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Ultrastructure of the Compound Eye of the Rice Brown Planthopper, *Nilaparvata lugens* (StåL) (Homoptera : Auchenorrhyncha : Delphacidae)

벼멸구 겹눈의 미세구조

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ABSTRACT The adult brown planthopper possesses two oval shaped compound eyes which, on their ventral borders, curve around the base of the antennae Compound eye of the adult brown planthopper is recognised apposition eye which each ommatidium is optically isolated from its surroundings, the rhabdoms receiving light only from their own corneal lens. Each ommatidium possesses its own dioptric apparatus formed from the cuticular cornea and an underlying crystalline cone The retinula cells lying immediately beneath the crystalline cone have their individual rhabdomeres tightly opposed to form one central, closed rhabdom. The rhabdom stretches from the apex of the crystalline cone nearly to the basement membrane and is approximately 110~120 μm in length The crystalline cone is surrounded by a pair of primary pigment cells and these in turn are surrounded by accessory pigment cells. Accessory pigment cells extend beyond the crystalline cone surrounding the retinular cells in the distal region of the eye The crystalline cone is surrounded by the distal-most regions of the retinula cells, the tip of the crystalline cone abutting onto the distal tip of the rhabdom formed from the fused rhabdomeres on the inner borders of the retinula cells. The distal region of the retinula cells show the presence of seven cells and sections taken proximally in the last quarter of the ommatidium before the basement membrane is reached, reveal the presence of a small, eighth retinula cell which also contributes to the central rhabdom. Each ommatidium has a central rhabdom formed from the modified inner border of all of the retinula cells. The rhabdom consists of microvilli arising from the inner wall of each retinula cell. In cross section the microvilli exhibit a characteristic honeycomb appearance. Pigment cells comprise the primary pigment cells enveloping the crystalline cone, the accessory pigment cells extending from the inner surface of the cornea to the basement membrane and the small pigment cells of the basement membrane

KEY WORDS Ultrastructure, compound eye, the rice brown planthopper, *Nilaparvata lugens*.

초　　록 벼멸구는 촉각 기부의 등쪽으로 알모양의 2개의 겹눈을 가지고 있다. 벼멸구의 겹눈은 각각의 단안이 분리되어 있고 각각의 낱눈이 단지 그들의 각막렌즈를 통해서만이 빛을 받는 연립상 겹눈이다. 각각의 낱눈은 큐티클성 각막렌즈와 그 안쪽에 수정체가 자리잡고 있다. 망막세포는 수정체 바로 아래쪽에 자리하며, 이들은 중심축쪽으로 감간소체들이 밀집결합되어 감간체를 형성한다. 감간체는 수정체 말단부분에서 시작되어 기저막에 까지 다달으며, 그 길이는 약 110~120 μm 정도이다. 수정체는 4개로 구성된 한쌍의 1차색소세포에 의하여 둘러 쌓여 있으며 이것은 또한 부속색소세포에 의하여 둘러 쌓여 있다. 수정체의 기저부위는 망막세포에 의하여 일부가 둘러 쌓여 있고 망막세포의 내벽에서 발생한 감간소체들로 구성된 감간체와 닿아있다. 낱눈의 상층부분은 7개의 망막세포로 구성되어 있으나 3/4부분에서 8번째의 망막세포가 자리잡고 있다. 중앙부위에 위치하고 있는 감간체는 미세융모들로 구성된 감간소체들로 구성되어 있는데, 이들 미세융모의 단면도는 6각형의 모양을 가지고 있다. 색소세포는 수정체를 감싸고 있는 1차색소세포, 기저막까지 닿아 있는 부속색소세포, 기저막 부위의 기저막색소세포 등 3가지의 색소세포들이 있다.

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The rice brown planthopper. *Nilaparvata lugens* (Stål) (Homoptera: Auchenorrhyncha: Delphacidae) have long been known as serious pests of rice in temperate regions of eastern Asia. The reasons for their dramatic increase in importance have not been definitely established although changing cultural practices may be responsible. The potential of these insects to become serious pests seems to depend on their high fecundity, tolerance to overcrowding, the dispersal ability of the adult insects and their adaptability to various types of rice plant.

N lugens can overwinter in the tropics, e.g., in the Philippines, Viet-Nam, Thailand and in southern China, however it a long-range, windborne migrant in temperate eastern Asia Because of the low winter temperatures in Korea and Japan, rice brown planthoppers cannot survive there throughout the year and invade annually from China on winds associated with rainy season depressions (Kisimoto, 1981). Since Asahina and Turuoka (1968) first reported catching *N. lugens* at sea, further studies (e.g., Kisimoto, 1976, Watanabe *et al.*, 1988) have demonstrated that it is capable of long distance migratory flights. If spreading by long-distance flight between geographical areas also occurs in the tropics, this could mean the potentially rapid spread of newly-evolved characters (such as resistance to insecticides or the capacity to damage rice varieties that currently resist insect attack) as well as the spread of rice diseases. This will affect the development of integrated management of this pest (Kenmore *et al.*, 1984).

The majority of adult insects possess a pair of well developed compound eyes with highly organized optic ganglia. The structure and function of the compound eyes of representative insects from most Orders have been examined by many authors. However, little is known of the role of vision or olfaction during long distance orientation of the Auchenorrhyncha. Indeed the plant played by vision in long-distance orientation is not well understood in many homopterans. Much of the information regarding visual orientation in the Auchenorrhyncha is anecdotal in nature Many species are attracted to light and to yellow traps, but whether vision is used during flight to locate potential host plants is unknown (Saxena *et al.*, 1974a, 1974b, Saxena and Saxena, 1975a, 1975b). Thorsteinson (1960) considers that visual signals, except at close range, can be relegated to a collateral role for insects on the grounds that they do not contribute significantly to unique identification of food plants by insects.

MATERIALS AND METHODS

The disposition of the compound eye in the head and their external structure was examined in fresh, brown planthoppers mounted intact under the light microscope (LM) or, after suitable preparation, using the scanning electron microscope (SEM). The general organization of the compound eye was investigated by means of sections taken for the light microscope or for the transmission electron microscope (TEM). Measurements of the height and width of the crystalline cone were measured at a magnification of ×900 for all samples under the Zeiss Photomicroscope II . The sections to be measured were selected from the approximate mid-point of the crystalline cone.

The number of facets in samples of adult -males and -females were counted for comparison of the male and female compound eye.

Semithin Sections of the Insect Compound Eye

Most of the sections of the compound eye taken for light microscopy were semithin resin sections about 0.5± 0.1 μm thick cut on an ultramicrotome. Vertical, horizontal and sagittal sections of the eye were cut. For the semithin sections, insects were initially immobilized by placing them in carbon dioxide (CO_2) for a few seconds. The best method of fixation was found to be to immerse the whole insect in 3% glutaraldehyde in 0.2 M cacodylate buffer (pH 7.2) for 2 hours at room temperature. They were post-fixed in 1% Osmium tetroxide (OsO_4) in caccodylate buffer at pH 7.2 for 2 hours at room temperature, followed by dehydration in an ethanol series. They were cleared in propylene oxide for two periods of 15 minutes and embedded in TAAB resin (25 *ml* TAAB, 22.5 *ml* DDSA, 2.5 *ml* MNA and 1 *ml* DMP 30) at room temperature.

Resin blocks were shaped using a hacksaw and a razor blade and the tissues were serially sectioned to 0.5 μm thickness using a Reichert OM U2 ultramicrotome. The sections were examined and photographed in a Zeiss Photomicroscope II.

Scanning Electron Microscopy (SEM) of the Compound Eye

Dehydration for 30 minute periods in 30, 50, 70 % ethanol stages followed. In 70% ethanol the brown planthoppers were transferred to an ultrasound bath. Three 20 second periods of sonication separated by changes of alcohol followed, in order to remove surface debris which covers the hopper's compound eyes Final dehydration in 90 and 100% ethanol took place. The specimens were attached to polished brass stubs, using silver loaded conductive paint, and then sputter-coated with gold palladium. Viewing of specimens took place under a JEOL 35SM scanning electron microscope.

Transmission Electron Microscopy (TEM)

After curing, thin sections were cut on a Reichert Om U2 ultramicrotome. When areas of interest were reached after TEM inspection of these sections, thinner sections of grey colour (40~50 nm) were taken for high magnification examination. Sections were picked up on 200 and 400 mesh copper grids and stained with uranyl acetate (3% in 70% alcohol) (Stempak and Ward, 1964), followed by Reynold's lead citrate (Reynolds. 1963). The specimens were viewed using a JEOL JEM-100S electron microscope at 80 KV.

RESULTS

External Structure of the Compound Eye

The adult brown planthopper possesses two oval shaped compound eyes which, on their ventral borders, curve around the base of the antennae. There are also two very small ocelli, around 150 μm in diameter, set close to the anterior surface of the compound eye. The facets of the compound eye are packed close together and take on an hexagonal form (Fig. 1). The adult females have more facets that the adult males 520 (average of 20 females) compared to 465 (average of 20 males), see Table 1. There are no obvious signs of external specialization in the eye, the facet diameters, at around 40~50 μm, seen to be very similar over the surface of the eye apart from a number of slightly larger ones around the margin of the eye.

Corneal hairs are irregularly distributed over the surface of the eye, between the facets (Fig. 1). The hairs are 40~50 μm long and they are set into a socket which lies between three adjoining facets. There is some evidence that the hairs are innovated (see below).

Internal Structure of the Compound Eye

Figs. 2, 3 and 6 show the general arrangement of the compound eye and reveal that it is an apposition-type eye. Each ommatidium possesses its own dioptric apparatus formed from the cuticular cornea and an underlying crystalline cone The retinula cells lying immediately beneath the crystalline cone have their individual rhabdomeres tightly opposed to form one central, closed rhabdom. The rhabdom stretches from the apex of the crystalline cone nearly to the basement membrane and is approximately 110~120 μm in length. The inner boundary of the compound eye is formed by the basement membrane which is pierced by the retinal cell axons passing centrally to the optic ganglia. The crystalline cone is surrounded by a pair of primary pigment cells and these in turn are surrounded by accessory pigment cells. Accessory pigment cells extend beyond the crystalline cone surrounding the retinular cells in the distal region of the eye. Deeper in the eye the accessory pigment cells are reduced in size so that they do not completely surround an ommatidium. At the inner margin of the eye, the retinula cell axons are surrounded by processes extending upwards from the basement membrane of pigment cells.

The Dioptric Apparatus

The dioptric apparatus comprises the cuticular corneal lens and the crystalline cone of each ommatidium. In surface view each facet appears as a convex lens of hexagonal outline. The diameter of the corneal facet is approximately 40~50 μm and its radius of curvature 50~70 μm. The total thickness

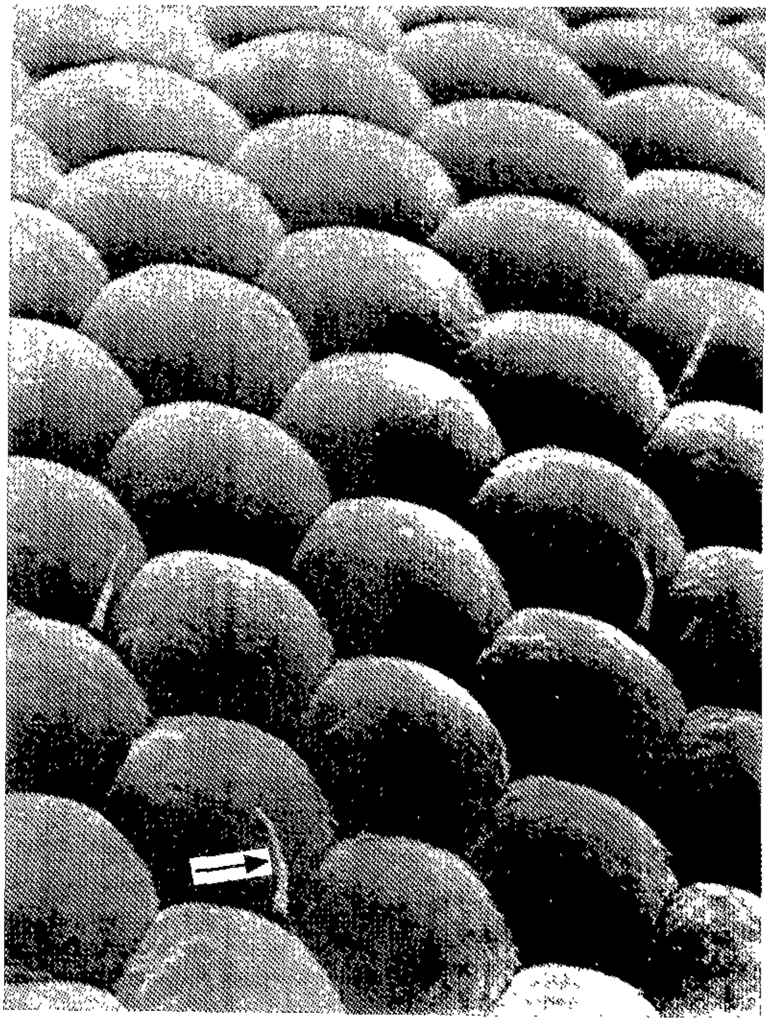

Fig. 1. Surface view of the cornea seen by scanning electron microscopy. The corneal hairs, arrow, are irregularly distributed between the facets. ×420.

of the corneal facet varies between 2~6 μm depending upon the section sites. The inner surface of the lens is separated from the crystalline cone by a narrow band of cytoplasm from the corneal pigment cells. The corneal lens is composed of layers of cuticular chitin of alternate electron dense and light bands. Canals penetrate the cuticular lens. Each pore canal consists of a cellular evagination of either a primary or an accessory pigment cell. The structure has a diameter of 0.15 μm and extends to about 0.6 μm below the outer surface of the corneal lens, the cellular component occupies only the proximal part of the canal.

The crystalline cone is composed of four closely apposed cells The symmetry of these four elements is characteristic of all of the cones examined in the brown planthopper. The four nuclei of the cone cells are situated distally, forming a densely staining cap. The crystalline cone cells lack organelles and appear to be filled with electron dense particles.

The crystalline cone is surrounded by the distalmost regions of the retinula cells (Fig. 3), the tip of the crystalline cone abutting onto the distal tip of the rhabdom formed from the fused rhabdomeres

Table 1. Number of facets of compound eye of *N. lugens*

	Number of Facets	
Sample No	Male	Female
1	453	531
2	445	523
3	466	531
4	468	531
5	482	519
6	463	514
7	480	527
8	468	518
9	476	526
10	453	513
11	469	508
12	457	509
13	459	523
14	479	507
15	455	514
16	469	531
17	469	537
18	482	504
19	449	524
20	457	513
Average	464.95	520.15
Standard Deviation	11.24	9 62

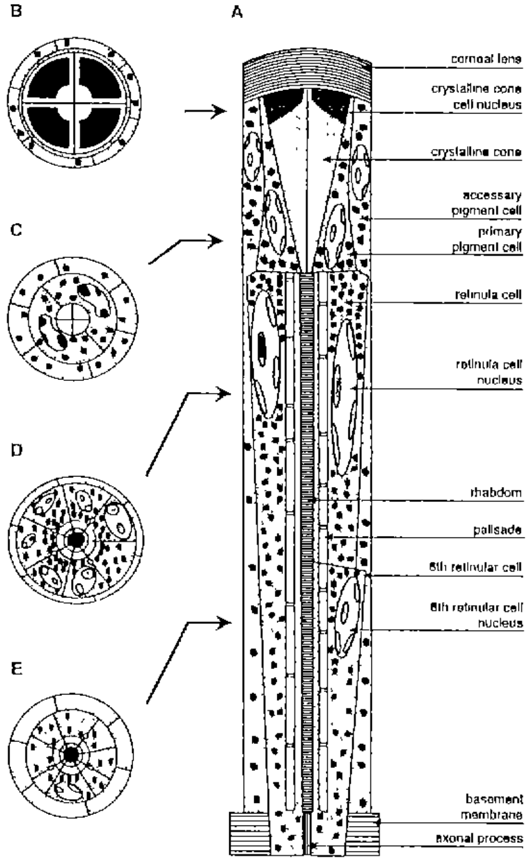

Fig. 2. Schematic illustration of an ommatidium of the compound eye of the brown planthopper. A, longitudinal view of the ommatidium; B, C, D and E, cross-sectioned views of the ommatidium at each line

on the inner borders of the retinula cells. In Fig. 4, a nearly horizontal section through the apex of the cone, it can be seen that the crystalline cone not only makes contact with the rhabdom, but is surrounded by the cytoplasm of the retinula cells. At this level desmosomes can be seen between the tips of the retinula cells and the crystalline cone as well as between the retinula cells themselves.

The crystalline cone is immediately surrounded by two primary pigment cells, which in turn are surrounded by accessory pigment cells (for description of these cells, see below). As the diameter of the crystalline cone decreases proximally, the cytoplasmic volume of the primary pigment cell increases so that the whole unit (crystalline cone+primary pigment cells) has a cylindrical form (Fig. 3).

Retinula Cells

Sections through the distal region of the retinula cells perpendicular to the long axis of the ommatidium show the presence of seven cells with the microvilli of their inner borders closely opposed to form one central, closed rhabdom (Figs. 2 and 5). Sections taken proximally in the last quarter of the ommatidium before the basement membrane is reached, reveal the presence of a small, eighth retinula cell which also contributes to the central rhabdom (Fig. 5). Desmosomes connect each retinula cell to its neighbour at their inner margins near the rhabdom. Four fibrillar processes, known as cone cell process (Walcott, 1971) descend between the retinula cells (Fig. 5). One retinula cell, always has a fibrillar process between it and its two neighbouring cells. This feature has been used to number the cells, the cell with two cone extensions on its border

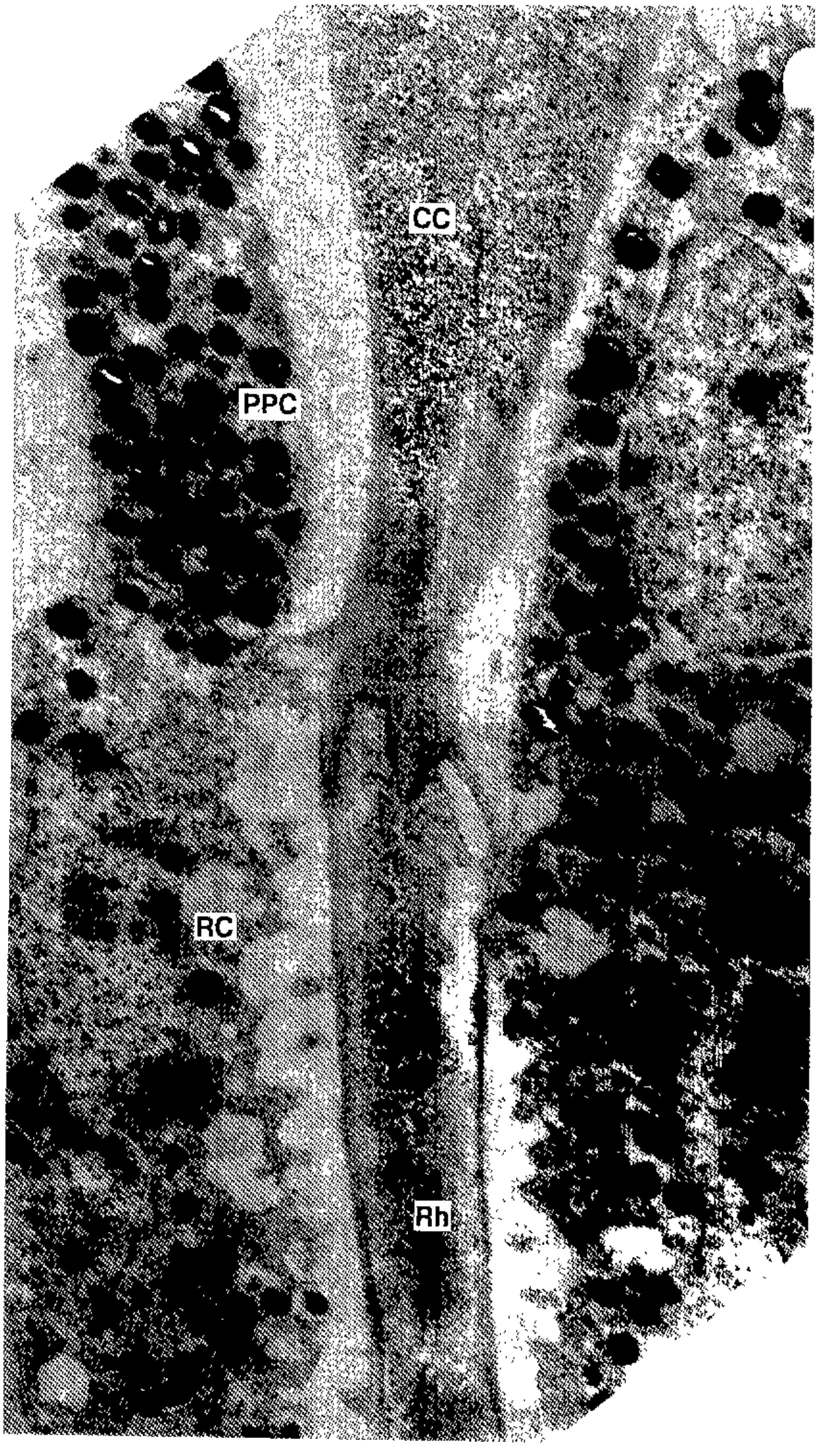

Fig. 3. Vertical section through the ommatidium shows the rhabdom engulfing the apex of the crystalline cone. The size of the pigment granules differs between the primary pigment cell and the retinula cell. CC: crystalline cone; PPC: primary pigment cell; RC: retinula cell; Rh: rhabdom. ×9,050.

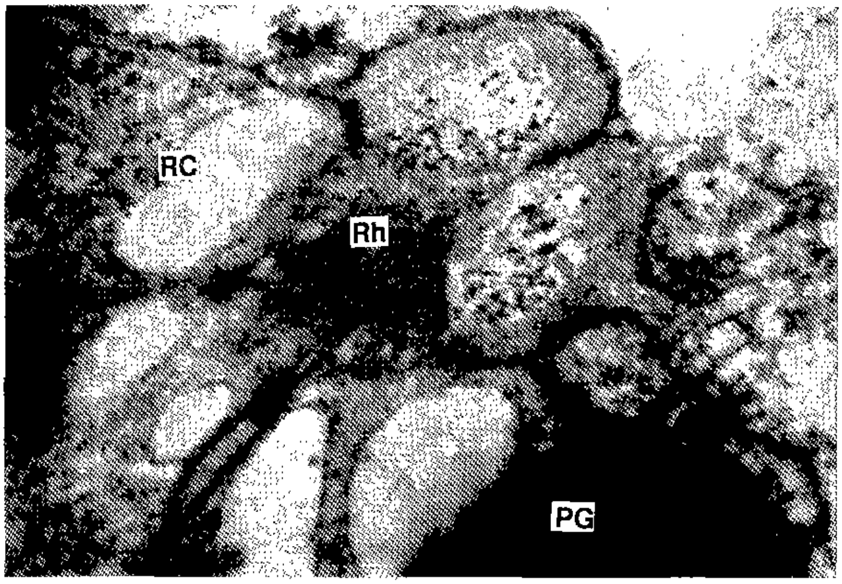

Fig. 4. A slightly oblique horizontal section through the base of the crystalline cone where it contacts the retinular cells. Note the desmosomes where the tips of the retinula cells contact the crystalline cone. CC: crystalline cone. PG: pigment granule: RC retinula cell; Rh: rhabdom. ×37,090.

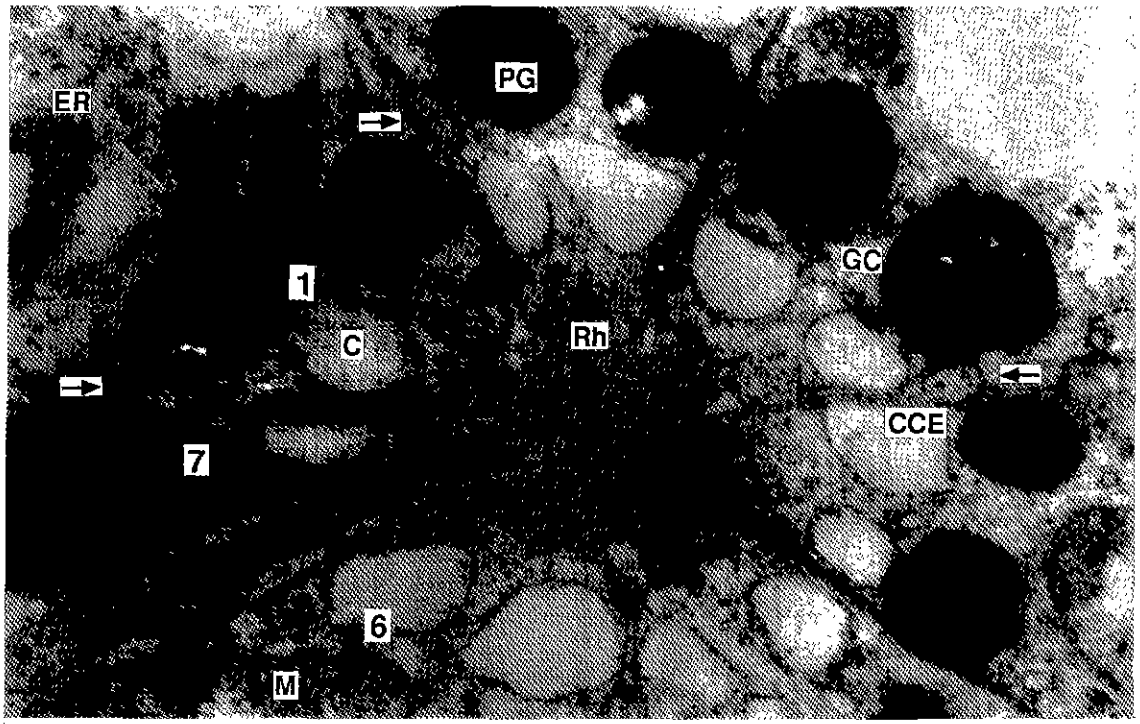

Fig. 5. Horizontal section of a lower part of single ommatidium; the eight retinula cells of the ommatidium can *be seen and cell numbering is arbitrary 8th retinula cell appeared. Four cone cell processes run proximally through* the retina between pairs of retinula cells with the exception of the 8th retinula cell. C: cisternae; CCE: crystalline cone extension; D: desmosome; ER: endoplasmic reticulum: GC· Golgi complex: M: mitochondria; PG· pigment granule, Rh. rhabdom. ×41,970.

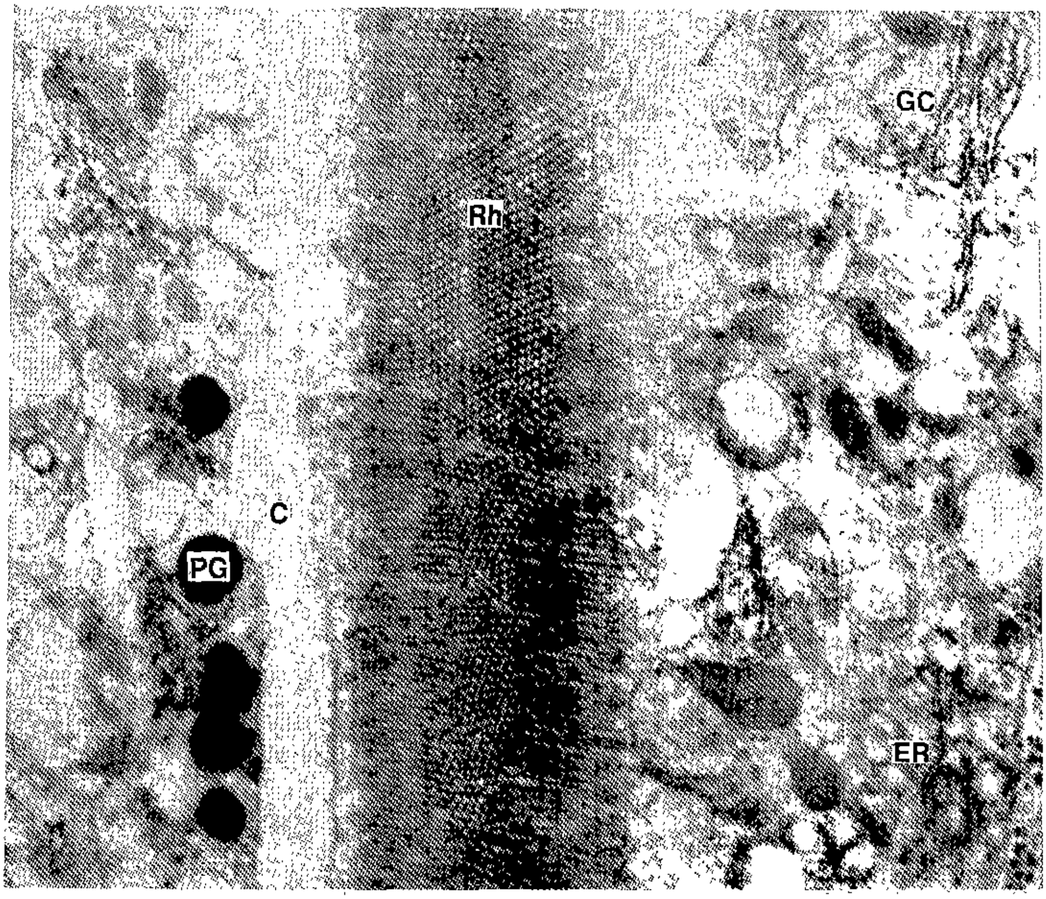

Fig. 6. A vertical section through part of a rhabdom. C: cisternae; ER: endoplasmic reticulum, GC: Golgi complex; PG: pigment granule, Rh: rhabdom ×17,020.

is referred to a cell 1. One fibrillar process runs between each of the two remaining pairs of cells with the exception of cell 8 (Fig. 2). This arrangement of the cone extension appears to be consistent in the brown planthopper unlike some insects (e.g., Wilson, 1975). The cells are numbered in a clockwise manner from cell 1 with the exception of cell 8 which protrudes proximally between cells 6 and 7.

Sections taken parallel to the long axis of the rhabdom show that the nuclei of cells 1~7 are situated in the distal-most region of the ommatidia, just below the crystalline cone (Fig. 3). The nuclei of these cells are irregular in outline but measure approximately 4~6 μm in width and 20~40 μm in length. The smaller nucleus of the 8th cell lies in the proximal quarter of the cell (Fig. 2).

Each ommatidium has a central rhabdom formed from the modified inner border of all of the retinula cells. The rhabdom consists of microvilli arising from the inner wall of each retinula cell (Fig. 6). The microvilli of each cell are oriented with their long axes perpendicular to the long axis of the cell (Fig. 6). Within that plane the orientation of the microvilli depends upon the cell to which they belong, so that there is a gradual change in the orientation of the long axis of the microvilli around the rhabdom. Each microvillus is about 40~45 nm in diameter and 450~530 nm long in the light adapted state. In cross section the microvilli exhibit a characteristic honeycomb appearance (Fig. 6). Observation at high power show that the microvilli are finger-like evaginations of the photoreceptor cell plasma membrane. These evaginations butt up against each other centrally to form the single rhabdom structure.

The Pigment Cells

Three types of pigment cell have been described in compound eyes, (rev. Trujillo-Cenóz, 1985), and all three appear to be present in the brown planthopper. These comprise the primary pigment cells enveloping the crystalline cone, the accessory pigment cells extending from the inner surface of the cornea to the basement membrane and the small pigment cells of the basement membrane.

The primary pigment cells are two large cells which surround the crystalline cone in each ommatidium (Fig. 3) and also the distal-most tips of the retinula cells. The distal part of the primary pigment cell near the corneal lens is narrow and at a this layer of the cells cytoplasm lies between the crystalline cone and the corneal lens. Microtubules are evident where the cell abuts onto the corneal lens The proximal region of the cell widens as the crystalline cone decreases in diameter and this region of the cell contains the nucleus (Fig. 3). The cell is rich in organelles other than pigment granules, e.g., mitochondria, endoplasmic reticulum, Golgi complexes. The pigment granules are concentrated in the proximal part of the cell and appear in two principal forms. Some granules are small, round and of homogeneous electron density rather like those of the retinula cell and the accessory pigment cells. The remaining pigment granules, which occur more frequently, are larger, 0.7~0.8 μm in diameter, and more irregular in shape.

The accessory pigment cells contact the corneal lens distally. They are comprisous as they surround the primary pigment cells and the distal-most region of the retina, containing large numbers of pigment granules of the same size and shape as those in the retinular cells. The nuclei of these cells lie at the level of the middle third of the crystalline cone. The accessory pigment cells become smaller as they descend through the retina and contain few pigment granules. Individual ommatidia are not completely ringed by accessory pigment cells but the retinula cells of one ommatidium are frequently apposed to those of the next ommatidium, the accessory cells occupying a relatively small area from the medial to the proximal region of the retina (Fig. 7).

The basal pigment cells are short and loaded with large granules of pigment. These cells are attached to the basement membrane, their cell bodies are located at that level and protrusions filled with pigment granules extend up between the descending retinula cell axons (Fig. 7)

The Basement Membrane

The basement membrane is 0.6~1 0 μm thick and composed of diffusely fibrous material, possibly collagen fibres (Fig. 7). Numerous tracheae (0 6~0.9 μm in diameter) penetrate through the basement membrane and run in longitudinal arrays between the retinula cells. The axons of the retinula cells descend through the basement membrane towards the first optic ganglion. The neural organization of the optic ganglia of *N. lugens* has not been examined in this study. It is not possible to say therefore whether all the retinular axons terminate in optic ganglion I or whether some axons descend to optic ganglion II.

DISCUSSION

Examination of the structure of the brown planthopper compound eye shows it to be a simple apposition eye similar to that described in the grasshopper (Fernández-Morán, 1958), locust (Horridge and Bernard, 1965; Horridge *et al.*, 1981; Williams, 1982), cockroach (Wolken and Gupta, 1961; Wilson *et al.*, 1978; Butler, 1973) and bee (Schinz, 1975). Each ommatidium contains a corneal lens, a crystalline cone formed from four cells and seven retinula cells stretching between the crystalline cone and the basement membrane, with a smaller eighth proximal retinal cell. The rhabdom formed by the modified inner border of these cells is a closed one. The crystalline cone cells are surrounded by two primary pigment cells containing pigment granules and these in turn are surrounded by accessory pigment cells that extend beyond the primary pigment cells to surround the distal region of the retinal cells. The accessory cells extend beyond this to the basement

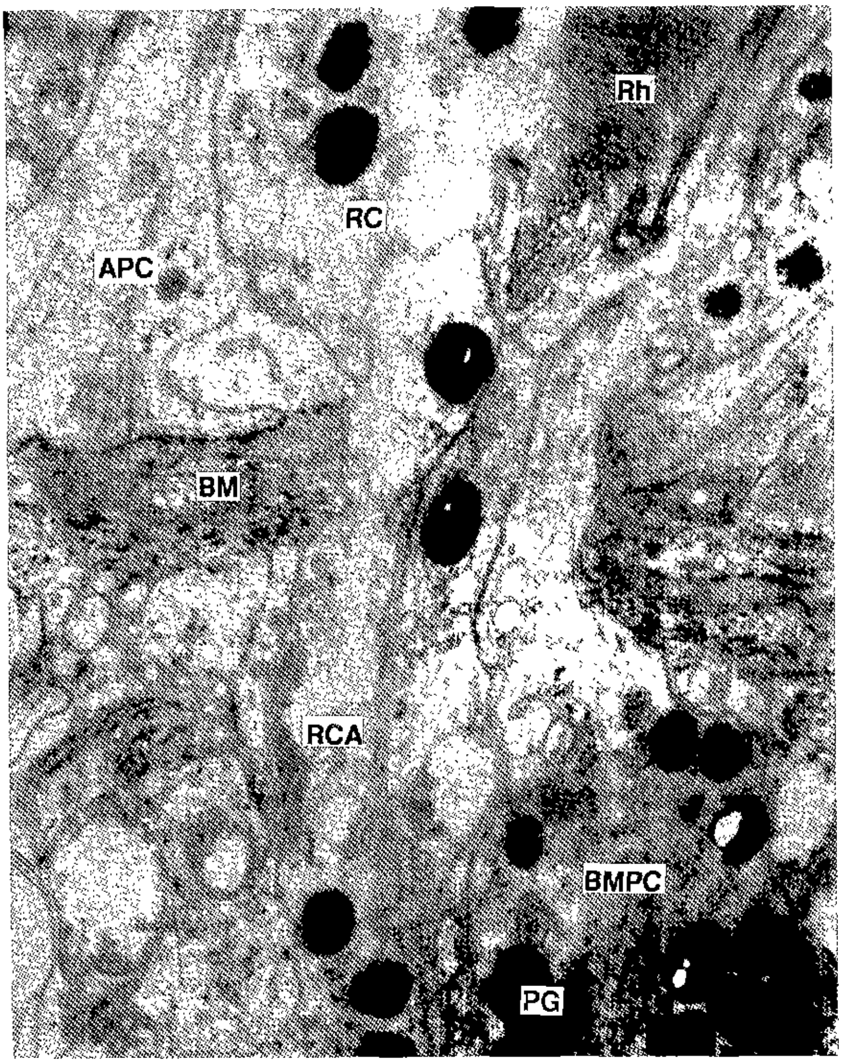

Fig. 7. Ultrastructure of the proximal retina and axons. The rhabdom narrows and, after it terminates, the retinula cell abruptly reduces in diameter forming an axon Note that some pigment granules are seen within the axon. The basement membrane pigment cells (BMPC), containing pigment granules (PG), protrude upwards through the basement membrane (BM) around the base of the retinula cells APC: accessory pigment cell, RC: retinula cell; RCA: retinula cell axon ×24,720

membrane but they become smaller as they descend so that they do not completely surround the retinal cells of each ommatidium in the medial and proximal retina. There some of the retinula cells of neighbouring ommatidium butt up against each other. The accessory pigment cells contain many fewer pigment granules as they narrow but the retinula cells themselves contain pigment granules and these presumably serve to screen the rhabdom in each ommatidium from its neighbours. The basement membrane is lined with cells containing pigment granules and projections from these cells push up between the retinal cell axons as they descend through the basement membrane. The retina is thus lined with black pigment granules presumably absorbing any light that has passed through and not been absorbed by the photoreceptor pigment. There is no sign of any reflecting tapetal layer in this eye. On passing through the basement membrane the retinal cell axons can be seen to swell and become irregular in outline forming terminals in the first optic ganglion, the lamina. The fine structure of the ganglia was not examined and it is not known whether all of the retinal axons terminate in this ganglion or whether some pass through to the medulla as, for example, in *Apis* (Goldsmith, 1962, 1964).

External examination of the eye by SEM does not reveal any obvious difference between the eyes of adult males and females except for a difference in size. There are more facets present in the eye of the female. Inspection of the corneal facets does not suggest that there are obvious areas of smaller facets that might form a 'foveal' region. However it cannot be deduced from this that there is little variation of ommatidial angle across the eye. Future studies in which the ommatidial angle is measured carefully across the eye at all levels are necessary to examine this point.

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