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THE COMPOUND EYE OF DIAMONDBACK MOTH, *PLUTELLA XYLOSTELLA* (L.) AND ITS PIGMENT MIGRATION

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Chung-Hsing Wang and Sze-Jih Hsu (1982) The Compound Eye of Diamondback Moth, *Plutella xylostella* (L.) and Its Pigment Migration. *Bull. Inst. Zool., Academia Sinica* **21**(1): 75-92. The compound eye of the diamondback moth, *Plutella xylostella* (L.) from the cornea to the basement membrane has been investigated with scanning and transmission electron microscopes.

The compound eye of the diamondback moth is composed of 1500-2000 ommatidia. Each ommatidium consists of corneal nipples, a lamellar cornea, a non-homogenous crystalline cone, 2 principal pigment cells, 6 shorten-type accessory pigment cells, 7 retinular cells with a basal retinula cell, trachea-tapetum and a fenestrated basement membrane. The characteristic features of the compound eye of the diamondback moth are similar to that of the nocturnal moth.

The pattern of the pigment migration in dark and light conditions was also discussed in this paper.

The structure and optical properties of the compound eye in Lepidoptera have been reported[2,9,10,19,24] and reviewed with a most detailed description with the conventional light microscope[28]. Because of the strides made in transmission electron microscopy, scanning electron microscopy, freeze-etching technique, electrophysiology and others, enormous advances in our understanding of the functional organization of insect photoreceptors have occurred recently[8]. The ultrastructure studies concerning the compound eye of Lepidoptera are the eccentric retinula cell in *Bombyx mori*[12]; the corneal nipples of nocturnal moth[3]; a clear-zone eye of *Ephestia*[14,16]; the superposition eye of skipper butterflied[17] and the superposition eye of diurnal moth, *Phalaenoides tristifica*[18].

The estimation of activity from the morphological structure of the compound eye of Lepidoptera had been describibed by Yagi and Koyama[28,29]. The nocturnal activity of the diamondback moth had been presumed by Yagi and Koyama[29]. Recently the activity of the diamondback moth has been studied at various seasons and has been emphasized that the temperature factor is more conspicuous than light intensity[1].

The objective of the present report is to demonstrate the fine structure of the compound eye of the diamondback moth and to point out certain features concerning the functional morphology of the diamondback moth as a basis for further work on it's activity in the field.

MATERIAL AND METHOD

The heads of the diamondback moths, *Plutella xylostella* (L.) were decapitated and then treated with different methods according to the apparatus ued for observation.

(A) **Light microscopy**

Samples (heads) were fixed in formoalcohol and embedded in paraffin. Sections are 7 μm in thickness. The preparations were stained with hematoxyline and eosin and examined with the bright-field microscope.

(B) **Transmission electron microscopy**

Samples were sliced in half in 2.5% glutaraldehyde in pH 7.2, 0.1 M phosphate buffer at 4°C and then post-fixed in 1% osmic acid in pH 7.2, 0.1 M phosphate buffer at 4°C. After dehydration in the acetone series, the compond eyes were embedded in Spurr epon. Ultrathin sections were cut and then stained with uranyl acetate and lead citrate and viewed with JEM 100S transmission electron microscope at 80 KV.

(C) **Scanning electron microscopy**

Two different methods were used: (1) Epon-fraction methods: The compound eyes were fixed, dehydrated and embedded with the same procedure as for transmission electron microscopy. The blocks of the compound eye were fractured with a razor blade. Carbon and gold were deposited over the eye fragments in a vacuum evaporator and observed with JSM 15 scanning electron microscope at 15 KV. (2) Dry-fraction method: The compound eyes were double-fixed with 2.5% glutaraldehyde and 1% osmic acid. Samples were dehydrated with gradated alcohol and dried in CO_2 critical point apparatus, and were fractured with a razor blade. The fragments were coated with carbon and gold and observed with JSM 15 scanning electron microscope at 15 KV.

(D) **Pigment migration**

(1) One group of the moths were decapitated in light, fixed in formoalcohol for routine histological section and stained with hematoxylin and eosin.

(2) Another group of the moths were put in the dark room for 2 hour, killed with boiling water in dark. The heads were also prepared for histological observation with the same procedure as[1].

The light absorption rate of ommatidium was measured with microspectrophotometer at 550 nm.

OBSERVATION AND DISCUSSION

The compound eye of the diamodback moth, *Plutella xylostella* is approximated hemispherical (Fig. 1) and composed of 1500–2000 hexagonal facets. The diameter of each facet is 17.79 ± 1.12 μm in male and 17.70 ± 0.92 μm in female. Like most moths, unequal number of facets is found in both sexes. There is a relatively small number of facets of the female diamondback moth in comparison with that of the male. The compound eye is surrounded by a dense layer of long hairs (Fig. 6). There are interfacet hairs between the facets. The length of the interfacet hairs is 4–13 μm in the male and 5–16 μm in the female.

The general structure of an ommatidium is illustrated in Fig. 2, with representative cross sections at different levels and a key to the location of the electron micrographs. The following account refers to details at progressively deeper levels based mainly on chemically fixed light-adapted eye. The structure of the ommatidium of the diamondback moth includes dioptric apparatus, light-insulation apparatus, retinula cells, trachea-tapetum and basement membrane. The minute structures of each part are described as follows.

1. **Dioptric apparatus**

Light reaches the retinula cells through a dioptric apparatus composed mainly of cornea, crystalline cone and crystalline tract (Fig. 2, 3a, b, c, d, 6, 7).

(a) Cornea

The cornea is plane-convex with a radius

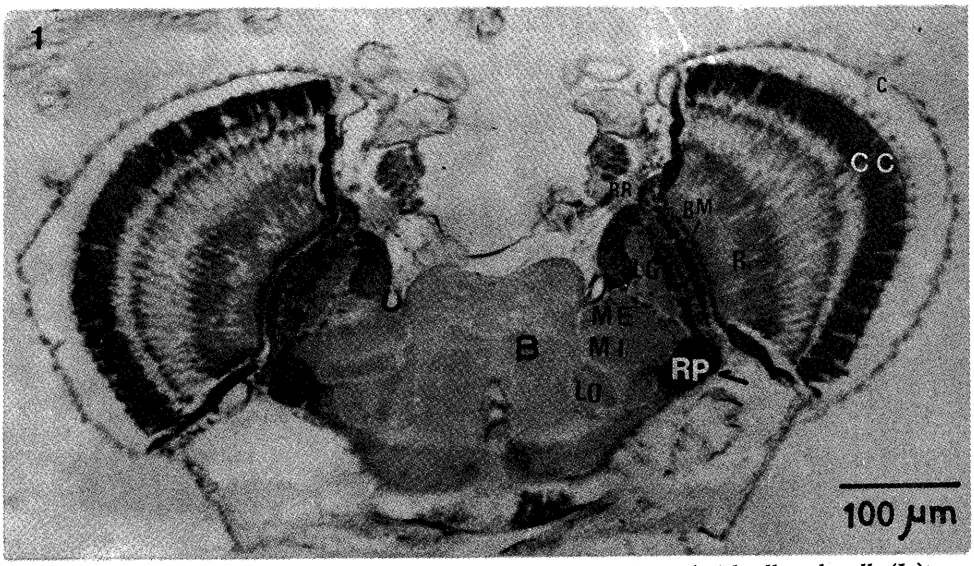


Fig. 1. A frontal section of the head of the diamondback moth, ***Plutella xylostella*** (L.), showing the structure of the compound eye. B: Brain; BM; Basement membrane; BR: Basal retinular cell; C: Cornea; CC: Crystalline cone; LG: Lamina ganglionaris; LO: Optic lobe; ME: Medulla externa; MI: Medulla interna; R: Rhabdom; RP: Rudimentary pigment cells of stemmata of larva.

of its curvature 4 μm and a diameter of 20 μm. Each corneal facet surface is covered with a perfect hexagonal array of 4500 corneal nipples (Fig. 8, 9) which are 200 mμ in diameter and 240 mμ high (Fig. 3b, 4). By the presence of corneal nipples, the surface area of the facets is increased 3 times.

The cornea which is treated with epon-fraction method shows that it is a lamellar structure with a periodicity of about 0.2 μm and at least has 19 layers (Fig. 3a, 4, 9). By comparing the results of SEM with those of TEM, the layer structure in SEM shows an electron-dense layer in the TEM preparation. The electron-lucent layers are about 0.13 μm thick in the facet center, except in the part just underneath the epicuticle which is about 0.29 μm thick. Therefore the electron-lucent layers may be the interlamellar matrix (Fig. 4). The curvature of the lamellar decreases from the outside toward the inside, so that the innermost layer is almost flat. The facets of the diamondback moth are collapsed in the center because the electron-lucent layers lost water in the high vacuum (Fig. 6). There is no corneal process at the inner side of the cornea (Fig. 10a). Both the structures of nipples and epicuticle are very similar (Fig. 4). It is proper therefore, to assume that the nipples are the protrusions of the epicuticle. It has been described that the color reflection patterns of the compound eye of Diptera, Coleoptera and some other insects, are caused by the lamellar structure of the cornea(6,7,13,22,23,25). Though the compound eyes of the diamondback moth have a lamellar structure in the cornea, they do not show color reflection. This result coincides with theory that the cornea nipple may decrease the reflection of light(3,4).

(b) Crystalline cone and tract

Beneatth the flat inner surface of the cornea, there is a conical shaped crystalline cone consisting of 4 parts formed by four corneagenous cells (Fig. 3b, 10c). The nuclei of corneagenous cells (Fig. 3b, 10c). The nuclei of corneagenous cells are homogeneous, about 5.5 μm in diameter, lying on the top of the crystalline cone (Fig. 3a). The cones, 15 μm wide at distal end, taper over their 24.2 μm and 3 μm wide at the proximal end. The distal surface of the crystalline cone is plane (Fig. 10b). The surface of the cone, distributed a lot of microtubules which run parallel to the long axis of the cone cells, can readily be seen Fig. 10c. About half the way down the cone, there is a slightly constricted ring, about 9 μm in diameter (Fig. 10a, b). It was suggested that the light rays would be forced to cross over near the constriction point in hour-glass cones[8], therefore the constriction of the diamondback moth cone may have the same function. However, its real significance remains to be elucidated. The cross section of the cone is nonhomogeneous and can be divided into four concentric zones with different electron density (Fig. 10a, b), which are presumably related to the gradient of the refractive index[8,18], and also one of the characteristic features of the nocturnal moth[20,27]. This morphological evidence coincides with the fact that the diamondback moth is a nocturnal moth as indicated by Yagi and Koyama[28,29].

The crystalline tract, about 8.13 μm long, 0.9 μm in diameter, extends from the proximal end of the cone downward to the distal retinula cell processes. The deeper it goes, the smaller the diameter is (Fig. 11). The crystalline tract has kept the four tetrameres (threads), as in a cone (Fig. 3c). The tract divides into two sectors, each containing 2 tetrameres, into which the retinula cell extends (Fig. 3d, 5). The rhabdom of the retinula cell is visible at the connection point. This type of connection is very simmilar to that of the mantis *Ciulfina* described by Horrige and Duelli[15]. As to the function of the crystalline tract, many authors suggested that the tract acts as a light guide or pipe[8,11,13,22].

2. **Light-insulating apparatus**

The light-insulating system of the diamohdback moth consists of two principal pigment cells and six accessory pigment cells.

The two principal pigment cells surround each crystalline cone and tract. The cell body extends from the cornea to the proximal end of the crystalline tract. The irregularly shaped nucleus lies near the tip of the cone. The highly electron-dense pigment granules and oval-shaped with a diameter ranging from 0.62 to 0.76 μm (Fig. 3c, d). A few microtubules are observed in the cytoplasm of the principal pigment cells.

The six accessory pigment cells, surrounding each ommatidium and shared with adjacent ommatidia, extende from the lens to the basement membrane (Fig. 3a–h). They are enlarged between the cone tip and the distal end of rhabdom columns (Fig. 5). At the six corneas of the hexagonal rhabdom column, the two or three-forked cell processes of the accessory pigment cells are thrust between tracheae or between retinula cells and trachea (Fig. 3g, h). It is remarkable that the pigment granules, which are 0.56–0.76 μm in diameter are restricted to the distal ends of these long cells (Fig. 5). All the nuclei of the accessory pigment cells lie at the same level near the crystalline tract, a little lower than the position where the nuclei of the principal pigment cells are located. The microtubules of the cytoplasm of the accessory pigment cells are more crowded than in the principal pigment cells (Fig. 3b, c, d, 5), therefore it is easily to distinguish the principal pigment cell from the accessory pigment cells. There are three types of the accessory pigment cells of Lepidoptera, a shortened type, a separated type and a lengthened type[28]. The shortened type to which the diamondback moth belongs is the most common type in nocturnally active moths.

The pigment granules of both pigment cells can migrate in response to light intensity. The pigment migration can be observed by the absorption curve measured with microspectrophotometer (Fig. 17, 18). In the light-adapted eye, the crystalline tract and the distal retinula cell processes are surrounded by pigment granules and only a few pigment granules are located around the cone (Fig. 7, 12, 17). On the other hand, the pigments of dark-adapted eye surround the cone and form a clear-zone between the cone tip and the rhabdom column (Fig. 1, 18).

Fig. 2

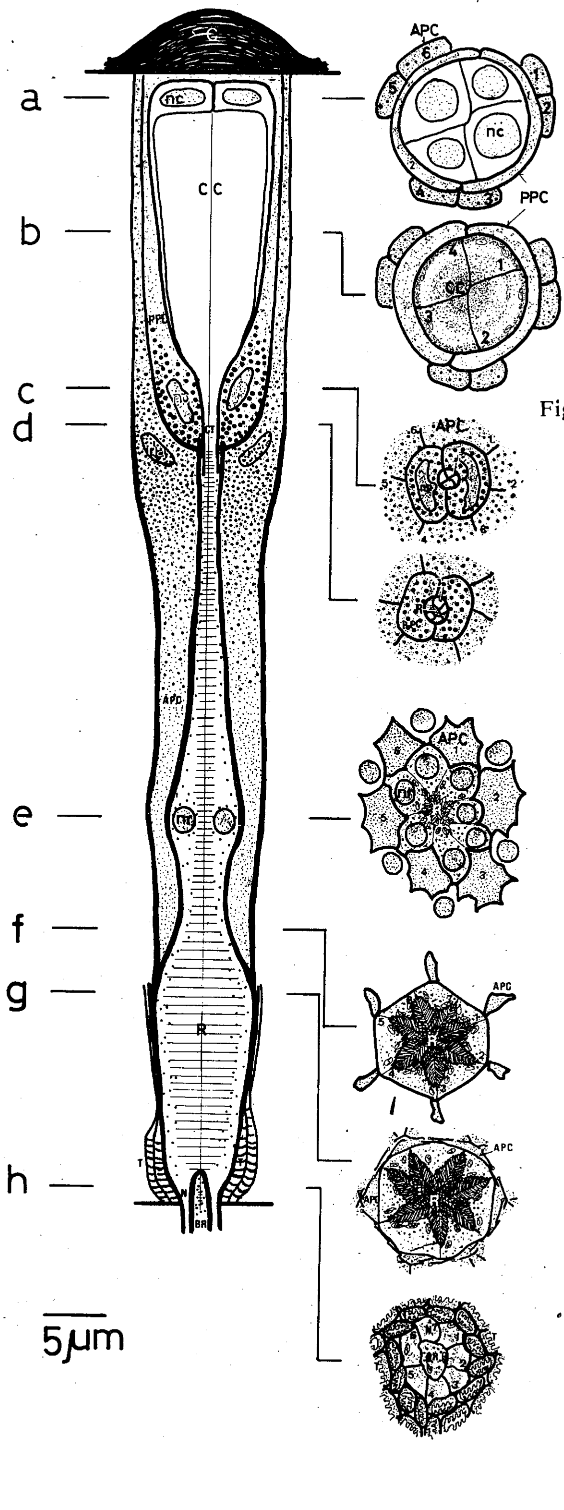


Fig. 2. Illustration diagrams of the ommatidium of *P. xylostella* (L.), showing a longitudinal section (left) and transverse sections (right) at the levels indicated with a-h.

a. nuclei of the corneagenous cells (nc). The cone is surrounded by 2 principal pigment cells (PPC) and 6 accessory pigment cells (APC) indicated by arabic numbers (1-6).
b. crystalline cone. Arabic numbers (1-4) indicate 4 parts of crystalline cone (CC).
c. crystalline tract. Arabic numbers (1-6) are 6 accessory pigment cells. np: nucleus of principal pigment cells.
d. the connection point of crystalline tract and retinula cell column (R).
e. the nuclei of retinula cells (nr).
f. the distal end of the rhabdom column (R.) 1-7: retinula cells.
g. the rhabdom column.
h. the retinula axon (1-7) surrounded by trachea.

Fig. 3. The ultra-thin sections (a-K) of the light-adapted ommatidium at progressively deeper levels.

a. An oblique section through the dioptric apparatus, showing the lamellar structure of cornea (C) and the homogeneous nuclei (N) lying on the crystalline cone top (CC).

b. A cross section of the crystalline cone (1-4), showing the cone surrounded by principal pigment cells (PPC) and accessory pigment cells (APC).

c. a cross section through the crystalline tract (CT) at the level of the principal pigment cell nuclei (N), showing the 4 tetrameres of the crystalline tract and the pigment granules of the principal pigment cells and accessory pigment cells around the crystalline cone in light-adapted eye.

d. A cross section just through the connection point, showing the crystalline tract dividing into two sectors, each containing 2 tetrameres into which the retinula cell extends (R).

e. A cross section through the narrow part of the retinula cell column at the level of the nuclei of 7 retinula cells (1-7), showing the desmosomes at the boundary of the rhabdomeres.

f. An oblique section of the retinula cell column near the expanded proximal part, showing the hexagonal structural of retinula cell column and the microvilli of rhabdom.

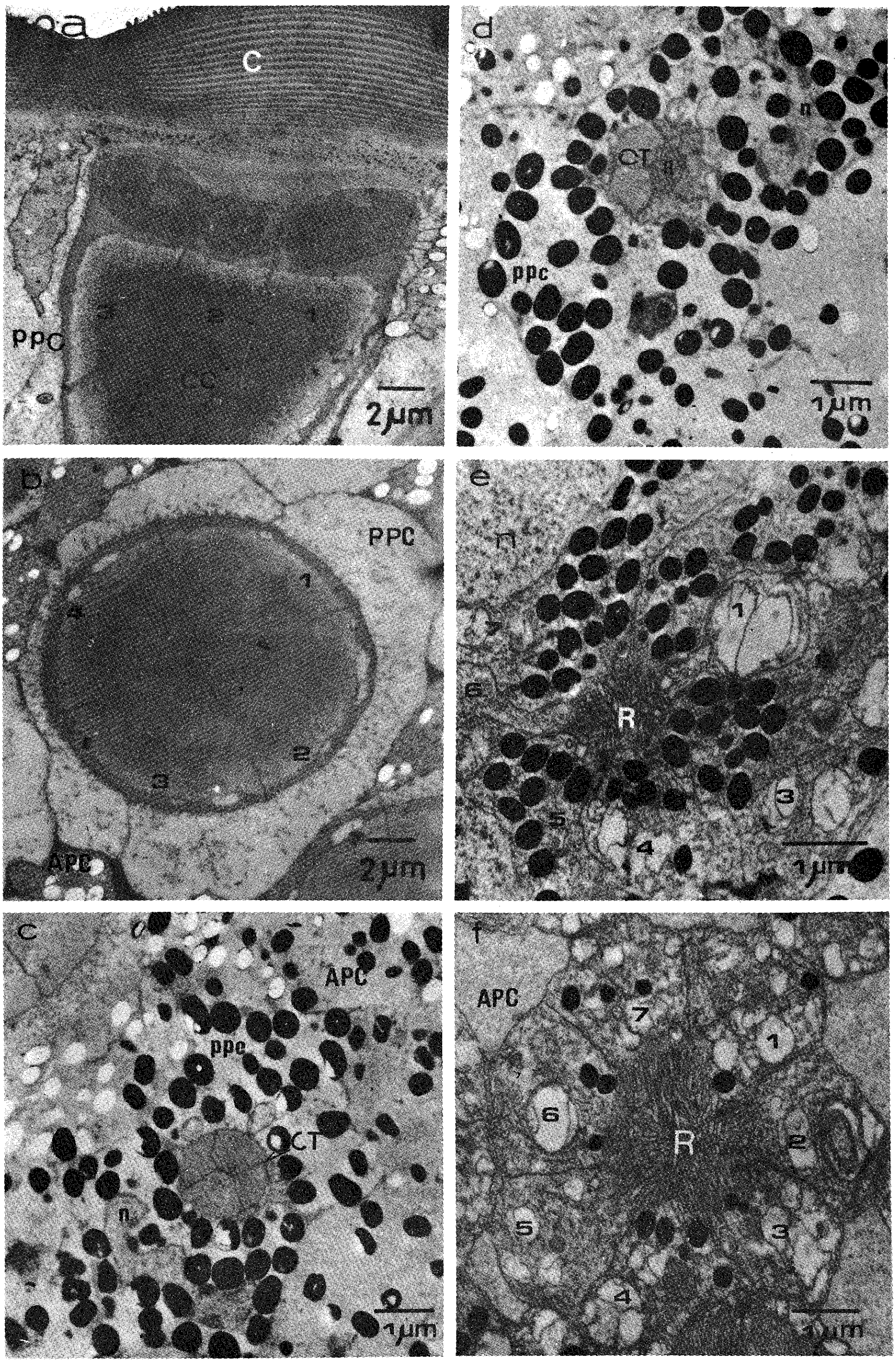
g. An oblique section through the transition level of the narrow distal part and the expanded proximal part (rhabdom colum), showing the rhabdom column surrounded by the collapsed tracheae (Arrow).

h. A cross section of the hexagonal rhabdom column, showing the accessory pigment cell (APC) divided into 3 cell processes by tracheae. Each cell processes thrusts into one of 3 adjacent corneas belonging to 3 neighboring rhabdom columns.

i. An oblique section through the proximal end of rhabdom column, showing retinula axons surrounded by trachea-tapetum (T).

j. A cross section just distal to the basement membrane, showing the rhabdomere (R) of the basal retinula cell.

k. A cross sectionr though the fenestrated basement membrane, showing the fibrous structure of basement membrane and it's perforation penetrated by retinula axons and tracheae.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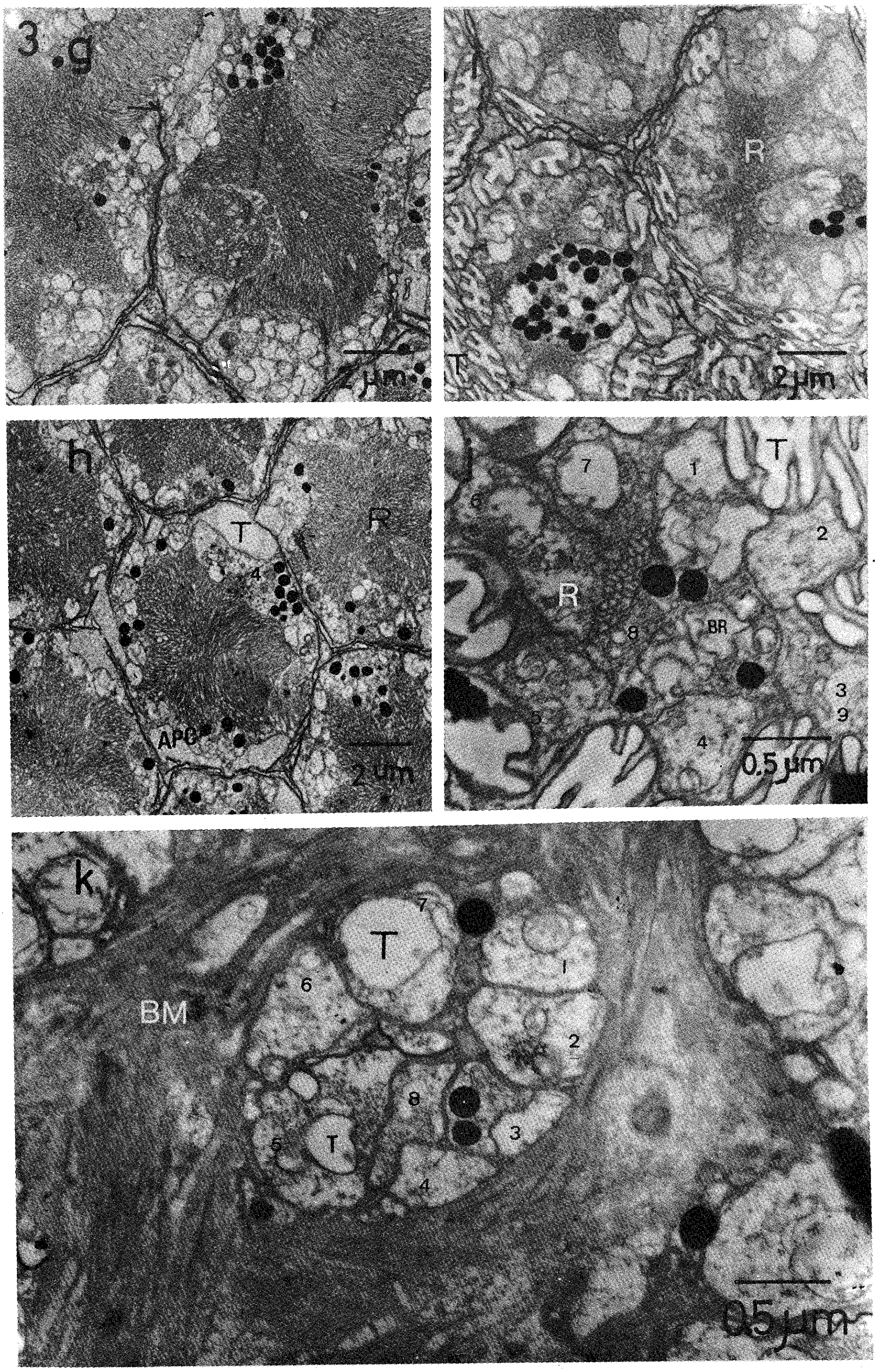
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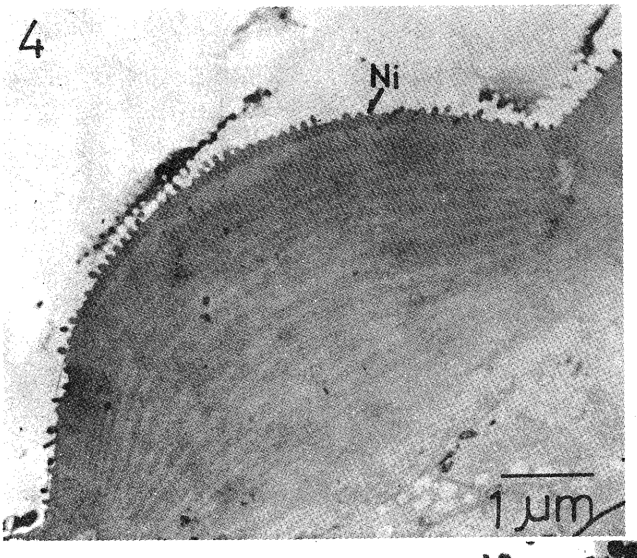


Fig. 4. A longitudinal section of a cornea, showing it's lamellar structure and the corneal nipples (Ni).

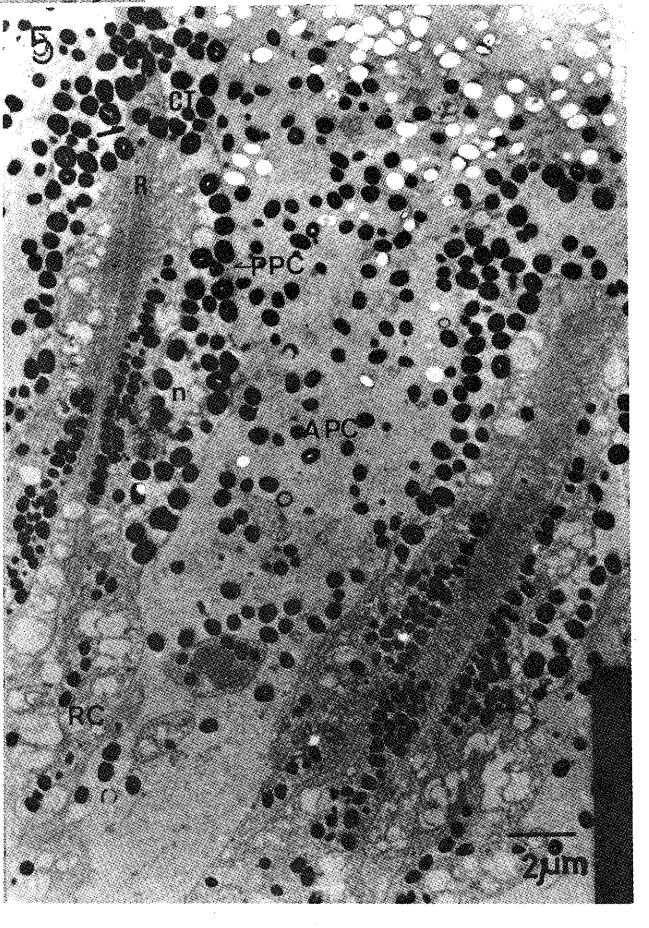


Fig. 5. A longitudinal section through the distal end of the narrow part of retinula cell column, showing the transition point of crystalline tract (CT) and retinula cell column (arrow). In this area, the crystalline tract and retinula cell column are insulated by the pigment granules of principal pigment cell and accessory pigment cells (PPC and APC).

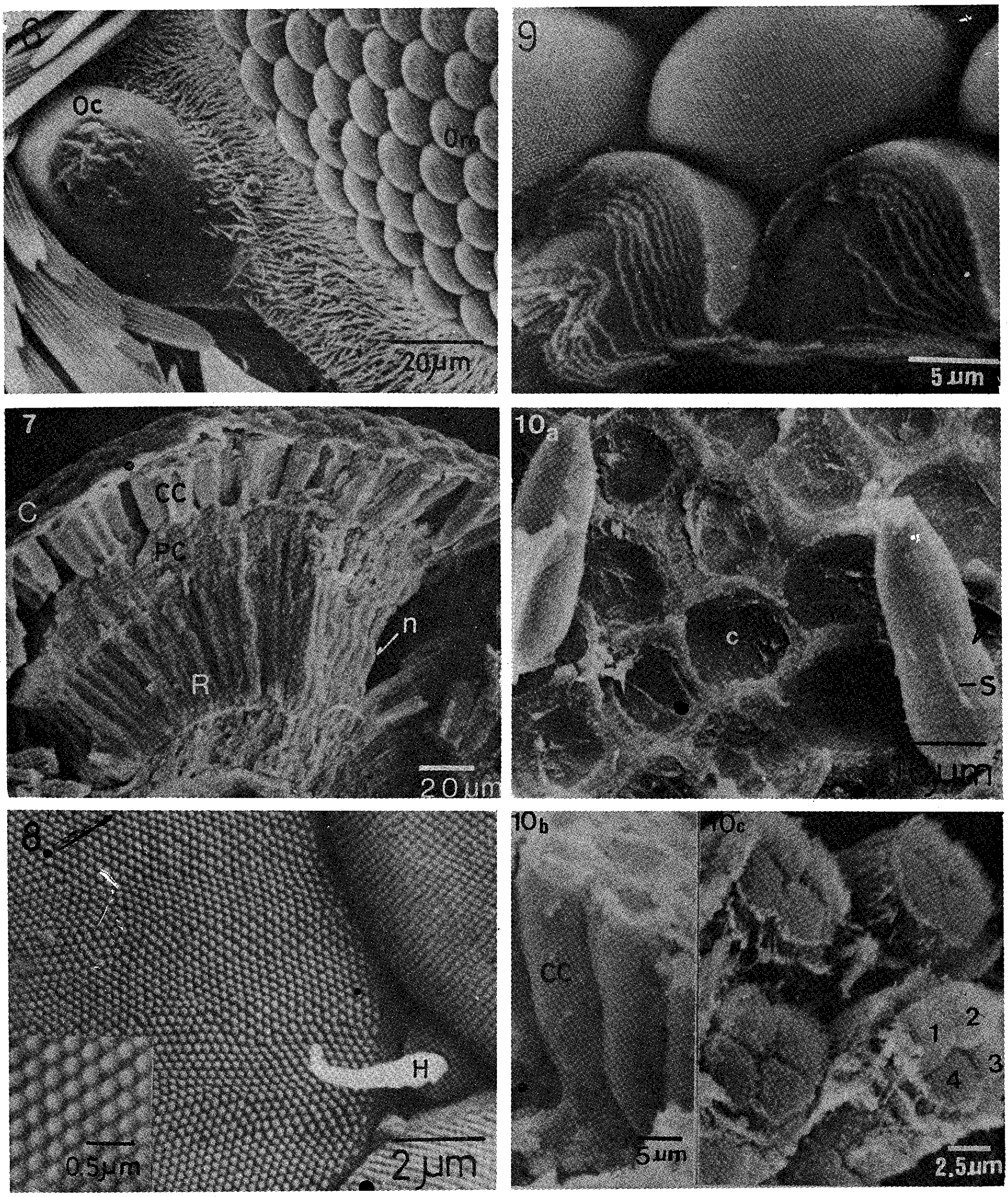
Figs. 6-10. Scanning electron microgarphs, showing the structures of the compound eye of ***P. xylostella.***

6. The surface structure of the hexagonal facets (CM), ocellus (OC) and the hairs surrounding the compound eye.
7. A fraction of the compound eye prepared by dry-fracture method, showing internal structures of the compound eye.
   C: cornea CC: crystalline cone PC: pigment cell R: retinula cell
8. The corneal nipples of the facets, showing their regularly hexagonal array. Insert is the higher magnification of corneal nipples.
9. A fraction of cornea prepared by epon-fracture method, showing the lamella structure of cornea.

10a. Two inverted crystalline cones with a constricted ring (arrow).
S: suture line of 2 corneagenous cells C: cornea

b. A cluster of the crystalline cones with the cornea removed.
CC: crystallin cone.

c. Four corneagenous cells of a cone, indicated by arabic numbers 1-4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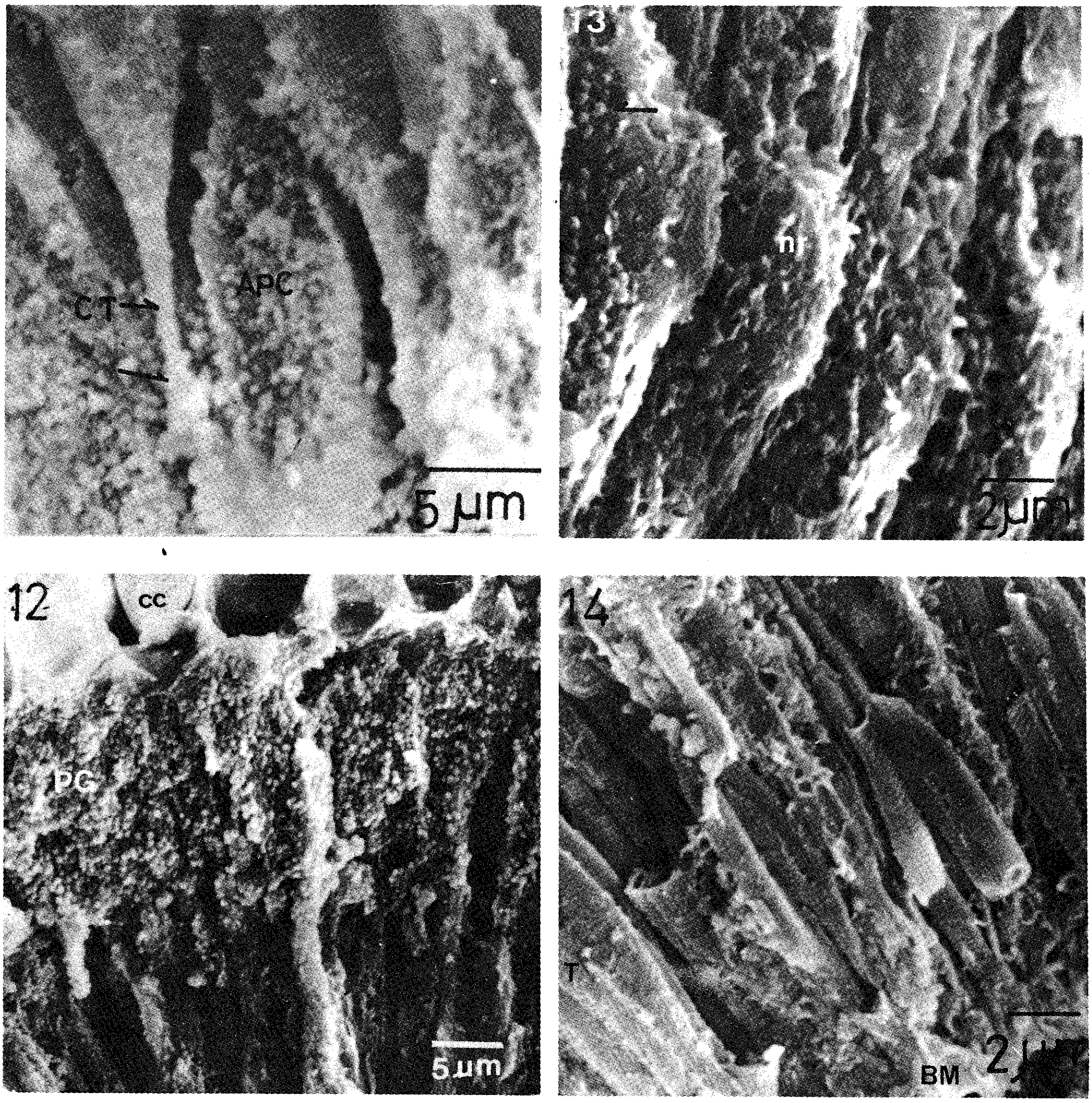
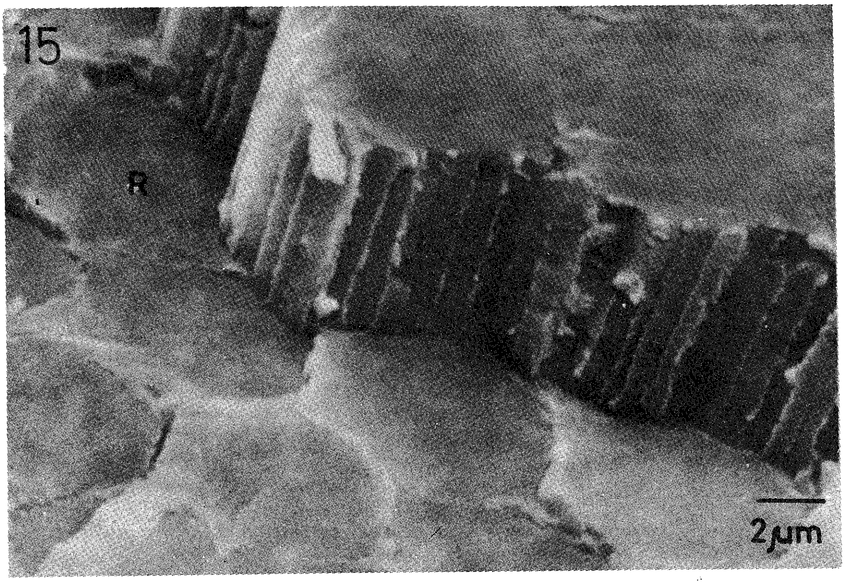
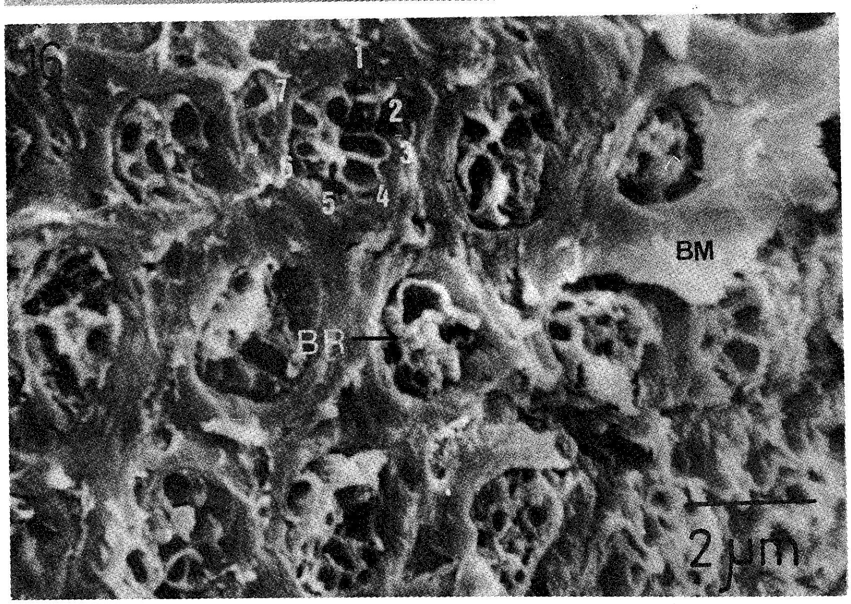


Figs. 11-14. Scanning electron micrographs, showing the internal structures of the compound eye of *P. xylostella*.

11. The crystalline tract (CT) and the distal end of the narrow part of retinula cell column (arrow).
12. The pigment granules of pigment cells (PG) surrounding the crystalline tract.
13. The nucleus (nr) of the retinula cell. The arrow shows the pigment granules of the retinula cell.
14. The trachea-tapetum (T) surrounding the proximal part of the rhabdom column BM: Basement membrane.



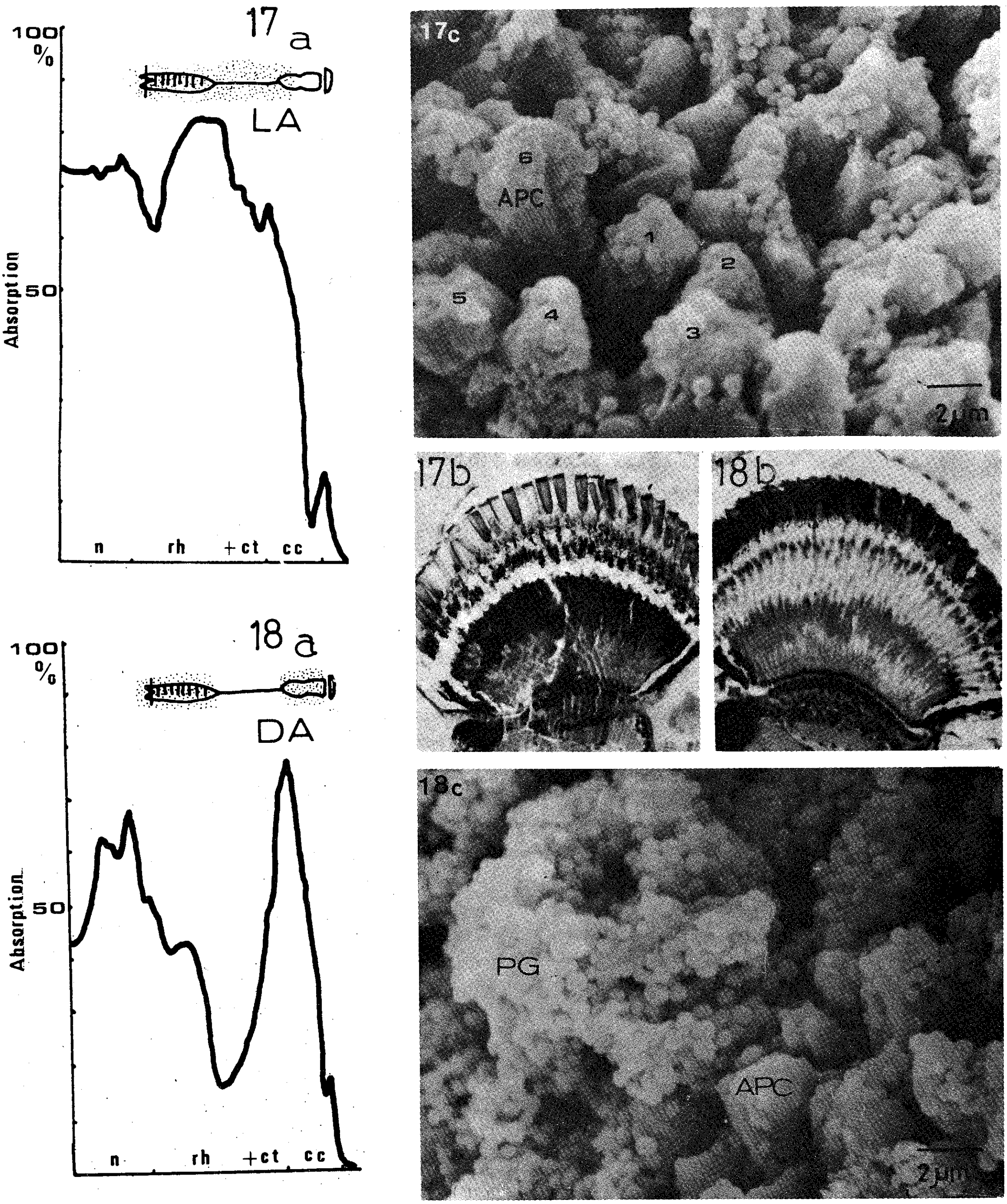


Figs. 15-16. The scanning electron micrographs, showing the structure of the compound eye of *P. xylostella*.

15. The fraction of the compound eye made by epon-fraction method, showing the hexagonal rhabdom colum (R) surrounded by the rows of trachea.
16. The fenestrated basement membrane (BM). Each perforation is penetrated by seven retinula axon and the cell processes of the basal retinula cell.

Figs. 17-18. The pigment migration of the compound eye of *P. xylostella* in response to the light.

17. The light-adapted eye. (LA)
    a. The light absorption curve of the ommatidium measured by microspectrophotometer from nerve (n) to the cornea. The crystalline tract and the narrow part of retinula cells show the maximum absorption.
    CC: crystalline cone Ct: crystalline tract LA: light-adapted eye
    n: nerve rh: retinula cell column
    b. A histological section of a light-adapted eye, showing the pigment granules migrated to the crystalline tract and the narrow part of retinula cell column.
    c. A scanning electron micrograph of the light-adapted eye, showing only a few pigment granules appearing in the distal end of accessory pigment cells (APC, 1-6).
18. The dark-adapted eye (DA).
    a. The light absorption curve of the ommatidium measured by microspectrophotometer from nerve (n) to the cornea.
    Both the crystalline cone and the proximal end of rhabdom column have a higher absorption rate.
    b. A histological section of a dark-adapted eye, showing the pigment granules migrated to the crystalline cone and the lower part of rhabdom.
    c. A scanning electron micrograph of the dark-adapted eye, showing the pigment granules appearing in the distal end of accessory pigment cells.
    PG: pigment granules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3. Retinula cells and traches-tapetum

There are seven retinula cells and a basal retinula cell per ommatidium. The retinula cell columns formed by seven retinula cells are 73 μm long and can be divided into two parts, the narrow distal part and the expanded proximal part. The narrow part is the extended cell processes of the retinula cells, which makes up almost 75% of the entire length of the retinula cell column (Fig. 5). The expanded part is a regular hexagonal array of retinula cells, in which the rhabdomeres of retinula cells are fused together to be a rhabdom column (Fig. 3g, h, i). The adjacent membranes of the neighbouring cells form desmosomes at the boundary of the rhabdomeres (Fig. 3e–j). These desmosomes appear from the proximal end of crystalline tract, and go down almost to the basement membrane. The nuclei of the seven retinula cells are located at the narrow distal part which is about 32 μm from the basement membrane (Fig. 3e, 7, 13). The cytoplasm of the retinula cell contains a great number of mitochondria and multivesi cular bodies as well as some pigment granules. The pigment granules, 0.31–0.46 μm in diameter, are smaller than those of pigment cells. They also can migrate in response to light intensity.

The rhabdom of the diamondback moth is a closed type. The rhabdomeral microvilli, run about 0.11 μm in diameter, perpendicularly to the axis of the ommatidium. The angle formed by two neighboring rhabdomeral microvilli is 47 degrees. A small basal retinula cell with a small rhabdomere is located at the proximal end of the retinula cell colum (Fig. 3j). The nucleus of this cell lies beneath the basement membrane. The number of the retinula cells in each lepidopteran ommatidium varies, 14–16 retinula cells in *P. tristifica*[18], 11 retinula cells in the silk moth and some Lycaenidae[16,18,21] and 8–9 retinula cells in most Lepidoptera[28]. These different numbers may be due to the more or less use[26,28].

In Lepidoptera, there are three kinds of rhabdoms. One has pillar like retinula cells with which the rhabdoms reach straight down from the crystalline cone to the basement membrane. Many diurnal insects belong to this type. The second type of rhabdoms is that of the diamondback moth and other nocturnal moths[19,24,28]. The third type is a transitional form between the typical day- and night-flying insects, as for instance the eye of the skipper butterfly (Superfamily Hesperioidea)[22].

The tracheae originate below the basement membrane and extend upward through the fenestration of the basement membrane and ascend distally parallel with the rhabdom column (Fig. 3g–j). The tracheae surrounding the distal end of the rhabdom column are in a collapsed state, therefore the tracheae look like a two packed double electron-dense layer. This feature may have some importance in the control of pigment migration and light reflection. There are 5 to 6 tracheae, 10.6 μm in width, on each side of the hexagonal structure of the rhabdom column (Fig. 3b, 15). Just underneath the rhabdoms and between the nerve fibers of retinula cells, many tracheae are crowded together to form the tapetum (Fig. 3i, j, 14). Accoring to the opinion of some authors, the light can be reflected from the trachea-tapetum back to the rhabdom. This mechanism is thought to improve contrast for a particular color[8,22].

4. Basement membrane

The fenestrated basement membrane can be observed by both, the transmissions and scanning electron microscope (Fig. 3k, 16). Each hole, about 3 μm in diameter, is penetrated by many tracheae, seven retinula axons and a basal retinula cell, surrounded by retinula axons. The basement membrane is composed of electron-dense fibers which lie irregularly around the perforations of the membrane.

In conclusion, this preliminary study presents the ommatidium of the diamondback moth, *P. xylostella* (L.), as a compact, bulb ampoule-shaped aggregation of seven retinula cells beneath a crystalline cone which, in turn, is surmounted by a plane-convex cornea. Though the rhabdomeres of retinula cells fuse together, the nerve fibers of the individual retinulacells remain separated. A basal retinula cell lying on the basement membrane is surrounded by those separated nerve fibers of the retinula cells. Other features present are a short, thin cylindrical extension of the crystalline cone, i.e. a crystalline tract, that separates the crystalline cone from the rhabdom. The cone, tract and rhabdom are shielded with pigment granules of 2 principal pigment cells, 6 accessory pigment cells as well as retinula cells. These insulating pigment granules are not in a fixed position, they can migrate in respose to the light. Due to the migration of these granules the ommatidium can control the intensity of the light which passes through the dioptric apparatus and goes into the retinular cells. The migration patterns of the granules are still under further investigation. We are especially interested in the question whether the pigment migration is correlated to different wavelengths, and how the pigment granules migrate in response to various wavelengths. We hope that this investigation could bring about a better understanding of the phototropic activity of the diamondback moth.

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小菜蛾複眼之構造與色素顆粒之移動

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本文爲利用各種顯微鏡術研究小菜蛾複眼之內，外部構造，並研究其複眼內色素顆粒之移動現象。