Microvillar Orientation in the Retina of a Pierid Butterfly

Tom M. Maida

Department of Biology, University of South Florida,
Tampa, Florida

The orientation of microvilli in the compound eye of the butterfly, *Pieris protodice*, has been examined using electron microscopy. The retinula cells comprising each ommatidium have been divided into four types based upon microvillar orientation, position of nucleus, and location within the ommatidium. The vertical and horizontal retinular types have microvilli in the distal one-third to half of the retina. There is alteration in the orientation of these microvilli of up to 90°. The rhabdom is dominated by the microvilli of the diagonal retinulae in the proximal retina. There is consistent orientation of the diagonal cell microvilli throughout the retina. In mid-retina, these microvilli undergo dramatic alteration in length, leading to a Crustacean-like organization, for some 50 μm. The basal, or eccentric, retinula cell is bilobed, and has only a few microvilli projecting a short distance into the rhabdom.

While microvillar orientation in the retina of numerous groups of insects has been described (*e. g.*, ant [1], bee [2], fly [3]), there has been only casual reference to rhabdomeral architecture in the Pierid butterflies. As a whole, the butterfly retina has been treated only at the level of the light microscope [4], in which finer details, such as microvillar patterns, are not resolved. As it is now well known that the orientation of visual pigment-containing microvilli is important in polarized light perception [5], the rhabdom and constituent cells have been examined at the electron microscope level in the Pierid butterfly, *Pieris protodice*.

In each ommatidium, there are four distal receptors, 4 proximal receptors, and one basal receptor. Their nuclei are located in the distal, proximal, and basal parts of the retina, respectively. The distal photoreceptors can be subdivided into two groups: one pair oriented dorsoventrally (vertical retinulae) and another oriented at 90° to the dorso-ventral axis (horizontal retinulae). The soma of the proximal receptors are oriented diagonally across the ommatidium at 45° to the left and right of the dorso-ventral axis, and are termed the diagonal retinulae. The U-shaped basal receptor is oriented vertically, and limited to the basal $35 - 40$ μm of the retina.

The microvilli of the vertical retinulae are limited to the distal 200 μm of the retina (Fig. 1B). These
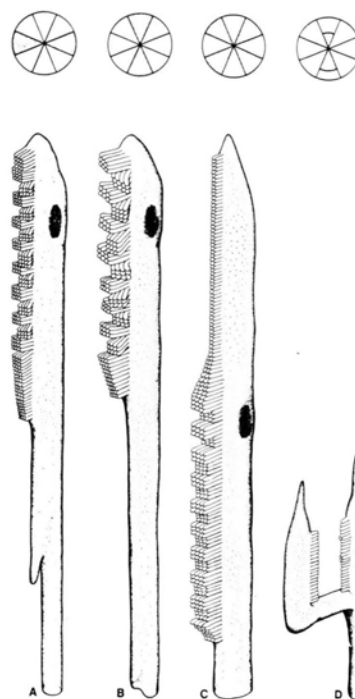
Fig. 1. Diagrammatical representation of the four receptor types in the retina. The stippled areas of the circles above indicate the position of each cell type within an ommatidium. A. The horizontal retinula cell. B. The vertical retinula cell. C. The diagonal retinula cell. D. The basal, or eccentric, retinula cell.

microvilli meet in the center of the rhabdom throughout this length (Figs 2 A, 2 B). The orthogonal layers — the microvilli of which are usually directed at 45° to the left and right of the vertical axis — are each $5 - 7$ microvillar layers thick. The 90° change in orientation is not constant, as some packets of microvilli are parallel with the dorso-ventral axis and at 45° to the adjacent layer. The microvilli of the vertical cells are generally oriented in this manner a few micrometers above the level of the axon, as well as in some packets in the more distal regions.

The microvilli of the horizontal cells are shorter than those of the vertical receptors (Figs 2 A, 2 B). While the microvilli are often parallel with the horizontal axis of the eye, orientation varies up to 30° from this axis (Fig. 1 A). The major microvillar contribution of these horizontal retinulae is limited to the distal 200 μm of the retina, as are those of the vertical receptors. In a few ommatidia, the soma contribute a few microvilli to the rhabdom in the proximal half of the retina. The horizontal, as well as vertical receptors, are axons in the proximal half of the retina.
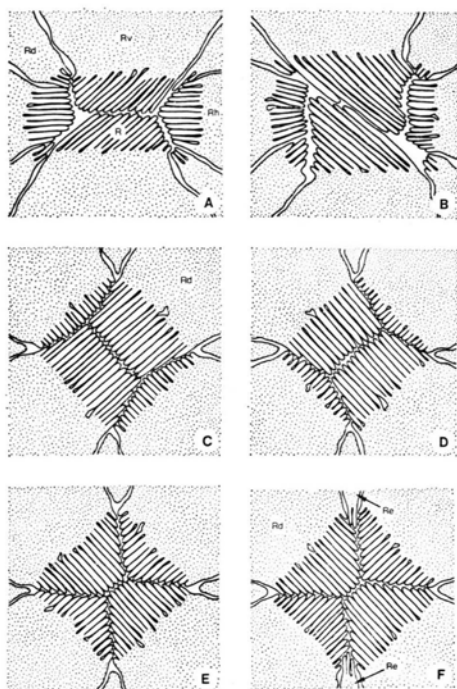
Fig. 2. Diagrammatical representation of rhabdoms at significant depths of the retina. Symbols: Rv, vertical retinula; Rd, diagonal retinula; Rh, horizontal retinula; Re, eccentric retinula. A and B. The distal retina, showin two representative microvillar patterns. C and D. The level of the diagonal cell nuclei, illustrating alteration of microvillar lengths. E. The level proximal to the diagonal cell nuclei, and distal to the eccentric cell. F. The level of the eccentric retinula cell.

The cell bodies of the diagonal retinulae extend from a few micrometers distal to the cone base to approx. 25 μm distal to the basement membrane of the retina. The microvilli of these cells are oriented throughout the length of the soma at 45° to the horizontal axis. Throughout the distal 200 μm of their length, the cells are small, and have relatively minor microvillar contribution to the rhabdom (Fig. 1 C). The microvilli are limited in this region to the corners of the rhabdom (Figs 2 A, 2 B). At the transition zone — the level where distal cell soma become axonal — these cells enlarge and there is equal microvillar contribution by all eight retinula cells. Proximal to the transition zone, the diagonal cells are larger, have more microvillar

contribution, and there are no microvilli associated with the distal cells. At their nuclear level, approx. 300 μm from the outer corneal surface, there is alteration of the length of the microvilli. For some distance, several microvillar layers thick, microvilli from opposing cells meet in the center of the rhabdom, and those of the alternate set are reduced in length (Fig. 2 C). In the orthogonal layer, the microvilli of the alternate set extend to the center of the rhabdom, and the adjacent cells' microvilli are reduced (Fig. 2 D). This dramatic alteration is limited to a region some 50 μm thick. Below that level, the rhabdomeres are tapered, with microvilli decreasing in length peripherally and meeting those of adjacent retinulae. There is minor alteration of microvillar length centrally, resulting in alternate sharing of this region by the four cells (Fig. 2 E).

The U-shaped soma of the eccentric, or basal, retinula cell replaces the vertical retinulae in the position immediately adjacent to the rhabdom (Fig. 1 D). Crossover of the eccentric cell, the thin strip of cytoplasm connecting the dorsal and ventral halves, is proximal to the rhabdom. The microvilli of the cell are very short, and project directly into the rhabdom (Fig. 2 F). There are only one-two microvilli present at any level of the eccentric cell.

Microvillar orientation in the butterfly compound eye is exceedingly complex. The microvilli of the vertically oriented retinulae show shifts in orientation of up to 90°, precluding the participation of these cells in the detection of plane polarized light orientation. The microvilli of the horizontal cells vary in orientation up to 60°. While the consistant orientation of microvilli provides a structural basis for the detection of the e-vector of plane-polarized light, it may limit the maximal response of the receptor to a single configuration [6]. There is consistant orientation of microvilli of the two pairs of diagonal cells, and of the eccentric cell. The behavioral significance of specific microvillar orientation in the eye of Pierids has not been demonstrated, nor have the necessary neural connections for processing of information concerning the e-vector of polarized light. In conjunction with future data obtained by stimulation with plane polarized light and intracellular recording, these findings will make possible immediate recognition of the cell recorded. It will also make identification of spectral cell types a more feasible undertaking.

[1] R. Menzel, T-I-T-J. Lif. 3 (3), 95 [1973].
[2] F. V. Valera and K. Porter, J. Ultra. Res. 29, 236 [1969].
[3] C. B. Boschek, Z. Zellforsch. 118, 369 [1971].
[4] M. Nowikoff, Z. wiss. Zool. 138, 1 [1931].

[5] R. Menzel and A. W. Snyder, J. Comp. Physiol. 88, 247 [1974].
[6] T. H. Waterman and K. W. Horch, Science 154 (3748), 467 [1966].