# Microvillar Orientation in the Retina of the Nymphalid Butterfly

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The photoreceptor cells of the nymphalid butterfly, *Agraulis vanillae*, have been structurally characterized. Four distinct types of retinulae can be found in each ommatidium. Two vertically oriented cells contribute microvilli to the rhabdom only in the distal retina. These microvilli are ordered into discrete packets. Although the distal-most microvilli enter the rhabdom in a dorsal-ventral axis, these rhabdomeral packets begin altering their direction of orientation becoming directed at 45° to the vertical alignment of the cells. Abrupt alternations in orientation produce microvillar packets oriented to each other at approximately 90° along the distal portion of each vertical cell. The vertical retinulae lose their microvilli at mid-retina and become axonal. Four retinular cells, oriented diagonally across the ommatidium, contribute microvilli to the rhabdom aligned at 45° to the vertical axis. These diagonal cells produce microvilli throughout the depth of the retina. Two horizontally ordered photoreceptors produce microvilli aligned along a horizontal axis, these cells contributing rhabdomeres along their entire length. A ninth bilobed eccentric cell is arranged in a vertical plane in the basal region of the ommatidium. A few short microvilli are added to the rhabdom from each lobe. These are oriented in a vertical direction.

The photoreceptor cells comprising the ommatidia of the nymphalid butterfly *Agraulis vanillae* have been structurally characterized. The nine receptors within a single ommatidium may be classed according to the depth in the retina at which their nuclei occur. Two vertical cells, having their nuclei located in the distal-most portion of the cell, are arranged in a dorsal-ventral orientation. Four diagonal retinulae, oriented 45° from the dorsal-ventral ommatidial axis, possess nuclei located in the central portion of the distal half of the retina. Two receptor cells with nuclei located near the middle of the retina are ordered across the ommatidium in a horizontal manner. While these vertical, diagonal, and horizontal retinula cells all possess nuclei in the distal half of the retina, a single basally located cell, the eccentric cell, has its nucleus just distal to the basement membrane. This ninth cell is oriented dorsal-ventrally across the ommatidium.

Microvillar projections from each of these four cell types meet to form a fused rhabdom extending the entire depth of the retina. In insects, rhabdomeres typically enter the rhabdom with a specific orientation. Except in the bee visual system, where the ommatidium gradually rotates through as much as 30° in a clockwise or counterclockwise direction before it reaches the basement membrane [1], the angle of entry for any particular cell type remains constant throughout the depth of the retina. Although three of the classes of photoreceptors in the butterfly retina appear to conform to this generality, a fourth type does not.

The vertical retinular cells contribute microvilli to the structure of the rhabdom only in the distal half of the retina (Fig. 1 B). These microvilli

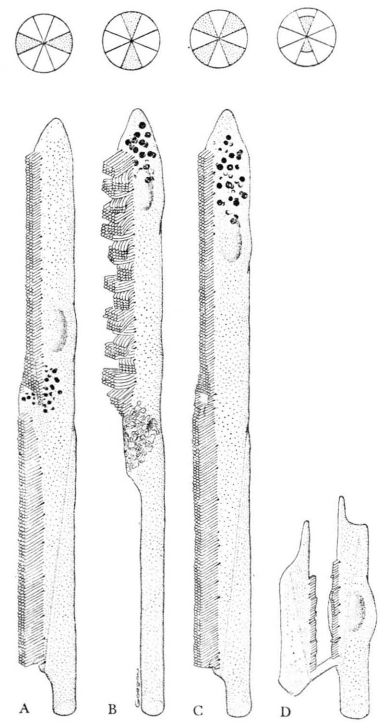


Fig. 1. A schematic representation of the four photoreceptor types found in the ommatidium. These cells are not drawn to scale. The small circle above each of the cell types indicates the position that cell occupies within an ommatidium. A. The horizontal retinula cell. B. The vertical retinula cell. C. The diagonal retinula cell. D. The eccentric retinula cell.

dominate the rhabdom extending across to meet each other. Initially, just proximal to the dioptric apparatus, these cells contribute vertically aligned microvilli. However, the orientation soon begins to change (Fig. 2 A). Packets of microvilli begin to alternate their orientation in the rhabdom, becoming directed first 45° to one side of the vertical cell

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alignment and then 45° to the other side. Rapid alternation occurs throughout the length of the microvillar column of the vertical cells. Rhabdomeral packets vary in thickness containing as few as three or as many as eleven layers of microvilli. Directional changes are abrupt. EM sections often catch portions of two sequential packets, demonstrating alternations of very nearly 90°. Occasionally, a packet will orient vertically in the rhabdom. At approximately mid-retina, the vertical cell microvilli become shortened and orient to the dorsal-ventral axis of these cells. At this point the vertical cells lose their microvilli and become axons (Fig. 2 C, D).

The microvilli of the diagonal retinular cells enter the rhabdom at the top of the retina as very short processes oriented at 45° to either side of the dorsal-ventral ommatidial axis. The diagonal cell rhabdomeres maintain this diagonal orientation

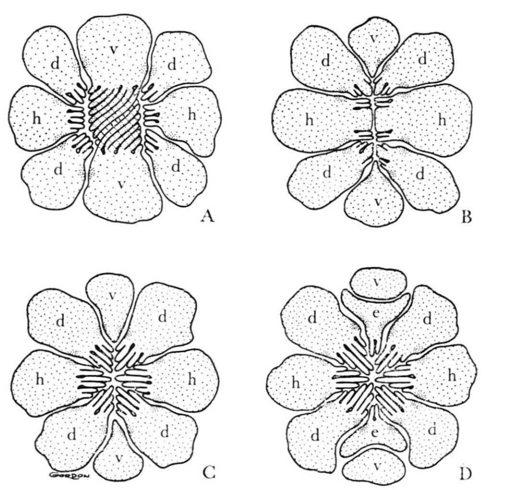


Fig. 2. Schematic cross sections of four levels in the ommatidium. Symbols: v, vertical retinular cell; d, diagonal retinular cell; h, horizontal retinular cell; e, eccentric retinular cell. A. Section through the distal portion of the retina revealing the angular displacement of the vertical cell microvilli. B. Section through the mid-retina demonstrating the "split" rhabdom. C. Section through the proximal portion of the retina in the region where the vertical cells have just become axonal. D. Section through the basal region showing the microvillar contribution of the eccentric cell.

along their entire length (Fig. 1 C). Because the central portion of the distal rhabdom is composed of vertical cell microvilli, the diagonal microvilli are reduced in length (Fig. 2 A). At mid-retina, just as the vertical cells lose their microvilli, the diagonal cells occasionally undergo a change. The short microvilli appear to move laterally so as to form a central region devoid of rhabdomere (Fig. 2 B). When this occurs, it happens for only a few micrometers. The microvilli rapidly expand centrally to fill any gap that might have occured. Because the vertical cells have now become axonal, the diagonal cell microvilli now lengthen (Fig. 2 C) and meet in the center of the rhabdom. These four cells continue in this manner to the base of the ommatidium just above the basement membrane. There, the diagonally oriented microvilli rapidly shorten and disappear.

The third class of receptors, the horizontal cells, also contribute microvilli throughout the entire depth of the retina. Microvilli enter the rhabdom in the distal portions of the ommatidium as very short processes (Fig. 1 A). The microvilli are oriented along a horizontal axis and demonstrate no deviation from this pattern. At mid-retina, the horizontal cells always undergo a change in microvillar distribution. The horizontal rhabdomeres split into two laterally occuring portions (Fig. 2 B) and finally all microvilli disappear. Centrally, the plasma membranes of the two horizontal cells become apposed. This occurs, as with the diagonal cells, only through a very narrow region of the retina. The rhabdomere is soon reconstituted while the microvilli now lengthen to meet in the central regions of the rhabdom (Fig. 2 C). The two horizontal cells contribute long, straight, horizontally oriented microvilli to the base of the retina where the rhabdomeres become shorter and rapidly disappear.

The basally located eccentric cell (Fig. 1 D), found only in the proximal one third of the retina, contributes relatively few microvilli to the structure of the rhabdom. This cell sends two processes distally along side the rhabdom. These two lobes are aligned in a vertical orientation. Eccentric cell microvilli are very short. EM sections show only one microvillus extending a short distance into the rhabdom from each process in a vertical orientation. Occasionally, two microvilli are observed side by side (Fig. 2 D). A thin cytoplasmic bridge crosses under the rhabdom. It is at this level of "crossover" that the microvilli of the eccentric cell, as well as of the diagonal and horizontal receptor cell types, finaly disappear.

The function of specific microvillar orientation in the eye of the nymphalid butterflies is unknown. Quite possibly, by incorporating a system of alternating microvillar packets arranged at approximately 90° to each other, the vertical retinular cells have considerably broadened their range of sensitivity to photic stimuli. Rigorous orientation in the eye of the desert ant *Cataglyphis bicolor* [2], as well as in specific dorsaly located ommatidia in the bee *Apis mellifera*[3], has been demonstrated to serve as a detection system of the plane of linearly polarized light. Behavioral orientation to the e-vector of polarized sky light has proved to be an important factor in the life of these social insects. It has not yet been shown that the butterfly orients to polarized light. Clearly, should the plane of linearly polarized light be an important environmental parameter to the nymphalids, only those retinular cells with a constant microvillar orientation could serve as detectors[4]. This would seem to preclude the vertical retinular cells as a reliable source of information concerning polarized light. The three remaining populations of retinular cells could possibly serve an e-vector detection function. Until electrophysiological data on the four cell types is accumulated, we can only speculate on the function of these photoreceptor elements in the eye of the nymphalid butterflies.

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