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THE LOBSTER OPTIC LAMINA
I. GENERAL ORGANIZATION

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SUMMARY

The lamina is 150–220 μ thick and has five layers: (*a*) ganglion cells (2nd-order neurons); (*b*) a thick-layered glial sheath; (*c*) more ganglion cells of the same kind; (*d*) columnar structures called optic cartridges, where retinula fibres terminate in inflated bags which are penetrated by numerous spines of the ganglion cell axons; and (*e*) a lower multilamellate layer of glial cells among which are neurosecretory cells with short centrifugal axons. Horizontal nerve fibres run along the lamina in the columnar region, where there is a 1:1 relation between ommatidia and cartridges. Retinula fibre terminals are recognized by numerous vesicles and by large pale mitochondria, ganglion cell spines by small dark mitochondria and lack of vesicles. Ganglion cell axons have neurotubules whereas transverse fibres do not. The latter have both synaptic and other vesicles. Some of the horizontal fibres are secretory in appearance.

INTRODUCTION

The optic lamina is the most superficial portion of the optic lobe. Situated close beneath the basement membrane of the retina, it is the first neuropile region, containing the first synapses on the visual pathway. No electrophysiological investigations as yet bear directly on the function of the lamina in Crustacea because all units so far recorded in the optic tracts (Waterman & Wiersma, 1963; Waterman, Wiersma & Bush, 1964; Wiersma, Bush & Waterman, 1964) could have their origins in more central neuropile regions. The only physiological recordings which are relevant to the function of the lamina in arthropods are from the retina in insects, showing that retinula fibres are small field 'on' units which can carry spikes in the drone bee (Naka & Eguchi, 1962) and in the locust (Scholes, 1966). The physiological work has reached the stage where a detailed knowledge of the structural relationships is essential. For comparison, reference will be made to a recent detailed description of part of the structure of the lamina of the blowfly (Trujillo-Cenóz, 1965).

Previous information on the neuron pattern of the crustacean lamina is restricted to the detailed paper of Hanström (1924). According to his investigations, based exclusively on Golgi preparations, different grades of complexity of the lamina can be distinguished even between decapod Crustacea. The simplest type, illustrated by *Pachygrapsus*, has only three layers, from distal to proximal: (*a*) the ganglion cell bodies; (*b*) a synapse area composed of a layer of columnar structures, called optic cartridges, each of which is a group of thickened terminations of retinula cell axons

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lying around a short spiny proximal region of a ganglion cell axon; and (*c*) a diffuse synaptic area. The most complicated type of lamina, Hanström found in *Palinurus*, where there were five distinct layers: (*a*) distal ganglion cell bodies; (*b*) a distal horizontal (tangential) fibrous layer; (*c*) proximal ganglion cell bodies; (*d*) a columnar synaptic area of optic cartridges; and (*e*) proximal horizontal fibres. The structure of the lamina in *Astacus* and *Homarus* appeared to be similar to that in *Palinurus*, though the Golgi preparations from these animals were not adequate to allow a detailed description. Irrespective, however, of the number of layers, the lamina is always a multilayered structure of the same basic constitution throughout the arthropods (Bullock & Horridge, 1965). Apart from the layer of cartridges, the most obvious feature of physiological significance is a regular crossing of the retinula fibres above or at the level of the ganglion cell bodies. This has the consequence that the seven axons from one ommatidium of the retina run to different (probably neighbouring) optic cartridges. There is therefore an ordered convergence and simultaneous divergence of the retinula fibres on to the second-order neurons. However, besides this regular pattern of retinula endings, there are arborizations of other fibres to take into account. Short, local fibres spring from cell bodies which lie on the central side of the lamina; horizontal fibres from distant unknown cell bodies have wide ramifications and centrifugal units with restricted dendrite spread may be present, as they are in insects (Cajal & Sánchez, 1915).

No electron-microscope studies have been made on this structure in Crustacea. The only examination in any arthropod has been upon the blowfly (Trujillo-Cenóz & Melamed, 1963; Trujillo-Cenóz, 1965). The dipteran optical cartridge consists of two ganglion cell axons surrounded by six retinula cell axon terminations which make synapses on them, with presynaptic ribbons but without postsynaptic spines. Each retinula ending is accompanied by two centrifugal axons which are presynaptic. Other fibre types are not described although the classical authors show a few horizontal fibres in the bee and dragonfly lamina.

This paper is concerned chiefly with the structure of the nerve cells and the general organization of the lamina, while the ultrastructure of the varied types of specialized synaptic contacts will be dealt with in the succeeding paper.

MATERIALS AND METHODS

Small pieces of the optic lobe of *Homarus vulgaris* containing the lamina were fixed for 1 h at 4 °C in 3·5 % glutaraldehyde made up in half-strength sea water, buffered with phosphate to pH 7·6. This was followed by a thorough washing in 50 % sea water for half an hour. The specimens were postfixed in 1 % buffered osmium tetroxide, dehydrated in a graded acetone series and embedded in Araldite. Sections 1–2 μ thick and stained with toluidine blue have been used for orientation of the lamina prior to thin sectioning. Pale gold to silver sections in the radial or horizontal planes were selected, mounted on bare grids, stained with lead citrate according to Reynolds (1963) and examined in a Siemens Elmiskop 1 electron microscope.

OBSERVATIONS

General organization of the lamina

The curvature of the optic lamina follows exactly that of the retina (Fig. 2). Radial and tangential planes are defined relative to this curvature. The retinula fibres converge in a radial pattern towards the lamina, and enter it already grouped into small bundles. We have been unable to determine the important fact whether one bundle corresponds to the seven retinula axons of one ommatidium. On the inner concave side, fibres again leave the lamina in numerous small bundles which decussate and form the first chiasma of the optic lobe.

In the lamina itself, which is 150–220 μ thick, one can easily recognize in silver preparations the five distinct layers described by Hanström (1924) for *Palinurus* (Figs. 3, 4). An important difference, however, from his description is that in the lobster the second or peripheral fibre region (*II*, Fig. 3), which separates the proximal and distal ganglion cells from each other, and the 5th or proximal fibre layer (*V*, Fig. 3), consist of a well-developed system of relatively thick horizontal fibres of non-nervous nature.

Light- and electron-microscope investigations of these horizontal fibres reveals that they are a specialized glial structure. Each is an especially compact layer of several very thin strata of elongated multipolar glial cells. The ultrastructure of these glial cells will be described in a succeeding paper, being beyond the scope of the present one. It is nevertheless obvious, even from 1–2 μ sections, that these two glial layers physically isolate the lamina on both sides. They are broken only to allow the retinula fibres to enter on the peripheral and the optic fibres to leave on the proximal side.

The columnar synaptic area, 80–140 μ thick, sandwiched between the two glial sheaths mentioned above, is characterized by its regular array of radially oriented cartridges, which give the whole central sheet of the lamina a columnar appearance. Each cartridge is composed of one or two central ganglion cell axons and 6–8 (probably 7) retinula fibre endings which are thickened to such an extent that they have a bulbous appearance (Figs. 5, 6), as is clear even in Golgi preparations. Retinula fibre bundles which arrive at the lamina split up as they pass through the pores in the glial envelope, and fibres of one pore frequently run to different cartridges. A third layer of horizontal fibres (*IV* in Fig. 3), containing at least two types of neurons, lies in the lower parts of the columnar region, where the retinula cell endings are found. A very thin glial sheath, distinct from the thick glial envelope of the lamina, covers the retinula fibre bundles; in the synaptic region this sheath is restricted to the outer surface of the inflated retinula fibre endings. This thin glial sheath alone isolates the individual cartridges from each other, but a number of elongated processes of areolar glial cells (sheet cells) of the peripheral layer spread down between the groups of retinula cell endings. We assume that this glial tissue with its numerous elongated processes has an especially important role in the nutrition of the synaptic region because no vascular system can be found here. It is quite different in appearance from the similarly located glia of 'epithelial cells' in the blowfly.

A second fibrous element of the columnar region stands out in electron-microscope surveys (Figs. 5, 6), and can be identified in the toluidine-blue stained sections which span the whole depth of the lamina (Fig. 7). The fibres are seen as round, oval or elongated profiles which fill the whole area between the cartridges; they are axons and correspond to the horizontal nerve fibres which are observed in silver preparations in the middle and lower parts of the columnar area in the lobster (Fig. 3), but are more obvious in the crab (Fig. 4). Horizontal fibres are more numerous and thicker in the lower part than in the upper part of this region. Occasionally, however, they are seen even near to the origin of the ganglion cell axons but always within the thick glial envelope. In the electron microscope horizontal fibres appear as watery profiles or as neurosecretory fibres, and there is reason to suppose that they are of at least two types, as set out below. Where they enter the optic cartridges, the horizontal fibres make synapses with both the retinula and ganglion cell axons, and synaptic contacts between the transverse fibres themselves cannot be excluded. The types of synapse found in this horizontal fibre system will be treated in detail in the next paper. Tracing these fibres in Golgi preparations, Hanström (1924) concluded that some (which we find to be secretory) spring from local cells in the fifth region of the lamina and ramify only locally, while a second type (which we find as empty profiles) originate in a more distant cell close to the medulla; some may even come from a more central portion of the optic lobe, or from the brain itself. No horizontal fibres were described by Trujillo-Cenóz (1965) in his study of the dipteran lamina.

Nerve cells of the lamina

Two types of neurons are outstanding and easily distinguished: (*a*) the ganglion cells of the first and third layers (Figs. 7, 8); and (*b*) larger nerve cells which are spaced out on the proximal side of the lamina in the inner glial envelope (Figs. 7, 9). Both types are monopolar, as is usual in invertebrates.

The ganglion cells are located in two layers as mentioned earlier, separated from each other by the layers of the peripheral glial sheath. The two layers together are 30–60 μ thick. One cell measures 6–16 μ. There are more cells situated outside than inside the sheath, but we have no reason to suppose that this difference in position implies a functional difference between the two ganglion cell layers. The function of the cell bodies is believed to be of a trophic nature, and it is suggested that a separation of ganglion cells into two layers is accidental, although electrophysiological recording may prove otherwise. Ganglion cells of both layers send their axons to the optic cartridges, where they establish similar synaptic connexions with retinula and transverse fibres. In Golgi preparations also the configuration and pathways of the axons of the ganglion cells are similar. In 1–2 μ sections the size, shape and structure of the nucleus and cell body are similar, and the axons of both ganglion cell layers have quite the same appearance. Electron-microscope observations of the synapses have so far revealed only one anatomical type of ganglion cell. In the comparable location in the blowfly, Trujillo-Cenóz (1965) found two structurally distinct types of unipolar neurons.

The initial part of the lobster ganglion cell axon is smooth, but in the region of the optic cartridges the axons form branches, as seen in Golgi preparations (Fig. 1). These

consist of a rich arborization of primary, secondary and tertiary spines; they are described in the next paper. In the fly lamina Trujillo-Cenóz found side branches of the initial part of the ganglion cell axons, which form a plexus peripheral to the layer of cartridges. These fibres were figured by Cajal & Sanchéz (1915) in the fly. We are unable to locate a comparable plexus in the lobster although it cannot be absolutely excluded.

The ganglion cells appear under the electron microscope as pear-shaped cells without plasmatic folds and with a rather crowded cytoplasm containing free ribosomes

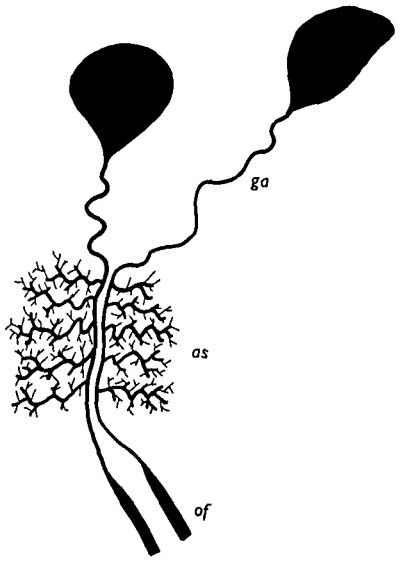

Fig. 1. Highly schematized drawing of ganglion cells from Golgi preparations. The initial thin portion of the axon (*ga*) is contorted, the middle part has spiny dendrites (*as*), and the third portion (*of*), which lies in the optic chiasma, is slightly thickened.

and membranes of the endoplasmic reticulum (Fig. 10). The most characteristic inclusions are large well-developed dictyosomes usually near to the nucleus (Figs. 5, 10, 11). Such large dictyosomes are never found in glial cells. The dictyosomes consist of crescentic stacks of agranular cisternae with some cisternae apparently fragmenting into a swarm of small vesicles. They are remarkably similar to the large dictyosomes of insect neurons (Smith & Treherne, 1963). In the synaptic region, to find an axon which definitely originated from a ganglion cell body, we had to search a large number of sections, because the axons are extremely thin in this region and not straight, as seen in Fig. 1. There is no specialized axon–hillock region. Although the ganglion cells may lie quite close to each other they are separated by at least one thin glial process (Fig. 10) except where two lie together in one optic cartridge.

The initial part of the axon contains plenty of ribosomes, which are found otherwise only in the perikaryon and in dendrites of multipolar vertebrate cells. The morphological discovery of these particles in the axon can be related to the recent chemical demonstration of RNA in axons, albeit in the cat (Koenig, 1965). In this part of the

axon, neurotubules are quite numerous, as in the blowfly, and are distributed in bundles (Fig. 12). Though a few neurotubules can be discerned in the cell body near the origin of the axon, they are numerous only in the axon. They are so highly characteristic of this type of axon as it makes its way through the lamina, that this feature has been utilized to distinguish ganglion-cell axons from the retinula axons and from some of the transverse axons. Even the postsynaptic and thickened part of the axon in layer 5 is filled with neurotubules (Fig. 13). No neurofilaments, as distinct from neurotubules, have been seen. The mitochondria of the ganglion cells are smaller and denser than those of the retinula cells.

The nerve cells of the 5th layer are larger than the ganglion cells; they are arranged regularly at intervals, are round, and measure 18–24 μ (Figs. 7, 9). They are mostly secretory and send their axons to the columnar region as horizontal fibres. Secretion in the cells has been demonstrated faintly by standard histological methods for neurosecretion. In the electron microscope the perikaryon is seen to be filled with secretory vesicles and dense-core vesicles (Figs. 13–15), but is not especially rich in endoplasmic reticulum. The mitochondria are small with few cristae, and no large dictyosomes have been found. Neurons of this type were not included in the study by Trujillo-Cenóz, although in Diptera there are cell bodies in this position, with centrifugal fibres (Cajal & Sánchez, 1915).

DISCUSSION

The optic lamina of the lobster is a well-developed multilayered structure of five distinct layers which do not correspond to Hanström's (1924) five layers, two of them being of non-nervous, glial origin. These two glial sheaths isolate the columnar synaptic region of optic cartridges from the underlying parts of the optic lobe and from the retina above. Anatomically this isolation is so complete that it suggests a functional isolation which may be related to the restriction of flow of ionic electric currents around the cartridges. The outer layer of ganglion cell bodies and the regularly arranged optic cartridges are similar to those long-known in insects (Cajal & Sánchez, 1915; Trujillo-Cenóz, 1965). The optic cartridges, like those of insects and similar structures in *Octopus* (Dilly, Gray & Young, 1963), appear as 'en passant' synapses between swollen presynaptic retinula bags and the ganglion cell axons. The insect lamina differs from that in crustaceans in having in addition basal retinula cell axons which, when they occur, run right through the lamina to end in the medulla (Cajal & Sánchez, 1915).

In the apterygote insect *Lepisma* Hanström (1940) found a 1:1 relationship between ommatidia and optic cartridges, there being only twelve of each on each side in this animal. Counts made on our silver preparations show the same relationship in the lobster. Each cartridge must receive seven retinula terminals because they do not branch and each ommatidium has seven retinula cells (Rutherford & Horridge, 1965). Each cartridge receives retinula fibres from different ommatidia by their interweaving, as has been found in all insects and crustaceans so far investigated. This means convergence of different ommatidia on one ganglion cell and divergence of one ommatidium

to different ganglion cells. The situation is complicated by the numerous transverse fibres of local neurosecretory cells and also of other more widely ramifying axons. The whole system bears a general resemblance to that in insects, as found by Zawarzin (1913) in the dragonfly and Cajal & Sánchez (1915), and partly illustrated in detail by Trujillo-Cenóz (1965), but is more complicated. As will be shown, the horizontal fibres are mainly postsynaptic to retinula and presynaptic to ganglion cell fibres, but we cannot say whether they are inhibitory or excitatory, or perhaps both. The finding of a class of secretory horizontal fibres complicates the situation.

The chief recognition feature of use in interpreting sections is the dense cytoplasm of the retinula cell bag terminals, with numerous vesicles and large pale mitochondria. The ganglion cells are recognized in sections by their large dictyosomes, which are comparable with those in many insect nerve cells, and by their small darkly staining mitochondria. Neurotubules of the ganglion cell axon are useful for distinguishing it from other axon types lower down in the lamina. Horizontal fibres are identified by their empty contours, without neurotubules but with presynaptic vesicles. The presence of the ribosome granules in the ganglion cell axon suggests a capacity to synthesize protein, and is a feature not commonly encountered in axons.

The second type of nerve cell, lying below the columnar region close to the fifth or lower glial layer, is secretory, and shows staining features and fine structure which are typical of neurosecretory cells in invertebrates, with secretory, synaptic and dense-core vesicles. Neurosecretory cells have not previously been reported from the lamina and there is no known end-organ or function. One can only suppose that their secreted product has some specific function, perhaps to modulate the activity of surrounding neurons, and that the time constants of control of synthesis and release of secretion are much longer than those of ordinary nervous action. Their presence suggests that they receive excitation which is available only here, such as that relating to general light intensity, from the primary visual fibres of the optic cartridges.

To make suppositions about the interactions of all these fibres we require information of their synaptic connexions with each other, all of which will be the topic of the succeeding paper in this series.

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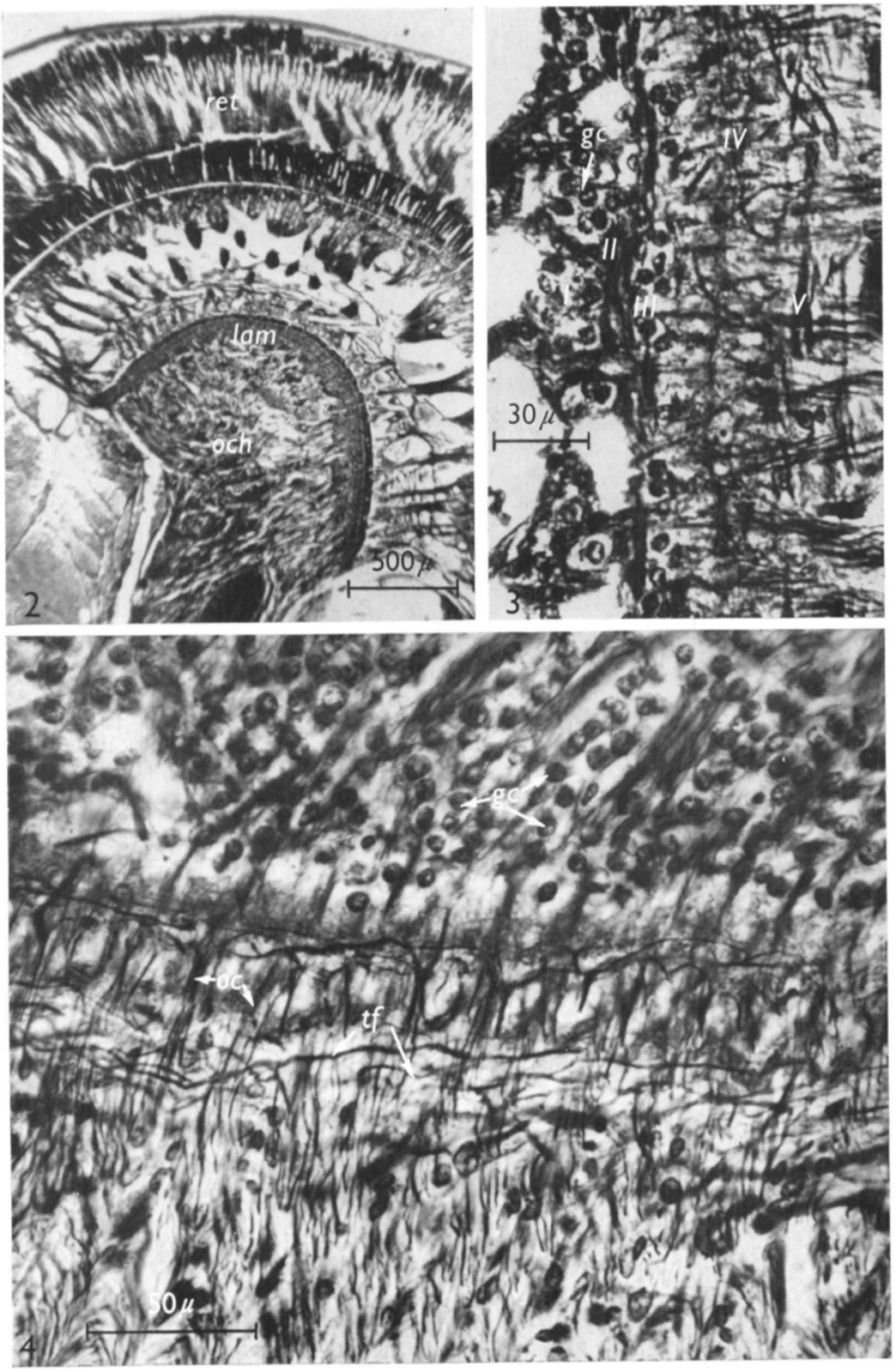
ABBREVIATIONS

b	haemocoel lacuna	*nc*	neurosecretory cell body
c	cisterna	*ng*	neurosecretory granule
cl	optic cartridge layer	*nt*	neurotubule
d	dictyosome	*ntf*	neurosecretory transverse fibre
ga	ganglion cell axon	*oc*	optic cartridge
gc	ganglion cell	*och*	optic chiasma
gl	glial layer	*of*	optic fibre
gp	glial process	*rb*	ribosomes
lam	lamina	*re*	retinula ending
m	mitochondrion	*ret*	retina
n	nucleus	*rf*	retinula fibre
na	neurosecretory cell axon	*tf*	transverse fibre

Fig. 2. Low-power light micrograph of silver-stained vertical section of the eye-stalk of the lobster showing retina (*ret*), lamina (*lam*) and first optic chiasma (*och*).

Fig. 3. Higher power of a Holmes silver preparation in the radial plane showing the five layers of the optic lamina in the lobster: *I*, first layer of ganglion cells (*gc*); *II*, transverse glial fibre layer; *III*, second layer of ganglion cells; *IV*, columnar synaptic layer; and *V*, second transverse glial layer. Note a layer of horizontal nerve fibres in the centre of the columnar region.

Fig. 4. Silver impregnation of the lamina of the crab *Carcinus*, showing widely ramifying transverse fibres (*tf*) of the region of the optic cartridges (*oc*). Note the great depth of the ganglion cell layer (*gc*).



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Figs. 5, 6. Low-power electron micrograph montage of the lamina of the lobster, continuous from the top of Fig. 5 to the bottom of Fig. 6. In Fig. 5 the retinula fibres (*rf*) and ganglion cell axon (*ga*) enter the columnar region between cells of the glial layer (*gl*). The retinula fibres and ganglion cell axons (the latter identified by their small, dense mitochondria) are separated from the surrounding ganglion cell bodies (*gc*) by a thin glial sheath (*gp*) which is continuous with the glial layer. In one ganglion cell is found a dictyosome (*d*). One of the retinula fibres widens to a bag which is filled with the synaptic vesicles characteristic of the retinula endings (*re*).

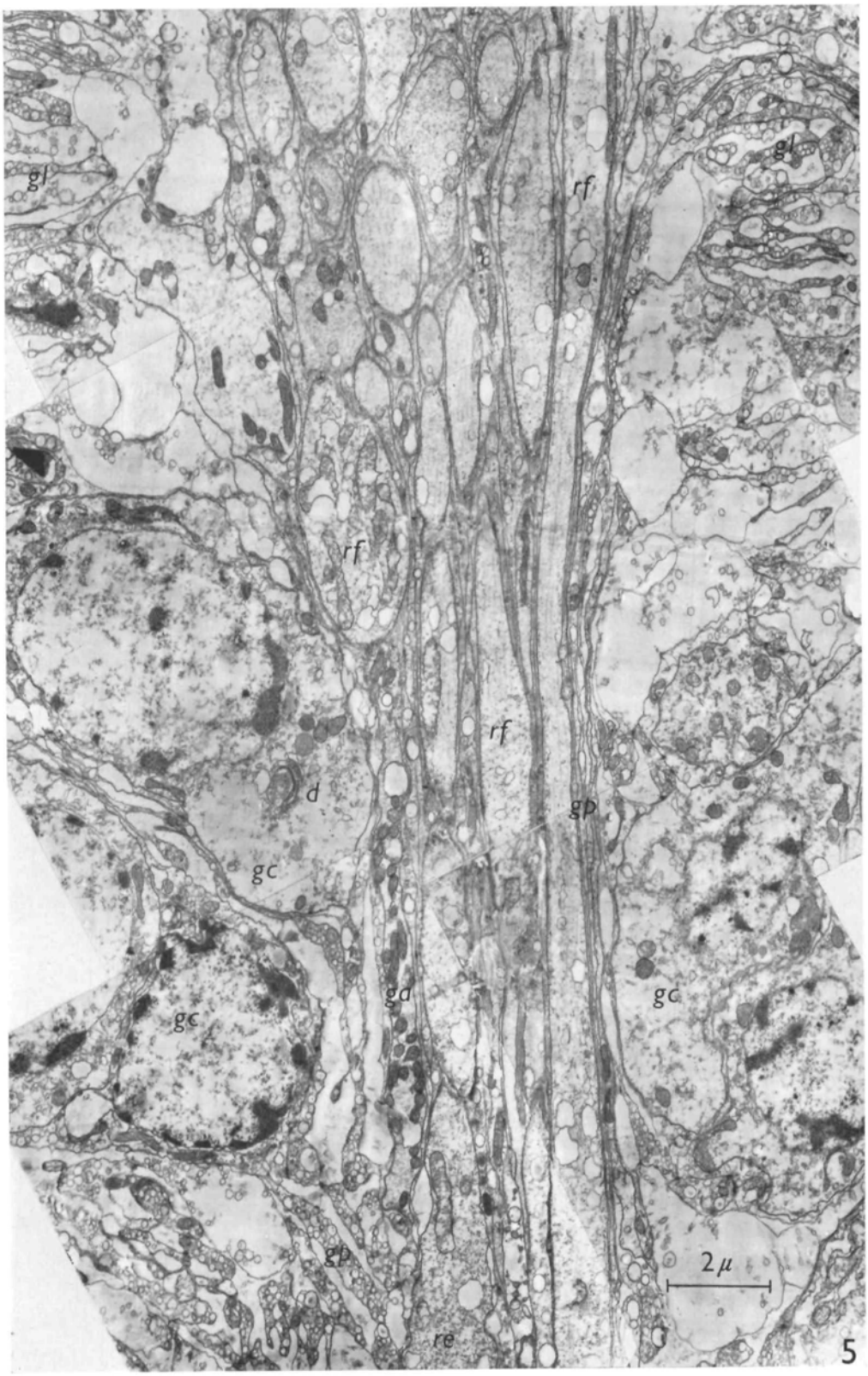

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Fig. 6. Continuation of Fig. 5 with the synaptic region. The widened retinula endings (*re*) with their characteristic large light mitochondria (*m*) constitute the optic cartridges (*oc*); the whole diameter of one optic cartridge is marked with a line. In the centre of the optic cartridges the smaller profiles with dense small mitochondria are the spines of the ganglion cell axons. Next to the optic cartridge are the large empty profiles of the transverse fibres (*tf*). Below the cartridge several axons (*ntf*) contain neurosecretory vesicles. The optic cartridges are covered and separated from each other by glial processes (*gp*).

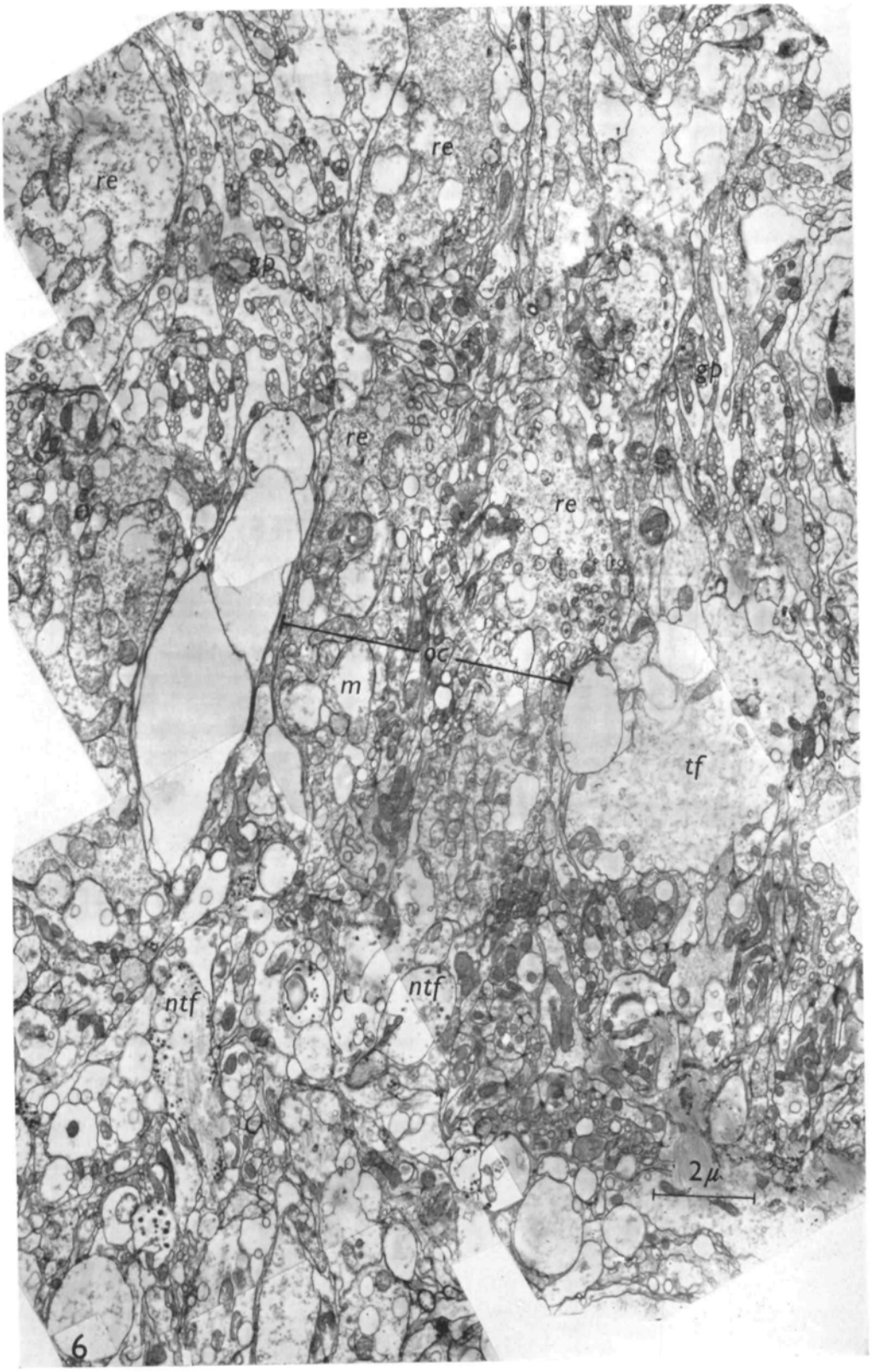

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Fig. 7. Light-microscope picture of the lamina from a 1-μ Araldite section stained by toluidine blue. The five layers of the lamina can be recognized. In the first lie ganglion cell bodies (gc_1); the second is a glial layer (gl_1) the thickness of which is marked by a line. Arrows show where the glial sheet is pierced at regular intervals to allow retinula fibres and ganglion cell axons to enter the columnar region. Below the glial sheet lie more ganglion cell bodies (gc_2) in one or two rows, which constitute the third layer. The fourth and thickest layer (*cl*) contains the optic cartridges which give it a columnar appearance. Some large neurosecretory cells (*nc*) are found in this and the next region. The fifth layer is of glia (gl_2) of a depth marked by the line. Ganglion cell axons or optic fibres (*of*) break up the sheet when leaving the lamina on the right. Framed areas are shown at higher power in Figs. 8, 9. Haemocoel lacunae (*h*) lie between the retina and lamina but do not penetrate the latter.

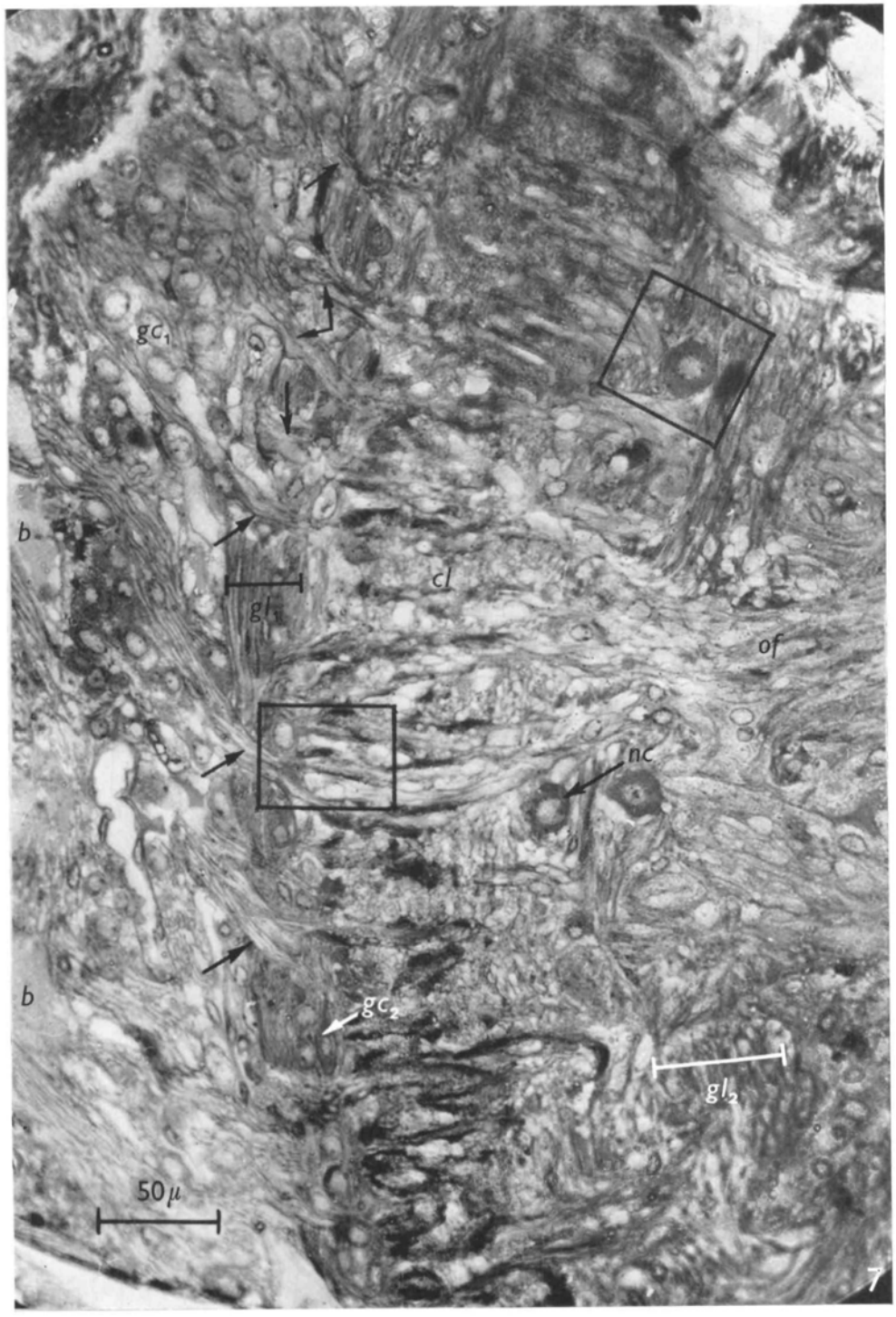

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Fig. 8. Enlargement of part of Fig. 7 showing retinula fibres (*rf*) entering the columnar region. Note that they separate and end in different optic cartridges (oc_1, oc_2 and oc_3). The axon (*ga*) emerging from a ganglion cell (*gc*) enters oc_1. Between the cartridges are transverse fibres (*tf*) in cross-section.

Fig. 9. Enlargement of part of Fig. 7 showing a neurosecretory cell body (*nc*) sending its axon (*na*) peripherally towards the cartridge region. Next to the cell are optic fibres (*cf*) leaving the lamina, and the lower glial layer (*gl*).

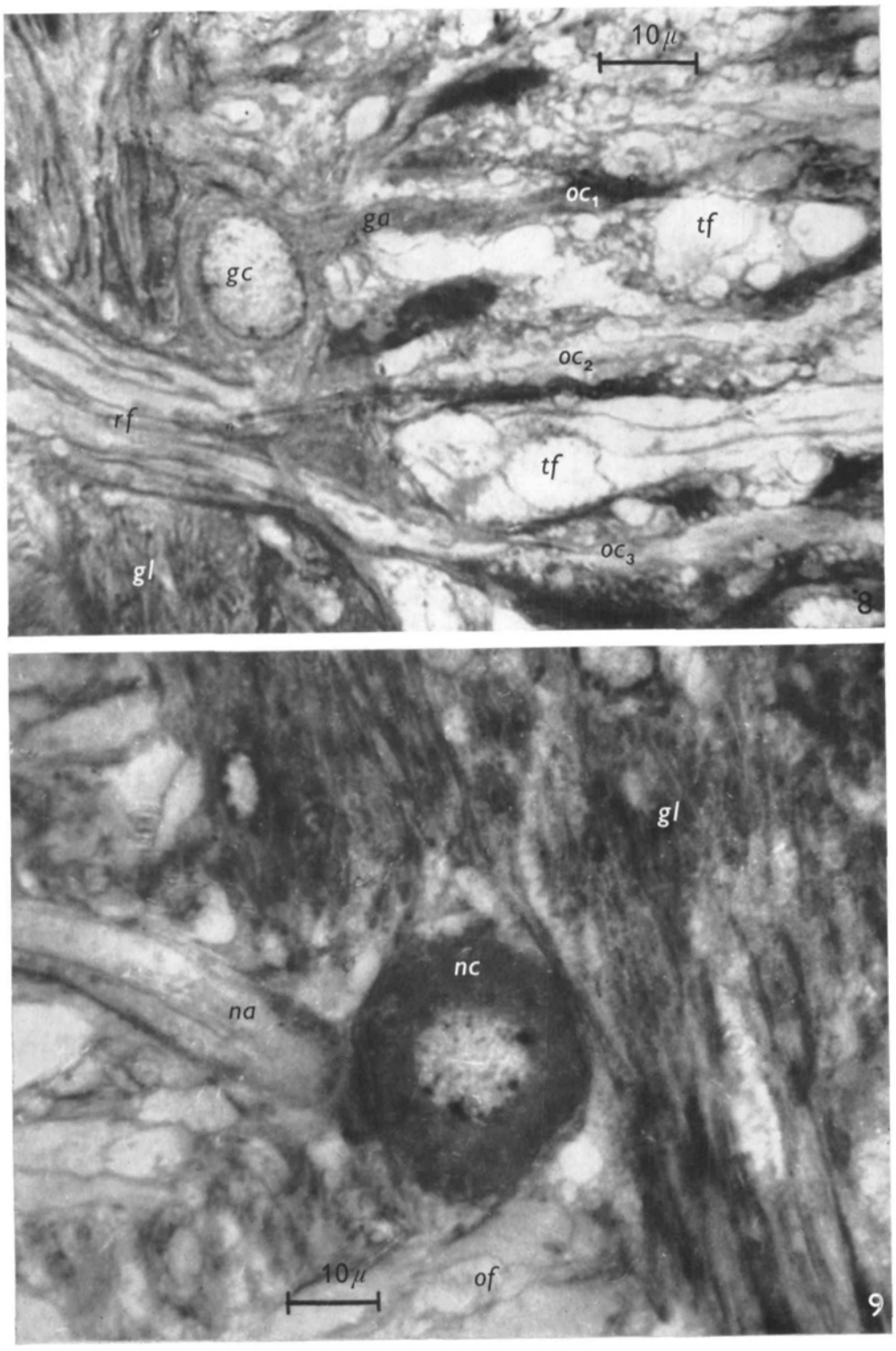

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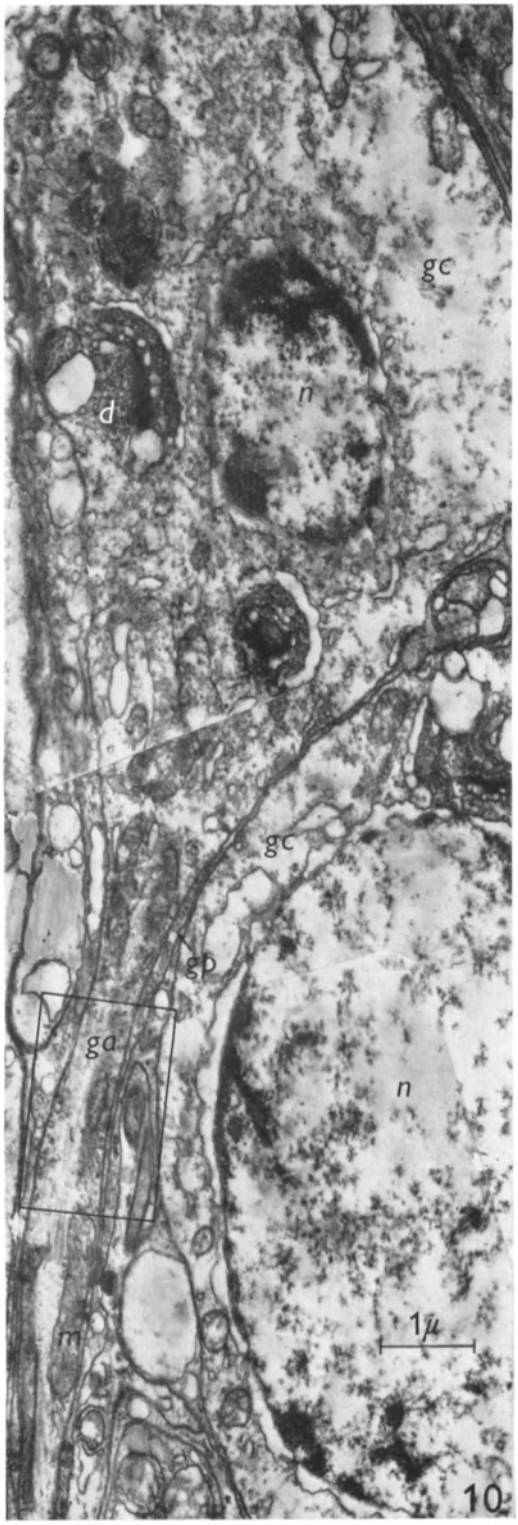
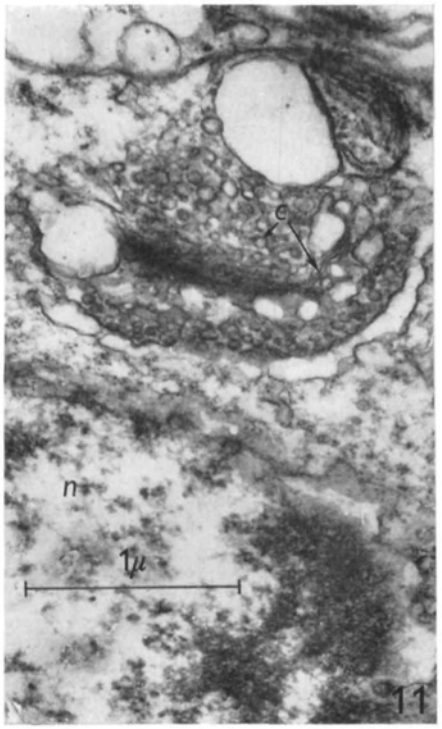
Fig. 10. Two ganglion cells (*gc*), the upper with an axon (*ga*) emerging from it. The nucleus (*n*) is large but in the upper cell is cut off-axis. Both cells contain dictyosomes (*d*) near to the nucleus. The two ganglion cells are separated from each other by a thin glial process (*gp*).

Fig. 11. The dictyosome (*d*) from Fig. 10 at higher power, with crescent-shaped stacks of smooth endoplasmic reticulum with cisternae (*c*) and a few larger empty vesicles.

Fig. 12. Details of the initial part of the axon which is framed in Fig. 10. The axon is ensheathed with glial processes (*gp*) and contains neurotubules (*nt*), ribosomes (*rb*), and elongated mitochondria (*m*).





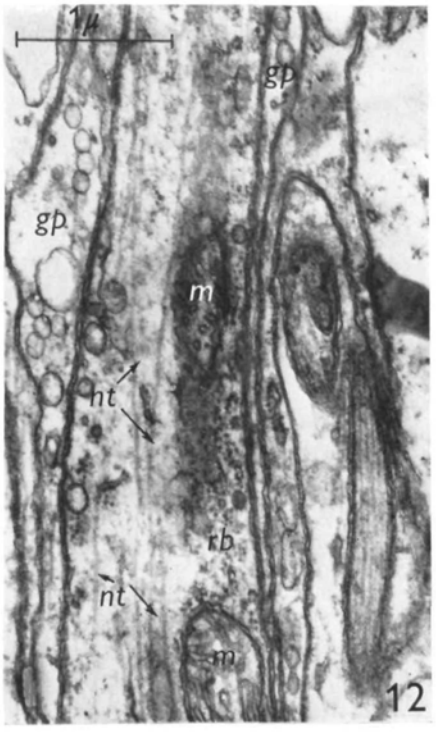


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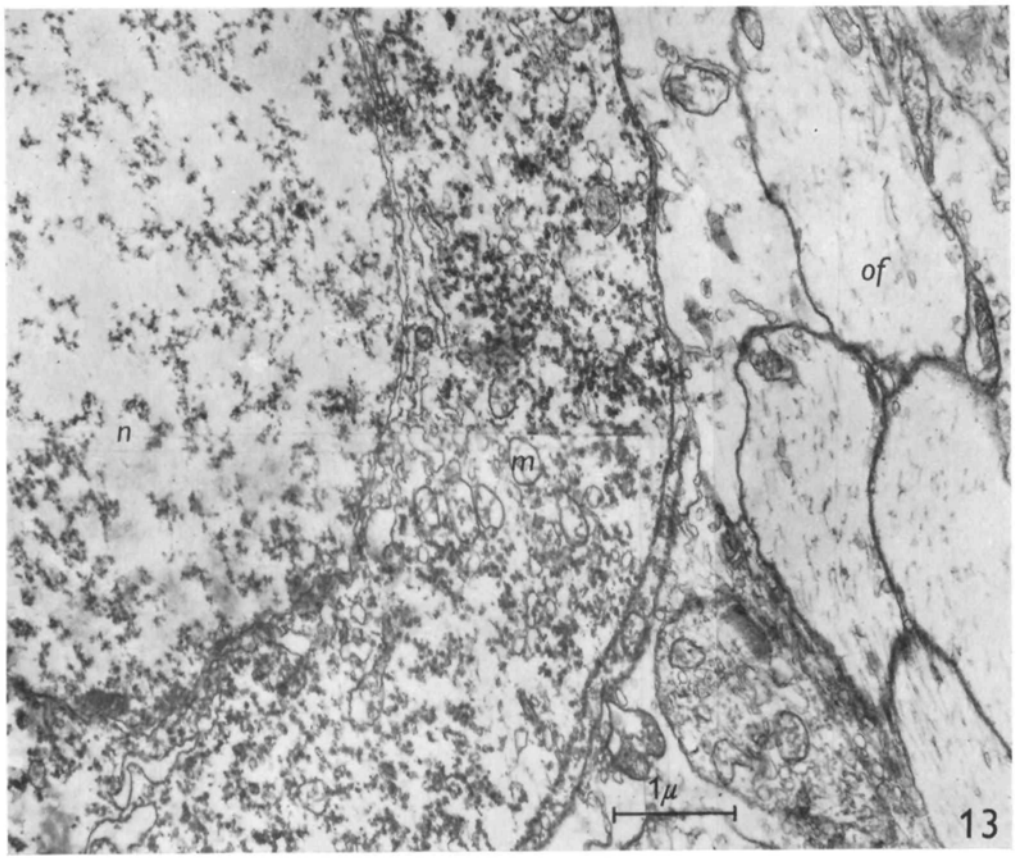
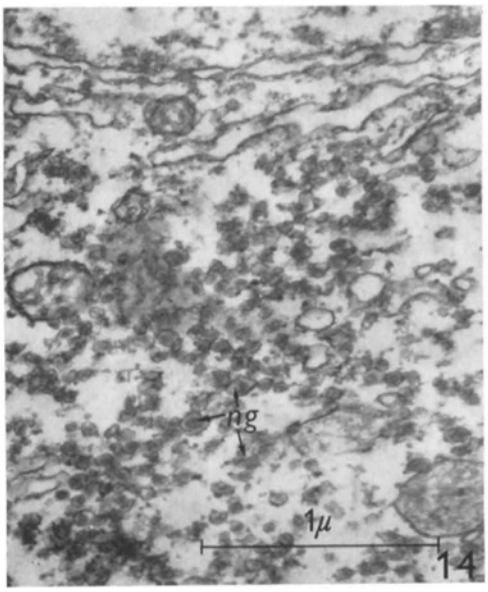
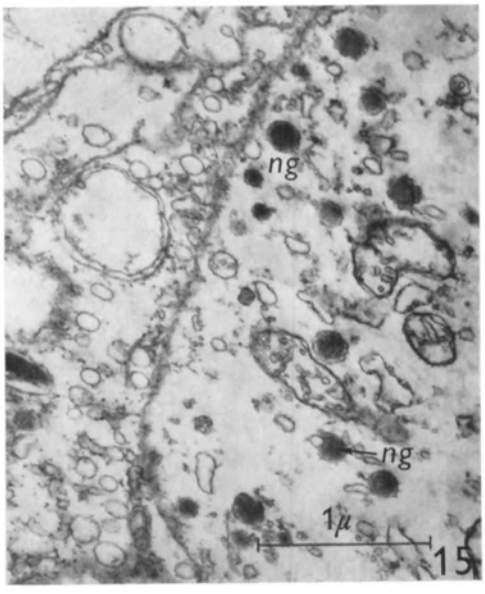
Fig. 13. Electron micrograph of the neurosecretory cell. The perikaryon is here filled mainly with vesicles which are similar to the widespread so-called dense-core vesicles and a few small mitochondria (*m*). Nearby are large optic fibres (*of*) containing neurotubules.

Fig. 14. Dense-core vesicles of the cytoplasm of the cell shown in Fig. 13.

Fig. 15. Part of another neurosecretory cell with neurosecretory elementary granules (*ng*).







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