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RECEPTORS IN INSECT

I. The Fine Structure of the Compound Eye of the Oriental Fruit Fly *Dacus dorsalis* Hendel

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Chin-Yih Wu, Chung-Shia Chang, Li-Chu Tung and Jin-Tun Lin (1985) Receptors in insect I. The fine structure of the compound eye of the oriental fruit fly *Dacus dorsalis* Hendel. *Bull. Inst. Zool., Academia Sinica* **24**(1): 27-38. The fine structure of the compound eye of the oriental fruit fly (*Dacus dorsalis* Hendel) were studied with scanning and transmission electron microscopy. There are about 4500 to 4600 ommatidia in each compound eye of both male and female flies. Each ommatidia consists of a lens covered with corneal nipples, a pseudocone and eight retinula cells surrounded by the primary pigment cells and longitudinal pigment cells. A cross section of the retinula cell cluster shows a rhabdomere structure. A superior retinula cell and an inferior retinula cell are projected into the central ommatidial cavity. The fine features of the compound eye of the oriental fruit fly are similar to that of other dipterans. The histology of the ommatidial elements is discussed.

The fine structure of the ommatidia of certain species of dipterans including flies have been reported and reviewed (Agee *et al.*, 1977, Chi and Carlson 1976, Carlson and Chi 1979, Davis *et al.*, 1983, Melamed and Trujillo-Cenoz 1968, Trujillo-Cenoz and Bernard 1972, Waddington and Perry 1963, Williams 1981). The ultrastructure of the retinula cell offers some hints to electrophysiological studies on the photoreceptor of insects. The present report is to describe the fine structure of the compound eye of the oriental fruit fly. This information will provide necessary guide to study the spectral sensitivity of the compound eyes and define the visual response by electrophysiological studies.

MATERIALS AND METHODS

The oriental fruit flies were fed with artificial diet in our laboratory. After light adapted for one hour, flies were decapitated and fixed for scanning and transmission electron microscopy.

1. Scanning microscopy

Flies were immobilized by chilling in refrigerator for about five minutes. The heads were then dissected out with a sharp razor blade and fixed in 2.5% glutaraldehyde buffered with 0.1M cacodylate (pH 7.3) at 4°C

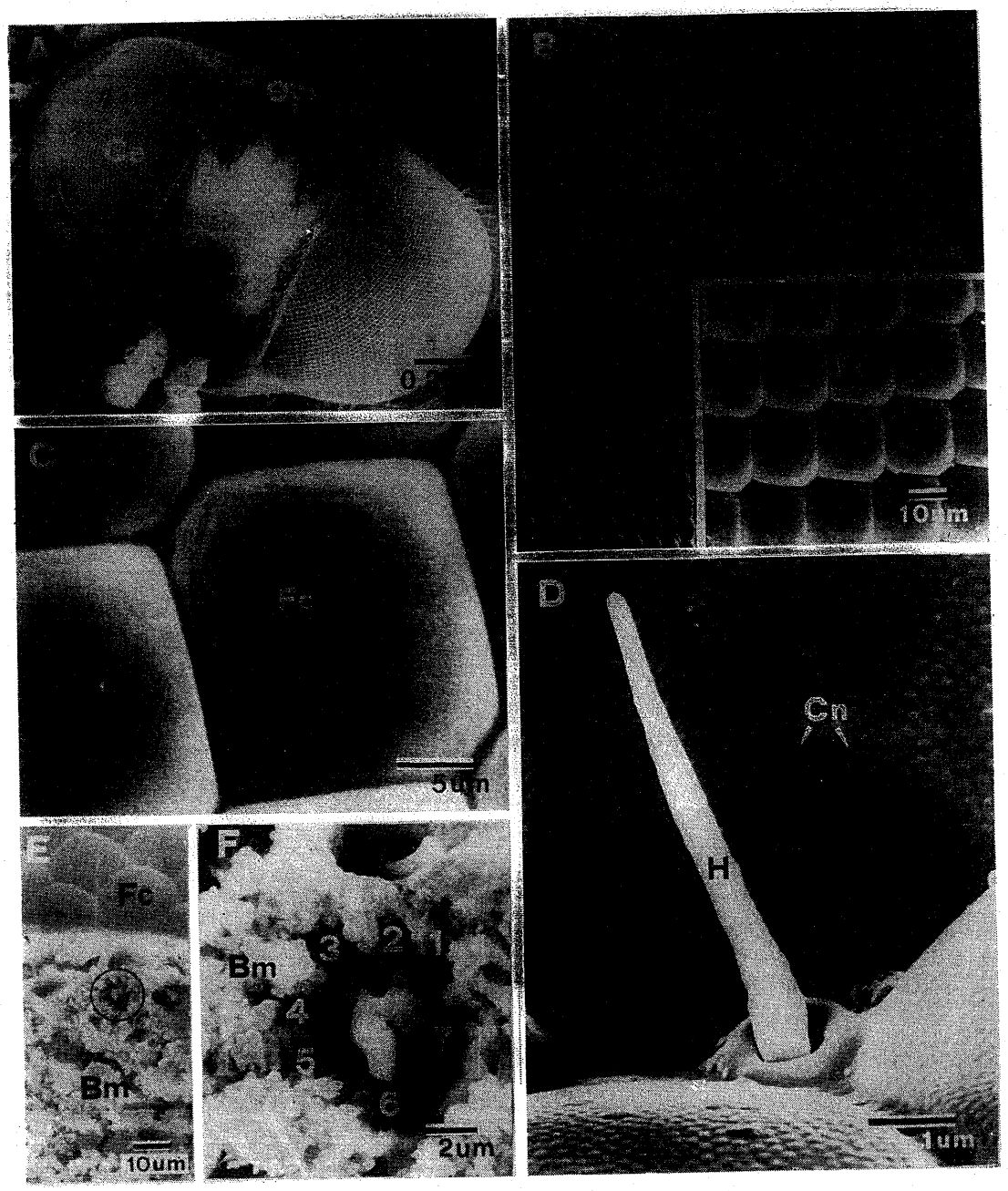


Fig. 1. Scanning electron microscopy of *Dacus dorsalis*

A. Whole aspect of the head.
B. Low magnification of the corneas. insert:facets at central region of the compound eye. (×420)
C. High magnification of facets and corneal nipples (dots).
D. Corneal nipples and an interfacet hair.
E. The facets and basement membrane after tearing.
F. High magnification of a part of fenestrated membrane showing the circle in Fig. E. Each perforation is surrounded by processes of seven retinula cells (1-7).

Bm: basement membrane Cn: corneal nipples Fc: facet
H: interfacet hair Ocl: ocellus Oe: ommatidial facet

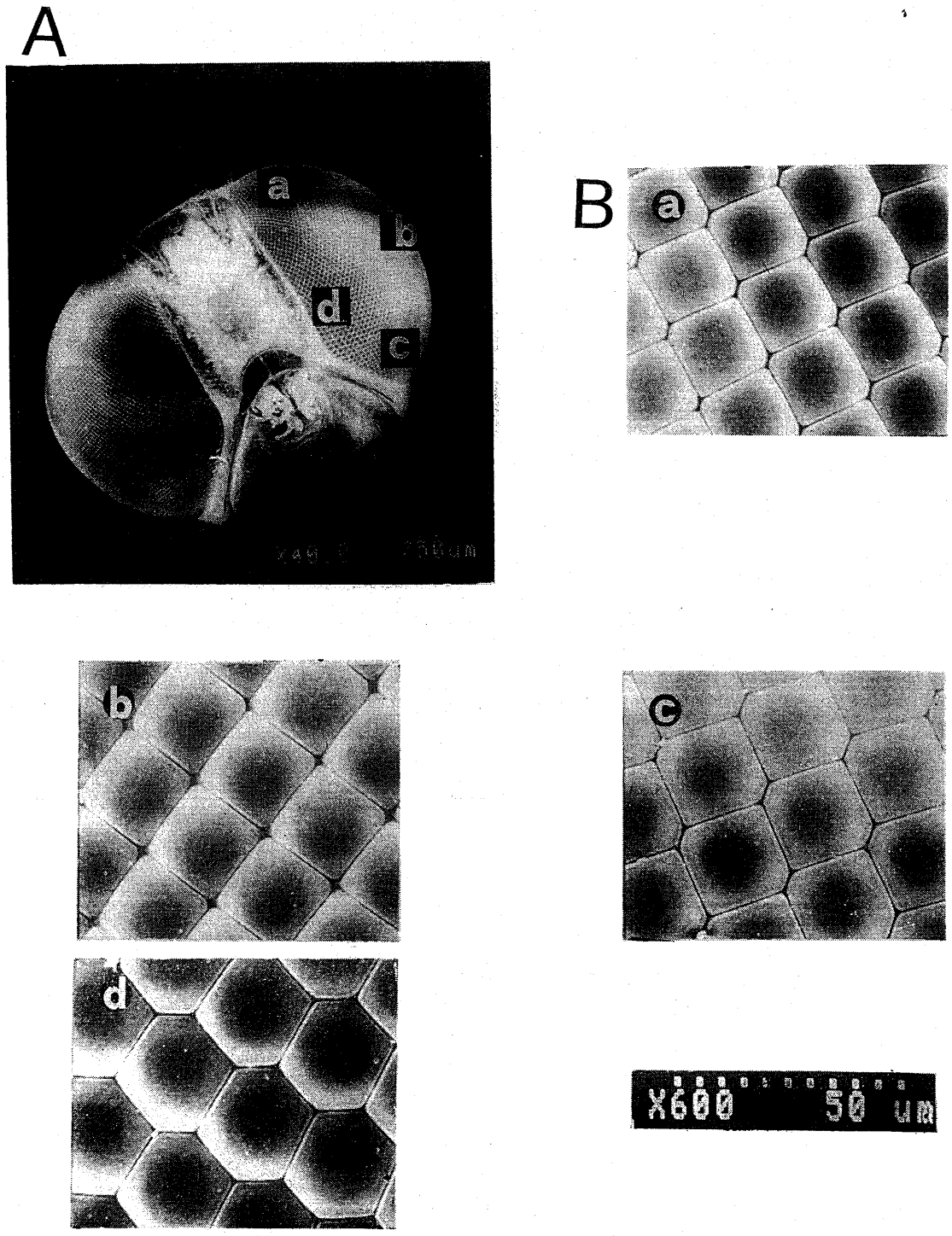


Fig. 2. Scanning electron microscopy of the ommatidum of *Dacus dorsalis*

A. The whole compound eyes. (×40)

B. Those a, b, c and d are taken from different places on the compound eye shown on A. The facets of ommatidia of a, b, c and d appear in various shapes. (×600)

for 2-3 hours. After brief washing with buffer, they were post-fixed with 1% OsO_4 at pH 7.4 for two hours. Samples were dehydrated and deposited with carbon and gold, and observed with Hitachi S-520 scanning electron microscope at 15 KV.

2. Transmission microscopy

The compound eyes were halved and fixed in 2.5% glutaraldehyde (0.1M cacodylate buffer, pH 7.2) for 4-5 hours and then post-fixed in 1% OsO_4 (0.1M cacodylate buffer, pH 7.2) at 4°C. The samples were then dehydrated with alcohol and embeded in spurr low-viscosity resin. Longitudinal and cross ultra-thin sections were stained with uranyl acetate for 15 minutes and in lead citrate for 7 minutes. The specimens were observed and photographed with a high voltage electron microscope (Hitachi H-500) at 75KV.

OBSERVATION AND DISCUSSION

There are two compound eyes on the head of oriental fruit fly, The compound eye is in oval shape (Fig. 1A, B, 2A) and in similar shape and size in both sexes.

Each compound eye has about 4500-4600 hexagonal facets on its surface (Fig. 1B, 2Ba-d). Facets located on the outer region of the compound eye are in typical hexagonal shape (Fig. 2Bd). They count about 2/5 of total facets. The facets located in the central part of the compound eye are in atypical hexagonal shape and count about 3/5 of total facets. The detailed morphology of an atypical facets is shown in Fig. 1C and 2Ba-c. The length and width of an atypical facets are 22 um and 18 μm respectively. There are numerous corneal nipples on all facets (Fig. 1C, D). The interfacet hair is frequently observed between facets (Fig. 1B, D). It has a length of 6-13 um and a diameter of 0.6-0.8 μm at base region of the hair.

Figures 3 and 4 show the longitudinal and cross sections of an ommatidium.

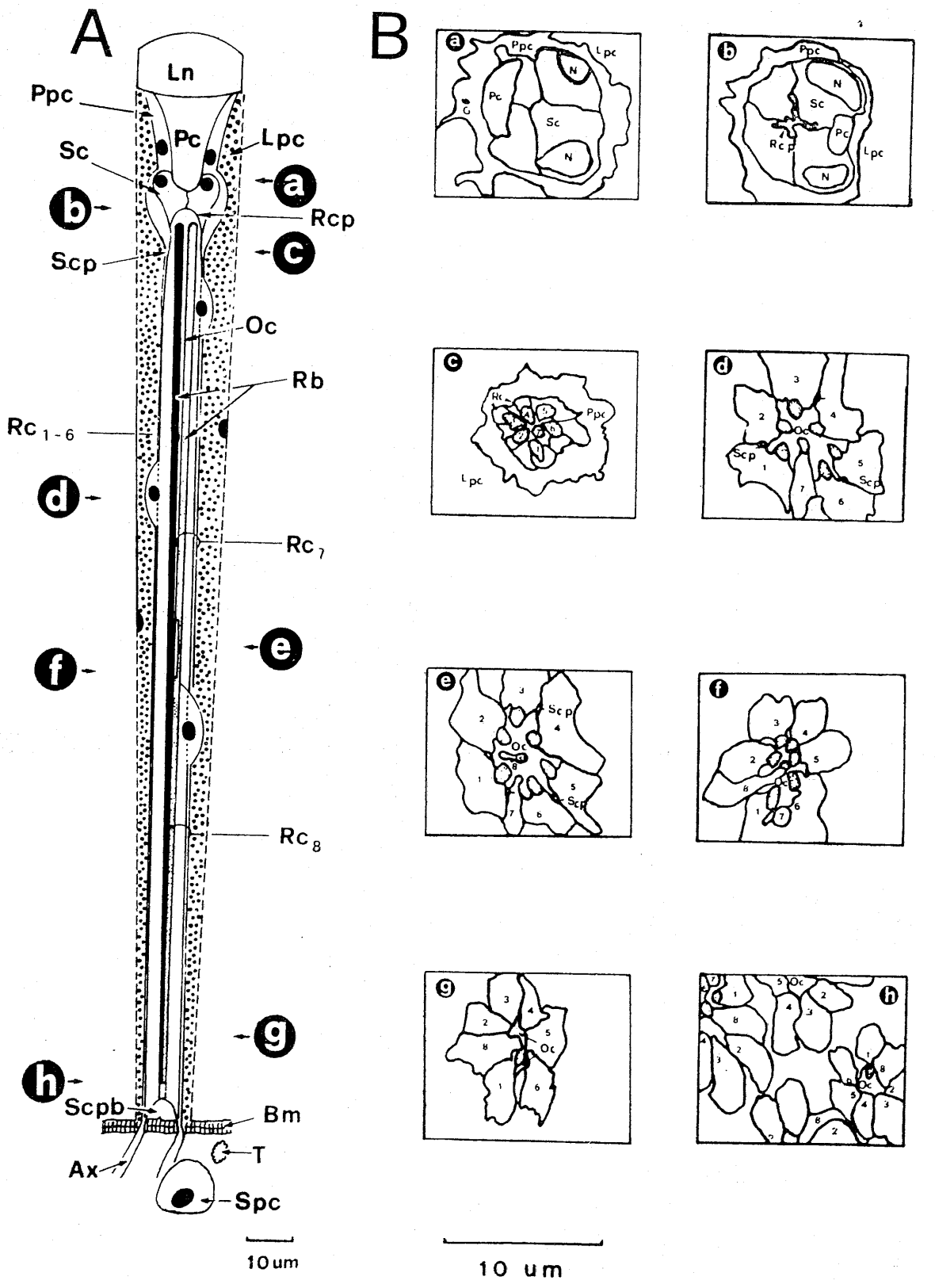
The length and the diameter of the ommatidium are 100-120 μm and 12-20 μm respectively (Fig. 3).

In general, an ommatidium consists of a lens, a pseudocone, four Semper cells and eight retinula (photosensitive) cells. Retinula cells and Semper cells are surrounded by primary pigment cells which extend to basement membrane (Fig. 3A).

The rhabdom of oriental fruit fly is formed by eight rhabdomeres. The arrangement of rhabdomere is similar to that found in other fruit flies (Agee *et al.*, 1977, Davis

Fig. 3. A. Longitudinal section of an ommatidium. a-h show the positions where the cross sections are cut (in B).
B. Various cross sections of ommatidium.
a: cross section is made near the proximal end of pseudocone.
b: cross section through rhabdomere cap.
c: sectioned through distal region of ommatidium showing retinula cells and rhabdomeres (Rb_1-Rb_7).
d: sectioned through middle region of ommatidium.
e: cross section made through proximal end of retinula cell 7, Rb_8 appears and occupied the place where Rb_7 was located. Rb_7 and Rb_8 are in rectangular relation.
f: cross section made through distal end of Rc_8. Rc_7 is almost disappeared.
g: section made through near the basement membrane. Rhabdomeres are centered within the ommatidial cavity.
h: section on the basement membrane. The space between ommatidium is wide.

Ax: axon Bm: basement membrane Ln: lens Lpc: longitudinal pigment cell
N: nucleus Oc: ommatidial cavity Pc: pseudocone Ppc: primary pigment cell
Rb: rhabdomere Rc: retinula cell Rcp: rhabdomere cap Sc: Semper cell
Scp: Semper cell process Scpb: Semper cell pigment body Spc: support cell
T: trachea-tapetum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et al 1983, Williams 1981). Essentially, it consist of central tiered rhabdomere, R_7 from distally, R_8 from proximally, and 6 outer rhabdomeres, R_1-R_6, from retinula cells (Fig. 3A, Ba-h, 4a-h).

1. Dioptric apparatus

Dioptric apparatus composes of a corneal lens and a gelatinous pseudocone (Fig. 3A, 5A).

a) Corneal lens:

The corneal lens is in slightly biconvex shape. The longitudinal section of lens shows that there are about 60 electron-dense and electron-lucent layers forming a lamella structure (Fig. 5A). It is covered with numerous corneal nipples (30-35 nipples/μm^2). Each nipple has a diameter of 0.2-0.3 μm and a height of 0.1 μm (Fig. 1C, D, 5A). Corneal nipples increase the surface area of facet (Wang and Hsu 1982) and reduce the corneal reflection to the light in order to get more light passing through retinula cells (Carlson and Chi 1979).

b) Pseudocone and retinula cell

The pseudocone is right underneath the lens and in a tumble shape. It is surrounded by four wedge-shaped Semper cells and many primary pigment cells (Fig. 3A, Ba-c). The proximal end of pseudocone has a diameter of 4-6 μm and the distal end of 10-12 μm and a length of 18-20 μm. Pseudocone has no organells, but is covered with microvilli on the inner surface (Fig. 5A, C). The pseudocone may be formed by Semper cells have numerous mitochondria and vesicles. Their nuclei have a diameter of 2 μm and are located at the bottom of the pseudocone.

Each Semper cell has a process along the proximal end extending to the Semper cell pigment body at the basement membrane (Fig. 3A, 5E). Between Semper cells, there is a belt desmosome which extends to the proximal region of the basement membrane along with the retinula cell (Fig. 6A). The rhabdomere cap and the ommatidial cavity are packaged tightly at distal region of the retinula cells (Fig. 3A, Bb, c, 4b, c).

In mediterranean fruit fly, the position relationship between retinula cell and Semper cell process is characterized (Davis *et al.*, 1983). This helps to identify each retinula cell. In this study, processes of Semper cell are found between retinula cells, R_1 and R_2, R_3 and R_4, R_5 and R_6, R_7 and R_1. Therefore, the locations of each retinula cell are identified (Fig. 4d, 6A). R_7 comes out between R_1

Fig. 4. Various cross sections of ommatidium. a-h show the positions where the cross sections are cut in fig. 3A.
a: near the proximal end of pseudocone, four Semper cells are seen around by primary pigment cells.
b: cross section through the rhabdomere cap.
c: distal region of ommatidium, showing seven retinula cells. Rabdomere 7 is in the center of the ommatidial cavity. Six rhabdomeres form an asymmetrical trapezoidal pattern.
d: middle region, showing rich cytoplasm and mitochondria in the retinula cells.
e: cross section made through proximal end of retinula cell 7 (Rc 7). The rhabdomeres are in an U-shape arrangement.
f: distal end of retinula cell 7.
g: near the basement membrane. Each rhabdomeres concentrates at the ommatidial cavity.
h: cross section through the most proximal end of the ommatidium. Some of the rhabdomeres begin disappearing.

Ax: axon Bm: basement membrane Ln: lens Lpc: longitudinal pigment cell
N: nucleus Oc: ommatidial cavity Pc: pseudocone Ppc: primary pigment cell
Rb: rhabdomere Rc: retinula cell Rcp: rhabdomere cap Sc: Semper cell
Scp: Semper cell process Scpb: Semper cell pigment body Spc: support cell
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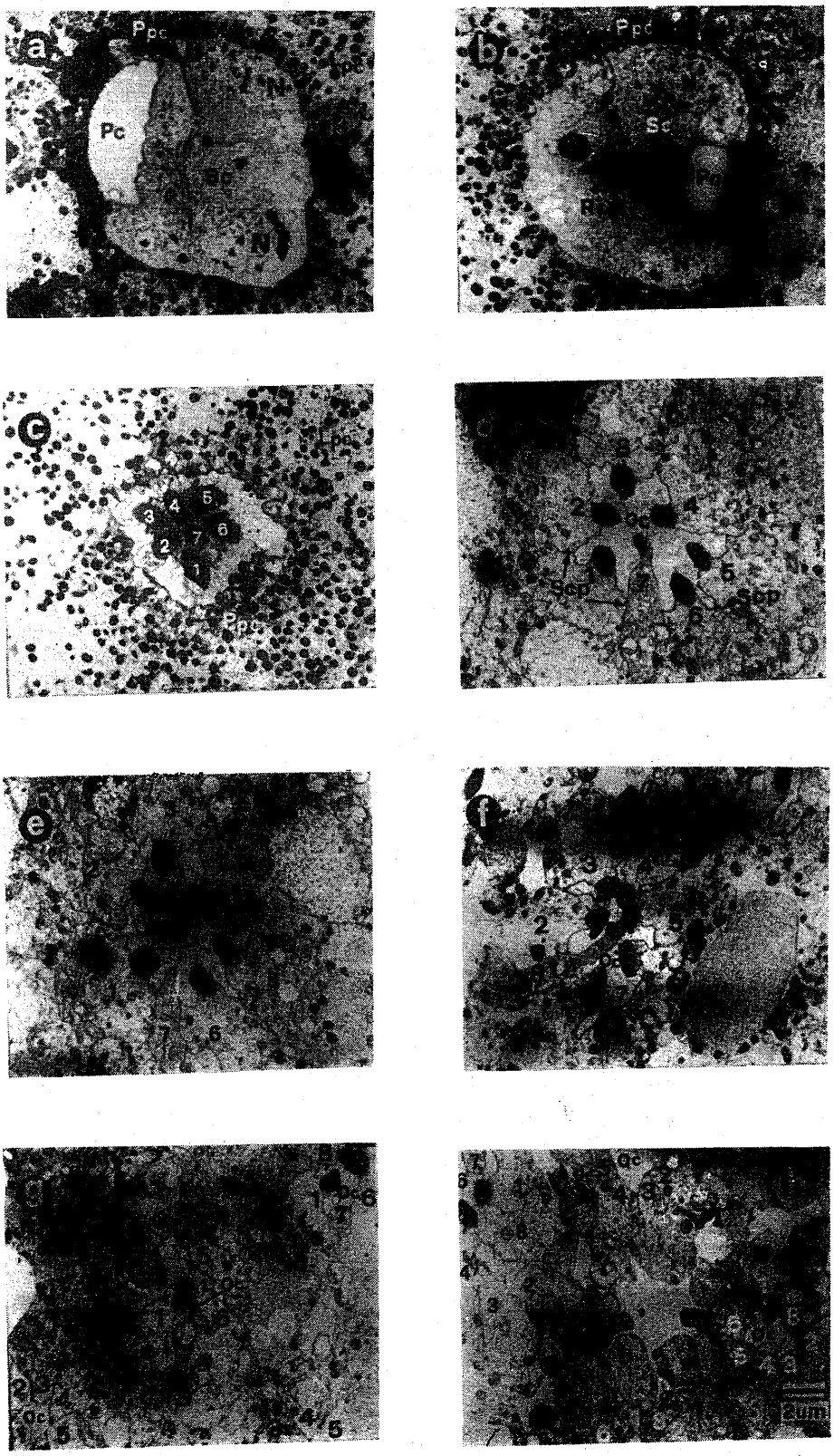
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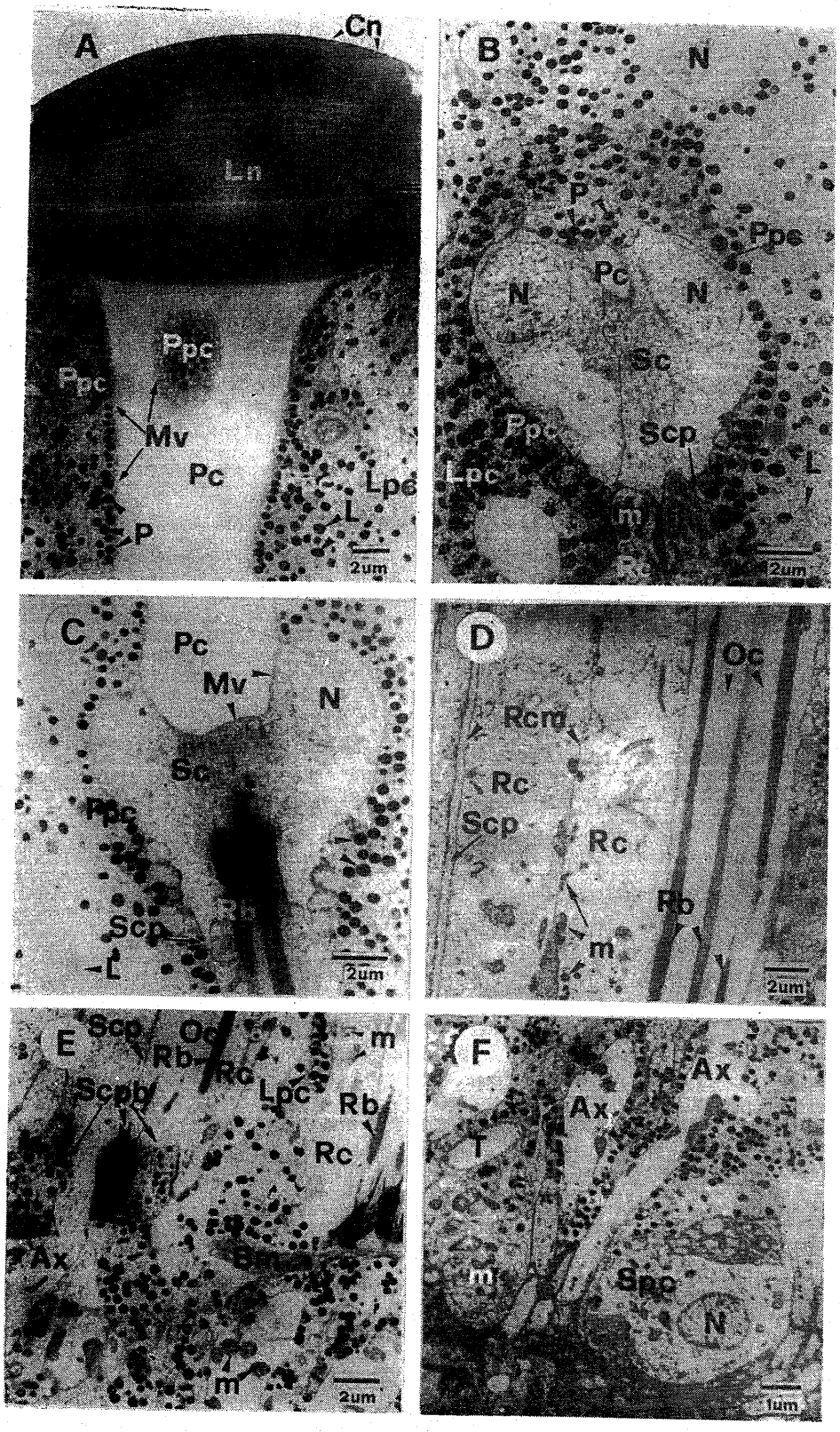
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and R_6 at the distal end and R_8 comes out between R_1 and R_2 at the proximal end. R_7 and R_8 are positioned with a rectangle toward the ommatidial cavity (Fig. 3Be, f, 4e, f).

2. Retinula cell

As mentioned above, the oriental fruit fly has eight photosensitive retinula cells. Each of these cells has rhabdomeric microvilli which extends toward basement membrane. The basement membrane is penetrated by seven retinula cell processes (Fig. 1E, F). The retinula cell is rich in mitochondria, nucleus, pigment granules, vacuoles, Golgi complex, centrioles and matrix.

Retinula cell axon locates at the proximal end of the cell body. The distal portion of the axon penetrates through the basement membrane and extends toward the lamina.

Six outer rhabdomeres form an asymmetrical trapezoidal pattern at the distal portion (Fig. 3Bc, d, 4c, d, 6A). It is typical in the cross section of those retinula cells. As the ommatidium extend toward basement membrane, the pattern change from the trapezoidal shape of rhabdomeres change to U-shape (Fig. 3Bf, 4f). This by looking the changing pattern of rhabdomere, we can locate the different levels when the cross sections of the ommatidium are shown.

Processes of Semper cell extend itself toward Semper cell pigment body that is directly contact with basement membrane (Fig. 5E).

From the cross section of the ommatidium, microvilli are found to connect with the plasma membrane in the retinula cell suggesting that both of them probably have same origin (Fig. 6B).

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Fig. 5. A: Longitudinal section through the dioptric apparatus, showing the lamellar structure of lens, corneal nipples, pseudocone, microvilli, primary pigment cells and longitudinal pigment cells.

B: A slightly oblique section of Semper cells (with their large nuclei), process and distal end of the retinula cells. Semper cells are surrounded by the thin layer of primary pigment cells and longitudinal pigment cells on the outside.

C: Showing Semper cells with their processes and nuclei. Retinula cells and rhabdomeres are inverted into Semper cells. Microvilli are seen between the pseudocone and Semper cells.

D: An oblique longitudinal section of retinula cells. The organells, such as mitochondria, vacuoles, pigment granules, rhabdomeres and matrix are seen in the retinula cell. Processes of Semper cell pass through the membrane of two retinula cells.

E: Basement membrane and proximal end of the retinula cell. Semper cell process is terminated in the Semper cell pigment body which occupied distal to the basement membrane. Axons take the place of retinula cell at basement membrane.

F: Section just below the basement membrane. Large support cells with large nuclei are located just below the basement membrane.

Ax: axon Bm: basement membrane Cn: corneal nipples L: lipid globules Ln: lens
Lpc: longitudinal pigment cell m: mitochondria Mv: microvilli N: nucleus
Oc: ommatidial cavity P: pigment granule Pc: pseudocone Ppc: primary pigment cell
Rb: rhabdomere Rc: retinula cell Rcm: retinula cell membrane Sc: Semper cell
Scp: Semper cell process Scpb: Semper cell pigment body T: trachea-tapetum

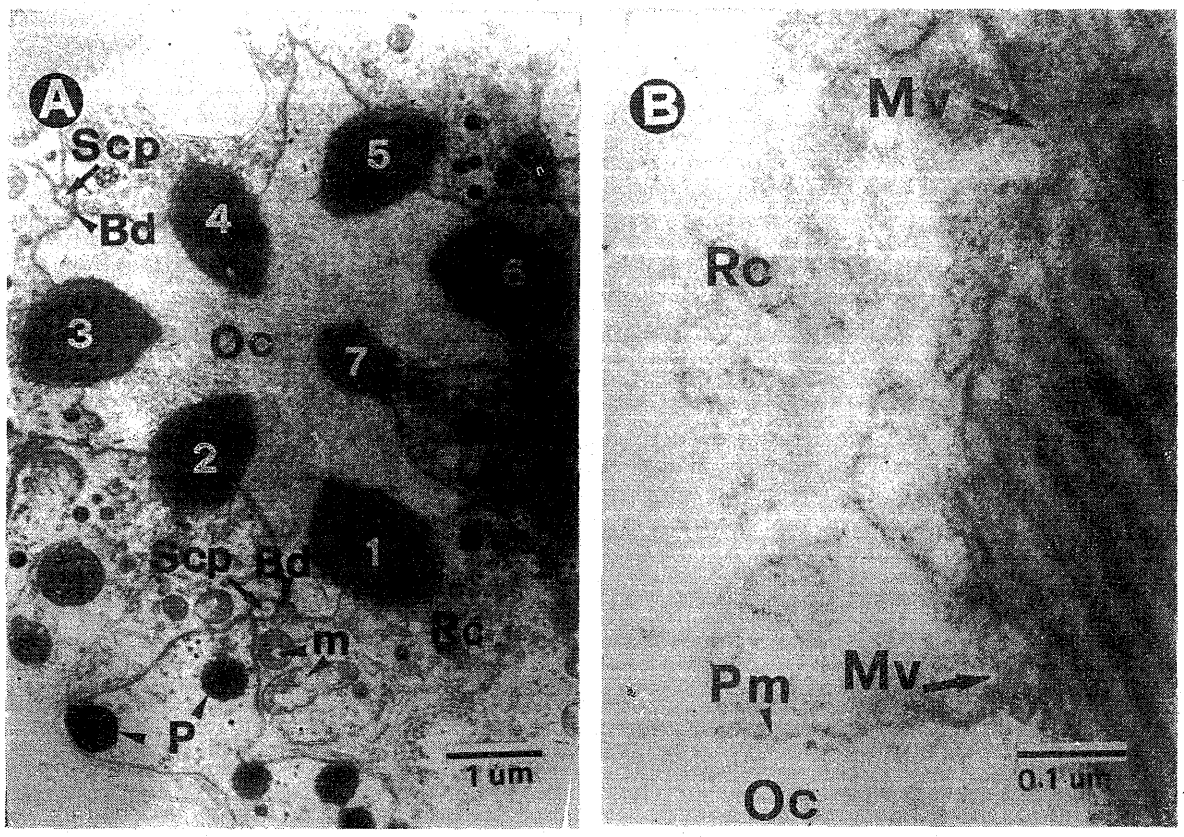

Fig. 6. Cross section of the ommatidia of *Dacus dorsalis.*

A: Cross section at distal end of the retinula cell. At this level, seven retinula cells are seen in a typical trapezoidal pattern. The superior central cell, 7, protrudes its rhbdomere to the center of the ommatidial cavity. Adjacent retinula cells are joined by belt desmosomes Semper cell processes extend along the Semper cell to the Semper cell pigment body which located just above the basement membrane (low magnification).

B: Invagination of the microvilli is seen in this cross section (Arrow, high magnification).

Bd: belt desmosome m: mitochondria Mvimicrovilli Oc: ommatidial cavity P: pigment granule Pm: plasma membrane Rc: retinula cell Scp: Semper cell process

REFERENCES

AGEE, H. R., W. A. PHILLIS and D. L. CHAMBERS (1977) The compound eye of the Caribbean fruit fly and the apple Maggat fly. *Ann. Entomol. Soc. Am.* **70**: 359-364.

CHI, C. and S. D. CARLSON (1976) The large pigment cell of the compound eye of the house fly *Musca domestica. Cell Tissue Res.* **170**: 77-88.

CARLSON, S. D. and C. CHI (1979) The functional morphology of the insect photoreceptor. *Ann. Rev. Entomol.* **24**: 379-416.

DAVIS, J. C., H. R. AGEE and E. A. ELLIS (1983) Comparative ultrastructure of the compound eye of the wild, laboratory reared and irradiated Mediterranean fruit fly *Ceratitis capitata* (Diptera: Tephritidae). *Ann. Entomol. Soc. Am.* **76**(3): 322-332.

MELAMED, J. and O. TRUJILLO-CENOZ (1968) The fine structure of the central cells in the ommatidia of Dipterans. *J. Ultrastructure Research* **21**: 313-334.

TRUJILLO-CENOZ, O. and G. D. BERNARD (1972) Some aspect of the retinal organization of *Sympycnus lineatus* Loiew (Diptera, Dolichopodiae). *J. Ultrastructure Research* **38**: 149-160.

WADDINGTON, C. H. and M. M. PERRY (1963) Interretinular fibers in the eyes of Drosophila. *J. Ins. Physiol.* **9**: 475-478.

WILLIAMS, D. S. (1981) Twisted rhabdomeres in the compound eye of a Tipulid fly (Diptera). *Cell Tissue Res.* **217**: 625-632.

WANG C. S. and S. S. HSU (1982) The compound eye of diamondback moth, *Plutella xylostella* (L) and its pigment migration. *Bull. Inst. Zool., Academia Sinica* **21**(1): 75-92.

昆 蟲 之 受 器

一、東方果實蠅 (*Dacus dorsalis*) 複眼之微細構造

吳京一 張春霞 童麗珠 林金盾

使用掃描式及穿透式電子顯微鏡觀察東方果實蠅複眼之構造。東方果實蠅頭部兩側由 4500～4600 個左右之個眼 (ommatidium) 成正及不正六角形所組成之複眼。每一個個眼包括有晶體，假圓錐眼，視細胞及外圍之色素細胞等，其晶體上有 30～35 個/μm^2 之晶體乳頭 (corneal nipples)。每個個眼具有能感光的感桿分體 (rhabdomeres) 共有 8 個，其排列方式和其他種類果實蠅相似。