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(Ernst-Mayr-Lecture am 9. November 1999)

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The origins of eyes

By the time of the Cambrian, when many of the present animal phyla rapidly attained the forms we recognise today, eyes of one sort or another were already present. These were not the impressive single-chambered eyes found today in vertebrates and cephalopod molluscs, nor were they the equally sophisticated compound eyes of modern insects and crustaceans. They would have been simple eye-cups capable of supplying small grazing invertebrates with just enough information to find the right light environment: light for animals that lived on plants, and dark for those preferring the detritus of the sea floor. Not much is needed for that. A few photopigment-containing receptors in a cup of dark shielding pigment would permit light detection with a modest degree of directional sensitivity. There are many such eyes with us still in the flatworms (Platyhelminthes), the annelid worms, the gastropod molluscs, chordates such as *Amphioxus*, and many of the smaller invertebrate phyla. During the Cambrian radiation explosion, which may have lasted for as little as 25 million years, some animal groups became carnivorous (Conway-Morris 1998). This meant that they needed much better eyesight to see and capture their prey; equally their prey needed better eyesight to detect predators and to avoid capture. A visual 'arms race' began, in which some – but not all – of the pre-existing eye types improved out of all recognition. This will be the subject of the second part of this review. First, however, I will discuss the pre-Cambrian origins of eyes, and concentrate on a question which was of great interest to Ernst Mayr: did eyes evolve only once, or many times?

In 1977 Salvini-Plawen and Mayr published a paper in which they reviewed the evidence relating to the origins of the various types of eye present in our current fauna. In their introduction they point out that part of their motivation was to see whether Darwin had been right in worrying quite as much as he did about eye

evolution. Both in the *Origin* (Darwin 1859) and later in a letter to Asa Gray ("the eye to this day gives me a cold shudder"), Darwin had admitted that he could not see clearly how an organ of such complexity and perfection as the human eye had arisen by the operation of natural selection on minor variations. He accepted that this was a failure of his imagination rather than the process itself, but he was openly nervous on this issue. A particular problem for Darwin was that the vertebrate eye lacked antecedents. Lampreys – the existing relatives of Ordovician agnathan fishes of 450 million years ago – have eyes that are so like our own that they give away nothing about the early evolution of the vertebrate eye, and we still know next to nothing about where our eyes came from. However, thanks largely to the anatomical studies of Richard Hesse (1900, 1904) we do have a quite clear idea of the way that single chambered eyes, similar to those of fishes, evolved in the molluscs. Fig. 1, from Salvini-Plawen & Mayr (1977), shows a series of eyes of modern gastropod molluscs. It starts with the very simple pigmented pit eye of a limpet (*Patella*), and ends with an eye with a fully developed lens. The series could easily be extended to encompass the much larger eyes of cephalopod molluscs such as *Octopus*, with a mobile iris and muscles to move the eye. If such a series had been available to Darwin, I doubt that his concerns would have been anything like so burdensome. Of course, there is no guarantee that a series derived from eyes of modern animals is actually the way that eye evolution proceeded half a billion years ago, but it demonstrates that there need be no missing links in the process, and that had been Darwin's underlying worry.

The results of Salvini-Plawen & Mayr's survey were remarkable. They concluded that eyes had evolved not once, but many times. "Adopting the most rigorous criteria of homology, at least 40 different lines of photoreceptor differentiation must be postulated". Their evidence came largely from key differences in anatomy at the gross and the cellular level. Some eyes are convex and compound, others are concave and single chambered; in some the eye is formed from epidermis, in others from neural tissue; in some the receptor axons emerge from the back of the eyecup (eversion), in others from the front (inversion); some eyes have achieved an extended photo-pigment-bearing membrane area in their receptors by means of microvilli, in others the membrane is formed from the elaborated folds of a cilium. (The electron microscope studies of Richard Eakin (1972) and his co-workers were crucial here). Since Salvini-Plawen and Mayr's paper other criteria for separating different lines of eye evolution have become available: the ionic mechanisms, membrane channels and biochemical transduction cascades are also of different types, in ways that are related to some of the anatomical differences. Once the various early eye lineages had adopted one or other combination of the characters just listed, they stuck to them. It is very rare to find instances where it seems that microvillous receptors have evolved into ciliary receptors, or compound eyes

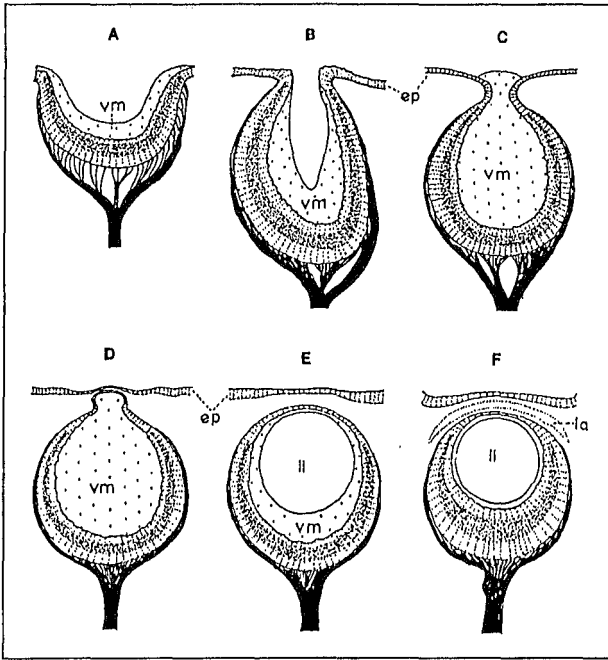


Figure 1

Sequence of development of lens eyes in prosobranch gastropod molluscs, based on living species. From Salvini-Plawen & Mayr (1977). A, pit eye of *Patella*; B, eye cup of *Pleurotomaria*; C, pinhole eye of *Haliotis*; D, closed cup of *Turbo*; E, Lens eye of *Murex*; F, lens eye of *Nucella*. (ep, epidermis or cornea; la, lacuna; li, lens; vm, vitreous mass.)

have turned into single chambered eyes (although this may have happened in the chelicerates: *Limulus* has compound eyes, but spider eyes are single-chambered). In general it seems that the characters chosen by Salvini-Plawen and Mayr are 'conservative' and unlikely to change, once established. This is the basis for thinking that each of the modern eye types had a separate origin. Had there been a single initial prototype eye that worked, one would not have expected to see such variation in its progeny. Thus separate origins seem more likely.

Recently this multiple origin view of early eye evolution has been challenged by evidence from molecular genetics (Gehring & Ikeo 1999). Gehring and his colleagues found that a gene that organises eye development in vertebrates (*Pax-6*) is very similar to a gene (*eyeless*) that serves a similar function in the fly *Drosophila* (Quiring et al. 1994). In a spectacular experiment (Halder et al. 1995) they showed

that the *Pax-6* gene from a mouse could, with suitable encouragement, induce the formation of ectopic eyes (i. e. eyes in unusual locations such as legs) in developing *Drosophila* embryos (the eyes formed were fly eyes not mouse eyes; the *Pax-6* gene initiates the process but does not define the structure). The conclusion drawn was that this gene had been associated with eye formation from a period that preceded the split up of the early eye lines in their remote past. This meant, it was claimed, that eyes had a common origin, from a prototype that involved a common agent (*Pax-6*) which organized photopigment, neurons and screening pigment into a proto-eye.

However, quite aside from the logic of the Salvini-Plawen and Mayr evidence, the *Pax-6* scheme has problems. There are animals which have no eyes, but do have *Pax-6* or its homologues (cnidarian corals, Catmull et al. 1998; the nematode *Coenorhabditis elegans*, Zhang & Emmons 1995). Further, *Pax-6* does not just organize eyes. In vertebrates it takes part in the organization of the neural tube and the olfactory epithelium. In the blind nematode *C. elegans* it is involved in patterning the head region, and in the development in a sense organ in the tail. Thus the nature of the association between *Pax-6* and eyes is far from clear. It is undoubtedly an ancient gene, and its role seems to be as a master organizer, initiating developmental processes that then proceed by their own logic. One view is that it had a role in organising the nervous system and especially the head region of early metazoan animals, and that this role extended to any sense organ that needed its services (Nilsson 1996). On the basis of present evidence, it seems likely that eyes did indeed have multiple origins in the Precambrian, and that organizers such as *Pax-6* were co-opted as required, as indeed were the other components needed to make an eye.

The Cambrian and After

Of the 40 or more Precambrian lines of eye differentiation listed in Table 1 of Salvini-Plawen and Mayr's paper, only about quarter gave rise to the much larger eyes capable of resolving an image (Land 1981). Most remained as small (<100 μm) pigmented pits. With a few interesting exceptions, 'good' eyes are found in only three phyla – the molluscs, arthropods and chordates. These eyes are illustrated in Fig. 2. They include the lens eyes of cephalopod molluscs and fish (c), the latter giving rise to the eyes of land vertebrates in which the cornea becomes the main refractive structure (d). This is a design we share with spiders, but few other animals. Other single-chambered eyes are the 'pinhole' eye of the ancient cephalopod *Nautilus* (a), and the mirror eye of the scallop *Pecten* (g). Amongst compound eyes the apposition eyes of diurnal insects and crustaceans are the most

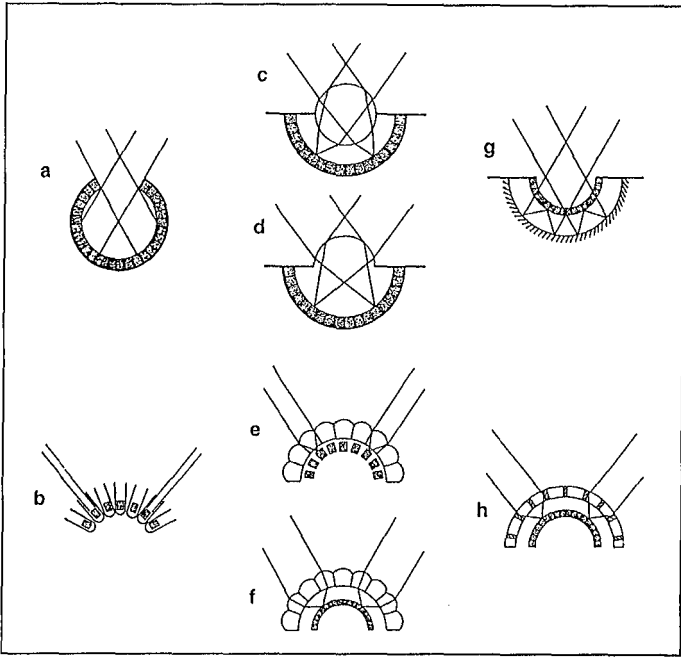


Figure 2

Principal types of optical system in modern eyes. a, pigment pit eye of *Planaria*, leading to pinhole eyes of *Haliotis* and *Nautilus*; b, proto-compound eye, similar to those of tube-worms such as *Sabella*; c, spherical lens eye of fish or *Octopus*; d, corneal eye of spiders and land vertebrates; e, apposition compound eye of diurnal insects and crustaceans; f, refracting superposition eye of beetles, moths and euphausiid crustaceans; g, spherical mirror eye of *Pecten*; h, reflecting superposition compound eye of decapod shrimps, lobsters and crayfish.

common type (e), in which each receptor cluster images a small angle in outside space through its own lens. These are undoubtedly ancestral to other varieties of compound eye. Two variants arose to provide a brighter image for use at night, or in the deep ocean. These are the superposition eyes, which use either lenses (f: moths, beetles, krill), or mirrors (h: decapod shrimps and lobsters). In superposition eyes many optical elements contribute to the image at any one point, and so the pupil is bigger and the image up to 100 times brighter than in the apposition type of eye. In one sense the distinction between an image-forming eye, and one capable only of supplying information about the general direction of light, is an arbitrary one. As optics get better, and receptor numbers increase to match this improvement, the feature that changes crucially is the acceptance angle of each receptor: that is,

the angular width of the cone of light that each receives from the surroundings (see Fig. 5b). In the pigment pit type of eye, illustrated in Fig. 1 and Fig. 2a this can be anything up to 90° . Within this angle nothing can be resolved, so there can be no chance of performing tasks such as finding prey, detecting a predator, avoiding obstacles during locomotion or recognising landmarks. Quite how narrow receptor acceptance angles have to be for these 'post-Cambrian' tasks to become possible is a matter of debate, but 5° seems to be a likely figure. This is approximately the acceptance angle in the eye of the tiny fruit fly *Drosophila* although many larger insects have acceptance angles closer to 1° . For the human eye the acceptance angle of a foveal cone is about 1 arc minute – 60 times better than a typical insect. With a 5° acceptance angle a 1 cm object can be detected at a distance of 11 cm, which is far enough to avoid collision for a slow flying insect. For a larger acceptance angle this would probably not be the case. Thus although acceptance angle is a continuously variable quantity, many tasks require that it should not exceed a particular value, and so a qualitative division in what different eyes can 'deliver' emerges from the continuum.

During the Cambrian explosion, optical systems capable of providing better image resolution were invented and perfected. Many of the interesting questions about this period and its aftermath concern one of the classical problems of evolutionary biology: are similar structures related by common descent (homology), or have they evolved in parallel from independent origins in response to similar needs (analogy)? Given that there is only a small number of workable optical systems that an eye can use (Fig. 2), it is almost inevitable that the same solution should have evolved more than once. In the sections that follow I shall explore three themes that all have a bearing on these problems.

First, I examine the parallel evolution of the kind of spherical lens that is found in the eyes of fish and cephalopods – perhaps the most successful 'invention' in the history of animal optics. It turns out that there is only one 'good' way to make such a lens, and that this has evolved at least four times, and probably many more. It is an impressive example of analogy, the parallel evolution of a uniquely competent structure. Second, I explore something of an evolutionary disaster, the compound eye. The multilens construction of compound eyes has prevented them from achieving a resolution better than about 1/100th that attainable by single chambered eyes such as ours, and yet arthropods have, in general, stuck with this flawed design. Why? Finally I look at two quite unexpected alternatives to the mainstream of eye evolution. Two remarkable 'one-off' optical arrangements that use mirrors rather than lenses to produce successful image-forming eye designs. I'm not sure what the moral is here, except that there is often no single 'best' solution, and evolution seems to find a way of exploring a range of possible alternatives. And they are both eyes in which I have taken a personal interest.

The Matthiessen lens

The route to a lens eye, shown in Fig. 1, finishes with a lens made of some refractile substance that has narrowed down the acceptance angle of receptors on the retina. But has it provided a well resolved image? If the lens is made of an optically homogeneous material the answer is certainly no. A homogeneous sphere produces a very poor image (Fig. 3), because the outer rays of a parallel ray bundle are over-focussed, and cross in front of the focus for central rays, resulting in a very blurred image. This lens defect is known as spherical aberration. Many great nineteenth century minds addressed this problem, including Thomas Young and James Clerk Maxwell, the latter allegedly "while contemplating his breakfast herring" (Pumphrey 1961). However, it was Matthiessen in the 1880s who provided the biological evidence that animals had solved this problem. He showed that the lenses of fish were not homogeneous, but had a gradient of refractive index. The index was highest in the centre and fell approximately parabolically to the periphery. He showed that such a gradient resulted in the bulk of refraction occurring within the lens, rather than at its interfaces. This had two useful consequences. First, it reduced spherical aberration, because the outer zones of the lens had relatively less ray-bending power than in a conventional, homogeneous, lens. And secondly it produced a more powerful lens, with the focal length coming down from about 4 lens radii (for a homogeneous lens with a refractive index of 1.52) to 2.5 radii (for an inhomogeneous lens with a *central* refractive index of 1.52). This ratio (focal length / lens radius = 2.5) had become known as Matthiessen's Ratio, and it is diagnostic for an inhomogeneous lens in which spherical aberration has been corrected. Because of this, it is easy to discover whether different evolutionary lines of lens-based eyes have 'discovered' this solution: if Matthiessen's ratio is about 2.5 then they have, if it is closer to 4 then they have not. Remarkably, independently evolved spherical lens eyes from 4 phyla all have Matthiessen's ratios of 2.5. It seems that, once an eye has headed down this evolutionary path, the pressure is very strong to get it right. There is no acceptable half-way alternative. The exact form of the gradient needed to make a lens free from spherical aberration was not worked out until the 1940's. It is not quite parabolic, as Matthiessen had believed, but rather more complicated. There is still no universal agreement, but the various solutions are reviewed by Jagger (1992). A particularly interesting, and complicating, question is the extent to which chromatic aberration is dealt with. Although there is no formal way of correcting this problem using watery, biological materials (there is no equivalent of flint glass and crown glass with different dispersions, as used in an achromatic doublet) it seems that fish lenses have gone some way to dealing with the problem by engineering several different focal lengths into their lenses (Kröger et al. 1999). In this way the (near) focus

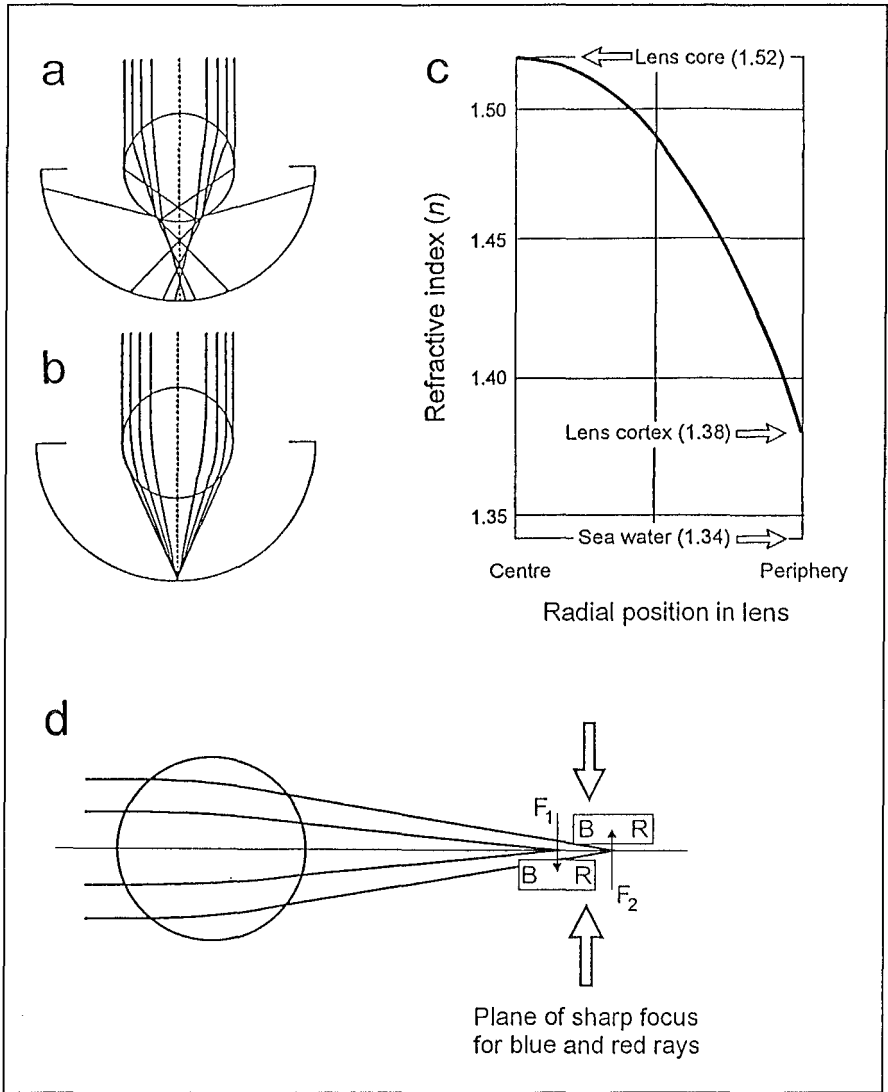


Figure 3

Optics of the lenses of fish eyes. a, spherical aberration of a lens with a homogeneous refractive index: the image is of unusably poor quality; b, a lens with an appropriate refractive index gradient has no spherical aberration (a & b based on Pumphrey 1961); c, form of the gradient needed to achieve the condition in b (based on Jagger 1992); d, mechanism proposed by Kröger et al. (1999) for minimising the effects of chromatic aberration. Separate images are formed at F_1 and F_2 , and their chromatic spread allows the red image of F_1 to coincide with the blue image of F_2 .

for blue light from a relatively long focal length region of the lens can be made to coincide with a (far) focus for red light from a shorter focal length lens region (Fig. 3d). The effect is that the retina, with its cones of several different chromatic sensitivities, can receive a reasonably well-focused image in a single plane. However, this does mean that the refractive index gradient of the lens must depart from the 'ideal' solutions proposed for spherical aberration correction. The gradient needed to produce a multi-focal-length lens is going to be a novel and challenging problem in optical physics. Incidentally, Darwin (1859) initially believed that the human eye was corrected for chromatic as well as spherical aberration, but Helmholtz later assured him that it was not. The new work on fish suggests that although Helmholtz was technically correct, natural selection has found an ingenious way round the problem.

How many animal taxa have found the solution to the problem of producing a lens free from spherical aberration? (The chromatic aberration version just discussed is perhaps a vertebrate refinement which we will ignore for now). Clearly the vertebrates achieved this early in their evolution. Cephalopod lenses (octopus, squid and cuttlefish) also conform to Matthiessen's ratio (Sivak 1982), so they

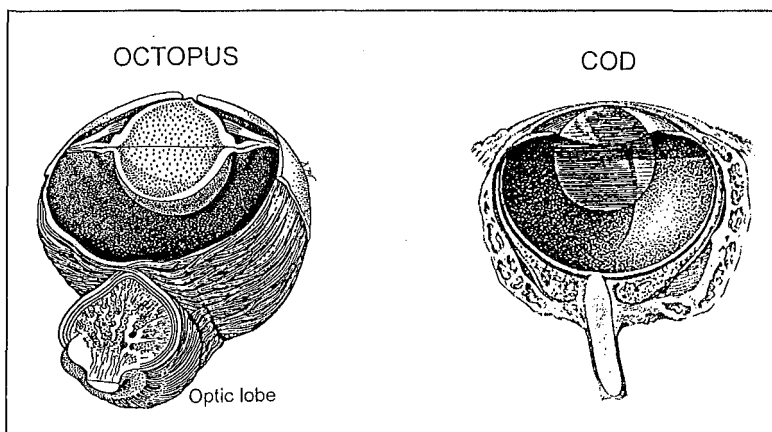


Figure 4

The eyes of fish and cephalopod molluscs are probably the most famous example of convergent evolution. (*Octopus* from J. Z. Young, 1964, *A Model of the Brain*, Oxford UP; cod from D. W. Soemmerring, 1818, *De Oculorum Homini Animaliumque*, Göttingen: Vandenhoeck & Ruprecht). In spite of their superficial similarity there are numerous differences in detail. *Octopus* receptors are microvillous but fish receptors use discs attached to a cilium; the *Octopus* retina is everse but the fish retina inverse; in *Octopus* the initial processing of the image occurs outside the eye in the optic lobe but in fish it occurs in the retina itself.

too have hit on this solution (Fig. 4). Other molluscs, including both pulmonates (*Lymnea*) and prosobranchs (the conch *Strombus* and heteropods such as *Pterotrachea* and *Oxygurus*) have similar lenses. It is hard to know whether all the mollusc eyes with good lenses inherited them from an early proto-gastropod stock that had discovered the trick, or whether this kind of lens evolved several times in the gastropods, and again (once or several times) in the cephalopods. Matthiessen's ratio lenses occur in two other phyla, both as remarkable 'one-offs'. In the annelid worms the Alciopidae became, uniquely for that phylum, visual predators of upper ocean waters. They evolved eyes with excellent optics and fine-grain retinas, and it will come as no surprise to learn that the lenses are have Matthiessen optics. Perhaps more surprisingly, in a phylum where compound eyes are the norm, one single crustacean group, copepods of the genus *Labidocera*, has also come up an eye with a spherical lens. Like the others, it has a focal length consistent with Matthiessen's ratio, and excellent imaging powers (Land 1984). It does seem that, once an eye of the single chambered type is launched upon an evolutionary career that requires good resolution, the route to the only correct solution to the problem is inevitable. There are no eyes that still try to produce images with the wrong (homogeneous) kind of lens.

How easy is it to get from the Precambrian type of pigment cup eye (Fig. 2a) to one that produces a good image? One might guess that this would have been a difficult and slow process that took hundreds of millions of years to get right. In an audacious study, Nilsson and Pelger (1994) tried to estimate how long this might have taken. First they showed that there were no major obstacles on the way (this had worried Darwin). By making small cumulative changes in such parameters as eye geometry and refractive index gradient, and making modest assumptions about selective advantage and heritability, Nilsson and Pelger estimated that it would take less than half a million generations to produce an effective, well-resolving eye from a simple photosensitive epithelium. For a small animal one generation takes about a year. So, half a million years will make an eye, if there are no other factors (evolving an appropriate brain could be a problem!) to be considered. One of the useful implications of this study is that it makes the Cambrian explosion – and the plethora of eye types that it spawned – less of a problem. Things can happen fast, when the pressure is on.

Remarkably, the ancient cephalopod *Nautilus* failed to make a lens. It retains a pinhole eye, even though it has had half a billion years to improve on this design. The problem is that *Nautilus* has a big eye, similar in size to *Octopus*, with perhaps a million receptors. The eye has a variable iris and extra-ocular muscles to stabilise it against the animal's rocking style of swimming. These are all features of an advanced eye, and yet it has no lens. If it stops the pinhole down to gain resolution it loses light, and if it opens it to gain light it loses resolution to a disastrous extent.

The problem, from an evolutionary point of view is that almost any blob of jelly, placed in the region behind the pupil, would improve both image quality and light gathering power. So many molluscs have achieved this in part or in full, with a Matthiessen lens often the result. Why did this not happen in *Nautilus*? I still find this a bigger mystery than the origin of really good eyes, which so concerned Darwin.

Compound eyes: a successful blind alley.

In the most straightforward type of compound eye, the apposition eye found in bees, grasshoppers, crabs and most diurnal arthropods, each group of receptors has its own lens, and the unit comprising optics, receptors and associated pigment cells is known as an ommatidium (Fig. 5a). Although the lens in each ommatidium produces a small inverted image, that image is not resolved by the photoreceptors. They all contribute photoreceptor membrane to a single central rod, the rhabdom, which behaves as a light-guide, and integrates all light reaching its distal end (Fig. 5b). The receptors in each ommatidial group – typically 8 or 9 – respond differently to wavelength and polarization, but they share the same field of view, which is typically about 1° . The situation in dipteran flies is intriguingly different (Kirschfeld 1967), where there is some resolution within each image, but I will not pursue this here. In an apposition eye each ommatidium contributes one ‘pixel’ to the overall erect ‘image’ – which is now neural in nature rather than optical.

In many ways this must have seemed an excellent arrangement for a Cambrian animal. The eye’s optics could be built out of the chitinous constituents of the head armour. The brain could be put inside the eye, saving the space that a large single-chambered eye would squander. But there was a flaw, which would not have made its presence felt during the early evolution of such eyes: they would become impossibly large when resolution greater than about 1° was called for.

The problem is diffraction. The gross features of the images in eyes or optical instruments can be determined by geometrical optics, i.e. by calculating the trajectories of rays through the system. However, to work out what happens to the finest detail in an image it is necessary to use wave optics, because ultimately the image is a diffraction pattern caused by the interference of light from all regions of the lens (or other image-forming structure). A consequence of diffraction is that the image of a point source of light is not a point, as it would be in geometrical optics, but a small circle of blur, known as the Airy disc, after its discoverer. The width of this disc varies *inversely* with the diameter of the lens (D , Fig. 5b). At half maximum intensity the width, in angular terms is given by $\theta = \lambda/D$ radians, where λ is the wavelength of light ($\sim 0.5 \mu\text{m}$). It is this inverse relationship that

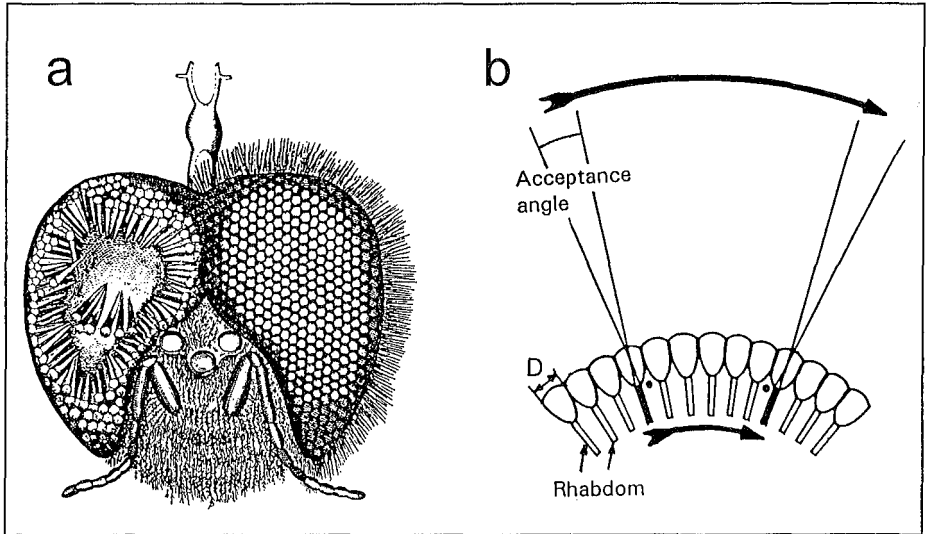


Figure 5

Apposition eyes of insects. a, partly dissected eye of a drone bee, showing the ommatidial units (from J. Swammerdam 1737, *Biblia Naturae*). b, Image formation in apposition eyes. Each lens forms a small inverted image at the distal tip of each rhabdom (dots), but there is no resolution within each rhabdom, and the overall image (arrow) is erect. The resolution of the eye depends on the acceptance angle of each rhabdom, and in the diffraction-limited condition that decreases as the diameter (D) of each facet lens increases.

makes it necessary to employ very large lenses or mirrors in telescopes that resolve distant stars. Equally, it ensures that very small lenses, such as those found in apposition compound eyes, have very poor resolving power. Applying the above formula to the ommatidia of a bee eye, where the lenses have a diameter of $25\ \mu\text{m}$, gives a blur circle of width 0.02 radians, or 1.15° . To get an idea of this extend your arm and look at the thumb nail: this is about the size of the minimum resolvable angle of a bee's eye. By contrast, the human pupil in daylight has a diameter of about $2.5\ \text{mm}$, a hundred times the diameter of a bee lens. And in practice this means that our resolution is a hundred times better with a blur circle smaller than 1 arc minute.

Supposing an insect with a compound eye needed to improve its resolution, by reducing its minimum resolvable angle from (say) 1° to 0.5° . The diffraction formula states that the diameter of each lens will need to be doubled, which on its own will double the size of the eye. But to exploit the improved optical resolu-

tion, there also needs to be an increase in the number of lenses, again by a factor of 2 along any lens row, and this again will require a doubling in the size of the eye. Thus a doubling of the resolution of a compound eye requires an increase in eye diameter by a factor of 4. In a single-chambered eye, with only one lens shared by all receptors, the required increase in size would only be a factor of 2. The consequences of this squared relationship between resolution and eye size were first pointed out by Mallock in 1894. He calculated the diameter of a compound eye with the same (1 arc minute) resolution as our eyes. It is a simple calculation to show that this comes to 12 metres – the size of a large house! In 1976 Kirschfeld pointed out that this is a little unfair, because the effective resolution of the human eye falls off rapidly away from the fovea. Taking into account this reduced peripheral resolution Kirschfeld came up with a minimal design about 1 m in diameter (Fig. 6). This is not quite as absurd as the Mallock eye, but unwieldy all the same, and certainly hard to fly with.

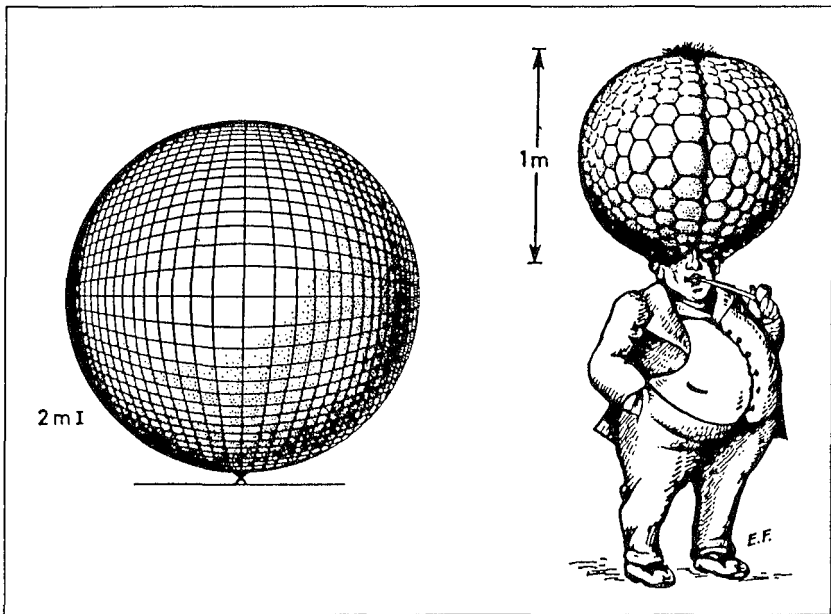


Figure 6

Compound eyes with the same resolution as the human eye. Left, an eye with 1 arc-minute resolution everywhere, based on the calculation of Mallock (1894). Right, an eye with 1 arc-minute resolution in the fovea only, and the peripheral resolution decreasing as in the human eye. Each 'facet' represents 10^4 actual facets. From Kirschfeld (1976).

Insects often do manage to squeeze in a small region of higher resolution into their eyes. In many insects the male often has such an 'acute zone' in the part of the eye that points upwards and forwards, and this is used in the pursuit of females on the wing (see Land 1989). In insects that prey upon other insects (robber flies, dragonflies) the acute zone is found in both sexes. The increased resolution has to be paid for, however, by enlarging the eye or reducing resolution elsewhere. As a consequence, no insect has resolution better than about 0.25° , which is awful by the standards of vertebrate eyes. Nilsson (1989) puts it very well: "It is only a small exaggeration to say that evolution seems to be fighting a desperate battle to improve a basically disastrous design".

Why have insects and crustaceans retained this design, when adopting a simple eye would not have handicapped them in this way? It is not easy to find an answer. One cannot argue that single-chambered eyes were not available to insects, because many possess them as larvae, and also as the dorsal ocelli of adults. Some of the larval single-chambered eyes are remarkably good. The largest ocelli of tiger beetle larvae (*Cicindelidae*) have about 6,300 receptors each (Friederichs 1931), and an inter-receptor angle of about 1.8° , which is quite comparable with the inter-ommatidial angle of the adult compound eyes. Thus insects *can* make single-chambered eyes when they try. Perhaps, having evolved a brain with a layout appropriate for an erect image, a change to an inverted-image geometry would have involved a dysfunctional intermediate. This is perhaps the answer, but it is not wholly convincing. In the Chelicerata it seems that just this happened. The ancient chelicerates (*Limulus* and the extinct eurypterids) had compound eyes, but present-day scorpions and spiders have single-chambered eyes. There are even one or two scattered examples where this has happened in both insects and crustaceans (e.g. the amphipod *Ampelisca*; Nilsson 1989). But it did not happen in the mainstream of either the insects or the higher Crustacea, and this remains a substantial evolutionary enigma.

Mirror alternatives to lens optics.

In optical technology images can be formed by mirrors; so too in eyes. Unexpectedly, and fairly recently, two very different optical systems have been discovered that use mirrors to produce the images that the animals see. The first was the concave mirror optical system of the single-chambered eyes of scallops (*Pecten*) (Fig. 2g), and the other was the radial mirror system in the compound eyes of shrimps, lobsters, crayfish and other long-bodied decapod crustaceans (*Macrura*) (Fig. 2h).

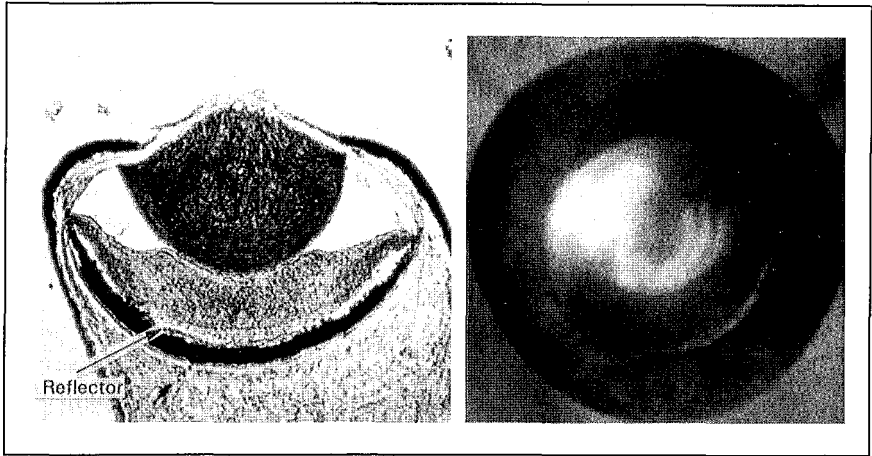


Figure 7

Eye of the scallop *Pecten maximus*. Left: frozen section of an eye showing the lens, the thick retina, and the spherical reflecting surface. The eye has a diameter of 1 mm. Right: the author's hand, photographed in the eye of a scallop.

Scallop eyes

The anatomy of the 100 or so eyes that look out between the tentacles of the mantle of a scallop was well described a hundred years ago, but it had been accepted that this was a lens eye, somewhere in the spectrum of those depicted in Fig. 1. A chance observation led me to question this (Land 1965). When I looked through a dissecting microscope into an eye of a scallop, I saw an inverted image of myself, looking down the microscope (Fig. 7, right). This is perhaps not so surprising, because eyes usually contain images, and these can be seen in eyes like ours with a suitable ophthalmoscope. The strange thing about the scallop image was that it was *in* the eye. Although the image in our eye is in the plane of the retina, to see it we have to view it through the lens, and this re-images it back close to infinity where it originated. Thus to see the image we would need a telescope focussed at infinity, rather than a microscope focussed on the eye. In other words, the image that I saw could not have been produced by the lens.

The other thing I noticed about the image was that it was very bright; it did indeed look like an image from a mirror. After a little while the solution became obvious. The mirror layer (argentea) at the back of the eye was actually forming the image. Some experiments showed that the so-called lens was very weak, and contributed very little to the formation of the image. (This is in contrast to a cat's eye where

there is also a mirror behind the retina, but its job is simply to recycle unabsorbed light back through the retina; it is the lens that forms the image). There are two layers of receptors in the scallop retina. One, the distal retina, is right behind the lens in the plane of the image. The other, the proximal retina, is almost touching the mirror, where there is no image. The two kinds of receptors are different morphologically: the distal cells have many cilia in their photoreceptive region, but the proximal cells have microvilli, which is typical for molluscs. As early as 1938 H. K. Hartline had recorded from the nerves from both retinæ, and found that whereas the proximal retina produced conventional 'on' responses, the distal retina responded only to the light going off.

I concluded that scallops see movement with their distal retina. A dark object will sequentially darken distal receptors as its image moves over them, and they will respond; for a light object the trailing edge will have the same effect. The impulses travel to the main ganglion which innervates the adductor muscle, and the animal closes its shells. The optical system provides the animal with an early warning device with which it can see animals coming at some distance. It gives the scallop an advantage over many other clams which simply have a shadow reflex; this only works when the predator is effectively on top of them, so the scallop's optical system buys time. The role of the proximal ('on') retina is less clear. In the absence of a resolved image it could function as a weakly directional light receptor, responsible for finding the appropriate light environment. Studies by Buddenbrock and Moller-Racke (1953) suggest that scallops need such a system to orient and migrate.

Where did these remarkable eyes come from? They possess two quite different receptor systems, which is unusual. Their optical system is an extreme refinement of an arrangement found in many 'primitive' eyes, where a mirror of some kind behind the receptors enhances sensitivity. Mayr & Salvini-Plawen (1977, Fig. 8) make the intriguing suggestion that the distal retina is novel, and is an adapted version of a free-standing ciliary receptor organ, which in other genera such as *Cardium* and *Tridacna* is in direct contact with the surrounding sea-water. If that were so, this would be a unique example of a sense cell changing its modality – from chemo- or mechanoreceptor to photoreceptor. Off-responding photoreceptors are known from other molluscs, both gastropods and bivalves, so it may be that the *Pecten* receptor appeared by a more conventional route. There is no doubt, however, that the bivalves are an odd lot. As well as *Pecten*'s unique optical discovery, the ark shells (*Arca*, *Pecunculus*) have evolved small but effective compound eyes, again apparently from no-where. Their role is the same as the eyes of scallops: to see motion at a distance. As Nilsson (1994) puts it, they are burglar alarms.

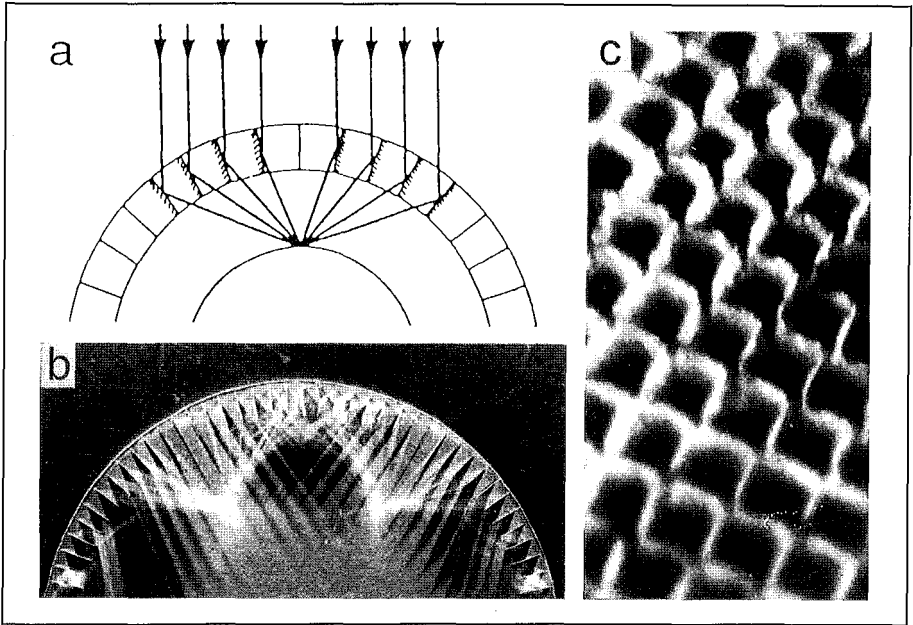


Figure 8

Image formation in the eye of a decapod shrimp. a, optical diagram showing how radial mirrors can produce an image of a point source. b, a model of the eye, made from silvered tape. The photograph shows the images of two light sources. c, the surface of the eye of a crayfish, showing the square array of the mirror tips. The squares are approximately $50\ \mu\text{m}$ across.

Gehring & Ikeo (1999) make the point that if strange things like this happened in the bivalve molluscs, why should not similar fluidity between optical systems and cell types have occurred at the time of the first origins of metazoan eyes. And thus, could not all eyes be derived from a common prototype? They have a point, but my interpretation of bivalve optical promiscuity is somewhat different. Bivalve eyes only ever had one function – to improve on the detection of shadow – and virtually any optical system would do the job. For a multi-purpose eye (like those of arthropods or vertebrates) the setting up of a nervous system able to extract information about motion, position and identity would prevent further radical changes in eye design, for reasons already discussed. The bivalves had the luxury of inventing anything they liked – although in fact few of them did. They were thus outside the mainstream of eye evolution, and their particular case has little to tell us about the origins of the major lines of eyes.

The compound mirror eyes of decapod crustaceans

For about 20 years, from the 1950's to the mid-1970's, shrimps and their relatives couldn't see. The advent of interference microscopy in about 1950 had made it possible to measure the refractive indices of the tiny optical structures that form images in compound eyes. Measurements on crayfish showed that the structures thought to be lenses had a low, homogeneous refractive index. Sigmund Exner, in his famous monograph of 1891, had thought that the eyes of decapods were like those of beetles and moths. These have superposition eyes in which the optical elements are lens-cylinders, structures with an internal refractive index gradient (a little like Matthiessen lenses) that act as single lenses in apposition eyes, or, in superposition eyes, as pairs of lenses operating as inverting telescopes (for details see Exner 1891 or Land 1981). However, to behave in this way the structures need to have a parabolic radial refractive index gradient, with a central refractive index greater than 1.5. The interference microscope measurements in the 1950s indicated a homogeneous index closer to 1.4. The eyes could not be working in the way that Exner had envisaged.

During the 1960's there was much speculation about the way these eyes might work, and even suggestions that Exner's ideas about superposition imagery might be wrong altogether (e.g. Horridge 1968, pp 160-162, 1971). The problem was solved in 1975, when Klaus Vogt, again studying crayfish eyes, showed that the low refractive index structures were, in fact, silvered with a multilayer mirror similar to that in *Pecten*. I found the same thing in a deep-sea shrimp the following year (Land 1976). These observations led us both to the solution shown in Fig. 8a. Parallel light beams reflected from the radially directed mirrors are redirected in such a way as to intersect at a focus half way out from the centre of the eye, which is where the retina is situated. This gives a ray path almost identical to that in the more common (refracting) type of superposition eye, except that the redirection of the rays occurs by reflection, not refraction (Fig. 2f and h). A full account of the optics of crayfish eyes is given in Vogt (1980).

There were clues to the existence of this mechanism that could have been picked up at any time in the preceding century. First, the eyes of living shrimps are impressively silvery in appearance; it is perhaps the fact that the mirrors do not survive long in formalin that led to this being overlooked. Second, the facets of shrimps and their relatives are square, not hexagonal (Fig. 8c). In general, if one takes a set of deformable rods and packs them tightly together, they will form a hexagonal array, because this geometry results in the smallest centre-to-centre packing distance. A square array is thus not what one would expect, and indicates the need for a special explanation. Square facets are almost unique to decapod crustaceans. All the other eyes that Exner believed to have superposition optics

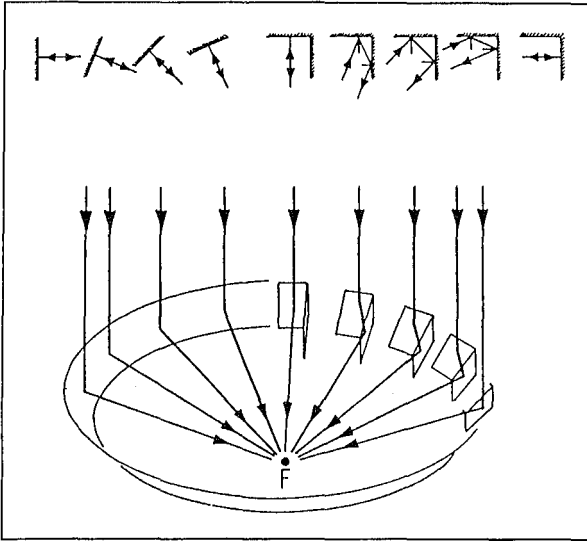


Figure 9

Explanation of the square facets. One 3-dimensional interpretation of Fig. 8a is that it represents a section through a stack of concentric mirror rings, one of which is shown here on the left of the main figure. Such a stack will form an image at F, but only for rays that are exactly aligned with the axis of the stack: other rays are reflected at increasingly inappropriate angles. The diagrams at the top show the paths of rays as seen from a point above the stack. On the right the single mirror strip has been replaced by a series of corner reflectors: these give virtually identical ray paths to the single strip, apart from a small lateral displacement. The right of the main figure shows that the corner reflectors also form an image at F, but the structure now no longer has a single axis, and so can operate over a wide angle.

From Land (1981).

have hexagonal facets, and they do indeed function by refracting superposition. This even includes the sister group of the decapod crustaceans, the euphausiids (krill), in which the optical elements are high-refractive index, bullet-shaped lens-cylinders, quite unlike the soft square structures in decapod shrimps.

There is indeed an intriguing reason for the square facets (Vogt 1977), and Fig. 9 is an attempt to explain it. The crucial feature is that two sides of each mirror box act as a "corner reflector". Corner reflectors have the property that rays directed towards them from whatever angle return along a reflected path at exactly 180° to the incident path. This means that such a mirror pair behaves as though it were a single mirror that is always at right angles to the incident ray. As Fig. 9 shows,

this property allows two sides of each mirror box to substitute for the single mirror in the idealised diagram (Fig. 8a). This also means that the eye as a whole has no one single "good" axis, as would be the case if the mirrors were single curved single strips. Since only 90° corners have these useful properties, and the 120° corners that a hexagonal lattice would produce do not, it follows that reflecting superposition eyes must have a square facet lattice. The corollary is also usually true: eyes with a wholly square facet lattice are of the reflecting superposition type. Interestingly, in *Gennadas*, a decapod shrimp which appears to have changed – remarkably – from the reflecting to the refracting type of eye, the facet pattern is mostly hexagonal, although there are still hints of squareness (Nilsson 1990). Macruran eyes do not start with square facets, but hexagonal ones which are clearly of the apposition type. Only rather late in development, around stage 15 in *Palaemonetes*, do the crystalline cones elongate and square off and the eye attains the superposition optics of the adult. Even the adult eye, however, retains the capacity for reverting to the apposition type during light adaptation, as screening pigment progressively cuts off the oblique rays that form the superposition image. Thus, from an evolutionary point of view, it seems that the reflecting superposition eye is a development of the apposition eye which it does not entirely supplant. Interestingly, the short-bodied crabs (Brachyura) which are thought to have evolved from the long-bodied Macrura, have only apposition eyes (or a different type of superposition eye known as parabolic superposition: Nilsson 1988). Whilst the macrurans tend to live in the plankton as larvae, and then migrate as adults to deeper (and darker) waters, where a more sensitive type of eye is an advantage, the crabs are generally surface-living and diurnal. One can guess that the capacity to produce reflecting superposition eyes was lost when it was no longer required.

Summary

This brief survey of eye evolution has not produced any new grand principles, but has, I hope, given a modern perspective on some of the questions that have concerned evolutionary thinkers for the last 150 years. Where did eyes come from in the first place? We know that the ingredients for eyes, in particular rhodopsin, has been available in the metazoan genome from the very beginning. So have other constituents: black pigment and something from which to make a transparent refractile structure (Land & Fernald 1992). How indeed could eyes have come about if these were not available? Now we also have *Pax-6* to stir into the mixture. Is this the *sine qua non* eye organizer gene, or simply an available gene capable of switching on a developmental sequence, which has been appropriated several times for the production of eyes?

When the dust had settled after the Cambrian radiation, a small number of eye types evolved into much more efficient eyes, able to supply new kinds of information: about motion, identity and location. Some of them, for example the Matthiessen lens eye, evolved many times; others, such as the reflecting superposition lens eye of shrimps, probably only once. The picture of why some were successful and others not is confusing. The apposition compound eye is a seriously flawed design in a physical sense, and yet, in terms of sheer numbers, it is the most successful of all eye types. Eyes that should have died out, the *Nautilus* eye for example, are still with us. Strange one-off image forming eyes such as the mirror eyes of scallops have also survived. Evolution does not seem to home in on the one 'best' design, to the exclusion of others. There is both an inventiveness in the evolutionary process that generates novelty, as well as a conservative process that preserves it against the odds.

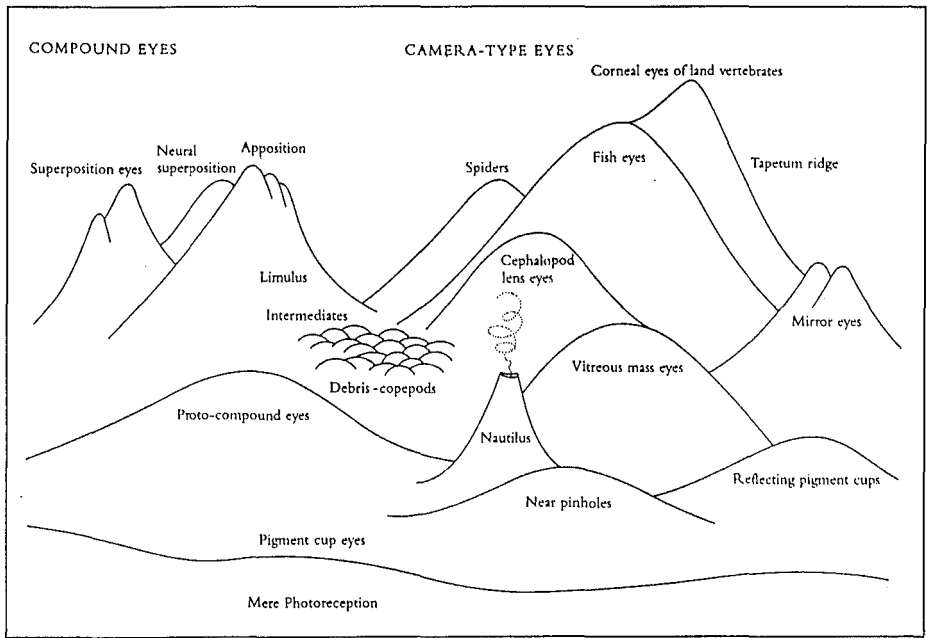


Figure 10

A landscape of eye evolution, in which height represents optical quality, and the ground plane evolutionary distance. The reader should not take the details too seriously. Climbing the hills is straightforward, going from one to the other near-impossible. Redrawn by Lala Ward from a sketch by me. From Dawkins (1996).

To finish this essay, I offer a pictorial summary. For his book 'Climbing Mount Improbable', Richard Dawkins (1996) asked me to sketch my version of the mountain range, and Fig. 10 was the result. The height of the mountains represents optical quality (something like the product of resolution and sensitivity, see Snyder et al. (1977) for a more profound discussion of what this might mean) whilst the ground plane is evolutionary distance. Again very roughly the z-axis, away from the reader, is evolutionary time, and the x-axis, left/right, is a measure of the optical difference between types of eye. The point is that it is relatively easy to climb the mountains; natural selection will do this. But it is very hard to get from one to another without passing through a zone of much reduced vision. The smoke from the *Nautilus* volcano indicates an eye type for whose continuing existence I still have no satisfying explanation.

References

- Buddenbrock, W. von & I. Moller-Racke: Über den Lichtsinn von *Pecten*. In: Publ. Zool. Staz. Napoli, 24 (1953), pp. 217-245.
- Catmull, J., Hayward, D. C., McIntyre, N. E., Reece-Hoyes, J. S., Mastro, R., Callaerts, P., Ball, E. E. & D. J. Miller: *Pax-6* origins – implications from the structure of two coral *Pax* genes. In: Dev. Genes. Evol., 208 (1998), pp. 352-356.
- Conway-Morris, S.: The Crucible of Creation, Oxford University Press, 1998.
- Darwin, C.: On the Origin of Species by means of Natural Selection, London: John Murray, 1859.
- Dawkins, R.: Climbing Mount Improbable. London: Penguin Books, 1996.
- Eakin, R. M.: Structure of invertebrate photoreceptors. In: Handbook of Sensory Physiology. Vol VII/1. (ed HJA Dartnall), Berlin: Springer, 1972, pp. 625-684.
- Exner, S.: Die Physiologie der facettierten Augen von Krebsen und Insekten, Leipzig-Wien: Deuticke. Translated into English by RC Hardie (1989), Berlin: Springer, 1891.
- Friederichs, H. F.: Beiträge zur Morphologie und Physiologie der Sehorgane der Cide-liden (Col.). In: Z. Morph. Ökol. Tiere, 21 (1931), pp. 1-172.
- Gehring, W. J. & K. Ikeo: *Pax 6*: mastering eye morphogenesis and eye evolution. In: Trends in Genetics, 15 (1999), pp. 371-377.
- Halder, G., Callaerts, P. & W. Gehring: Induction of ectopic eyes by targeted expression of the *eyeless* gene in *Drosophila*. In: Science, 267 (1995), pp. 1788-1792.
- Hartline, H. K.: The discharge of impulses in the optic nerve of *Pecten* in response to illumination of the eye. In: J. Cell. Comp. Physiol., 11 (1938), pp. 465-477.
- Hesse, R.: Untersuchungen über die Organe der Lichtempfindung bei niederen Thieren. VI. Die Augen einiger Mollusken. In: Z. Wiss. Zool., 68 (1900), pp. 379-477.
- Hesse, R.: Das Sehen der niederen Tiere, Jena: Fischer, 1908.
- Horridge, G. A.: Alternatives to superposition images in clear zone compound eyes. In: Proc. R. Soc. B, 179 (1971), pp. 97-124.

- Horridge, G. A.: Interneurons, San Francisco: WH Freeman, 1968.
- Jagger, W. S.: The optics of the spherical fish lens. In: *Vision Res.*, 32 (1992), pp. 1271-1284.
- Kirschfeld, K.: Die Projektion der optischen Umwelt auf das Raster der Rhabdomere im Komplexauge von *Musca*. In: *Exp. Brain. Res.*, 3 (1967), pp. 248-270.
- Kirschfeld, K.: The resolution of lens and compound eyes. In: Zettler, F. & R. Weiler (eds.), *Neural Principles in Vision*, Berlin: Springer, 1976, pp. 354-370.
- Kröger, R. H. H., Campbell, M. C. W., Fernald, R. D. & H.-J. Wagner: Multifocal lenses compensate for chromatic defocus in vertebrate eyes. In: *J. Comp. Physiol. A*, 184 (1999), pp. 361-369.
- Land, M. F.: Image formation by a concave reflector in the eye of the scallop *Pecten maximus*. In: *J. Physiol. (Lond.)*, 179 (1965), pp. 138-153.
- Land, M. F.: Superposition images are formed by reflection in the eyes of some oceanic decapod crustacea. In: *Nature*, 263 (1976), pp. 764-765.
- Land, M. F.: Optics and vision in invertebrates. In: Autrum, H. (ed.), *Handbook of Sensory Physiology*. Vol VII/6B, 1981, pp. 471-592.
- Land, M. F.: Crustacea. In: Ali, M. A. (ed.), *Photoreception and Vision in Invertebrates*, New York: Plenum, 1984, pp. 401-438.
- Land, M. F.: Variations in the structure and design of compound eyes. In: Stavenga, D. G. & R. C. Hardie (eds.), *Facets of Vision*, Berlin: Springer, 1989, pp. 90-111.
- Land, M. F. & R. D. Fernald: The evolution of eyes. In: *Ann. Rev. Neurosci.*, 15 (1992), pp. 1-29.
- Mallock, A.: Insect sight and the defining power of compound eyes. In: *Proc. R. Soc. B*, 55 (1894), pp. 85-90.
- Nilsson, D.-E.: A new type of imaging optics in compound eyes. In: *Nature*, 332 (1988), pp. 76-78.
- Nilsson, D.-E.: Optics and evolution of the compound eye. In: Stavenga, D. G. & R. C. Hardie (eds.), *Facets of Vision*, Berlin: Springer, 1989, pp. 30-75.
- Nilsson, D.-E.: Three unexpected cases of refracting superposition eyes in crustaceans. In: *J. Comp. Physiol. A*, 167 (1990), pp. 71-78.
- Nilsson, D.-E.: Eye ancestry: old genes for new eyes. In: *Current Biology*, 6 (1996), pp. 39-42.
- Nilsson, D.-E.: Eyes as optical alarm systems in fan-worms and ark clams. In: *Phil. Trans. R. Soc. B*, 346 (1994), pp. 195-212.
- Nilsson, D.-E. & S. Pelger: A pessimistic estimate of the time required for an eye to evolve. In: *Pro. R. Soc. Lond. B*, 256 (1994), pp. 53-58.
- Pumphrey, R. J.: Concerning vision. In: Ramsay, J. A. & V. B. Wigglesworth (eds.), *The Cell and the Organism*, Cambridge University Press, 1961, pp. 193-208.
- Quiring, R., Walldorf, U., Kloter, U. & W. Gehring: Homology of the *eyeless* gene of *Drosophila* with the *small eye* gene in mice and *aniridia* in humans. In: *Science*, 265 (1994), pp. 785-789.
- Salvini-Plawen, L. von & E. Mayr: On the evolution of photoreceptors and eyes. In: *Evol. Biol.*, 10 (1977), pp. 207-263.

- Sivak, J.: Optical properties of a cephalopod eye (the short-finned squid, *Illex illecebrosus*). In: J. Comp. Physiol. A, 147 (1982), pp. 323-327.
- Snyder, A. W., Laughlin, S. B. & D. G. Stavenga: Information capacity of eyes. In: Vision Res., 17 (1977), pp. 1163-1175.
- Vogt, K.: Zur Optik des Flusskrebsauges. In: Z. Naturforsch., 30c (1975), p. 691.
- Vogt, K.: Ray path and reflection mechanism in crayfish eyes. In: Z. Naturforsch., 32c (1977), pp. 466-468.
- Vogt, K.: Die Spiegeloptik des Flusskrebsauges. The optical system of the crayfish eye. In: J. Comp. Physiol., 135 (1980), pp. 1-19.
- Zhang, C. S. & S. W. Emmons: Specification of sense-organ identity by *Caenorhabditis elegans Pax-6* homologue. In: Nature, 377 (1995), pp. 55-59.