

Fig. 1. Electron micrographs of freeze-fractured rhabdomere microvilli from vitamin-A enriched (a), and vitamin-A deprived (b) blow flies. The figures above are examples of numerous micrographs made from a total of 23 vitamin-A deprived and 37 vitamin-A enriched flies. Eyes were excised, fixed in glutaraldehyde for one hour and treated with 25% glycerin for 12 h before freezing. The arrows indicate the direction of carbon-platinum shadowing (× 120,000).

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## Rhodopsin Particles in the Photoreceptor Membrane of an Insect

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Electron-microscopic examination of freeze-fractured fly retinae has revealed the presence of particles, 80 to 100 Å in diameter, on the photoreceptor membrane. Flies which were raised on a vitamin-A deficient diet show a substantial reduction in the density of such particles. The reduction in particle density is in agreement with the reduction in visual-pigment concentration as measured spectrophotometrically for these flies. These results suggest that the particles are identical with molecules of the visual pigment, rhodopsin.

Fernandez and Nickel <sup>1</sup> have shown by freeze-fracture preparation of crayfish photoreceptors that the A-face (cytoplasmic layer) of the rhabdomere-microvillus membrane contains particles 80 Å in diameter which are separated from each other by a mean distance of 120 Å. This corresponds to a packing density of 6600 particles/ $\mu$ m<sup>2</sup>. Comparable electron-microscopic data has also been obtained for rhabdomeres of ants <sup>2</sup>.

These results are in agreement with the molecular structure of the disc membrane of vertebrate photoreceptors where similar particles incorporated into the A-face have been identified as rhodopsin molecules. Thus in photoreceptor membranes of arthropods as well as in those of vertebrates the particles are localized on the inner phospholipid layer while

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\* Figs 1 a and 1 b see Plate on page 762 d.

the extracellular layer (B-face) appears to be

The visual pigment  $(P_{490})$  concentration in the photoreceptors of the blowfly (Calliphora erythrocephala) depends directly on the vitamin-A content in the diet as shown by difference spectrophotometry (Schwemer, unpublished data) <sup>3</sup>. The largest ratio of  $P_{490}$  concentration in vitamin-A enriched strains compared to vitamin-A deprived strains was 100:2.

In the present study, a comparison of freezefracture preparations showed a very dense packing of particles on the rhabdomeres of vitamin-A enriched strains (Fig. 1 a) \* whereas on the rhab-domeres of the vitamin-A deprived strains only a few scattered particles could be found (Fig. 1b). The size of the particles was 80 to 100 Å, the same dimension as in crayfish. The packing density of the particles was found to be as great as  $6400 \,\mu\text{m}^2$  in A-enriched animals and in A-deprived strains as low as  $100/\mu m^2$ . The mean values for the two strains were: A enriched = 3800/\mu m^2 and A deprived =  $650/\mu m^2$ , corresponding to a significant ratio of 100:16. This ratio of particle density agrees well with the ratio of pigment concentration 100:12 as determined spectrophotometrically for these particular strains. This result strongly supports the interpretation that the particles seen on the freeze-fractured membranes are identical with the visual pigment (P<sub>490</sub>) in the photoreceptors

Biochemical analysis of rhabdomere membranes of the cephalopod *Eledone* as well as those of *Calliphora* have demonstrated a constant phospholipid to visual pigment ratio of about 70:1. From this ratio the mean distance between pigment molecules was estimated to be 80 Å <sup>4</sup>. The molecular weight of visual pigment is about 40000 corresponding to a mean-molecular diameter of 40 Å. The discrepancy between the electron-microscopically determined particle size and the diameter as postulated by molecular weight might be explained by the hypothesis that three or four molecules tend to aggregate to form the particles.

<sup>1</sup> R. F. Fernandez and E. E. Nickel, J. Cell. Biol. **69**, 721 [1976].



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S. Razmjoo and K. Hamdorf, J. Comp. Physiol. 105, 279 [1976].

<sup>&</sup>lt;sup>4</sup> K. Hamdorf and J. Schwemer, in Photoreceptor Optics (A. W. Snyder and R. Menzel, ed.), p. 263, Springer Verlag, Berlin 1975.