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# The Superposition Eye of *Cloeon dipterum*: The Organization of the Lamina ganglionaris

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**Summary.** The lamina ganglionaris of the superposition eye of *Cloeon dipterum* is composed of separate optic cartridges arranged in a hexagonal pattern. Each optic cartridge consists of one central, radially branched monopolar cell (Li) surrounded by a crown of seven retinula cell terminals and two more unilaterally branched monopolar cells (La1/La2) situated close together outside the cartridge. Projections to neighbouring cartridges have not been observed.

In most cases, synaptic contacts could be seen between a presynaptic retinula cell and more than two other postsynaptic profiles, which belong to monopolar cells or sometimes to glial cells.

Seven retinula cell fibers of one ommatidium pass in a bundle through the basement membrane, run into their respective cartridges without changing orientation and terminate at approximately equal levels in the lamina. Long visual fibers with endings in the medulla are not visible in the superposition eye lamina, but are present in the lateral apposition eye. The relationship between the behaviour of the animal, optic mechanisms of the superposition eye and the structure of the lamina is discussed.

**Key words:** Superposition eye – Lamina ganglionaris – *Cloeon dipterum* – Light- and electron microscopy.



## Introduction

It is a characteristic feature of the family Ephemeridae (May flies) that the eye of the male is bifunctional, containing two morphologically different parts. This sexual dimorphism is most striking in the species *Cloeon dipterum*, where

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the male has two separate types of compound eyes, a dorsal "turban-shaped" superposition eye covering the whole dorsal head region and a lateral apposition eye (Zimmer, 1897; Priesner, 1916; Hanström, 1928; Streble, 1960; Horridge, 1976; Wolburg-Buchholz, 1976). In contrast, the female possesses only the smaller, lateral apposition eye. The biological significance of the enlarged dorsal eyes of *Cloeon dipterum* is not clear, but they may be used to detect and capture a single female flying overhead in a swarm during the "mating dance" at dusk (Zimmer, 1897). Insects with enlarged dorsal eyes seem to be able to recognize small objects against the sky; to do this successfully, their eyes require a spectral sensitivity to match the background and also a narrow angular sensitivity (Horridge, 1976). Together with the separation of a superposition from an apposition part of the retina, a corresponding division of the optic neuropils also occurs, in the sense that there exists a divided lamina ganglionaris and medulla. The dorso-ventral parts of medullae project into what appears to be homogeneous lobula and lobulus neuropils.

The present account attempts to resolve the neuronal network of the lamina in the superposition eye of the male of *Cloeon dipterum*. Further, it is of particular interest to compare the laminal wiring of both eye types joined together in one individual and to find the neuronal substrate for different functional properties.

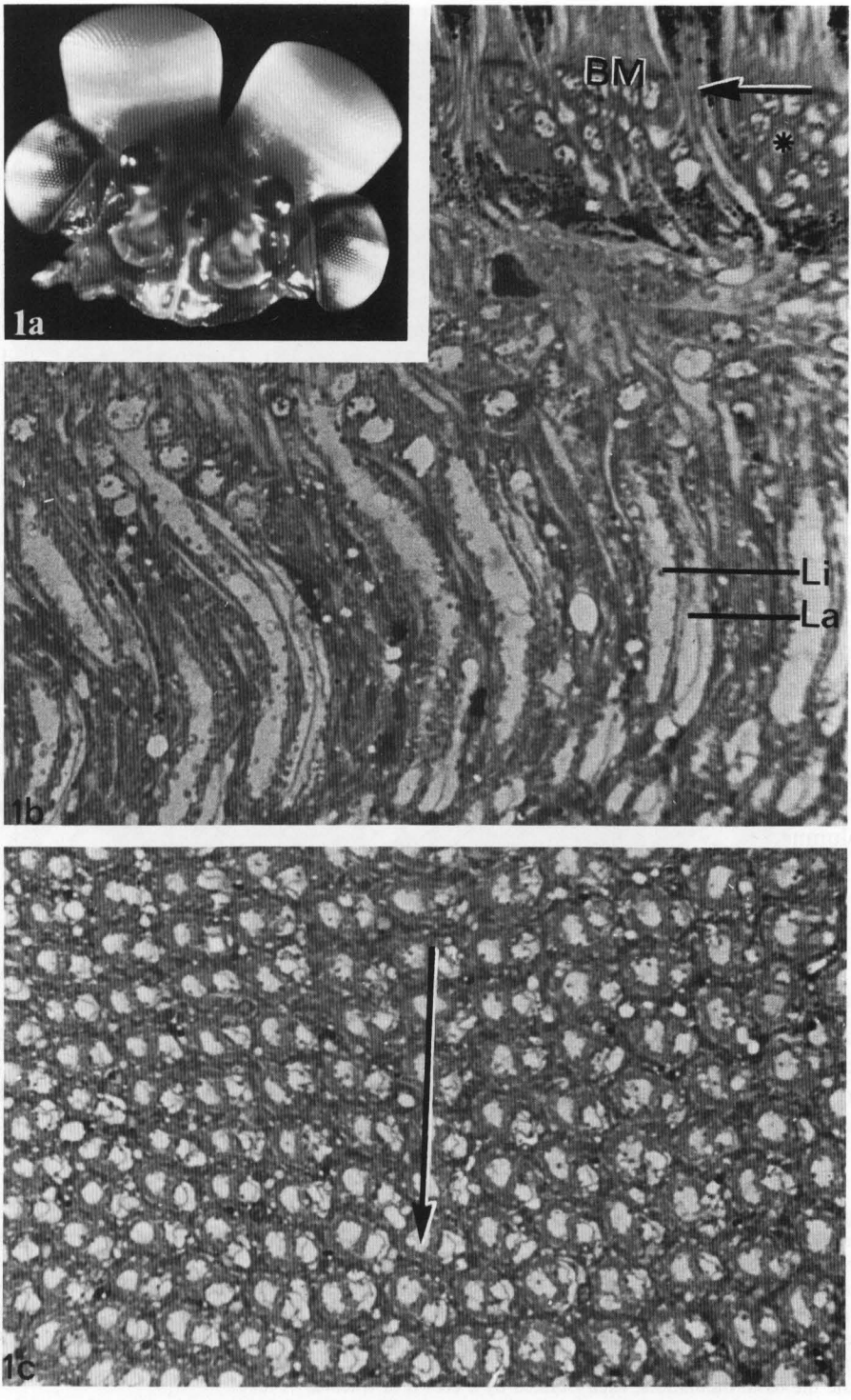
## Materials and Methods

Larvae of *C. dipterum* were collected from ponds in Schönbuch, near Tübingen and reared to adults in the laboratory. Investigations were carried out on the male imago, to a lesser extent on larvae and subimagos.

*a) Golgi Methods.* Most preparations were made using the Golgi-Cox procedure (according to Weiss, 1972a and Ramón-Moliner, 1970). Whole heads were impregnated and kept in several concentrations of staining solutions for about two months. For comparison, some specimens were stained with the Golgi-Colonnier method (Colonnier, 1964; see also Strausfeld, 1976). The silver impregnated, Durcupan-embedded heads (polymerization at about 60°C for 10 h) were cut horizontally or vertically 30–50 µm on a sliding microtome and mounted under coverslips with Permount. Relevant sections were reembedded in Durcupan and fully polymerized for electron microscopic investigations. These sections were stained with uranyl acetate and sometimes lead citrate also. Drawings from Golgi preparations were made on millimeter paper with reference to a calibrated eye-piece net graticule.

*b) Electron Microscopic Methods.* Dissected heads were fixed in Karnovsky's glutaraldehyde-formaldehyde, postfixed with $OsO_4$, dehydrated in ethanol and embedded in Durcupan ACM. Serial sections were prepared for light (1–2 µm) and electron microscopy on an LKB-ultratome. Ultrathin sections were stained with lead citrate and examined in a Philips EM 300 electron microscope.

**Fig. 1. a** Frontal aspect of the whole head of the male *Cloeon dipterum* with enlarged dorsal superposition eyes, lateral apposition eyes and three ocelli. ×50. **b** Horizontal section of the lamina (2 µm thick). Retinula cell fibers penetrate the basement membrane (*BM*) in bundles (→) and form an optic cartridge after leaving the fenestrated and monopolar cell body layer together with the monopolar cell axons (*Li*/*La*); cell body layer belonging to the optical tapetum (*). **c** Hexagonal arrangement of the neuroommatidia in the right eye (2 µm thick tangential section); → indicates the direction of z-axis. ×1050


1a
BM
*
Li
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## Results

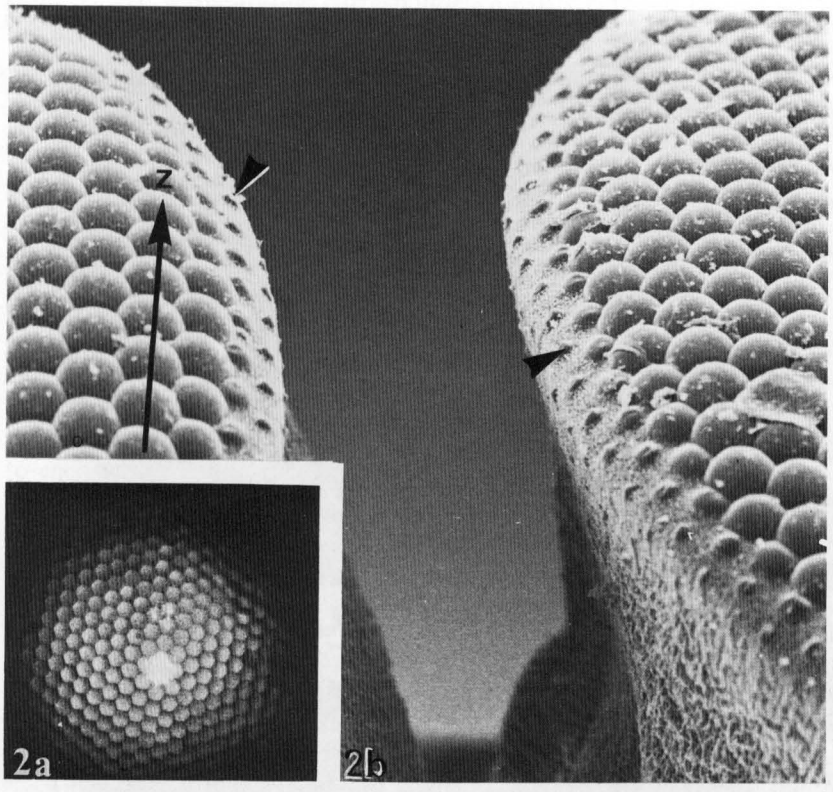
### *I. Retina*

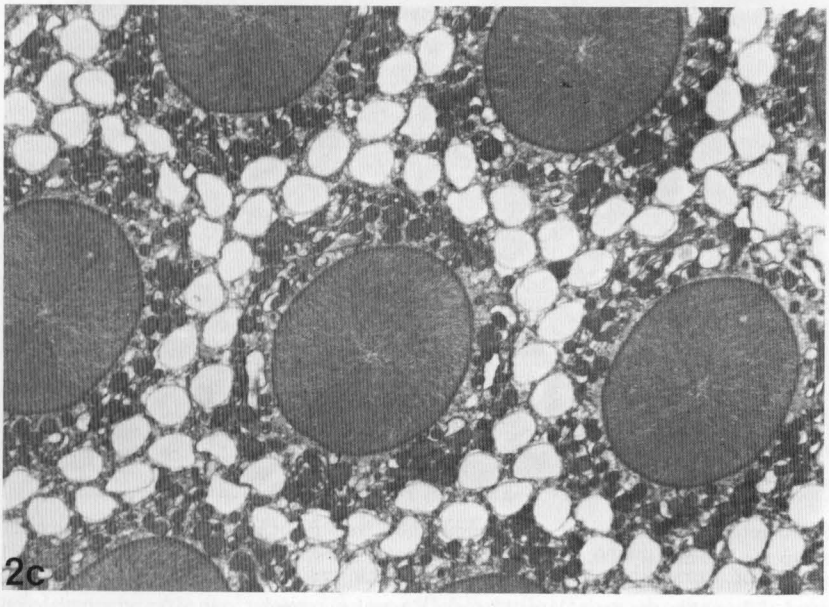
The male of *C. dipterum* has large, cylindrical, dorsal superposition eyes (1 mm wide and 6 mm high) occupying half of the whole head (Fig. 1a). During transformation from subimago to imago the superposition eyes increase in size, because hemolymph is secreted and separates the dioptric apparatus from the basal receptors (Zimmer, 1897; Wolburg-Buchholz, 1976). The eye remains smaller and spherical when the moulting process from subimago to imago is prevented. The epidermal eye cylinder is limited by a slightly curved elliptical surface consisting of about 500 cornea facets, arranged in a hexagonal array with one vertical (z) and two oblique (x/y) axes (Fig. 2b). The retina is composed of about 20 (z) and 35 (x/y) rows of facets. In the superposition eye of *C. dipterum* the chiasma twists dorsoventrally just as it twists fronto-posteriorly in the Musca eye (Braitenberg, 1967, 1970). For this reason, the vertical rows running parallel to the body axis were termed (z) and are homologous to the horizontal (z)-rows of the optical system of Musca. The morphology of the retina was described elsewhere by Horridge (1976) and Wolburg-Buchholz (1976); however, it is necessary to point out that the greater part of the ommatidia in the superposition eye retina has two rhabdomes at different levels: a small apical one, directly beneath the cristalline cone, and a large basal one, each formed by seven retinula cells. In the lateral ommatidia (of about 5 (z)-rows) the retinula cells extend to a dioptric apparatus with incompletely developed facets (Fig. 2b) or end proximally from the cornea in the lateral part of the eye. For this reason, the number of basal ommatidia exceeds the number of facets. Further, it can be assumed that all basal ommatidia seem to be functionally intact since each of them, even the lateral ones, project to corresponding lamina and medulla columns.

### *II. General View of the Lamina*

It is a well known fact that at different levels of the insect optic system a certain pattern is repeated almost identically; for example, the number of lamina units is equivalent to the number of receptor units. These lamina units have been termed neuroommatidia (Viallanes, 1891) or optic cartridges (Cajal, 1915; Trujillo-Cenóz and Melamed, 1963). In the lamina of May flies the array of cartridges reflects the arrangement as mentioned above for the retina mosaic

**Fig. 2. a** Eye glow in the superposition eye: Illumination of a single facet of the dark adapted eye causes a patch of facets (350 μm in diameter) to glow; the glow is due to a reflection of the incident light by the basal tracheal tapetum. (I would like to thank E. Buchner for his advice and assistance in the illumination experiments.) **b** Scanning electron micrograph showing the hexagonal arrangement of facets in the superposition eye (*arrow* indicates the horizontal *z*-axis). Note the incomplete facets (►) on the border of the eyes. (SEM, courtesy of B. Boschek); ×260. **c** Transmission electron micrograph. Cross section through the basal receptor layer of the retina. Note the basal ommatidia, each isolated by a crown of trachea. ×4800


z
2a
2b


2c

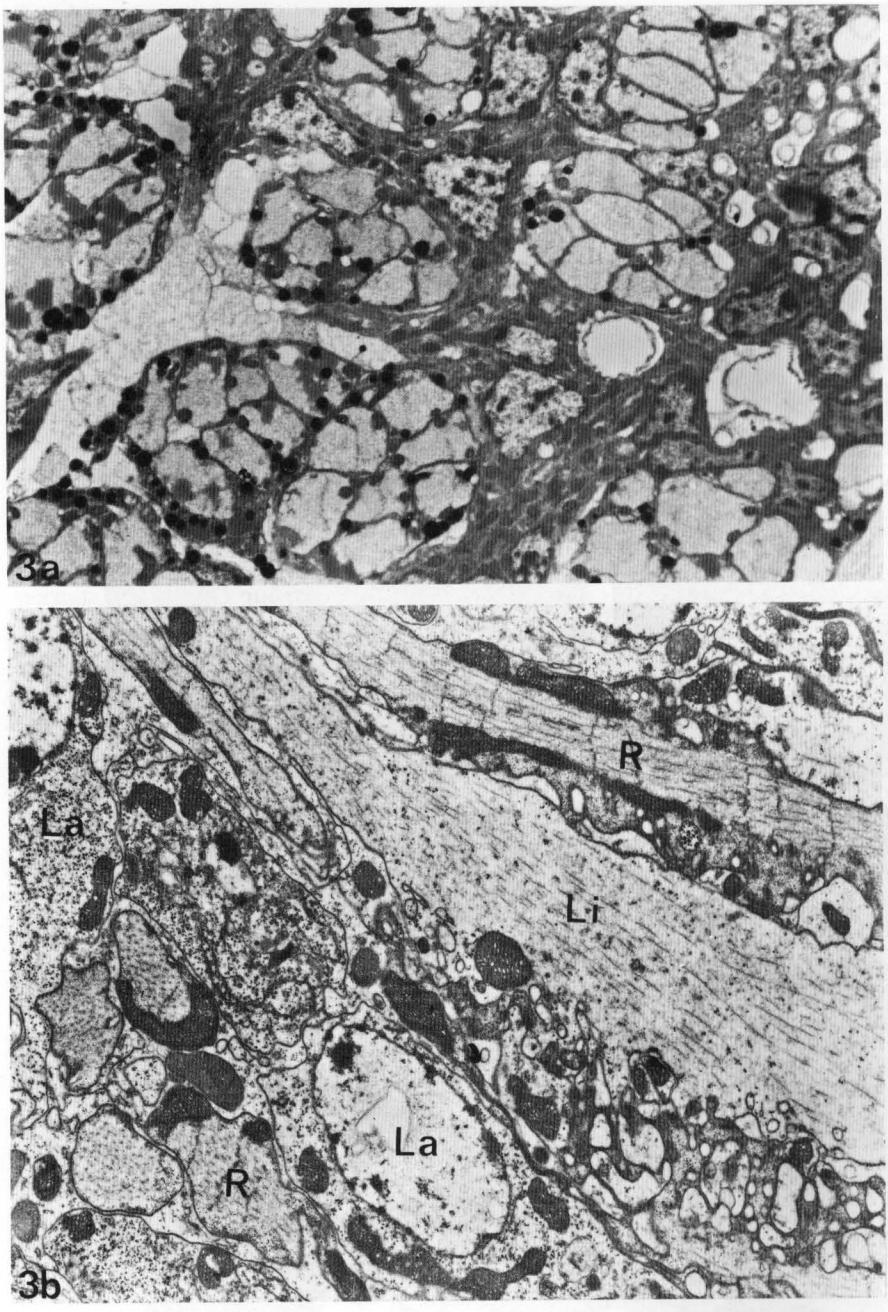



**Fig. 3. a** Seven retinula cell axons of each ommatidium run in bundles through the basement membrane into the lamina. ×4500. **b** Electron micrograph showing the distal part of the external plexiform layer, where retinula cell fibers (*R*) join together with monopolar cells. Note the regularly spaced smooth ER within the retinula cell axons. Central monopolar cell (*Li*); monopolar cell bodies (*La*). ×9600

(Figs. 1c, 7). A one-to-one correspondence exists between lamina columns and the basal retina receptors.

In the lamina three distinct layers from distal to proximal are recognizable (Fig. 5): a fenestrated layer (FL) (about 30 μm thick), a monopolar cell body layer (MCBL) (about 30 μm thick) and an external plexiform layer (EPL) (about 70 μm thick). The whole lamina, measured from the basement membrane up to the beginning of the outer chiasma, is about 130 μm thick.

The axons of seven retinula cells pass in bundles through the basement membrane (Fig. 3a), penetrate the fenestrated layer concurrently with neighbouring bundles and after entering the monopolar cell body layer terminate in the corresponding neuroommatidia (Figs. 1b, 3b). By means of combined series of semi-thin and ultra-thin sections of Golgi-stained material reembedded for electron microscopy, it was possible to trace the path of seven retinula cells from the basal receptor layer into the lamina columns. It was clear that neither the retinula cells nor their corresponding axons change their positions relative to each other during passage through the fenestrated layer into the plexiform layer.

The cell body layer consists of monopolar cell perikarya of different sizes. This is similar to what was found in the fly by Trujillo-Cenóz (1965a), who classified the monopolar cells into two morphological groups, type I and type II. More distally, larger cell bodies, 7.5 μm in diameter, are visible and directly beneath those of about 5 μm in diameter. In direct apposition to the monopolar cell body layer follows the external plexiform layer, where the receptor axons R1–R7 from their respective ommatidia join together with monopolar cell axons and other nerve profiles to form the optical cartridges (Figs. 1c, 7).

The lamina is interwoven with glial and tracheal cells. The cell bodies directly beneath the basal membrane belong to tracheae which form the basal retinal tapetum (Figs. 1b, 2c). From his morphological observations, Horridge (1976) concluded that this tapetum in *C. dipterum* does not function as a light reflector, isolating neighbouring rhabdomeres optically. That the basal tapetum must be regarded as optically significant, however, is evident from illumination experiments (Fig. 2a) using the method of Kunze (1972): Light projected onto a single facet of the dorsal eye leads to a bright "glow" covering more than 100 facets. This eye glow is the result of a diffuse reflection of the incident light by the basal tapetum. This experiment shows, according to the arguments used by Kunze, that the dorsal eye of *C. dipterum* behaves optically as a superposition eye in the classical sense of Exner (1891). During prolonged illumination the eye glow does not decrease. This is due to the fact that the screening pigment cannot spread across the clear zone with light adaptation because the accessory pigment cells do not cross the clear zone (Horridge, 1976 and personal observations).

### *III. The Elements of the Optic Cartridges*

*1. Retinula Cells.* The seven axons of each ommatidia can be recognized in Golgi preparations running in parallel bundles from the basement membrane into their respective cartridges, where they terminate at approximately equal

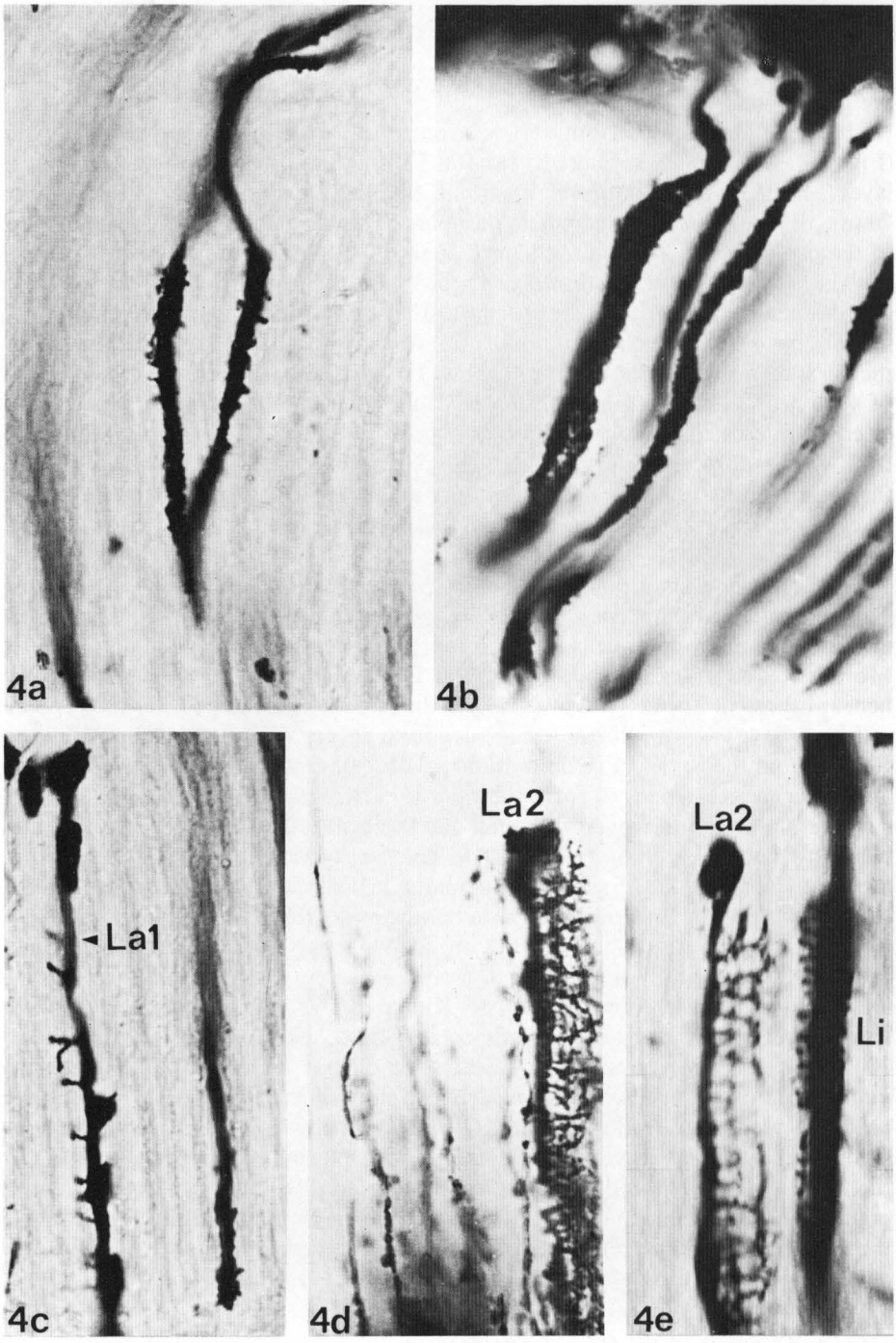



**Fig. 4a–e.** Golgi-Cox preparation of the lamina ganglionaris. **a, b** Retinula cell endings in the lamina with few short lateral spines. **c** Monopolar cell type (*La1*) with few spines only on one side of the main fiber. **d** Basket-like fiber profiles coming from the medulla and surrounding more than one cartridge. **d, e** Monopolar cell type (*La2*) unilaterally branched. In the right part of the figure **e** a central, radially branched monopolar cell (*Li*) of a neighbouring cartridge is visible. a–e $\times 1050$

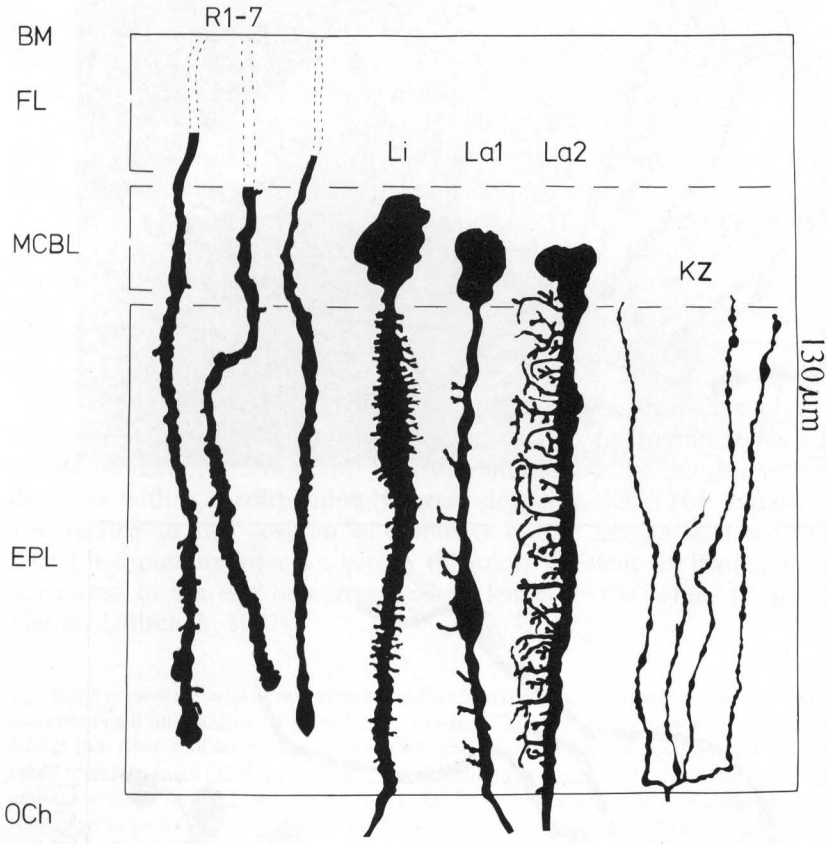



**Fig. 5.** Drawings of retinula cell axons and monopolar neurons of the superposition eye lamina. Basement membrane (*BM*); fenestrated layer (*Fl*); monopolar cell body layer (*MCBL*); external plexiform layer (*EPL*); outer chiasma (*OCh*); short visual fibers (*R1–7*); bilaterally branched monopolar cell (*Li*); unilaterally branched monopolar cells (*La1*/*La2*); basket-like fibers (*KZ*)

levels, vary in shape and show irregular swellings and a few short lateral spines (Figs. 4a, b, 5). Electron microscopy reveals that the retinula axons increase in diameter to 1–1.5 µm when entering the cartridge and change their fine structural appearance. The regularly scattered cisternae of smooth endoplasmic reticulum as well as microtubules decrease in number, while mitochondria, glycogen and synaptic vesicles appear in the axon termination (Fig. 3b).

Long visual fibers, found in other insect species with fused (Ribi, 1974; Ohly, 1975) and unfused (Campos-Ortega and Strausfeld, 1972; and for summary, Strausfeld, 1976) rhabdomes, are not visible. In contrast to these findings, it is certain that in the apposition eye of the male *C. dipterum* two of the eight retinula cells with thinner axons have synaptic endings in the medulla (Fig. 6).

*2. Monopolar Cells.* In Golgi preparations three distinct types of monopolar cells can be identified by means of their branching patterns (Fig. 5). The first

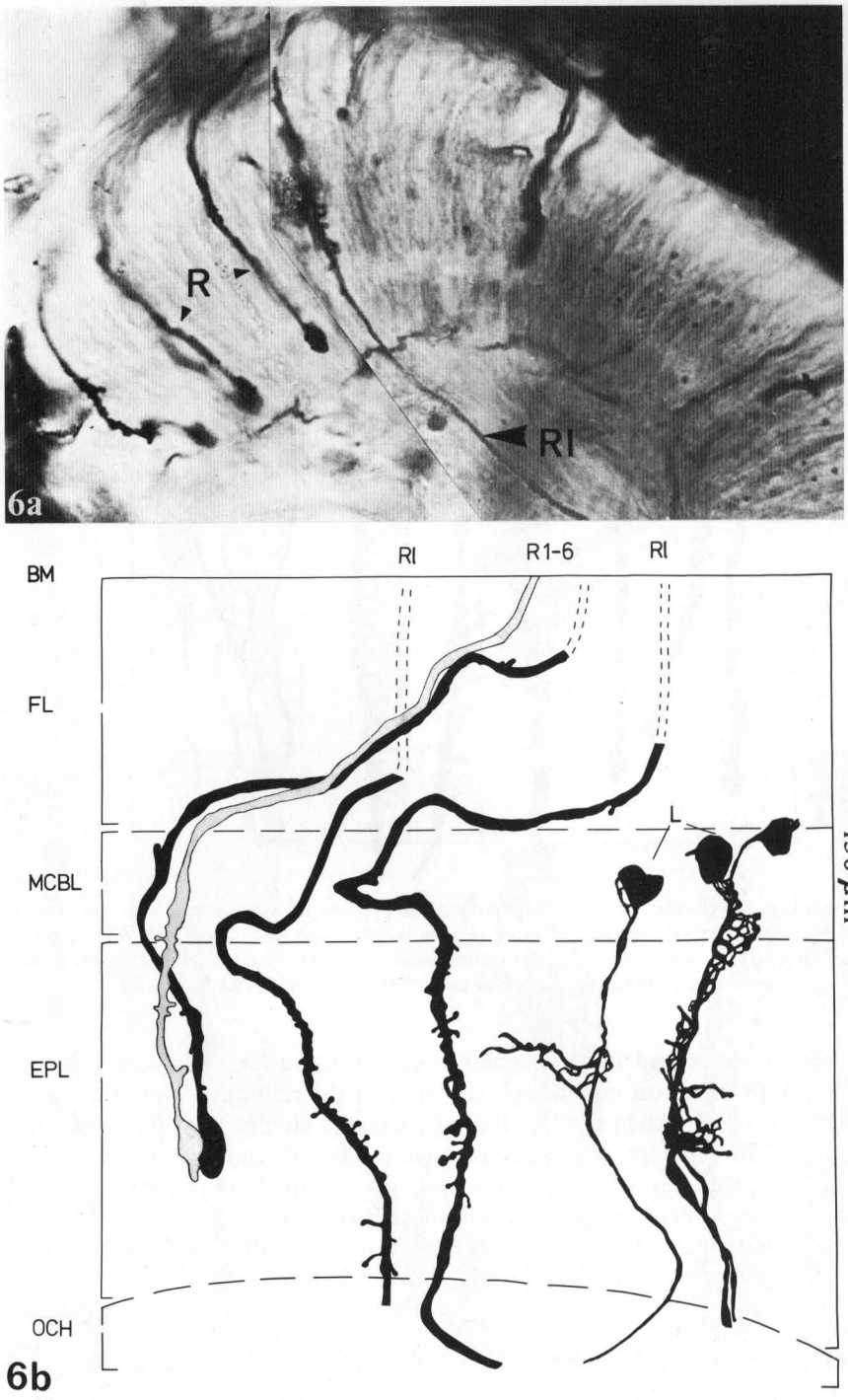



**Fig. 6.** Photograph **a** and drawing **b** of a Golgi-Cox impregnated lamina of the lateral apposition eye. Basement membrane (*BM*); fenestrated layer (*Fl*); monopolar cell body layer (*MCBL*); external plexiform layer (*EPL*); outer chiasma (*OCh*); short visual fibers (*Rl–6*) with endings in the lamina; long visual fibers (*Rl*) with endings in the medulla; different types of monopolar cells (*L*). ×750

type of monopolar cell, termed here Li, has a thick main fiber (approximately 7.5 μm) with short branches throughout the cartridge (Figs. 4e, 5). Studies of serial sectioned, Golgi-EM-embedded material show clearly that the processes of Li extend into the spaces between retinula axons in more than two directions (Fig. 10). The lamina portion of the Li cell types are connected with the larger, more distally situated cell bodies as mentioned above.

The two remaining second order neurons (La1/La2) belong to the smaller perikarya in the cell body layer. La1 possesses a thin main fiber (5 μm in diameter) with large swellings and is branched unilaterally (Figs. 4c, 5). The third cell type, La2 (5 μm in diameter), also has an unilateral arrangement of dendritic processes, but compared to La1, these processes are more numerous, larger in size and much more branched (Figs. 4d, e, 5).

In general, each monopolar cell type varies in size, depending on their localization in the lamina. Centrally, where the neuroommatidia correspond to the ommatidia having two sets of rhabdomes, the neurons have a larger diameter with a correspondingly larger dendritic field. The variation of fiber size related to the position of elements of the lamina is a striking feature seen for dipterous insects where a thickness gradient of lamina neurons was correlated to the size of corresponding lenses in the retina (Braitenberg and Hauser-Holschuh, 1972).

In the present material it was extremely difficult to recognize other cell types identified as medulla-to-lamina cells and lamina tangential cells. In some Golgi-Cox preparations it was possible to find basket-like fiber profiles in the lamina surrounding one or more cartridges (Figs. 4d, 5). These could represent small field elements belonging to cell bodies near the medulla sending their brush-like endings to the lamina. These fiber elements may be comparable to the $\alpha$–$\beta$ neuron system described for dipterous insects by Trujillo-Cenóz (1965a), Campos-Ortega and Strausfeld (1973) and Burkhardt and Braitenberg (1976).

## IV. Arrangements of the Cartridge Elements

Seven retinula cell axons form a crown around one central second order fiber Li; two more second order fibers La1/La2 run close to each other outside the bundle of retinula fibers R1–R7, always in a position near R1 (Figs. 7, 8a, 9). Each cartridge is embedded in a stroma of glial and tracheal cells (Figs. 7, 8b). In the more proximal part of the lamina the central monopolar fiber Li is no longer separated from the other two fibers La1/La2 by the retinula cell terminal R1 (Fig. 7). The three monopolar cell fibers run together into the inner chiasma.

The retinula cell axons have been numbered in the following way: the retinula axon separating Li from La1/La2 is termed R1; numbering of the other fibers occurs clockwise in the right and counterclockwise in the left superposition eye (Fig. 9). The arrangement is mirror-symmetrical between the right and left eye, but there is no plane of mirror symmetry dividing each eye and the ganglia into an upper and lower half, as has been shown in flies (Braitenberg and Hauser-Holschuh, 1972).

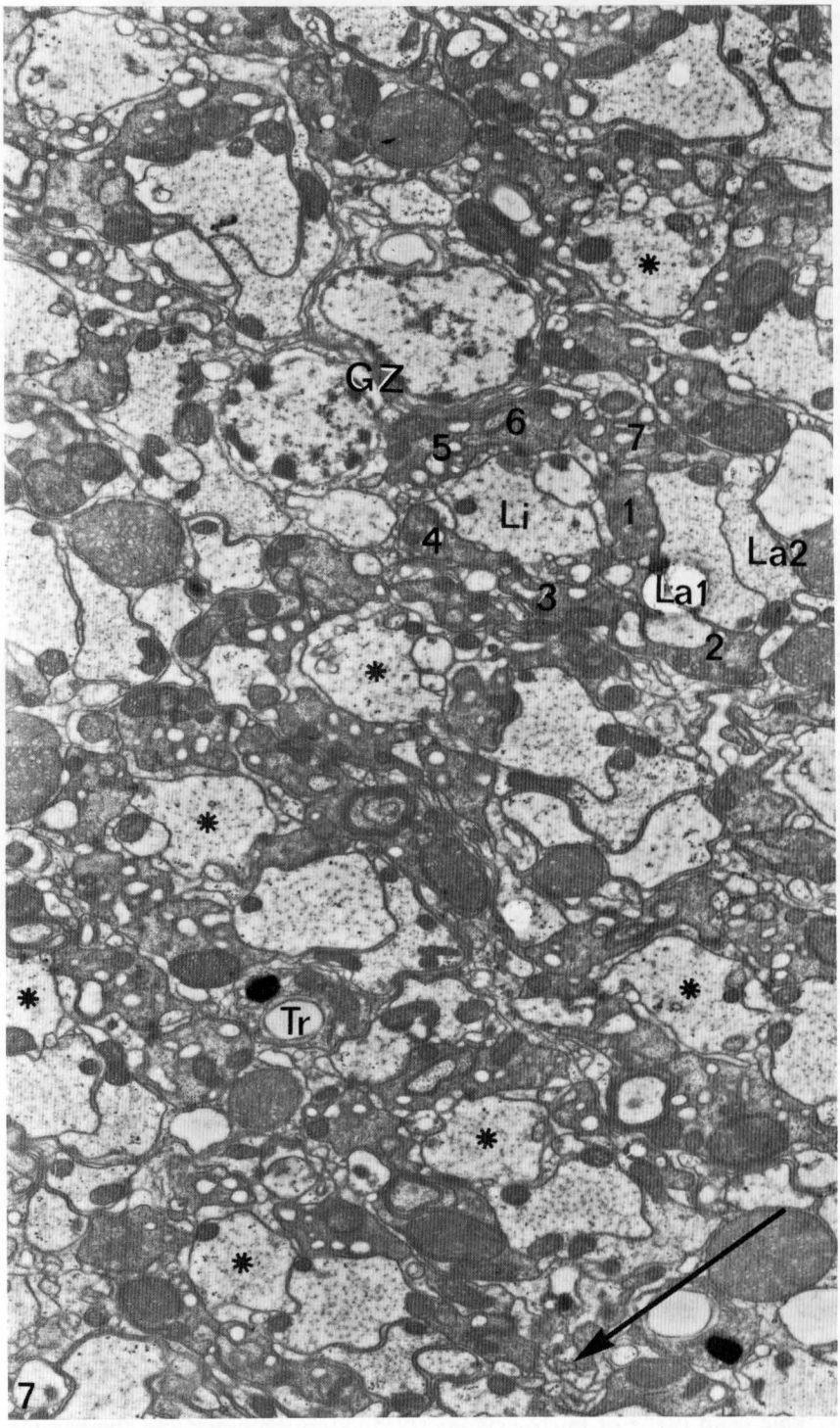



**Fig. 7.** Montage of two electron micrographs showing two rows of cartridges (*). The cartridges were sectioned more proximally near the inner chiasma, where the three monopolar cell types come together. *Arrow* indicates the direction of *z*-axis. Monopolar cells (*Li/La1/La2*); retinula cell axons (*1–7*); glial (*GZ*) and tracheal cells (*Tr*). ×12,000

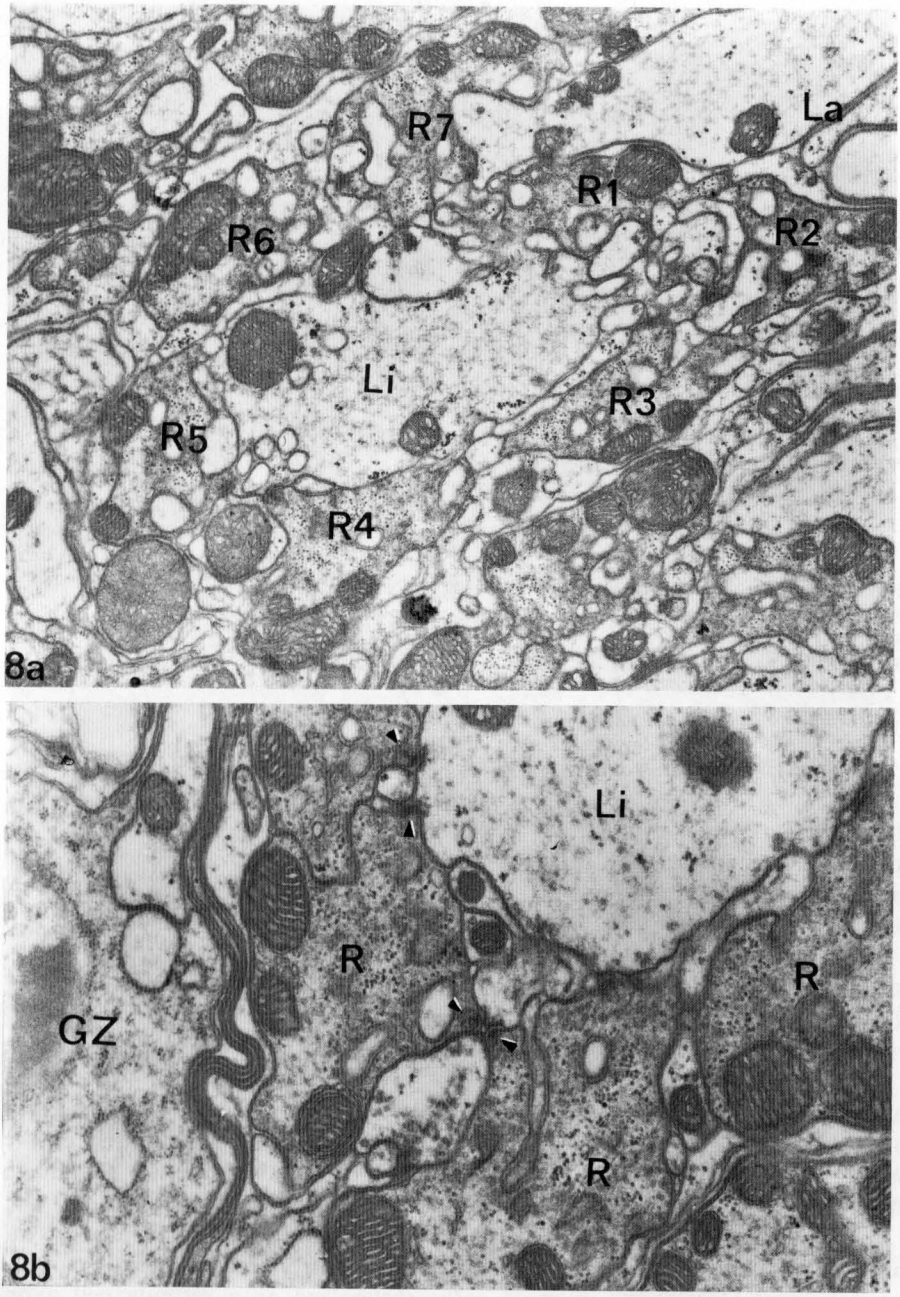



**Fig. 8. a** Electron micrograph showing a cross section of one cartridge. The central monopolar cell (*Li*) is surrounded by seven retinula cell axons (*R1–7*). Monopolar cell (*La*) sends branches in the direction of Li. ×17,000. **b** Retinula fibers (*R*) filled with large mitochondria and synaptic vesicles. Two neighbouring R-cells are presynaptic to the same spine of a monopolar cell (►). Monopolar cell (*Li*); glial cell (*GZ*). ×28,400

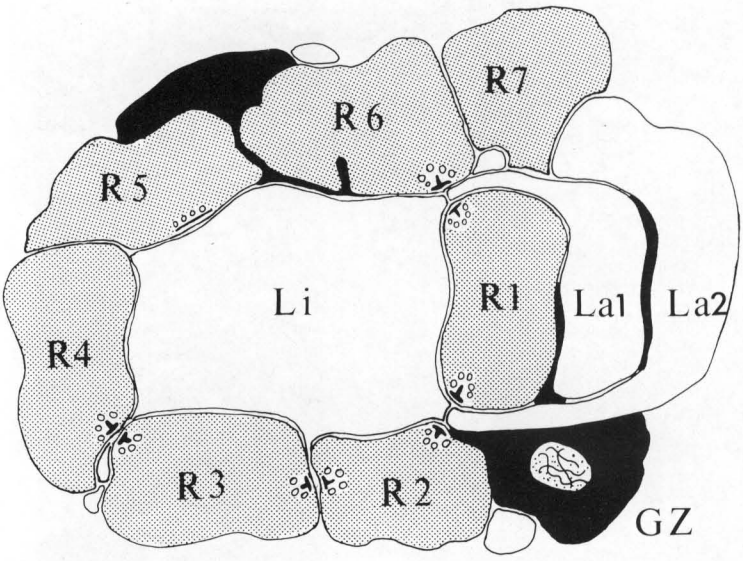



**Fig. 9.** Diagram showing the organization of a cartridge in the right eye. Synaptic contacts are possible between two monopolar cell fibers (postsynaptic) and one retinula fiber (presynaptic), sometimes glial profiles are involved; retinula cell fibers (*R1–7*); monopolar cells (*Li/La1/La2*); glial cell (*GZ*)

*V. Synaptic Organization*

Numerous descriptions of synaptic junctions in insect neuropils have been reported (summarized by Strausfeld, 1976). In this study only those synaptic contacts where ribbon-like structures could clearly be seen were identified as such.

In the lamina of the superposition eye of *C. dipterum*, synaptic contacts are observed between the monopolar cell dendrites of Li and all surrounding retinula cell axons R1 to R7. In most cases two neighbouring R-fiber terminals, perhaps R1 and R6 (Figs. 8a, 9), are presynaptic to one and the same spine of the central monopolar cell Li. The other two identified monopolar cells La1/La2 lying outside the retinula cell crown send their dendrites to the neighbouring R-cell axons R1/R2 and R6/R7 as well to the opposite part of the cartridge to fibers R3, R4 and R5. Identification of this projection was made with facility in thin serial sections of Golgi-stained material (Fig. 10).

All synaptic contacts, described for this lamina, are so-called divergent synapses, i.e. a single fiber is presynaptic to more than one postsynaptic element. The presynaptic elements, in most cases recognized as a retinula cell axon terminal, are characterized by a bar-shaped synaptic ribbon (Fig. 11). Some synaptic vesicles appear aligned along the bar density. Figures 11b and d show a T-shaped presynaptic density of an R-axon termination as it appears when the plane of the section is normal to the long axis of the bar-shaped ribbon. The organization of the presynaptic area, shown here, differs from that of the three-

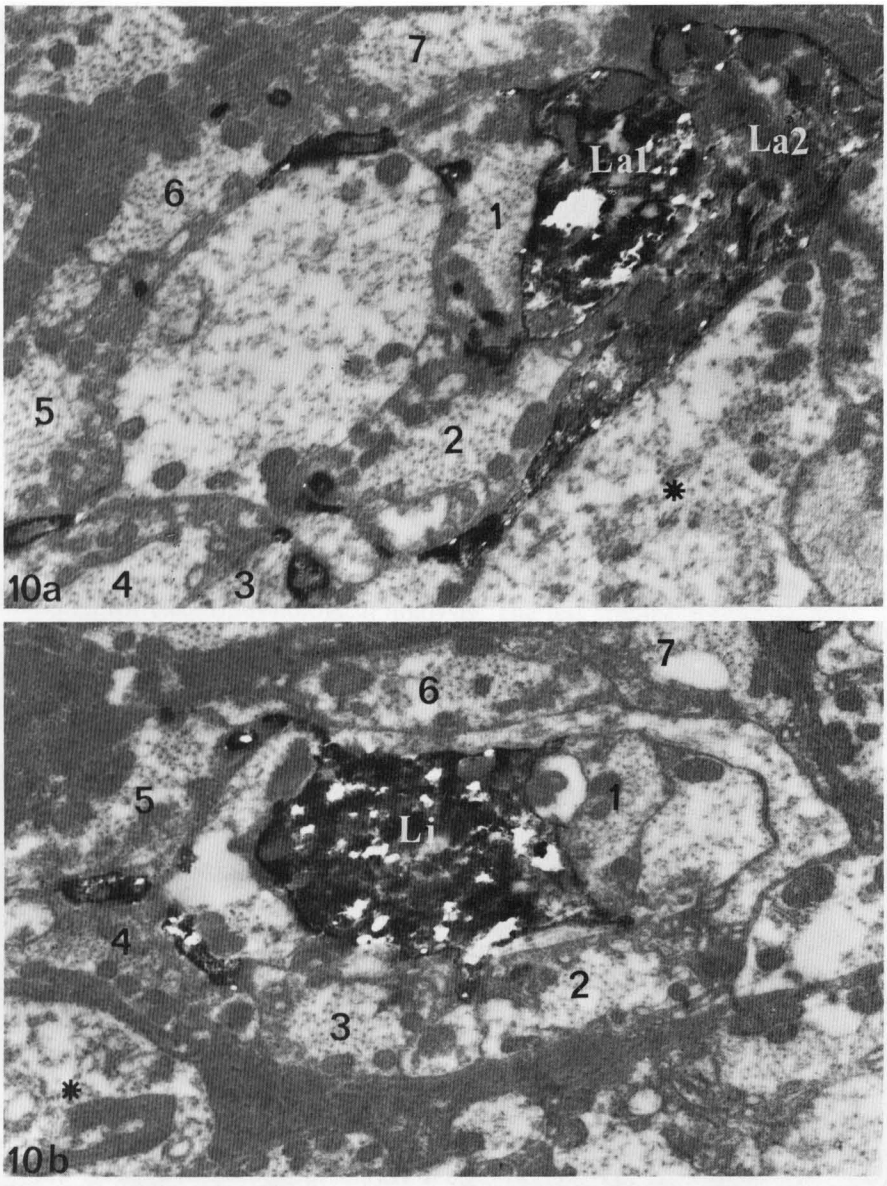



**Fig. 10a and b.** Electron micrograph of Golgi-Cox impregnated material; cross section through the lamina near the monopolar cell body layer. Figure **a** shows the branching pattern of the two outside running monopolar cells (*La1*/*La2*) and **b** a radial branched monopolar cell (*Li*); retinula cell terminals (*1–7*); perikarya of monopolar cells (*). ×12,900

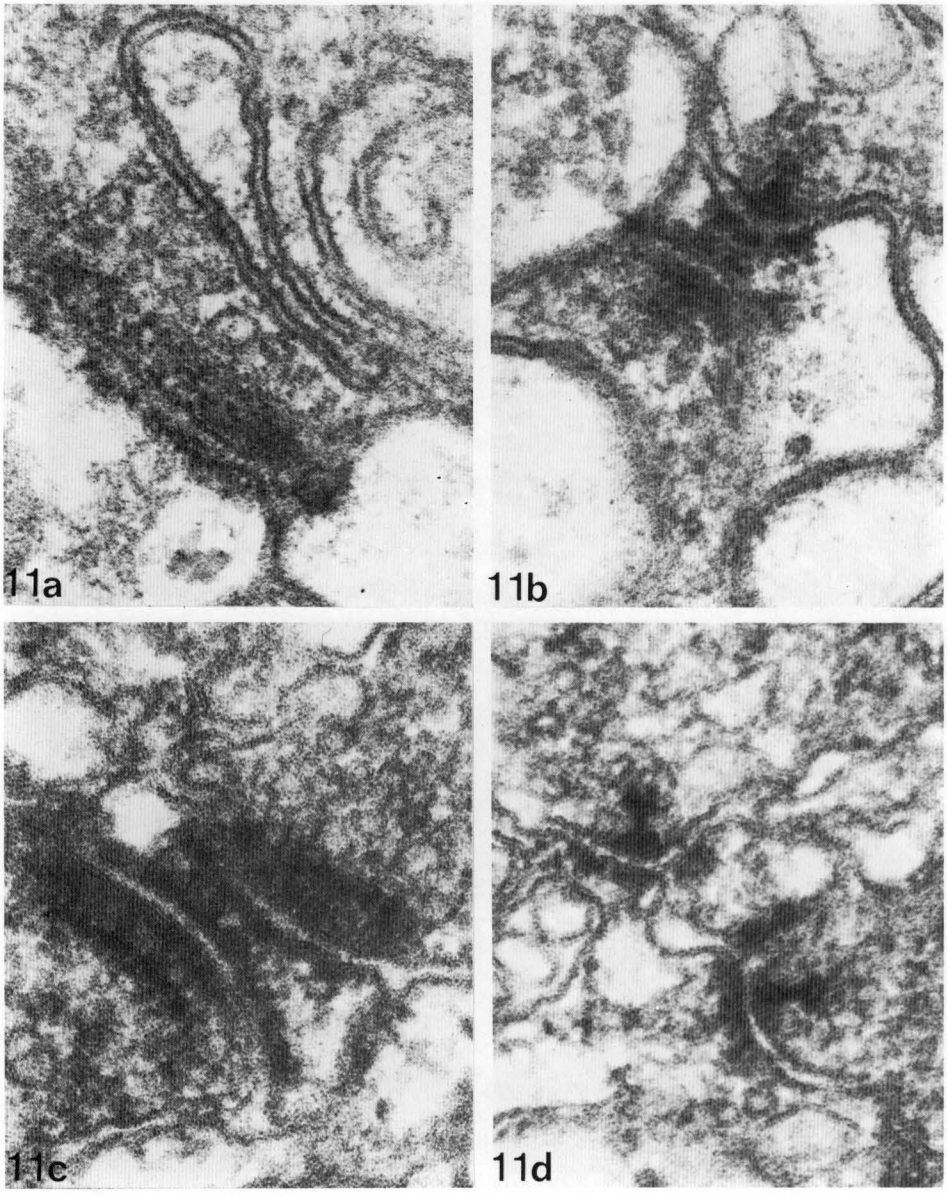



**Fig. 11a–d.** Synapses between R-fibers and monopolar cells as they appear in section planes perpendicular to each other; (a, c) parallel to the long axis of the bar-shaped ribbon; (b, d) normal to the long axis of the bar-shaped ribbon. In Figure **a** few synaptic vesicles appear aligned along the bar density; **b, c** show two opposite R-fibers with presynaptic specialization to one and the same monopolar cell spine. In contrast, in **d** two opposite R-fibers are presynaptic to two different monopolar cell spines. (c, d) Fixation with $OsO_4$ alone. $\times 120{,}000$

dimensional model, presented for the so-called R-L-synapse of *Musca domestica* (Burkhardt and Braitenberg, 1976), and resembles more closely the presynaptic specialization of synapses in the neuropil of *Formica lugubris* (Lamparter et al., 1969) or synaptic structures in the retinula cell endings in the compound eye of the crayfish (Hafner, 1974). Postsynaptic elements are spine-like processes of the different monopolar cells Li or La1/La2 (Figs. 8b, 9, 11d). The postsynaptic site of the contact shows an electron dense fuzzy material. The participation of glia at the postsynaptic site seems to be quite common (cf. Burkhardt and Braitenberg, 1976). Cell contact specialization between glial processes and $\beta$-fibers, called "gnarls", and glial invaginations of R-fibers, so-called "capitate projections" (cf. Hauser-Holschuh, 1975; Burkhardt and Braitenberg, 1976) are not visible in the cartridges of *C. dipterum*.

## Discussion

Since the early anatomical work on compound eyes, especially on optic ganglia, some insect species have been preferred, such as flies, bees and locusts. Bees and flies were chosen because of their interesting behaviour, while locusts were favoured for electrophysiological analysis. The less studied species of May flies are of interest because they belong to a primitive insect group, with a distinct sexual dimorphism, obvious from the enlarged turban-shaped superposition eye of the male and from the different behaviour between the sexes.

The organization of the different lamina neurons and incoming retinula terminals within a cartridge is variable. The cartridge may be quite separated as seen in flies, *Pieris* and now in *C. dipterum* or indistinct, as in locusts, bees and some species of water-bugs. The distribution of the retinula axon terminals from one ommatidium among the cartridges of the lamina is of two types: either each terminal is distributed to different cartridges as in flies (Braitenberg, 1967; Kirschfeld, 1967) and water-bugs (Meinertzhagen, 1971, and personal observations on *Gerris*), or the terminals end in a single cartridge, as in all fused rhabdome eyes so far examined, including the May flies.

It was shown in the cartridges of this lamina that three types of monopolar cells Li and La1/La2 make synpatic contacts with seven retinula cells, but it is not clear whether La1/La2, in spite of their external localization, receive the same input as the central fiber Li. Another point is that Li, with its radial arrangement of spines, probably has the same function as L1/L2 together in the cartridge of dipterous insects (Boschek, 1971).

Monopolar neurons have been reclassified by Strausfeld and Blest (1970) into small (those with dendrites belonging to one and the same cartridge) and large neurons (those with overlapping fields of lateral dendrites connecting more than one cartridge). The latter is seen in L4 neurons of the fly lamina (Strausfeld and Braitenberg, 1970; Strausfeld and Campos-Ortega, 1973; Braitenberg and Debbage, 1974) or the L4-type of the bee lamina (Ribi, 1974), where axon collaterals may pass to adjacent cartridges. In the lamina of the May fly superposition eye, it was not possible to obtain an indication of intercations between cartridges formed by dendrites or collaterals of monopolar cells.

This is surprising because Strausfeld and Blest (1970) have shown that the wide field dendrites of monopolar cells are common features for example of nocturnal lepidoptera and especially of insects with superposition eyes. In contrast, they are relatively rare for apposition eyes. But it seems improbable that the basket-like fibers in May flies play a role in wide field lateral interaction.

The structure of the superposition eye lamina of the male *C. dipterum* is in many features similar to other investigated insects with fused or unfused rhabdomere-eyes. The primary conclusion of the present account is that in *C. dipterum* one cartridge of the superposition eye lamina receives seven inputs from the same retinula and gives off at least three large monopolar cell axons, but there exists no long visual fiber running through the lamina to the medulla. In contrast to other insect laminae, the second synaptic neuropil of the superposition eye of *C. dipterum* receives no information directly from the first order neurons. In other insects so far investigated, most of the retinula cell axons from one ommatidium terminate in the lamina, but usually one pair passes as so-called long visual fibers directly to the medulla. These originate either from central retinula cells in the open-rhabdomere eye or from the smaller one in the fused-rhabdomere apposition eye type (see Meinertzhagen, 1971). In the fused-rhabdomere apposition eyes of the bee the colour types of receptors correspond to classes of terminals as follows: the UV or polarized-light sensitive receptors are retinula cells belonging to long visual fibers, while green and blue receptors have their retinula cell terminals at different levels in the lamina (Ribi, 1975; Menzel and Snyder, 1974). The fact that in the lamina of Musca the axons of the retinula cells R7 and R8 bypass the complex system of optical cartridges and go directly to the medulla agrees with the two-system hypothesis of Kirschfeld and Franceschini (1968). According to this concept, in the fly compound eye there are two physiologically distinct populations of receptor cells, which are also definable by their morphological projections. Thus, when two types of retinula cells are present in insect compound eyes, they could be divided by physiological means in a scotopic (for Musca R1–R6) and a photopic (for Musca R7/R8) system. In the superposition eye of the male *C. dipterum* only one system, i.e. the scotopic one, is present. On the other hand, the lateral apposition eye of the males and females possesses both receptor systems.

In order to understand why the female *C. dipterum* requires superposition and apposition eyes, it was necessary for comparative purposes to investigate the lamina of the apposition eye. However, it was difficult to interpret from the electron microscopical material if this lamina is composed of separate cartridges and, furthermore, to identify their single cartridge elements, because fiber profiles are extremely small. So far, it is clear, especially from Golgi studies (see Fig. 6) that eight retinula cells from each ommatidium pass the basement membrane with six short retinula cells ending in the lamina plexiform layer and two retinula cells terminating in the medulla.

Some evidence exists that the male requires its superposition eye only in dim light with lower sensitivities to find the flight swarm of females. As a morphological correlate in the lamina, only the scotopic system analogue to R1–R6 of Musca is represented. Further, there is some question as to the optical function of the dorsal eye of *C. dipterum*. Horridge (1976) concluded that it is not an optical superposition eye according to Exner, but acts in a different way by means of light guides, connecting the proximal tips of the crystalline cones

with the basal rhabdomes. Two observations, however, clearly favour a function similar to the concept of Exner: 1. the eye glow (Fig. 2a) and 2. the fact that the number of basal rhabdomes within the retina is significantly higher than the number of cornea facets (Wolburg-Buchholz, 1976). Both facts can be explained by the theory of Exner; the second finding, in particular, is incompatible with a light guide hypothesis. Nevertheless, the functional significance of the distal rhabdom in the *Cloeon* eye is not yet clear.

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