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# THE EVOLUTION OF EYES

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## INTRODUCTION: EVOLUTION AT DIFFERENT LEVELS

Since the earth formed more than 5 billion years ago, sunlight has been the most potent selective force to control the evolution of living organisms. Consequences of this solar selection are most evident in eyes, the premier sensory outposts of the brain. Because organisms use light to see, eyes have evolved into many shapes, sizes, and designs; within these structures, highly conserved protein molecules for catching photons and bending light rays have also evolved. Although eyes themselves demonstrate many different solutions to the problem of obtaining an image—solutions reached relatively late in evolution—some of the molecules important for sight are, in fact, the same as in the earliest times. This suggests that once suitable biochemical solutions are found, they are retained, even though their "packaging" varies greatly. In this review, we concentrate on the diversity of eye types and their optical evolution, but first we consider briefly evolution at the more fundamental levels of molecules and cells.

### *Molecular Evolution*

The opsins, the protein components of the visual pigments responsible for catching photons, have a history that extends well beyond the appearance of anything we would recognize as an eye. Goldsmith (1990) recently



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compared the opsins' evolutionary lineages in detail. These molecules consist of seven transmembrane helices with short loops on both sides of the membrane. Covalently attached to the molecules is a highly conjugated molecule, the chromophore, which is one of a family of only four close relatives of vitamin A. The chromophore accepts the photon of light; as a result, the molecule flips from the 11-*cis* to the all-*trans* form, which in turn triggers a biochemical cascade that leads to excitation of the receptor cell. These features are common to all metazoan opsins. Based on the degree of similarity in their DNA, they must share a common ancestry. Two regions of the molecule, particularly the cytoplasmic loop between helices 1 and 2 and the site of attachment of the chromophore molecule in helix 7, show very close similarity in opsins from vertebrates, insects, and *Octopus*, whose ancestries diverged in the Cambrian. Within the vertebrates, the primary structure of the rod and cone opsins clearly has a phylogeny that maps onto the phylogeny of the parent species. With the recent work by Nathans and coworkers (e.g. Nathans 1987) we have begun to understand the molecular and phylogenetic basis of color vision at a molecular level.

Although metazoan opsins have apparently evolved along several separate lines from a common ancient ancestor, what happened earlier is not so clear. Interestingly, "bacteriorhodopsin" from *Halobacterium* does not show significant amino acid similarity with cattle rhodopsin, and it is double-bond 13 of the chromophore, rather than 11, that is altered by light. Nevertheless, like metazoan opsins, bacteriorhodopsin seems to belong to a larger superfamily of proteins, all of which have seven transmembrane helices and operate by activating second-messenger cascades (e.g. Hall 1987). These proteins include the $\beta$-adrenergic receptor and the muscarinic acetylcholine receptor. Whether these similarities indicate a very ancient common ancestry or a more recent appropriation of one protein to another function, is not yet clear. For further discussion and detailed references, consult Goldsmith's excellent review (1990).

Opsins are not the only visual proteins with an interesting history. Vertebrate lenses are formed from modified epithelial cells, which contain high concentrations of soluble proteins known as "crystallins" (e.g. Bloemendal 1981) because of their highly organized packing. The distribution of these proteins is responsible for the remarkable refractive index gradients in these lenses, which underlie their optical properties (see below). Of the ten crystallins now known, $\alpha$-A is the most ubiquitous, as it is only missing in bony fishes. Once thought to be "dull proteins" (de Jong et al 1988), the production and arrangement of lens proteins instead offers a tantalizing glimpse at the versatile bag of tricks used during the evolution of optical structures.

Phylogenetic trees based on DNA sequences of α-A crystallin reveal strongly directional selection in vertebrates that require increasingly flexible lenses. However, how the observed amino acid substitutions contribute to flexibility is unknown (de Jong et al 1988). The consequences of relaxed selection can be seen in the crystallins of the subterranean rodent *Spalax ehrenbergi*, which is completely blind and has only rudimentary eyes. The gene for α-A crystallin changes four times as fast as in sighted rodent relatives, but at only one fifth the rate for neutral evolution found in pseudogenes (Hendriks et al 1987). Because *Spalax* still responds to photoperiods for thermoregulation (Haim et al 1983), perhaps some feature of α-A is required for functionality, or, as Hendriks et al (1987) suggest, α-A may play a role in the development of the eye. In any event, the severity of the constraints on lens construction are mirrored in the extent of evolutionary selection for α-A lens protein. For other lens proteins, there are other themes and variations, but these give no clear idea of how selection is acting.

Until recently, all crystallins were thought to be unique to lens tissue and to have evolved for this specialist function. However, this is apparently only partly true, as crystallins fall into two distinct groups. One group, the Alpha and Beta-gamma crystallins, are indeed specialized lens proteins. Each is the product of gene duplication and divergent evolution from distinct ancestors with a role in stress responses. Alpha crystallins are related to ubiquitous and ancient heat-shock proteins and to a schistosome egg antigen; Beta-gamma crystallins are relatives of a bacterial spore coat calcium-binding protein (Wistow & Piatigorski 1988). The other group of lens proteins are enzymes or their close relatives, which are often used as enzymes elsewhere in the animal (e.g. Wistow et al 1988a). Moreover, some taxon-specific lens proteins are actually products of the same genes as the enzymes (Hendriks et al 1988; Wistow et al 1988b). One gene coding for a protein with two entirely different functions has been called "gene sharing" (Wistow et al 1990) and is considered an evolutionary strategy that preceeded gene duplication and specialization (Piatigorski & Wistow 1989). Such shared genes are subjected to two or more different selective constraints, which makes evolutionary change complicated at best.

Why have enzymes been recruited as vertebrate lens tissue, which comprises up to 40% of the lens? There is considerable speculation on this point (e.g. Wistow & Kim 1991), but no compelling insight. Whatever the reason, this molecular opportunism in vertebrates is apparently such a good idea that molluscs independently evolved the same strategy (Doolittle 1988). Squid eyes, which are interesting for their convergence with fish eyes at the organ level (see below), have lenses whose protein content is almost 100% the enzyme glutathione S-transferase (Tomarev & Zinovieva

1988). This convergence of molecular strategy hints that "enzyme as lens" might have a deeper structural basis. Or, as Piatigorski et al (1988) suggest, gene regulation of enzymes conveniently lends itself to exploitation for tissue-specific expression. Thus, enzymes may be used to make lenses because either that type of protein makes good lenses, or it may just be easy to get lens cells to make a lot of enzyme, or there may be less obvious reasons for this strategy.

Edwards & Meyer (1990) reported that conservation of a crystalline cone constituent exists throughout the insects and crustacea. This suggests that just as α-A crystallins in vertebrates show a monophyletic line, so do at least some lens proteins in arthropods, even though at the organ level arthropods show every known type of optical structure. We end this section with a remark of Goldsmith (1990), which summarizes the multilevel nature of eye evolution: "The eyes of cephalopods, arthropods, and vertebrates are not homologous, yet at the molecular level some of their constituents are."

## *Cellular Evolution*

After molecules, receptor cells are at the next level of organization. At the receptor cell level, there are interesting indications of ancient common ancestries. As Eakin (1963) first pointed out, the protostomes (the annelid-mollusk-arthropod line) tend to have receptors in which the expanded photopigment-bearing membrane is composed of microvilli; in the deuterostomes (the echinoderm-chordate line), however, the receptors have membranes derived from cilia, which are expanded into plate- or disklike structures. Eakin's analysis, which suggests a simple dual phylogeny for photoreceptor cells, ran into difficulties because of many anatomic exceptions: Many of the microvillous (rhabdomeric) structures contained at least part of a cilium, for example (Eakin 1972). In terms of physiology, however, our knowledge tends to support Eakin's original scheme. The microvillous receptors of mollusks and arthropods depolarize to light, and the eventual result of photon absorptions is the opening of $Na^+$ channels in the receptor membrane (e.g. Fuortes & O'Bryan 1972). The ciliary receptors of vertebrates, on the other hand, hyperpolarize to light by the closing of $Na^+$ channels (e.g. Yau & Baylor 1989). An exception to this scheme seems to be the receptors in the primitive chordate *Salpa*, which are microvillous, but hyperpolarize (Gorman et al 1971).

One other physiologic class of receptor, which is found infrequently in the mollusks and annelids, hyperpolarizes to light like vertebrate receptors (Leutscher-Hazelhoff 1984). Here, however, the mechanism is different, as it involves an increase in the conductance of $K^+$ ions (Gorman & McReynolds 1978). Anatomically, these receptors are characterized by

the presence of many expanded cilia. Functionally, they all seem to be concerned with simple defensive "off" responses to shadow or motion (Land 1968; Salvini-Plawen & Mayr 1977). Thus, a case can be made on both anatomic and physiologic grounds that there may be a rather small number of anatomic and physiologic types of photoreceptor cell, possibly with independent evolutionary origins. Alternatively, they may have repeatedly arisen because they represent the only ways to utilize the available membrane machinery in the service of photoreception. The answer may lie in the relationship of the physiologic response to the cells' specific microanatomy, which at present remains unexplored and enigmatic.

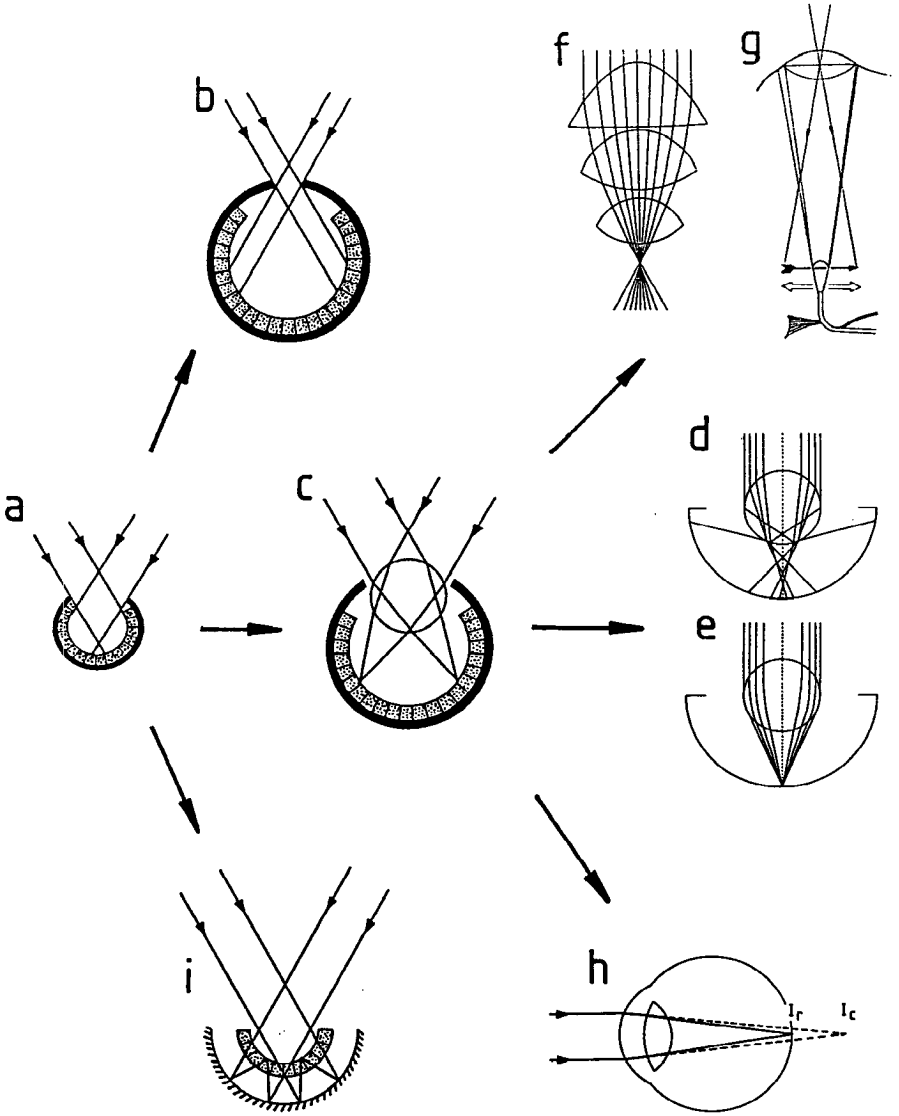
The rest of this review addresses evolution at the level of the whole organ, the eye itself. Here, we are largely concerned with the ways that the preexisting molecular and cellular building blocks have been assembled to provide various solutions to the problem of obtaining and transmitting an image.

## THE EVOLUTION OF OPTICAL MECHANIMS

### *Parallel Evolution in Optical Design*

When we trace the evolution of different kinds of eye, the greatest problem lies in deciding whether similarity in structure is due to evolutionary convergence or to common descent. There is a relatively small number of ways to produce an eye that gives a usable image, and most have been "discovered" more than once, thus giving rise to similar structures in unrelated animals. Citing the most notorious example, the phylogenetically unrelated eyes of squid and fish are similar in a great many details, presumably because the logic of the production of large, camera-type eyes necessitates a spherical lens, iris, eye-muscles, etc. (Packard 1972). By contrast, human and fish eyes are related by common descent, although optically they are rather different from each other. A superficial study of the eyes does not always allow such a distinction to be made, and lineages in eyes must be traced by either knowing the phylogeny of the animals in advance, or looking at other characters that are related less to optical "design principles." In the case of fish and cephalopods, the inverted and multilayered structure of the fish retina, compared with the simpler, noninverted retina of octopus and squid, demonstrates most clearly the unrelatedness of the eyes themselves.

Eye evolution has proceeded in two stages. In almost all the major animal groups, one finds simple eye-spots that consist of a small number of receptors in an open cup of screening pigment cells (Figure 1*a*). In an impressive analysis of the detailed structure, anatomic origins, and phylogenetic affinities of these eye-spots, Salvini-Plawen & Mayr (1977)



concluded that such structures had evolved independently at least 40 times, and probably as many as 65 times. These eye-spots are useful in selecting a congenial environment, as they can tell an animal a certain amount about the distribution of light and dark in the surroundings. However, with only shadowing from the pigment cup to restrict the acceptance angle of individual receptors, the resolution is much too poor for the eye to detect predators or prey, or to be involved in pattern recognition or the control of locomotion. All these tasks require the eye to have an optical system that can restrict receptor acceptance angles to a few degrees or better. This second stage in eye evolution, the provision of a competent optical system, has occurred much less frequently than the first, in only six of the 33 metazoan phyla listed by Barnes (1987): the Cnidaria, Mollusca, Annelida, Onychophora, Arthropoda, and Chordata. These are, however, the most successful phyla, as they contribute about 96% of known species. Perhaps the attainment of optical "lift-off" has contributed to this success.

The most exciting feature of the later stages of optical evolution has been the diversity of mechanisms that have been tried out in various parts of the animal kindgom. At last count, there were ten optically distinct ways of producing images (Figures 1 and 2). These include nearly all those known from optical technology (the Fresnel lens and the zoom lens are two of the few exceptions that come to mind), plus several solutions involving array optics that have not really been invented. Some of these solutions, such as the spherical graded-index lens (Figure 1*e*), have evolved many times; others, such as the reflecting superposition eyes of shrimps and lobsters (Figure 2*j*), have probably only evolved once. Four or five of these mechanisms have only been discovered in the last 25 years, which is remarkable given that excellent anatomic descriptions of most of these eyes have been available since the 1900s or earlier.

As most textbooks continue to refer to "the lens eye" or "the compound eye," as though these represented the totality of optical types, it seems appropriate to provide a brief review of all known mechanisms of image formation in eyes. We concentrate here on the new mechanisms, but do

*Figure 1* The evolution of single-chambered eyes. The arrows indicate developments, rather than specific evolutionary pathways. See text for details and references. Compiled from many sources.

(*a*) Pit eye, common throughout the lower phyla. (*b*) Pinhole eye of *Haliotis* or *Nautilus*. (*c*) Eye with lens. (*d*) Homogeneous lens. (*e*) Inhomogeneous "Matthiessen" lens. (*f*) Multiple lens eye of male *Pontella*. (*g*) Two-lens eye of *Copilia*. Solid arrow shows image position; open arrow, the movement of the second lens. (*h*) Terrestrial eye of man with cornea and lens; *Ic*, image formed by cornea alone; *Ir*, final image on retina. (*i*) Mirror eye of the scallop *Pecten*.

not omit those that have been understood for much longer. Thus, the remainder of this chapter is mostly devoted to the mechanisms, capabilities, evolutionary origins, and affinities of the many kinds of "advanced" image-forming eye. The conventional division of eyes into "simple," i.e. single-chambered or camera-like, and "compound" is retained, because the mechanisms involved really are very different and represent topologically "concave" and "convex" solutions to the problem of image formation (Goldsmith 1990). Useful, supplementary accounts of optical mechanisms in the invertebrates are given by Land (1981a), and in several chapters in Ali (1984). Nilsson (1989) gives an excellent account of compound eye optics and evolution. Walls (1942) still provides the best comparative account of vertebrate eye optics, but Hughes (1977, 1986) and Sivak (1988) offer important new perspectives.

## *Simple Eyes*

PIT EYES These eye-spots are of interest here only because they must have provided the ancestors for optically more advanced eyes (Figure 1*a*). These eyes are typically less than 100 $\mu$m in diameter and contain from only 1 to about 100 receptors. They are found in all but five of the 33 metazoan phyla. They may be derived from ciliated ectodermal cells or, less commonly, from nonciliated ganglionic cells. The eyes may be "everse," i.e. the receptors are directed towards the light, and the nerve fibers pass through the back of the eye-cup. Or, they may be "inverse," i.e. the nerve fibers emerge from the front of the cup (Salvini-Plawen & Mayr 1977). Burr (1984) has reviewed behaviors that these eyes can mediate. There are three ways to improve the performance of an eye-spot. An enlarged cup and reduced aperture produces a pinhole eye (Figure 1*b*). The incorporation of a refractile structure into the eye sharpens the retinal image and thus improves directionality (Figure 1*c*). And, the provision of a reflecting layer behind the receptors has two effects: First, it increases the amount of light available to the receptors; second, if the receptors move forward in the eye, it throws an image on them (Figure 1*f*). One can discern the beginnings of all these processes in the eye-spots of different invertebrate groups (reviews in Ali 1984).

PINHOLES The only one good example of a pinhole eye is found in the ancient cephalopod mollusk *Nautilus* (Figure 1*b*). A few other mollusks have what one might describe as "improved pits." In the abalone *Haliotis*, the eye-cup is 1 mm long with a 0.2 mm pupil, and perhaps 15,000 receptors (Tonosaki 1967; Messenger 1981). The *Nautilus* eye, however, is quite different. Except for the absence of a lens, it is an advanced eye in all respects. It is large, almost 1 cm in diameter; it has an aperture that can

be expanded from 0.4 to 2.8 mm (Hurley et al 1978); and it has extraocular muscles that mediate a response to gravity, thus stabilizing the eye against the rocking motion of the swimming animal (Hartline et al 1979).

Optically, however, this is a poor eye. The point-spread function (blur circle) on the retina cannot be smaller than the pupil, which limits resolution to several degrees at best. Muntz & Raj (1984) used the animal's optomotor response to test resolution and found that the minimum effective grating period was 11–22.5°, which is worse than expected. The real problem with this eye is that a reduction of the pupil diameter to improve resolution means a serious loss of retinal illuminance, and vice versa. Even at full aperture, the image is six times dimmer than in the eye of an octopus or fish, and the resolution is awful. The real mystery is that the pinhole has been retained. Almost any lens-like structure, however crude, placed in the aperture would improve resolution, sensitivity, or both. Thus, it must remain an evolutionary conundrum that this simple modification has not occurred here, when it has so often elsewhere.

SPHERICAL LENSES In aquatic animals, the most common optical system in single-chambered eyes is based on a spherical lens (Figures 1*c–e*). Initially, such a lens would have arisen by an increase in the refractive index of the material within the eye-cup, brought about by the addition of protein or carbohydrate. Eyes with such undifferentiated (or "Fullmasse") lenses can still be found in some gastropod mollusks and annelids (see Land 1981a for earlier references). However, such a lens can only reduce the diameter of the blur circle on the retina, not form a sharp image, because the focal length cannot be shortened enough to fit the eye. In more advanced lens eyes, the required reduction in focal length is achieved because the lens has a special inhomogeneous construction, with dense, high refractive index material in the center, and a gradient of decreasing density and refractive index toward the periphery. In 1877, Matthiessen discovered this gradient in fish lenses (see Pumphrey 1961; Hughes 1986; Axelrod et al 1988). He was struck by the short focal length (about 2.5 radii, known as "Matthiessen's ratio"); if the lens were homogeneous, the refractive index would be 1.66, an unattainable value. In fact, the central refractive index is about 1.52, which falls to less than 1.4 at the periphery. The effect of the gradient is twofold. First, the focal length is reduced (and, concommitantly, the relative aperture increased) because light is continuously bent within the lens, not just at its surfaces. Second, with the correct gradient the lens can be made aplanatic, i.e. free from the spherical aberration, which makes homogeneous spherical lens virtually unusable (Pumphrey 1961) (Figure 1*d* and *e*). The exact form of the gradient that permits this condition was not achieved theoretically until quite recently

(Luneberg 1944; Fletcher et al 1954), although Matthiessen had proposed a parabolic gradient that was very similar. In spite of a recent suggestion by Fernald & Wright (1983) that fish lenses might have a substantial homogeneous core, it now seems that a continuous gradient, like that of Matthiessen or Luneberg, must be present to account for the observed ray paths (Axelrod et al 1988).

By measuring the focal length, it is easy to tell whether a particular group of animals has "discovered" how to make this kind of lens. If the focal length is around 2.5 radii, then the lens must have a gradient construction. A homogeneous lens with the same central refractive index would have a focal length of 4 radii. By this criterion, "Matthiessen" lenses have evolved at least eight times: in the fish, in the cephalopod mollusks (excluding *Nautilus*), at least four times in the gastropod mollusks (littorinids, strombids, heteropods, and some pulmonates), in the annelids (alciopid polychaetes), and once in the copepod crustaceans (*Labidocera*). Details are given in Land (1981a, 1984a). The remarkable lens eyes of cubomedusan jellyfish (Piatigorsky et al 1989) are not included here, as their optical properties have not been examined. Interestingly, the above list does include all aquatic lens eyes of any size; none have homogeneous lenses. One can conclude that there is one right way of producing such lenses, and that natural selection always finds it. Matthiessen lenses are indeed of excellent optical quality, as they offer high resolution with high light-gathering power. Their only residual defect is chromatic aberration (Fernald 1990), which need not have a serious effect.

Lens construction accounts for one aspect of the remarkable convergence between fish and cephalopod eyes. The identity of Matthiessen's ratio in the two groups, itself a result of the refractive index of the dry material of the lens center, and the inevitable spherical symmetry of the image effectively dictate the eyes' shape and proportions. The presence of eye muscles can be explained from the need to stabilize the image. This need grows with image quality, if that quality is not to be compromised by blur. Similarly, the need for an accommodation mechanism is determined by eye size, in the same way that focusing becomes more critical for camera lenses as the focal length increases. Thus, many of the convergent features that seem so remarkable (Packard 1972) are inevitable, given a particular type and size of eye.

MULTIPLE LENSES Among aquatic eyes (Figure 1*f* and *g*), there are alternatives to the single spherical lens, but they are certainly not common. Two of the most interesting are found in copepod crustaceans, in which they are derived from parts of the single median eye. In *Pontella*, the lens is a triplet (Figure 1*f*); two elements are actually outside the eye in the

animal's rostrum, and a third element is close to the retina of only six (!) receptors (Land 1984a). The eyes are sexually dimorphic—the females only have a doublet—and the animals themselves are conspicuously marked in blue and silver, which suggests a role for the eyes in the recognition of species and potential mates. Optically, the intriguing feature of the eyes is the first surface, which is parabolic. Ray tracing shows that this configuration can correct the spherical aberration of the other five interfaces in the optical system to provide a point image. This seems to be an interesting alternative solution, as an aspheric surface achieves the same result as the inhomogeneous optics of the Matthiessen lens.

Another copepod, *Copilia*, has fascinated biologists for more than a century. Its eyes are constructed strangely (Figures 1*g* and 3*b*), and they move to and fro in the longitudinal plane, thus scanning the water in front of the animal (Exner 1891). Each eye has two lenses that are arranged like a telescope: A large, long focal length "objective" lens forms an image on or close to a second, short focal length "eyepiece" lens immediately in front of the cluster of five to seven photoreceptors (Wolken & Florida 1969; Downing 1972). The second lens and receptors move together as a unit during scanning. The function of this astonishing system is still not well understood, but we discuss the possible role of scanning later in this review.

CORNEAL REFRACTION In our own eyes, two thirds of the optical power lies in the cornea (Figure 1*h*). The lens, which is entirely responsible for image formation in our aquatic ancestors, is now mainly concerned with adjustments of focus. The use of a curved air/tissue interface for image formation is limited to terrestrial animals, and is actually a rather uncommon optical mechanism. Apart from the land vertebrates, the only other large group to use corneal refraction are the spiders (Land 1985a), whose eyesight can be remarkably acute. Williams & McIntyre (1980) estimate that the interreceptor angle in the jumping spider *Portia* is only 2.5 arc min. Considering the size of the animal (1 cm), this compares quite favorably with 0.5 arc min in the human fovea. The larvae of some insects also have simple eyes that form an image by using the cornea; the most impressive are the eyes of tiger beetle larvae (*Cicindela*), in which the interreceptor angle is about 1.8°. This is quite comparable in performance to the compound eyes of the adults that supplant them (Friederichs 1931; Land 1985b). The dorsal ocelli of adult insects are of the same general design, but are profoundly out of focus. They are concerned with stabilizing flight relative to the sky, and not with imaging.

For an eye of the corneal type to realize its maximum possible (diffraction limited) acuity, it must be corrected for spherical aberration. There are two ways this might be done: The cornea itself might be aspherical, as

the surface that directs all parallel rays to a single point is not spherical, but elliptical; alternatively, an inhomogeneous lens might be used to produce the correction. According to Millodot & Sivak (1979), the cornea of the human eye is aspheric and thus corrected; the lens corrects itself by being inhomogeneous. The penalty of an aspheric correction is that the eye loses its radial symmetry, and thus has one "good" axis and reduced resolution elsewhere. Where all-round vision is needed, it may be better to go for the other solution. In the rat eye, which has a nearly spherical cornea, the lens is in fact overcorrected for spherical aberration, thus compensating for the cornea (Chaudhuri et al 1983). One further trick that seems to obtain a little more resolution from the eye is the inclusion of a negative lens, which is formed from the retinal surface, into the fovea, immediately in front of the receptors. This produces a system with telephoto properties and a locally enlarged image. Snyder & Miller (1978) first described this arrangement in an eagle, in which the eye's focal length effectively increased by 50%; a similar mechanism also occurs in some jumping spider eyes (Williams & McIntyre 1980).

The transition from lens-based to cornea-based optics, which accompanies the evolution of terrestrial life, must have involved a weakening of the power of the lens as the cornea became effective, much as happens today during metamorphosis in anurans (Sivak & Warburg 1983). Greater problems arise when an animal needs to operate effectively in both media at the same time. There seem to be two solutions. One solution is to retain all the power in the lens and have a flat cornea without power in either medium. This is approximately the situation in penguins and seals (Sivak 1988). An interesting variant of this occurs in porpoises (*Phocoena*), in which the cornea retains some power by having different inner and outer radii and an internal refractive index gradient. When the porpoise focuses in air, the cornea is flattened further (Kroeger 1989). The alternative to a nearly flat cornea is to provide the lens with huge powers of accommodation. This occurs in some diving birds, in which the powerful ciliary muscle squeezes the lens into, and partly through, the rigid iris, thus deforming the front surface into a locally very high curvature. In diving mergansers, this mechanism can produce as much as 80 diopters of accommodation, compared with 3–6 diopters in nondiving ducks (Sivak et al 1985).

CONCAVE REFLECTORS Small eye-spots, in which the pigment cup is overlaid by a multilayer mirror, are found in some rotifers, platyhelminthes, and copepod crustaceans (see Ali 1984). However, none of these eyes are large enough to form usable images. In scallops (*Pecten*) and their relatives, the situation is different (Figure 1*i*). They have up to 100 respectable-sized

(1 mm) eyes around the edge of the mantle, each of which contains a "lens," a two-layered retina, and a reflecting tapetum. If one looks into the eye through the pupil, a bright inverted image is visible. Its location indicates that it could only have been formed by the concave reflector, not by the weak, low refractive index lens (Land 1965). The image visible to an observer is indeed the same one the animal sees. It falls onto the distal layer of the retina, where there are receptors that give "off"-responses. Thus, the animal sees moving objects—and shuts—as the image crosses successive receptors. These eyes represent an evolutionary line that is apparently quite unrelated to other molluskan eyes (Salvini-Plawen & Mayr 1977, Figure 8). The only other large eye that uses a mirror as an imaging device—rather than just a light-path doubler, as in the tapetum of a cat's eye—is in the deep-water ostracod crustacean *Gigantocypris*. These large (1 cm) animals have a pair of parabolic reflectors that focus light onto blob-like retinae at their foci. The resolution is probably very poor, but the light-gathering power is enormous, with a calculated F-number of 0.25 (Land 1984a).

## *Compound Eyes*

In the last 25 years, we have seen a great revival of interest in compound eyes, with the discovery of three new optical types (reflecting and parabolic superposition and afocal apposition), the reinstatement of a fourth (refracting superposition), and rediscovery and naming of a fifth (neural superposition). In fact, the only type of compound eye to have avoided recent reappraisal is the classical apposition eye of diurnal insects and crustaceans, in which the erect image in the eye as a whole is built up from the elementary contributions of all the separate ommatidia (Figure 2*b*). Even that mechanism, proposed in the 1826 "mosaic theory" of Johannes Müller, came close to eclipse in the mid-nineteenth century and had to be revived by Sigmund Exner in his great monograph on compound eye optics (Exner 1891). Exner, the undisputed father of the subject, made two major discoveries, which we discuss below: the lens cylinder and the principle of superposition imagery. As seems to be the fate of ideas about compound eye function, they also came close to abandonment in the 1960s (see Land 1981a; Nilsson 1989), but survived the challenge undamaged. For readers interested in the history of the subject, Hardie's new (1989) translation of Exner's monograph, which includes a modern appendix, is a feast.

APPOSITION EYES These are the best-known and most common compound eyes, and their relative simplicity strongly suggests that they are the ancestral type in each lineage. Each unit, or ommatidium, consists of a lens that

forms an image onto the tip of the rhabdom, a light-guiding structure of photopigment-containing membrane formed from the contributions of a small number of receptor cells. The presence of the small, inverted image behind each facet caused confusion in the nineteenth century, but its role here is only to delineate each rhabdom's field of view and increase its brightness; the image is not resolved within the rhabdom. The animal itself sees the overall erect image across the eye, which is formed by the apposed "pixels" contributed by the individual ommatidia.

Apposition eyes are found in all three arthropod subphyla; the Chelicerata, Crustacea, and Uniramia (myriapods and insects). There is, however, no universal agreement regarding the number of times they evolved. Manton & Anderson (1979) favor separate origins of the three main groups, whereas Paulus (1979) believes that the groups are monophyletic, and that the original arthropods possessed faceted eyes. Among chelicerates, the horseshoe crabs (*Limulus*) have apposition eyes, and the prevailing view is that the simple eyes of scorpions and spiders are derived from these by reorganization under single lenses. The opposite appears to have occurred in the centipede *Scutigera*, in which a compound eye has apparently reevolved from scattered single elements. In insects and crustaceans, the compound eyes take many forms. However, there are sufficient detailed similarities in the way that individual ommatidia are constructed for a common ancestry to be a distinct possibility (Paulus 1979), although Nilsson (1989) takes the opposite view. Outside the arthropods, there are two remarkable examples of independently evolved apposition eyes, one in the annelids (on the tentacles of sabellid tube worms) and one in the mantle eyes of bivalve mollusks of the family *Arcacae* (see Salvini-Plawen & Mayr 1977; Land 1981a). In both cases, the eyes' function is to detect the movements of predators. In some of the tube worms, the eyes are little more than collections of pigmented tubes with receptors at the bottom.

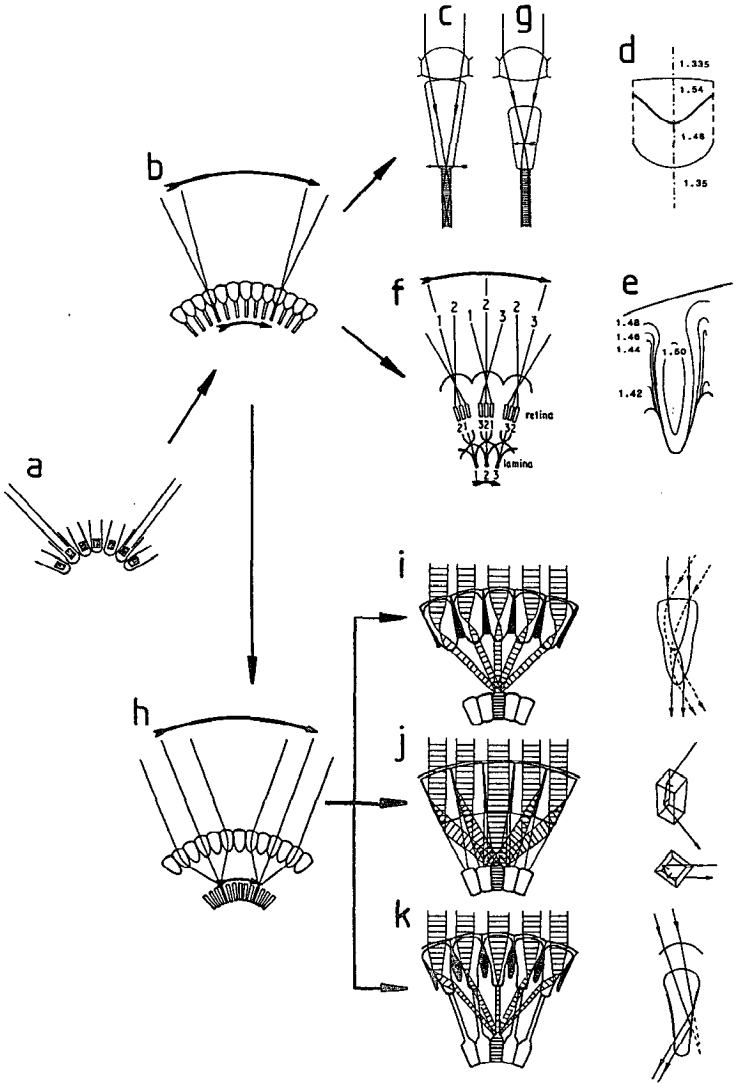


*Figure 2* The evolution of compound eyes. Arrows indicate developments, rather than specific evolutionary pathways, which are more complex. For further details and references see text. Compiled from many sources.

(*a*) Hypothetical ancestor with receptors in pigmented tubes. (*b*) Apposition eye. (*c*) Focal apposition ommatidium with image at rhabdom tip. (*d*) Multiinterface lens (*Notonecta*). (*e*) Lens-cylinder (*Limulus*); numbers in *d* and *e* are refractive indices. (*f*) Neural superposition in a dipteran fly; the numbers indicate the receptors and laminar structures that view the same directions in space. (*g*) Afocal apposition optics with intermediate image and collimated exit beam. (*h*) Superposition eye with deep-lying image. (*i*) Refracting superposition; inset shows axial and oblique ray paths. (*j*) Reflecting superposition; inset shows two views of ray paths through mirror box. (*k*) Parabolic superposition (*Macropipus*); inset shows focused beam recollimated by parabolic mirror.

This was probably how compound eyes originated in the mainstream of the Arthropoda (Figure 2*a*).

The image in each ommatidium may be produced in three different ways. In terrestrial insects, the curved cornea nearly always forms the image (Figure 2*c*). This mechanism is not available underwater; the



alternatives are the use of other lens surfaces (*Notonecta*, Schwind 1980), or a lens with a variable refractive index (*Limulus*, Exner 1891) (Figure 2*d* and *e*). Exner discovered the latter mechanism, which has affinities with the Matthiessen lens. He described it as a lens cylinder and showed that such a cylinder would form an image if the gradient of refractive index fell in an approximately parabolic fashion from the axis to the circumference. Eighty years later, interference microscopy made it possible to confirm Exner's farsighted conjecture in *Limulus* (Land 1979) and in the superposition eyes of many species (Figure 2*i*, see below).

The most serious limitation to the resolving power of apposition eyes, and of compound eyes in general, is diffraction (Mallock 1894; Barlow 1952; Snyder 1979). Image quality depends on lens diameter; the smaller the lens, the more blurred the image. The half-width of the diffraction image of a point source is given by $\lambda/D$ radians. Thus, for green light ($\lambda = 0.5$ $\mu$m) and a lens diameter $D$ of 25 $\mu$m, the diffraction image is 1.1° wide. The minimum angle that separates ommatidial axes cannot usefully be much smaller than this, which severely limits the quality of compound eye vision. By comparison, humans resolve 100 times better, as they have a single lens and a daylight pupil 2.5 mm in diameter. An improvement in the resolution of a compound eye requires an increase in both the sizes and number of the facets, which quickly results in structures of absurd dimensions. This is beautifully illustrated in Kirschfeld (1976).

NEURAL SUPERPOSITION EYES In the dipteran flies, there is a variant of the apposition eye in which the elements (rhabdomeres) that comprise the rhabdom are not fused, but separated from each other (Figure 2*f*). In these insects, each inverted image is really resolved by the seven receptive elements in the focal plane, which raises all the problems of how the many inverted images are put together to form the overall erect image. The solution to this was first proposed by Vigier (1908, translation in Braitenberg & Strausfeld 1973), and rediscovered and proved by Kirschfeld (1967). The angle between the visual directions of the rhabdomeres within an ommatidium is the same as that between the ommatidial axes themselves, so that the six eccentric rhabdomeres in one ommatidium all have fields of view that coincide with the central rhabdomeres in adjacent ommatidia. Beneath the retina, the axons of all the retinula cells that view the same direction (eight, as the central rhabdomere is double) from seven adjacent ommatidia, collect up into the same "cartridge" in the lamina, after an impressively complicated piece of neural rewiring. Therefore, there is no difference between these eyes and ordinary apposition eyes at the level of the lamina. Dipterans thereby gain a sevenfold increase in the effective size of the photon signal and do not have to sacrifice resolution

by increasing rhabdom size and, hence, acceptance angle. Thus, the flies have about an extra 15 minutes of useful vision at dawn and sunset.

AFOCAL APPOSITION Butterflies have apposition eyes, but with an unusual construction (Figure 2*g*). The cornea forms an image, just as in the eye of a bee or grasshopper. Unlike those insects, however, the image is not at the rhabdom tip, but at the front focus of a second lens contained (as a lens cylinder) in the crystalline cone. This lens, which is of very short focal length, then recollimates the light, so that it emerges into the rhabdom as a parallel beam, not a focused spot (Nilsson et al 1984, 1988). This construction is basically the same as in a two-lens astronomical telescope, with an angular magnification of about $\times 6$. It is considered "afocal" because there is no external focus, in contrast to the "focal" arrangement of an ordinary apposition eye (Figure 2*c*). As far as the resolution of the eye is concerned, the acceptance angle of each ommatidium is not determined by the angular subtense of the rhabdom tip, but by the critical angle for total internal reflection, which is set by the refractive index of the rhabdom itself. In practice, the situation is a little more complicated because the narrowness of the rhabdoms (ca. 2 $\mu$m) means that waveguide effects are important (Nilsson et al 1988; van Hateren 1989). Overall, the performance of the afocal apposition eye is marginally better than its focal equivalent (van Hateren & Nilsson 1987).

The afocal apposition eye is an important link between the apposition and superposition types, which we discuss next. It can be derived from an ordinary apposition eye by assuming that the second lens arises as a waveguide "funnel," which improves the transfer of light into the rhabdom. According to van Hateren & Nilsson (1987), such a structure can evolve into a lens without impediment. Once the second lens is present, and the system is afocal, it can further evolve into a superposition eye by an increase in the focal length of the second lens and a sinking of the retina to a more proximal position (Figure 2*h*). This type of transformation has apparently occurred several times in both the Lepidoptera and Coleoptera.

REFRACTING SUPERPOSITION EYES In the eyes of many nocturnal insects and crustaceans, the rhabdom tips are not immediately behind the facet lenses, as they are in apposition eyes, but lie much deeper, with a zone of clear material that separates them from the optics (Figure 2*i*). Exner (1891) demonstrated that in the eye of the firefly *Lampyris*, a real, erect image is formed at the level of the retina. This image is produced by the superposition of rays from many elements across the eye surface. Exner also showed that such imagery is not possible if the optical elements behave as simple lenses. However, a single image will be produced by the array if each element behaves as a two-lens telescope that inverts the light path,

but (unlike afocal apposition) has little actual magnification. A problem with this mechanism seemed to be that in *Lampyris*, and in other eyes of this type, the optical elements do not have sufficient optical power in their curved surfaces to function as telescopes. Exner's solution was again to postulate the presence of lens cylinder optics (see Apposition Eyes, above). These lens cylinders differ from those of *Limulus*, however, as they are twice the length, with a focus in the middle, not at the tip. Each half of the structure then behaves like one lens of a telescope, and overall the system becomes an afocal inverter, with a parallel output beam. Disbelief in both lens cylinders and superposition optics arose during the 1960s, and the modern reinstatement of Exner's ideas followed accurate refractive index measurements by Seitz (1969) and Hausen (1973) (see also Kunze 1979).

The feature crucial to the optical performance of all types of superposition eye is the accuracy with which the beams from each telescopic element coincide at the deep focus. In spite of an historic belief that there cannot be perfect coincidence, we now know that the superposition is so good in some diurnal moths that the eye operates at the diffraction limit for a single facet, which means that optically these eyes are as acute as equivalent apposition eyes (Land 1984b). By having a large effective pupil and large receptors, superposition eyes gain a 100-fold, or even a 1000-fold, increase in sensitivity; hence, their popularity in dim-light situations. McIntyre and colleagues have published a particularly fine series of studies, which explores all these issues, on the design of scarab beetle eyes (McIntyre & Caveney 1985; Warrant & McIntyre 1990a,b).

REFLECTING SUPERPOSITION EYES Exner (1891) was actually wrong once. He thought that the eyes of long-bodied decapod crustaceans (shrimps, crayfish, lobsters) had superposition eyes of the refracting kind discussed above. However, attempts in the 1950s and 1960s to demonstrate lenses or lens cylinders in these eyes failed. Instead, these studies, which found square, homogeneous, low refractive-index, box-like structures, caused considerable confusion because no optical function could be ascribed to such elements. Thus, shrimps were blind, for about 20 years. This serious problem was resolved by Vogt (1975), who studied crayfish, and Land (1976), who studied shrimp. They discovered that the ray-bending was not done by lenses, but by mirrors in the walls of each "box." A comparison of Figures 2*i* and 2*j* shows that both telescopes and mirrors have the ability to invert the direction of a beam of light, so both can give rise to a superposition image. In many ways, the mirror solution seems more straightforward than the complicated telescope arrangement. This, however, is only true for the rather idealized case of Figure 2*j*, which

illustrates rays in a section along a perfect row of mirrors in the center of the eye. Most rays away from the eye's plane of symmetry do not encounter a single mirror, but are reflected from two sides of the mirror "box" that makes up each optical element. There are, then, two important questions: What is the fate of these doubly reflected rays? Do all initially parallel rays reach a common focus? Here, the square arrangement of the facet array—almost unique to the decapod crustaceans—turns out to be crucial. Image formation is only possible if most rays encounter a "corner-reflector."

Consider first a simpler arrangement for producing a point image by reflection. This consists of a series of concentric "saucer rims," each angled to direct rays to a common focus; Figure 2*j* would then be any radial section through this array. The problem here is that such a stack has a single axis, and only rays nearly parallel to that axis form an image; other rays are reflected chaotically around the stack. The alternative is to replace the single reflecting strips with an array of mirror-pairs set at right angles. This substitution is possible because rays reflected from a corner go through two right angles and leave in a plane parallel to the incident rays (Figure 2*j*, inset). In other words, the rays behave almost as though they had encountered a single mirror at normal incidence, as in the saucer rim array. The beauty of the corner-reflector arrangement is that the orientation of each mirror pair is no longer important, unlike the situation in the single mirror array. Thus, the structure as a whole no longer has a single axis and can be used to make a wide-angle eye (Vogt 1977; Land 1981a). Clearly, this mirror-box design only works with right-angle corners and not hexagons, which accounts for the square facets. Various other features of these eyes are important for their function. The mirror boxes must be the right depth, about twice the width, so that most rays are reflected from two faces, but not more. Rays that pass straight through are intercepted by the unsilvered "tail" of the mirror boxes, whose refractive index decreases proximally to provide the appropriate critical angle for reflexion (Vogt 1980). Finally, there is a weak lens in the cornea of the crayfish. This lens "pre-focuses" the light that enters the mirror box, thus giving a narrower beam at the retina (Bryceson 1981). All these features provide an image comparable in quality to that produced by refracting superposition optics (Bryceson & McIntyre 1983; Nilsson 1989).

Reflecting superposition eyes, which are only found in the decapod crustaceans, presumably evolved within that group back in the Cambrian. The nearest relatives of the decapods, the euphausiids (krill), have refracting superposition eyes. The larval stages of decapod shrimps have apposition eyes with hexagonal facets, which change at metamorphosis into superposition eyes with square facets (Land 1981b; Fincham 1984; Nilsson 1983, 1989). Presumably, this transformation would have been no more

difficult in evolution than in ontogeny. Interestingly, most of the true crabs (Brachyura), normally regarded as "advanced" decapods, have retained the apposition eyes into adult life. Undoubtedly, this reflects the crabs' littoral or semiterrestrial environment, in which light levels are high compared with the benthic or pelagic environment of shrimps and lobsters.

PARABOLIC SUPERPOSITION EYES This final type of eye is the most recently discovered (Nilsson 1988) and the most difficult to understand. From an evolutionary viewpoint, it is also the most interesting because it has some characteristics of apposition eyes, as well as both other types of superposition eye (Figure 2*k*). It was first discovered in a swimming crab (*Macropipus* = *Portunus*). Each optical element consists of a corneal lens, which on its own focuses light close to the proximal tip of the crystalline cone, as in an apposition eye. Rays parallel to the axis of the cone enter a light-guiding structure that links the cone to the deep-lying rhabdom. Oblique rays, however, encounter the side of the cone, which has a reflecting coating and a parabolic profile. The effect of this mirror surface is to recollimate the partially focused rays, so that they emerge as a parallel beam that crosses the eye's clear-zone, as in other superposition eyes. This relatively straightforward mechanism is complicated because rays in the orthogonal plane (perpendicular to the page) encounter rather different optics. For these rays, the cone behaves as a cylindrical lens, thus creating a focus on the surface of the parabolic mirror. It then recollimates the rays on their reverse passage through the cone. This mechanism has more in common with refracting superposition. Thus, this eye uses lenses and mirrors in both apposition and superposition configurations and it would be the ideal ancestor of most kinds of compound eye. Sadly, the evidence is against this, as all the eyes of this kind discovered to date are from the brachyuran crabs or the anomuran hermit crabs, neither of which is an ancestral group to other crustaceans (Nilsson 1989). However, this eye does demonstrate the possibility of mixing mirrors and lenses, thus providing a viable link between the refracting and reflecting superposition types. This is important because such transitions do appear to have occurred. The shrimp *Gennadas*, for example, has a perfectly good refracting superposition eye, whereas its ancestors presumably had reflecting optics as in other shrimps (Nilsson 1990).

## *Zero-, One-, and Two-Dimensional Eyes*

A novel classification of eye types that cuts across the scheme just presented is worth a brief comment. Most eyes, of whatever type, resolve surrounding space onto a two-dimensional retinal sheet; the third dimension is added by the brain on the basis of further clues, such as binocular disparity, and

motion parallax. However, there are a few eyes in which the retina is essentially one-dimensional: a line of receptors, rather than a sheet. For a century, we have known that the eyes of heteropod sea-snails have linear retinae, three to six receptors wide and several hundred receptors long. A study of one of these, *Oxygyrus*, demonstrated that the retina works by scanning, and the eye tilts through 90° in about a second (Land 1982). In this way, the receptor row samples the surrounding water and presumably detects food particles (Figure 3*a*). A rather similar scanning system is found in the copepod *Labidocera*. Here, however, there are only ten receptors in the line, and only the males have the specialized eyes, which implies a role in mate detection (Land 1988). The principal eyes of jumping spiders (Salticidae) provide a third example. These have complex layered retinae, five to seven receptors wide by about 50 long (Land 1972; Blest 1985). They move the retinae from side to side (at right angles to the long dimension) and rotate them while examining novel stimuli (Land 1969). Interestingly, this scanning system operates in parallel with the fixed two-dimensional retinae of the antero-lateral eyes, which detect movement and act as "viewfinders" for the principal eyes. The last example is found in



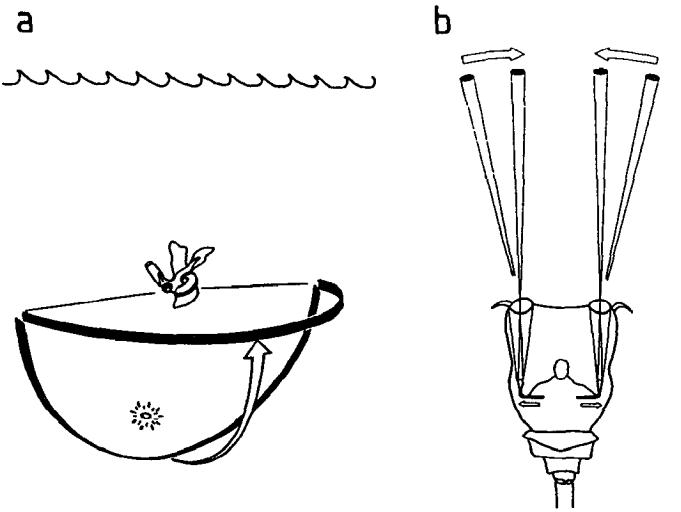



*Figure 3* Alternatives to the two-dimensional retina. (*a*) The heteropod sea-snail *Oxygyrus* has a linear retina that scans the upwelling light in the ocean. (*b*) The copepod *Copilia* has retinae that only subtend 3° and scan through a total of 14°.

the apposition compound eyes of mantis shrimps (Stomatopoda). These have conventional, two-dimensional retinae, except that each eye has a strip of six rows of enlarged ommatidia that passes through the center. The eye keeps its remarkable octochromatic color-vision system in this strip, whose field of view is less than 5° by 180° (Cronin & Marshall 1989). This arrangement means that for the animal to determine the color of the stimulus, the eye must center it on the band and scan across it, which is indeed what happens. The eyes show both targeting movements and slow, small scanning movements (Land et al 1990). Whether the rest of the eye can function during scanning is not clear; the mantis shrimps do not have the extra stationary pair of eyes available to the jumping spiders.

The only convincing example of a zero-dimensional eye is the copepod *Copilia*, whose optical system was discussed earlier (Figure 1*g*). Each eye has a field of view only about 3° wide, and within this the image is probably not further resolved. Although the eyes move back and forth through about 14° (Downing 1972), they still only scan a minute fraction of the space around the animal (Figure 3*b*), which raises the obvious question, What can *Copilia* find to look at? Moray (1972) points out that although the scanning movements are horizontal, the predominant movements of the plankton on which *Copilia* feeds are vertical. Thus, the prey itself may provide a second dimension to the scanning. Without such additional motion, it is hard to imagine that the eyes are of much value.

## *Evolutionary Fine Tuning: Sampling the Environment*

Thus far, we have only considered the broad types of eye and their macro-evolution, but not the way that each eye is adjusted to particular conditions. In general, one finds only a weak relationship between eye-type and the ecological niche of the animal; no one type is obviously more useful than the others in a given set of conditions. This is because all eye types can be built with higher or lower resolution, or absolute sensitivity, by varying the sizes of the eye itself, the optical components, the receptors, or the ganglion cell pools (see Land 1981a). The only real limitations on the uses of the different types are that compound eyes are diffraction limited to a resolution of about one degree and that superposition compound eyes are intrinsically more sensitive, size for size, than apposition ones, and so are more common in nocturnal or deep water arthropods.

One can often find a detailed correspondence between eye structure and niche in the way the image is sampled by the retina. The best-known example of such a relationship is in the distribution of ganglion cells in mammals. Animals that inhabit flat, open environments usually have "visual streaks" of high ganglion cell density that correspond approxi-

mately to the horizon (cheetah, plains kangaroo, rabbit); however, arboreal species, and those whose lateral view is generally obscured by vegetation (human, tree kangaroo, rat), typically have a radially symmetric pattern (Hughes 1977). Similar conclusions apply in birds (Meyer 1977; Martin 1985; Hayes & Brooke 1990). Many sea-birds, such as the manx shearwater and fulmar petrel, whose important visual world is the few degrees around and below the horizon, tend to have a horizontal, ribbon-like area of high ganglion cell density. Woodland birds, however, have varying arrangements of nonlinear areas that contain one or often two foveas. In reef fish, the same patterns occur. Collin & Pettigrew (1988a,b) found that fish that swam over sandy bottoms or below the open surface tend to have elongated horizontal high density areas, but those that live in holes and cracks in the reef itself had more circular areas (Figure 4*a* and *b*). One particularly interesting case is the surface-feeding fish *Aplocheilus*, which has two horizontal streaks separated by about 40°. One views the surface from below; the other, which views the surface from above, looks out of the water just above the edge of Snell's window (Munk 1970).

Interestingly, the visual system's priorities and interests in vertebrates show up at the level of the ganglion cells—the third-order neurons at the point where information must be compressed before transmission to the brain. There are differences in the densities of the receptors, the ultimate sampling stations, but they are much less striking than those seen in the ganglion cell layer. By contrast, in arthropods with compound eyes, variations in sampling related to the structure of the environment are found in the layout of the most peripheral structures, the ommatidia (Land 1989). Presumably, this difference arises because the information bottleneck in compound eyes is at the periphery, as the relatively low optical resolution is provided by the diffraction limited lenses. In any event, the equivalents of visual streaks and acute zones of various kinds appear when one maps the directions of the ommatidial axes onto a sphere around the animal (Figure 4*c* and *d*). Some common patterns include a region of enhanced vertical resolution around the horizon in many flying insects and in crabs that inhabit flat sandy or muddy shores (Zeil et al 1986); forward-pointing acute zones related to the velocity flow field in forward flight (Land & Eckert 1985; Land 1989); and special regions of high acuity, which usually point forwards and upwards, that are concerned either with sexual pursuit, in which case they are confined to males (Collett & Land 1975; van Praagh et al 1980), or with the capture of other insect prey on the wing, as in the eyes of dragonflies (Sherk 1978) (Figure 4*d*). There is even a remarkable analogue of the two horizontal streaks of *Aplocheilus*,

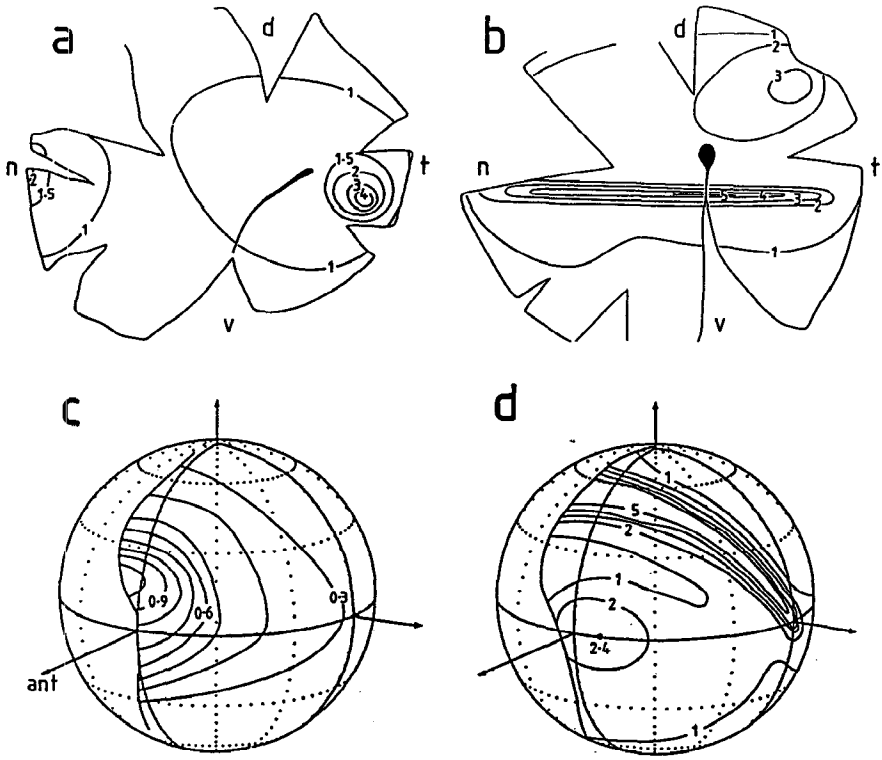



*Figure 4* Adjustments of retina to habitat in fish (*a* and *b*) and insects (*c* and *d*). (d = dorsal, v = ventral, n = nasal, t = temporal.)

(*a*) Ganglion cell density map of the left retina of the reef rish *Cephalopholis miniatus*, which lives in cavities in the coral and has a forward-pointing acute zone. (*b*) A similar map for *Lethrinus chrysostomas*, which lives in open water and has a "visual streak" that images the underwater horizon. Numbers are thousands of ganglion cells per $mm^2$. Modified from Collin & Pettigrew (1988a,b). (*c*) Map of visual field of the left eye of a male blow-fly *Calliphora erythrocephala*, which shows an acute zone pointing forward and slightly dorsal. (*d*) Similar map for the dragonfly *Anax junius*, which has a streak of elevated resolution crossing the dorsal quadrant. Figures show the numbers of ommatidial axes per square degree of field. ant; anterior direction. (From Land 1989.)

in the eye of the surface-feeding backswimmer, *Notonecta* (Schwind 1980). In many instances, the provision of an acute zone in a compound eye necessitates an improvement in the diffraction limit, which can only be achieved by locally increasing the sizes of the facet lenses. In dipteran flies and dragonflies, this leads to the paradoxical situation in which the region of highest acuity appears superficially to have the coarsest mosaic.

## CONCLUSIONS

1. At the molecular level, vision has an ancestry that predates the appearance of recognizable eyes. Thus, all metazoan opsins are sufficiently similar at the amino acid level to be regarded as having a single ancient origin. They may have originated from an earlier family of transmembrane proteins. In contrast, the many proteins responsible for refraction in vertebrate lenses are neither related to one another, nor have a single origin. Two, which appear in all vertebrates, are relatives of different stress response proteins of ancient origin, whereas most others double as enzymes. Various amounts of these different proteins are used to make lenses following rules that have thus far eluded discovery.

2. The number of anatomically and physiologically distinct receptor types seems to be small and may represent ancient lineages. As a general rule, the microvillous receptors of Protostomes depolarize by an increase in $Na^+$ conductance, whereas vertebrate ciliary receptors hyperpolarize to light by a $Na^+$ conductance decrease. A further class of multiciliate receptors also hyperpolarizes, but via an increase in $K^+$ conductance.

3. Eyes with well-developed optical systems evolved many times at the end of the Cambrian period. There are now about ten optically distinct mechanisms. These include pinholes, lenses of both multi-element and inhomogeneous construction, aspheric surfaces, concave mirrors, apposition compound eyes that employ a variety of lens types, and three kinds of superposition eye that utilize lenses, mirrors, or both.

4. Because the number of physical solutions to the problem of forming an image is finite, convergent evolution has been very common. The best example is the inhomogeneous Matthiessen lens, which has evolved independently in the vertebrates, several times in the mollusks and annelids, and once in the crustaceans. Similar cases of convergence can be found among compound eyes.

5. Not all eyes employ two-dimensional retinae to receive the image. In one crustacean (*Copilia*), the surroundings are scanned with a pair of receptors that have point-like fields. A number of mollusks and crustaceans have one-dimensional strip-like retinae, which scan at right angles to their long dimension.

6. Both simple and compound eyes may show very specific adaptations to environment and way of life. In vertebrates, these are usually manifest as variations in ganglion cell density across the retina. However, in the compound eyes of insects, in which the optics are limiting, these variations are seen in the size and disposition of the ommatidia.

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