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# The fine structure of the ocelli of *Triatoma infestans* (Hemiptera: Reduviidae)

T. C. Insausti, C. R. Lazzari

**Abstract.** The morphology and fine structure of the ocelli of *Triatoma infestans* have been analyzed by means of light and electron microscopy. The two dorsal ocelli of this species are located behind the compound eyes, looking dorsally and frontally. Externally, the ocelli are marked by the corneal lenses virtually spherical in form and limited internally by a cuticular apodeme. The lens focuses the incoming rays beyond the retina. A single layer of corneagen cells lies below the cuticular lens. The corneagen cells and photoreceptors are arranged in a cup-like fashion beneath the cuticular lens. A distal retinal zone comprises the rhabdoms, which are laterally connected in an hexagonal meshwork. A middle retinal zone comprises the receptor cell segment free of rhabdom, and a proximal zone their axons. In the middle zone, the oviform nuclei and spheroids are located. Screening pigment granules are present within the retinal cell. Spherical mitochondria are homogeneously distributed in the cytoplasm of the cell body. In the axonal zone, mitochondria are found in the peripheral region. Axons from receptor cells extend into the ocellar neuropile at the base of the ocelli, to synapse with second order neurons. The large axons of second order neurons are bundled by glial cells. The ocellar plexus exhibits a high diversity of synaptic unions (i.e. axo-dendritic, axo-axonic, dendro-axonic, and dendro-dendritic).


**Keywords:** vision, ocelli, ultrastructure, triatominae, *Triatoma infestans*, insect

## Introduction

Dorsal ocelli offer an attractive preparation for students of insect visual physiology, providing a readily accessible layer of receptor cells innervated by a small number of interneurons, which include some of the largest neurons within the brain. The function of these photoreceptors remains elusive in most cases. Different functional roles have been ascribed to these organs, e.g. modulation of the muscular tonus to the flight system, flight equilibrium control (Stange & Howard, 1979; Wilson, 1978; Stange, 1981; Rowell & Pearson, 1983), orientation in walking flies (Wehrhahn, 1984) and ants (Fent & Wehner, 1985) and, possibly, the dorsal light response used during flight (Kalmus, 1945; Goodman, 1965). Several hypotheses ascribe them a role in flight control and as modulating the compound eyes sensitivity. A possible function of the ocelli in the stabilization of flight at dusk has been suggested in locusts (Wilson, 1978) and dragonflies (Stange & Howard, 1979; Stange, 1981; Taylor, 1981a,b), a hypothesis that has not been tested in triatominae bugs. Among nocturnal insects, the ocellar system has been extensively examined in its anatomy and physiology in the cockroach (Mizunami et al., 1982; Mizunami, 1995; Mizunami & Tateda, 1986, 1988a,b; Ohyama & Toh, 1990a,b; Toh & Hara, 1984; Toh & Sagara, 1984).

*Triatoma infestans*, the main vector of Chagas disease in southern South America, is a nocturnal insect that posses two

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well developed ocelli. They spend daylight hours assembled in dark refuges and its activity pattern splits in two discrete temporal windows, one at dusk and another at dawn (Lazzari, 1992). Therefore, their visual system must be able to operate in a broad range of light intensities. Although the ability of *T. infestans* to sustain quite long dispersive flights has been described (Lehane & Schofield, 1978; Schofield et al., 1992), the aerial medium is not the most important in the life of this species, as does in other insects such as flies or bees. Triatominae are mainly walking insects that ensue dispersing flights under certain particular conditions (e.g. starvation). Recently, it has been demonstrated for the first time in an insect, that the ocelli of *T. infestans* are able to mediate by they own the negative phototactic behavior of these bugs, i.e. not through the modulation of the sensitivity of the compound eyes (Lazzari et al., 1998).

For those reasons aforementioned, haematophagous reduviids are particularly convenient for studies of the ocellar system. They possess two well-developed and spatially separated ocelli; each innervated by 10 large first-order interneurons, ranging from 8 μm to more than 25 μm in diameter. The central projections of these fibers have been described in considerable detail (Insausti & Lazzari, 1996). Furthermore, there are few ultrastructural data of the ocellus of *Rhodnius prolixus* (Goodman, 1981) and, so far as we know, there are no data about the neural organization of the synaptic plexus in Heteroptera insects.

In the present study, the dorsal ocelli of *T. infestans* were observed by light, scanning and transmission electron microscopy. This paper should enrich the information about the ocellar system of insects, especially Heteroptera, with fine structural investigations and some functional implications.

## Materials and methods

Males of *T. infestans* were used throughout in this work. The bugs were reared in the laboratory at 30 °C, 70% relative humidity and fed on citrated cow blood using an artificial feeder (Nuñez & Lazzari, 1990).

### Transmission electron and light microscopy

Small head pieces containing the ocelli were processed following the technique described by Ribi (1987) for insect preparations. Briefly, pieces were fixed in buffered solution of 2.5% glutaraldehyde and 2.0% paraformaldehyde with sucrose and $CaCl_2$ added (pH 7.3) for 2–3 h, and post fixed in 1% $OsO_4$ for 1–2 h. After dehydration in an ethanol series, the pieces were embedded via propylene oxide into hard Araldite or Durcupan. For electron microscopy, ultrathin sections were taken with an ultramicrotome using a diamond knife. The sections were doubly stained by uranyl acetate and lead citrate and observed with a Zeiss EM 109 T electron microscope.

For light microscopic examinations, semithin sections were taken with the same ultramicrotome using a glass knife and stained with methylene blue 1% or toluidine blue. Serial cross-sections were taken from the whole length of the ocelli for observing the branches of the distal processes of the second-order neurons.

### Scanning electron microscopy

Two different microscopes were used for observations. Some preparations were fixed as for TEM, dehydrated in acetone, critical-point dried over $CO_2$, coated with gold and observed in a Phillips SEM. Some whole insects killed and conserved into 70% ethanol with any further preparation. A few hours later, they were observed in an environmental scanning electron microscope (ESEM).

### The measure of the ocellar focal plane

The principal focal plane of the corneal lens was established by means of the method described by Wilson (1978). Briefly, the ocellar cornea was excised and cellular material carefully removed and floated in Ringer solution on a microscope slide with its inside surface down. With the aid of an inverted microscope, the position of the plane where parallel rays were focused by the cornea was determined, relative to the inner surface of the cornea.

## Results

### General morphology

The two dorsal ocelli of *T. infestans* are marked externally by two shining brown hemispheric lenses (about 370 μm in diameter), easily distinguishable from the dark brown head capsule. They are located behind the compound eyes, looking dorsolaterally and frontally (Fig. 1). The distance between the ocelli reaches about 815 μm.

The corneal lens is thick and, considering only the center is biconvex and approximately spherical in shape (about 455 μm in depth) being asymmetrical on the inner lateral surface (Figs 2–4). It could be established that the principal focal plane of the ocellar cornea lies at a distance of $114 \pm 18$ μm ($n = 8$) beyond the inner surface of the lens.

A one-layered epithelium of corneagenous cells (about 2.4 μm thick) with large oviform nuclei lies beneath the cuticular lens. The cytoplasm of the cells, and sometimes also the nucleus, can extend processes between two retinal cells, making a broad contact with them (Fig. 5, arrow). Corneagenous cells are laterally join together by septate desmosomes (Fig. 6, arrow). In young adults, the apical membrane of these cells presents processes like microvilli that relate them with the still developing cornea (Fig. 7, arrow).

At the outer rim of the lens, there is a layer of irregular pigmentary cells. In mature animals, the latter encircle the lens like a thin ring (Fig. 8). In young images, the ring appears as a kind of broad 'iris' that give rise to a narrow elongated false 'pupil' that gradually expands for a period of about 3 weeks (Insausti & Lazzari, 2000a,b). During this time, the apparent iris is formed by pigmentary cells that lie beneath the corneagenous cells (Fig. 9).

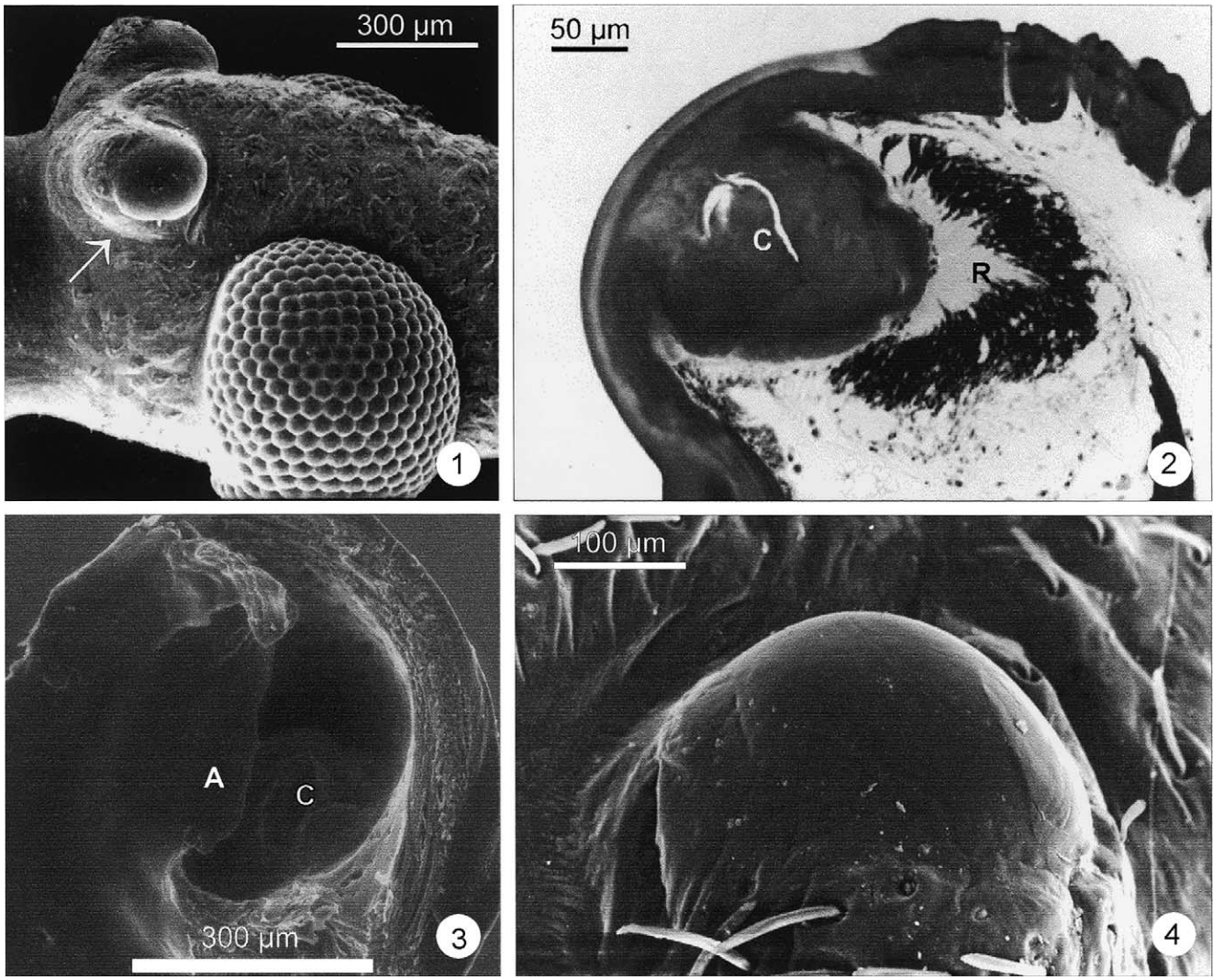


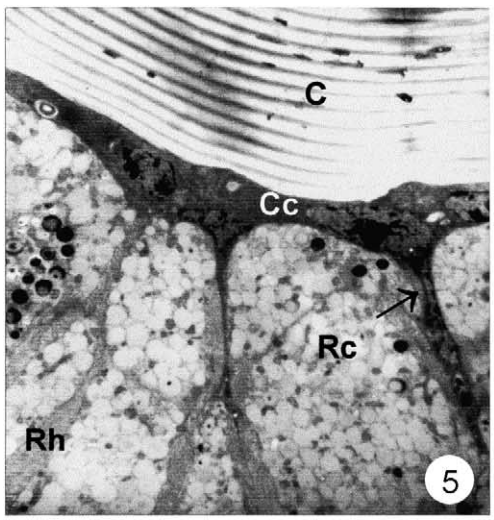

**Fig. 1** Scanning electron micrograph of the head of *T. infestans* in lateral view. The paired ocelli (arrow) are placed behind the compound eyes, looking dorsolaterally. **Fig. 2** Longitudinal section through the dark adapted ocellus. The rhabdomeric zone is shown as a clear zone just below the corneal lens. Note the pigment granules that concentrate in the middle zone of the cells. C, corneal lens; R, retina. **Fig. 3** Scanning electron micrograph of the inner surface of the ocellar cuticular portion. A, apodeme; C, corneal lens. **Fig. 4** Scanning electron micrograph of the ocellar lens.

The corneal epithelium is followed proximally by the retinal cells, which comprise the main mass of the ocellus (Figs 5 & 6). The corneagenous cells and receptor cells are arranged in a cup-like fashion beneath the cuticular lens (Fig. 2). All the ocellus is invested by a layer of thin flat epithelium with pigment granules into the cells (Fig. 10).

A broad apodeme of the cephalic capsule forms a cuticular cup enclosing the ocellus, being the pharyngeal dilator muscles attached to the opposite side (Fig. 3).

**Ocellar retina**

One ocellus has about 2800 elongated retinal cells arranged perpendicularly to the internal surface of the corneal lens. The total cell length from the distal tip to the proximal synapses reaches between 53 and 119 µm, according if they are located in the center or the periphery. Three zones can be recognized in a retinal cell: (i) a distal rhabdomeric zone (about 50–70 µm length × 5–6 µm diameter), (ii) a middle zone free of rhabdom (50–69 µm length × 6–8 µm diameter), where the nuclei are located, and (iii) a proximal zone, comprising from the origin of the axon up to its synaptic contacts into the neuropile with secondary neurons (Figs 34 & 36), which cell bodies are located in the brain (Fig. 33) (Insausti & Lazzari, 1996). In the dark-adapted ocellus, many screening pigment granules are present in the middle zone (Fig. 2). In light-adapted conditions the pigment granules move upward to the distal region where the rhabdomeric meshwork is located (Insausti, 1996, 1997). Glial cell processes invest the retinal cells in the zone free of rhabdom. The cytoplasm of these cells is characteristically denser than that of receptor cell and this condition is readily visible in electron micrographs. Numerous pigment granules are present into glial cells located between photoreceptors (Figs 16 & 17).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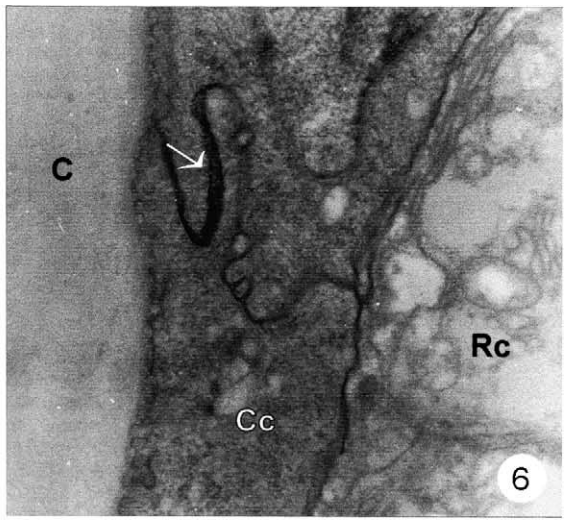
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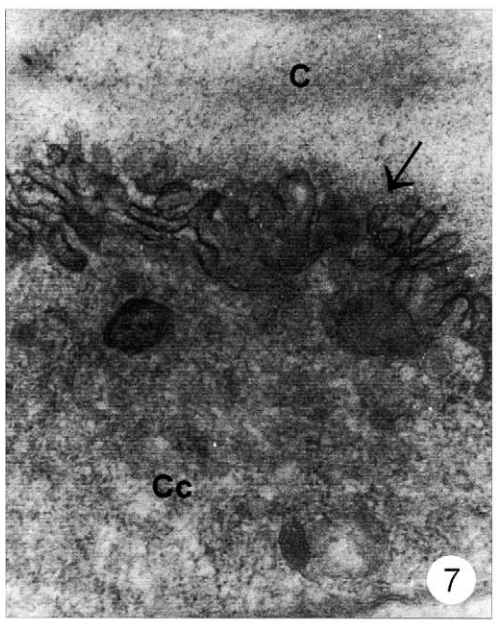
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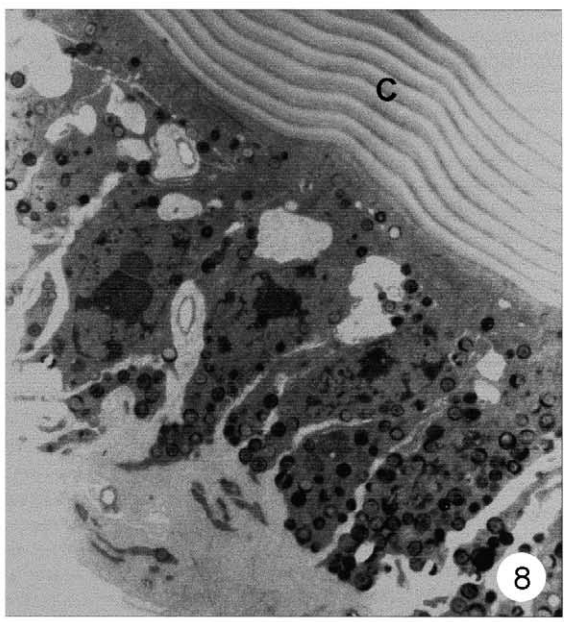
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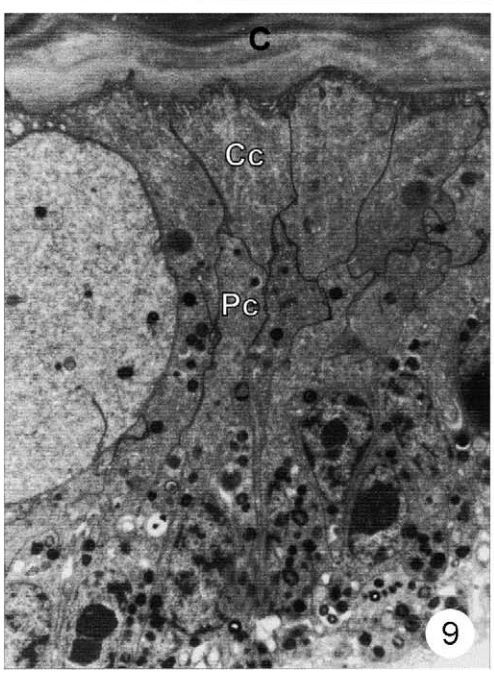
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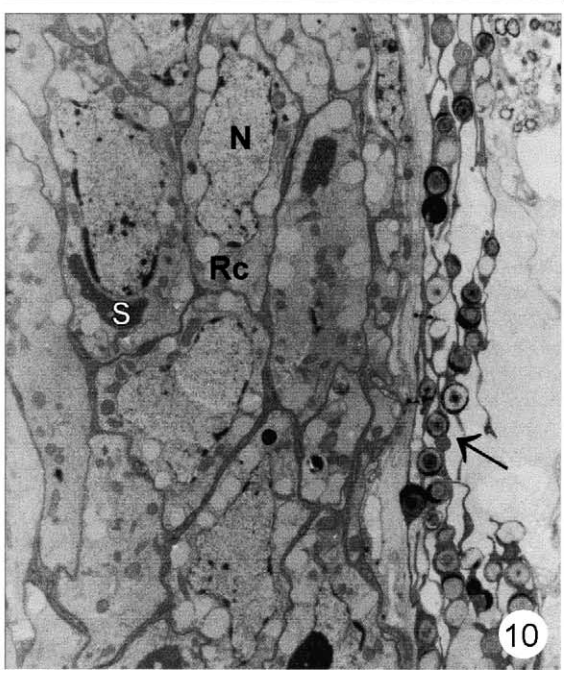
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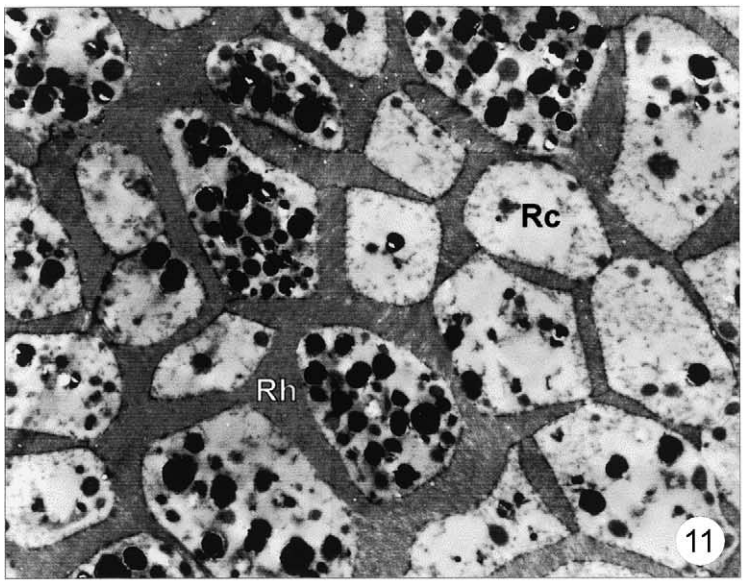
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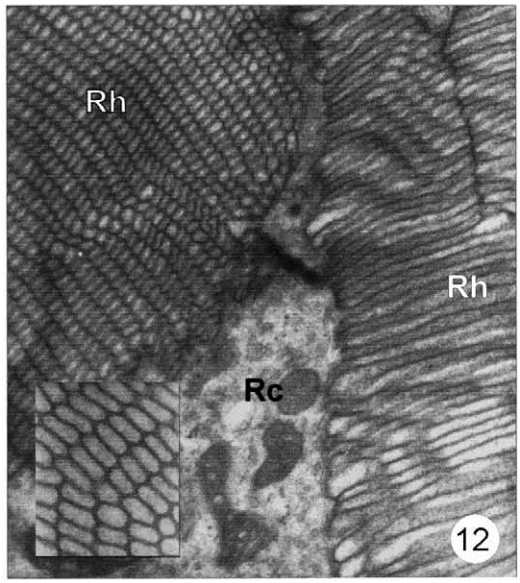
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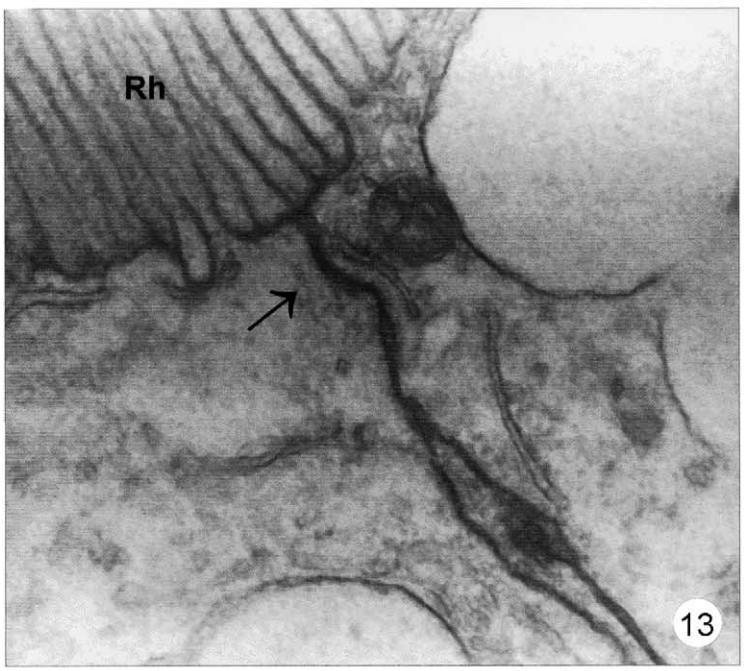
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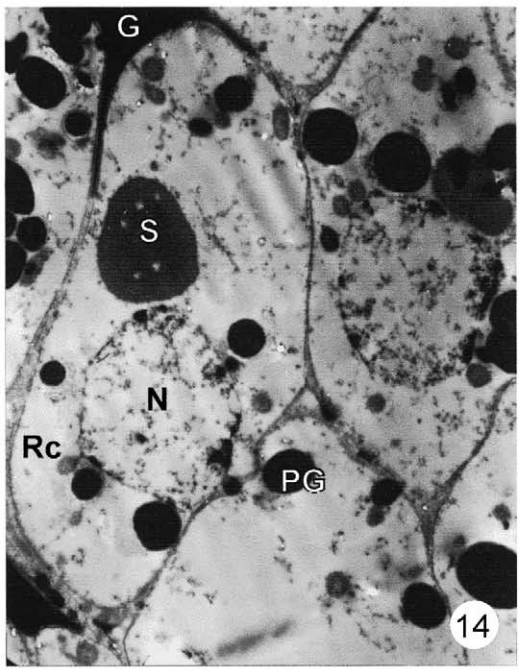
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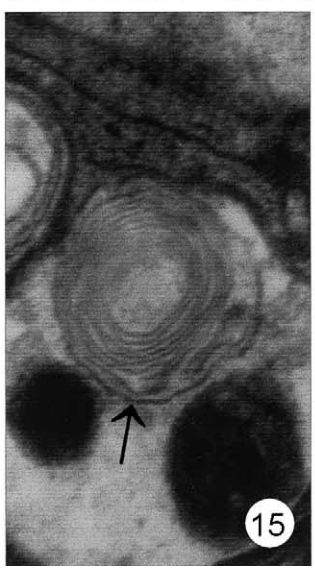
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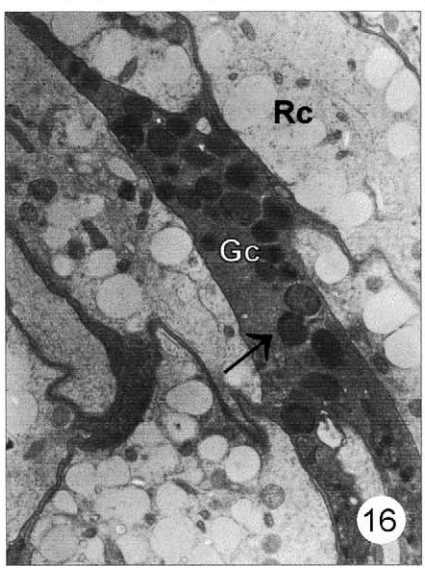
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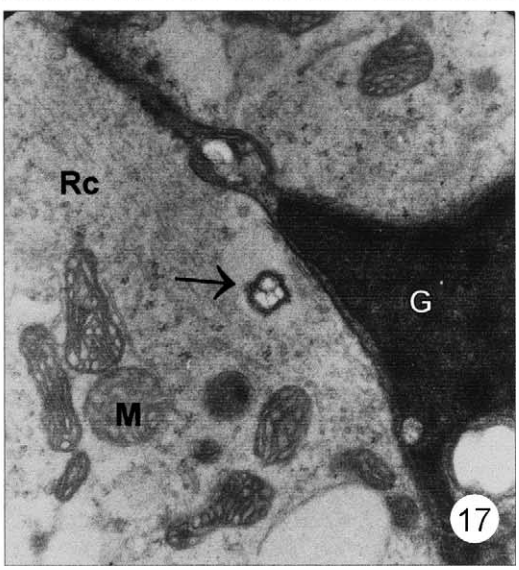
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**Fig. 5** Longitudinal section of the ocellus. The corneagenous cells with large nuclei are shown. The arrow shows the cytoplasm processes of corneagenous cells between two retinal cells. C, corneal lens; Cc, corneagenous cells; Rc, retinal cells; Rh, rhabdom. ×3 000. **Fig. 6** Longitudinal section of the ocellus near the corneal lens (C) showing the junction of corneagenous cells (Cc). Septate desmosomes are visible (arrow). Rc, retinal cells. ×20 000. **Fig. 7** Longitudinal section of the ocellus showing the upper border of corneagenous cells, with microvillar processes (arrow) related with the developing cornea. C, corneal lens; Cc, corneagenous cells. ×30 000. **Fig. 8** Longitudinal section of the ocellus through the outer rim of pigmentary cells. C, corneal lens. ×3 000. **Fig. 9** Longitudinal section of the ocellus through the 'iris' in young adults. The apparent iris is formed by pigmentary cells (Pc) that lie beneath the corneagenous cells (Cc), surrounding the developing cornea. C, corneal lens. ×7 000. **Fig. 10** Cross-section through the middle zone of ocellar retina. The ocellus is invested by a layer of thin flat epithelium with pigment granules into the cells (arrow). N, nucleus; Rc, retinal cell; S, spheroid. ×3 000.

**Fig. 11** Cross-section of the ocellus through the distal zone of the retinula cells showing the rhabdomeric meshwork. Rc, retinal cell; Rh, rhabdom. Note the pigment granules inside the receptor cells. ×3 000. **Fig. 12** Cross-section of the ocellus through the distal zone of the retinula cells with rhabdomeric microvilli cut transversally and longitudinally to their axis. ×20 000. Inset, higher magnification of rhabdomere cut transversally. ×140 000. Rc, retinal cell; Rh, rhabdom. **Fig. 13** Cross-section through the distal part of the rhabdomeric meshwork and beginning of the middle zone. Rh, rhabdom; arrow, desmosome. ×50 000. **Fig. 14** Cross-section of the ocellus through the middle zone of the retinula where the cell nuclei are located. Note the spheroid (S) near the nucleus. G, glia; N, nucleus; PG, pigment granule; Rc, retinal cell. ×5 000. **Fig. 15** Cross-section of a retinula cell showing the concentric arrays of endoplasmatic reticulum (arrow) at the origin of an axon. ×50 000. **Fig. 16** Oblique section through the middle zone of the retinula. Pigment granules are present in the cytoplasm of the glial cells (arrow). Gc, glial cell; Rc, retinal cell. ×4 000. **Fig. 17** Cross-section through the middle zone of the retinula. Arrow, multivesicular body; G, glia; M, mitochondria; Rc, retinal cell. ×14 000.

In the distal zone, the entire lateral faces of each retinal cell are modified to form microvilli, which are connected with those of neighboring photoreceptors, forming a hexagonal thick meshwork of rhabdomeres (about 1.1 μm thick) (Fig. 11). Rhabdoms cut along their long axis reveal dense packing of microvilli of about 70 nm diameter (Fig. 12). The neighboring retinal cells are connected to each other by desmosomes located at the portion adjacent to the rhabdomeric structure (Fig. 13, arrow). The cytoplasm of the receptor cell contains, in this zone, a large number of mitochondria exhibiting diverse shapes, i.e. spherical, elongated, irregular, generally concentrated near the microvillar border. Also present in the cytoplasm, smooth and rough endoplasmic reticulum can be found (Figs 11 & 12).

In the middle zone, the retinal cells are often oval in section, sometimes irregular. The nuclei of different cells are homogeneously distributed over this area of the retina. The nuclei are large (about 5.5 μm × 3.6 μm) and their shape follows the cell form. They contain peripherally concentrated chromatin and conspicuous nucleoli. A more electron-dense spherical body without membrane surrounding it, is present next to the nuclei (Figs 10 & 14). Mitochondria are homogeneously distributed over the cytoplasm of the cell body (Figs 16 & 17). Also present in the perinuclear cytoplasm are smooth and rough endoplasmic reticulum, several Golgi complexes as well as multivesicular bodies (few vesicles of about 0.16 μm in diameter) (Figs 13 & 17 arrow). Frequently, just before the beginning of the axon, the smooth endoplasmic reticulum runs in several concentric layers, given a winding body of about 0.6 μm in diameter (Fig. 15). The glial processes surround the retinal cell (except the desmosomes) filling most of the inter-cellular space (Figs 16 & 17).

In the proximal zone, the retinal cell tapers off into the axon (with about of 1.9 μm in diameter). In this region, large mitochondria (generally round in shape) are found in the peripheral position (Figs 19 & 22). Also present in the axoplasm are onion bodies (0.3–0.4 μm in diameter) multivesicular bodies and neurotubules (Figs 20, 21 & 23). The glial elements may invest single visual cell axons or groups of such axons, thus, forming a separate sheath around the bundles of axons (Fig. 19). The visual axons in this region diverge from the bundles and extend to the ocellar neuropile at the base of the ocelli to synapse with second order neurons (Figs 34 & 36). The terminal of the axoplasm contains a great quantity of neurotubules and synaptic vesicles. They contact synaptically with many branches of the distal process of the second-order neurons (Fig. 22). The branches of large ocellar nerve fibers may be distinguished from those of the visual axons, since they are less electron-dense and contain a smaller number of neurotubules and synaptic vesicles. Both types of neurons contrast with the highly electron-dense glial cells (Figs 19, 22 & 24). The retinular cell axons are connected by bulb junctions (Figs 23 & 24).

## Synapses

The ocellar neuropile (Figs 34 & 36) is a flattened structure, which is connected to the protocerebrum by an ocellar nerve (440 μm long and 45–65 μm thick, Fig. 33). The second-order neurons are highly branched into many fine dendritic strains in the distal part of the ocellar nerve. Nevertheless, in its proximal part, which joins the brain mediodorsally, the ocellar nerve comprises only 10 giant fibers (>8 μm) and an indeterminate number of small fibers (<5 μm) (Insausti & Lazzari, 1996) (Figs 33–36).

Synaptic interactions are complex within the neuropile, since all kinds of relationships can be found. At contact points between receptor cell axons and interneuron dendrites, different types of synapses are present (Fig. 18) which can be described as follows:

Type 1. *Axo-dendritic contacts*: a retinal axon is pre-synaptic to an ocellar nerve fiber. These synapses are normally characterized by the presence of a button-like pre-synaptic structure formed by accumulation of electron-dense material (Figs 25 & 27). Bar synapses elements can also be found (Figs 31 & 32).

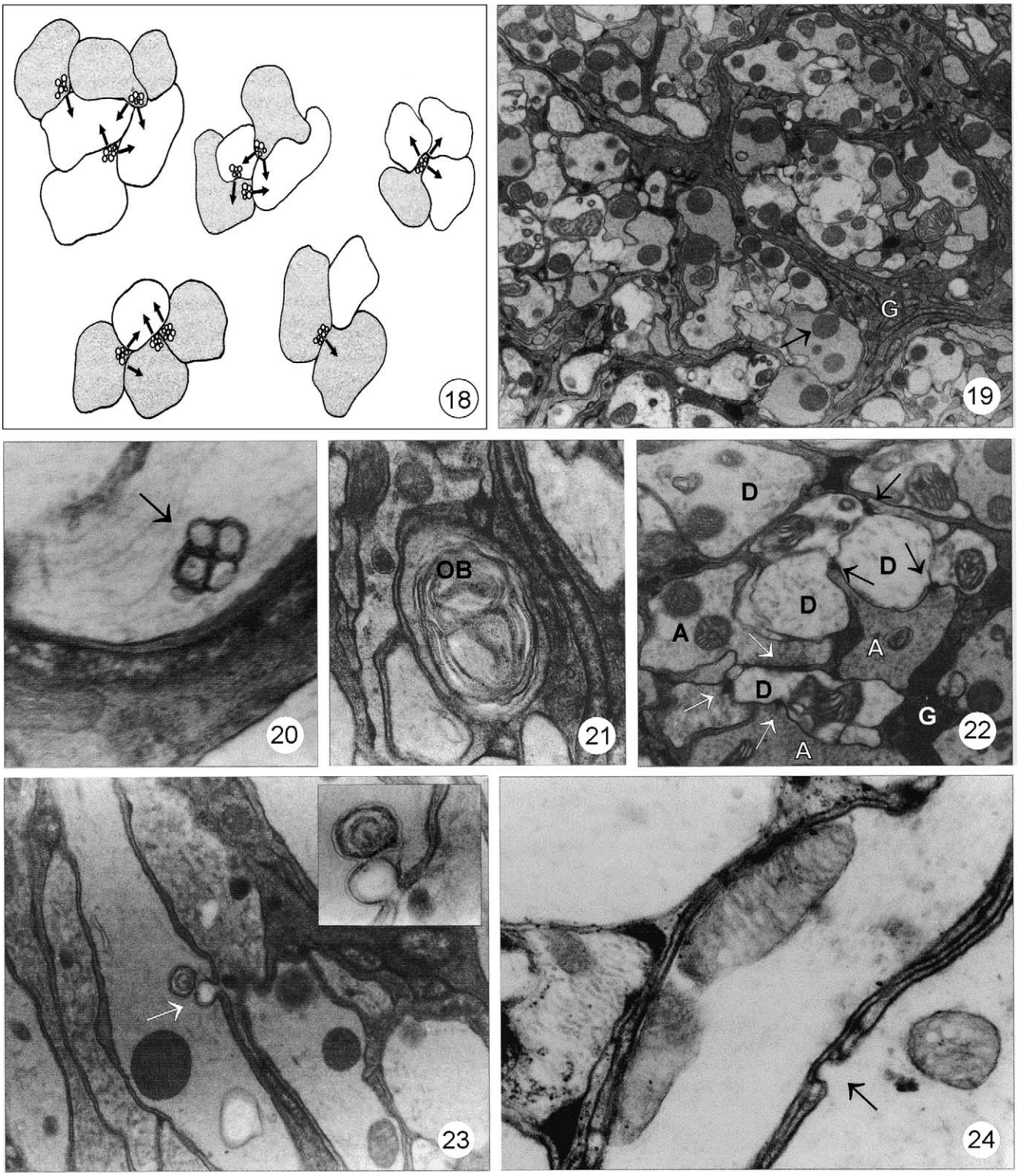
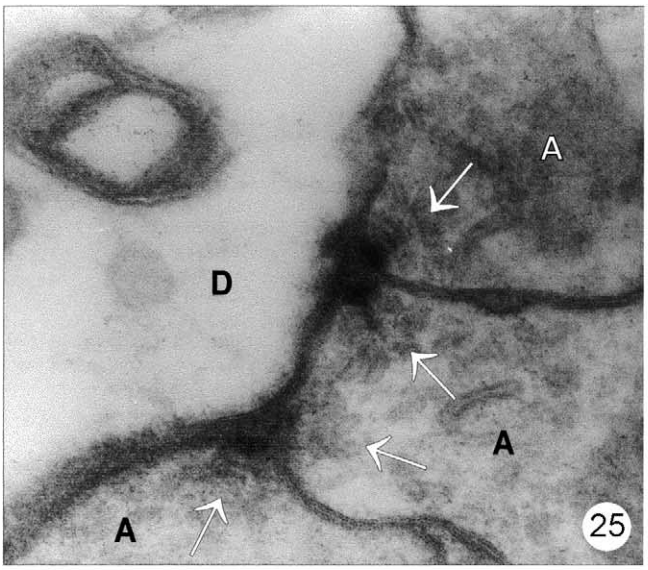



**Fig. 18** Diagram illustrating some of the microcircuits between interneuron dendrites and retinula cell processes in the ocellar neuropile (synaptic plexus). Grey areas, retinular axons; white areas, ocellar nerve fibres. **Fig. 19** Characteristics of the neural elements in a cross-section through the synaptic region. The retinula cell axons are bundled individually or in groups by glia (G, dark cytoplasm). Note the arrangement of round mitochondria (arrow). ×7 000. **Fig. 20** Oblique section through a retinula cell axon showing a multivesicular body (arrow). ×20 000. **Fig. 21** Oblique section through a retinula cell axon showing an onion body (OB). ×85 000. **Fig. 22** Cross-section through the synaptic region. The axoplasm of the retinular axons (A) appears granular and more electron dense than dendritic elements (D). The synaptic loci are indicated by arrows. The black arrow indicated a divergent triad. G, glia. ×20 000. **Fig. 23** Oblique section through retinula axons showing a bulb junction between adjacent cells (arrow). ×12 000. An onion-like body with concentric layers of membrane is associated (inset, ×85 000). **Fig. 24** Oblique section through retinula axons showing a bulb junction between adjacent cells (arrow). ×26 000.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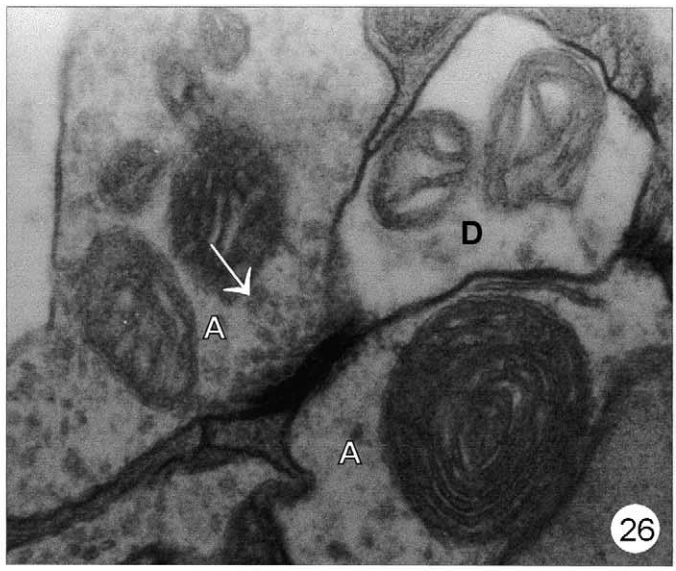
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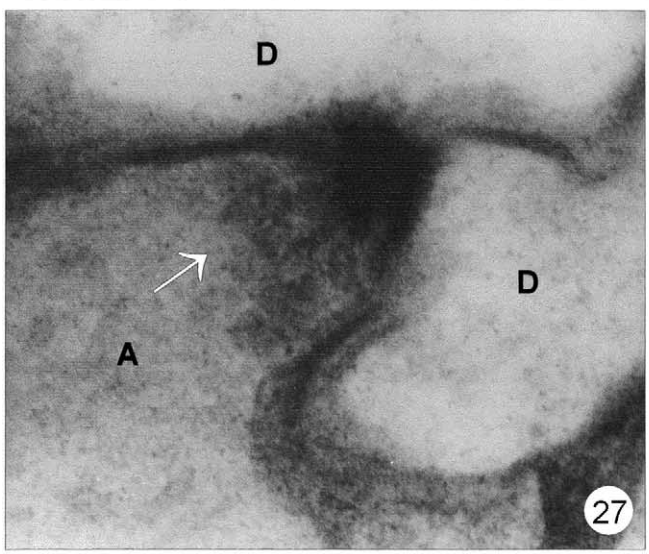
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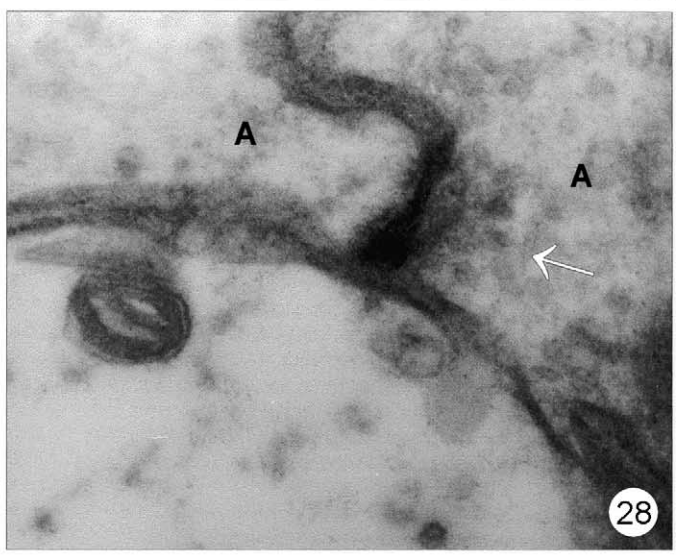
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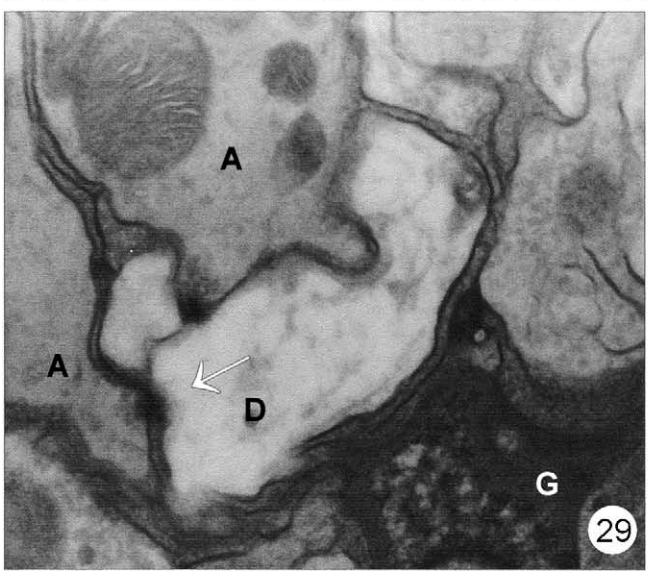
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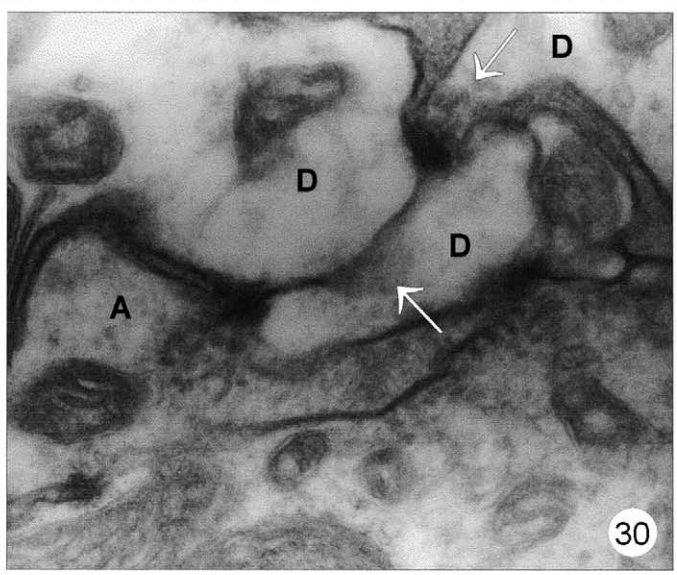
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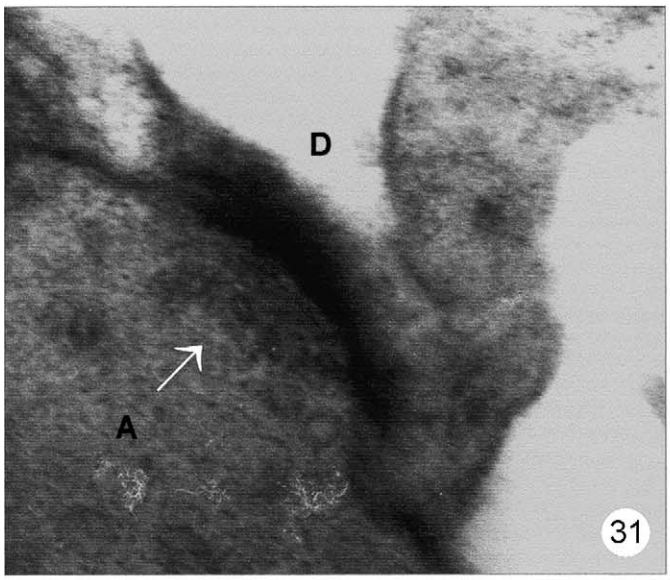
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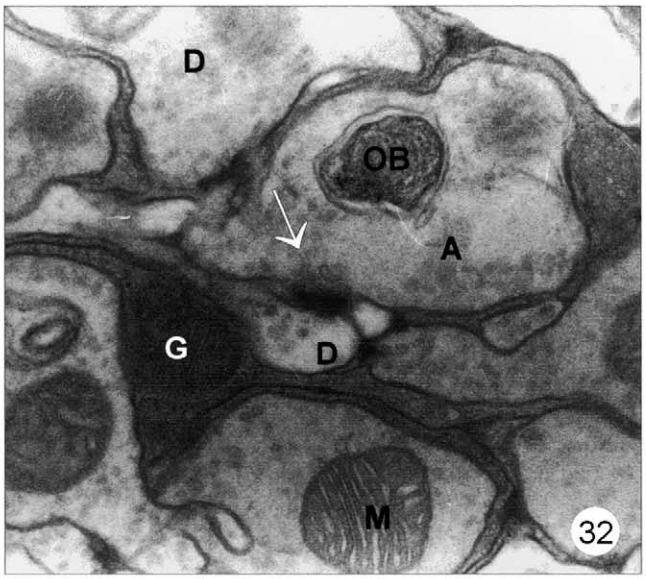
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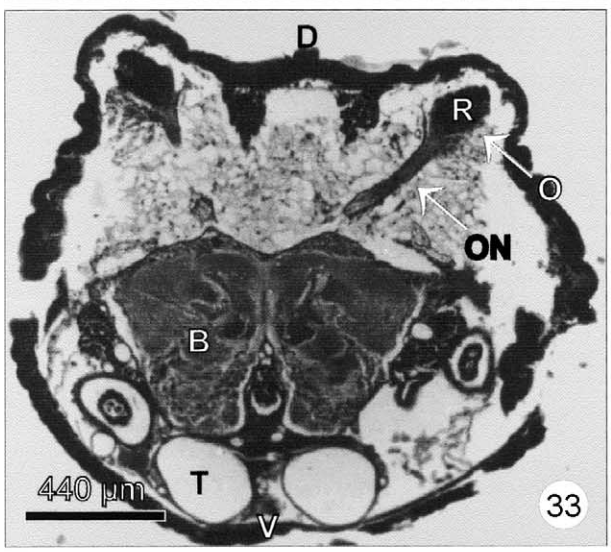
D
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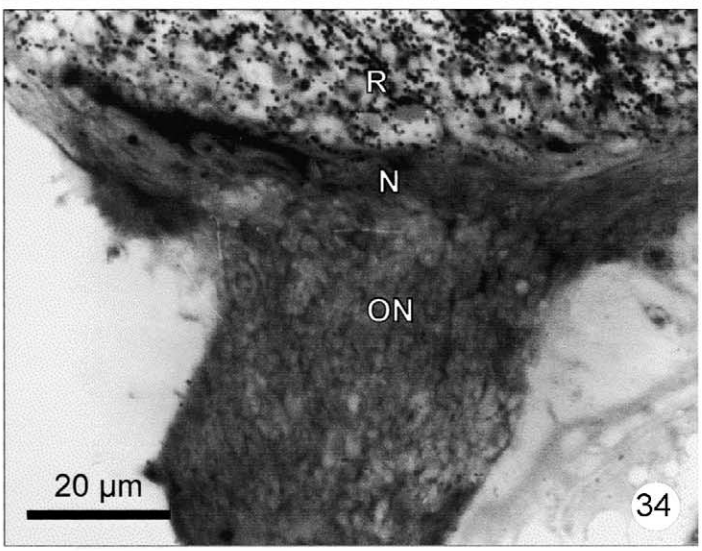
33


R
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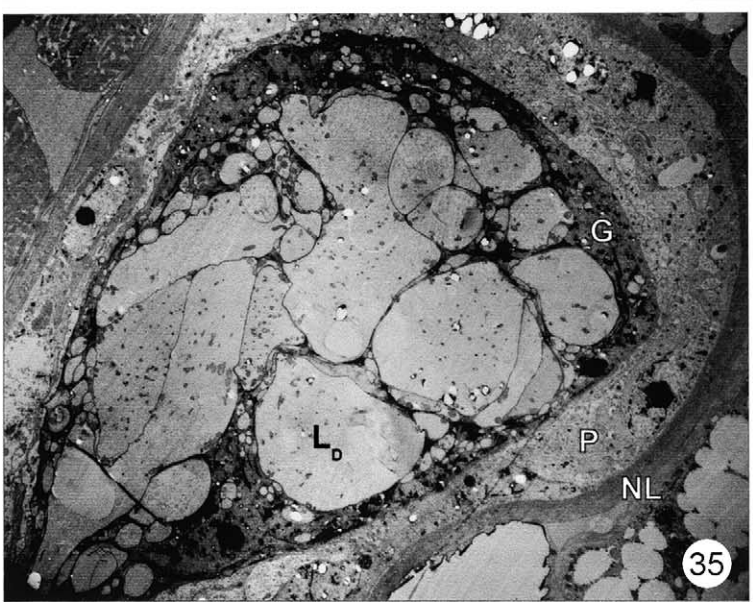
20 µm
34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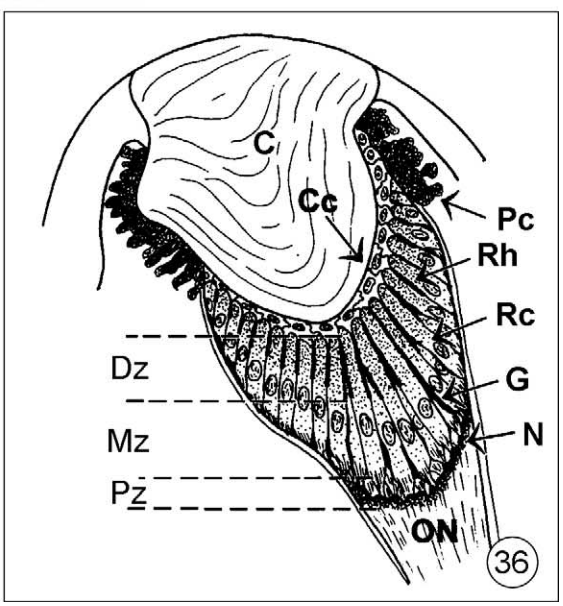
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36

**Fig. 25** Synaptic contacts (arrows) of two axons (A) onto a dendrite (D) (axo-dendritic contact, convergent dyad) with serial button-like presynaptic structures. ×85 000. **Fig. 26** Bar-shaped presynaptic contact (arrow) of one axon (A) onto another (axo-axonic connection). ×50 000. **Fig. 27** Simple button synaptic contact (arrow) of one axon (A) onto two dendrites (D) (axo-dendritic contact, divergent dyad). ×140 000. **Fig. 28** Bar-shaped presynaptic connection (arrow) of one axon (A) onto another (axo-axonic contact). ×85 000. **Fig. 29** Feedback synaptic contact (arrow) of one dendrite (D) onto one axon (A) (dendro-axonic connection with pre-synaptic bar-shaped structure). ×30 000. **Fig. 30** Reciprocal synaptic contacts between dendrites (D) (arrows) (dendro-dendritic contact with a button-like presynaptic structure). A, axon. ×50 000.

**Fig. 31** Bar-shaped presynaptic contact (arrow) of one axon (A) onto a dendrite (D) (axo-dendritic contact). ×85 000. **Fig. 32** Bar-shaped presynaptic contact (arrow) of one axon (A) onto a dendrite (D) (axo-dendritic contact). G, glia; M, mitochondria; OB, onion body. ×30 000. **Fig. 33** Light micrograph of a cross-section through the head of a young adult of *T. infestans*, showing the position of the brain (B), the long ocellar nerve (ON) and the ocellus (O). D, dorsal; R, retina; T, tacheae; V, ventral. **Fig. 34** Light micrograph through the lower portion of the ocellus showing retina (R), the neuropilar zone (N) and the ocellar nerve (ON). **Fig. 35** A cross-sectioned ocellar nerve showing the large and small processes of the first order interneurones and the outer sheaths. A large fibre ($L_D$) is labelled. G, glia; NL, neural lemma; P, perineural layer. ×1 000. **Fig. 36** A schematic drawing of the longitudinal section through the occellus, based upon the light microscopic observations. C, corneal lens; Cc corneagenous cells; Dz, distal zone; G, glial cells, Mz, middle zone; N, neuropilar zone; ON, ocellar nerve; Pc, pigmentary cells; Pz, proximal zone; Rc, retinal cell; Rh, rhabdom.

Type 2. *Dendro-dendritic contacts*: an ocellar nerve fiber is pre-synaptic to another one. These contacts are characterized by button-like pre-synaptic structures (Fig. 30).

Type 3. *Dendro-axonic synapses*: an ocellar nerve fiber is pre-synaptic to a retinal axon. These contacts are characterized by bar synapses (Fig. 29).

Type 4. *Axo-axonic contacts*: a retinal axon is pre-synaptic to another one. Characterized by bar synapses (Figs 26 & 28).

In many cases, a single pre-synaptic fiber may make synaptic connection with two postsynaptic units (divergent dyad) (Figs 22 & 27). In these cases contacts are characterized by pre-synaptic structures of axons that are button-like. We also found cases where two pre-synaptic fibers make synaptic connection with one postsynaptic unit (convergent dyad, Fig. 25) and in another cases a single pre-synaptic fiber may make synaptic connection with three postsynaptic units (divergent triad, Fig. 22, black arrow).

Figure 36 depicts an anatomical reconstruction of the ocellus of *T. infestans*, based on the morphological characteristics revealed by the present study.

## Discussion

In the present study, the fine structure of the dorsal ocellus, ocellar nerve and peripheral neuropil has been examined in the haematophagous bug *T. infestans*. It could be established that these organs exhibit an unusual degree of complexity, as compared with other insects.

The corneal lens of *T. infestans* is thick and its external surface is hemi-spherical in shape, whereas the inner one is quite irregular. In the middle, it is biconvex and quite spherical. In the boundaries, the curvature of the inner surface does not follow that of the external surface. In the related species *R. prolixus*, the lens has a complex form and its inner surface is hemispherical (Goodman, 1981). In other well-analyzed group of nocturnal insects, the cockroaches, the corneal lenses are slight thickenings in windows of transparent cuticle (Goodman, 1981). In other insects, the ocellar lens is very thick, being plane-convex, biconvex, concave–convex or virtually spherical in its form. In the honeybee, for example, the lens is thick and has an asymmetrical inner surface (Goodman, 1981). The comparative analysis shows that, even through *T. infestans* has nocturnal habits (as cockroaches), the form of the ocellar cornea is more similar to that present in diurnal insects.

As in other insects investigated up to date, the ocelli of *T. infestans* are unfocused. Whereas the rhabdomeric zone of retinal cells extends up to a maximum of 70 μm from the inner surface of the cornea, parallel incoming rays converge at about 114 μm. The fact that incoming light rays are focused far beyond the retina, makes them unable to form images.

In most insects (e.g. bees, dragonflies, cockroaches) just a portion of the borders of retinal cells is involved in the formation of the rhabdom (Toh & Kuwabara, 1974; Ruck & Edwards, 1964; Cooter, 1975; Weber & Renner, 1976). In *T. infestans*, like in *R. prolixus* (Goodman, 1981), the rhabdom has the structure of a network that involves all the lateral walls of the photoreceptive cells. The entire faces of the distal zone of each retinal cell are modified to form microvilli, which interdigitate with those of neighboring cells to form a real thick network. A comparable network arrangement of rhabdomeres has been reported in dipteran's ocelli, where each retinal cell has a good deal of its border modified to form rhabdom, so that the retinal layer approaches a meshwork (Redikorzew, 1900; Toh et al., 1971; Hertweck, 1931; Toh & Kuwabara, 1975; Wunderer et al., 1988). The particular arrangement of the ocellar rhabdom of *T. infestans* could be related with a specific functional characteristic, such as an increased sensitivity to light or the perception of polarized light. Future work should reveal the relation between structure and function of these simple eyes.

Pigment granules could be observed inside photosensitive cells, inside glial cells and inside pigmentary cells. The formers move around the rhabdom during light adaptation and migrate down, towards the proximal region of the cell, in the dark-adapted ocellus (Insausti, 1996, 1997).

In the photoreceptor cells of the *T. infestans* ocellus is remarkable the presence, in the proximity of the nucleus,

of an electrodense spherical body. It closely resembles the 'spheroid' present in retinular cells of the compound eye of *R. prolixus* (Müller, 1970) and *T. infestans* (Reisenman et al., 2002). Müller (1970) reported that, in compound eye photoreceptors, this structure duplicates its diameter from 5 to 10 μm in the course of the adaptation from light to darkness. In *R. prolixus*, it is a round structure, free of membrane, of finely granulated electrodense material, that reaches its maximal size 60 min after transferring the bugs to complete darkness. This *spheroid*, which as far as we know has been never described in other insects, seems to be exclusive to photoreceptor cells of both compound eyes and ocelli of triatomines.

Inside the ocellar photoreceptor cells of *T. infestans* we also noted the presence of multivesicular organelles, composed by 4–5 vesicles surrounded by electrodense material. These organelles, typically present in compound eyes, use to be associated with the rhabdom. Among others, it has been suggested that they would participate in the formation of the rhabdomeric tubules. The presence of acetylcholine/acetylcholinesterase inside these vesicles suggests that they could participate in photic transduction (Goodman, 1970). Even though their function remains to be elucidated, is it worth to mention that in the ocelli of *T. infestans* multivesicular bodies are composed by just few vesicles and are found not only in the proximity of the rhabdom, but also in the axonal cytoplasm and in zones of the cell free of rhabdom.

In the cytoplasm of photoreceptor cell, near to the origin of the axon, a membrane structure formed by concentric layers of smooth endoplasmic reticulum can be seen. This structure presents as more or less dense, it means, with a variable number of concentric rings of membrane, in different insects. Comparatively, the situation of *T. infestans* is intermediate between the high development observed in *Periplaneta* by Weber and Renner (1976) and that reported in *Schistocerca* by Goodman (1970). In the last named species, the axonal origin is clearly marked by concentric rings or smooth endoplasmic reticulum (Goodman, 1970).

The ultrastructural study revealed the presence of organelles formed by concentric membrane layers with an electrodense center, resembling the 'onion bodies' described by other authors (Goodman, 1970; Dow & Eaton, 1976; Toh & Sagara, 1984). These structures have been found in diverse arthropods, inside photoreceptors of compound eyes and ocelli (Goodman, 1970). In the ocelli of *T. infestans* they localize mainly in the axonal cytoplasm of photoreceptive cells, sometimes associated to the cell membrane.

The ocellar plexus exhibits a high diversity of synaptic unions (i.e. axo-dendritic, axo-axonic, dendro-axonic and dendro-dendritic). More frequently, the pre-synaptic elements in the ocellar plexus of *T. infestans* presented bar shaped ribbons or button synaptic structures. We often observed the association of one pre-synaptic with two post-synaptic elements (divergent dyad; Strausfeld, 1976). The opposite, i.e. two pre-synaptic elements contacting one post-synaptic (convergent dyad) was also observed. Less frequent were divergent triads, where one pre-synaptic element joined three postsynaptic ones.

The ocellar plexus revealed a high degree of complexity, which is consistent with other characteristics of the ocelli of *T. infestans* already described. According to the literature, marked differences do exist in the synaptic organization of the ocellar plexus in different insects. In dragonflies (Dowling & Chappell, 1972), locusts (Goodman et al., 1979), cockroaches (Cooter, 1975; Toh & Sagara, 1984) and bibionids (Wunderer et al., 1988) many synaptic contacts among photoreceptors have been observed. In the moth *Trichoplusia ni*, electrotonic joins between photoreceptors have been reported by Dow and Eaton (1976). In cockroach, however, the occurrence of synapses between photoreceptor axons is not frequent (Toh & Sagara, 1984). In the wasp *Paravespula vulgaris*, axo-axonic contacts have not been found (Kral, 1979). Reciprocal synapses between photoreceptors have been found neither in flies (Toh et al., 1971; Toh & Kuwabara, 1975), nor in honeybees (Toh & Kuwabara, 1974). Eaton and Pappas (1977) have proposed that the synapses between photoreceptors could act, by means of reciprocal excitation, as generators of the synchronized activity in the axons or receptor cells. Feedback synapses have been found from L-neurons to photoreceptors in dragonflies (Dowling & Chappell, 1972), locusts (Goodman et al., 1979), the moth *T. ni* (Eaton & Pappas, 1977), wasps (Kral, 1979) and the fly *Drosophila* (Stark et al., 1989), being this one of the more conspicuous characteristics of the ocellar plexus. This kind of synapses is not frequent in cockroaches (Toh & Sagara, 1984). Apparently, in honeybees (Toh & Kuwabara, 1974) and flies (Toh et al., 1971; Toh & Kuwabara, 1975), L-neurons do not make feedback synapses over photoreceptors. In these insects, L cells seem to be always post-synaptic in the ocellar plexus. The functional role of feedback synapses over photoreceptors has not been elucidated so far. In *T. infestans*, the synaptic organization of the ocellus exhibits all type of synaptic contacts, i.e. axo-dendritic, dendro-axonic (feedback synapses), axo-axonic, and dendro-dendritic. Some of the synaptic contacts could originate from interneurons back to the receptor terminal, but others would correspond to neurons originating in the protocerebrum. Indeed, the cobalt filling revealed the occurrence, in *T. infestans*, of first-order ocellar interneurons that project bilaterally to both ocelli and also arborize in the posterior slope of the protocerebrum and the lamina (Insausti & Lazzari, 1996).

In the pre-synaptic fibers of the optic ganglion of muscoids Diptera (*Lucilia*, Trujillo-Cenóz, 1965, 1969; *Musca domestica*, Boschek, 1971) and in the ocellus of the fly *Boettcherisca peregrina* (Toh et al., 1971) differentiated T-shaped synaptic structures have been described. In the central nervous system of the cockroach *Periplaneta americana*, the occurrence of structures similar to those found in flies was reported (Boeckh et al., 1970). Dowling and Chappell (1972) recognized two types of synaptic contacts in the dragonfly ocellus, one conventional (based on criteria used in vertebrates by Gray & Guillery, 1966) and a second with a button-shaped pre-synaptic structure. In the bee *Apis mellifera*, Toh and Kuwabara (1974) informed that the synaptic locus and its polarity are not easily identified,

due to the lack of differentiated pre-synaptic structures in this insect. In *T. infestans*, the synaptic locus and its polarity (pre- or post-synaptic) can be recognized easily, since in these insects the joins always exhibit a pre-synaptic structure differentiated either as a button or as a simple bar. Besides, synaptic vesicles can be recognized to be present in the pre-synaptic element. No T-shaped synapses could be found, which appear to be typical from dipterous.

We observed the presence of *bulb junctions* between axons of retinular cells. These unions have been described in *Schistocerca gregaria* (Goodman et al., 1979) and in *T. ni* (Dow & Eaton, 1976), where this structure is referred as gap junction.

The studies of the ocellar system have been conducted on insects that occupy all the temporal niches. Some are diurnal in habits (flies, wasps, bees) others are nocturnal (cockroaches, moths) and others display activity at both, dusk and dawn (trichopterous). In the moth *T. ni*, the ocellar input determinates the light-intensity threshold for flying and regulates small changes in the phase relationship with the daily cycle of illumination (Eaton et al., 1983). *Triatoma infestans* display spontaneous locomotion activity twice a day, at dusk and dawn (Lazzari, 1992). The comparative analysis of the ocellar morphology does not reveal any apparent organization pattern that could be related with the light intensity to what the insect are exposed due to their habits.

The function of the ocelli has been often related with flying. Indeed, in those insects ascribed as 'good-flyers' the ocellar input is involved in fly stabilization (Wilson, 1978; Stange & Howard, 1979; Stange, 1981; Rowell & Pearson, 1983). Triatomines are mostly walking insects, which can accomplish disperssive flights under given conditions (e.g. fasten). Although the ability of *T. infestans* to sustain prolonged flights during the night hours (Lehane & Schofield, 1978, 1982; Schofield et al., 1992), the aerial medium is not the main one in the life of these insects, as does for flies or bees. The relationship between the ocellar system and flight remains to be investigated in this species. However, the high degree of development evinced by the ocellar morphology and the central projections of the ocellar interneurons (Insausti & Lazzari, 1996) does not seem to correlate with the low flying activity that these bugs display. It is probably that the organization of the ocellar system conveys a compromise among diverse adaptive functions in a given species. In this sense, one of the most striking characteristics of *T. infestans* is their strong photonegative reaction (Reisenman et al., 1998). This response is mediated by a directional response to light, i.e. negative phototaxis. The detailed experimental analysis of this behavior has revealed that it is far from being a stereotyped one, being finely modulated by endogenous and exogenous factors, such as the intensity and spectral quality of the light, the age, the occurrence of mutations, etc. (Reisenman, 2000). Remarkably, it has been demonstrated that negative phototaxis in *T. infestans* rely on two parallel visual inputs, the compound eyes and the ocelli (Lazzari et al., 1998). This means that the ocelli can mediate by their own the photonegative response of this species, an ability that has not been shown in other insects.

In conclusion, the ocellar system of triatomine bugs appears as relatively complex in all aspects, when compared with the available information about other insects. The degree of development of the ocelli, the disposition of the rhabdom, the diversity of pigments, the synaptic interactions in the ocellar plexus (including feed-back synapses) and the projections of first-order interneurons into the central nervous system are some of the elements where this complexity becomes more evident. We should add to this the existence of an apparent 'pupil' that change with the age of the adults, which corresponds to the growth of the corneal lens (Insausti & Lazzari, 2000a,b) and has not been described in any other insect.

All these characteristics make the triatomine ocelli very noteworthy. Unfortunately, with the exception of some comments relative to *R. prolixus* included in the comprehensive review by Goodman (1981), there are not data on the ocellar system of hemiptera that could help us to comprehend its organization (e.g. number of ocelli, extended rhabdomeric areas, etc.). Even more difficult results to speculate about the functional role of the ocelli, since the insects analyzed so far differ from *T. infestans* not only in their habits, but also are phylogenetically distant. Indeed, the most fruitful studies have been those related with the association of the ocelli to flight. This fact could have biased the election towards experimental models like bees, wasps, flies, dragonflies and locusts, which can be easily induced to fly in the laboratory, provided that this is a main locomotion modality in these insects. As mentioned, the only function evinced up to now for the ocelli of *T. infestans* is to add the negative phototactic reaction of this species (Lazzari et al., 1998).

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