

Extracellular Shedding of Photoreceptor Membrane in the Open Rhabdom of a Tipulid Fly

David S. Williams and A.D. Blest

Department of Neurobiology, Australian National University, Canberra, Australia

Summary. The compound eyes of the Australian tipulid fly, *Ptilogyna*, shed the bulk of their rhabdomeral membrane to extracellular space during turnover. The rhabdomeres of the retinulae lie in a common extracellular space (ECS), which is subdivided in the proximal retina. Before dawn, a distal region of the microvilli in each rhabdomere differentiates and becomes less electron-dense after conventional fixation. The differentiated region then dilates and develops an irregular profile. A few hours after dawn, the transformed tips break off and form a detritus in the ECS. The degraded membrane is internalised back into the retinula cells by mass endocytosis. Retinulae develop pseudopodia at sites bordering the ECS and engulf the membrane detritus, which comes to lie first of all in vacuoles within the receptor cells and then forms very large multivesicular bodies. The latter transform to multilamellar and residual bodies and are, presumably, lysed. Surrounding these secondary lysosomes are rough endoplasmic reticulum and smooth tubular systems, tentatively considered on comparative grounds to provide hydrolases. The literature concerning the ultrastructure of compound eyes offers a small number of instances where extracellular shedding can be suspected for morphological reasons. Attention is drawn to analogies with the shedding of photoreceptor membranes in vertebrate retinae.

Key words: Open rhabdom – Microvillus – Extracellular membrane shedding – Pseudopodial uptake – Secondary lysosomes – Fly, *Ptilogyna spectabilis* (Skuse).

Photoreceptors of the anterior lateral eyes of the salticid spider, *Plexippus*, shed membrane from the microvilli of their rhabdomeres to extracellular space (ECS),

Send offprint requests to: D.S. Williams, Department of Neurobiology, Research School of Biological Sciences, Australian National University, P.O. Box 475, Canberra City, A.C.T. 2601, Australia

Acknowledgements: The authors thank Prof. G.A. Horridge for drawing their attention to *Ptilogyna* as potential material for these studies, and Denis Anderson and Bruce Ham for collecting flies in the field. Rod Whitty and the staff of the Electron Microscopy Unit provided technical advice and support, and Chris Snoek prepared Fig. 1.

from which it is retrieved by processes of the nonpigmented glia (Blest and Maples, 1979). Previously, a similar route of shedding had been suspected to be implicated during turnover of rhabdomere membrane in another spider, *Dolomedes* (Blest and Day, 1978). The former authors suggested that an extracellular route might explain the apparent absence of products of membrane degradation in the receptor cytoplasm of flies with open rhabdoms (Melamed and Trujillo-Cenoz, 1968; Boschek, 1971). Preliminary examination of receptors of the blowfly, *Lucilia*, has not so far resolved this question, although intracellular shedding via pinocytosis has been shown to take place (Williams, in preparation).

In the present report, massive extracellular shedding in the retina of a tipulid fly is described, and it is shown that the receptors retrieve products derived from the shed membrane by endocytosis from the ECS.

Materials and Methods

Both sexes of the large crepuscular and nocturnal Australian tipulid *Ptilogyna (Plusiomyia) spectabilis* (Skuse) (Dobrotworski, 1971) were collected at Captain's Flat, Karwarrie, and at Braidwood, both in New South Wales. Some specimens were fixed at the site of capture, but most were conveyed to the laboratory in Canberra in plastic bags resting on ice in a polystyrene container with a window to sustain the normal daily cycle of illumination. They were then stored in a room exposed to daylight which was well-diffused to prevent exposure to direct sunlight. The temperature of the room was not controlled other than to avoid heating above ambient environmental temperatures and to avoid cooling below 20°C at night. The range of temperatures experienced by these flies was probably narrower than that of the external environment. Flies were fixed for electron microscopy at various times throughout the 24 h light cycle up to 48 h after capture; some were also sampled after being held in the dark for up to three days and then exposed to various durations of natural daylight.

Retinae were dissected so as to expose tissue to the fixative as rapidly as possible. The nature of the effects described below means that very rapid fixation is important; Griffiths and Boschek (1976) and Griffiths (1979) have shown that significant ultrastructural changes of the fly retina are evident as soon as 3 min after injury to the receptors. Flies were decapitated and the lateral margins of the eyes trimmed with microscissors under primary fixative at 4°C so that only a small block of the central retina remained. The whole dissection was completed in less than 1 min, and the procedure was performed under light filtered by Schott RG 665 (red cut-off) and KG3 (heat) filters. Room lighting was either on or off to coincide with day or night.

Primary fixatives were: (a) 2.5% glutaraldehyde in 0.1 M cacodylate buffer at pH 7.3 with 0.07 or 0.14 M sucrose and 2 mM CaCl₂; (b) 2.5% glutaraldehyde and 2% paraformaldehyde in 0.1 M sodium dihydrogen orthophosphate-NaOH buffer at pH 7.3 with 0.07 M D-glucose and 0.9 mM CaCl₂; (c) 2.5% glutaraldehyde in 0.1 M PIPES-NaOH buffer at pH 7.3 with 0.07 or 0.14 M sucrose and 2 mM CaCl₂.

The best results were obtained with fixatives (a) and (b); 0.07 M sucrose provided the better tonicity. After a brief wash, tissues were post-fixed for 0.5–1 h in 1% OsO₄ in the same buffer. They were embedded in Araldite, and grey to silver-grey sections were collected on formvar-coated slot grids, or on 400-mesh grids without a supporting film, and examined in a Jeol 100C or Hitachi H500 electron microscope.

Results

General Anatomy

A full account of the dark- and light-adapted eye will be given separately (Williams, in preparation). The gross anatomy of the retinae of five genera of

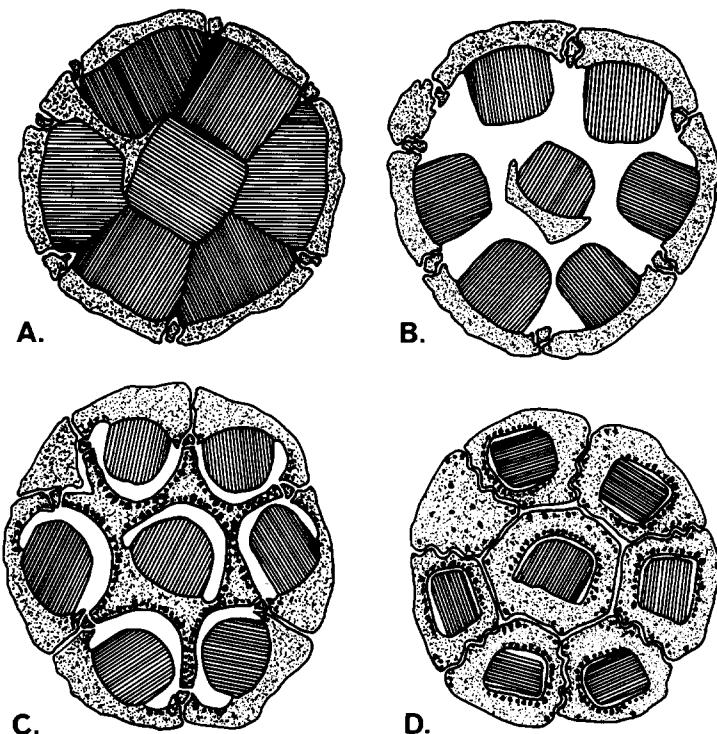


Fig. 1. Diagram illustrating the four different regions of the rhabdom in transverse section. A–D are profiles taken at increasing distances from the cornea

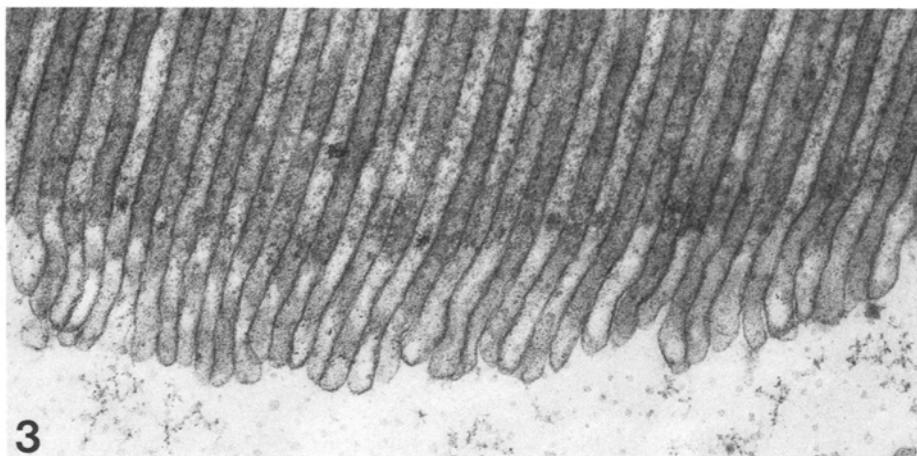
European Tipulidae was described by Sotavalta et al. (1962), on the basis of light microscopy alone. At that level of resolution our results agree basically with those of Sotavalta et al., but the latter did not resolve an eighth cell and concluded that each ommatidium possessed seven retinulae only.

The organisation of a single ommatidium is illustrated in Figs. 1 and 2. Figure 1 shows a series of transverse sections taken at different levels. Distally, beneath the crystalline cone, the rhabdomeres of six retinulae (R1–6) are contiguous with each other laterally, and centrally with the short rhabdomere of R7. There is no large ECS, resulting in a distal fused rhabdom composed of the rhabdomeres of R1–7 (Fig. 1A). Beneath this region, there is a short segment of the ommatidium with a large common ECS. Here, the rhabdomeres of R1–6 are for the most part separated, and the central rhabdomere of R8 lies free of them (Fig. 1B). More proximally, processes from R8 extend around its own rhabdomere and laterally to the margins of the rhabdom to form the tops of "pockets", in which the proximal parts of the rhabdomeres of R1–6 and 8 lie (Fig. 1C and 2). In the basal part of the rhabdom the lateral processes of R8 are replaced by extensions from R1–6 so that each retinula encloses its own rhabdomere and continues the "pocket" (Fig. 1D). The seven pockets, which appear in transverse section to contain small isolated ECSs around individual rhabdomeres, are thus connected to the large common central ommatidial ECS in the distal rhabdom.

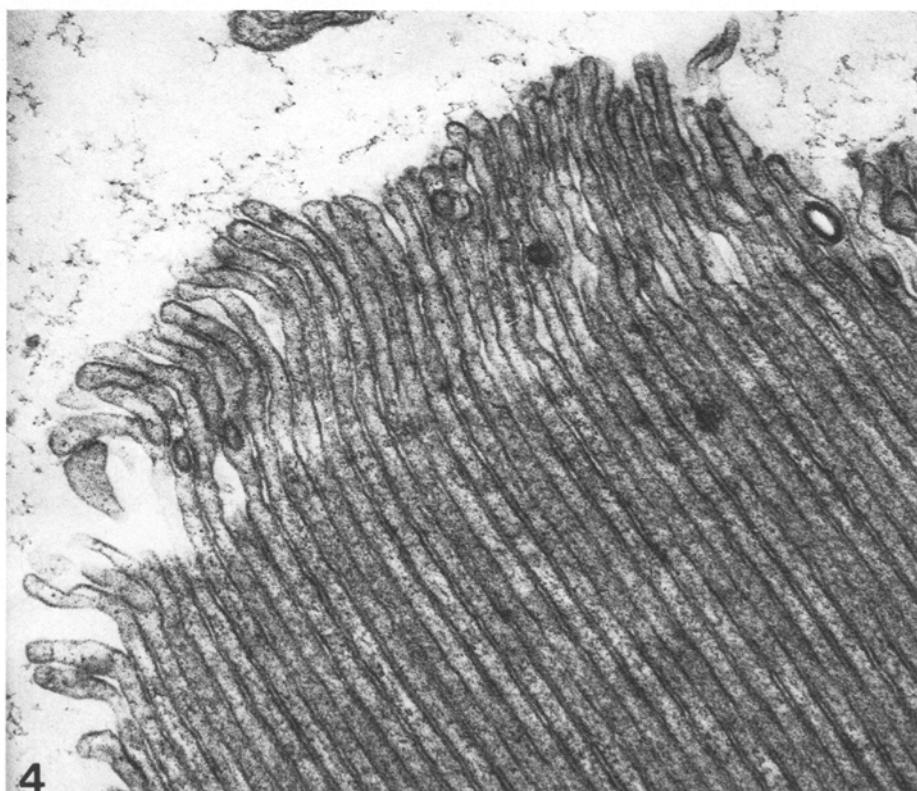


Fig. 2. Approximately transverse section of an ommatidium fixed in the afternoon. The top portion of the profile is slightly more distal than the bottom. The section samples the distal part of the region where the rhabdomeres lie in "pockets" formed by extensions of the retinulae. Retinulae are numbered. $\times 7,000$. Scale = $2 \mu\text{m}$

Each rhabdomere of R1–6 twists down its length in a manner that cannot be artefactual, a feature that will be discussed later (Williams, in preparation). The rhabdom is short ($50 \mu\text{m}$) occupying only half of the distance between the lenslet and basement membrane. The bulk of the cytoplasm of the retinulae, together with their nuclei, lie proximal to the rhabdom. The retinulae contain pigment granules, and the assembly of retinulae is surrounded by pigment cells.



3



4

Fig. 3. Microvilli from a rhabdomere of an eye fixed immediately before dawn. Their tips have become less electron-dense and are irregular in profile. $\times 54,000$

Fig. 4. A slightly later stage than Fig. 3. The tips of the microvilli are more disorganized. $\times 54,000$

The shedding of distal segments of microvilli into ECS, described below, occurs in all parts of the rhabdom, including the fused region.

Extracellular Shedding of Distal Segments of Microvilli

Before dawn, the tips of the microvilli undergo a transformation. They become less electron-dense, dilate, and show signs of vesiculation (Figs. 3 and 4). After dawn these changes are exaggerated, and entire tissue fragments consisting of microvillus tips break off from their rhabdomeres to yield an irregularly vesicular detritus in the ECS (Figs. 5–7).

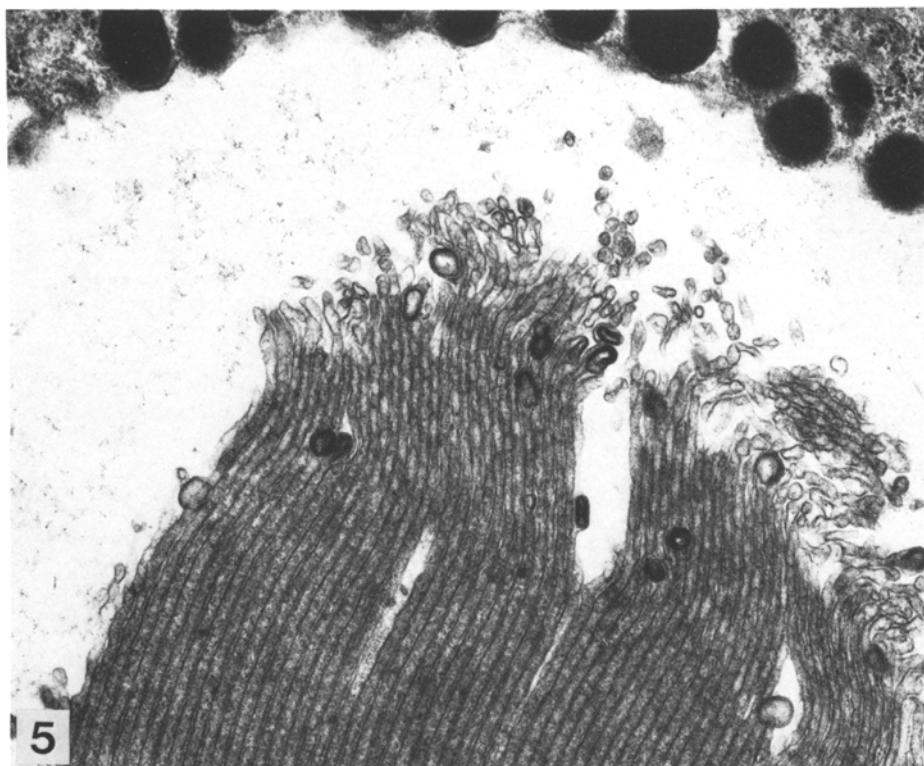
At this stage in the cycle, the state of the receptors implies that shed membrane is endocytosed back into the retinulae. The surfaces of the retinulae adjacent to the rhabdomeres acquire pseudopodial processes (Figs. 7, 8 and 10) and sparse coated endocytotic pits (Fig. 8). Vacuoles within retinulae now contain vesicles, profiles of which match those of vesicles in the ECS, and amorphous material, that appears similar to the material scattered throughout the ECS (Figs. 8 and 9). In the normal retina pseudopodial uptake is not readily observed, probably because it happens very rapidly. It is signalled most conspicuously by the presence of vacuoles in the retinulae. When, however, flies are held in continuous darkness for 2–3 days and then exposed to a normal dawn, very large masses of membrane are shed, and pseudopodial profiles (Figs. 7, 8 and 10) are readily observed.

Endocytosed membrane products eventually aggregate as multivesicular bodies (mvbs) in the cytoplasm of the retinulae around the rhabdom. By midday, very large mvbs are present (Fig. 14), and may be easily seen with the light microscope. Later in the afternoon, large vacuoles containing only a few vesicles are more abundant here (Fig. 11). This suggests that after midday the amount of membrane being shed decreases, but phagocytosis continues, taking up more extracellular fluid than membrane. Small residual bodies are found in retinulae in the morning and large residual bodies by the afternoon (Fig. 16). These secondary lysosomes presumably result from degradation of mvbs via multilamellar bodies (Figs. 15–17), similar to that described by White (1967, 1968), Eguchi and Waterman (1976), and Blest et al. (1978a).

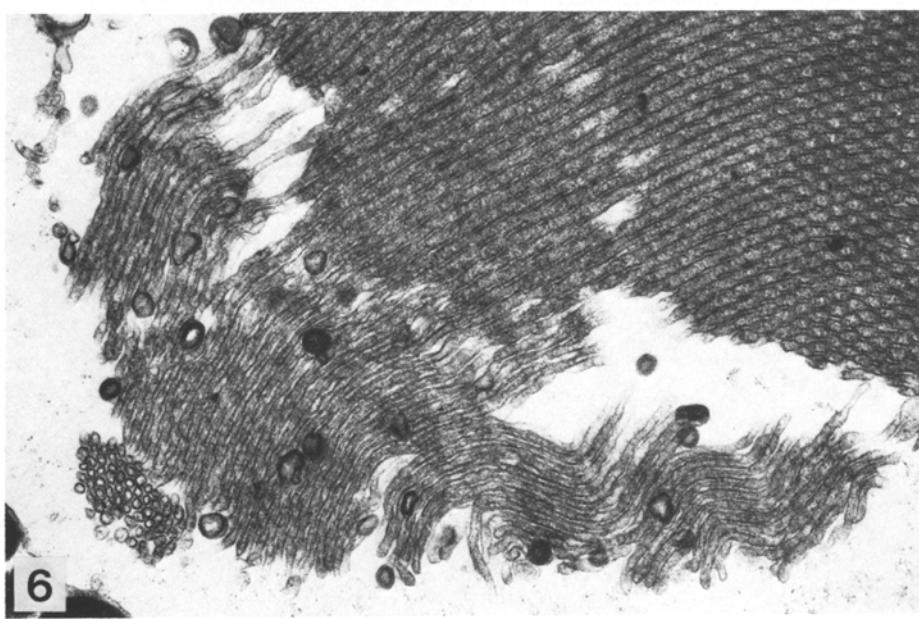
From late morning until mid-afternoon, secondary lysosomes occupy a significant proportion of the cytoplasmic volume of the retinulae, and become surrounded by fields of smooth endoplasmic reticulum, tubules and vesicles. The latter probably contain acid hydrolases, for similar organelles derived from the endoplasmic reticulum and associated with mvb degradation have been described in retinae of a spider *Dinopis* (Blest et al., 1978b) and in the grapsid crab *Leptograpsus* (Blest et al., 1980). In both the crab and the spider (Blest et al., 1979), they have been shown to be acid phosphatase-positive, and have been discussed as a specialised GERL system.

Timing of the Cycle

The timing of events outlined above is not precise, although some generalisations can be made. Receptors sampled between midnight and 04.00 h lack secondary



5



6

Figs. 5 and 6. Microvilli from rhabdomeres of eyes fixed after dawn. The tips of the microvilli are more transformed than in Figs. 3 and 4, and have begun to detach from the rhabdomere. $\times 37,000$

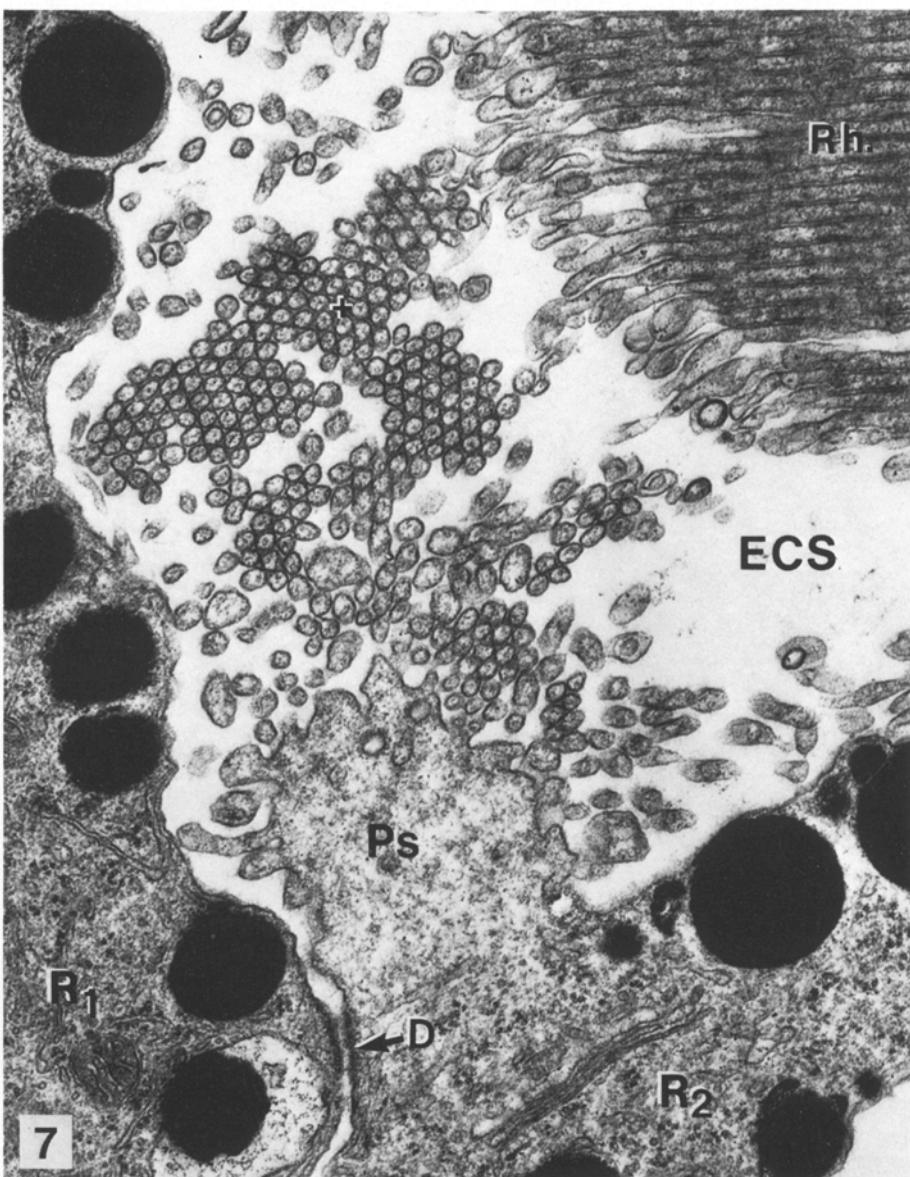
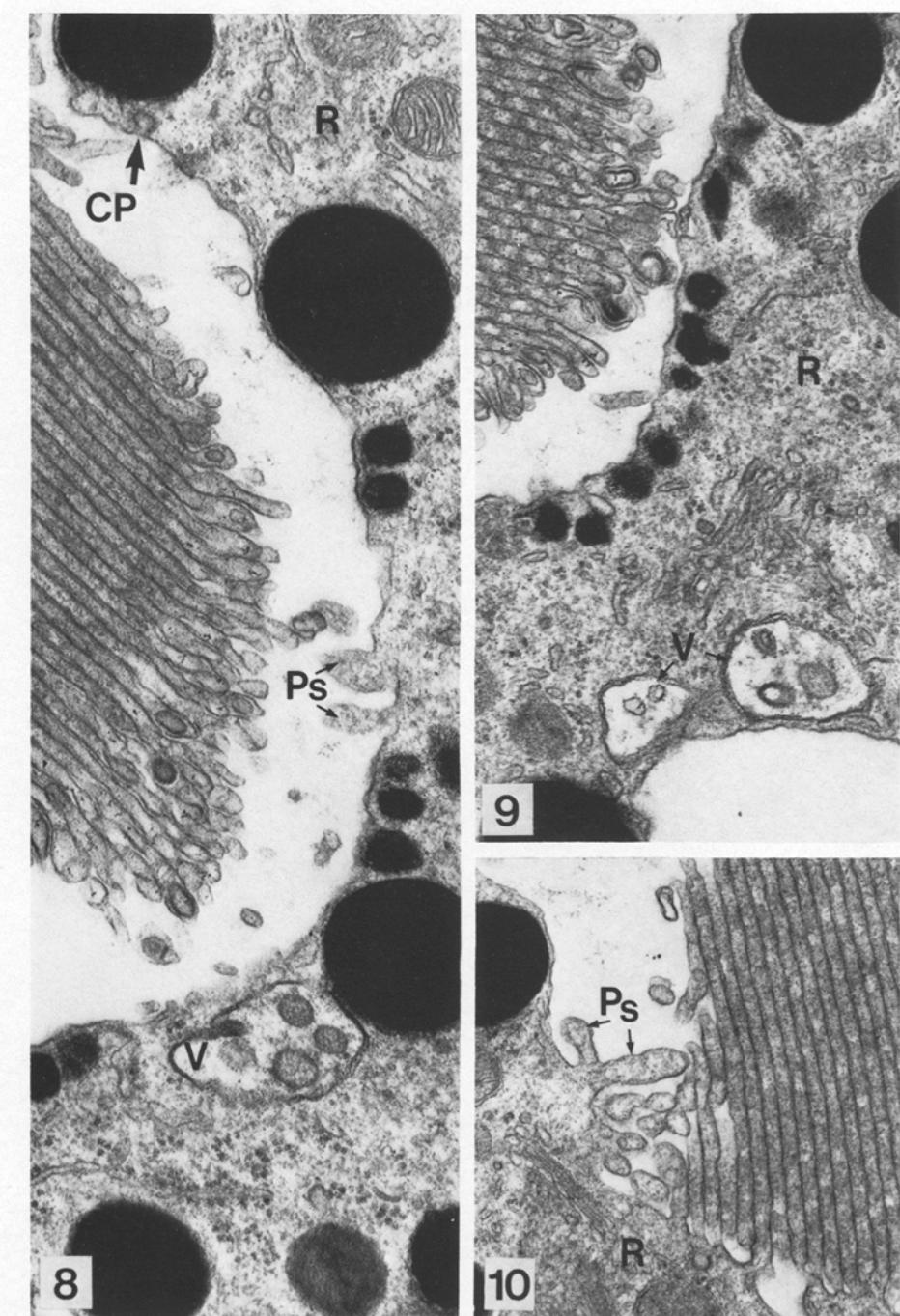


Fig. 7. Pseudopodia (*Ps*) extend from a retinula (*R*2) into the extracellular space (*ECS*) around a shedding rhabdomere (*Rh*). Some microvilli are in transverse section (+). They still show the organisation of intact microvilli, including axial filaments, and are probably still attached to the rhabdomere beyond the plane of section. *R*1 retinula neighbouring *R*2; *D* desmosome at junction of *R*1 and *R*2. $\times 43,000$



Figs. 8–10. Profiles of retinulae (*R*) with pseudopodia (*Ps*) projecting into ECS, and small vacuoles (*V*) containing vesicular profiles considered to be derived from shed microvilli. *Cp* coated pit. Fig. 8, $\times 47,000$; Fig. 9, $\times 44,000$; Fig. 10, $\times 39,000$

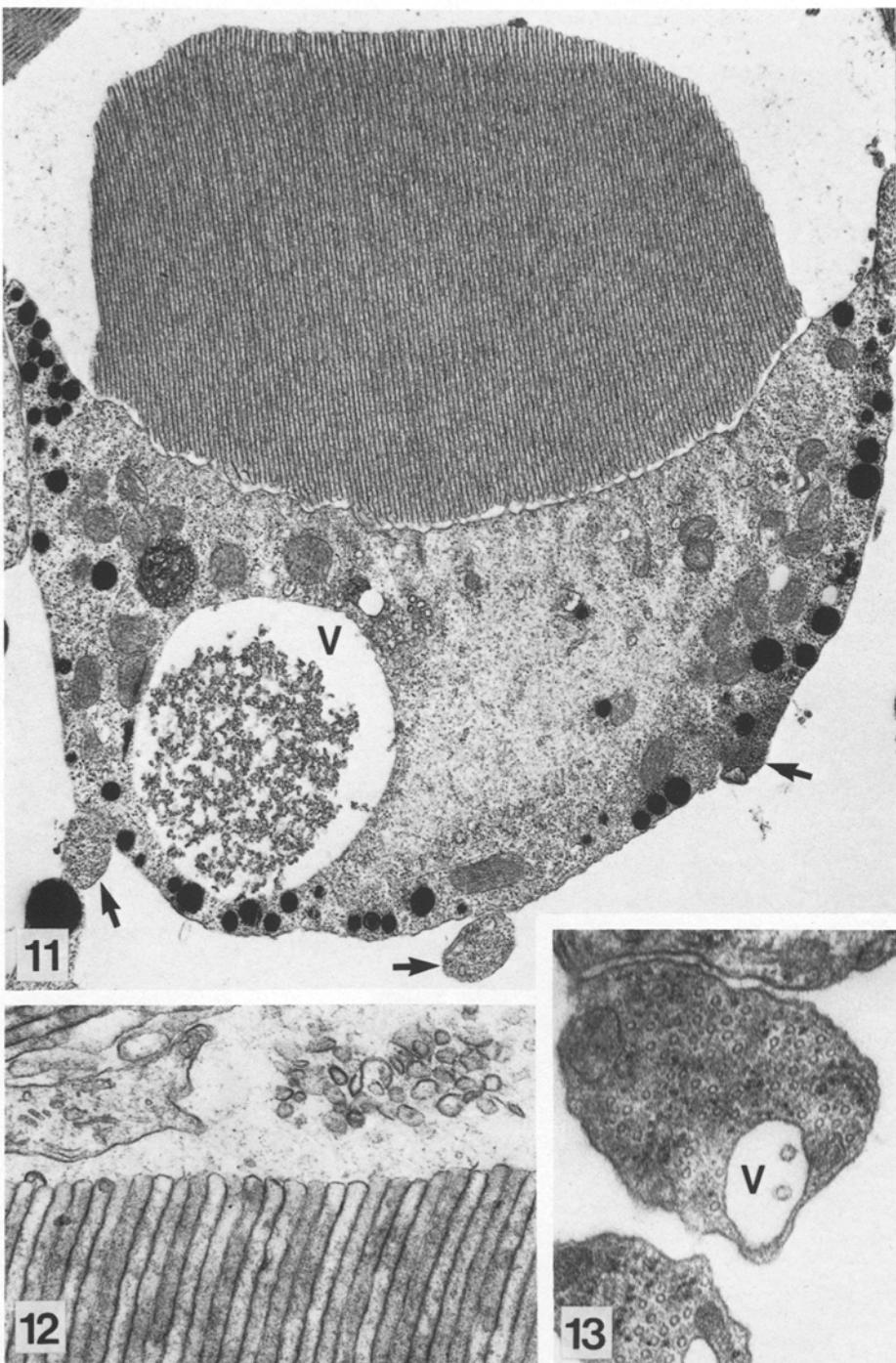
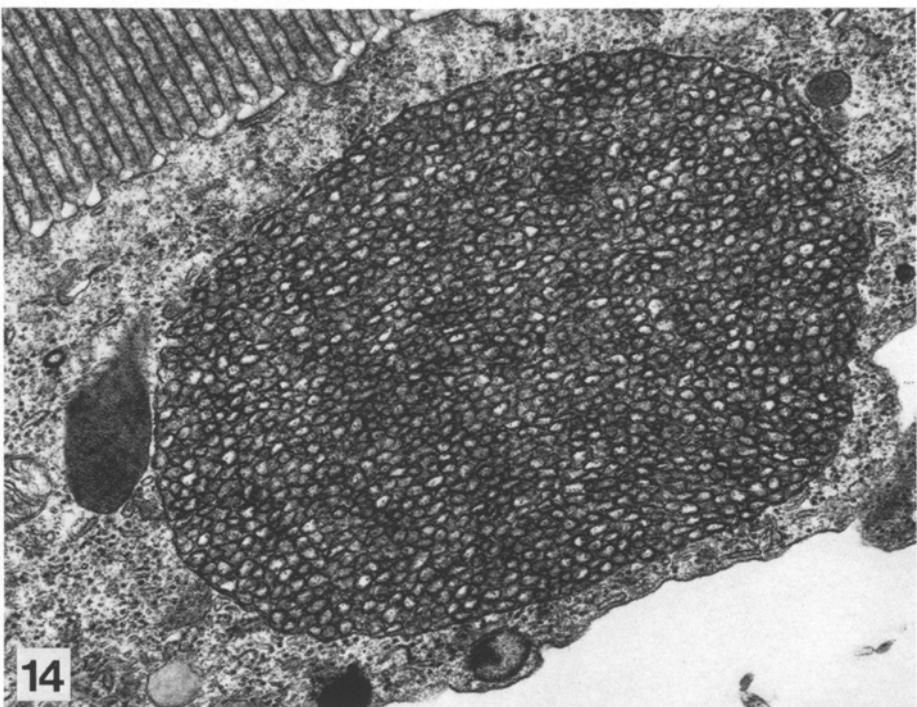


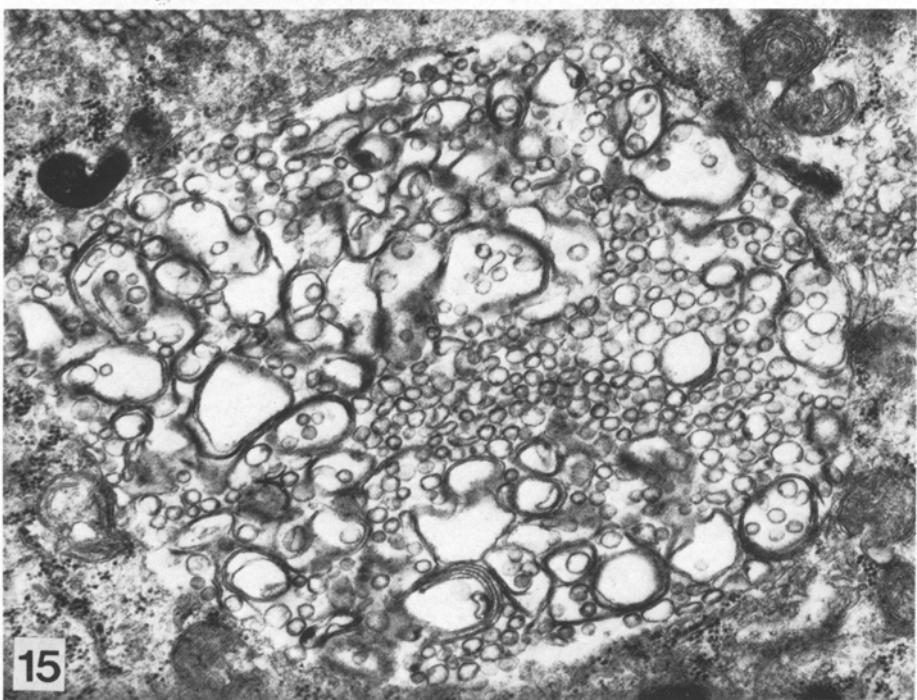
Fig. 11. Retinula fixed in the afternoon. The tips of the microvilli are orderly. The cytoplasm contains a large vacuole (*V*) only partially filled with vesicles derived from shed photoreceptor membrane. Arrows indicate secondary pigment cells. $\times 13,000$

Fig. 12. Distal tips of microvilli fixed in the afternoon. $\times 35,000$

Fig. 13. Transverse section of columns of secondary pigment cells in the region of the rhabdom. Vacuole (*V*) contains two vesicles. $\times 57,000$



14



15

Fig. 14. Large, tightly-packed multivesicular body in retinula fixed at midday. $\times 36,000$

Fig. 15. Multivesicular body at later stage than Fig. 14. Vesicles are reorganising to form lamellae. $\times 36,000$

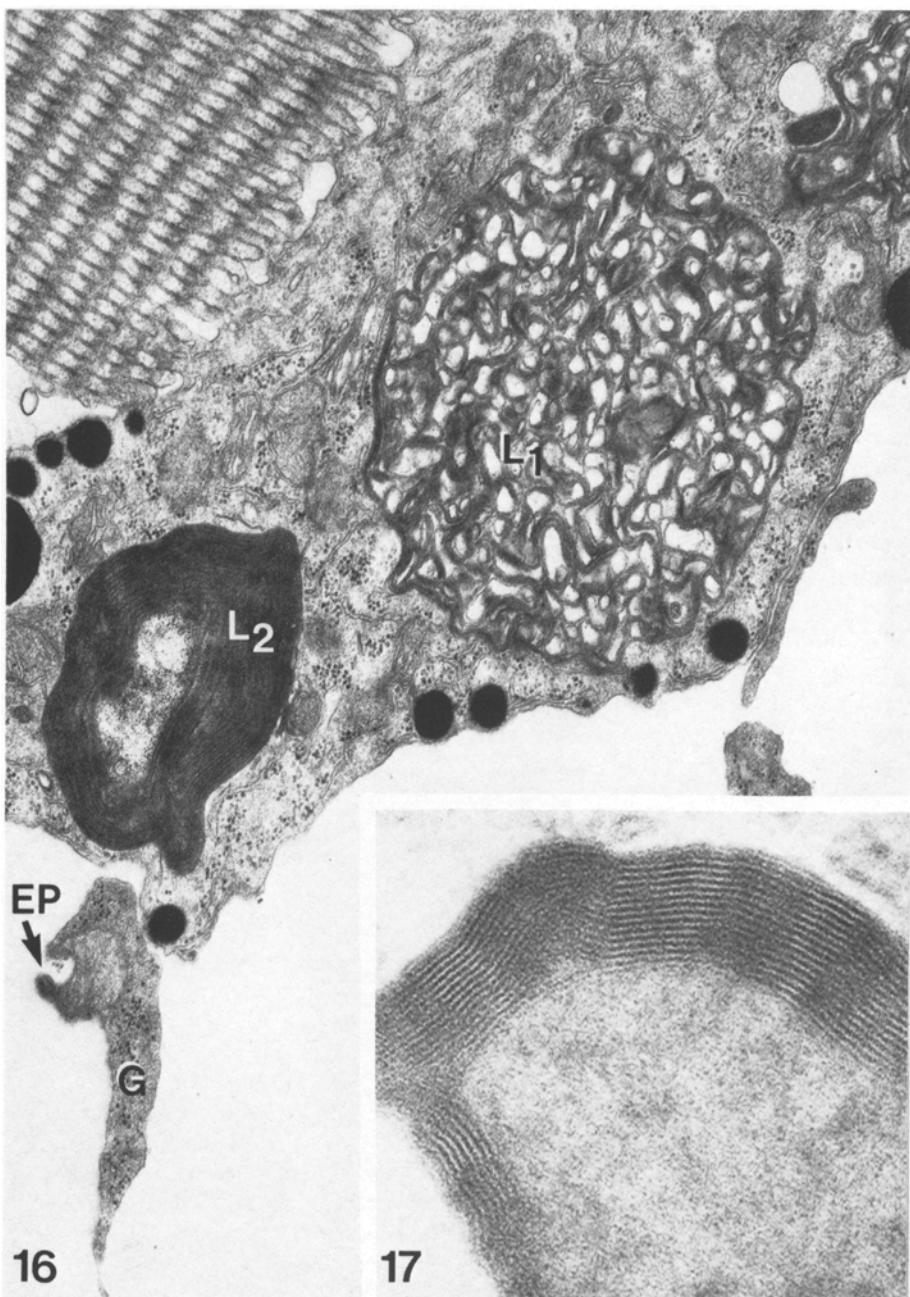


Fig. 16. Secondary lysosomes (*L*1 and *L*2) in more advanced states of degradation than shown in Fig. 15. In *L*1 vesicles have reorganized to multilamellae bodies. *L*2 represents a later stage, consisting of multiple layers of phospholipid lamellae, some of which have partially coalesced. *G* secondary glial cell; *Ep* endocytotic pit. $\times 29,000$

Fig. 17. Parallel lamellae in a secondary lysosome at a stage slightly prior to *L*2 in Fig. 16. $\times 190,000$

lysosomes, and the tips of their microvilli were intact and untransformed (Figs. 11, 12). All receptors fixed between dawn and mid-morning were found to be in the process of shedding. Between 12.00 and 16.00 h some cells had completed shedding to the point shown in Fig. 11, but the majority had not. Small mvbs are present in the retinulae by 2 h after dawn and residual bodies soon after; however, it is only during the middle of the day that mvbs of the massive size depicted in Fig. 14 appear. It can be concluded that shedding begins just before dawn, continues throughout the day, and has a pronounced peak around mid-morning. Degradation of membrane products probably begins in earnest after midday.

Shedding as a Normal Process

Shedding was established as a normal process by dissecting and fixing *Ptilogyna* in the field. Rhabdomeres were in identical stages of the cycle for given times of day as were those sampled after being held for up to 2 days in storage in Canberra.

Participation of the Secondary Pigment Cells in Membrane Uptake

The common ECS around the rhabdomeres of a single ommatidium appears to be isolated from the ECS outside the ommatidium by the juxtaposition of R1–7 to their neighbours (Fig. 2; Williams, in preparation); often there is a desmosome at the junction two neighbouring cells (Fig. 8). Therefore, there is little to suggest that material can leak from the central ECS to the extra-ommatidial ECS. Nevertheless, columns of secondary pigment cells outside the central region of the ommatidium can be seen to possess endocytotic pits (Fig. 16) and occasionally small vacuoles, which may contain vesicles or other less well-defined material (Fig. 13). Profiles of receptors sometimes suggest that the retinulae may produce small pseudopodia into the extra-ommatidial ECS. If these pseudopodia were to break off and be endocytosed by the pigment cells, this might account for the fragments seen in vacuoles in the pigment cell columns.

Internalisation of Membrane by Pinocytosis

Pinocytosis of rhabdomere membrane at the bases of the microvilli occurs as a minor mechanism of internalisation. Coated vesicles can be seen still attached to microvilli, and free in the cytoplasm, but they are not frequent, and are at no time seen in sufficient quantities to account for mvbs of the sizes observed.

Involvement of Fixation Artefacts

One component of the shedding profiles illustrated in this paper is probably of artefactual origin: the dense vesicles or "micro-whorls" shown in Figs. 5 and 6 will be shown to be similar to artefacts produced in rhabdomeres of another dipteran,

Lucilia, by prolonged primary fixation or when calcium concentrations no greater than those in the present fixatives are used (Williams, 1980). Other features are independent of fixation method.

Discussion

The present results confirm the reality of extracellular shedding of photoreceptor membrane in the compound eyes of arthropods. In the jumping spider, *Plexippus*, it appears to be a relatively slow event. *Ptilogyna* sheds in bulk, with a dawn peak, and the amount of membrane lost appears to be of similar order to the quantities shed by the spider *Dinopis* (Blest, 1978), and the crabs *Grapsus* (Nässel and Waterman, 1979) and *Leptograpsus* (Stowe, in preparation), although it is not as great. Both *Dinopis* and grapsid crabs show intracellular shedding only. Yamamoto and Yoshida (1978) demonstrate extracellular shedding and phagocytosis of microvilli by the photoreceptors of the simple eye of a holothurian.

Extracellular shedding has not been suspected in insects, despite a wealth of comparative studies of the ultrastructure of compound eyes. It seems likely that it may occur wherever ommatidia contain open rhabdoms whose rhabdomeres abut on extracellular space. Published electron micrographs are uninformative. Schneider and Langer (1969), have presented interesting micrographs of the receptors of the Hemipteran *Gerris*; transverse sections reveal filopodia from the receptors projecting into the intra-ommatidial ECS which they share. One micrograph has large, irregular vacuoles in retinulae. Others disclose conventional mvbs and pinocytotic vesicles. The eyes of this group of Hemiptera require re-examination in relation to the daily cycle, as do those of any arthropod possessing rhabdomeres with non-uniform microvilli.

Trujillo-Cenóz and Bernard (1972) describe the receptors of compound eyes of the dolichopodid fly, *Sympycnus*. The microvilli have a sharply-delimited, distal, tapered and disordered region in most of the receptors shown in their micrographs. It resembles the shedding zone in *Ptilogyna*, and probably has the same functional significance. Surprisingly, microvillar tips of the Megalopteran *Archicauloides* also have a well-defined pale zone, although the rhabdomeres to which they belong form a fused rhabdom, so that the microvillar tips of different retinulae are contiguous (Walcott and Horridge, 1971). Thus, there would seem to be no space available for extracellular shedding. The eye has not yet been examined at the day/night transitions, so that the significance of this pattern of organisation is equivocal.

The control of extracellular shedding is of interest. Transformation of tips of the microvilli occurs well before dawn, so that the sequence leading up to shedding is clearly not a result of simple damage to transductive membrane consequent upon performance. It may be a developmental change that anticipates shedding and allows it to be initiated at the appropriate time. The nature of this change, and the mechanism that defines the zone of transformation so clearly, are not understood. In well-fixed material, transverse sections of microvilli show axial filaments, while adjacent sections of transformed tips do not (Fig. 7). This suggests that shedding may involve or even be controlled by cytoskeletal changes affecting the stability of the microvillar conformation. In the dragonfly, *Hemicordulia*, Laughlin and

McGinness (1978) find that rhabdomeres of the dorsal retina fixed in the light-adapted state show proximal zones where the basal segments of the microvilli are of lower electron-density and are dilated or slightly deformed. This region may prove to be a shedding zone occupying the bases of the microvilli, but it should be remembered that the rhabdoms of crabs, which shed membrane in bulk at dawn (Nässel and Waterman, 1979; Blest et al., 1980), are not regionally differentiated in this way, although those of *Dinopis* may be (Blest, 1978).

Why has the extracellular route been evolved by jumping spiders and craneflies? For the jumping spider, Blest and Maples (1979) suggested that for shedding at the bases of the microvilli to be possible, the twin rhabdomeres of each cell would have to be separated, and that this geometry would not be compatible with the sharp angular sensitivity functions of the receptors (Hardie and Duelli, 1978) and the high spatial resolution of the eyes. These arguments cannot apply to the tipulid eye, which is designed primarily as a nocturnal eye with low resolution, and has a quite different optical geometry (Williams, in preparation).

Extracellular shedding in both *Ptilogyna* and *Plexippus* offers analogies to vertebrate photoreceptor membrane shedding, although it should be noted that the construction of vertebrate photoreceptors does not allow them to internalise transductive membrane (Young, 1978; Anderson et al., 1978). At present, little is known concerning the addition of membrane material to rhabdomeral microvilli. Attachment of preassembled membrane to the bases of microvilli has been proposed (Itaya, 1976), while autoradiography suggests that membrane proteins or their components can be inserted anywhere in the rhabdomere (Perrelet, 1972; Hafner and Bok, 1977). Such diverse strategies of membrane addition could have very different consequences when membrane is shed. It is clear, however, that distal shedding could allow membrane addition to proceed exclusively at the bases of the microvilli, so that all components would be shed as a function of the time they had been in the rhabdomeres. This hypothesis seems to allow the most economical strategy for turnover, and is suggested to underlie the evolution of extracellular shedding of the kind described in this paper. It rests, however, on the assumption that the high cholesterol content of microvillar membranes reduces their fluidity (Zinkler, 1974), so that translational diffusion of membrane proteins is severely limited. This prediction has been confirmed for crayfish photoreceptors by Goldsmith and Wehner (1977) and Wehner and Goldsmith (1975), but has yet to be extended to other arthropods.

References

- Anderson, D.H., Fisher, S.K., Steinberg, R.H.: Mammalian cones, disc shedding, phagocytosis and renewal. *Invest. Ophth.* **17**, 117-133 (1968)
Blest, A.D.: The rapid synthesis and destruction of photoreceptor membrane by a dinopid spider: a daily cycle. *Proc. R. Soc. Lond. B.* **196**, 463-483 (1978)
Blest, A.D., Day, W.A.: The rhabdomere organisation of some nocturnal pisaurid spiders in light and darkness. *Phil. Trans. R. Soc. Lond. B.* **283**, 1-23 (1978)
Blest, A.D., Maples, J.: Exocytotic shedding and glial uptake of photoreceptor membrane in a salticid spider. *Proc. R. Soc. Lond. B.* **204**, 105-112 (1979)

- Blest, A.D., Kao, L., Powell, K.: Photoreceptor membrane breakdown in the spider *Dinopis*: The fate of rhabdomere products. *Cell Tissue Res.* **195**, 425–444 (1978a)
- Blest, A.D., Powell, K., Kao, L.: Photoreceptor membrane breakdown in the spider *Dinopis*: GERL differentiation in the receptors. *Cell Tissue Res.* **195**, 277–297 (1978b)
- Blest, A.D., Price, G.D., Maples, J.: Photoreceptor membrane breakdown in the spider *Dinopis*: localisation of acid phosphatases. *Cell Tissue Res.* **199**, 455–472 (1979)
- Blest, A.D., Stowe, S., Price, D.G.: The sources of acid hydrolases for photoreceptor membrane degradation in a grapsid crab. *Cell Tissue Res.* in the press (1980)
- Boschek, B.C.: On the fine structure of the peripheral retina and lamina ganglionaris of the fly, *Musca domestica*. *Z. Zellforsch.* **118**, 369–409 (1971)
- Dobrotworski, N.V.: The Tipulidae (Diptera) of Australia. III. The genus *Ptilogyna* (Westwood). *Aust. J. Zool. Suppl.* **1**, 1–41 (1971)
- Eguchi, E., Waterman, T.H.: Freeze-etch and histochemical evidence for cycling in crayfish photoreceptor membranes. *Cell Tissue Res.* **169**, 419–434 (1976)
- Goldsmith, T.H., Wehner, R.: Restrictions on rotational and translational diffusion of pigment in the membranes of a rhabdomeric photoreceptor. *J. Gen. Physiol.* **70**, 453–490 (1977)
- Griffiths, G.W.: Transport of glial cell acid phosphatase by endoplasmic reticulum into damaged axons. *J. Cell Sci.* **36**, 361–389 (1979)
- Griffiths, G.W., Boschek, C.B.: Rapid degeneration of visual fibres following retinal lesions in the dipteran compound eye. *Neurosci. Lett.* **3**, 253–258 (1976)
- Hafner, G.S., Bok, D.: The distribution of ^3H -leucine labelled protein in the retinula cells of the crayfish retina. *J. Comp. Neurol.* **174**, 397–416 (1977)
- Hardie, R.C., Duelli, P.: Properties of single cells in posterior lateral eyes of jumping spiders. *Z. Naturforsch.* **33**, 156–158 (1978)
- Itaya, S.K.: Rhabdom changes in the shrimp, *Palaemonetes*. *Cell Tissue Res.* **166**, 265–273 (1976)
- Laughlin, S.B., McGinniss, S.: The structures of dorsal and ventral regions of the dragonfly retina. *Cell Tissue Res.* **188**, 427–447 (1978)
- Melamed, J., Trujillo-Cenóz, O.: The fine structure of the central cells in the ommatidium of dipterans. *J. Ultrastruct. Res.* **21**, 313–334 (1968)
- Nässel, D.R., Waterman, T.H.: Fast massive photoreceptor membrane turnover in crab eye light and dark adaptation. *J. Comp. Physiol.* **131**, 205–216 (1979)
- Perrelet, A.: Protein synthesis in the visual cells of the honeybee drone as studied with electron microscope autoradiography. *J. Cell Biol.* **55**, 595–605 (1972)
- Schneider, L., Langer, H.: Die Struktur des Rhabdoms im "Doppelauge" des Wasserläufers *Gerris lacustris*. *Z. Zellforsch.* **99**, 538–559 (1969)
- Sotavalta, O., Tuurala, O., Oura, A.: On the structure and photomechanical reactions of the compound eyes of crane-flies (Tipulidae; Limnobiidae). *Ann. Acad. Sci. Fenn. A.* **62**, 1–14 (1962)
- Trujillo-Cenóz, O., Bernard, G.D.: Some aspects of the retinal organisation of *Sympycnus lineatus* Loew (Diptera, Dolichopodidae). *J. Ultrastruct. Res.* **38**, 149–160 (1972)
- Walcott, B., Horridge, G.A.: The compound eye of *Archicauroides* (Megaloptera). *Proc. R. Soc. Lond. B.* **179**, 65–72 (1971)
- Wehner, R., Goldsmith, T.H.: Restrictions on translational diffusion of metarhodopsin in the membranes of rhabdomeric photoreceptors. *Biol. Bull.* **149**, 450 (1975)
- White, R.H.: The effect of light and light deprivation upon the structure of the larval mosquito eye. II. The rhabdom. *J. Exp. Zool.* **166**, 405–425 (1967)
- White, R.H.: The effect of light and light deprivation upon the structure of the mosquito larval eye. III. Multivesicular bodies and protein uptake. *J. Exp. Zool.* **169**, 261–278 (1968)
- Williams, D.S.: Ca^{++} -induced structural changes in photoreceptor microvilli of Diptera. *Cell Tissue Res.* in the press (1980)
- Yamamoto, M., Yoshida, M.: Fine structure of the ocelli of a synaptid holothurian, *Ophiodesoma spectabilis*, and the effects of light and darkness. *Zoomorphologie* **90**, 1–17 (1978)
- Young, R.W.: Visual cells, daily rhythms and vision research. *Vision Res.* **18**, 573–578 (1978)
- Zinkler, D.: Zum Lipidmuster der Photorezeptoren von Insekten. *Verh. Dtsch. Zool. Ges.* **67**, 28–32 (1974)