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STRUCTURE AND FUNCTION OF INSECT PHOTORECEPTOR

by

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ABSTRACT

The connections between the retinula cells of the compound eye and the neural elements in the optic lobe in fleshfly (Boettcherisca peregrina) were observed by electron microscopy. The ommatidium consisted of eight retinula cells: six ordinary retinula cells, one central retinula cell and one basal re retinula cell. The axons of ordinary retinula cells (short fibers) terminated at the lamina, whereas two extraordinary retinula cells extended their proximal axons (long fibers) to the medulla. Five or six short fibers crowded around two axons of monopolar ganglion cells at the lamina, constituting the "neurommatidium", where they held the repeated synaptic contacts with the monopolar axons. Many "spherical invaginations" were discovered at the axon membranes of short fiber in the neurommatidium. Such peculiar structures as well as the cytoarchitecture at the lamina were discussed in relation to possible functions.

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INTRODUCTION

In the compound eye of insect, axon of the retinula cell extends proximally through the basement membrane to hold direct connections with the neural elements in the optic lobe. Such neural connections of the compound eye have been studied by several workers using the light microscope. According to Ramon y Cajal and Sanchez (3), there are two types of axons of retinula cells in the compound eyes of flies: long and short fibers. Long fibers pass through the lamina without having the synapses and probably have their endings in the medulla. Short fibers, which are the more numerous, terminate around the axons of monopolar ganglion cells in the lamina, where they form the group referred to as the "neurommatidium" (10) or the "optical cartridge" (21).

A number of electron microscopic studies on the retinula cells of insect compound eyes have been published during the past decade (6, 7, 8, 9, 22, 23, 24, 25). They were chiefly concerned with the fine structures of the retinula cells, especially with the rhabdomeres which are the light trapping sites in the receptor cell of the compound eye. It has been confirmed from these studies that the rhabdomere consists of the closely packed arrays of microtubules, oriented perpendicularly to the long axis of the ommatidium. In addition, it has been shown that the rhabdomeres are in a difinite arrangement within the ommatidium, according to the species of insects.

On the other hand, very little is known about the synaptic organization at the proximal ends of the retinula cells by electron microscopy. There has been only a brief discription with respect to this region, which did not amply shown the synaptic architecture of the retinula axons (21).

We have observed the fine structure of the synaptic region in the lamina of a fleshfly (Boettcherisca peregrina). As a result, there were found two types of terminations of the retinula cells derived from a single ommatidium. In addition, the peculiar doughnut-shaped structure was discovered in the synaptic areas of "short fibers". Characteristic profiles of the "neurommatidium" were also clarified.

MATERIAL and METHODS

The adult fleshflies (Boettcherisca peregrina), which had been raised in our laboratory, were decapitated and the heads were immersed in cold fixative immediately. After a short time, the compound eyes were dissected and put into the fresh fixative for 30 to 120 minutes. Fixatives employed in this study were as follows: (1) 2.5% osmium tetroxide buffered with s-Collidine at pH 7.4 (2), (2) 1% osmium tetroxide buffered with Millonig's buffer at pH 7.4 (14), (3) 5 or 6% glutar-

aldehyde buffered with s-Collidine at pH 7.2, and (4) 6.25% glutaraldehyde buffered with phosphate buffer at 7.2 (17). In the glutaraldehyde fixation, the postomification was followed by 2.5% osmium tetroxide with s-Collidine buffer, after washing by s-Collidine buffer. Among the fixatives mentioned above, the "double fixation" by glutaraldehyde with s-Collidine buffer and osmium tetroxide with s-Collidine gave the best preservation for this material. The specimens were rapidly dehydrated through a graded concentrations of cold ethanol, and then embedded in Epon 812 (13). Sections were cut with a Porter-Blum MT-2 microtome, stained with lead citrate (18), and examined by a Hitachi HU-11 electron microscope.

OBSERVATION

The optic lobe of the fly consists of three main neuropile masses. They have been called by a variety of names (10). In this paper, the author will employ "the lamina", "the medulla" and "the lobula" as their names from the periphery inward, according to Horridge's opinion (11).

In the present study, the region from the retinula of compound eye to the lamina will be divided into four layers: the receptor layer, the basement membrane layer, the ganglion cell layer, and the neurommatidial layer. Such subdivision is convenient for the discription and has not clear lines of demarcation. The rough boundaries of four layers are as shown in Fig. 1 drawn schematically based on the present observation.

Receptor layer

In the compound eye of fleshly, each ommatidium consists of eight retinula cells. The cylindrical retinula cells are radially arranged around the ommatidial axis occupied by the central matrix. Adjacent cells adjoin each other by the desmosomes situated at the inner edges. The retinula cell contains several kinds of cytoplasmic organelles: numbers of mitochondria with various sizes, granular endoplasmic reticulum, ribosomes, Colgi complex, small dense granules, vacuoles, and multivesicular bodies. At the proximal portion of receptor layer, seven retinula cells protrude the individual rhabdomeres toward the ommatidial axis, but one does not bear its own rhabdomere (Fig. 2). Seven rhabdomeres keep the specific pattern for *Diptera* ommatidia: they are not fused each other but separated individually by the central matrix, being quite different from the fused-type rhabdomeres of other various insects. They are composed of many closely packed arrays of microtubules, as already demonstrated in various types of compound eyes (8, 23).

Two retinula cells in a single ommatidium usually display the different profiles from other six cells. One is rather

small and can be tentatively called the "central retinula cell", because of its feature protruding more centrally the rhabdomere. The nucleus of central retinula cell is at more proximal level than those of the other six. Another retinula cell is extremely thin at the middle portion of receptor layer, whose nucleus is situated near the basement membrane. Consequently, it will be provisionally named the "basal retinula cell". Its rhabdomere could not be detected through the present observation. Since the basal retinula cell extends its processes in both directions, proximally and distally, it can be considered as a certain kind of bipolar neuron.

Basement membrane layer

It has been shown by light microscopy that the basement membrane of insect compound eye was a thick wall of about 1 micron in width and fenestrated in places for passage of retinula axons, cytoplasmic processes of basal pigment cells, and tracheoles (20). However, it is found in the present observation that the basement membrane is made up of two layers: the inner pale layer with thicker width and the outer thin layer with densely lined loops (Fig. 5). The inner layer contains many fine filaments and dense ground substances. This layer is continuous with the cytoplasm of the basal pigment cell, whereas the limiting plasmamembrane can be found at the bottom surface of this layer. This implies that the most portion of the classical "basement membrane" is a specialized part of basal pigment cell. The outer hairpin-shaped dense lines may possibly be the extracellular structure secreted from the basal pigment cell.

The basal pigment cell has a lot of pigment granules, mitochondria, granular endoplasmic reticulum, ribosomes, and fine tubular filaments. Its nucleus is beneath the basement membrane. This cell extends its cytoplasmic processes among the ommatidia in the receptor layer.

A group of retinula cells from a single ommatidium pass together through the same fenestration of the basement membrane, where these processes display axonal appearances with neurotubules and a few mitochondria. Eight axons of retinula cells, originated from a single ommatidium, run in a bundle in a considerable distance beneath the basement membrane (Fig. 4). They are enclosed by glial cell, exhibiting mesaxons. This mesaxon occasionally shows the ladder-like desmosomes. Thus, no intercellular spaces are discovered around the axons in this region, except about 150 A spaces between the apposed plasma membranes. It is noticeable that two out of eight axons in one group is smaller in diameter than the others. They belong to the basal retinula cell and the central retinula cell. Such two axons possess a small quantity of neurotubules and dense ground substance at this level.

It can be judged from the observation on many serial

sections that eight retinula axons from a single ommatidium redistribute at the proximal level of this layer. Two thin axons of basal and central retinula cells run in pairs away from the bundle of the other axons. One or two axons of six large retinula cells also get out of the ommatidial group and run obliquely in this layer till they join the neighbouring ommatidial group.

Ganglion cell layer

The nucleus of the monopolar ganglion cell is located at the distal portion of the lamina. This cell is conspicuous with its relatively large nucleus. Its cytoplasm contains a lot of ribosomes, some mitochondoria, Golfi complex, multivesicular bodies, and granular endoplasmic reticulum. Of those organelles, a somewhat large amount of ribosomes draw a distinction between the surrounding glial elements and itself. The monopolar ganglion cell is entirely covered with a glial element. Fig. 5 shows the monopolar ganglion cell and its axon extending proximally. Fine neurotubules appear in the axoplasm as the axon departs from the cell body. The axon often emits small collateral branches or buds along its course. Some of these branches have the definite with the contiguous small processes bearing a number of synaptic vesicles, showing the increased density of the apposed membranes. These are presumed to be the synapses between the monopolar axon and the small branches from retinula axons. Although such synaptic contracts are found at the axonal portion of about 3 μ from its perikaryon, there are no synaptic contacts between the cell body of monopolar ganglion cell and the other neuronal processes. In the neighboring region, many small processes containing synaptic vesicles are present. They may be from either ganglion axons or retinula axons, and occasionally come in the synaptic contacts with each other.

The retinula axons, excluding smaller axons, contain a lot of synaptic vesicles and mitochondria in this layer. Besides, there are often seen small spherical thick-membraned structured (about 30 mμ in diameter) near the axon membranes. Such characteristic profiles will be demonstrated in detail in the next layer.

Neurommatidial layer

It is shown by cross section that there are many groups composed of five or six retinula axons in the lamina, proximal to the ganglion cell layer (Fig. 6). The groups always embrace two axonal processes of monopolar ganglion cells at more proximal level (Fig. 7). Such a group was designated as the "neurommatidium" by Ramon y Cajal and Sanchez (3). As a whole appearance, the neurommatidium has the following composition: five or six cylindrical trunks of thick retinula axons gather in a bundle around two axonal processes of monopolar

ganglion cells and run parallel with each other extending over the distance of about 50 micra. On the other hand, two thin axons of the central and [illegible] retinula cells proceed among the neuromatidia [illegible] the [illegible], [illegible] do not participate in the [illegible] layer. Accordingly, it is [illegible] thick axons [illegible] spond to the "short fibers" and [illegible] with the "long fibers".

Short fibers often [illegible] branches. Both trunks and branches contain many synaptic vesicles and mitochondria. [illegible] the intimate contacts [illegible] the synaptic profiles [illegible] are usually occupied by glial processes. [illegible] axons have the different cytoplasmic characteristics [illegible] retinula axons, containing only a few synaptic [illegible] small quantity of axoplasmic [illegible] frequently conjunct with one another by the desmosome-like structures. The attenuated glial elements intervene also among the monopolar axons and the short fibers. There are rarely occasional contacts between the trunks of the monopolar and the receptor.

It has been described that monopolar axons extend many side branches [illegible] the short fibers in the [illegible] layer, showing [illegible] such branches are [illegible] because their shapes are [illegible] like the [illegible]. However, most of minute [illegible] branches of short fibers are seemed to [illegible] branches from the monopolar axons. [illegible] the synaptic contacts between the [illegible] short fibers. Thus the retinula short [illegible] the monopolar axons [illegible] layer.

In the short [illegible] layer, the long rod-shaped, small granular [illegible] occur with relatively [illegible] continuous with the [illegible] membrane. It can be confirmed at higher magnification that the peculiar structure is composed of the small pouch of axon membrane and the conformable spherical projection of a probable glial cell (Fig. 8). In addition, it shows the electron-dense material between the opposed membranes [illegible] substance [illegible] emboss the spherical [illegible]. It can be confirmed also by serial sections [illegible] its outlets leading to the [illegible]. It will be provisionally named the "spherical [illegible]" in the following description.

The spherical [illegible] is confined to the neuromatidial trunk of short fibers, but has no intimate association with synaptic vesicles. Such [illegible] has never been reported by the electron microscopic [illegible] on the nervous tissue of [illegible]. [illegible], it is shown

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that the cytoplasmic expansion thrust into the spherical invagination is a highly flattened glial process (Fig. 9). This demonstration probably suggests it functional role.

The rounded basal pole of the short fiber is located at the deepest proximal portion of the lamina. In the longitudinal section through this portion, there is seen the termination of the short fiber and followed by the ending of the cytoplasmic expansion of surrounding glial cell (Fig. 10). The axon of monopolar ganglion cell extends into the chiasma between the lamina and the medulla.

Long fibers, distinct from the omatidial group, run through among neurommatidial groups (Fig. 6). Two long fibers are infolded in pairs by the another glial element being different from ones filling up among neurommatidial groups. A pair of these fibers always accompany a thin tracheole along the entire course through the neurommatidial layer. They have far smaller diameters (about 1.5 μ) than those of short fibers, and have neither synaptic profiles nor collateral branches in the lamina. Their prolongations toward the medulla are seen in Fig. 11, although their terminal endings are not caught as yet.

The other cells

Other elements can be seen among the neural elements over the entire layers beneath the basement membrane. These cells project complicatedly their finger- or leaf-shaped cytoplasmic processes, exhibiting a complex cellular architecture in this region. Thus any neural elements are not free from the envelopment by the other elements in the region beneath the basement membrane.

At the level of the basement membrane's fenestration (Fig. 3), the retinula axons are tightly enveloped by the attenuated processes of basal pigment cell. A cell containing a large quantity of tiny filaments embrace the retinula axons at the tracheolar region between the basement membrane and the lamina. It constructs the "megaxon" with characteristic ladder-shaped desmosomes around the retinula axons. Occasionally its horizontal [illegible] has the intimate contact with the large tracheole. [illegible] contiguous with both the basal pigment cell and the glial element in the lamina by sharing a differrent type of desmosomes.

In the ganglion cell layer, two types of cell occur. Their cytoplasmic profiles contrast with each other: one is pale and the other strongly dark. The nucleus of the pale cell is close to the cell body of the monopolar ganglion. Its ramified processes fill up the spaces among the neural elements and occasionally embrace the small tracheole. The cytoplasm of this cell consists of many mitochondria, rosettes of ribosomes, granular endoplasmic reticulum, fine filaments,

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but small quantity of ground substances. On the other hand, the perikaryon of the cell which is conspicuous with its dark profile is located at the distal region of the lamina. It expands the star-shaped arms, frequently reaching to the central portion lacking the monopolar axons in the distal level of the neurommatidium.

A glial cell expanded between the neurommatidial groups is the largest one of these elements (Figs. 6 and 9). The nucleus of this cell is situated at the middle portion of the lamina. Its plasma membrane always displays some layers of infoldings around the short fiber. In addition to such highly flattened processes, a large number of mitochondria are particularly prominent within its cytoplasm. Whereas the granular endoplasmic reticulum is dispersed throughout its cytoplasm, the array of agranular endoplasmic reticulum is also present in the proximal layer. As already noted, the minute processes of this element build up the "spherical invagination" with the membrane of short fiber.

DISCUSSION

The existence of two types of retinula axons has been described by the classic pictures obtained by light microscopic observations (3, 11). However, there was no available evidence about that two types of axons were derived from any types of retinula cells in the ommatidium, though it was assumed that short fibers were of large retinula cells. Even the number of the long fiber from a single ommatidium was not determined. By the present observation, the long fibers were first demonstrated to belong to both the central and basal retinula cells in each ommatidium. Therefore, it is possible that these cells have the quite different function from the ordinary retinula cells. Moreover, the basal retinula cell is not provided with the rhabdomere but is a kind of bipolar neuron, and in this sense differs from the central retinula cell. From these results, there are at least three types of retinula cells in a single ommatidium of the fleshfly compound eye.

It has been generally recognized that the number of the retinula cells in a single ommatidium in Diptera is usually eight (16). One of them is extremely small and has been overlooked by many earlier electron microscopists. Recently, Waddington and Perry (22) demonstrated it in the developing Drosophila eye as the "eight retinula cell". Such a distinctive type of cell has been observed also in the superposition-type compound eye of the silkworm moth (Bombyx mori), which has been called the "eccentric retinula cell" (6). Both eighth retinula cell and eccentric retinula cell have their own rhabdomeres and consequently work as photoreceptor cells. On the other hand, it is noteworthy that the basal retinula cell of the fleshfly has not the rhabdomere, so that it does not play the part of photoreceptor. Moreover, this cell evidently extends long axon to the medulla, without syn-

aptic relation to the monopolar ganglion cell in the lamina. It follows that the basal retinula cell has a quite different functional role from the eccentric and eighth retinula cells. To estimate the roles of such different types of retinula cells, of the central and basal ones in particular, more precise physiological approaches on the cellular level should be accumulated hereafter.

The earlier observations using the light microscope have shown that there are various types of neurons in the lamina, including the monopolar ganglion cells, the multipolar ganglion cells, the arborizations of centrifugal fibers, and the tangentially arranged fibers. Although such numerous types of neurons could not be identified, we obtained the evidence suggestive of theexistence of the tangential fibers. A neuron extending tangentiallywits processes is often seen at the proximal level of the lamina (Fig. 9). This neuron seems to have many synapses with the short fibers in neighbouring neurommatidia. It follows from this finding that short fibers from neighbouring ommatidia inhibit each other their visual activities at the level of lamina. It was also clear that short fibers from adjacent ommatidia intersected each other at the ganglion cell layer, terminating to the axons of monopolar ganglion cell within the same neurommatidium. Such an architecture may suggest that there are the integrating mechanisms between neighbouring ommatidia at this level.

We discovered the spherical invaginations in the synaptic area of the short fibers of the fleshfly. From our unpublished data, however, they could not be found in the retinula axons of honeybee, whereas the short fibers in the lamina of *Drosophila* were studded with many spherical invaginations. Considering these, the spherical invaginations are probably restricted to the short fibers of the *Diptera* compound eyes.

It is noteworthy that the inner pouch of spherical invagination is the spherical protrusion of the supposed glial cell. Such a relationship between neural and glial elements has been demonstrated also in some invertebrate axons (*Helix* and *Aplisia*) [1, 17]. The structures found in *Helix* and *Aplisia* axons, however, have different profiles from the spherical invagination of fleshfly, in respect that they consist of long infoldings of axon membrane and trabeculae of glial process. In addition, they have no relation to the synaptic area, in contrast to the spherical invaginations localized within the synaptic area of short fibers. Although it will be necessary to analyze the spherical invagination histochemically in evaluating its functional significance, it is presumable that the lpherical invagination is a specialized part to perform metabolic work for synaptic activity.

Many investigators have observed the fine structures of thesynapses between the receptor and the bipolar cells of the retinas in various vertebrates (4, 12, 18). It has become

obvious by their observations that the synapses have the characteristic structures in common with many vertebrate retinas, consisting of the synaptic pedicles of receptor cell, the synaptic lamellae or ribbons, the paired terminations of the bipolar cell, and the accumulated synaptic vesicles at the both synaptic sites. Among these characteristics, the synaptic lamellae or ribbons have been identified at only the receptor-bipolar synapses of the vertebrate retinas. No function has been suggested for this structure. Therefore, we assumed that there might be the synaptic ribbons also at the receptor-ganglion synapses in the optic lobe of insects, if they are necessary for the first synaptic transmitting mechanism of the photoreception in the differentiated eye. Beyond our expectation, however, the insect synapse had no such a peculiar apparatus.

The complexity in the cytoarchitectures of the insect optic lobe was presented. The various types of glial cells differed from the glial elements in the central nervous system of vertebrate. Their complicated cytoplasmic processes entirely filled up the spaces among the neural elements. Most of them have not been referred to so far. Their cytoplasmic characteristics are different from the vertebrate glia. This may owe to the circulating system of insect body fluids, which is in contrast to the closed circulating system in the vertebrate. The role of the spherical invagination should be considered also from this point of view.

The electron microscopic observation about the compound eye-optic lobe region in insect has just started. It is assumed that the synaptic architectures in the compound eye will show a great deal of variation depending upon various species of insects. Numerous comparative histology by the electron microscopy on this field is required. This will make the way leading not only to the follow-up of the visual pathway of insect but also to the elucidation of the configuration of the insect brain.

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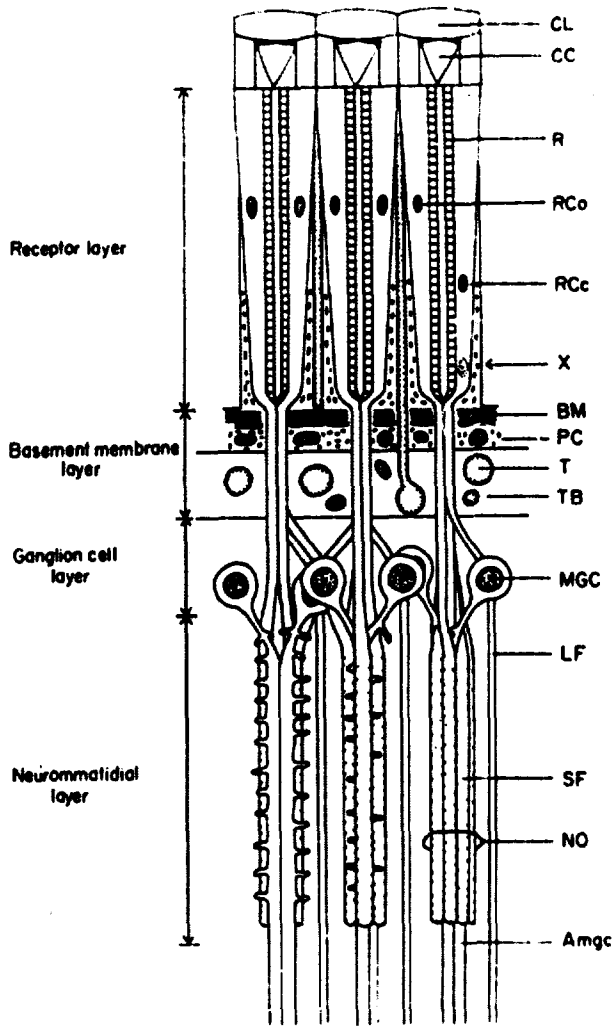

Fig. 1. Diagram of the receptor layer and the lamina of the fleshfly compound eye. Abbreviations: CL, corneal lens; CC, crystalline cone; R, rhabdomere; RCo, ordinary retinula cell; RCc, central retinula cell; X, position of nuclus of basal retinulacell; BM, basement membrane; PC, basal pigment cell; T, tracheole; TB, tracheoblast; MGC, monopolar ganglion cell; LF, long fiber of retinula cell; SF, short fiber of retinula cell; NO, neurommatidium; Amgc, Axon of monopolar ganglion cell.

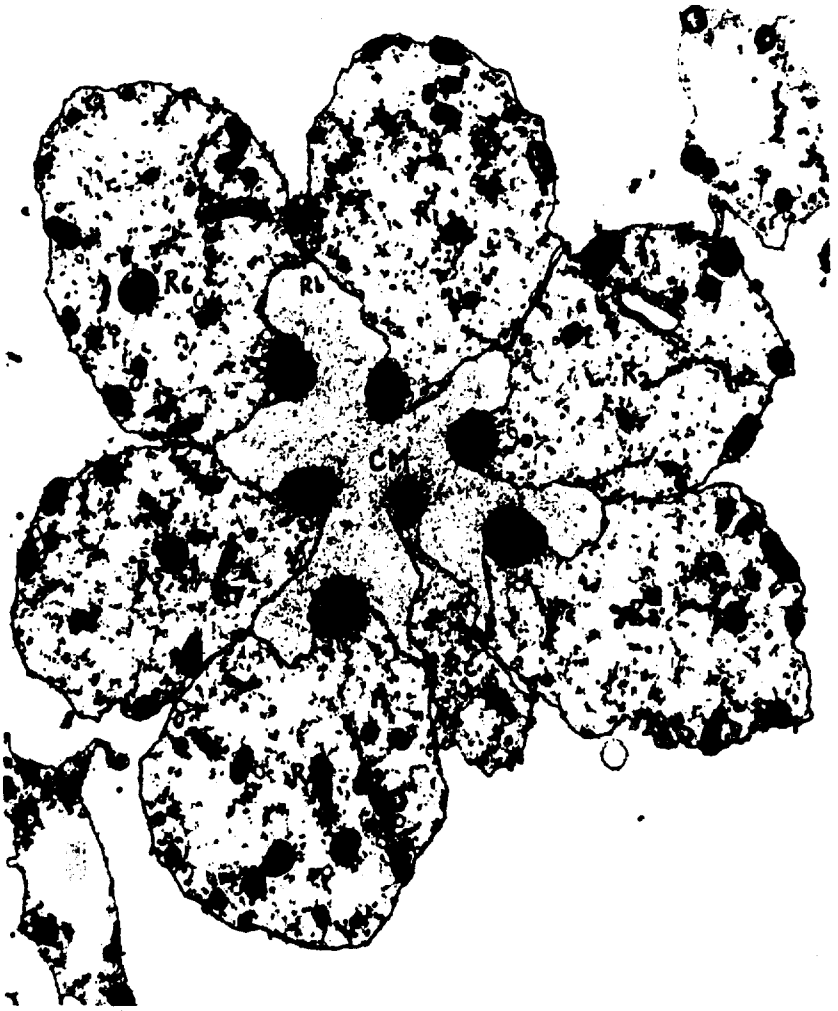

Fig. 2. Transverse section through the receptor layer. The ommatidium consists of six ordinary retinula cells (R1 - R6), one central retinula cell (Rc), and one basal retinula cell (Rb). Seven rhabdomeres are separated by the central matrix (CM). x 8,000.

Fig. 3. Oblique longitudinal section through the basement membrane. Eight axons of retinula cells (A1 - A8) from the same ommatidium are in a bundle beneath the basement membrane (BM). PC, basal pigment cells; T, tracheole, x 9,000.

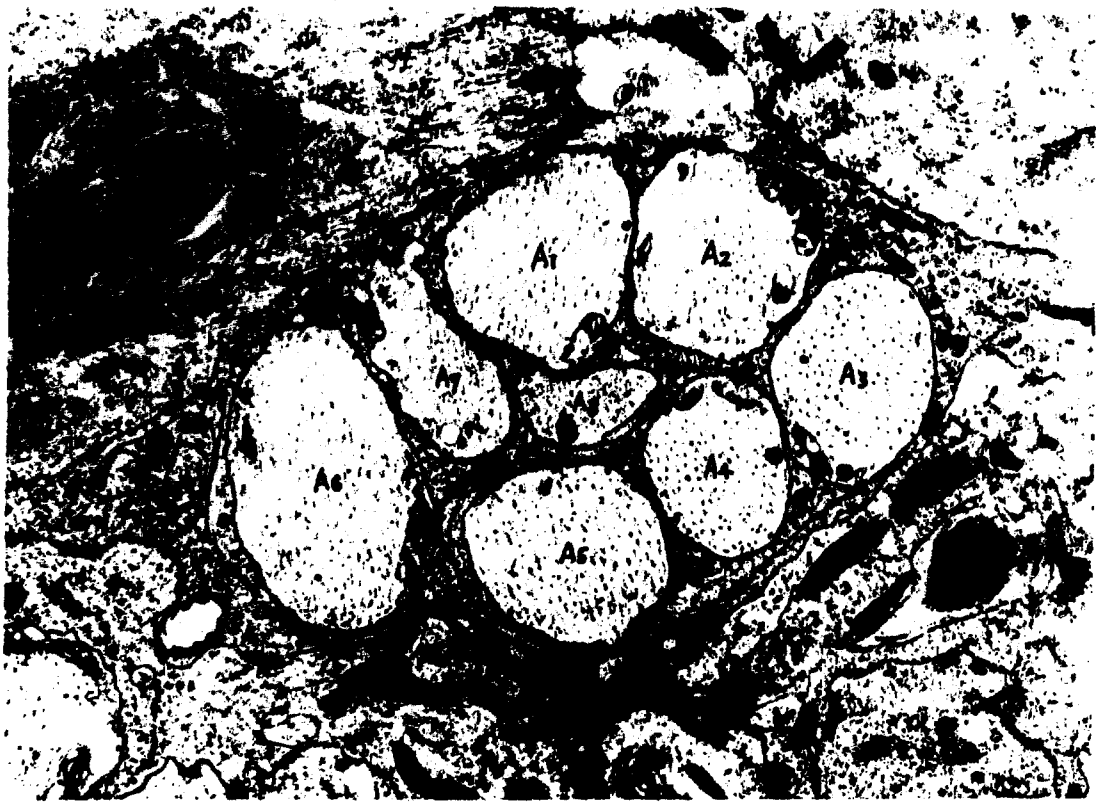

Fig. 4. The ommatidial group of retinula axons in the proximal basement membrane layer. Eight axons (A1 - A8) are enclosed by the glial element. Two small axons (A7 and A8) are supposedly from the central retinula cell and the basal retinula cell. x 8,000.

Fig. 5. Oblique longitudinal section through the ganglion cell layer. Monopolar ganglion cell (RA) extends proximally the axon. Large retinula axons (RA), short fibers, contains many synaptic vesicles and spherical invaginations. In the region among these axons, there are a lot of small neural processes occasionally holding the synaptic contacts (sy). x 8,000.

Fig. 6. Transverse section through the distal neurommatidial layer. Six large retinula axons, i. e. short fibers, (SF) gather in a group. Glial cells (C) intervene between these axons. Two long fibers (LF) of retinula cells run in pairs among the neurommatidial groups. T, tracheole. x 9,000.

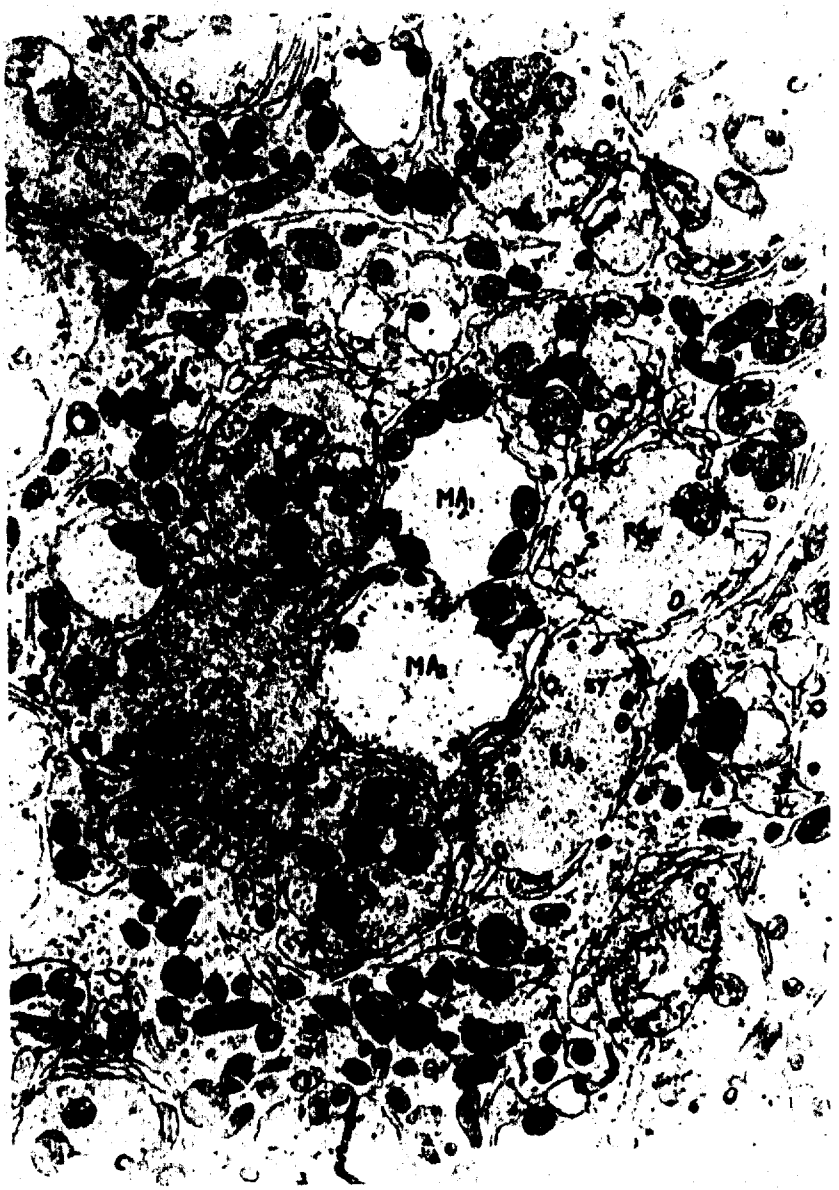

Fig. 7. Transverse section through the neurormatidial [illegible]. Two [illegible] (MA1 and MA2) of monopolar ganglion cells [illegible] retinula axons (RA1 - RA6). Such a group [illegible] "[illegible]". Many spherical invaginations [illegible] of retinula axons. Some [illegible] (ay) [illegible] seen. G, glial cell. x 9,000.

Fig. 8. Longitudinal section through the short fibers of retinula cell (RA) in the neurommatidial layer. Spherical invaginations (s) are clearly seen. sv, synaptic vesicles; G, processes of glial cell; m, mitochondria. x 32,000.

Fig. 9. Longitudinal section through the proximal neuro-ommatidial layer. Basal end of short fiber (SF) are shown. Spherical invaginations (s) clearly hold the relationship to the glial cell (G). The supposed tangential neuron (TN) is situated at this layer. x 8,000.

Fig. 10. Longitudinal section through the most proximal layer of the lamina. Axon of monopolar ganglion cell (MA) run toward the chiasma between the medulla and the lamina (arrow) while the basal end of short fiber of retinula cell (SF) are at this layer. Synapse (sy) between retinula axon and monopolar axon are shown. G, glial cell. x 6,500.

Fig. 11. Longitudinal section through the same layer as shown in Fig. 10. Paired long fibers run toward the chiasma. G, glial cell; T, trachoole. x 8,700.