LIGHT DEPRIVATION AND PRESUMED PHOTORECEPTOR CELLS IN *Hydra littoralis*

by

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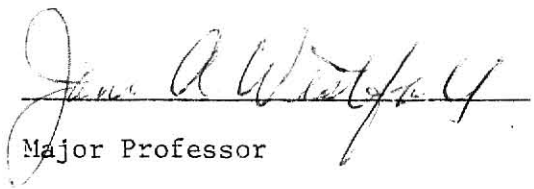

Major Professor

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INTRODUCTION

The photosensitivity of a fresh-water coelenterate, *Hydra*, was first reported by Trembley (1744). Later Wilson (1891) and Haug (1933) confirmed that *Hydra* are most responsive to the shorter wavelengths of light within the visible spectrum. In neither of these studies was an anatomical basis for this photosensitivity demonstrated. In the 1960's the application of electrophysiological recording techniques were applied to studies of *Hydra*; they provided an important new method for measuring this animal's reactions to light. Passano and McCullough (1962) demonstrated that light shone on an entire *Hydra* or focused on the basal disk inhibited the regular rhythmicity of the rhythmic pulses, which they believed were generated by pacemakers in the gastrodermis. They also reported that light focused on the hypostome-tentacle junction was able to block coordinated epidermal muscle contractions. Rushforth et al. (1963) observed that *Hydra* contract when exposed to light and that excision of the tentacles had no effect on this response. Light also affected isolated portions of *Hydra* (Rushforth and Burke, 1971); in particular, isolated tentacles responded to illumination by increasing both the frequency and number of bursts associated with contraction of the longitudinal musculature.

The above studies have not resolved the anatomical location of the photoreceptive cell(s) in *Hydra*. However, they have demonstrated both behaviorally and electrophysiologically that the photoreceptive areas may include the tentacles, hypostome, hypostome-tentacle junction, and the basal disk, and that the animal need not be intact for a response to light

to be elicited. Also, none of the extensive morphological studies done on *Hydra* have identified an unequivocable photoreceptor cell. Lentz (1966) and later Westfall and Kinnamon (1978) suggested a possible photosensory role for the sensory cells in *Hydra* based on the similarity of these cells to the ciliary photoreceptor cells of other animals (Eakin, 1972). In fact, Westfall and Kinnamon (1978) observed in tentacles of *Hydra* sensory cells with a basal swelling of the cilium and pigment-like granules in the apical cytoplasm. In this study I have also observed in the base of the tentacle similar cells with a basal swelling of the cilium and pigment-like granules in the apical cytoplasm; the significance of these cells will be discussed later. A gastrodermal (= endodermal) photoreceptor has also been suggested (Feldman and Lenhoff, 1960) based on studies involving starvation-associated depigmentation of gastrodermal cells in *Hydra littoralis*.

This study was undertaken in an attempt to show by morphological methods the exact location of photoreceptor cells in *Hydra littoralis*. My experimental protocol was based on the premise that photosensitive cells will undergo detectable ultrastructural changes after long periods of light deprivation. Previous ultrastructural studies in other invertebrate species have demonstrated such changes to occur in animals kept in the dark (Röhlich and Tar, 1968; Carpenter et al., 1974; Roach and Wiersma, 1974; Bedini et al., 1977; Yamamoto and Yoshida, 1978; Eguchi and Waterman, 1979; Bloom and Atwood, 1981).

I have therefore examined the head region of *Hydra littoralis* (head region consisting of base of the tentacle, hypostome, and hypostome-tentacle junction) in light-deprived animals in order to determine if this light deprivation had any effect on the ultrastructure of the neurons. There are two types of neurons found in *Hydra*: sensory cells located in the periphery of the epidermis (= ectoderm) and ganglion cells located

near the myonemal bases of the epitheliomuscular cells. Both types of neurons were examined because structurally they are similar, containing a cilium-stereociliary complex, neurosecretory type granules, and ultrastructural evidence of interneuronal and neuromuscular synapses; both could therefore theoretically serve a photoreceptive function.

MATERIALS AND METHODS

Experimental Protocol

Specimens of *Hydra littoralis* (from Carolina Biological Supply Company) were acclimated to laboratory conditions for one week prior to experimentation. Two groups of experimental animals were then formed. One group, termed the normal-light animals (NL), were maintained under normal laboratory lighting conditions consisting of approximately 12 hours of light per day from overhead fluorescent lamps with an intensity of 65 foot-candles incident upon the animals, as measured by a Gossen Luna Pro light meter (Gossen Inc., West Germany). The second group of animals, termed the light-deprived animals (LD), were maintained under conditions of constant darkness except for a brief exposure to dim red light (Kodak Red Filter #1, Eastman-Kodak, New York) every other day during feeding and cleaning. This red light delivered an intensity of approximately six foot-candles incident upon the animals. Both groups of animals were kept in culture dishes containing P-19 culture solution (Elias et al., 1972) at 23°C and were fed on brine shrimp nauplii every other day. Under these conditions the animals remained healthy and continued to grow and reproduce.

Five animals from both groups were fixed for electron microscopy at 42 hours, 5, 14, and 40 days after the start of the experiment. All fixations were done in the early afternoon. In order to test for a diurnal

change in photoreceptor structure, a second experiment was done in which the animals were fixed at midnight, corresponding to the "night-eye" concept of Horridge et al., (1981). For this experiment, the LD animals were kept in constant darkness for 6 hours prior to fixation, and the NL animals were kept under the standard laboratory lighting conditions from 0800 until fixation at 2400 hours.

Fixation Procedures

Twenty-four hour starved animals from each group were fixed identically, except that the LD animals were fixed under dim red light. To prevent the *Hydra* from contracting, a few drops of 2% urethane (Macklin, 1976) were added to the vials containing the *Hydra* in the P-19 culture solution. Once the animals were relaxed, a solution of 2.5% glutaraldehyde in 0.05 M cacodylate buffer (approximately 350 mOsmol) at pH 7.3 was added to the vials at room temperature. Fresh fixative was added and the vials were stored on ice for one hour. Following several rinses in buffer, the tissue was postfixed in a solution of cold 1% OsO_4 in 0.05M cacodylate buffer for 90 minutes, rinsed briefly in distilled H_2O, and dehydrated in a graded series of ethanol. The tissue was then infiltrated overnight in a 1:1 acetone-Epon/Araldite mixture under a light vacuum and then slowly cured for two days in a fresh Epon/Araldite mixture.

Procedures for Microscopy

For orientation using light microscopy, thick (0.5-1.0 μm) sections were cut on a Sorvall MT-2 ultramicrotome, placed onto glass slides, stained with a 1% toluidine blue in sodium borate solution, and photographed with a Zeiss Ikon camera mounted on a Zeiss RA 38 light microscope (Carl Zeiss Inc., Germany). For transmission electron microscopy, thin (<0.1 μm) sections

were cut with a diamond knife, placed on 200 hex copper grids or Formvar-coated slot grids, poststained with uranyl acetate followed by a triple lead stain (Sato, 1968), and coated with carbon. The sections were subsequently viewed on a Philips EM-301 operating at 60 or 100 kV.

RESULTS

An ultrastructural examination of the head region, defined to include the tentacle base, of a total of 19 *Hydra* from all experimental periods of LD and NL animals revealed that light deprivation had no observable effects upon the fine structure of the sensory and ganglion cells. Also, neurons from animals fixed at midnight showed no ultrastructural changes from those of animals fixed in early afternoon.

Sensory cells

Approximately 40 sensory cells from the base of the tentacles and from around the mouth (Fig. 1) were examined and found to exhibit the same fine structure in both the LD and NL animals (Figs. 2-6). The cells were long (8-10 μm) and narrow (2-4 μm) with a short cilium (1-2 μm) projecting from the apical end. Several stereocilia surrounded the sensory cilium, which was connected to the cytoplasm by a basal body with ciliary rootlets (Fig. 3). The cytoplasm adjacent to the rootlets was rich in mitochondria and also contained numerous ribosomes and microtubules.

The proximal portion of the cell contained a prominent heterochromatic nucleus and tapered into one or more neurites projecting towards the base of the surrounding epitheliomuscular cell. The perikaryon of the sensory cell contained several Golgi complexes (Fig. 2), dense-cored vesicles (of probable Golgi origin), occasional dense bodies, and diffusely distributed ribosomes.

Morphological variations in sensory cells

In both the LD and NL animals the sensory cells from the base of tentacles and from around the mouth exhibited two variations in their general morphology: (1) a modification of the sensory cilium by formation of a swelling at its basal end (Fig. 4); and (2), incorporation of oval (260 by 150 nm) or round (110-150 nm) pigment-like granules into the apical cytoplasm (Fig. 5). In a few sensory cells serial sections demonstrated the presence of both a basal ciliary swelling and pigment granules in the same cell (Figs. 5 and 6).

Ganglion cells

More than 100 ganglion cells, from the base of the tentacle, around the hypostome (Fig. 1), and at the hypostome-tentacle junctions of both the LD and NL animals were compared and found to show similar fine structure (Figs. 7-9). Ganglion cells were characterized by a heterochromatic nucleus with a prominent nucleolus. A cilium-stereociliary complex was situated near the nucleus; it had a sensory cilium with basal body and striated rootlets projecting in a direction opposite to the surrounding stereocilia (Figs. 7 and 8). Mitochondria were found in the perikaryon and near the cilium-stereociliary complex, although not in as great abundance as in the sensory cells. Other typical organelles found in the ganglion cells included Golgi complexes, ribosomes, glycogen, occasional dense bodies, and dense-cored vesicles. As in the sensory cells, no detectable changes were observed in the general features of ganglion cells from the LD animals as compared to those from the NL animals.

Neuronal organelles

The ultrastructure of organelles of sensory and ganglion cells in both LD and NL animals were compared with each other and with data reporting

organellar changes in light deprived and light adapted states of other invertebrate photoreceptors (Table 1). All comparisons were qualitative; owing to the complexity and uncertainties of this type of study, no quantitative measurements were made nor statistical analyses attempted.

Mitochondria were most abundant in the apical region of the sensory cells and in the perikarya of ganglion cells. They contained prominent cristae surrounded by dense matrices. The mitochondria appeared somewhat larger and more numerous in sensory cells compared to ganglion cells; however, in neither cell was there any apparent change in the number or structure of the mitochondria with light deprivation (Figs. 10 and 11).

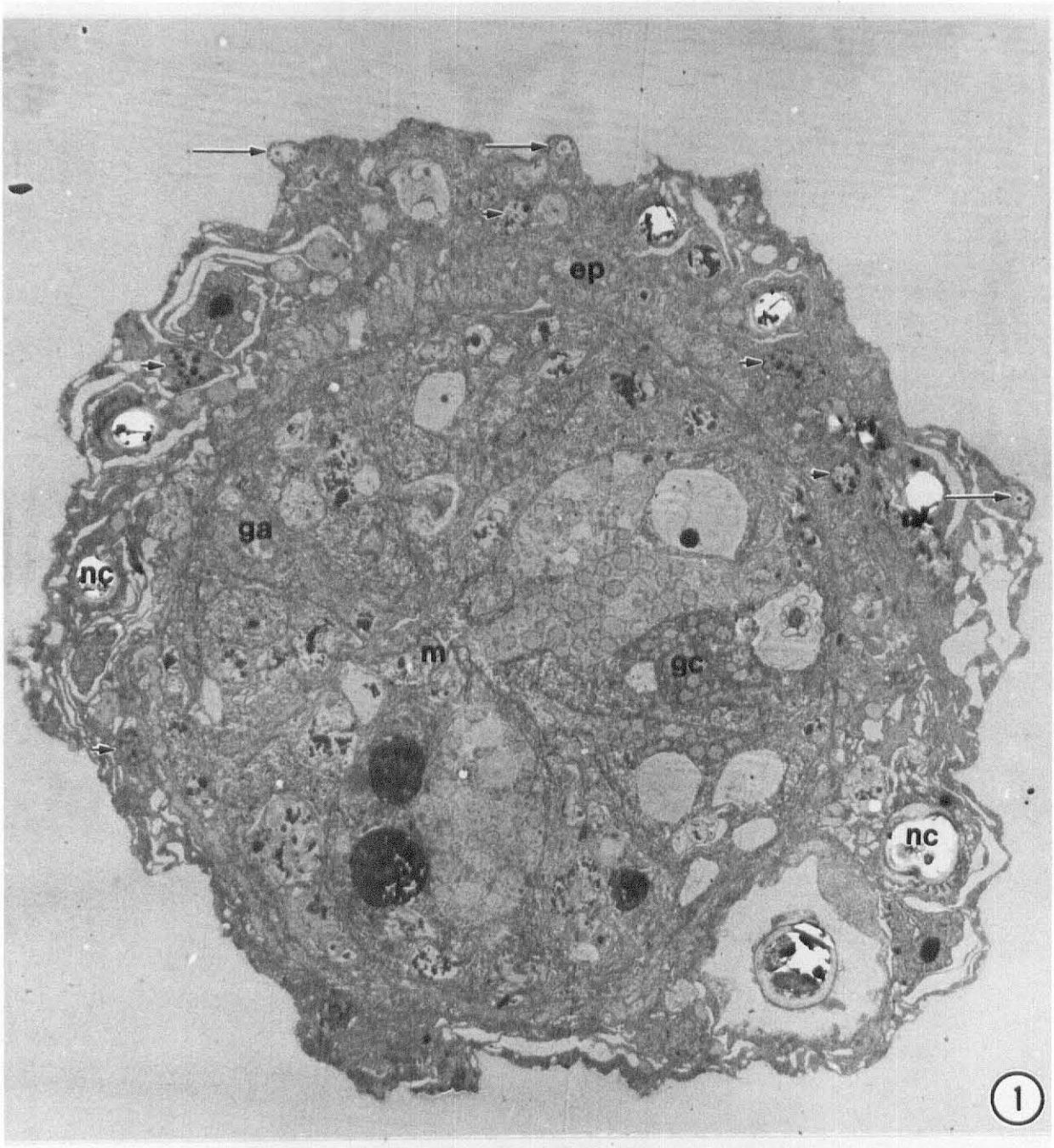
One or more Golgi complexes were situated in the perikarya of both sensory and ganglion cells. Often 3-4 Golgi complexes were seen in the sensory cells, whereas only 1-2 were found in the ganglion cells. The complexes consisted of 5-6 saccules with an amorphous material in the peripheral swellings of the saccules. No ultrastructural differences were observed between the Golgi complexes of LD and NL animals (Figs. 12 and 13).

Accumulations of glycogen in the perikarya of ganglion cells were prominent, but occurred infrequently in the sensory cells from both LD and NL animals. The glycogen was usually found in the form of individual β-particles, although α-rosettes occasionally appeared throughout the cytoplasm. In ganglion cells the glycogen accumulated in large masses near the nucleus; however, no differences in glycogen form or content were observed between the LD and NL animals (Figs. 14 and 15).

Occasional dense bodies were found in the perikaryon near the cilium-stereociliary complex of ganglion cells and in close proximity to the nucleus in sensory cells. The number of dense bodies as well as their appearance did not change in the LD animals as compared to the NL animals (Figs. 16 and 17).

PLATE I

Fig. 1. Electron micrograph of transverse section through hypostome of a light deprived (LD) animal with sensory cells (arrows) peripheral to ganglion cells (arrowheads). Note glandular cells (gc) around mouth (m) and nematocysts (nc) in epidermis (ep). X 1,824.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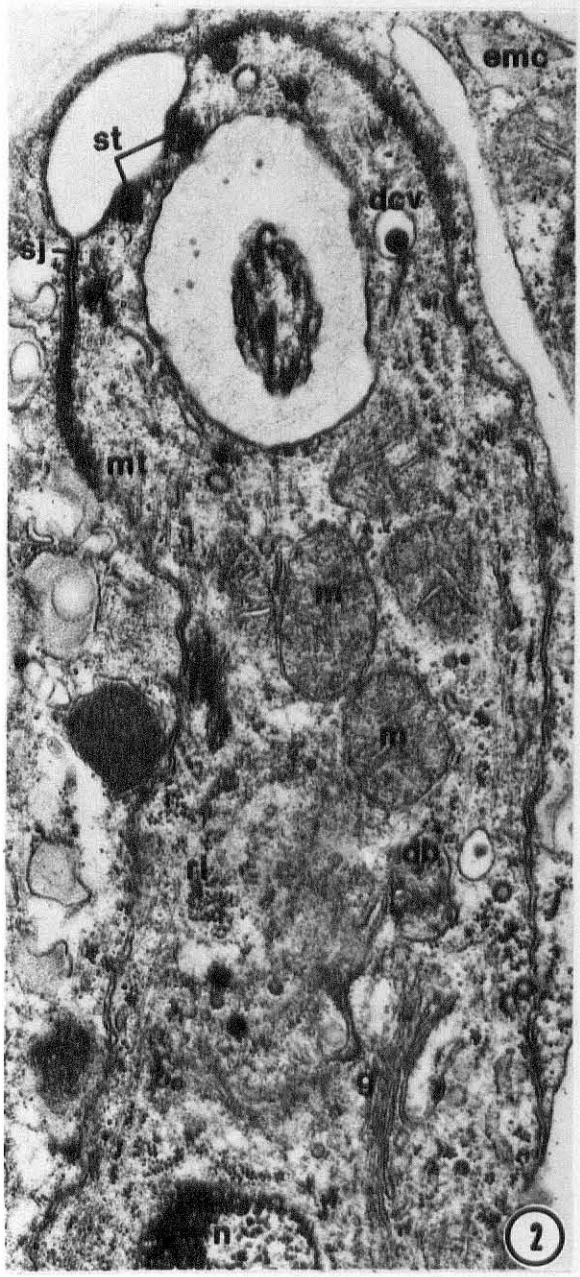
1

PLATE II

Fig. 2. Apical portion of sensory cell from base of tentacle of LD animal with sensory cilium (c) surrounded by cores of several stereocilia (st). Note numerous mitochondria (m), Golgi complex (g), dense body (db), microtubules (mt), and dense-cored vesicles (dcv) in region apical to nucleus (n). emc, epitheliomuscular cell; sj, septate junction. X 22,440.

Fig. 3. Apical portion of sensory cell from base of tentacle of NL animal with slight swelling of ciliary membrane (arrow) and pigment-like granules (pg) in periciliary cytoplasm. Note similarity of mitochondria (m) and other organelles with LD animal (Fig. 2). c, cilium; db, dense body; dcv, dense-cored vesicle; emc, epitheliomuscular cell; mt, microtubules; ri, ribosomes; sj, septate junction; st, cores of stereocilia. X 22,400.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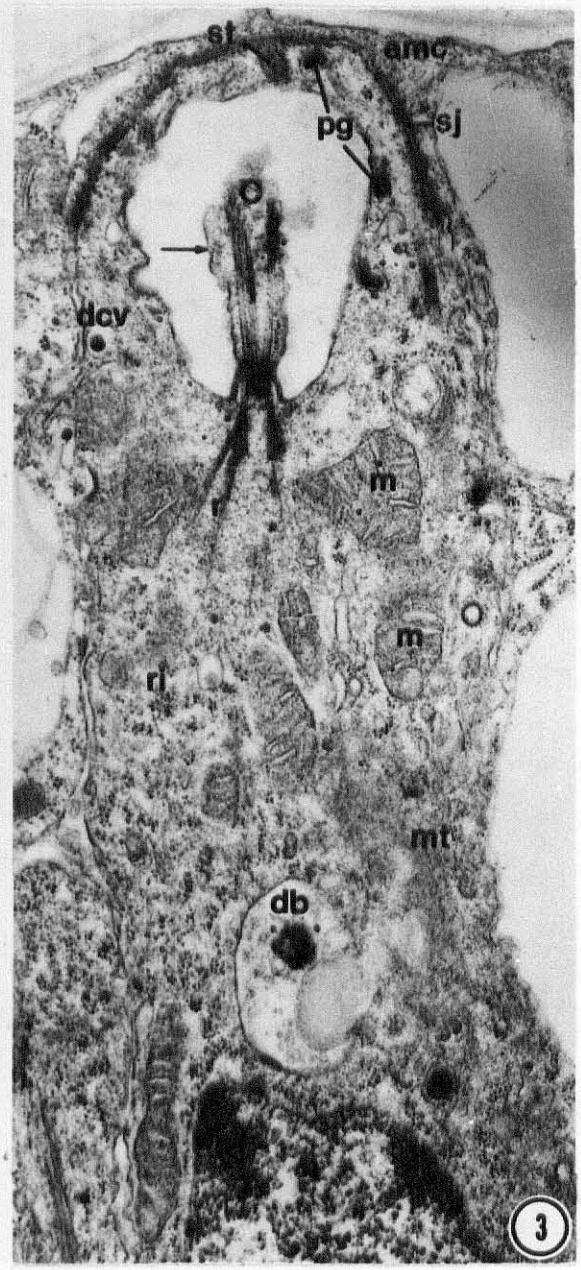
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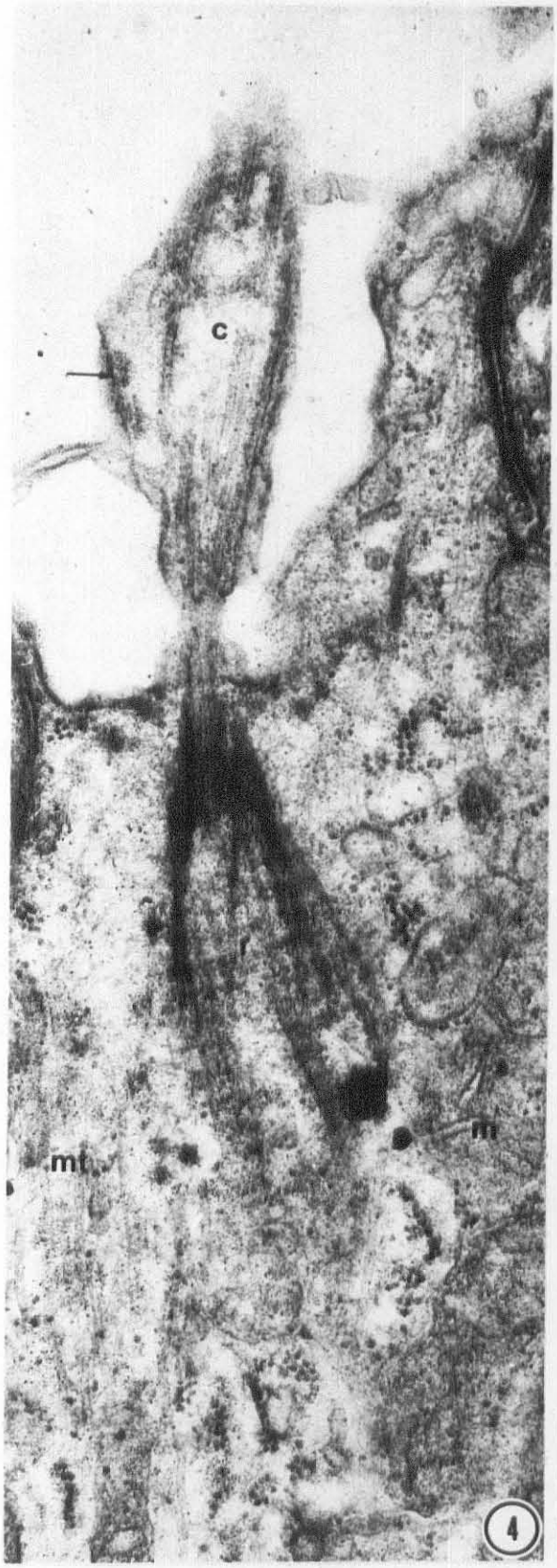
PLATE III

Fig. 4. Basal swelling on cilium (c) of sensory cell from hypostome of a LD animal. Note dense material (arrow) associated with flared membrane of cilium. mt, microtubules; m, mitochondrion; r, rootlets. X 49,590.

Fig. 5. Pigment-like granules (pg) near centriole (ce) in apical region of sensory cell from base of tentacle of LD animal. Note mitochondria-rich region of cytoplasm below the centriole. emc, epitheliomuscular cell; m, mitochondria; v, vacuole. X 27,200.

Fig. 6. Slight basal swelling (arrow) on cilium (c) in serial section of sensory cell shown in Fig. 5. Note numerous mitochondria (m) near rootlets (r) of cilium. emc, epitheliomuscular cell; n, nucleus; st, cores of stereocilia. X 19,080.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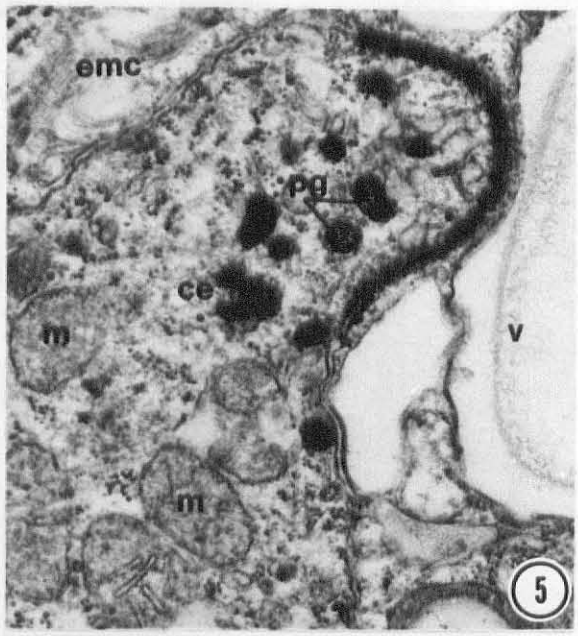
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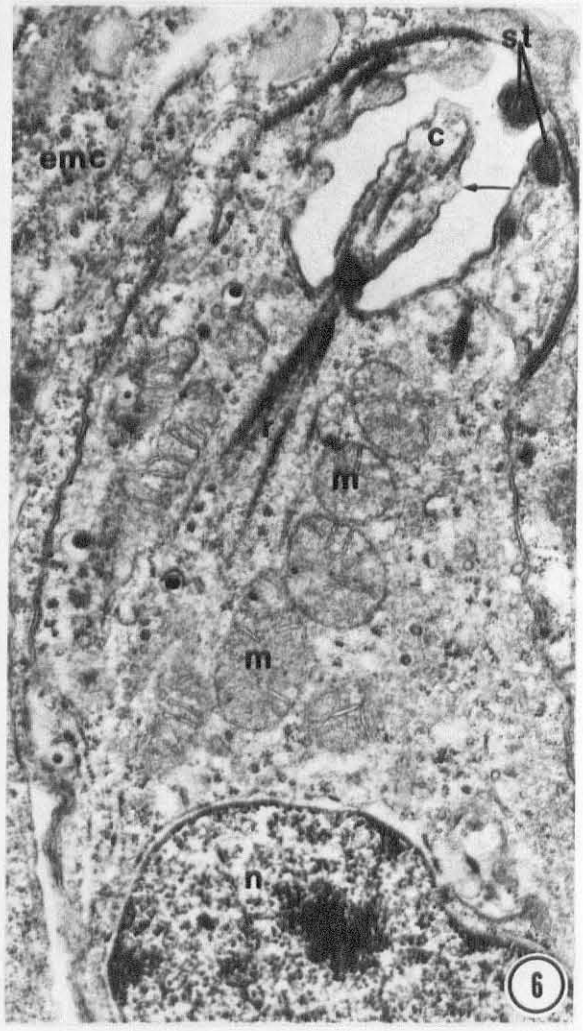
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PLATE IV

Fig. 7. Longitudinal section of cilium-stereociliary complex in ganglion cell from LD animal. Note presence of mitochondria (m), ribosomes (ri), glycogen (gl), microtubules (mt), and dense-cored vesicle (dcv) around nucleus (n). c, cilium; r, rootlets; st, stereocilia. X 18,700.

Fig. 8. Longitudinal section of cilium-stereociliary complex in ganglion cell from NL animal. Note similarity of cilium (c), stereocilia (st), and other perikaryal organelles with those of NL animals (Fig. 7). db, dense body; dcv, dense-cored vesicle; mt, microtubules; m, mitochondria; n, nucleus; ri, ribosomes. X 18,700.

Fig. 9. Cross section of ganglion cell cilium with 9 doublets of microtubules surrounding 3 singlets. Note filamentous cores of stereocilia (st) in periciliary cytoplasm. X 64,625.

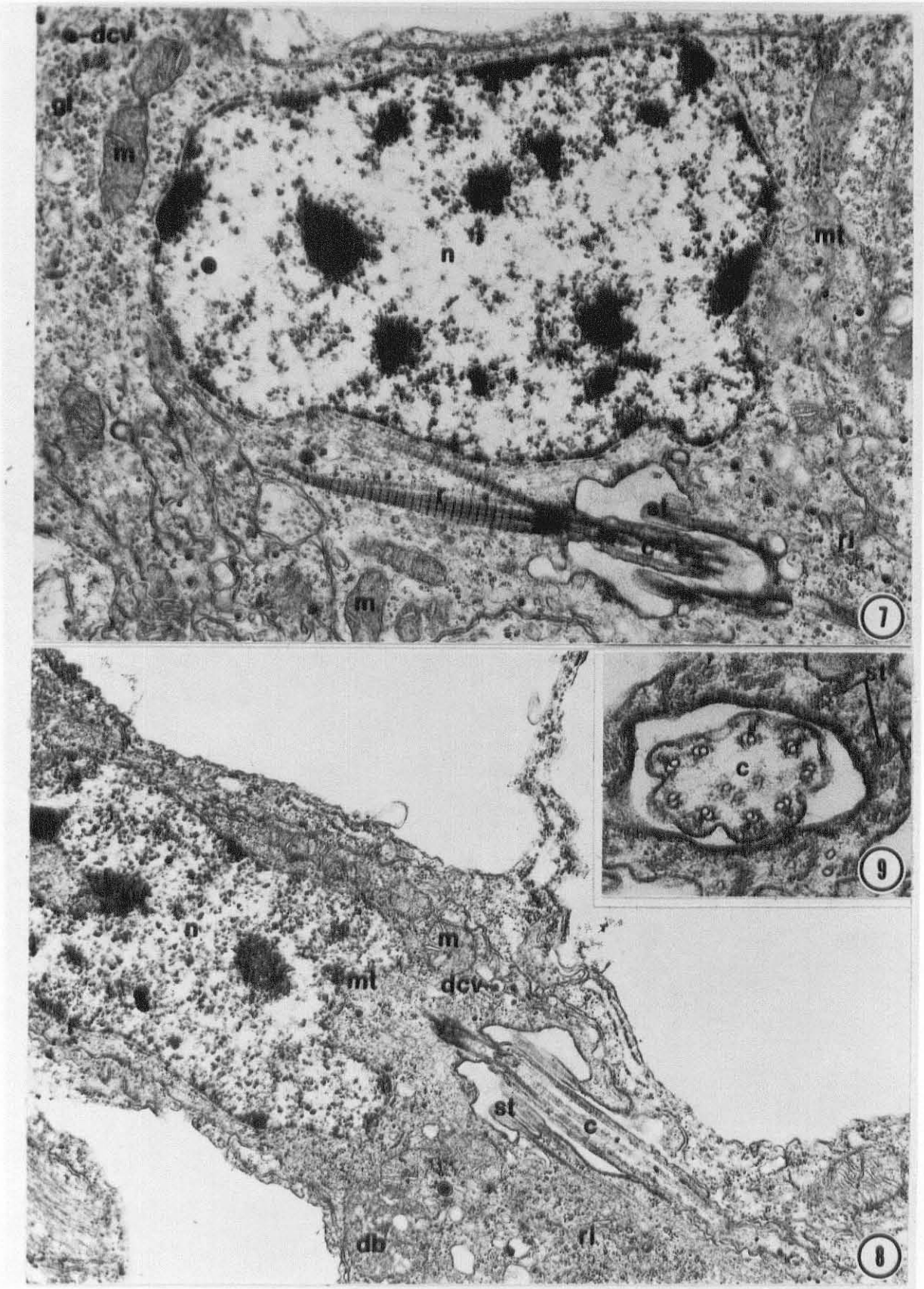
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PLATE V

Fig. 10. Part of ganglion cell perikaryon with numerous mitochondria (m) near ciliary complex of LD animal. Note prominent cristae surrounded by dense matrix in mitochondria. n, nucleus; st, stereocilia; v, vacuole. X 21,080.

Fig. 11. Part of ganglion cell perikaryon with numerous mitochondria (m) near ciliary complex of a NL animal. Note similarity of mitochondria to those from a LD animal (Fig. 10). n, nucleus; st, stereocilia. X 21,080.

Fig. 12. Part of ganglion cell perikaryon with Golgi complexes from a LD animal. Note characteristic 5-6 saccules per Golgi complex (g) and amorphous material in the distal ends of some saccules. gl, glycogen; n, nucleus. X 31,000.

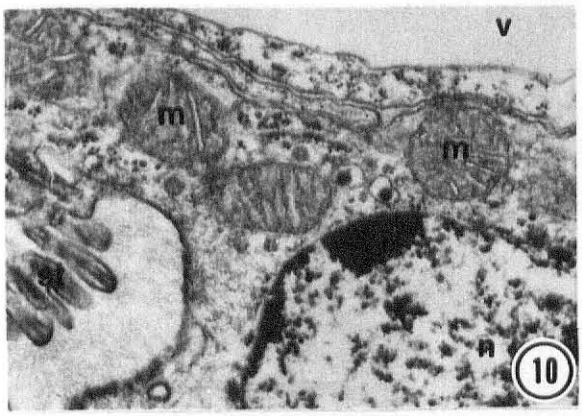
Fig. 13. Part of ganglion cell perikaryon with Golgi complex form a NL animal. Note that Golgi saccules and amorphous contents (arrow) are similar to those from a LD animal (Fig. 12). m, mitochondrion; n, nucleus; v, vacuole. X 31,000.

Fig. 14. Part of ganglion cell perikaryon from a LD animal with accumulation of glycogen particles (gl). Note both α and β particles of glycogen near mitochondria (m) and nucleus (n). X 24,800.

Fig. 15. Part of ganglion cell perikaryon from a NL animal with accumulation of glycogen particles (gl). Note similarity of α and β particles to those of a LD animal (Fig. 14) and association with mitochondria (m) and nucleus (n). X 24,800.

Fig. 16. Part of ganglion cell perikaryon with dense body (db) near ciliary complex (c) of a LD animal. gl, glycogen; m, mitochondrion; n, nucleus. X 24,800.

Fig. 17. Part of ganglion cell perikaryon with dense body (db) near ciliary-stereociliary complex of a NL animal. Note similarity of location and appearance of dense body with that of a LD animal (Fig. 16). c, cilium; gl, glycogen; g, Golgi complex; st, stereocilia. X 24,800.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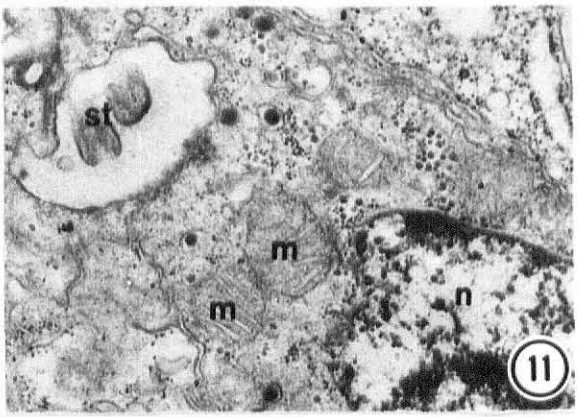
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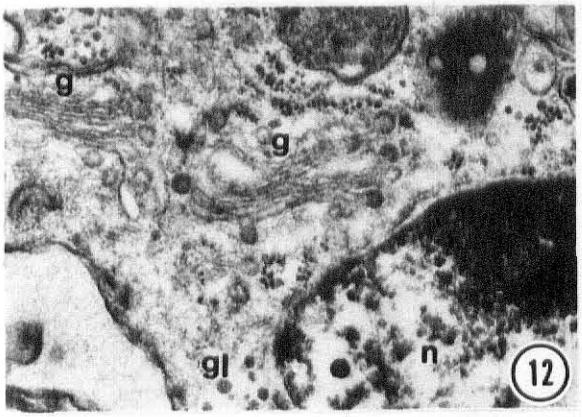
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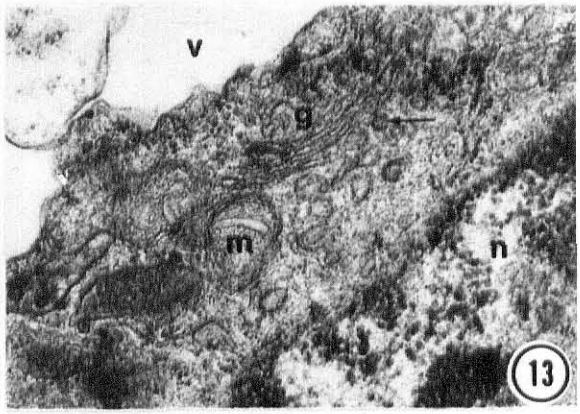
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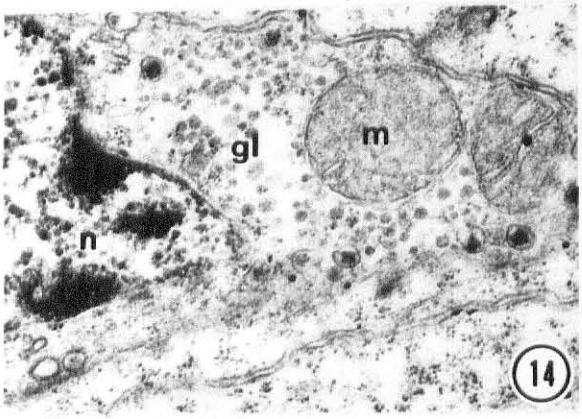
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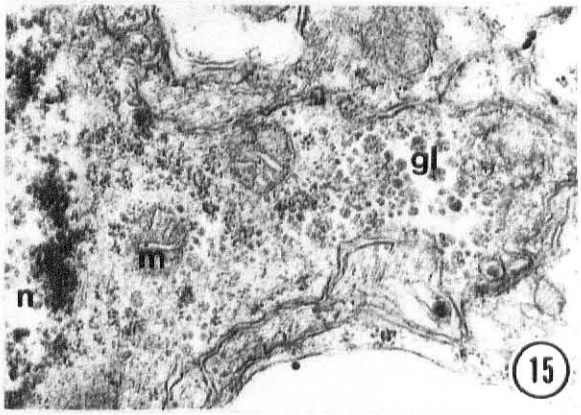
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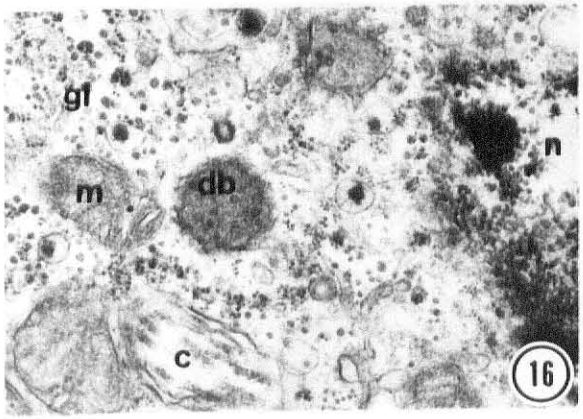
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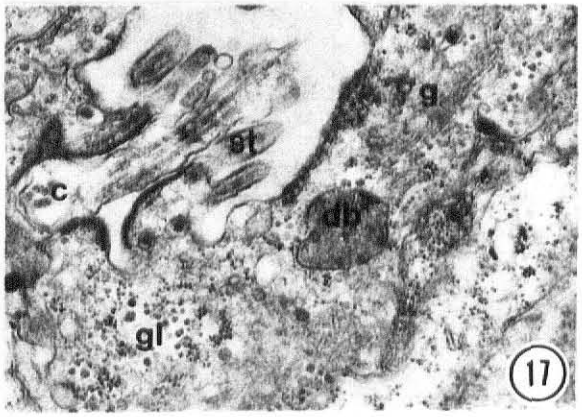
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TABLE 1. Comparison of effects of light deprivation on ultrastructural components of photoreceptor cells in various invertebrate species with those on neurons of Hydra littoralis.

EFFECTS OF LIGHT DEPRIVATION	OTHER INVERTEBRATE SPECIES	Hydra littoralis
MITOCHONDRIA	Shrunken, *Dense Matrix*[1]	NC[+]
GLYCOGEN	Increased Accumulations[1]	NC
ENDOPLASMIC RETICULUM	Enormously Swollen[1]	NC
MICROVILLI	A. Disarrayed & Irregular[1,2,3,4,5]	NC(?)
	B. Longer, more regularly arrayed[6,7]	
DENSE BODIES	Decreased Number[2]	NC

1. Planarian, from Carpenter et. al., 1974.
2. Crayfish, from Eguchi & Waterman, 1979.
3. Locust, from Bloom & Atwood, 1981.
4. Crayfish, from Roach & Wiersma, 1974.
5. Planarian, from Rohlich & Tar, 1968.
6. Echinoderm, from Yamamoto & Yoshida, 1978.
7. Echinoderm, from Eakin & Brandenburger, 1979.

+- No change

DISCUSSION

In this investigation I found that light deprivation had no gross effects upon the ultrastructure of either sensory or ganglion cells in the head region of *Hydra littoralis*. Yet electrophysiological studies have specifically implicated this part of the animal in its response to light (Passano and McCullough, 1962; Rushforth et al., 1963; Rushforth and Burke, 1971). Ultrastructural changes as a result of light deprivation were expected because it has been shown in other invertebrate species that light deprivation produces observable ultrastructural changes within the photoreceptive cells (Carpenter et al., 1974; Bedini et al., 1977; Eguchi and Waterman, 1979; Yamamoto and Yoshida, 1978; Eakin and Brandenburger, 1979; Bloom and Atwood, 1981).

Comparison of ultrastructural changes after light deprivation

The closest animal phylogenetically to *Hydra* in which light deprivation studies have been done is the planarian *Dugesia dorotocephala* (Carpenter et al., 1974). In this animal after nine days of light deprivation the rhabdomeric microvilli became disarrayed, and within the cytoplasm of the photoreceptive cells the mitochondria were shrunken in appearance with a dense matrix, the endoplasmic reticulum was greatly swollen, and glycogen accumulation had increased. A disruption of rhabdomeric microvilli following light deprivation has also been shown in a rhabdocoel flatworm (Bedini et al., 1977) and in a locust (Bloom and Atwood, 1981). Crayfish studies (Eguchi and Waterman, 1979) showed more variable effects of light deprivation on rhabdomeric microvilli. During the first two weeks of light deprivation the diameter of the rhabdomeric microvilli increased, the number of lysosome-related structures near the rhabdom decreased, and the diameter of particles

(visualized by freeze-fracture) on the receptor membrane decreased, although their number increased. However, after four weeks in constant darkness the photoreceptor microvilli became disarrayed and the number of membrane particles fell to about half their initial number. In my study on *Hydra* no ultrastructural differences could be detected between short (42 hours and five days) and long (14 and 40 days) periods in darkness in any of the cells observed.

In several species of echinoderms the photoreceptive microvillar membranes became elongated and neatly arranged with light deprivation (Yamamoto and Yoshida, 1978; Eakin and Brandenburger, 1979); however, these observations may have been the result of rather short periods of light deprivation (30-40 hours). Whether or not disruption of the membranes would have occurred with longer periods of light deprivation remains to be established.

In all of the studies mentioned so far the effects of light deprivation upon rhabdomeric photoreceptors have been presented. However, a presumed photoreceptor cell in *Hydra* would be ciliary in origin. Eakin (1965) has shown that rods and cones of a tadpole differentiate and develop normally in the absence of light, and remain intact during prolonged light deprivation. It is possible then that ciliary derived photoreceptors are not altered by light deprivation. This could perhaps explain why I found no ultrastructural changes in the ciliated neurons of *Hydra* which had been light deprived. However, more organisms with ciliary photoreceptors need to be examined in light deprivation before any conclusions can be made.

Why did light deprivation have no observable effects on Hydra neurons?

The above reports by several investigators on the photoreceptor cells of various light-deprived invertebrates have demonstrated that distinct

ultrastructural changes occurred in photosensitive cells maintained under constant darkness. Yet light deprivation had no detectable effects on any cells observed in *Hydra littoralis*. How can this result be explained in view of the findings in other invertebrates that were light-deprived? One possible explanation stems from the work of Westfall (1973) and Westfall and Kinnamon (1978). In these studies they presented ultrastructural evidence of a multifunctional nature for both sensory and ganglion cells in *Hydra*. By classifying the synaptic contacts of the above cell types, along with the presence of a cilium, they have suggested that these cells can function as sensory neurons, motor neurons, and interneurons, i.e., the three types of neurons recognized in the vertebrate nervous systems. Because *Hydra* is a member of the phylogenetically most primitive group of animals recognized to possess a nervous system, Westfall (1973) has suggested that the sensory and ganglion cells of this animal may represent "a primitive nerve cell from which specialized neurons in higher nervous systems have been derived." If this is in fact the case, then perhaps simply depriving the neuron of a "specific" or an "adequate" sensory stimulus would not have affected its ultrastructure in a detectable way because it would still have to perform its motor and interneuronal functions. The photoreceptive membrane may have been altered, but not in a way that could be detected with the methods used in this study. This does not eliminate the fact that a change may well have occurred. For example, the swelling in the ciliary membrane may have been changed in size as a result of light deprivation, yet it would not have been observed in this qualitative study. Also, any alteration of intramembranous particles presumably present in light sensitive membranes would not have been visualized without using the freeze-fracture technique. Thus one must be careful in making a blanket statement that light deprivation had no observable effects on neurons in *Hydra*.

An alternative hypothesis may also be argued. The structure of the cilium-stereociliary complex, which is presumed to be the transducing element of the sensory and ganglion cells, resembles that of the vertebrate hair cell, which has been shown to subserve a mechanoreceptive function (Hudspeth and Corey, 1977). If we consider that the multifunctional *Hydra* neurons may be evolutionary progenitors of separately functioning neurons it may be feasible that some of these early cells first functioned as mechanoreceptors and in later forms evolved the incorporation of a photopigment into a modification of the ciliary membrane. These later cells thus could have become photosensitive and yet retained their mechanoreceptive abilities to the present day; therefore, depriving them of one type of stimulus (light) may not have affected the ultrastructure in a detectable way because they could still be performing mechanoreceptive functions.

A non-neuronal photoreceptor in Hydra?

The above hypotheses assume that the photoreceptive cell(s) in *Hydra* are neuronal. Is there evidence for a non-neuronal photoreceptor? North and Pantin (1958) suggested that in the sea anemone *Metridium*, a salt-water relative of *Hydra*, the parietal cells of the muscular system may themselves be sensitive to light. This hypothesis was based on the fact that isolated mesenteries of *Metridium* contracted when exposed to light. If the photoreceptor in *Metridium* could be part of the muscular system, then by analogy could the epitheliomuscular cells of *Hydra* also be photosensitive? There are several arguments against this hypothesis. First, it is quite possible that the isolated mesenteries of North and Pantin (1958) contained thin strands of nervous tissue which may have been responsible for initiating the contraction. Removal of any remaining neurites could well result in the same response reported by Campbell et al., (1976) who found that "nerve-free"

Hydra do not respond to light; they did not produce the electrical potential that is elicited from normal *Hydra* when light stimulated. If the epitheliomuscular cell were photosensitive, then one could expect some sort of electrical potential to be produced by light stimulation of the cell whether or not nerves were present. Second, there was no ultrastructural evidence of any change between the epitheliomuscular cells in LD and the NL animals in this study. Finally, epitheliomuscular cells do not possess the basic criteria for a photosensitive cell (Eakin, 1972): swelling of the cilium to house a photopigment, and pigment granules to act as a shading device.

The best candidate for a photoreceptor cell in Hydra

Having considered the fact that light deprivation had no gross effects on the ultrastructure of sensory, ganglion, and epitheliomuscular cells in *Hydra littoralis*, what can be said about the identity of the photoreceptive cell? It appears that by employing morphological techniques alone we will not be able to solve the *Hydra* photoreceptor mystery. Other techniques, such as electrophysiological recording, biochemistry, and freeze-fracture may need to be utilized in conjunction with conventional transmission electron microscopy to solve the problem. However, I can offer certain conjectures as to the presumed photoreceptive cell in *Hydra*. Westfall and Kinnamon (1978) described pigment-like granules in sensory cells of the mid-tentacle region of *Hydra* and proposed that these cells might function as photoreceptors owing to their similarity to ciliary photoreceptor cells in other invertebrates (Eakin, 1972). Such sensory cells were modified by a basal swelling on the cilium and pigment granules in the apical cytoplasm. I have observed similar cells at the base of the tentacle and around the mouth. This type of sensory cell fits the criteria set forth by Eakin (1972) for a primitive photoreceptive cell: a swelling of the sensory cilium where

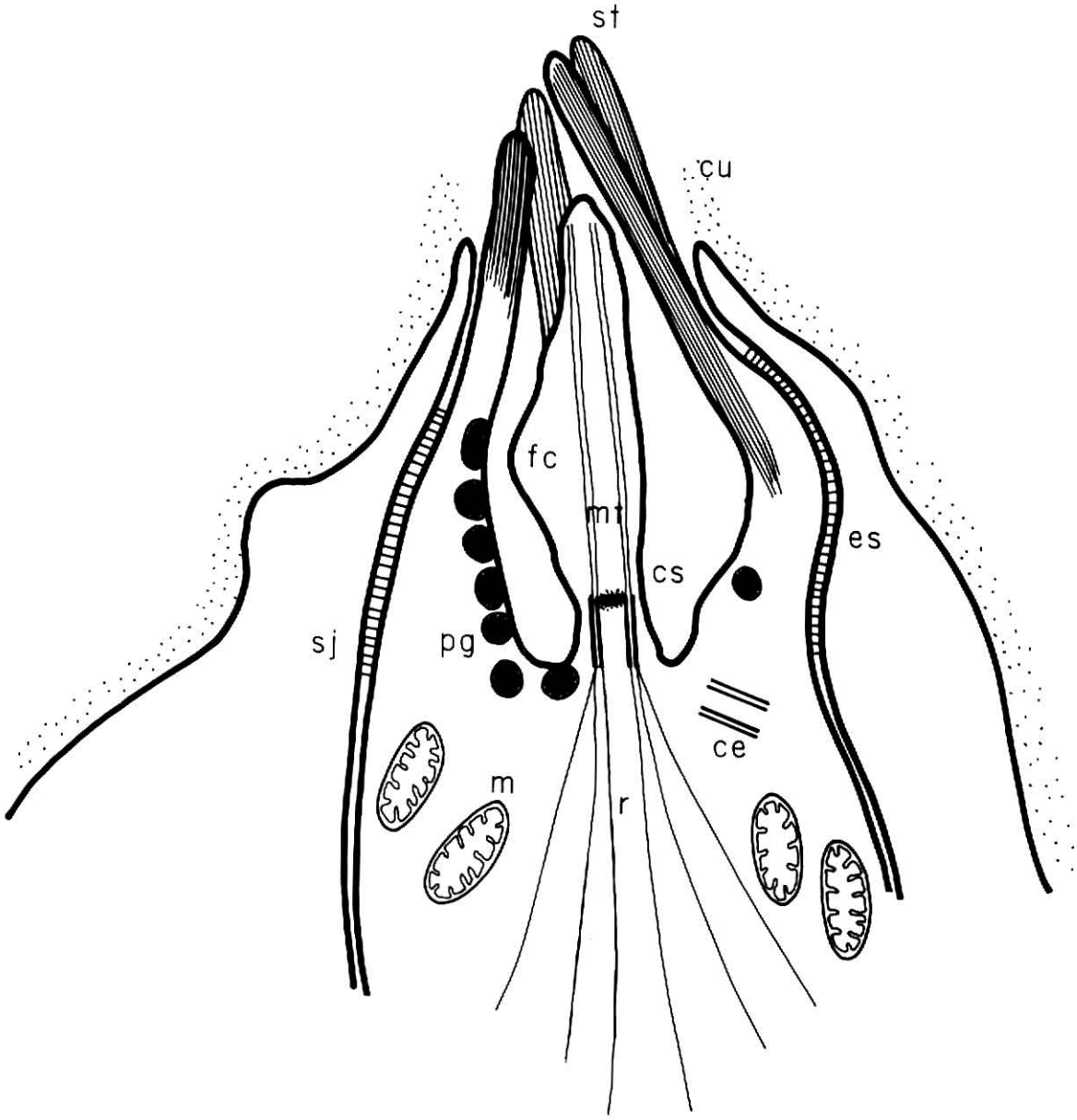
a photopigment might be incorporated into the membrane, and pigment granules in the cytoplasm around the cilium to act as a shading device and provide directional sensitivity to the animal. I believe that sensory cells fitting the above description represent the best candidates for the photoreceptor cells in *Hydra*; a schematic diagram illustrating such characteristics found in some *Hydra* sensory cells is shown in Figure 18. The anatomical location of these sensory cells (tentacles and around the mouth) correlates with the photosensitivity of *Hydra* as demonstrated electrophysiologically. I observed this type of sensory cell only five times; thus careful studies are needed to see if it occurs in greater numbers and to demonstrate if it is the specific photoreceptor of the animal.

Evolutionary significance of presumed *Hydra* photoreceptors

Based upon its morphology (Fig. 18) the presumed photoreceptor in *Hydra* seems to lie between the protists and the pelagic coelenterates in Eakin's proposed evolutionary scheme (Eakin, 1982). It may be that during evolution the free-swimming medusae required a more complex, structured type of photoreceptor as found in *Polyorchis* and *Bougainvillia* (Eakin and Westfall, 1962; Singla, 1974), whereas the sessile polypoid coelenterates, such as *Hydra*, may have required a less complex form of photoreceptor because of their sedimentary life-style. This type of presumed photoreceptor cell, similar to that of *Euglena* (Osafune and Schiff, 1980) may then have evolved and remained to this day in *Hydra*.

PLATE VI

Fig. 18 Diagram illustrating apical region of a presumed photoreceptor cell from head region of *Hydra littoralis*. ce, centrioles; cs, circumciliary space; cu, cuticle; es, epitheliomuscular cell sheath; fc, flared cilium; mt, microtubules; m, mitochondria; pg, pigment granules; r, rootlet; sj, septate junction; st, stereocilia.



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LIGHT DEPRIVATION AND PRESUMED PHOTORECEPTOR CELLS IN *Hydra littoralis*

by

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ABSTRACT

A fresh-water coelenterate, *Hydra*, has been shown both behaviorally and electrophysiologically to be light sensitive, yet no unequivocal photoreceptive cell has been identified. Photoreceptor cells are usually neurons having a photopigment incorporated into a ciliary or microvillar membrane. In a variety of organisms these cells have been shown to undergo detectable ultrastructural changes when kept in the dark. These changes consist of breakdown of the photoreceptive membrane and alterations of cytoplasmic organelles. Therefore, I chose to examine and compare ultrastructurally the two types of neurons, ciliary sensory and ganglion cells, in *Hydra* after light adaptation and light deprivation.

Specimens of *Hydra littoralis* maintained under normal lighting conditions (NL) for 42 hours to 40 days and animals light-deprived (LD) for the same periods of time were fixed for electron microscopy. Serial sections were cut of the hypostome and tentacle bases from both groups of experimental animals. The ultrastructure of organelles of sensory and ganglion cells in both NL and LD animals were then compared with each other and with data reporting organellar changes in dark and light adapted states of other invertebrate photoreceptors. Mitochondria, Golgi complexes, glycogen, dense bodies, and cilium-stereociliary complexes exhibited the same fine structure in the sensory and ganglion cells of both experimental groups.

The fact that comparison of NL and LD animals did not reveal changes in the sensory or ganglion cell organelles does not indicate that these cells

may not function as photoreceptors. On the basis of their synaptic contacts and the presence of a cilium, it has been suggested that the sensory and ganglion cells in *Hydra* may possess a multifunctional nature and have the ability to act as sensory neurons, motor neurons, and interneurons. Therefore, depriving these cells of a sensory input may not noticeably alter their ultrastructure because they could still function as motor neurons and interneurons. Alternatively, it is possible that the neurons of this phylogenetically primitive animal may respond to more than one type of stimulus and that depriving the cells of one type of stimulus may not have altered their ultrastructure in a detectable way.

Based upon the above results and previous studies the most likely candidate for a photoreceptor cell in *Hydra* is a sensory cell modified by a basal swelling of the cilium and containing pigment-like granules in the cytoplasm. Such a cell, which was observed in the present study at the base of the tentacle, has been previously seen in other parts of the tentacle. In order to unequivocally identify, ultrastructurally, that this cell is a photoreceptor in *Hydra*, its distribution in the animal must be determined. Further, other techniques, such as freeze-fracture, biochemistry, and electrophysiological recording must be pursued along with conventional transmission electron microscopy in such a study.