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Effects of light and dark on photoreceptors in the polychaete annelid *Nereis limnicola*

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Summary. The effects of light and dark on photoreceptors of the brackish-water polychaete annelid *Nereis limnicola* were studied by electron microscopy. Animals dark-adapted for one or two days exhibited well-formed straight microvilli (rhabdomeres) on the sensory cell processes. Continuous illumination of worms for one or two days caused extensive breakdown of the microvilli into vesicles and debris. Thirty minutes to three h of exposure of dark-adapted animals to light produced increasing severity of degradation of photoreceptoral microvilli. Light-adapted worms placed in darkness for one-half to three h showed progressive restoration of the microvilli to the dark-adapted condition. The products of degradation were internalized by both sensory and pigmented supportive cells by phagocytosis and pinocytosis.

Key words: Photoreceptors, annelid, polychaete – Light, degeneration – Dark, regeneration – Membrane recycling – Endocytosis

There have been many investigations of structural changes in photosensitive organelles in various taxa in relation to the amount of light entering an eye or ocellus. References are given in the succeeding paper (Brandenburger and Eakin 1985). To our knowledge cycling of photoreceptoral membranes in annelids has not been studied, although some effects of light on polychaete eyes have been described. Bocquet and Dhainaut-Courtois (1973), Fischer (1963), Fischer and Brökelmann (1966), Hauenschild and Fischer (1969) and Singla (1975) variously observed shifts in the position of pigment granules, changes in the diameter of the pupil, and alterations in the shape of the lens and the length of the sensory processes when the amount of illumination of a specimen is increased or decreased. Bocquet and Dhainaut-Courtois (1973) reported that the absence of light for 5 to 21 days produced variable changes in photoreceptoral processes in the eyes of both anterior and posterior zooids of *Syllis amica*. In an extreme instance the microvilli were replaced by numerous vesicles, and the apical processes of the supportive cells were said to disappear. For a general account of annelid photoreceptors see Verger-Bocquet (1984).

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The genesis of this study was a search for a good electron micrograph of a nereid rhabdomere for a review of polychaete photoreceptors. None had been published, including micrographs from our laboratory. Initially we thought that the apparent damaged condition of the photoreceptoral microvilli in earlier studies was due to poor fixation. Accordingly, we preserved the eyes of freshly collected *Nereis limnicola* in various fixatives. The result: all preparations showed damaged microvilli. We then discovered that the microvilli in dark-adapted worms exhibited good morphology. We concluded that the derangement and vesiculation of the microvilli of illuminated specimens were caused by the damaging effects of light.

Materials and methods

Young adult (25–50 mm in length) brackish-water polychaete annelids, *Nereis limnicola* (Johnson 1901), used in this study were obtained from Lake Merced in San Francisco, California. For dark-adaptation 6–8 worms removed from their flimsy tubes were placed in a large bowl of continuously aerated Lake Merced water. The bowl was enclosed in a light-proof box at 12° C. Light-adapted animals were similarly maintained except that they were continuously illuminated by light from a small fluorescent lamp giving 5 foot-candles at specimen level. After 24 to 48 h of adaptation, followed in some experiments by reversal of illumination or darkness, the animals were prepared for electron microscopic examination of the two pairs of cerebral eyes situated above the brain. Animals were decapitated, and their heads were bisected, trimmed with microscissors, and dropped into a fixative of 1.25% glutaraldehyde in 0.1 M cacodylate buffer, pH 7.3, with 0.75% sucrose, for 1 h at room temperature. For dark-adapted specimens the above procedures were conducted in the dark with the aid of a ruby light from a 25W lamp whose beam was concentrated and heat-filtered by a 25 ml volumetric flask filled with water. The treatment of light-adapted specimens was performed in the light. Following several rinses in buffer (0.2 M cacodylate plus 0.75% sucrose), at which time the hemiheads were further trimmed with a microknife, all specimens were postfixed for 1 h in chilled 1% OsO_4 in 0.1 M cacodylate plus 0.75% sucrose. After additional rinses in buffer the small pieces, each containing two eyes, were dehydrated, embedded in Spurr's resin or Epon, thick and thin sectioned, and sections examined with light and electron (Siemens 102) microscopes.

Each of the above experiments was repeated at least three times, with one exception, and in each experiment 5 or 6 animals were used, giving 6 to 10 good hemiheads (specimens). The exception was the reversal of light and dark for 30 min. This experiment was conducted once using 12 animals (6 for light reversal and 6 for dark reversal). Usually only three specimens were selected for EM study from each subgroup of similarly treated animals if their results were uniform.

In addition to the aforementioned experiments two special studies were conducted. On one cool, cloudy, late morning adult worms of *N. limnicola* were removed from the bottom of Lake Merced, one at a time, immediately placed in the above fixative, decapitated, and the head bisected under a dissecting microscope brought to the shore of the lake. The specimens were transported to Berkeley in vials of fixative embedded in crushed ice. The purpose of this procedure was to ascertain the ultrastructure of the photoreceptors in animals preserved immediately upon removal from their environment under low intensity of light.

The second special investigation was a long term (16 and 32 days) of dark-adaptation using the set-up previously described. Small amounts of commercial fish food were added occasionally to the bowl containing the worms. The purpose of this study was to confirm the observations of Bocquet and Dhainaut-Courtois (1973) that the absence of light causes degenerative changes in the eyes of a polychaete (see Discussion).

Results

1. Receptoral microvilli (rhabdomeres)

a) Dark-adapted eyes. The ocelli of animals dark-adapted for one or two days, under the conditions given above, showed the rhabdomeres consisting mostly of straight microvilli with the usual narrow attachments to the tips and sides of the sensory cell processes. There were only minor irregularities in the shape of the microvilli. Fig. 1 typifies the appearance of dark-adapted rhabdomeres. Note that they closely resemble normal photoreceptors of arthropods, onychophorans, cephalopods, gastropods and hirudinean and alciopid annelids (see Eakin 1972). Here and there, however, a few microvilli exhibit swollen tips (arrowheads, Fig. 1), and sometimes there is an adjacent vesicle (arrows, Fig. 1) that may have been abscised from the end of a microvillus.

The eyes of the worms dark-adapted for 16 days showed good morphology of the microvilli, although the tips of many were swollen and sunken into depressions of the cell membranes of sensory processes and pigmented supportive cells (not figured). In many rhabdomeres the microvilli were slightly smaller in diameter than those of eyes dark-adapted for only one or two days. Free vesicles and debris, however, were not present in the opticoels of nereids deprived of light for 16 days. Their sensory cell processes exhibited an unusually large amount of endoplasmic reticulum (ER) cisternae; multivesicular bodies were numerous in the somata of many receptor cells; and the sensory cell nuclei frequently contained large nucleoli.

The eyes of specimens dark-adapted for 32 days were characterized by: derangement and further narrowing of the microvilli (Fig. 3); considerable debris in the opticoels; there was reduction in the number of multivesicular bodies in the receptor cells, but an increase in the number of putative secondary lysosomes. The processes and somata of the sensory cells showed a decrease in ER, microtubules and mitochondria but a pronounced increase in cytoplasmic granules and particles of glycogen – sometimes to the extent of filling parts of a cell.

In both experiments of long-term dark-adaptation the pigmented supportive cells, their processes and the lenses showed no perceptible effects of the deprivation of light.

b) Light-adapted eyes. The ocelli of animals light-adapted under the conditions described above revealed extensive breakdown of the microvilli into vesicles (Fig. 2). Sometimes entire microvilli were detached from a sensory process resulting in their becoming narrow and irregular. In places, however, some microvilli appeared to be undamaged, although upon closer inspection one could see that their tips exhibited dilation and vesiculation. A group of good microvilli was infrequently observed.

The eyes of specimens removed from Lake Merced in the late morning of a cloudy day and immediately fixed did not exhibit the extensive degradation observed in the ocelli of animals that were light-adapted in our laboratory experiments. The microvilli of the former, however, showed more morphological irregularities, such as dilated and electron lucent tips (Fig. 4) than did the microvilli of dark-adapted worms.

c) Reversal of light- and dark-adaptation. If dark-adapted animals were exposed to 30 min of illumination, the number of dilated microvilli and nearby vesicles was increased (Fig. 5) compared with that in a dark-adapted rhabdomere (Fig. 1). After one h of exposure to light further breakdown of microvilli into vesicles was observed (Fig. 6). Some microvilli (MV_1, Fig. 6) became condensed and separated from the processes, and the tips of many were being phagocytosed by adjacent sensory cell processes (Fig. 6 inset). After three h of illumination the microvilli exhibited extensive vesiculation (Fig. 7).

In the converse experiments (light-adapted animals placed in darkness for 30 min to three h) the results were less uniform than those just described. Figs. 8 and 9 are selected to present the average state of the microvilli in the one and three h periods of dark-adaptation respectively. Much of the variation in the nature of the microvilli is due to the specific area of the retina sampled. Restoration of the microvilli seemed to progress more rapidly at the bases of the sensory cell processes and in rhabdomeres near the lip of an eyecup. By the end of the three h in darkness most microvilli in all sections of a retina exhibited good morphology.

2. Other cytoplasmic organelles and inclusions

a) Cytomembranes. Stacks of cytomembranes or cisternae (a few to 25) were frequently observed in sensory cell processes of light-adapted eyes (Fig. 10) and also of those fixed at the lake on a cloudy day. They were seen occasionally in dark-adapted ocelli (Fig. 11). In places these membranes appeared to be fused with broader submicrovillar cisternae (arrows, Fig. 11). Whorls of membranes were occasionally noted in the retinal cells (Fig. 16).

b) Endocytic vacuoles and vesicles. Evidence of phagocytosis of vesicles and debris, resulting from degradation of photo-

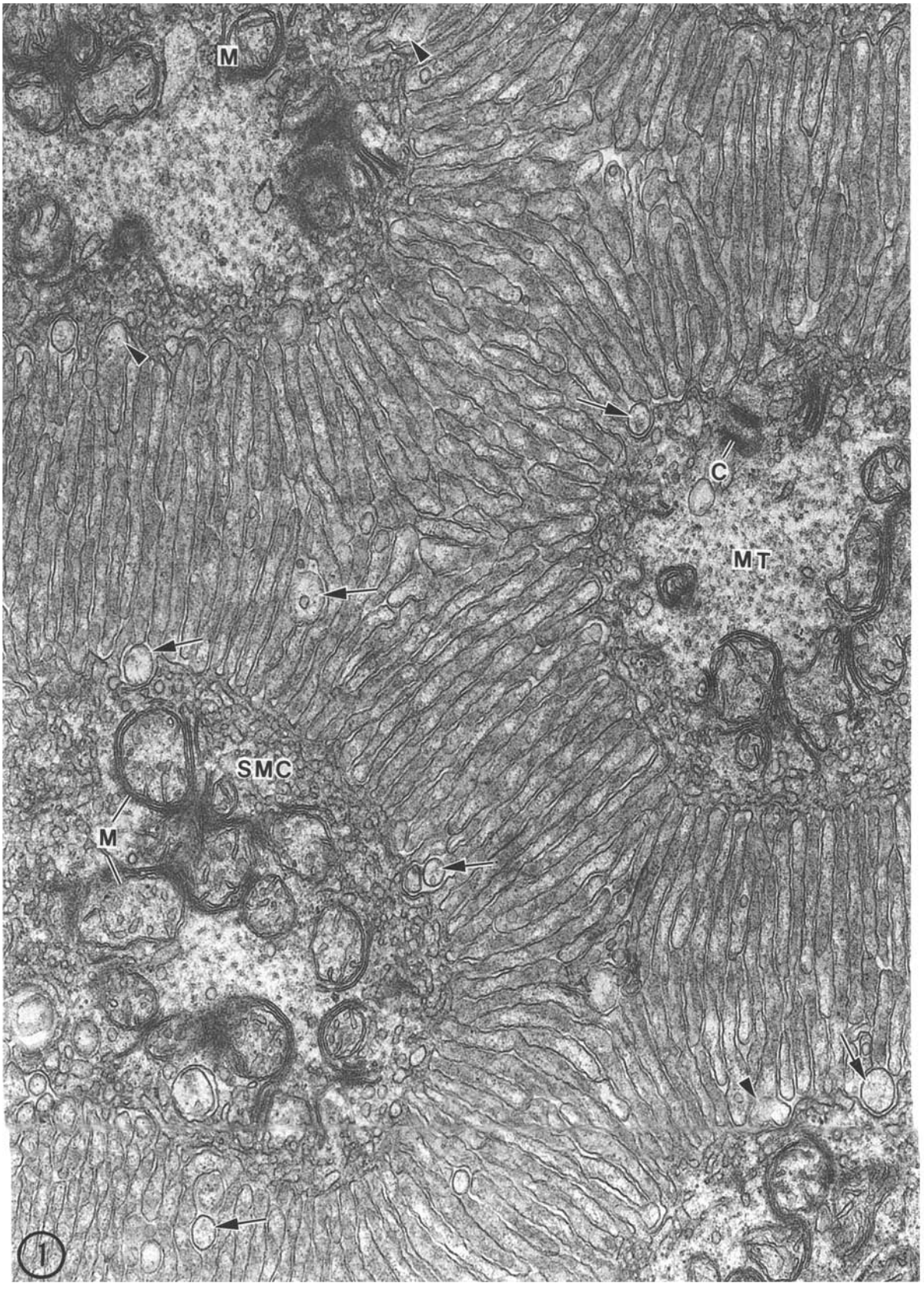


Fig. 1. Transverse view of four sensory cell processes and longitudinal view of their microvilli in a dark-adapted eye. *C* centriole; *M* mitochondria; *MT* microtubules; *SMC* submicrovillar cisternae; *arrows* occasional vesicles abscised from microvilli; *arrowheads* swollen microvillar tips. × 32000

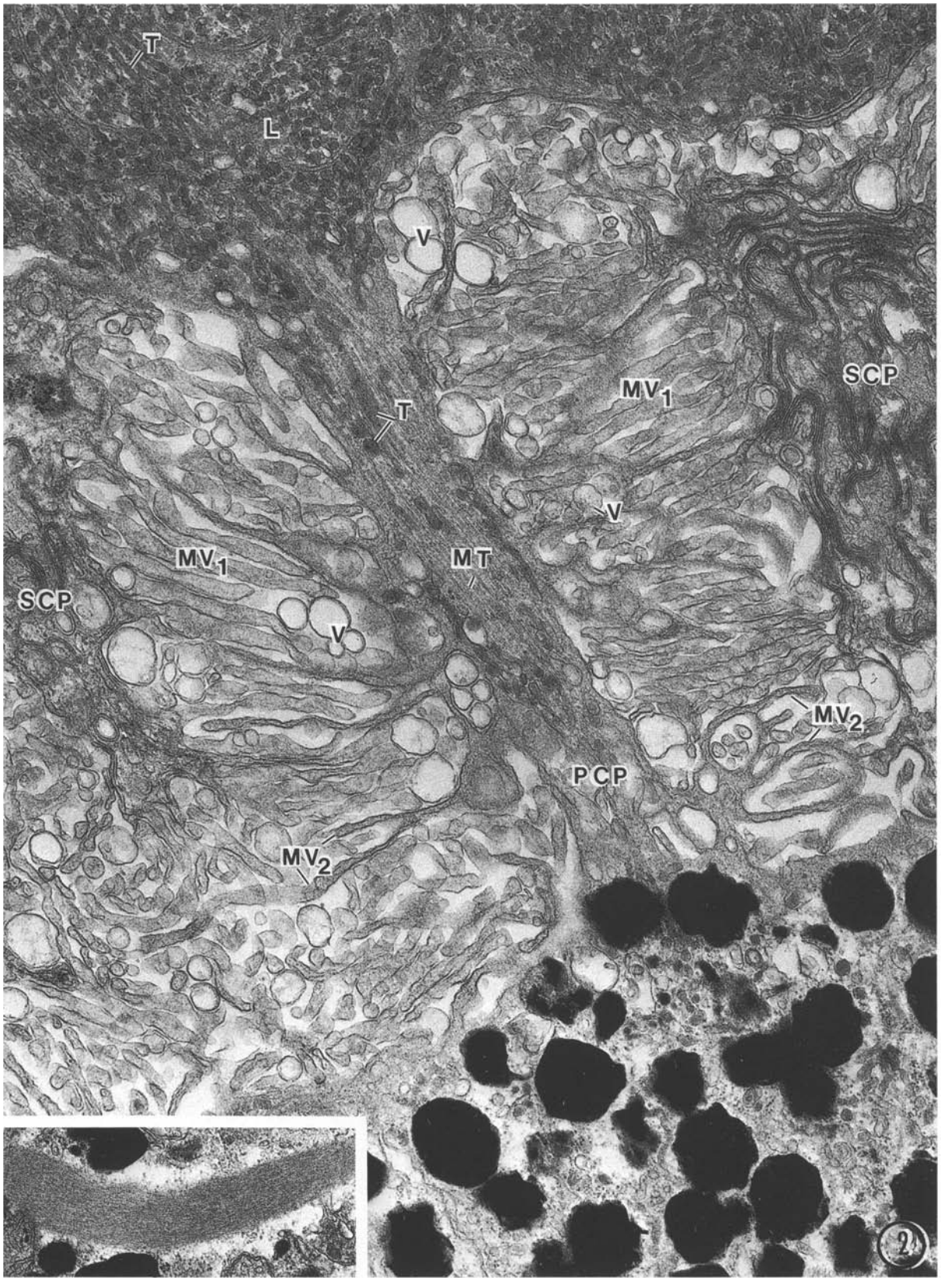


Fig. 1. Part of a radial section of an eye illuminated for 24 h. *L* lens compartments that are extensions of pigmented cell processes; *MT* microtubules; MV_1 degenerating microvilli of sensory cells; MV_2 microvilli of pigmented cells; *PCP* pigmented cell process; *SCP* sensory cell processes; *T* dense tubules in pigmented cell process and in lens compartments; *V* vesicles from breakdown of sensory microvilli. × 32000 *Inset*. Bundle of tonofilaments that runs lengthwise in a supportive cell. × 32000

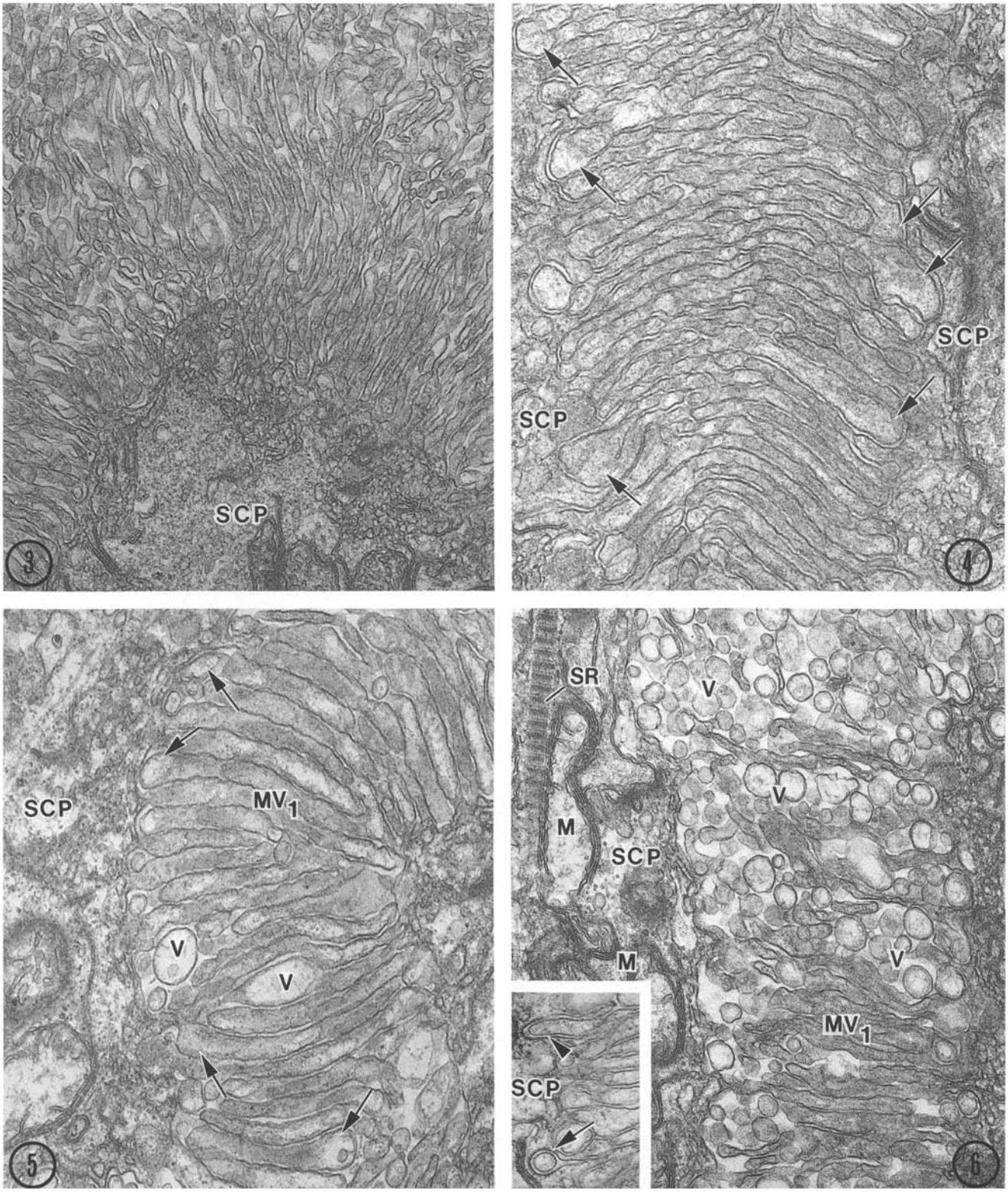


Fig. 3. An example of the effects of 32 days of dark-adaptation: derangement and narrowing of photosensory microvilli, but no vesiculation. *SCP* granular sensory cell process. × 32000

Fig. 4. Two adjoining rhabdomeres in a specimen fixed at Lake Merced under weak daylight, showing dilated microvillar tips (*arrows*) partially embedded in adjacent sensory cell processes (*SCP*). No vesiculation. × 38000

Fig. 5. An example of the effects of thirty-min illumination of a dark-adapted eye. MV_1 microvilli; *SCP* sensory cell process; *V* vesicles; *arrows* swollen microvillar tips. × 32000

Fig. 6. An example of the effects of one-h exposure to light of a dark-adapted eye. *M* mitochondria ensheathed by membranes; MV_1 shrunken and detached microvilli; *SCP* part of sensory cell process; *SR* striated rootlet; *V* vesicles from microvillar breakdown. × 32000 *Inset:* Phagocytosis by a sensory cell process (*SCP*) of a vesicle (*arrow*) and tip of a microvillus (*arrowhead*). Note coated membranes of incipient phagosomes. × 32000

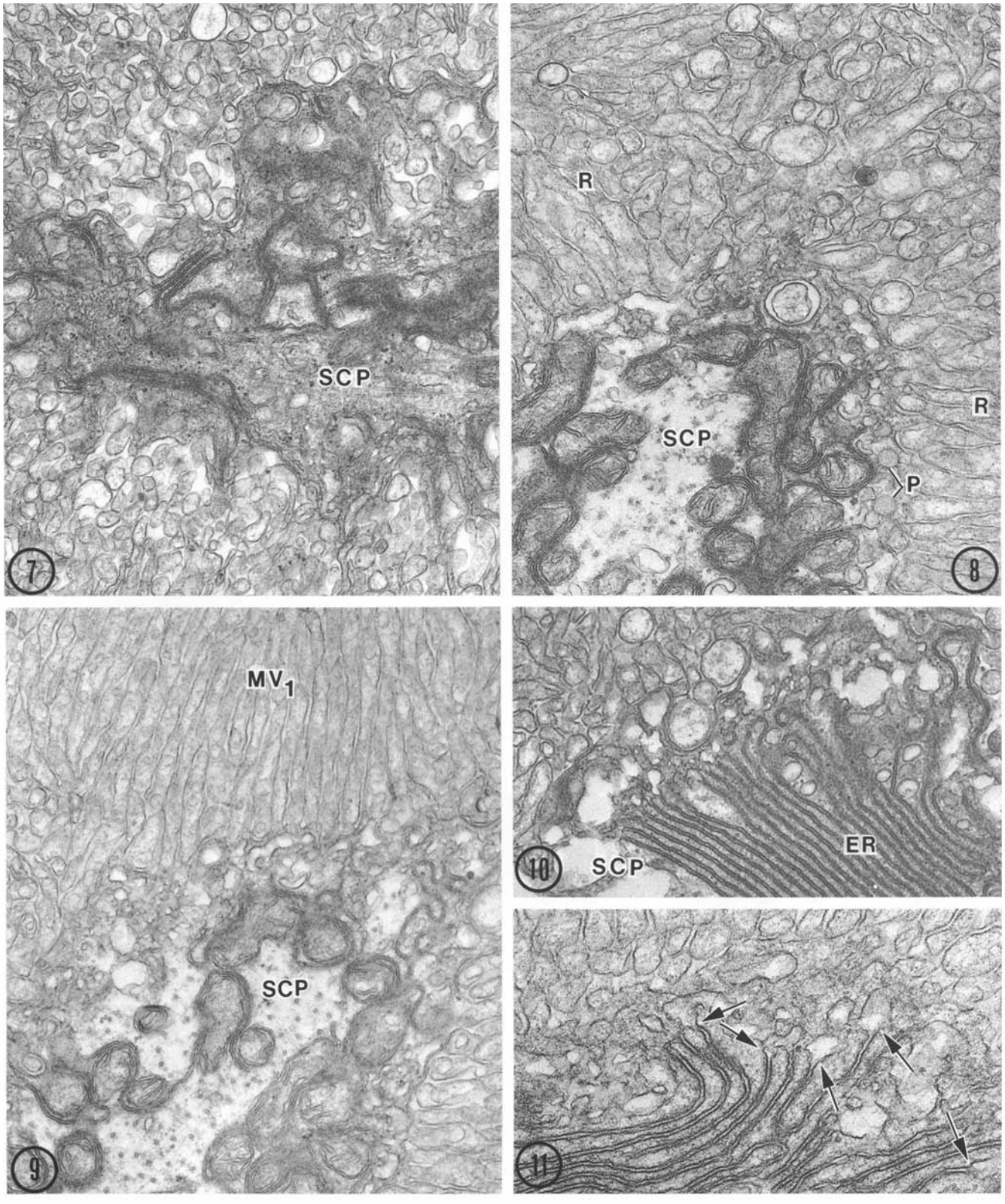


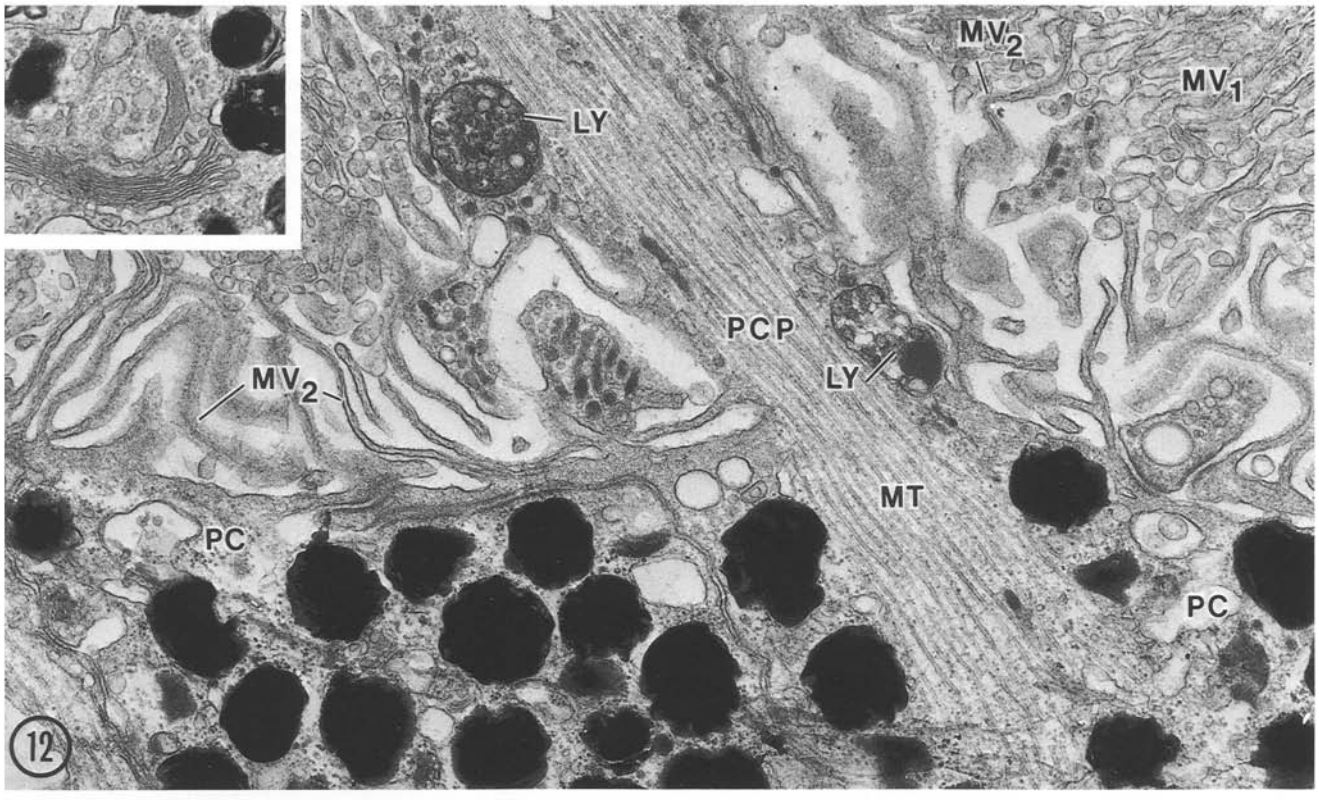
Fig. 7. An example of total degradation of microvilli into vesicles after three-h exposure to light of a dark-adapted eye. *SCP* part of a sensory cell process containing many membrane-enclosed mitochondria. × 32000

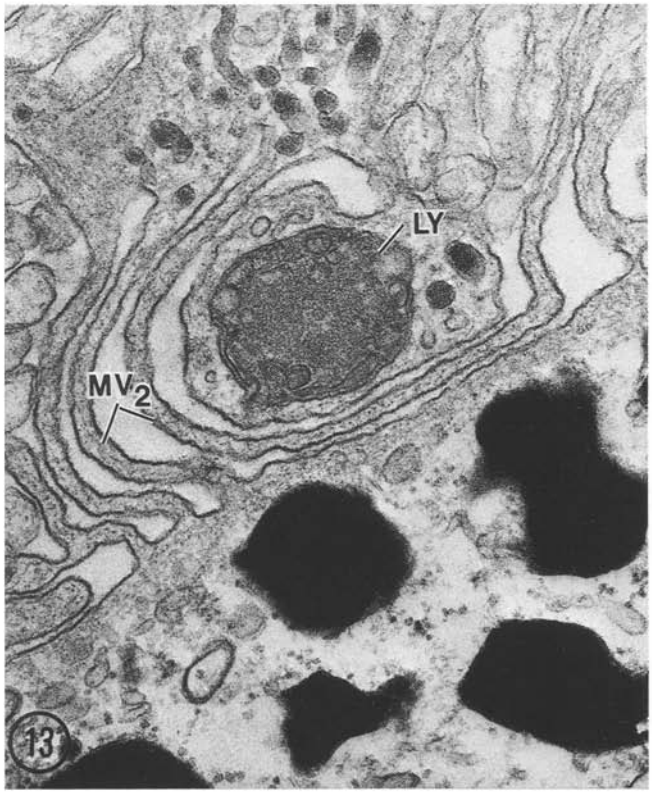
Fig. 8. An example of beginning regeneration of a rhabdomere (*R*) in a light-adapted eye after 1 h in the dark. *P* pinosomes or coated vesicles; *SCP* tip of sensory cell process containing microtubules and membrane-enclosed mitochondria. × 32000

Fig. 9. An example of almost complete restoration of microvilli (MV_1) in a light-adapted eye following 3 h in the dark. *SCP* part of a sensory cell process. × 32000

Fig. 10. Part of a light-adapted sensory cell process (*SCP*) containing a stack of endoplasmic cisternae (*ER*). × 32000

Fig. 11. Suggested fusion (*arrows*) of narrow endoplasmic cisternae with broader submicrovillar cisternae in a dark-adapted eye. × 57000





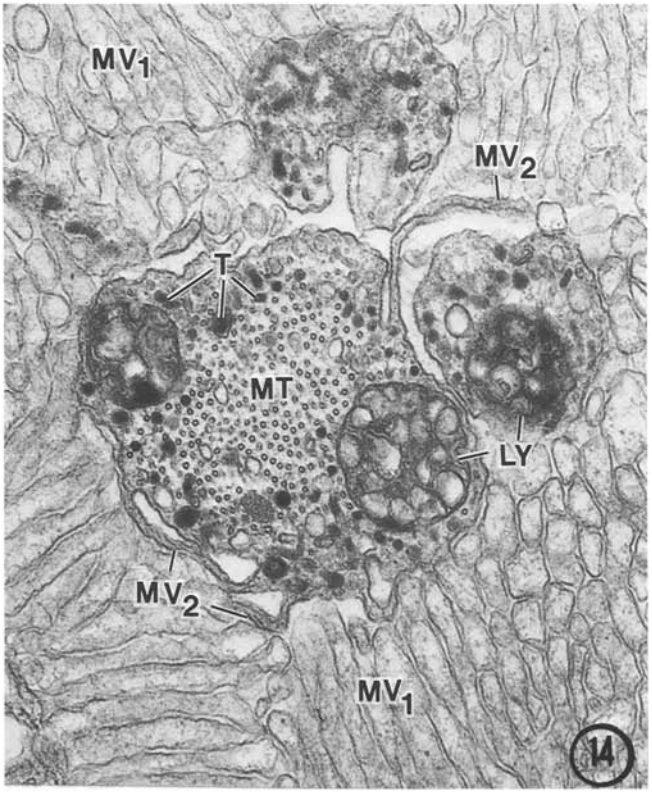


Fig. 12. Distal ends of two pigmented supportive cells (*PC*) in a dark-adapted eye. The process (*PCP*) of the right one extends into the lens (not shown). *LY* putative lysosomes; *MT* microtubules; MV_1 microvilli of sensory cells; MV_2 microvilli of pigmented cells. × 32000 *Inset:* Golgi apparatus and an adjacent large tubule filled with dense material in the distal end of a pigmented cell. × 32000

Fig. 13. Distal end of a pigmented supportive cell with long microvilli (MV_2) that exhibit phagocytosis. *LY* putative lysosome. Dark-adapted specimen. × 57000

Fig. 14. Cross sections of several processes of pigmented supportive cells. *LY* putative lysosomes; *MT* microtubules; MV_1 microvilli of sensory cells; MV_2 microvilli of pigmented cells; *T* dense tubules. Dark-adapted specimen. × 32000

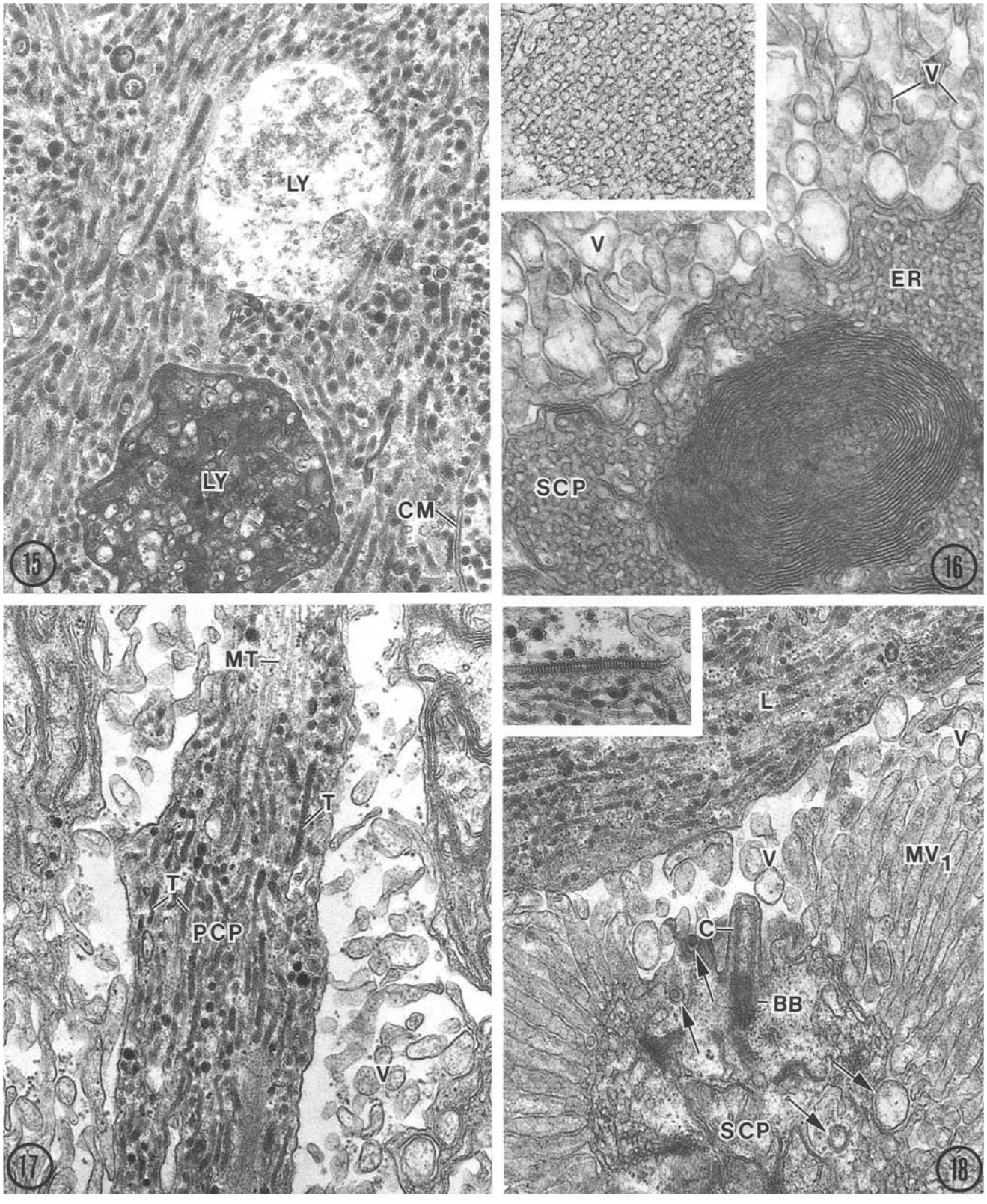


Fig. 15. Lens compartments filled with dense, spaghetti-like tubules. *CM* cell membranes of two lens compartments (extensions of pigmented cell processes); *LY* putative secondary lysosomes or residual bodies. Light-adapted specimen. × 32000

Fig. 16. Sensory cell process (*SCP*) filled with endoplasmic reticulum (*ER*) and containing a whorl of membranes. *V* vesicles from microvillar breakdown. Light-adapted specimen plus 1 h in the dark. × 40000 *Inset:* Crystalloid body near the nucleus of a sensory cell. × 45000

Fig. 17. Process of a pigmented supportive cell (*PCP*) containing microtubules (*MT*) and dense tubules (*T*). *V* vesicles from microvillar breakdown. Dark-adapted specimen plus 3 h of illumination. × 32000

Fig. 18. Distal end of a sensory cell process (*SCP*) with its microvilli (MV_1) and vestigial cilium (*C*). *BB* basal body ; *L* a lens compartment with its many dense tubules; *V* vesicles from degraded microvilli; *arrows* incipient phagosomes (?). Dark-adapted specimen. × 26000 *Inset:* Septate junction between two lens compartments. × 32000

receptoral microvilli, was observed in both pigmented supportive and sensory cells in both light- and dark-adapted worms. Some phagosomes contained a single vesicle; others (multivesicular bodies) enclosed a heterogeneous mass of vesicles, fragments of membranes and debris. Multivesicular bodies were especially numerous in the sensory cells of worms fixed at the lake under weak daylight. The phagocytosis exhibited by the supportive cells appeared to be accomplished in part by the activity of their microvilli acting as pseudopodia (e.g., Figs. 12–14). Incidentally, these microvilli were not damaged by light or by lack of illumination for 32 days.

Pinocytosis – the incorporation of extracellular fluid with solutes and suspensions – also occurred in both types of experimental animals and by both kinds of cells, but especially by the sensory ones. The evidence for this conclusion is the presence within the somata and processes of these cells of small, clear, coated vesicles (P, Fig. 8) and by curved, internally coated indentations of the plasmalemma, interpreted as incipient pinosomes.

c) Presumed lysosomes and residual bodies. The large, irregular, sometimes dark bodies (Figs. 12, 13) observed within the supportive cells or their processes and in the somata of sensory cells are putative lysosomes (see the following paper by Brandenburger and Eakin 1985). Similar structures were sometimes seen within the lenses of both light- and dark-adapted specimens (Fig. 15). Granular vacuoles were regarded as residual bodies resulting from lysosomal activity.

d) Tubules. The cores of processes of both sensory and pigmented supportive cells contained many clear, longitudinally arranged microtubules, 25 nm in diameter (Figs. 1, 2). They were surrounded by mitochondria in the sensory processes and by larger, more irregular, densely stained tubules, 37 to 140 nm in diameter (T, Figs. 2, 14, 17) in the supportive cell processes. These same tubules packed the interwoven compartments of the lens (Fig. 15) that are extensions of the supportive cell processes. Dark material present in cisternae adjacent to a Golgi apparatus (Fig. 12 inset) had an appearance similar to that in the dense tubules. Light- and dark-adapted ocelli showed no apparent difference in the number and nature of these cytoplasmic tubules.

e) Ciliary structures. Vestigial cilia (Fig. 18), centrioles or basal bodies (Fig. 1), and striated rootlets (Fig. 6) were observed in the sensory cell processes of both types of experimental animals.

3. Heretofore undescribed features

As fringe benefits of this investigation, we noted and photographed some structures not previously observed in a nereid eye: crystalloid bodies in photoreceptoral cells (Fig. 16, inset), large bundles of fibers (? tonofilaments) in pigmented supportive cells (Fig. 2, inset), and long belts of septate junctions between lens compartments (Fig. 18, inset). Paracrystalline bodies, similar to those reported here, were observed in the photosensory cells of the polychaete *Syllis* (Bocquet and Dhainaut-Courtois 1973).

Discussion

1. Daily breakdown and restoration of photoreceptors

A discussion of this topic will be presented in the following paper (Brandenburger and Eakin 1985).

2. Long-term deprivation of light

Bouquet and Dhainaut-Courtois (1973) observed profound effects of darkness on the photoreceptoral microvilli in the polychaete *Syllis* after only 12 days of absence of light. In one instance of a 12-day specimen (see their Fig. b, Plate V) the microvilli were completely broken down into vesicles and membranous debris, and the apical processes of the supportive cells were said to have disappeared, although in the text the authors state that the ultrastructure of the supportive cells is not significantly modified by darkness. We did not observe vesiculation of the microvilli in our specimens, even in those maintained in darkness for 32 days, and we found no evidence of degeneration in the processes of the supportive cells. We examined many sections of one eye in each of three worms in each experiment. The results were uniform. At the conclusion of each period of dark-adaptation (16 and 32 days) about six to eight worms were removed from the darkened aquarium and tested for activity under a red light before fixing their eyes (see Materials and methods). All were vigorous swimmers and seemingly healthy. We wonder if the one instance described and figured by Bouquet and Dhainaut-Courtois (1973) was an animal in poor health. The number of syllids examined was not stated.

We did observe, however, damaging effects of prolonged darkness upon the photosensory cells of *Nereis limnicola* that were more severe after a month of absence of light than after two weeks in the dark. The photoreceptoral microvilli began to shrink in diameter and became increasingly deranged, although there was little increase in debris in the opticoels of the eyes. Bodies regarded as secondary lysosomes became increasingly numerous. Concurrently, there was a progressive decline in the number of cytoplasmic organelles and an increase in cytoplasmic granularity and accumulation of glycogen. These trends suggest a drift of the receptoral cells into a state of inactivity and degeneration when deprived of light for several weeks.

3. Miscellany

a) Ciliary structures. The stunted cilium, basal body, and striated rootlet in the process of each sensory cell are regarded as vestigial structures (see Eakin and Westfall 1964; Eakin 1982). The rootlet, which often extends far down the sensory process, is probably useful as a supporting rod. According to one theory of evolution of photoreceptors (Vanfleteren and Coomans 1976; Coomans 1981; Vanfleteren 1982) cilia induce the formation of the photoreceptoral microvilli in eyes that are typically rhabdomeric. We see no evidence in this study to support that hypothesis. The vestigial cilia appear to play no role in the regeneration of the microvilli during dark-adaptation. Many reforming villi are at the bases of the sensory cell processes and seemingly too remote to receive any putative inductive stimulus from the distally situated cilia. A critique of this and other theories of evolution of photoreceptors plus a new hypothe-

sis, termed component selection, has been published recently (Burr 1984).

b) Tubules. There appear to be two kinds of tubules. The first is the standard microtubule found in both sensory and supportive cells and their processes and in the compartments of the lens. These tubules are small in diameter (25 nm), straight, presumably inflexible, and centrally placed in the processes. We surmise that they are supportive in function, and perhaps serve as guides in a cytoplasmic flow, first suggested by Dorsett and Hyde (1968). A discussion of the role of microtubules in photoreceptors is given by Ali and Klyne (1984).

The second type of tubule is larger and variable in diameter (37 to 140 nm), apparently flexible, peripherally situated in the supportive cell processes, and filled with a darkly staining material (Figs. 2, 14). They are not present in sensory cell processes. The extensions of the supportive cell processes that comprise the lens are filled with these tubules (Figs. 2, 15, 18). They look like strands of spaghetti. Earlier workers stated that these structures were vesicles or short rods, not tubules. Verger-Bocquet (1983) called them canaliculi. The differences in terminology may be due to differences in species studied, age of the specimens, plane of sectioning, and fixatives used. For example, Eakin and Westfall (1964) reported the structures in question to be vesicular in the ocellus of *Nereis limnicola*, the same annelid used in this investigation. We believe that our present interpretation of the tubule is correct, at least for adult worms.

The origin of the dense tubules and the material they contain has not been determined. Dorsett and Hyde (1968) did not find "lens material" in the bases of the pigment cell processes, but concluded it was a secretion. We observed, however, tubules bearing the osmiophilic substance not only in the basal parts of the pigmented cell processes but also in the subcortical regions of the same cells. Moreover, tubules or cisternae bearing a similar substance were seen adjacent to a Golgi apparatus (see Fig. 12, inset), the organelle we believe to be the source of the dense tubules and their contents, in agreement with a similar inference drawn by Zahid and Golding (1974) in their study of *Nephtys*. Whether the "lens material" moves distally in the tubules or is passively carried by elongation of the tubules is not known. We favor the latter hypothesis. The function of the tubules is also unknown. It is assumed that they give the lens its refractive properties.

The extensions of the supportive cells that traverse the photoreceptoral layer of a nereid ocellus have been variously referred to as fibers (Pflugfelder 1932), septa (Eakin and Westfall 1964; Singla 1975), filaments and pillars (Dorsett and Hyde 1968), apical prolongations (Bocquet and Dhainaut-Courtois 1973), and processes (Hauenschild and Fischer 1969, and in this paper). Another semantic problem: the large body in the eye of a polychaete worm has been termed a *Füllmasse* or *Glaskörper* (Hesse 1899; Pflugfelder 1932; Fischer and Brökelmann 1966; Hermans and Cloney 1966; Hauenschild and Fischer 1969). Other investigators, including us, use "lens," believing that the body has refractile properties that, so far as we know, have not been established (see Verger-Bocquet 1984, for discussion of polychaete lenses).

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