**Final version published in Photoreception and Vision in Invertebrates, M.A. Ali (ed). New York: Plenum Press, 1984. 131-178.**

# EVOLUTION OF EYES AND PHOTORECEPTOR ORGANELLES IN THE LOWER PHYLA

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The eye altering alters all.

William Blake, The Mental Traveller, 1800.

## INTRODUCTION

How could such a complex organ as the vertebrate eye have evolved by natural selection of numerous, successive, slight modifications? Charles Darwin posed this question but could not answer it satisfactorily because of the rather limited knowledge of invertebrate eyes in his day.

However he indicated how it should be answered:

> "If numerous gradations from a perfect and complex eye to one very imperfect and simple, each grade being useful to its possessor, can be shown to exist; if further, the eye does vary ever so slightly and the variations be inherited, which is certainly the case; and if any variation or modification in the organ be ever useful to an animal under changing conditions of life, then the difficulty of believing that a perfect and complex eye could be formed by natural selection, though insuperable by our imagination, can hardly be considered real" (Darwin, 1859).

For the vertebrate eye, though genetically inheritable variations are known, the question cannot be answered even today because of the lack of examples to fill the huge gap between the relatively primitive pigment-cup eyes of chordate ancestors and the fully-developed lens eye of the simplest vertebrates. Fortunately, as we now know, the lens eye has evolved independently several other times, and stepwise evolution is suggested by the existence of intermediate grades along those distinct lines.

Examples of well-developed lens eyes of alciopid annelids, certain gastropods, cephalopods, crustacea and arachnids are described by Land (1981; 1983a,b). In this chapter I intend to show how eyes could have evolved using examples chosen from the lower invertebrate phyla. The topic splits conveniently into two: evolution of the eye as an organ, and evolution of photoreceptor organelles.

The gradation in complexity of known light-receiving organs is so fine that it is difficult to draw a line indicating what is an eye and what is commonly referred to as an ocellus. I will avoid the problem by referring to, as an eye, any organ more complex than a single, unpigmented photoreceptor cell. The term 'photoreceptor' is commonly used to refer to either a photoreceptive organ, cell or organelle. Since it is the organelle that is specialized to detect photons, I will call it the photoreceptor and refer to the other structures by 'eye' and 'photoreceptor cell'.

## EVOLUTION OF EYES

The most common eye type, the pigment-cup eye, apparently has evolved in several different ways. Examples from Bryozoa, Nematoda and Cnidaria will be used to illustrate several possible sequences. Examples from Cnidaria will also indicate one way a lens eye might have been formed from a pigment-cup eye.

### Bryozoan line

Though the adult bryozoan is sessile, the larvae have a brief swimming phase during which positive and/or negative phototaxis is observed. Pigment spots are observed in the epidermis, the number and structure depending on species. In the 7 species studied by Woollacott and coworkers, a single ciliated photoreceptor cell is found in each pigment spot. This is associated with other epithelial cells in what Hughes and Woollacott identify as 3 levels of topological complexity (Hughes & Woollacott, 1980; Zimmer & Woollacott, 1977; Woollacott & Zimmer, 1972). A few more levels of morphological complexity are discernable and I have taken the liberty to arrange them in an order that suggests one possible sequence by which a pigment-cup eye could have evolved.

The simplest example is found in Bugula simplex and B. pacifica. Their larvae have 3 and 2 pairs of eyes, respectively. The sensory cell lies flush with the surface of the epithelium and because it is not invaginated, the tufts of 50-100 cilia that project from it lie above the surface (Fig. 1). The clump of cilia, thought to be the photoreceptor, would be shaded by the pigment found in the putative photoreceptor cell and adjacent corona cells. It would appear that the cilia of one of the corona cells (ciliated locomotory cells of the larvae) have become modified for photoreception and the cytoplasm of the cells of the immediate region has become pigmented to provide directional sensitivity.

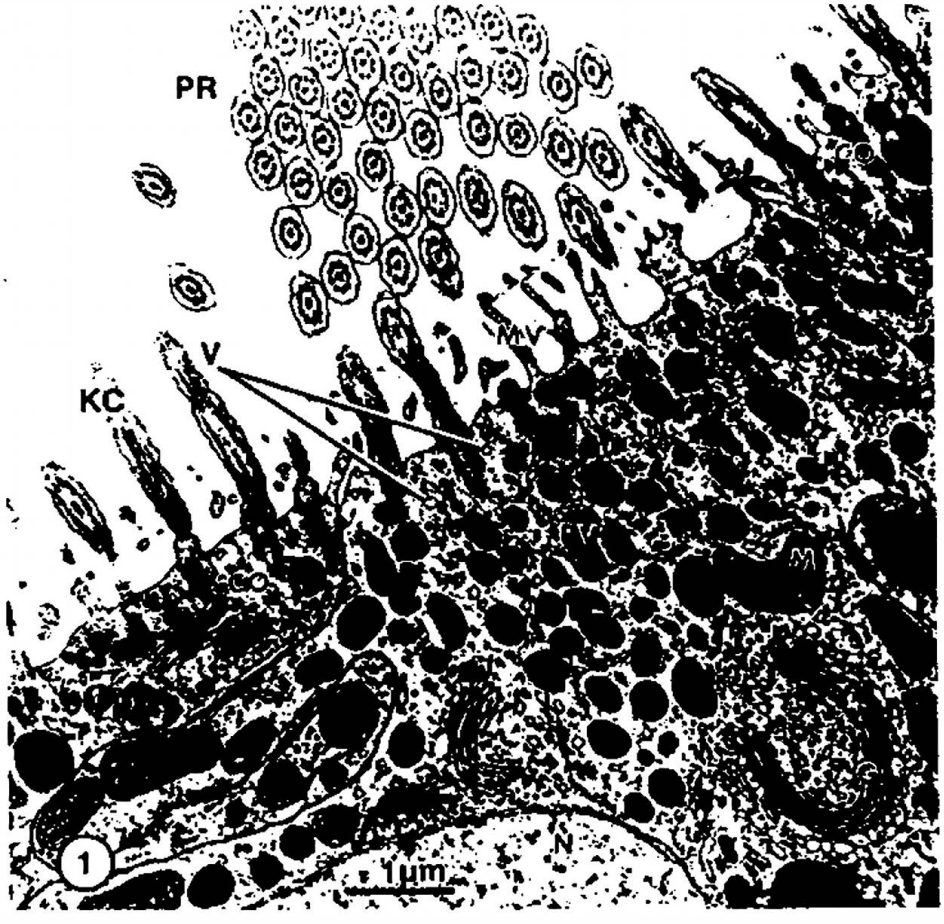


Fig. 1. Eye of Bugula simplex larvae (Bryozoa). A tuft of probably photoreceptive cilia (PR) projects from a single cell which connects to the nervous system. Pigment granules (PV) are present in both this cell and neighboring corona cells (CO). The latter bears kinocilia (KC). Branching microvilli (MV) project from both cell types. G, golgi network; M, mitochondrion; V, membrane vesicles. After Hughes and Woollacott (1980).

An earlier step in the evolution might have been a photoreceptor cell without shading pigment. An example may yet be found in bryozoa because larvae of certain species are known to be photosensitive though they lack pigment spots (Hughes & Woollacott, 1980).

A possible later step is illustrated by the eyes of B. stolonifera in which the apical surface of the photoreceptor cell is indented to form a shallow cup. Otherwise the eye structure is similar to that of B. simplex and B. pacifica. A deeply-indented

sensory cell is found in B. turrita. The pair of posteriolateral eyes are separately located, but the anteromedial ones (Fig. 2) are nearly adjacent. In this species each eye appears to be composed of a single cell in which are incorporated both the shading and photosensory functions. The advantage of sinking the photoreceptor into a cup, besides a protective one, is that the directionality of photoreception is improved. The 2 anteromedial eyes appear to collect light entering through different but overlapping sectors of space (Fig. 2).

If the photoreceptor lay deeper in the pigment cup the directionality would be further improved. This occurs in the eyes of B. neritina and Tricellaria occidentalis. In these eyes, the sensory cell is at the base of an epidermal invagination, the third topological grade of Hughes & Woollacott (1980).

Among the eyes of these 2 species, 3 grades of structural complexity are seen. The posterolateral eyes of T. occidentalis are composed of a single sensory cell at the base of a depression. Modified parts of two corona cells form the sides and rim. In the cytoplasm of all 3 cells, the pigment granules are concentrated towards the depression. The two corona cells are further modified from their normal form by the absence of cilia in the pigmented zone.

The anteromedian eye of T. occidentalis is constructed of 2 modified corona cells and 2 sensory cells. Of the bryozoan larvae described to date, this is the only example of a multireceptor-cell pigment-cup eye. Since the photoreceptor cilia interdigitate, the 2 cells would receive light from the same directions. The advantage of such an increase in complexity therefore, is not clear in this case.

In the eyes of B. neritina we find a significant increase in complexity. The surface of the pigment cup is made up of a single receptor cell at the base and walls of modified corona cells as before. The pigment, however, is located in special pigment cells as is common in most pigment-cup eyes. In B. neritina these are subepidermal in location (Woollacott & Zimmer, 1972).

From these bryozoan examples one can reconstruct a plausible stepwise sequence for the evolution of pigment-cup eyes. Of the species included, only T. occidentalis is not in the same genus, and that example could be discarded without affecting the conclusion. Nevertheless, inferring an evolutionary sequence from modern examples is rather a risky venture, and the following sequence should be regarded as only one possibility which could have occurred: 1) formation of an unpigmented photoreceptor cell from a ciliated motor cell, 2) addition of shading pigment to the photoreceptor cell and neighbouring epithelial cells, 3) indentation of the receptor cell, 4) invagination of the epithelium to form a deeper cup, and in several steps, 5) increased specialization of photoreceptor cells, epithelial cells and pigmented cells of the eye. Each of these successive slight increases in complexity can be seen to be useful to the organism.

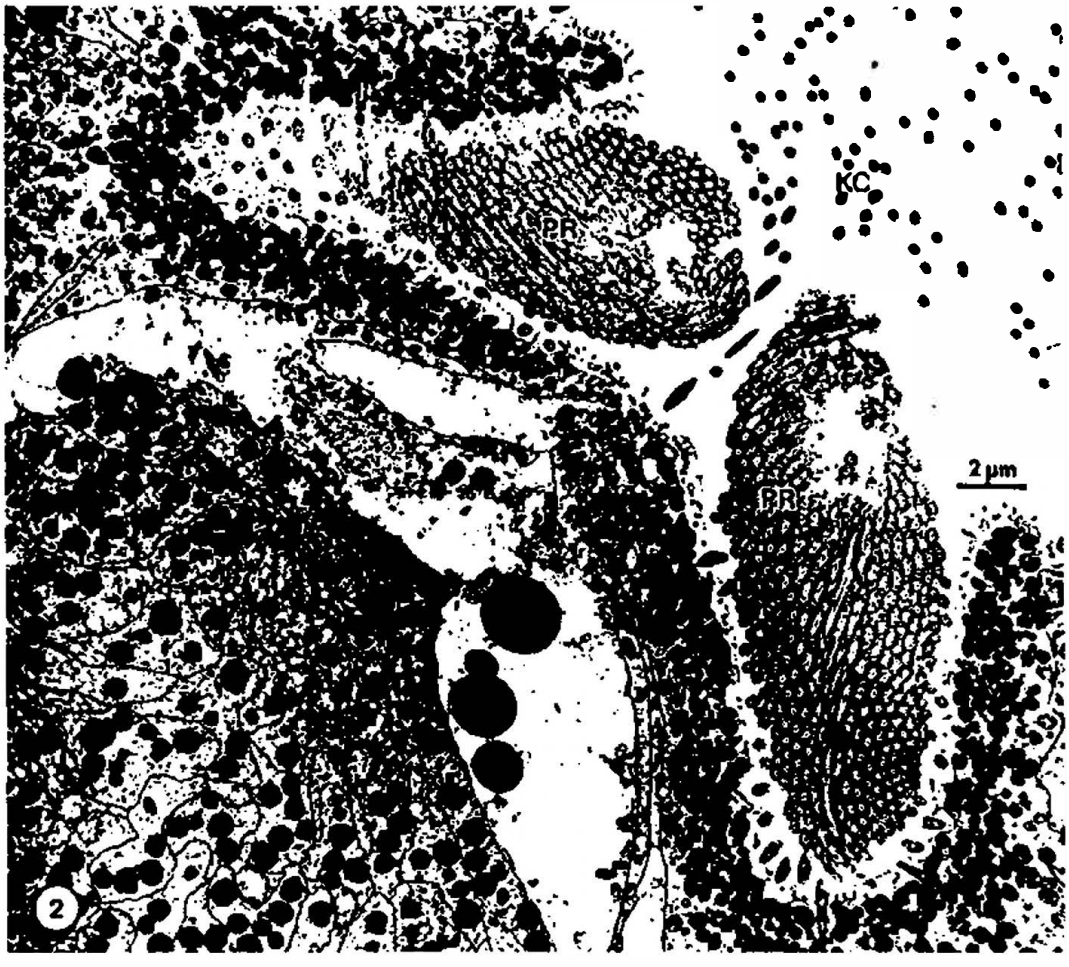


Fig. 2. Anteromedial eyes of Bugula turrita larvae (Bryozoa). The two pigment-cup eyes are separated by projections of underlying cells. KC, PR, PV as in Fig. 1. PG, pyroform gland. After Hughes and Woollacott (1980).

Further, individual variation of the structures is observed (Hughes and Woollacott, 1980). Therefore Darwin's criteria for "believing" that a pigment-cup eye can evolve by natural selection are met in Bryozoa.

Nematode lines

A small number of marine and aquatic nematodes have a noticeable pair of pigment spots in the anterior. A variety of structures has been noted and the morphology in 5 species has now been described at the electron microscope level (Siddiqui & Viglierchio, 1970; Croll et al., 1972; 1975; Burr & Burr, 1975).

Negative phototaxis has been observed in 3 of these species and photoklinokinesis has been observed in at least one species that lacks pigment spots (Burr, 1983).

Each eye contains a single photoreceptor and a shading pigment which is usually located within an anterior cell of the pharynx. The three examples in Fig. 3 indicate the range of morphologies described so far. The following evolutionary sequence could have occurred: 1) formation of the photoreceptor, 2) pigmentation of a nearby pharyngeal cell, 3) evagination of the pigmented cell, 4) formation of a pigment-cup from the pigmented cell. Steps 2, 3 and 4 are represented by the modern examples shown in Fig. 3.

A number of differences are noticeable between the nematode and bryozoan lines though the morphological result is the same: a cup-shaped shading structure containing a single photoreceptor. In the bryozoan larvae (excepting B. neritina), the pigmentation occurs in the photoreceptor cell or another epithelial cell, both of which are very similar to the ciliated motor cell (corona cell) of the epidermis and probably evolved from it. In the nematodes, however, the pigment and photoreceptor cells have originated from totally different cells which were already highly differentiated for other purposes. The photoreceptor cell probably evolved from a neuron whereas the pigment is located in the pharynx, the cells of which have a very different embryological lineage, at least in Caenorhabditis elegans (J.E. Sulston, E. Schierenberg, J.G. White, J.N. Thompson and G. von Eherenstein, personal communication). The pharynx is enclosed by a basal lamina which prevents any contact with the photoreceptor cell, whereas the 2 cell types of Bryozoa are in direct contact (Woollacott & Zimmer, 1972).

The existence of unique eye structures suggests that evolution of nematode eyes may have occurred independently at least 4 times. In Deontostoma californicum (Siddiqui & Viglierchio, 1970), Chromadorina bioculata (Croll et al., 1972), Chromadorina sp. (Croll et al., 1975) and Enoplus anisospiculus (Bollerup & Burr, 1979; Burr, unpublished), the shading pigment is concentrated in a region of a marginal cell of the pharynx, which continues to also maintain its normal function to support the cuticular lining of the lumen. The photoreceptor organelle is lamellar and a ciliary axoneme is absent. In Oncholaimus vesicarius, on the other hand, the pigment is located in the anterior of a pharyngeal muscle cell, the bulk of which is filled with myofilaments for its role in swallowing (Burr & Burr, 1975). The photoreceptor is a cluster of modified cilia. A third possible line has culminated in Araeolaimus elegans, in which the shading pigment is located outside the pharynx and is different ultrastructurally and spectrally from the pharyngeal pigment (Croll et al., 1975). The photoreceptor is lamellar. A fourth possible line is represented by Mermis nigrescens in which the presumptive shading pigment is located in large expansions of the anterior hypodermis (Ellenby & Smith, 1966; Croll et al., 1975; Burr, unpublished) and is an oxyhemoglobin (Ellenby, 1964; Burr et al., 1975), whereas the

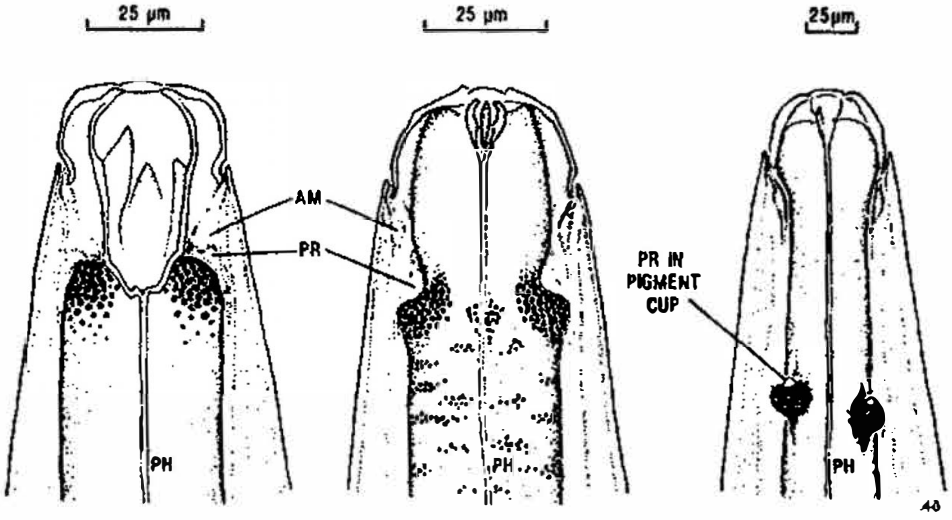


Fig. 3. Eye structure in 3 nematode species. A. In Oncholaimus vesicarius a multiciliary photoreceptor (PR) occurs in an olfactory organ anterior to a pigmented region in a pharyngeal muscle cell. Original, based on live worms and electron micrographs (Burr & Webster, 1971; Burr & Burr, 1975). B. In Enoplus anisospiculus a multilamellar, epigenic photoreceptor (PR) lies anterior to a pigmented evagination of a pharyngeal marginal cell. Original, based on live worms and unpublished electron micrographs. C. In Deontostoma californicum the pigmented region of a marginal cell is cup-shaped. Original, based on Siddiqui and Viglierchio (1970) and Hope (1967). PH, pharynx; AM, amphid, an olfactory organ.

pigment of the pharyngeal shading structures is probably a melanin (Bollerup & Burr, 1979). A photoreceptor has not yet been identified in Mermis, but the nature of the positive phototaxis (Cobb, 1926; 1929; Croll, 1966; Burr, to be published) suggests that a photoreceptor is shaded by the cylindrical pigmented region.

Cnidarian lines

The Cnidaria include the Hydrozoa, Scyphozoa (true jellyfish) and Anthozoa (sea anenomes). Their life cycles include 2 forms: polyps which are photosensitive but probably lack eyes, and medusae. They are thought to be phylogenetically more primitive than other metazoans, having only ectodermal and endodermal tissue and a limited degree of organ development. Surprisingly, one of the few evolutionary lines that lead to a lens eye occurs in medusae of certain Scyphozoa.

Eyes ranging in complexity from the flush epithelial grade to multireceptor pigment-cup eyes occur in the free-swimming medusae of Hydrozoa. Two examples are illustrated in Figs. 4 and 5. In Leuckartiara octona the ciliary photoreceptor cells are flush with the epidermis, as in Bugula simplex, but have only one cilium per cell (Fig. 4). The shading pigment is located in other epithelial cells and many photoreceptor cells occur in each eye (Singla, 1974).

In Bougainvillia principis (Fig. 5) the epidermis is invaginated to form a pigment cup. Each photoreceptor cell dendrite passes through the pigmented layer and projects 1-3 cilia into the cup. Microvilli, formed from the ciliary membrane, lie in clumps at the base of the pigment cup and probably constitute the photoreceptors. Branched projections of the pigment cells form a transparent mass that fills the center of the cup. Whereas the bryozoan pigment cup was open to the exterior, that of Bougainvillia is closed by a layer of epidermal cells (Singla 1974).

Eye complexity intermediate between Leukartiara and Bougainvillia is found in Polyorchis penicillatus and Sarsia tubulosa (Eakin & Westfall, 1962; Singla & Weber, 1982a,b). A pigment cup is formed of pigment and receptor cells. Each receptor cell projects a single cilium into the cup. Microvilli form from the ciliary membrane. In both species, microvilli also evaginate from the pigment cell membrane, from the apical surface and from a projection ("distal process"). These microvilli intermingle with the receptor cell microvilli in the cup. Distal to the presumed photosensory region of ciliary microvilli, the photoreceptor cilia of Sarsia swell into large vesicles and are covered by a mucous layer. In Polyorchis, on the other hand, the pigment cells form a similar layer of swollen tips. In both examples the pigment-cup eye is otherwise open; it is not enclosed by an epidermal layer as in Bougainvillia.

Bougainvillia eyes may have evolved from undifferentiated epithelium in the following sequence, a modification of one suggested by Singla (1974): 1) formation of photoreceptor cells in epithelium (There are several light-sensitive examples that lack pigment spots). 2) pigmentation of neighbouring cells to provide directional sensitivity (Leukartiara), 3) invagination of the epithelium (Polyorchis, Sarsia), 4) formation of distal processes of the pigment cells and microvillar elaborations of ciliary membrane (Polyorchis, Sarsia), 5) modification of the tip of distal processes into a large vesicle (Polyorchis) or branched projections (Bougainvillia) to form a transparent mass, 6) enclosure of the pigment cup by projection (Cladonema radiatum, Weber, 1981) or migration (Bougainvillia) of adjacent epithelial cells. All of the examples are Anthomedusae (Hydrozoa, Cnidaria).

The pigment-cup eyes of Polyorchis, Sarsia, Bougainvillia and Cladonema are examples of the everted type: one in which the photoreceptor cells enter the eye by penetrating through the layer of pigment cells. Inverted pigment-cup eyes occur in another

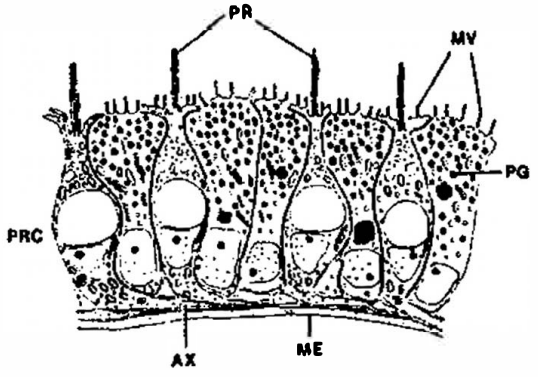


Fig. 4. Eye of Leukartiara octona medusae (Hydrozoa, Cnidaria). A single cilium (PR) and several microvilli (MV) project from each of many photoreceptor cells (PRC). Pigment granules (PG) are found only in the pigment cells. AX, axon; ME, mesoglea. After Singla (1974).

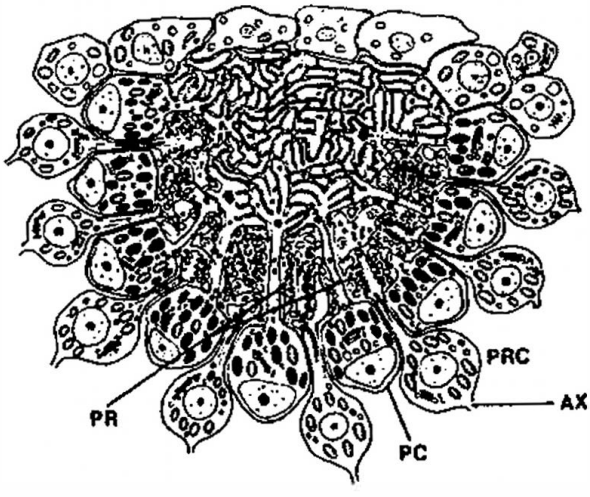


Fig. 5. Pigment-cup eye of Bougainvillia principis medusae (Hydrozoa, Cnidaria). A dendrite of the photoreceptor cell (PRC) passes between pigment cells (PC) and projects 1-3 cilia from its apical surface. Microvilli (PR) are formed from the ciliary membrane. Tubular projections of pigment cells (PC) branch to fill the center of the cup with a transparent füllmasse. AX, axon. After Singla (1974).

hydrozoan medusa, Tiaropsis multicirrata (Singla, 1974) and in the smaller eye of two types in a scyphozoan medusa, Aurelia aurita (Yamasu & Yoshida, 1973). In this type, only pigment cells form the cup and the numerous photoreceptor dendrites enter via the cup opening. Unlike in the other, larger eye of Aurelia and in other medusan eyes, the pigment cells of these 2 eyes are of endodermal origin and are separated from the photoreceptors by mesoglea. They could represent a second line of evolution in medusae.

Evolution of a lens

The transparent mass of the Bougainvillia eye, or füllmasse, may help maintain its shape by filling-up space. The swollen vesicles in Polyorchis and Sarsia may serve the same function. This type of structure is common in invertebrate eyes and is regarded as being a possible forerunner of a lens. In another

hydromedusan, Cladonema radiatum, the füllmasse of a similar eye becomes filled with spherical granules during development. These later change into compact crystalline bodies (Weber, 1981). A later stage in evolution of the lens may be represented by the distal eye of the cubomedusan, Tamoya bursaria (Cnidaria, Scyphozoa) described by Yamasu and Yoshida (1976). This eye (Fig. 6 A,B) has many structural similarities to that of Bougainvillia and Cladonema. It is everse, the putative photoreceptors are villi derived from ciliary membrane, the pigment cells project distal processes through the region of ciliary microvilli, and the eye is closed by a layer of epithelial cells. The lens of Tamoya replaces the füllmasse and it appears to have partly a space-filling function. The cells of the lens are separated from the retina by a capsule of extracellular material.

The eye of Tamoya is obviously considerably more complex than the other examples, with a shaped lens and a retina composed of hundreds of photoreceptors. To evolve from an ancestor like Bougainvillia, or Cladonema however, no new tissues or structures need be added, only further proliferation of photoreceptor and pigment cells and a modification of the füllmasse into a lens. By natural selection, the optimum shape should evolve easily. The cells that make up the lens of Tamoya, however, have an uncertain origin. Because they may have arisen by further specialization of some of the pigment cells that form the füllmasse of Bougainvillia or Cladonema, it would be interesting if it could be shown in Tamoya that the lens cells have an ontogeny common with that of pigment cells.

In comparison with the eyes of fish or squid, Tamoya's eye is still quite primitive. Still lacking are a well-developed iris diaphragm, a focussing mechanism, muscles of ocular movement, and geometry for optimum resolution of the image. For possible sequences in the evolution of lenses of some higher invertebrates see Salvini-Plawen and Mayr (1977) and Land (1981, 1983a,b).

The question of whether or not the distal eye of Tamoya can actually form an image is an interesting one. The formation of a retina containing hundreds of photoreceptor cells would appear to be a waste of energy unless information could be derived from at least a low resolution image. The proximal edge of the lens, however, is adjacent to the retina and this usually indicates that an image cannot be formed on the retina (Land, 1981). However, the curvature of the lens is greater for the region of distal surface not covered by pigment cells (Fig. 6B), and the ratio f/r (Land 1981, p. 514) estimated from the drawing ranges from 2 to 3,8 if f and r are measured from the center of curvature to the receptor organelle layer and the distal surface, respectively. With a Matthiessen's ratio as high as 3,8 an image could be formed within the layer by a lens material of reasonable refractive index. The range of f/r reflects the thickness of the receptor organelle layer. Because of this thickness the image could never be in focus

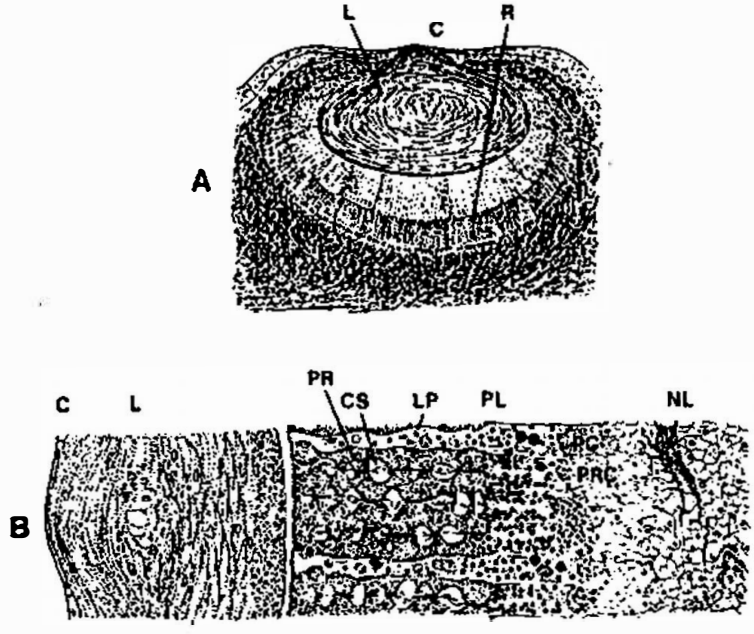


Fig. 6. Distal eye of Tamoya bursaria (Scyphozoa, Cnidaria). A, distal eye; B, details of structure. The eye is composed of a cornea (C), lens (L) and a retina which includes a receptor layer, pigmented layer (PL) and nerve layer (NL). Pigmented photoreceptor cells (PRC) project a cilium which swells at intervals (CS) and evaginates numerous microvilli (PR). Pigment cells (PC) send a long process (LP) through the layer of microvilli. After Yamasu and Yoshida (1976).

everywhere in the layer, and consequently the information collected by the retinal cells would have a low resolution.

The lens is structurally inhomogeneous with rounded cells in the center and flattened cells peripherally (Fig. 6B). If a lens is optically inhomogeneous as well, with a higher refractive index in the center, as in the fish, the ideal lens without spherical aberration is approached (Land, 1981). Demonstration of the presence of an advanced lens design in such a phylogenetically primitive organism would be of considerable interest.

Compound eyes and other eye types

Compound eyes appear only in the higher Protostoma: annelids, molluscs and arthropods, and they will be treated by others in this volume. Clusters of small pigment-cup eyes, seen in some Platyhelminthes, may be precursors of this type.

In terrestrial animals the cornea can act as the primary refracting surface. This eye type is common in terrestrial

vertebrates and arachnids and occurs also in land snails and insect larvae (Land, 1981). The compound eye predominates in adult insects. Eyes that incorporate image-forming reflectors are found only in the scallop, Pecten, and the giant deep-sea ostracod Gigantocypris (Land 1981, 1983a,b).

Conclusions

The examples chosen from 3 unrelated phyla illustrate not only that stepwise evolution of eyes is a reasonable possibility, but equally important, that more than one independent line leading to pigment-cup eyes must have occurred within two of the phyla. In a review of all of the phyla, Salvini-Plawen and Mayr (1977) enumerated numerous examples of this among the "40 or 65" phyletic lines they identified.

In 2 of the lines I described above, both photoreceptor and pigment cells appear to have originated from relatively undifferentiated ciliated epithelial cells, but the everse pigment-cup eyes that resulted are different in many details. In the nematode examples, the eyes appear to have evolved from cells that were previously in an advanced state of differentiation for other purposes. In these and other known examples there is much fodder for the theorist.

The scyphozoans (Cnidaria) provide the only example of a lens eye in the lower Metazoa. Why are they lacking in such important groups as the platyhelminthes, aschelminthes, echinoderms and lower chordates even though pigment-cup eyes are common? (See Fig. 7 for possible relationships). Why did lens eyes arise in only a few isolated lines of the higher phyla, e.g. fishes, cephalopod molluscs, prosobranchs (gastropod molluscs), and alciopids (polychaete annelids) (Land, 1981; 1983a)? The occurrence in Cnidaria and absence in many phylogenetically more advanced phyla indicates that phylogenetic or tissue grade is unimportant; neither mesodermal tissue nor a coelom is required. Indeed, the occurrence of a lens eye in the predatory dinoflagellate, Erythropsis (Protista), shows that even a multicellular grade is unnecessary (Couillard, 1983).

A common feature of all the organisms with lens eyes is a fast-moving, free-swimming habit and moderate to large size. All but the cubomedusan are active predators. By contrast there are no examples of lens eyes in the phyla that are predominantly sessile, slow-moving, benthic, interstitial or parasitic. There may be selection towards medium resolution eyes of other types in these organisms. An example is the scallop, which has image-forming mirror optics in lieu of a lens (Land, 1981; Land, 1983a). Other examples are given by Salvini-Plawen and Mayr (1977).

The very small size of rotifers may have prevented their eyes from developing past the pigment-cup stage even though they are active swimmers. Their eyes, at about 5 μm in diameter, are 1/10 the size of the lens eye of Erythropsis. Since resolution is

limited by eye size (Land, 1981), selection pressures for small body size may oppose pressures for increasing eye resolution and formation of lens eyes.

## EVOLUTION OF PHOTORECEPTORS

Darwin's criteria can also be applied to the question of how photoreceptors evolved. Richard Eakin, over the past 20 years, has made a noble attempt to demonstrate a stepwise sequence in two lines of evolution, a ciliary line following along the deuterostomate phyla to the vertebrates, and a rhabdomeric line following along the protostomate phyla to the arthropods and molluscs (Eakin, 1963, 1979). His observations, ideas and review articles have been a major catalyst to research in the area. However his original idea is now contradicted by many exceptions. Ciliary and rhabdomeric organelle types appear to have newly arisen many times, even both types within the same phylum. With the increasing number of examples being described in the lower and minor phyla, other relationships are becoming more evident. New theories, proposed by Vanfleteren and Coomans (1976), Salvini-Plawen and Mayr (1977) and Clément (1980) nicely explain many observations. Nevertheless Eakin's is the only proposal so far that attempts to explain the noticeable trend towards rhabdomeric receptors in the Annelida, Mollusca, and Arthropoda.

The diversity of photoreceptor structure has been reviewed several times (Eakin, 1972; Salvini-Plawen & Mayr, 1977; Coomans, 1981; Vanfleteren, 1982). In this chapter I will present current ideas that appear to me to be most significant to the understanding of photoreceptor evolution and then will add a conceptual model which may be increasingly useful as the problem unfolds. Some of the ideas are traceable to Eakin (1979; 1982), Vanfleteren (1982) and Salvini-Plawen (1982). However the emphasis, the model and other ideas of this chapter are new to the field. Examples will be chosen primarily from lower phyla that are not reviewed in detail in other chapters of this volume.

### Ciliary and rhabdomeric photoreceptors

All known photoreceptors have originated in cells of epidermal origin. The most common and best known are the ciliary and rhabdomeric types, distinguishable by whether or not the organelle is formed from the membrane of a cilium or of microvilli, respectively. Here I depart from Eakin's definition of rhabdomeric photoreceptors: all types in which the organelle is derived from the cell membrane proper. By restricting rhabdomeric photoreceptors to those formed of microvilli, I omit only one rare type included by Eakin's definition, to which I will give another name (see section on epigenous photoreceptors).

Eakin's definition assumes that photoreceptors composed of microvilli originally arose de novo by evagination of the cell membrane. It is much more likely that microvilli developed first

for other purposes and acquired photosensitivity secondarily. This is what Eakin proposes for photoreceptors derived of cilia. As for cilia, the cytoskeleton of photoreceptor microvilli resembles other types. The central cytoskeleton of squid rhabdomeric microvilli consists of a core of actin filaments connected to the membrane by side-arms. Thus it resembles the cytoskeleton of the microvilli of the intestinal brush border, except for its much smaller diameter (Saibil, 1982). The core filament bundle of leech rhabdomeres is larger. The apparent absence of a bundle in some photoreceptor microvilli may be due to inadequate fixation (Saibil, 1982). It would be hard to explain how the cylindrical shape can be maintained without such a cytoskeleton, and it is likely that the core is a characteristic of all microvilli, however modified. It is only in the membrane envelope where qualitative differences between microvilli are seen.

The distinction between rhabdomeric and ciliary photoreceptors is not always clear. In many medusae (Cnidaria), the organelle is composed of a clump of microvilli that project from the membrane of a cilium. Though a few microvilli also originate from the apical cell membrane in some medusae (Singla, 1974; Singla & Weber, 1982a) the bulk of them project from the membrane of the cilium. In Tamoya the ciliary microvilli sometimes coalesce into compact parallel-hexagonal arrays as do the rhabdomeric microvilli in the rhabdomeres of higher protostomes (Yamasu & Yoshida, 1976). In many arthropods, the rhabdomeric organelles commonly appear adjacent to a cilium and the two arise simultaneously during development (Vanfleteren, 1982). Critical to classification in these confusing cases is the location of the boundary between the photosensitive membrane and the rest of the plasma membrane. This will be the subject of a later section.

Epidermal cells of all metazoa are similar in being able to produce microvilli and cilia on their external surface. Therefore, the genome of all metazoa must contain the genetic information necessary for their manufacture and maintainance. Cilia and microvilli are specialized domains of the external cell membrane and they contain the cytoplasmic and membrane components that maintain their special shape and function.

The evolution of photoreceptors probably occurred in the following stages: 1) evolution of a photosensitive cell membrane, 2) localization of photosensitivity in a particular domain of the cell membrane such as the ciliary or microvillar membrane 3) further increase in surface area of the membrane and 4) increase in organization of the organelle. Only stages 3 and 4 can be inferred from metazoan examples; the other stages must have occurred earlier in evolution.

## Evolution of photosensitivity

Photosensitive behavior is clearly present in bacteria and Protista of many types. A rhodopsin-like, retinal-protein

photopigment in Halobacterium is known to be involved in photobehavior but rhodopsin has not yet been positively identified in Protista (Hildebrand, 1978). Behavioral action spectra implicate a carotenoprotein, perhaps rhodopsin, as the photopigment of some phytoflagellates such as Volvox, Chlamydomonas and Platymonas (evidence discussed by Nultsch & Häder, 1979; Foster & Smyth, 1980). At least 2 additional classes of photopigment are implicated for other unicell species.

Much less work has been done on lower Metazoa. Since rhodopsin is the photopigment of vertebrates, arthropods and molluscs, it can be inferred that rhodopsin arose in a common ancestor. It is reassuring that ocellar potentials of a planarian (Turbellaria, Platyhelminthes, Brown et al., 1968) and of two hydromedusans (Weber 1982a,b) have action spectra resembling the absorbance spectrum of rhodopsin. From schema such as that of Fig. 7 one can infer that rhodopsin arose in Protista or a primitive metazoan.

Some components of sensory transduction now being discovered in unicells resemble those of vertebrates and arthropods. Paramecium has been the most extensively studied. Mechanical stimulation to the anterior opens a $Ca^{++}$ channel and depolarizes the cell. Touching the posterior opens a $K^{+}$ channel and hyperpolarizes the cell. A depolarizing receptor potential triggers a regenerative depolarization by opening $Ca^{++}$ channels located in the ciliary membrane. The resulting increase in intraciliary $Ca^{++}$ concentrations inactivates the $Ca^{++}$ channels and reverses ciliary beating (Eckert & Brehm, 1979). A similar, but light-induced, electrical response coupled to ciliary reversal has been recorded in another ciliate, Stentor (Wood, 1976). Receptor potentials have not yet been recorded intracellularly in flagellates, however several lines of evidence indicate that photopotentials and $Ca^{++}$ are involved in light-induced reversals (Nultsch & Häder, 1979; Foster & Smyth 1980).

In Metazoa, intracellular recordings have been obtained of chordate, arthropod and mollusc photoreceptor potentials but none in the other phyla. Of those studied, most ciliary photoreceptors hyperpolarize due to light-activated closing of $Na^{+}$ channels in the ciliary membrane, and most rhabdomeric photoreceptors depolarize due to light-activated opening of $Na^{+}$ channels. However the hyperpolarization of the ciliary photoreceptor of the scallop (Pecten, Mollusca) is due to the opening of $K^{+}$ channels (McReynolds & Gorman, 1974; Gorman & McReynolds, 1978). This is probably the case also in a rhabdomeric photoreceptor in Salpa democratica (Tunicata, Chordata. Gorman et al., 1971; McReynolds & Gorman, 1975) and in the ciliary photoreceptor of the pineal organ of the trout (Vertebrata. Tabata et al., 1975).

We can conclude that, in Metazoa and some Protista, receptor potentials are generated by the modulation of ion permeabilities in a variety of ways. Until similar studies are done in other phyla,

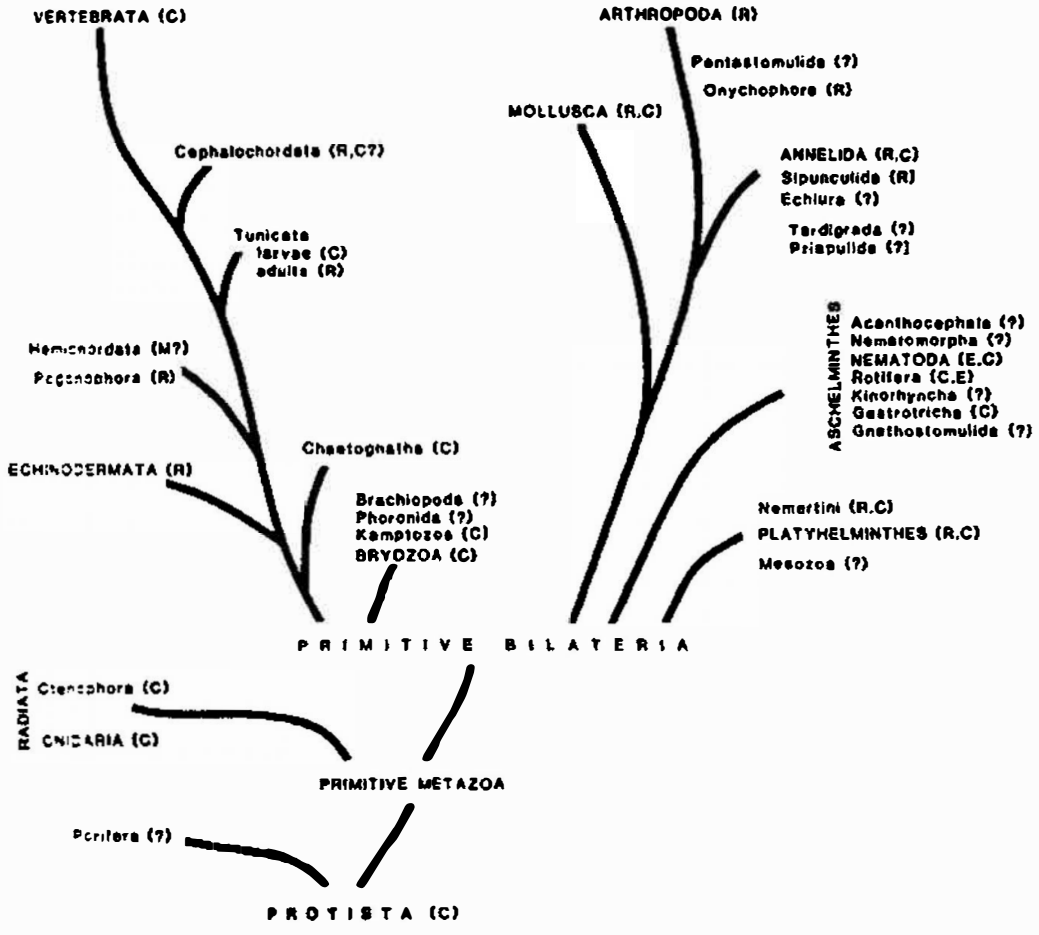


Fig. 7. Distribution of photoreceptor types among the phyla. C, ciliary; R, rhabdomeric; E, epigenous; M, mixed; ?, none yet identified or identification debatable. After Vanfleteren (1982).

however, it will be impossible to infer how each type of transduction mechanism has evolved.

Localization of photosensitivity

The localization of photosensitivity in special domains of the cell membrane occurs even in phytoflagellates. A primitive example is shown in Fig. 8, an electron micrograph of a freeze-fracture preparation of Chlamydomonaa reinhardii. A cluster of 8-12 nm intramembrane particles (IMP's) at high density (6500/$\mu m^2$) are apparent in the protoplasmic face (p-face) of the split membrane. These are restricted to the region of cell membrane overlying the shading pigment or eyespot (Melkonian & Robenek (1980a). IMP's 16-20 nm in diameter are excluded from this zone. Newly released

Fig. 8. Photoreceptive domain (between arrows) of plasma membrane of Chlamydomonas reinhardii (phytoflagellate, Protista). In the p-face leaflet, a high concentration of 8-12 nm particles is seen in the region overlying the stigma. The size and density of particles outside this region differs. After Melkonian and Robenek (1980a).

zoospores of the green alga Chlorosarcinopsis gelatinosa have a similar specialized zone which, unlike the shading pigment, disappears at the time the zoospore settles and becomes no longer phototactic (Melkonian & Robenek, 1980b). As yet there is no proof that the IMP's of these patches in the cell membrane are composed of photopigment, however similar p-face IMP's in vertebrate rod outer segment and crayfish microvillar membranes are probably aggregates of rhodopsin (see below).

There is a selective advantage to localization of the photopigment in a zone where it can be shaded by a pigment spot. It provides a simple mechanism for detecting the direction of the incident light. Without localization there would always be unshaded regions of the cell membrane that are light sensitive, and directional sensitivity would be poor. In multireceptor

pigment-cup eyes, the greater the localization, the better the resolution would be.

For localization to exist, the intramembrane particles must somehow be prevented from diffusing over the surface of the membrane. They could be tied together somehow or they may be held by some kind of molecular fence. Various components of the membrane or the underlying cytoskeleton have been proposed for this role (Nicholson, 1979; Cherry, 1979; Satir, 1980; Saibil, 1982).

Ciliary domain. Another restricted domain of the plasma membrane is the envelope of the cilium (or flagellum). Sooner or later, advantage would be taken of this pre-existing structure for localization of photosensitivity. This may have occurred in an ancestor of the phytoflagellate Chromulina psammobia (Fig. 9), in which an entire modified flagellum is shaded by a trough-shaped pigment spot (Fauré-Fremiet & Rouiller, 1957). Localization to the ciliary membrane must have occurred early in metazoan evolution, if not in Protista, since it is evident in photoreceptor cells of medusae (Cnidaria). The density of 8-10 nm IMP's is much higher in p-face leaflets of the ciliary shaft and ciliary microvilli than in those of the photoreceptor cell body or of the microvilli and cell body of pigment cells (Takasu & Yoshida, 1982).

Localization of rhodopsin to ciliary membranes is evident in rod and cone cells. IMP's observed in the p-face are characterized by a high density (4400-4700 per $\mu m^2$), relatively random distribution and homogeneous particle size in the 8-12 nm range. There is a variety of evidence that these IMP's must consist of rhodopsin (for references see Besharse & Pfenninger, 1980). Rhodopsin is an intrinsic component of both discs and outer segment plasma membrane and is known to traverse the membrane. The p-face 8-12 nm IMP's are thought to be aggregates of 4-5 rhodopsin molecules. Individual molecules protrude from the intra-discal surface (Roof & Heuser, 1982). Several investigators have shown similar-appearing 8-12 nm p-face IMP's in membranes reconstituted from purified rhodopsin and lipid.

IMP's with the same size and density are present in the p-faces of the membrane discs, outer segment plasma membrane, ciliary stalk membrane and the periciliary region of the inner segment plasma membrane. In contrast, the p-face IMP's of the plasma membrane outside the periciliar region, including that of the calycal processes, are less homogeneous in size, smaller on the average and 2/3 the density (Besharse & Pfenninger, 1980). The border of the ciliary domain is probably located just inside the ring of calycal processes (Fig. 10). This segregation of IMP's is the same in both rods and cones. Because rhodopsin is known to diffuse laterally in the membranes of rod and cone outer segments (Poo & Cone, 1974) one must assume that some kind of molecular fence prevents it from escaping from the ciliary domain. It is clear that the fence is not associated with the ciliary necklace or

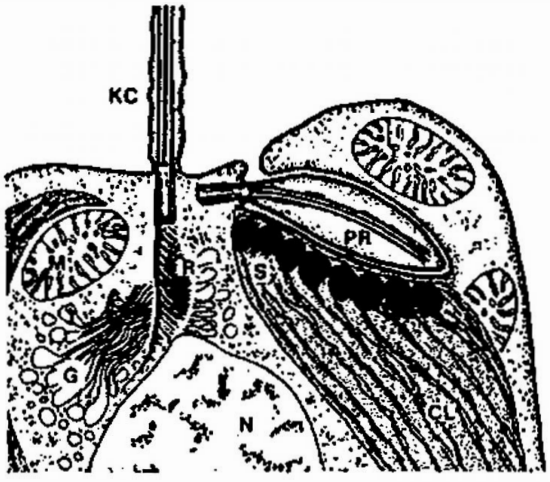


Fig. 9. Eye of Chromulina psammobia (phytoflagellate, Protista). Anterior to the stigma (s) lies an entire modified cilium (PR), the putative photoreceptor. CL, chloroplast; G, golgi network; KC, kinocilium; M, mitochondrion; N, nucleus; R, ciliary rootlet. After Fauré-Fremiet (1961).

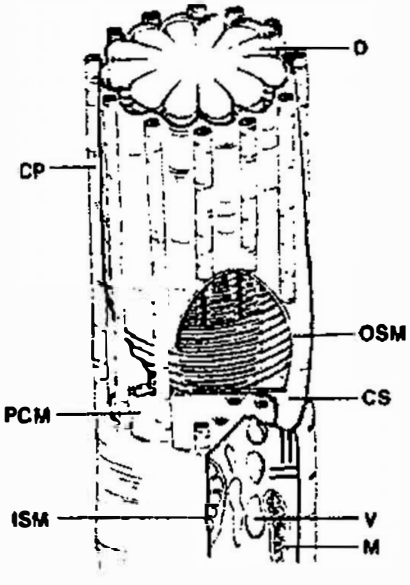


Fig. 10. Junction between inner and outer segments of an amphibian rod photoreceptor. Membrane vesicles (V) appear to fuse with the periciliary membrane (PCM). From there, photoreceptor membrane flows up the ciliary stalk (CS) to the outer segment membrane (OSM), from which the membrane discs (D) are formed at the base of the outer segment. The calycal processes (CP) lie outside the domain of the ciliary membrane. M, mitochondrion. After Besharse and Pfenninger (1980).

bracelet particles which are universally present in all cilia: they are in the wrong location - on the ciliary stalk (Röhlich, 1975).

There are at least 3 advantages of the ciliary membrane for localization of photosensitivity. 1) It is a restricted membrane domain where integral membrane proteins such as rhodopsin can be localized, 2) the genetic information necessary for its construction and maintainance is already available in the genome of metazoan epidermal cells, and 3) its surface area is large, therefore the amount of photopigment that can be shaded is greater than for a planar patch such as in Chlamydomonas. A possible fourth advantage, certain ion transport and regulatory proteins, useful in

phototransduction, may already have been segregated to these domains. For example, calcium-ion channels and pumps are localized to the membrane of kinocilia (Eckert & Brehm, 1979; Dentler, 1981). Another advantage of localizing photosensitivity in a cilium is suggested by Fig. 9. The stiffness provided by the axoneme probably facilitates indentation of the cell by the cilium. It may provide needed support to ciliary organelles of metazoan sensory cells.

Microvillar domain. The microvillar membrane has the same advantages. Though microvilli occur on the apical surface of epithelial cells of Hydromedusae (Cnidaria), the lowest phyla in which rhabdomeric photoreceptors have been found are Platyhelminthes and Echinodermata. Thus the colonization of the microvillar domain by photopigment could have first occurred in a common primitive bilateral ancestor (see Fig. 7).

In the crayfish, Procambarus (Fernández & Nickel 1976; Eguchi & Waterman, 1976), the p-face of the microvillar membrane contains 8-10 nm particles in high density. Digitonin, which extracts rhodopsin from membranes, gradually removed the IMP's. In the perimicrovillar plasma membrane of the dendrite, the IMP's have a much lower density even right up to the base of each microvillus (Fernández & Nickel, 1976). Either some kind of molecular fence must be located at the base of the microvillus or the particles are not mobile. The latter is suggested by other studies (Goldsmith & Wehner, 1977; Saibil, 1982). The plasma membrane remote from the rhabdom contains p-face particles in a broader range of sizes and with a smaller mean diameter (Eguchi & Waterman, 1976). In Drosophila, on the other hand, the p-face IMP density is about the same in the microvillar and plasma membranes of the retinula cells. Vitamin-A deprivation and 3 mutations decreased the partical density of both membrane domains as well as rhodopsin concentration (Schinz et al., 1982). Vitamin A-deficient blow flies have substantially fewer than normal IMP's in the rhabdomal membranes, and the rhodopsin content is lower by the same proportion (Boschek & Hamdorf, 1976). In the land snail, Helix aspersa, 7 nm p-face IMP's are more abundant in microvillar membranes of dark-adapted rhabdomeres than after prolonged treatment with light (Brandenberger et al., 1976). In the ant, however, 8,5 nm p-face IMP's of green- and UV-sensitive rhabdomes are not affected by various amounts of light-adaptation (Nickel & Menzel, 1976). Differences in the light treatments of the two studies may explain the divergent results.

Thus the p-face IMP's are correlated with the presence of rhodopsin in rhabdomeres of several higher invertebrates. In the crayfish they appear to be confined to the microvillar domain, whereas in Drosophila they are not. There have been no freeze-fracture studies of rhabdomeric photoreceptors of lower invertebrates. However there is reason to believe that one would find evidence of localization. First, localization of

photosensitivity is present in Protista, as already described. Second, in pigment-cup eyes, so common among lower invertebrate phyla, there is a clear advantage to localization of photoreceptive membranes to the interior of the cup. A photoreceptor cell would lose its directional sensitivity if the plasma membrane of the dendrite, soma and axon were photosensitive. Third, if a means of localizing visual pigment to microvilli were not developed early, the septate junctions could provide a fence. Septate junctions, equivalent to the vertebrate tight junction, are present in all invertebrate phyla except Chordata (where vertebrate-like tight junctions are found) and form a gasket-like seal around the apical circumference of cells lining an external or internal surface (Green & Bergquist, 1982). One might expect these junctions to be as effective a fence as the tight junctions of vertebrate olfactory cells cited in the next section. At what point in evolution photosensitivity became limited to the microvillar membrane is an interesting question for future study.

Chemosensory membranes. The advantages provided by the ciliary or microvillar membrane domains should also be useful for localization of chemosensitivity or mechanosensitivity. In metazoa, the apical end of neurons specialized for these functions usually project one or both of these structures. Surprisingly, however, the fence of vertebrate olfactory dendrites appears to be located at the tight junctions formed with the adjacent supporting cells rather than in the more restricted domain of the cilia or microvilli. P-face IMP's 8-12 nm in diameter are distributed over the entire apical surface of the dendrite (Kerjaschki & Hörandner, 1976; Menco et al., 1976; Usukura & Yamada, 1978). The density depends on species. Large, rod-shaped IMP's predominate in the apical membrane of adjacent supporting cells and IMP's were rare in motile cilia of "respiratory" cells of the same olfactory epithelium. Thus the 8-12 nm p-face IMP's probably have an olfactory function and, by analogy with the rhodopsin IMP's, may be chemoreceptive proteins.

Where both microvilli and cilia are present on olfactory dendrites, the particles are found in the membranes of both structures. These particles are rare on the lateral surfaces beyond the tight junctions. Apparently, in olfactory cells, it is sufficient to limit chemosensitivity to the entire exposed surface, and the microvilli and cilia both serve to increase the surface area.

In the newt the olfactory cells are of two types: one with several cilia and short microvilli and the other with only long microvilli. The apical surfaces and processes of both types contain the same 11 nm, randomly-distributed, p-face IMP's. However they occur at a higher density in the nonciliary type (Usukura & Yamada, 1978). Non-ciliated microvillar olfactory cells have been found in several other vertebrates (Bannister, 1965; 1968) and are analogous to rhabdomeric photoreceptors. The

microvilli never become as densely packed or tightly organized as they do in rhabdomeres. This reflects the difference in selection pressure. For efficient chemoreception the microvillar surfaces must be accessible to diffusing odorant molecules. For photoreception this is not a requirement and microvilli can be packed together to maximize the likelihood of capturing a photon.

Mixed-type photoreceptor cells. In view of the probable occurrence of chemosensory ciliary and microvillar projections in the same olfactory receptor cell, could photoreceptor cells exist in which both structures are photosensitive? This question calls to mind the examples mentioned earlier that are hard to classify. Where is the fence located in the photoreceptor cells of the hydromedusae Leukartiara and Polyorchis? Both microvilli and a cilium arise from the apical membrane of these species and in the latter species these microvilli intermingle with microvilli formed of the ciliary membrane (Singla & Weber, 1982a). The freeze-etch study of Takasu and Yoshida (1982) stops short of distinguishing between these two domains. In asteroid eyes, the microvilli are now known to arise from the apical membrane, not the ciliary membrane (Eakin & Brandenburger, 1979), but could the membrane of the adjacent cilium also be photosensitive? Eakin and Brandenburger argue that only the microvilli become disrupted by strong light, but could not the axoneme prevent disruption in cilia? A better indication comes from a freeze-fracture study: 8-12 nm p-face IMP's are present in high density in the microvillar and not the ciliary membrane (Yoshida, personal communication). The asteroid photoreceptor, therefore, would appear to be rhabdomeric, not a mixed type. It has been suggested (Brandenburger et al., 1973) that the photoreceptor cell of the tornaria larvae of a hemichordate is a mixed-type.

Synthesis and turnover of photoreceptive membranes

In the preceding section the occurrence of localized domains for photoreception was documented, and the need for a fence to segregate the domains was established. Also needed is a mechanism for inserting newly synthesized sensory proteins and other membrane proteins, specifically, within these domains. Along with this is the need to remove excess or worn out material from the domains. These mechanisms are now being studied intensively in both vertebrate and arthropod eyes. I will only summarize the prevailing view and leave discussion of arguments and evidence to the many reviews. I will then review the current evidence for synthesis and turnover in eyes of turbellarians and other lower invertebrates.

Vertebrates. Even though membrane turnover in rods and cones has received much attention in the last decade, the current understanding of some steps is still somewhat speculative (reviews: Whittle, 1976; Holtzman & Mercurio, 1980; Olive, 1980; Papermaster

& Schneider, 1982). Opsin, evidently, is synthesized on granular endoplasmic reticulum (GER) of the inner segment, and from then on, remains integrally associated with membrane. It is glycosylated initially on the ribosomes and terminally in the Golgi apparatus. GER and agranular endoplasmic reticulum (ER) are both involved with lipid metabolism. Labelled opsin or lipids appear in the ciliary stalk plasma membrane and flow to the outer segment where the membrane forms into the membrane discs. The discs were formerly thought to originate by invagination of the outer segment membrane but new evidence indicates that disc surfaces develop by evagination, and the opposing paired membranes are zippered by a separate mechanism (Steinberg et al., 1980). Incorporation of the 11-cis retinal, synthesized in the pigment epithelium, occurs within the outer segments (Bok et al.,1977). Membrane discs of rods slowly migrate up the outer segment and are ultimately shed and then phagocytized by the pigment epithelium. Since cone disc membranes retain their connection to the outer segment plasma membrane in most vertebrates, new opsin and lipid can diffuse throughout the outer segment. Cone outer segment tips are also shed and phagocytized. In a diurnal cycle, rods shed their tips in the morning after illumination begins, and cones shed theirs in the evening soon after it ends.

The mechanisms of transport of opsin and membrane from GER to golgi and from golgi to the ciliary stalk are still being debated. There is much evidence suggesting that membrane vesicles are the carriers (Papermaster & Schneider, 1982). These are seen near the distal end of the inner segment, near the Golgi apparatus and in the intervening ellipsoid region. It is thought that these structures insert membrane by fusion, as in exocytosis, with the periciliary membrane. Since this region lies within the fence around the ciliary membrane domain, it is only necessary for the added membrane to flow from there along the plasma membrane via the ciliary stalk to the outer segment. IMP's of the appropriate size distribution but at a lower density have been observed in these vesicles (Besharse & Pfenninger, 1980). Immunohistochemically demonstrable opsin is present (Papermaster et al, 1979), and labeled protein appears in vesicles near the cilium at the appropriate time. Pinocytotic coated vesicles that are commonly seen near the periciliary membrane may selectively remove material from the membrane, such as excess lipid deposited by the vesicles.

An essential step in bulk transport by exocytotic fusion of vesicles is the recognition of the target membrane (Palade, 1975). Presumably rhodopsin-containing vesicles fuse with the periciliary membrane, and $Na^+/K^+$ ATPase-containing vesicles fuse with the lateral membrane of the inner segment. Membrane recognition systems have been proposed for other cells and it is thought that the Golgi apparatus adds this component to the vesicle (Palade, 1975; Whaley & Dauwalder, 1979).

Arthropods and Molluscs. Membrane turnover in rhabdomeric photoreceptors is less well understood (for a recent review see Waterman, 1981). The cytoplasm near the rhabdomere typically contains GER, elements of ER, vesicles and tubules of ER, coated vesicles, multivesicular bodies and lysosomes. The role of each of these actors in the synthesis, transport and degradation of the rhabdomere is still uncertain. The amount of each component as well as the size of the rhabdomere varies with time of development, time of day and diurnal or long-term exposure to light or darkness, and it is by the control of these variables that the mechanism is being explored. The current view is that new rhabdomeric membrane may reach the base of microvilli via vesicles in some species and directly via flow along a tubular or ellipsoidal reticular system in others. Golgi complexes are comparatively rare in arthropod photoreceptor dendrites and are little affected by light or dark. "Photic vesicles" originate from Golgi saccules in photoreceptors of the snail (Brandenburger & Eakin, 1970) where, unlike in vertebrates, vitamin A is incorporated.

There is good support for the hypothesis that in arthropods membrane removal occurs by pinocytosis at the base of the microvilli, forming coated vesicles, and degradation occurs in the photoreceptor cell via a sequence of multivesicular bodies, lysosomes and residual bodies. Extracellular shedding followed by phagocytosis by the photoreceptor cell, hemocytes or other cells is an alternative route. Further discussion of the complexity and great variety of turnover mechanisms in arthropod and mollusc photoreceptors should be sought in Waterman (1981).

Lower invertebrates. Evidence of turnover in lower invertebrate phyla comes chiefly from studies of the effect of light and darkness on turbellarian (Platyhelminthes) eyes. Many of these studies were done long before the recent explosion of interest in photoreceptor membrane turnover and concerned the effects of long-term darkness on various Tricladida (Röhlich & Török, 1962; Röhlich & Tar, 1968; Carpenter et al., 1974b). A recent investigation of changes during normal diurnal light/dark periods was done on a rhabdocoel (Bedini et al., 1977). The microvilli degenerate in the dark and regenerate in the light. As they degenerate the microvilli become shorter and their tips disorderly. At their base, tubules, vesicles, multivesicular bodies and broken membranes are observed. Vesicles, large vacuoles and multilamellar whorls are distributed in the cytoplasm. Bristle-coated vesicles, normally seen pinching off from the microvillar base, are absent. When 12-hour darkness-treated eyes are exposed to light the microvilli are reconstructed with most of the change occurring between the 5th and 10th minute! The rapidity of restoration is even greater than observed in a dinopid spider, in which it occurs at dusk (Blest, 1978). The authors suggest that preassembled membranes are stored in the cytoplasm for the rapid

regeneration at dawn. Membrane appears to be transported to the base of the microvilli via vesicles.

Membrane degradation in the normal light-adapted eye of turbellarians can be inferred from the presence of coated vesicles (apparently originating by pinocytosis of the proximal end of the microvillar membrane), multivesicular bodies and lysozomes. Transport of new membranes in the fully light-adapted eye may utilize the same mechanisms as observed in regeneration; smooth-surfaced ER vesicles are present. In the light-adapted eye of D. dorotocephala, Carpenter et al. (1974a) observed ER in the form of long columns, parallel to the axis of the dendrite, which appear to merge with the microvilli. This has also been observed in other triclads (Stewart, 1966).

We can surmise that the mechanism of turnover in rhabdomeric photoreceptors is essentially the same in turbellarians and arthropods: degradation via a sequence of pinocytotic vesicles, MVB's and lysosomes, and bulk transport of new membrane via vesicular or tubular elements of the endoplasmic reticulum. Certainly the necessary equipment is there. The dynamics are still to be shown conclusively.

Development or regeneration of ciliary receptors has not been studied in lower invertebrates. The only hint of the mechanism of synthesis, transport and degradation of ciliary membrane comes from the structure of the apical cytoplasm. The nematode olfactory dendrite appears to have a particulary high rate of membrane turnover, as inferred from an extensive tubular and vesicular reticulum leading up to the periciliary membrane and evidence of shedding at the distal end of the cilium exposed to the sea water (Burr & Burr, 1975). Because of the cuticle, phagocytotic recovery of the shed membranes would be impossible.

Since the Cnidaria are regarded to be an early offshoot in the evolution of the Bilateria from phytoflagellates, it is interesting that their cilia contain the same structures involved in turnover of the ciliary membrane of vertebrates. This should be no surprise, since the same structures are well developed in phytoflagellates too. In Tamoya, the possibility that shed ciliary membranes are phagocytized by the pigment cell is suggested by the presence of many large multivesicular bodies and myelinated bodies (lysosomes?) in the long extension which extends though the network of microvilli derived from the ciliary membranes (Yamasu & Yoshida, 1976). Thus these pigment cells of the lowly Cnidaria may be analogous in this function to the pigment epithelial cells of vertebrates!

Increase in surface area

Because of the advantages of increased photosensitivity, natural selection has favored an increase in the surface area of the photosensitive membrane. Ciliary or microvillar membranes can be increased in area either by increasing the number of organelles per cell, by enlargement, or by pleating of the organelle membrane

in various ways. In order to preserve the shading properties of simple eyes, or the resolution of multi-receptor eyes, the larger membrane area would have to occupy a small volume. Selection is likely, therefore, to lead to a high membrane density in photoreceptors.

Multiple cilia have been observed in Bryozoa, Kamptozoa and in a nematode, however in these examples the organelles are likely to have evolved from cells which already contained multiple cilia. In bryozoan larvae the photoreceptive cilia have axonemes that are morphologically identical to those of the motile cilia of the neighbouring corona cells from which they probably evolved (Hughes & Woollacott, 1980). In Bugula simplex, both cell types have numerous cilia with the same spacing (Fig. 1). In the nematode example, Oncholaimus vesicarius, a clump of 10 cilia arise from a single dendrite in an olfactory organ but are enclosed and lie adjacent to a pigment spot (Fig. 3) rather than (like the similar chemoreceptors) passing through a cuticular opening to the exterior (Burr & Burr, 1975). Their location, and the nature of the phototaxis of this organism (Burr, 1979), implicate the cilia as photoreceptors. Their structural similarity to the chemoreceptive cilia and location in the olfactory organ suggest that they may have evolved by modification of one of the chemoreceptor cells (Burr & Burr, 1975). If so, they probably inherited the multiple cilia since the chemoreceptor cells are multiply ciliated. The multiple cilia of the chemoreceptors are undoubtedly a result of selection pressures for increased chemosensitivity.

Enlargement of a cilium is described in a kamptozoan (syn. entoproct). The unpleated multiple cilia lack arms on the a-microtubles, suggesting that the photoreceptor has been modified more than those of the closely related phylum, Bryozoa. The cilia also expand in diameter 1 μm above the basal body, giving the ciliary membrane a modest increase in surface area (Woollacott & Eakin, 1973). "Ampulla-shaped cilia" are found in rotifers (Clément, 1980) and the phytoflagellate, Chromulina (Fig. 9). Flattened cilia or "sacs" (Eakin, 1972) found in certain polychaete worms also represent a simple enlargement of the ciliary membrane area.

A much higher membrane area per unit volume can be obtained by pleating the ciliary membrane. The microvillar projections from cilia of cnidarian medusae have already been noted and illustrated (Figs. 5-6). It is interesting that a possible prior evolutionary step is illustrated by Leukartiara which has a single, unpleated cilium as a putative photoreceptor (Fig. 4). Pleated ciliary photoreceptors are found in many animal phyla. The various forms have been called lamellae, paddles, digits, tubules and discs (Eakin, 1972; Salvini-Plawen & Mayr, 1977). Lamellar expansions of the ciliary membrane that project into a cavity invaginated into the photoreceptor cell are found in Rotifera and Platyhelminthes (Clément, 1980; Clément & Wurdak, 1983; Fournier, 1983). These resemble similar structures, called phaosomes, of rhabdomeric

photoreceptor cells of Annelida and Pogonophora (Eakin, 1972; Vanfleteren, 1982).

In the case of rhabdomeric organelles, the surface area of the microvilli has been enlarged by increasing their number, by elongation and by branching (Eakin, 1972). Pleating of microvillar membranes is not observed. A high density is possible without pleating because of the already small size of microvilli.

Evolution of organelle complexity

In many phyletic lines there is evidence that photoreceptor membranes, after an increase in surface area, have been modified further towards greater organization and specialization. First, photoreceptor cells of the most advanced phyla have exquisitely structured organelles such as the rhabdomeres of crustacea (Fig. 11), insects and cephalopods, and the rods and cones of vertebrates. Secondly, in many lines, one can arrange examples in order of increasing complexity. My example is chosen from Cnidaria. From Leukartiara (Fig. 4) to Polyorchis the ciliary membrane changes from the unpleated form to one projecting loose microvilli which have varying diameters (Eakin, 1972). From Polyorchis to Sarsia the ciliary microvilli increase in density, and from Sarsia to Bougainvillia (Fig. 5) to Cladonema one can discern an increase in order towards a columnar arrangement of the organelle. In the scyphomedusan Tamoya the column is lengthened further (Fig. 6B). Intermittent swellings of the ciliary membrane, accompanied by a periodic fraying of the axoneme, provide a surface from which microvilli project. The microvilli have a more even diameter and sometimes are grouped into parallel - hexagonal clumps reminiscent of the arrangement in arthropod and mollusc rhabdomeres. It is striking that along the same stepwise sequence a comcomitant increase in specialization, complexity and organization occurs in the pigment cells and the eye as a whole. A comparison of the central nervous systems of these examples would be interesting.

The various forms that photoreceptor organelles have taken are catalogued by Eakin (1972). The rationale for each form is not

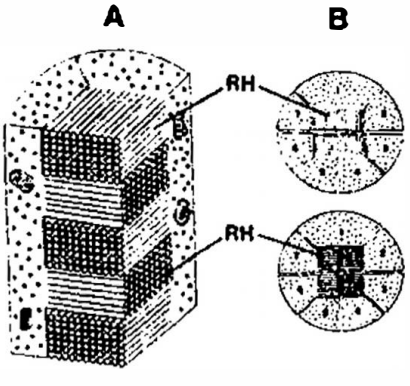


Fig. 11. Rhabdom of compound eye of the crayfish Procambarus clarkii (Crustacae, Arthropoda). A. Stereo diagram showing perpendicular orientation of the microvilli projecting from two photoreceptor cells. B. Transverse sections at two levels showing the organization of the rhabdomeres (RH) of the 7 photoreceptor cells of one ommatidium of the compound eye. After Eguchi (1965).

always obvious, except for the ones in which parallel microvilli are oriented perpendicular to the direction of propagation. Such a structure is likely to be sensitive to the direction of polarization of light. Two such rhabdomeres, oriented perpendicular to each other and located in different cells, are common in Crustacea and Insecta. Behavioral and physiological studies have demonstrated their role in the detection of polarization angle of light (Waterman, 1981). Parallel microvilli are also found in the interesting eyes of the Müller's larvae of Pseudoceros canadensis (Turbellaria, Platyhelminthes). As seen in Fig. 12, the right eye contains 3 rhabdomeres, oriented at different angles. Theoretically, it could detect polarization angle. The left eye, for some reason, contains a ciliary organelle as well (Eakin & Brandenburger, 1981).

Many photoreceptor forms appear to minimize polarization sensitivity. Though the disc membranes of rods and cones are perpendicular to the direction of propagation, rotational diffusion

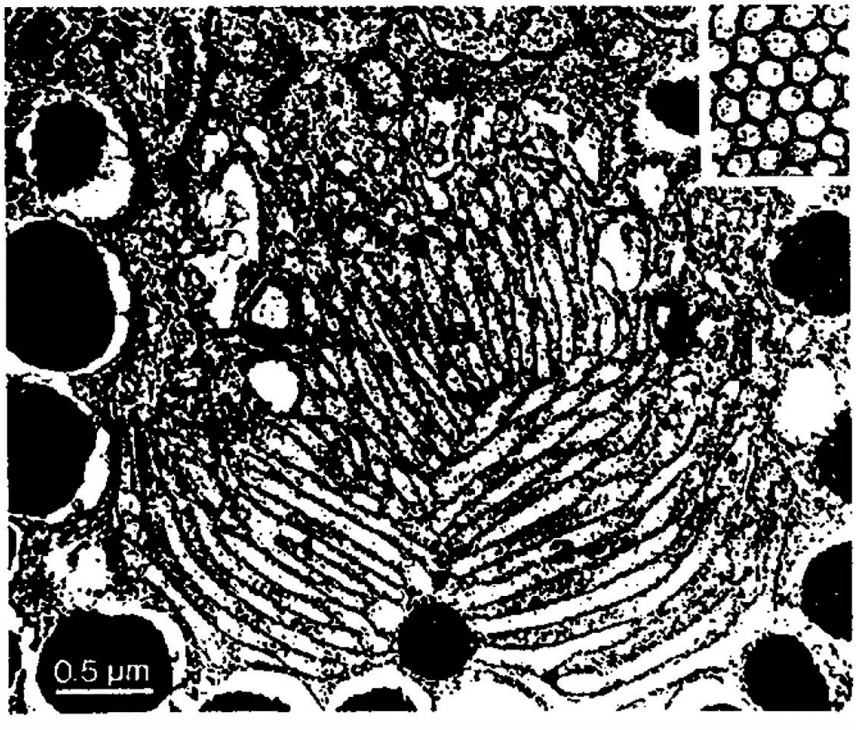


Fig. 12. Right-hand pigment-cup eye of Müller's larvae of Pseudoceros canadensis (Turbellaria, Platyhelminthes). Ordered microvilli of the 3 rhabdomeric receptors are shown. The left-hand eye has, in addition, another receptor composed of a clump of cilia (not shown). INSET, transverse section of microvilli. After Eakin and Brandenburger (1980).

randomizes the absorption vector of rhodopsin in the disc plane. The pigment molecules of Dugesia lugubris (Turbellaria, Platyhelminthes) are unlikely to be sensitive to the polarization vector because the microvillar membranes are parallel to the direction of propagation (Röhlich & Török, 1961). Disordered microvilli, such as those of the pigment-cup eye of the sipunculid worm (Fig. 13) may actually be "organized" in such a way to minimize sensitivity to polarization.

To make an ordered cellular structure, the cytoskeleton and extracellular material must be precisely designed and located. The ability to do this is evident even in the lowest phyla, cnidaria and platyhelminthes. Versatility and precision, however, appear to be greatest in the higher phyla.

Epigenous photoreceptor organelles

In addition to rhabdomeric and ciliary organelles, there are a few examples of photoreceptive organelles, in Nematoda and Rotifera, that are not composed of ciliary or microvillar membranes, being lamellar extensions of the apical membrane of a dendrite. Salvini-Plawen and Mayr (1977) propose that these are independently evolved from deep-lying, cerebral cells already differentiated for a neural function, and call them "ganglionic diverticular" organelles. In this category they also include other acilious examples that have microvillar membrane elaborations. This is puzzling because these microvilli appear the same, within variation, as rhabdomeric microvilli. Eakin (1972, 1979) includes both types of ganglionic organelle in his definition of a rhabdomeric receptor: any which are formed of non-ciliary plasma membrane. Salvini-Plawen (1982) admits of the difficulty of deciding whether ganglionic organelles arose from an acilious cerebral cell or by modification of a rhabdomeric cell. Also, Clément (1980) disagreed with Salvini-Plawen's new category, pointing to the historical difficulty of identifying cerebral neurons of Rotifera and to the presence of "cerebral" neurons bearing ciliary organelles. I propose that only clear morphological characters be used in the classification of photoreceptors, not presumed origins. Thus 'rhabdomeric' should refer to those organelles that are modified microvilli and 'ciliary' to those that are modified cilia. Accordingly, the microvillar type of "ganglionic" photoreceptor should be classified as a rhabdomeric photoreceptor. The lamellar type of acilious photoreceptor, then, is left unnamed. I propose the term 'epigenous' [growing on the surface] for any type of photoreceptor organelle that is formed of the cell membrane proper, not of a microvillar or ciliary membrane. This would include the special lamellar type identified above or any other form of projection of the cell membrane such as the cylindrical ones identified in the rotifer, Rhinoglena frontalis (Clément, 1980; Clément & Wurdak, 1983). A membrane patch like that of Chlamydomonas (Fig. 8) may be a precursor of epigenous photoreceptors. On the other hand,

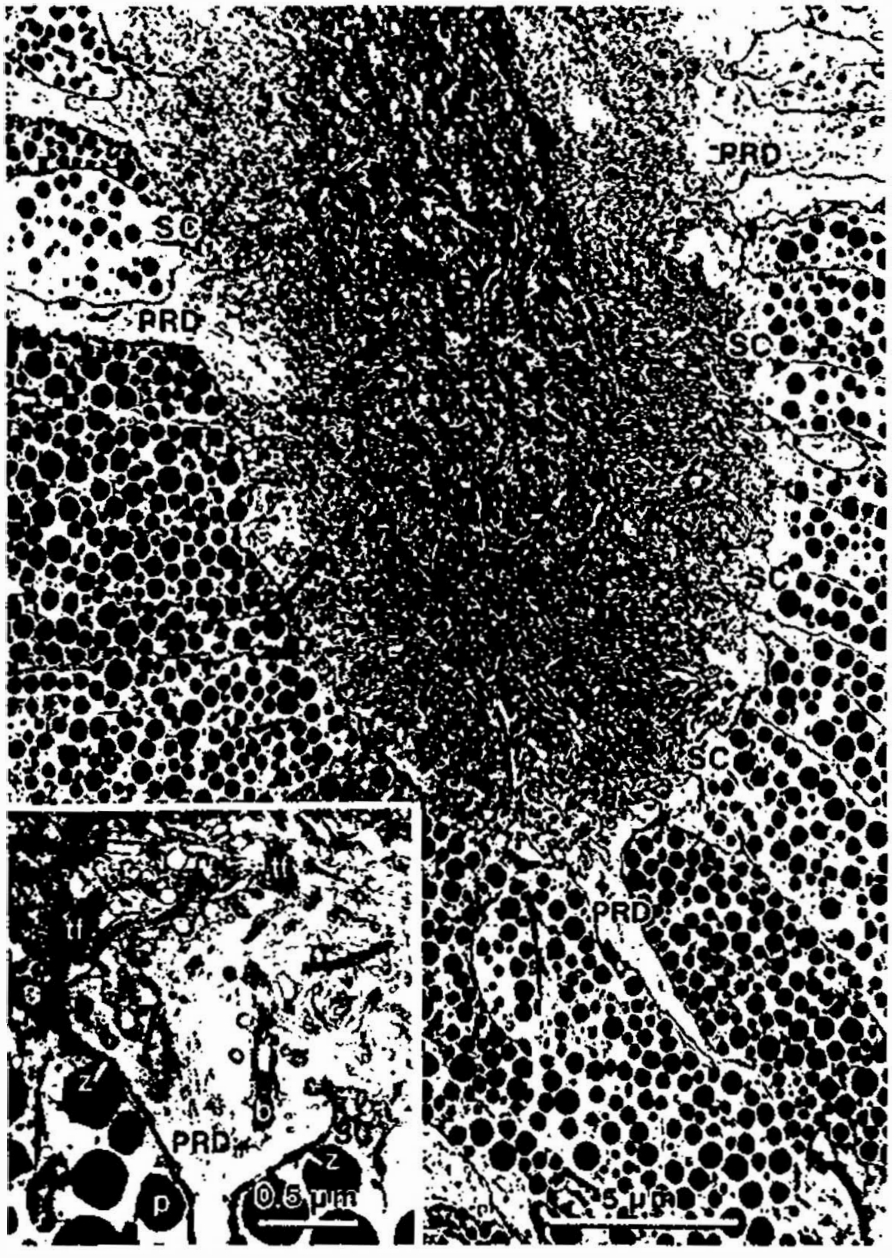


Fig. 13. Everse pigment-cup eye of Phascolosoma agassizii (Sipunculida), a marine worm. Photoreceptor dendrites (PRD) penetrate through the layer of pigmented supporting cells (SC). INSET. Detail of apical part of photoreceptor cell showing randomly arrayed microvilli (PR) and adventitious cilium (AC) that project from it. b, basal body; p, pigment granule; tf, tonofilaments; z, "zonula adhaerentes" (probably a septate junction). After Hermans and Eakin (1969).

epigenous organelles could be collapsed cilia which have had their axonemes suppressed during development.

Distribution among the phyla and trends

Four basic types of photoreceptor have been identified: ciliary, rhabdomeric, mixed and epigenous. In which phyla are they found? Figure 7 presents our current knowledge as summarized recently by Vanfleteren (1982). It is readily seen that the ciliary type has been found in all but five of the many phyla examined. There is a chance that ciliary examples may yet be found in some of these five because in only one of them, Arthropoda, have more than a few eyes been investigated. The rhabdomeric type has been found in all but 9 of the metazoan phyla investigated, and of the exceptions, only Vertebrata has been extensively studied.

Not only are both rhabdomeric and ciliary photoreceptors widespread, but each type appears to have arisen many times in metazoan phylogeny. Either ciliary or rhabdomeric organelles can occur in apparently cenogenic (newly arisen) eyes, as well as in well-established lines. Salvini-Plawen and Mayr (1977) argue that this disproves Eakin's hypothesis that there are 2 main lines of photoreceptor evolution.

There are some clear trends, however. Vertebrates have only ciliary, and Arthropods only rhabdomeric, photoreceptors in spite of the common occurrence of the opposite type of chemoreceptors and mechanoreceptors in these taxa. In the Platyhelminthes and Annelida, rhabdomeric photoreceptors predominate. In Annelida and Mollusca only rhabdomeric photoreceptors occur in cerebral eyes (Eakin, 1982). The ciliary photoreceptors of these phyla are found in caudal, branchial, epidermal, tegmental or mantel eyes. These are more likely to be cenogenic since they evolved in tissues that were not orginally photoreceptive (Salvini-Plawen & Mayr, 1977; Rosen et al., 1978; Eakin 1979, 1982).

Thus there is excellent evidence for a major trend towards rhabdomeric organelles in the protostomate line leading from ancestors of Platyhelminthes to Annelida, Mollusca and Arthropoda (Fig. 7). Minor trends are identifiable in two cases, each involving only two related phyla: 1) the clumped cilia of Bryozoa and Kamptozoa, and 2) the ciliary discs of ascidian tadpole larvae and vertebrates.

Though ciliary examples may yet be found, the apparent lack of ciliary photoreceptors in Echinodermata (Yamamoto & Yoshida, 1978; Eakin & Brandenburger, 1979; Eakin, 1982) has severely shortened the "ciliary line of evolution" originally proposed by Eakin (1963). The presence of ciliary photoreceptors in cephalochordates remains to be proven (Vanfleteren, 1982). What is left is the minor trend mentioned above.

The two other basic types of photoreceptor, epigenous and mixed, have only a few examples and appear to occur rarely (Fig. 7). Epigenous lamellar organelles have been discovered in Nematoda and Rotifera, and a cylindrical organelle has been found in

Rotifera. These appear to be no more nor less cenogenic than other types in the same phyla.

The mixed type has been proposed in only two phyla, Cnidaria (Singla, 1974) and Hemichordata (Brandenburger et al, 1973). Still needed is some kind of proof that the cilium and the (non-ciliary) microvilli are both photoreceptive. There are many rhabdomeric photoreceptors which have adventitious cilia adjacent to the microvillous organelle. In most cases it is unknown whether the ciliary membrane is also photosensitive. Freeze-fracture electron microscopy appears to be a promising approach to this problem; it has shown that olfactory neurons are usually of the mixed type (see earlier section on chemosensory membranes).

Conclusions and questions

Evolution of ciliary and rhabdomeric organelles may have occurred in four stages: 1) evolution of photosensitivity (in Protista or early Metazoa), 2) localization to restricted membrane domains such as the membrane of cilia (in Protista) or microvilli (in primitive Bilateria), 3) increase of surface area of microvillar or ciliary membranes by increase in number, enlargement, or in the case of ciliary types, pleating of the membrane, and 4) increase in complexity by greater organization and more precise form. Following Darwin, step-wise sequences increasing in membrane area and organelle complexity can be arranged for photoreceptors, provided closely related examples within phyla are chosen. Steps 3) and 4) are paralleled by increases in specialization and complexity of pigment cells and the eye as a whole.

As is the case for eyes, photoreceptors appear to have arisen many times in metazoa: many independent lines can be distinguished. Despite this, two major trends can be distinguished in the distribution of organelle type and complexity among phyla. One is towards greater versatility and precision of organelle structure as one proceeds toward higher phyla. The other is the selection, predominantly, of rhabdomeric organelles in cerebral eyes of the Platyhelminthes, Annelida, Arthropoda and Mollusca. Two minor trends toward modified cilia are also identifiable.

How can ciliary or rhabdomeric photoreceptors have newly arisen so many times? It must have been vastly easier for these organelles to evolve than, for example, mitochondria or endoplasmic reticulum. Why is versatility and precision of organelle structure so much greater in the higher phyla? Why are photoreceptors exclusively ciliary in Vertebrata and rhabdomeric in Arthropoda? Comparative anatomy, by itself, appears not to be able to answer these questions. In the next section I propose a mechanism of evolution that may help.

## ACKNOWLEDGEMENTS

The author is grateful to Richard M. Eakin, Merrill B. Hille and Michael J. Smith for reading the manuscript and offering suggestions. The author also appreciates the careful work of Wendy Yee in preparing the manuscript camera-ready for publication.

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