE 364

FIG. 1 *A*. Photograph of a cross-section through the third thoracic ganglion of the cockroach. The cortical portion of the ganglion has nerve cells; the large medullary area contains nerve fibers coursing in all directions. Unipolar nerve cells are seen on the right lower side of the ganglion; an apparently bipolar nerve cell is in the left upper part. The nerve cell nuclei are impregnated heavily by protargol and frequently the karyoplasm is displaced to one side of the nucleus. Bodian's protargol method. × 100.

FIG. 1 *B*. Photograph of a cross-section of an abdominal ganglion of the cockroach stained with cresyl violet. Four types of nuclei can be seen in the ganglion. Dark and elongated nuclei which usually rest on the sheath of the ganglion are indicated by number *1*. The nuclei of the perilemmal cells (*2*) occur inside and next to the homogeneous neural lamella (*NL*) and are dark but not so elongated or so flattened as are the aforementioned nuclei. The nuclei of the neuroglial cells (*3*) are larger than the other two, are relatively lightly stained, and contain large clumps of chromatin, frequently next to the nuclear membrane. Nucleoli are prominent. The nucleus of the nerve cell (*4*) is the largest of the four types. It is light staining but has granules, which do not usually accumulate on the nuclear membrane. Its nucleolus is prominent. The cytoplasm of the nerve cell sometimes appears vacuolated. Some of the metachromatically stained pink processes of the glial cells can be seen running along the lower portion of the photograph. × 470.

FIG. 1 *C*. Photograph of a cross-section of an abdominal ganglion of the cockroach, stained with cresyl violet. The nerve cells are distributed in the cortical portion of the ganglion; the large fibrous medullary area is unstained except for glial nuclei. The network of fibers at the junction of the cortex and medulla of the ganglion are metachromatically stained neuroglial processes. Neuroglial nuclei are present in the medullary area of the ganglion, frequently in the midline, as well as in the cortical portion. × 100.

FIG. 1 *D*. Photograph of two nerve cells in a section of an abdominal ganglion of the cockroach, stained with cresyl violet. The nuclei have large clumps of chromatin. The cell on the left exhibits a prominent nucleolus. The nerve cells stain darkly with cresyl violet; however, Nissl bodies are not apparent. × 470.

FIG. 1 *E*. Photograph of a section through an abdominal ganglion of the cockroach stained with cresyl violet and illustrating two neuroglial cells. Strands of metachromatically stained pink neuroglial cytoplasm enclose the neuroglial cell nuclei. × 470.

FIG. 1 *F*. Photograph of a section through an abdominal ganglion of the cockroach stained with cresyl violet and showing two nerve cells. The cytoplasm appears vacuolated. In other preparations, these vacuoles are not colored by a stain thought to be specific for proteins. The nucleus and prominent nucleolus are seen in the cell on the right. × 470.

FIG. 1 *G*. Photograph of a section through an abdominal ganglion of the cockroach stained by cresyl violet, illustrating two neuroglial cells. Strands of metachromatically stained pink neuroglial cytoplasm enclose and are most frequently evident near the neuroglial cell nuclei. × 470.

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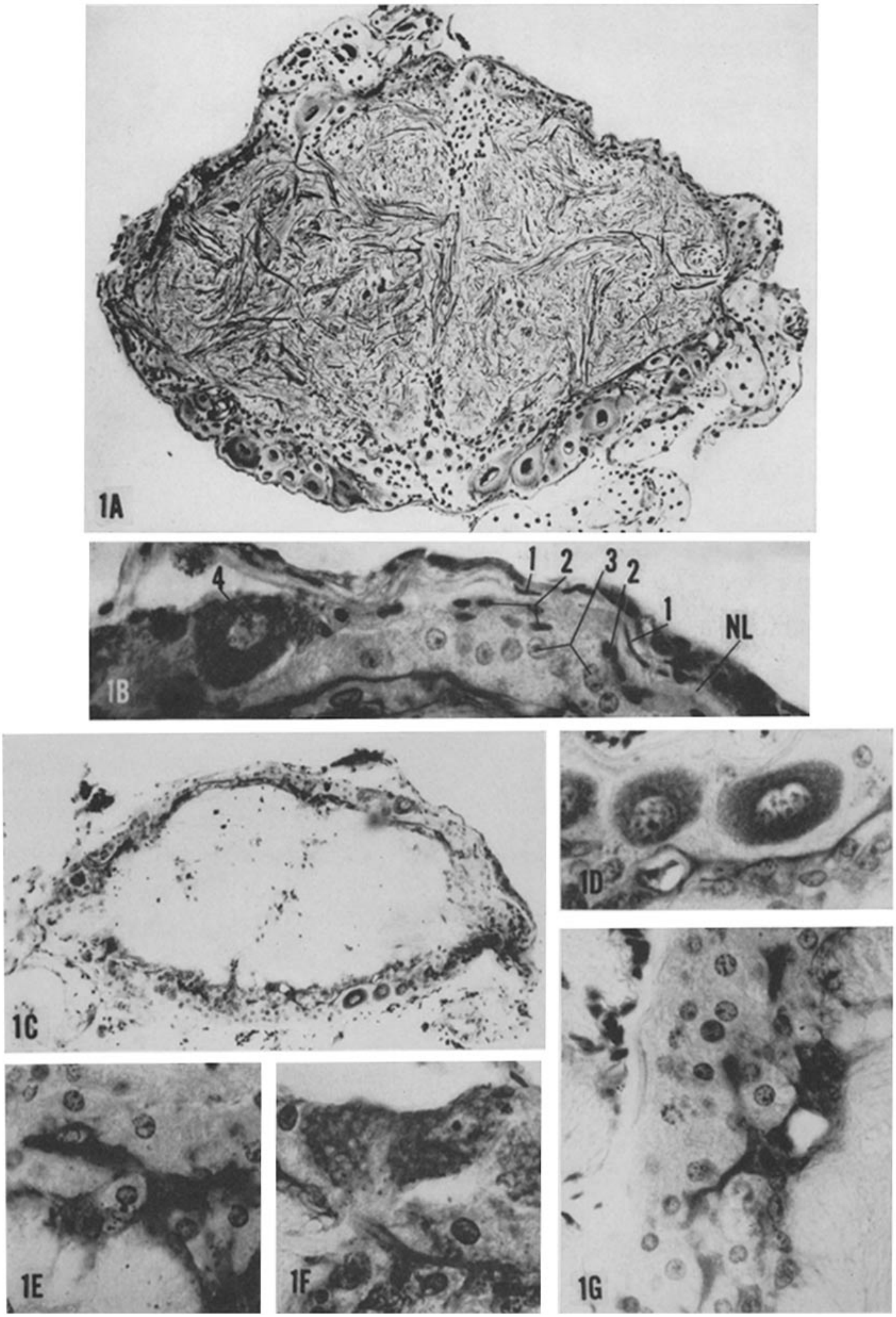
PLATE 364
VOL. 4



(Hess: Nerve cells and fibers of cockroach)

PLATE 365

FIG. 2. Electron micrograph of "dark" and "light" nerve cells in the third thoracic ganglion of the cockroach. In the cell at the bottom, the cytoplasm is dense, and clear spaces between the cytological elements are small and infrequent. The cell at the top is much lighter in the electron micrograph and clear spaces between the cytological elements are relatively large and frequently encountered. The nucleus (*N*) contains granules evenly distributed throughout its extent. The nucleolus (*NO*) occurs as a dark area in the nucleus. The dark cell at the bottom has granules dispersed almost evenly throughout its cytoplasm; the light cell at the top contains the granules in small aggregations or clumps. The mitochondria (*M*) of the light cell appear as dense bodies, while those of the dark cell, surrounded by a relatively dark cytoplasm, are similar in structure but do not appear as prominent as do those of the other cell. Lipochondria (*L*) are far more numerous in the dark cell type. The neuroglial cell processes form a thin sheath (*NE*) consisting of several alternating overlapping membranes and layers of cytoplasm around the nerve cells. The inner layer of this glial cytoplasm sometimes penetrates into the neuron. In some places, the origin of the glial cell cytoplasm is not seen and the glial cell process appears as an inclusion (*I*) in the neuron. $\times$ 8000.

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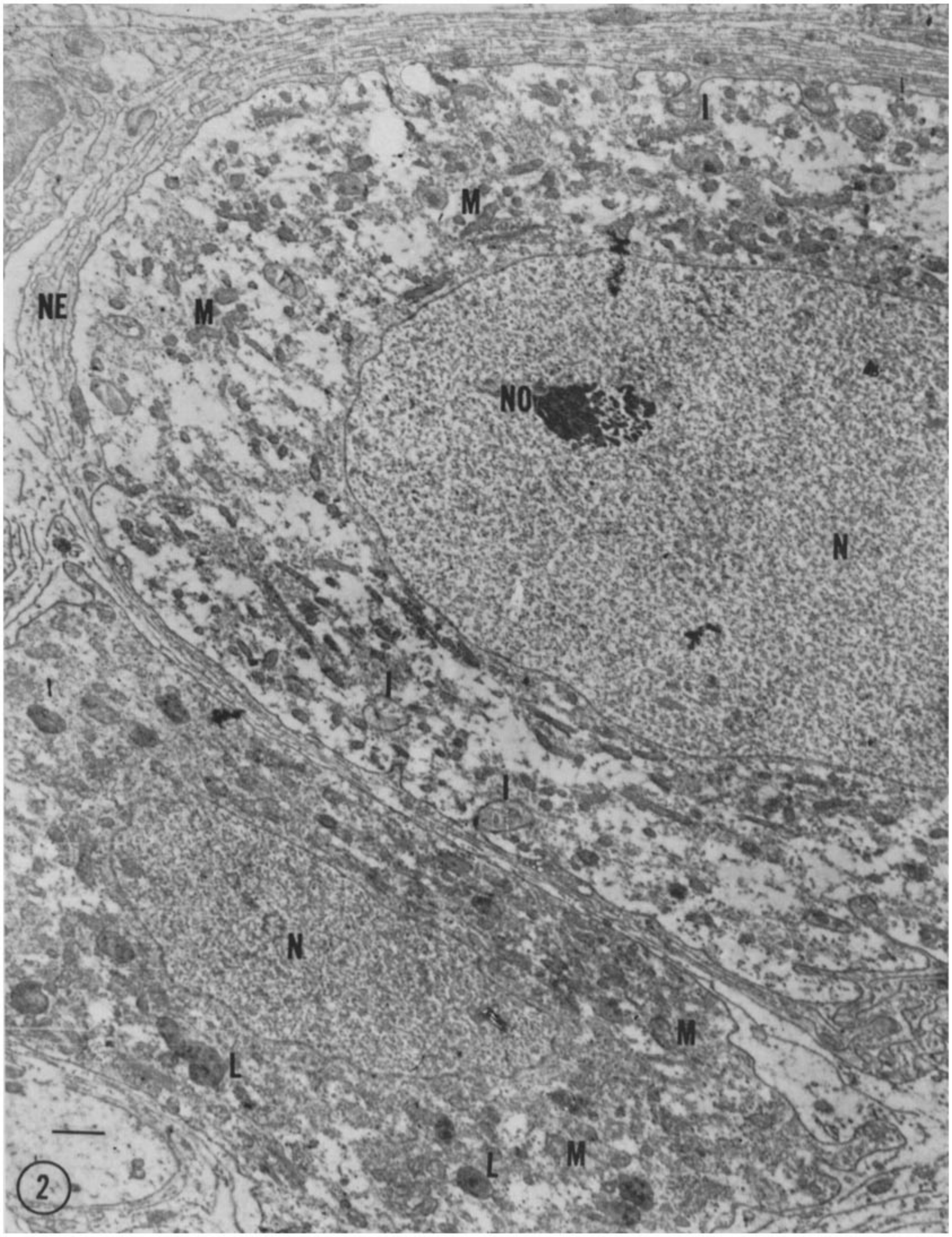
PLATE 365
VOL. 4



(Hess: Nerve cells and fibers of cockroach)

PLATE 366

FIG. 3. Electron micrograph of the third thoracic ganglion of the cockroach, illustrating numerous and elaborate glial processes (*I*) penetrating into the nerve cell (*NC*) from the surrounding neuroglial sheath (*NE*). × 8000.

FIG. 4. Electron micrograph of the third thoracic ganglion of the cockroach, showing the alternating layers of membrane and cytoplasm of neuroglial cell processes (*NE*) ensheathing the neuron. The innermost layer of neuroglial cytoplasm penetrates into the neuron. The cytoplasmic process (*I*) contains vesicles (*V*) and mitochondria (*M*). Its connection to the outside of the neuron is missed sometimes in section, and the process appears as an inclusion (*O*) in the neuron. A Golgi apparatus of the neuron is shown at *G*. × 16000.

FIG. 5. Electron micrograph of a cross-section of an abdominal connective of the cockroach. The neural lamella (*NL*) consists of fibers which appear in cross- and longitudinal section, and is thinner than that of the ganglion in Fig. 13. Neuroglial cell nuclei (*N*) are found under the sheath. The cytoplasm (*C*) around the neuroglial cell nucleus has interweaving processes covered by plasma membranes which pass into the substance of the connective in thin extensions of the cell and ensheath (*S*) the nerve fibers (*F*). × 8000.

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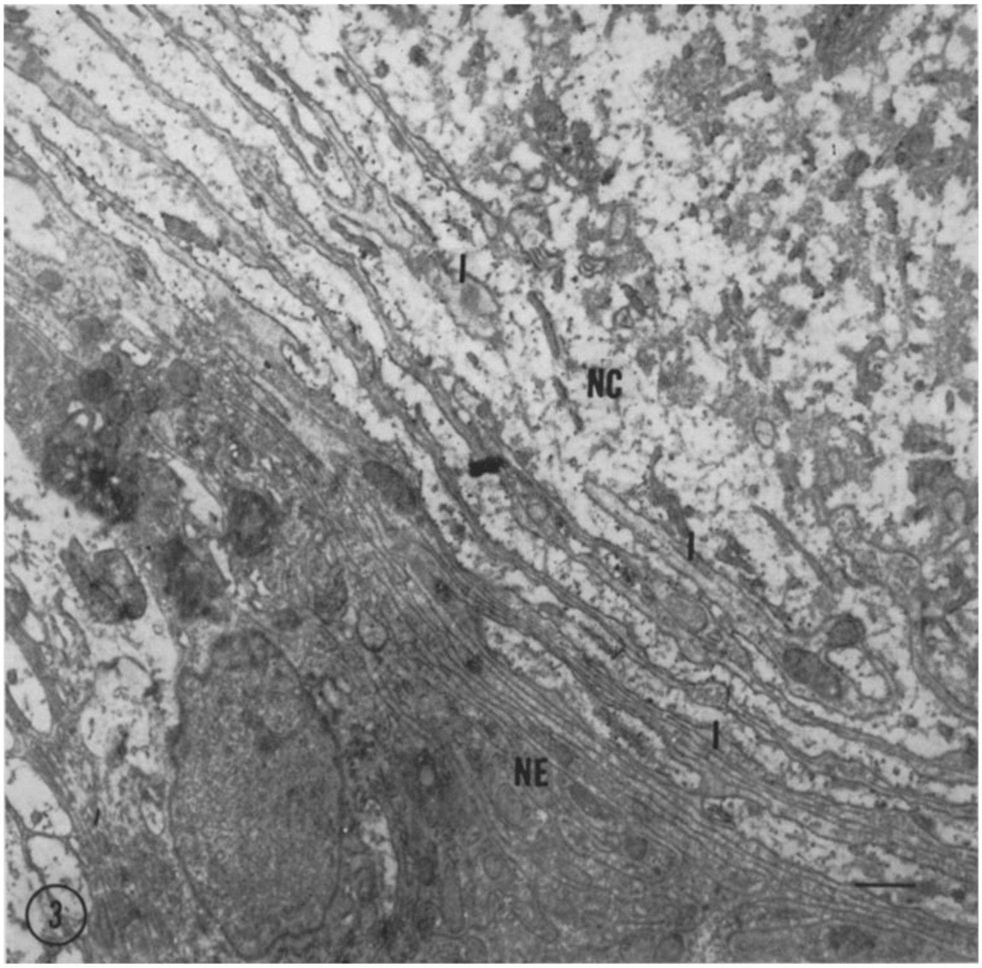
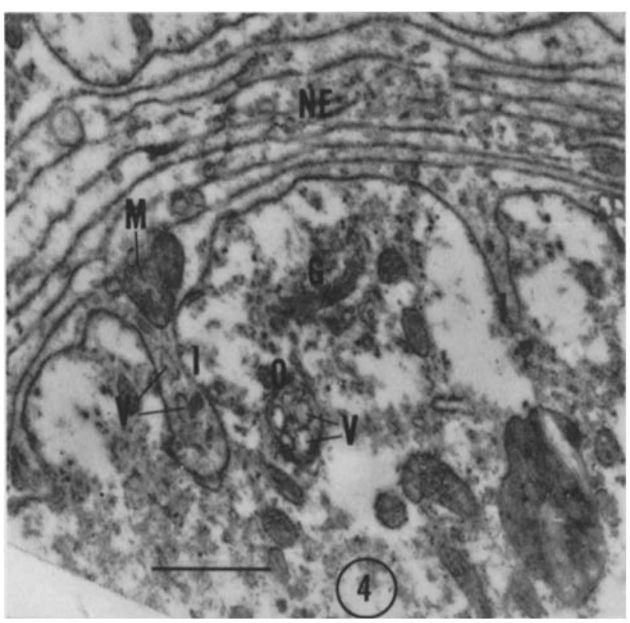
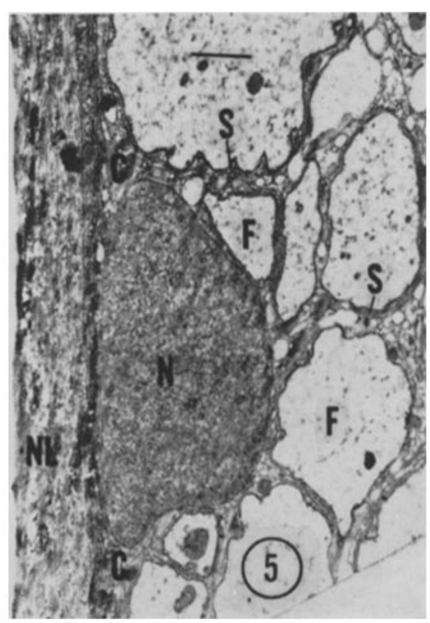






(Hess: Nerve cells and fibers of cockroach)

PLATE 367

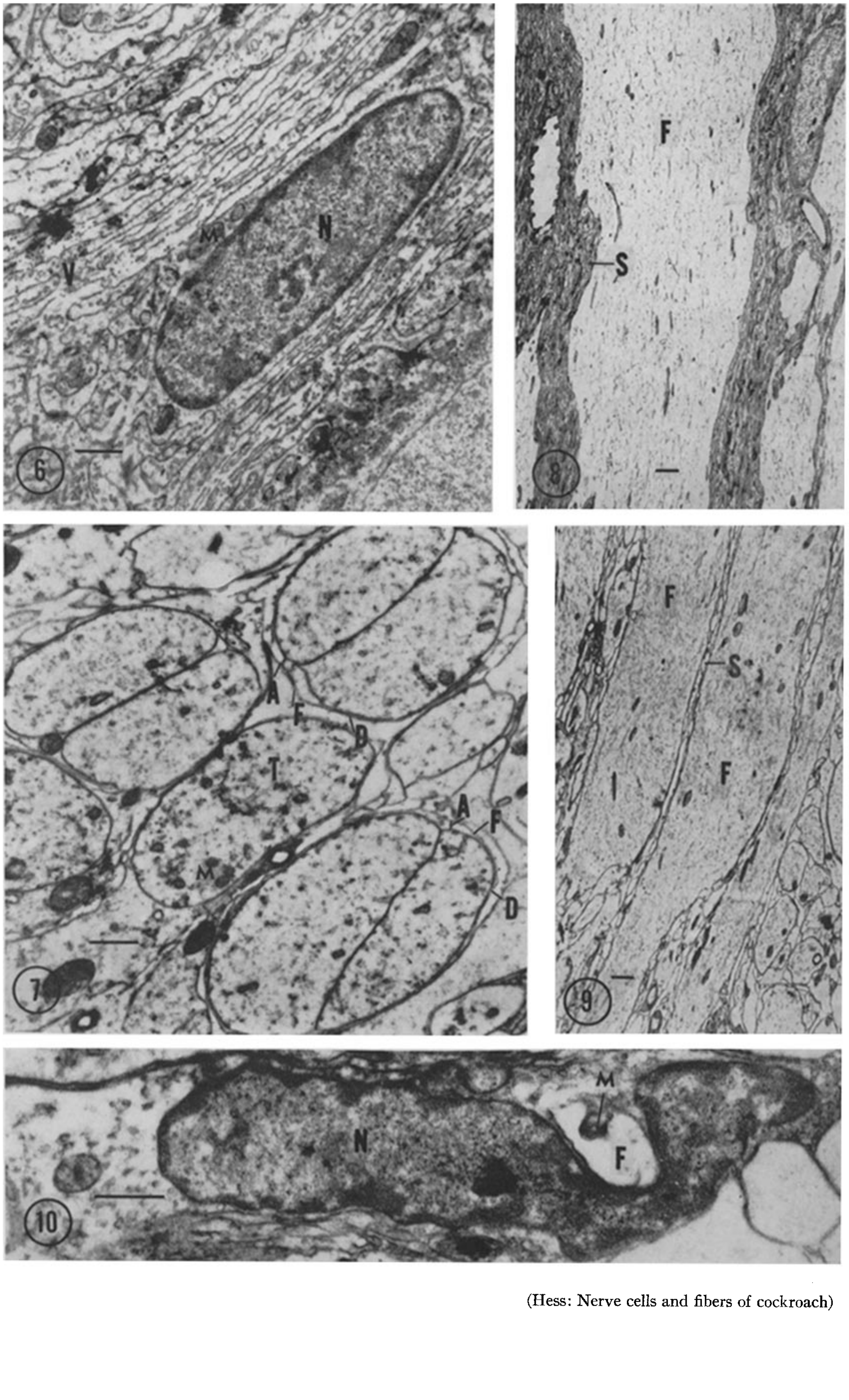
FIG. 6. Electron micrograph of a neuroglial cell in the third thoracic ganglion of the cockroach. The nucleus (N) is granular and contains dense accumulations of granules apposed to the nuclear membrane. Uninterrupted glial cell cytoplasm is restricted to a small area around the nucleus. The remaining cytoplasm consists of thin processes covered by plasma membranes and oriented so that a series of two to twenty overlapping layers consisting alternately of cytoplasm and membranes run in the same direction. The membranes are interrupted for short distances. The cytoplasm contains mitochondria (M) and vesicles (V), some of which may be cross-sections of the plasma membrane. × 8000.

FIG. 7. Electron micrograph of nerve fibers in the third thoracic ganglion of the cockroach. The fibers are granular and contain mitochondria (M) and some vesicles or tubules (T). The medium sized fibers are gathered into groups of two. The nerve fibers are ensheathed by glial cells. A membrane of the glial cell enclosing the two nerve fibers is seen at F. The fibers probably are not entirely enclosed by the glial cell, since a connection to the exterior through apposed glial plasma membranes is frequently demonstrable; indications of such mesaxons are seen at A. The glial cell cytoplasm enclosing the nerve fibers is sparse, and the nerve fibers are surrounded by at least three membranes (D), one belonging to the axon, the other two to the glial cell. × 8000.

FIG. 8. Electron micrograph of a longitudinal section of a nerve fiber in the connective between the third thoracic and first abdominal ganglia. Compare with Fig. 9. The fiber (F) and its sheath (S) are thicker than those of the fibers in Fig. 9. × 4000.

FIG. 9. Electron micrograph of a longitudinal section of the nerve fibers at their entrance into the third thoracic ganglion. Compare with Fig. 8. The fibers (F) and their sheaths (S) are thinner than those of the fiber in Fig. 8. × 4000.

FIG. 10. Electron micrograph of the third thoracic ganglion of the cockroach showing a small nerve fiber (F), containing a mitochondrion (M), resting in an indentation of a glial cell nucleus (N). × 12000.

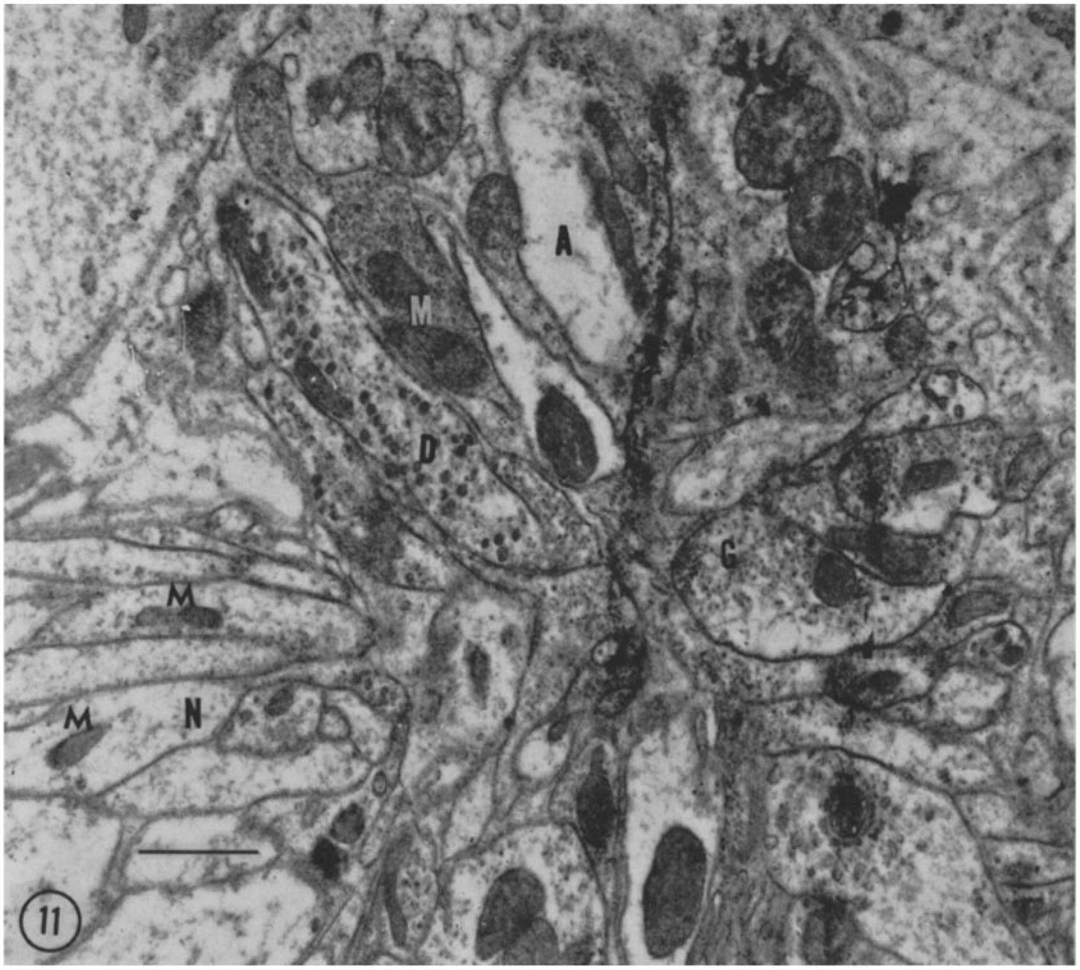


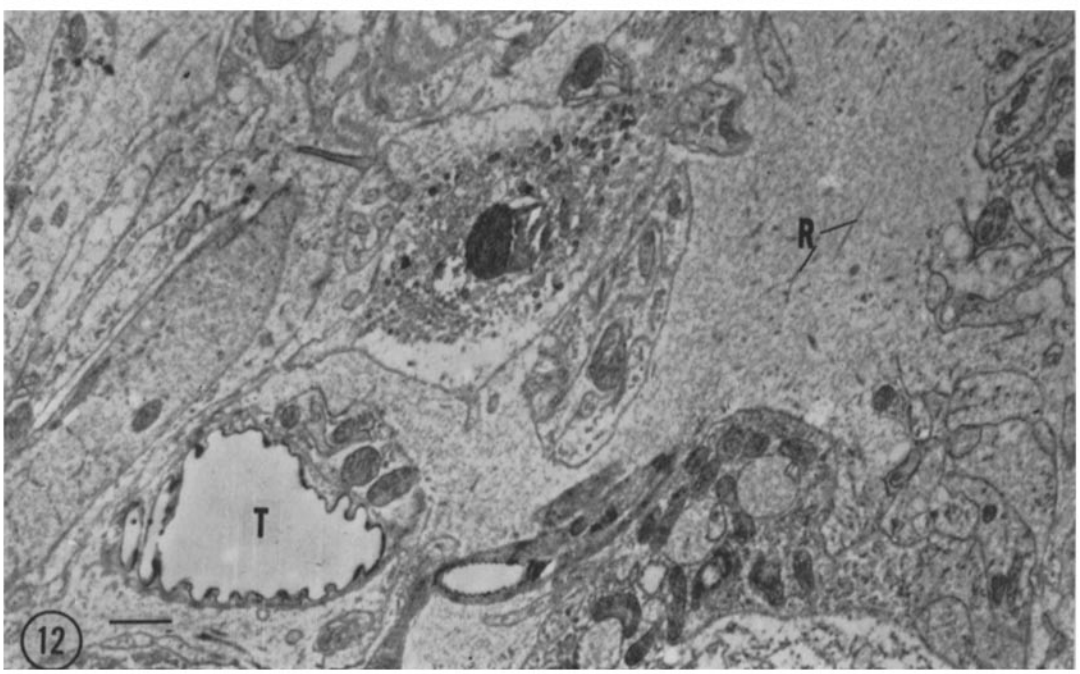
(Hess: Nerve cells and fibers of cockroach)

PLATE 368

FIG. 11. Electron micrograph of the medullary fiber portion of the third thoracic ganglion of the cockroach. Nerve fibers (*N*) are seen containing mitochondria (*M*). Occurring between the fibers are oblique or cross-sections of structures containing droplets (*D*), granules (*G*), and mitochondria (*M*). The structure marked *G* has only small granules; that marked *D* has both granules and larger and more dense droplets. The mitochondria in the particle-containing structures are more numerous and frequently larger than those in the nerve fibers. The appearance of the portion of these structures devoid of granules (*A*) is entirely similar to that of the nerve fibers. These structures appear to be nerve fibers near their termination (see text). × 16000.

FIG. 12. An extracellular space in the third thoracic ganglion of the cockroach. These granular areas contain a few electron dense thin elongated rods (*R*). Tracheoles (*T*) can often be seen. × 8000.





(Hess: Nerve cells and fibers of cockroach)

PLATE 369

FIG. 13. Electron micrograph of a cross-section of the neural lamella and perilemmal cells of the third thoracic ganglion of the cockroach. The fibrous feltwork and the thin granular or homogeneous outermost layer (*O*) of the neural lamella (*NL*) are seen. A sharp line (*BM*) divides the fibrous neural lamella from the cellular perilemma. The nuclei (*N*) of the perilemmal cells tend to be round with clumps of chromatin present throughout the nucleus and along the nuclear membrane. The cytoplasm is light. The mitochondria (*M*) are relatively large, dense, and conspicuous. × 8000.

FIG. 14. Electron micrograph of a cross-section of the neural lamella of the third thoracic ganglion of the cockroach. The outermost layer (*1*) of the sheath is thin and finely granular or homogeneous in appearance. Next to this layer (*2*) the fibers are cut predominantly in cross-section. Then, proceeding inward, the fibers appear sectioned longitudinally (*3*). Still farther inward (*4*), cross-sections of fibers predominate. The longitudinally sectioned fibers in the layer numbered *3* exhibit periodicity. × 20000.

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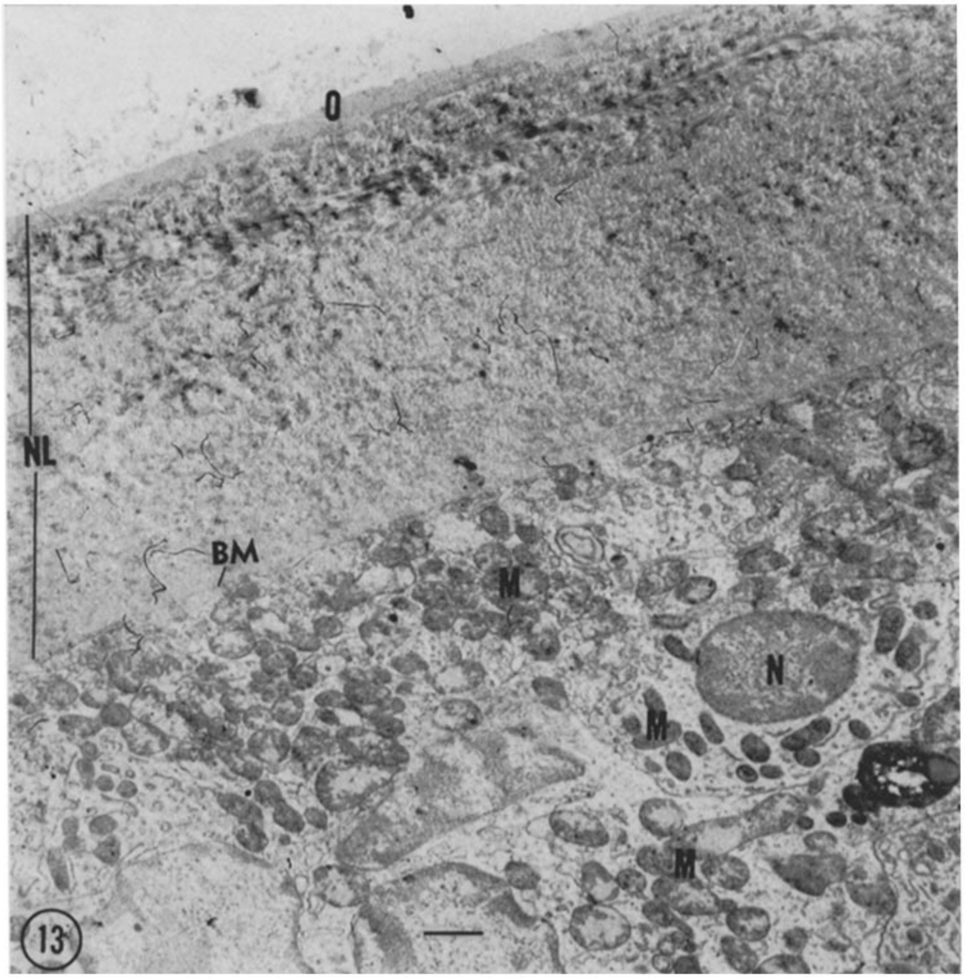
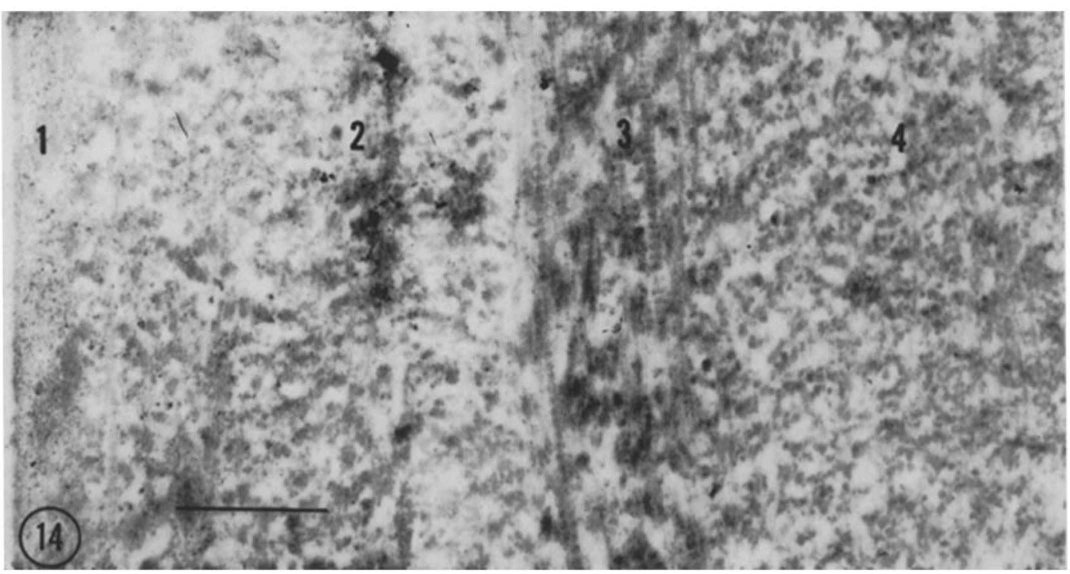
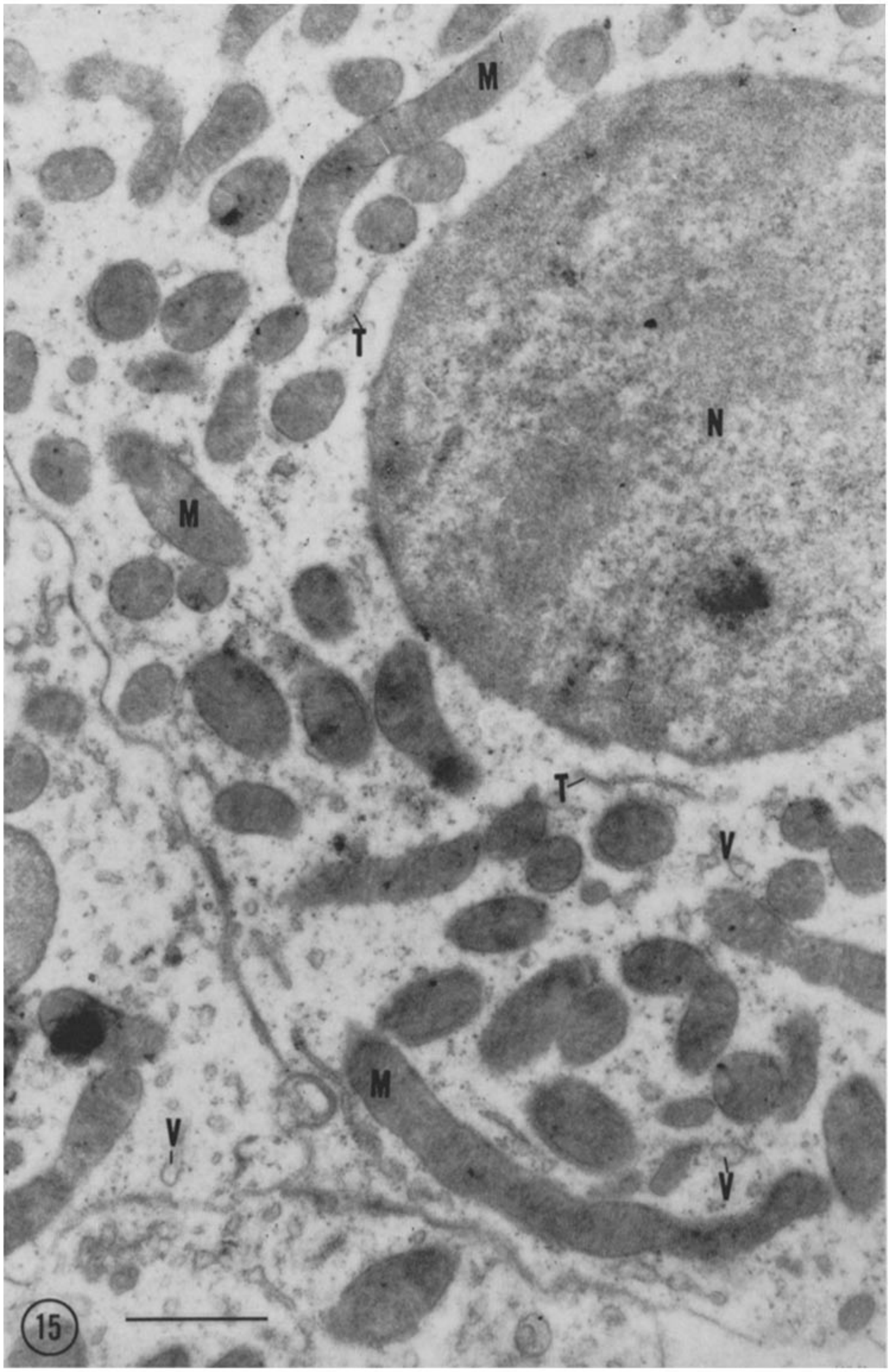




(Hess: Nerve cells and fibers of cockroach)

PLATE 370

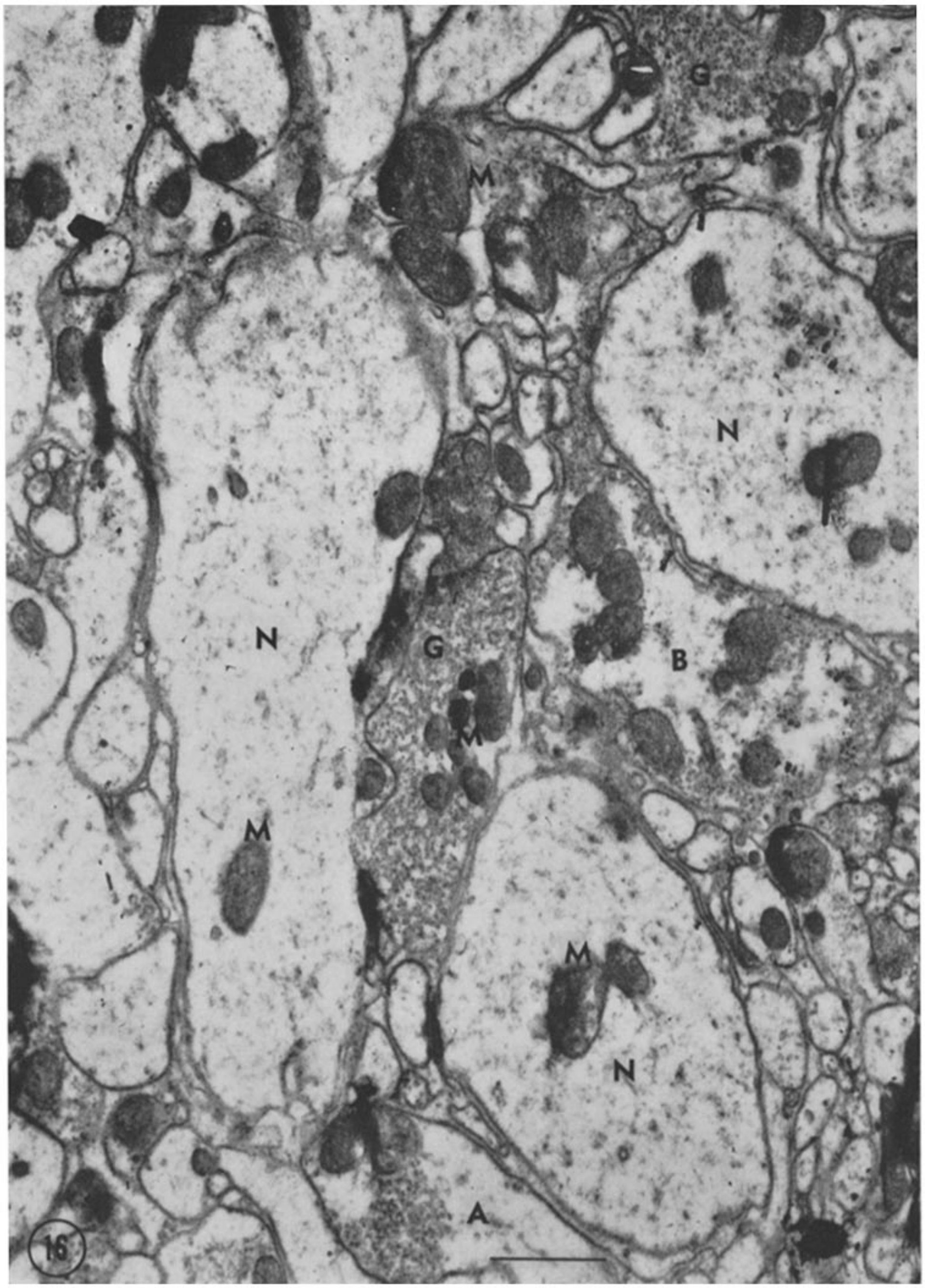
FIG. 15. Electron micrograph of a perilemmal cell ensheathing the third thoracic ganglion of the cockroach. The round nucleus (*N*) is seen. Chromatin clumps are present throughout the nucleus and along the nuclear membrane. The cytoplasm is light. Narrow short tubules (*T*) are seen in the cytoplasm, and small vesicles (*V*) with dark borders and clear centers, some of which may be cross-sections of these tubules, are also found. The cells are roughly cuboidal in shape and the cytoplasm can be seen clearly surrounding the nucleus. The outstanding structural characteristic of this cell is the mitochondria (*M*). These are relatively large, dense, with clearly defined, numerous folds. $\times$ 20000.



(Hess: Nerve cells and fibers of cockroach)

PLATE 371

FIG. 16. Electron micrograph of the medullary fiber portion of the third thoracic ganglion of the cockroach. Nerve fibers (*N*) are seen containing mitochondria (*M*). Occurring between the fibers are oblique or cross-sections of structures containing granules (*G*) and mitochondria (*M*). These structures appear to be nerve fibers near their termination. The granules are located at one end of the fiber marked *A* or in the beginning of the branches of the fiber marked *B*. Mitochondria are large and numerous in the synaptic area. $\times$ 16000.

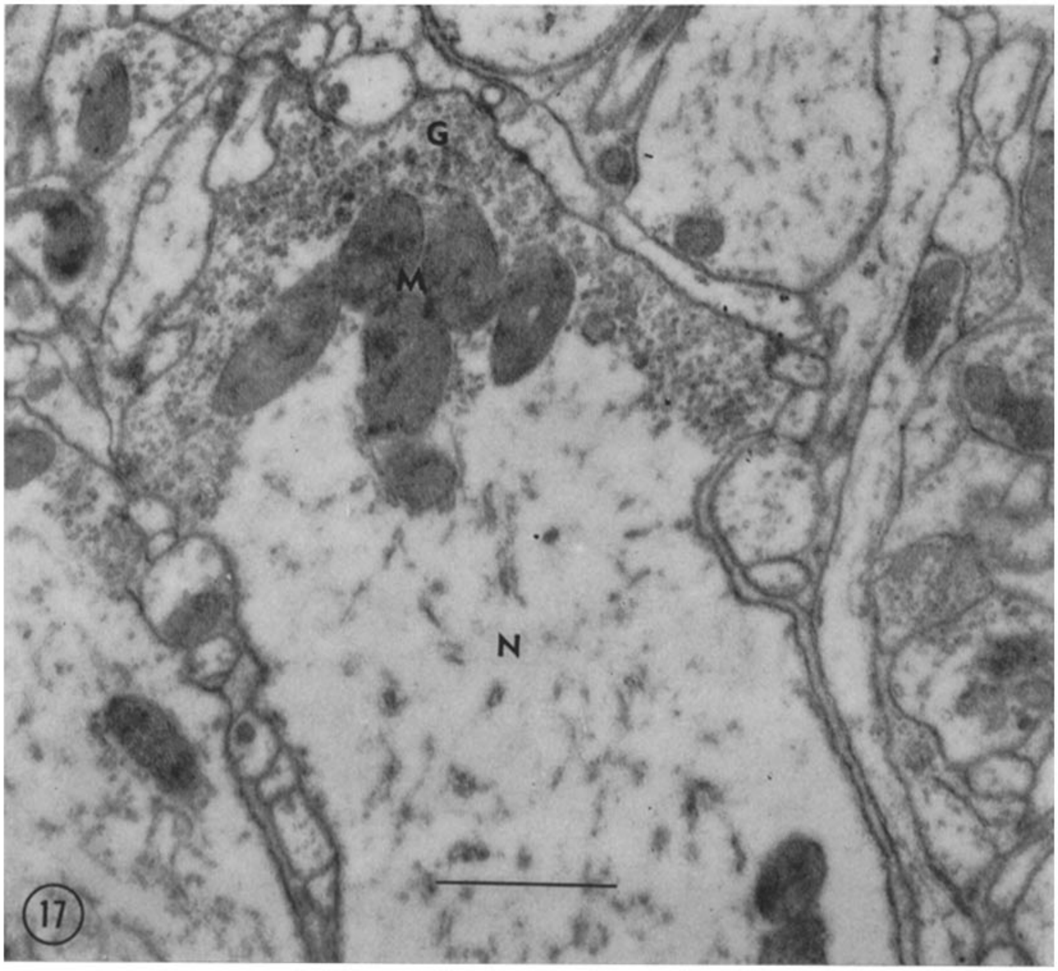


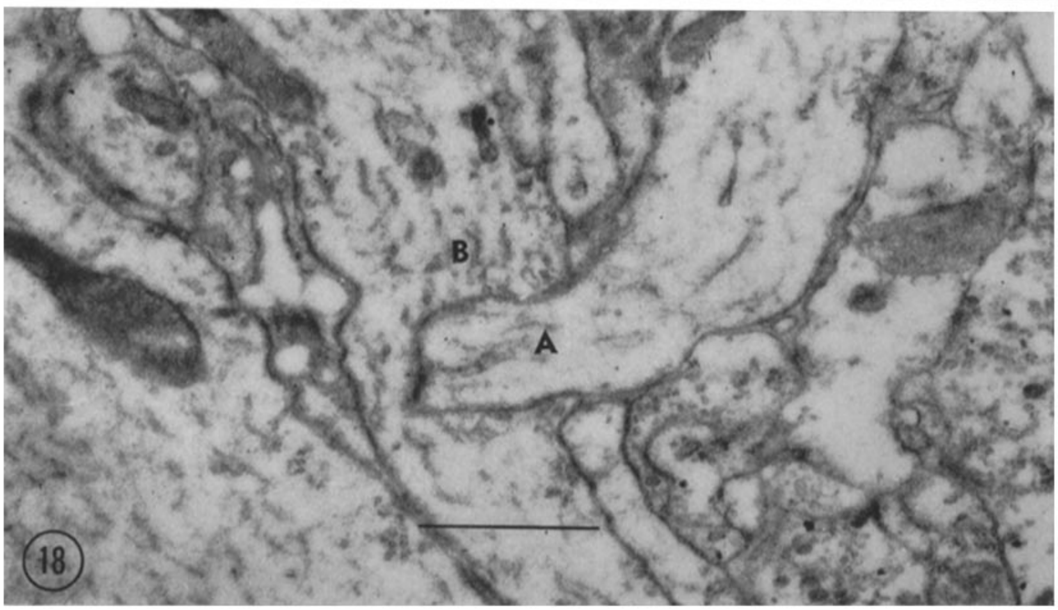
(Hess: Nerve cells and fibers of cockroach)

PLATE 372

FIG. 17. Electron micrograph of the sixth abdominal ganglion of the cockroach. The nerve fiber (*N*) has granules (*G*) and large and numerous spirally organized mitochondria (*M*). This nerve fiber is presumably approaching its termination, and this micrograph illustrates the continuity of the portions of a nerve fiber without and with particles. × 24000.

FIG. 18. Electron micrograph of an abdominal ganglion of the cockroach, showing one nerve fiber (*A*) indenting another nerve fiber (*B*) with no striking accumulation of particles in either. × 24000.

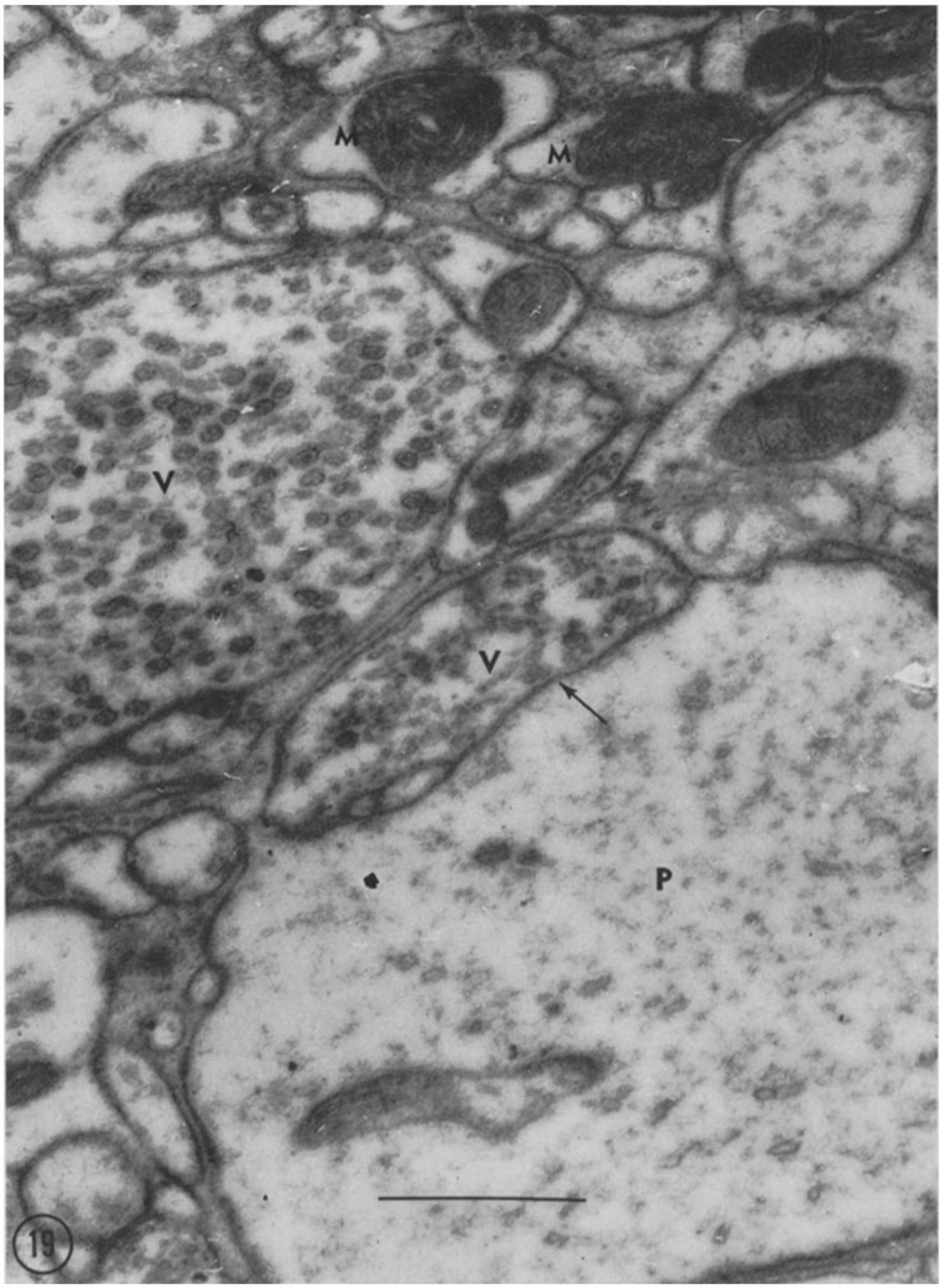




(Hess: Nerve cells and fibers of cockroach)

PLATE 373

FIG. 19. Electron micrograph of an abdominal ganglion of the cockroach, showing vesicle-containing nerve fibers (*V*). Granules are also seen among the vesicles. The small vesicle-containing, presumably presynaptic fiber appears to be ending on the large light fiber (*P*). Some indication of orientation of structures is seen along the membrane (arrow) of the presumably postsynaptic fiber (*P*). Mitochondria (*M*) with a spiral organization are seen in the synaptic region. $\times$ 28000.



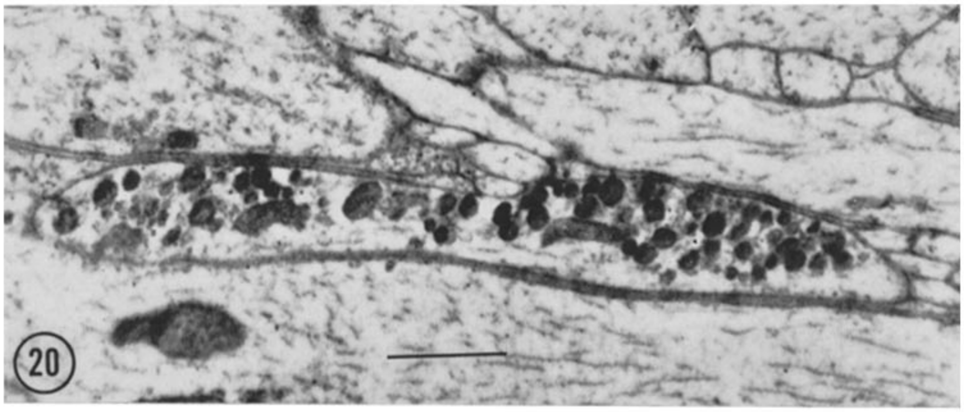
(Hess: Nerve cells and fibers of cockroach)

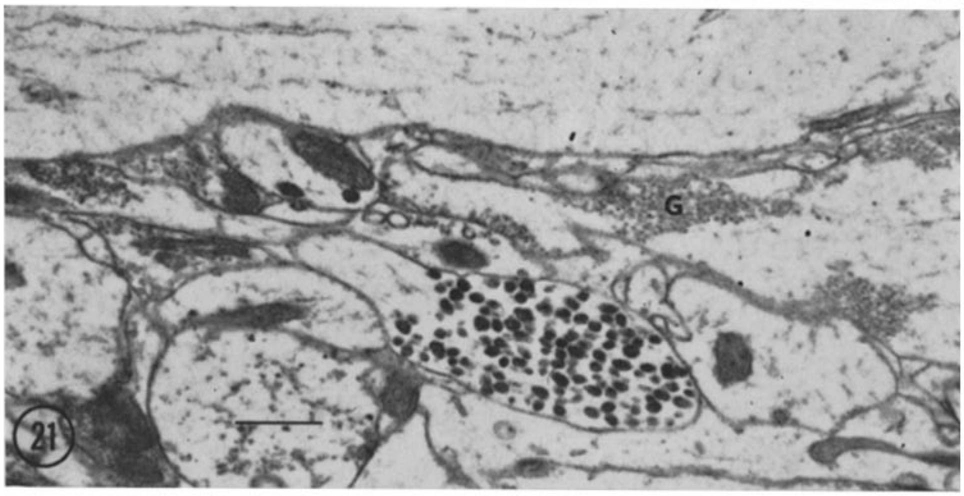
Plate 374

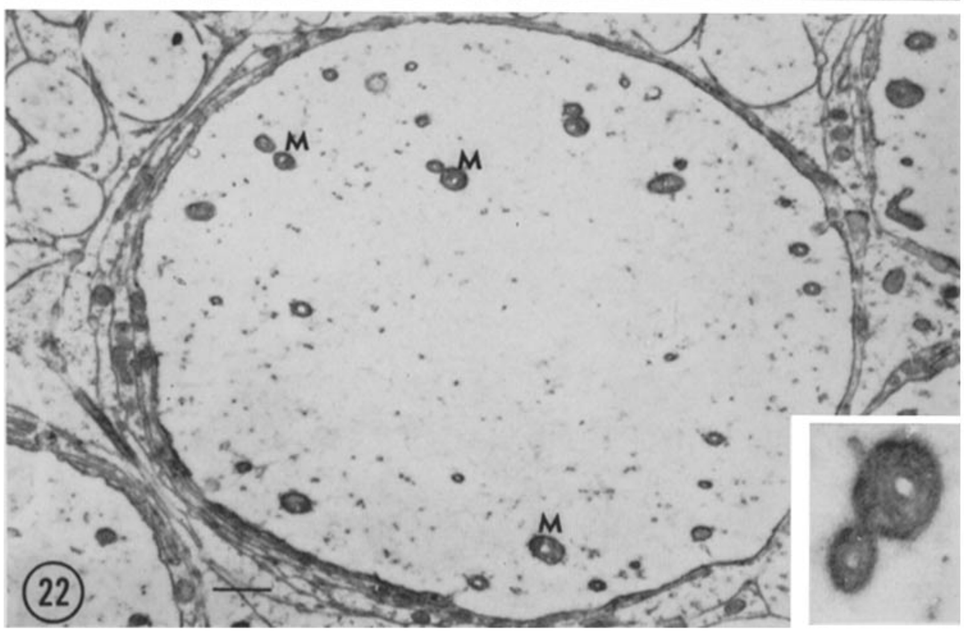
Fig. 20. Electron micrograph of an abdominal ganglion of the cockroach, showing a fiber containing droplets. Granules are scattered among the droplets. The fibrils in the structure with dense droplets are entirely similar to the fibrils of neighboring nerve fibers. × 16000.

Fig. 21. Electron micrograph of the third thoracic ganglion of the cockroach, showing a fiber containing droplets. Granules are present among the droplets and are also seen in neighboring nerve fibers (*G*). The fibrils in the structure with dense droplets are entirely similiar to the fibrils of neighboring nerve fibers. × 12000.

Fig. 22. Electron micrograph of a nerve fiber of the peripheral nerve in the cercus, showing mitochondria (*M*) with central holes (× 8000) and an apparent spiral organization (inset, × 30000).



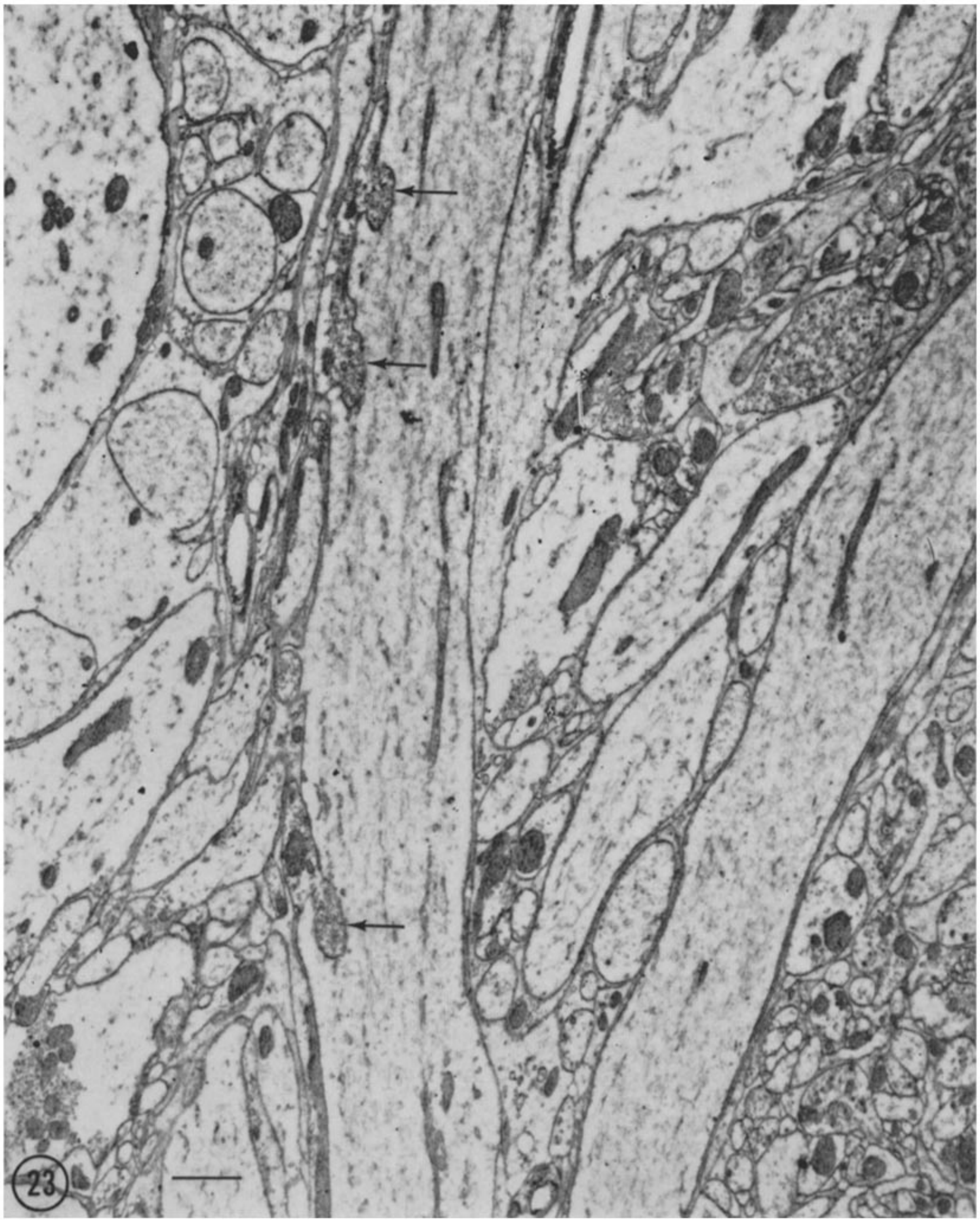




(Hess: Nerve cells and fibers of cockroach)

Plate 375

Fig. 23. Electron micrograph of a longitudinal section of a nerve fiber in the sixth abdominal ganglion of the cockroach with apparent granule-containing terminations of smaller fibers, indicated by arrows, pushing into it. $\times$ 10500.



(Hess: Nerve cells and fibers of cockroach)