4
A review of vertebrate and invertebrate ocular filters

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4.1 Introduction

The spectral information available to an animal's visual system depends both on the wavelengths reaching its outer segments and the visual pigments contained within them. The former is governed not only by the chromatic stimuli present in the environment, but also by the degree to which these are modified through intraocular filters, before being absorbed by the visual pigments. Although the ocular media of the majority of animals are transparent to light above about 310 nm, their primary function being either refractive or nutritive, in some, pigments are present that filter the spectral content of the light reaching the retina. Light impinging on the visual pigments may have its spectrum further modified by both filters within the retina itself and by reflective structures behind the retina.

This review sets out to describe the spectral characteristics of such ocular filters in both vertebrates and invertebrates, and outlines their location, the biochemical nature of the filtering pigments, and their function. In the following sections, filters are described by sequentially following the path of light through the eye's optical components from the outside world into the photoreceptors and, where present, reflection back by a tapetum. Most vertebrate filters, whatever their origin and placement, remove short wavelengths. Their function is therefore dealt with in a separate section. The eyes of invertebrates are more varied in their design and consequently possess a greater variety of functionally distinct filters. Their suggested functions are detailed within each section.

4.2 Vertebrate ocular filters

4.2.1 General spectral characteristics

Even in the absence of a specific short-wave absorbing filter, no ocular structure will transmit significant amounts of radiation below about 310 nm due to absorption by its nucleic acids and various structural protein components, such as aromatic amino acids. In such unpigmented structures the decline in

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transmission in the UV is smooth and the 'cut-off' wavelength (often defined as the wavelength of 50% transmission or the wavelength of half maximum optical density; Lipetz 1984a; Douglas & Thorpe 1994) is generally between 310 – 350 nm and depends primarily on the structure's thickness. The presence of specific short-wave absorbing pigments will result in further absorption in the UV/blue part of the spectrum. The transmission spectrum of a structure at short wavelengths is, therefore, the product of both 'background' absorption by its proteins and nucleic acids, and light loss caused by any specific filtering pigments. At longer wavelengths, transmission is generally above 90%, especially if living tissue free from any possible *post-mortem* artefacts is examined (e.g. van Best *et al.* 1988). In the infra-red, the spectral characteristics of most ocular media resemble those of pure water (e.g. Brainard *et al.,* 1994; van den Berg and Spekreijse 1997).

4.2.2 Cornea

The corneas of most animals contain no significant amounts of short-wave absorbing pigments and consequently transmit most light down to around 310 nm (e.g. *Mammals* – Hemmingsen & Douglas 1970, Chou & Cullen 1984, van den Berg & Tan, 1994; Ambach *et al.* 1994; *Birds* – Hemmingsen and Douglas 1970, Emmerton *et al.,* 1980, Govardovskii and Zueva 1977, Maier 1994; *Reptiles* – Thorpe 1991, Ellingson *et al.,* 1995; *Amphibia* – Thorpe 1991). Figure 1 (curve i) shows the smooth and rapid decline in transmission of a monkey cornea at short wavelengths, which is characteristic of all such unpigmented corneas.

Pigmented corneas are almost entirely restricted to fish, among whom they are quite common, the only exceptions being a small amount of pigmentation, which may have little or no effect on vision, found in the corneas of the frog, *Rana pipiens*, and the ground squirrel, *Citellus beecheyi* (Figure 1, curves ii & iv). The degree of pigmentation in fish differs markedly between species. While some have corneas which, like most other vertebrates, contain no short-wave absorbing pigments (e.g. McCandless *et al.,* 1969, Douglas 1989, Douglas and McGuigan 1989), and others have heavily pigmented, visibly yellow, corneas absorbing radiation above 400 nm (Heinermann 1984; Kondrashev *et al.,* 1986; for reviews, Figure 1, curve v), a significant number have a small, possibly inconsequential, amount of pigmentation, betrayed by irregularities in their absorption spectra in the near UV (e.g. Douglas and McGuigan 1989; Figure 1, curve iii).

Teleost corneal pigments are often restricted to, or are densest in, a dorsal 'eye-shade' region above the pupil (e.g. Muntz 1973, 1976a, 1982; Douglas 1989; Plate 1h*). Since the distribution of light underwater is very directional (Lythgoe 1975, 1976), such 'eyeshades' will selectively reduce the amount of

*Colour plates will be found between pages 124 and 125.

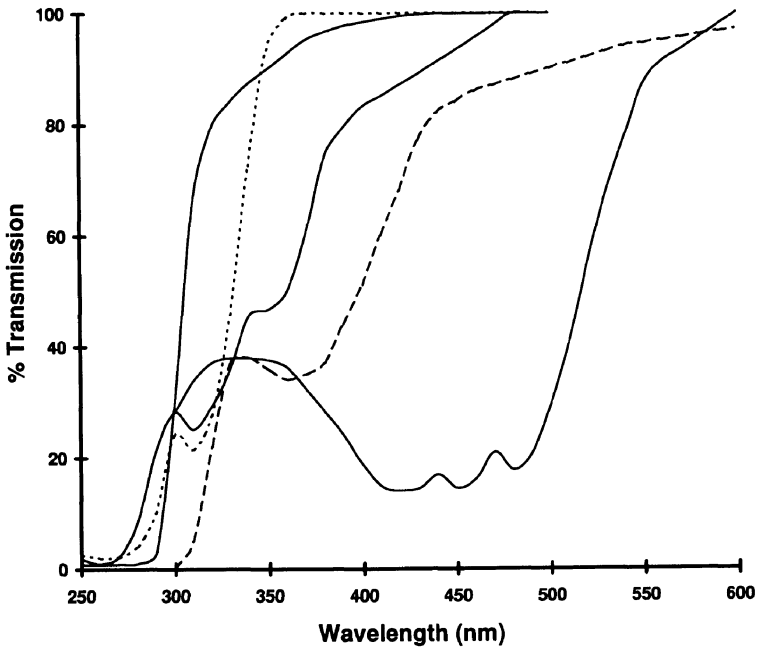


Figure 1 Transmission spectra of intact vertebrate corneas. (from left to right) (i) Primate, *Macaca fascicularis* (Thorpe 1991), with no detectable amounts of pigmentation, (ii) Frog, *Rana pipiens* containing small amounts of an unidentified pigment (Thorpe 1991, dotted line), (iii) Fish, *Herotilapia multispinosa*, displaying 2 absorbance maxima at 325 and 360 nm characteristic of the mycosporine-like amino acids palythine and palythene (Thorpe 1991), (iv) California ground squirrel, *Citellus beecheyi* (Hemmingsen & Douglas 1970, dashed line) (v) Dorsal cornea of the fish *Ctenopoma oxyrhynchus*, containing a carotenoid pigment (Thorpe 1991)

bright downwelling light, while leaving the less intense light, entering the eye along the optic axis, relatively unaffected.

The spectra of heavily pigmented corneas are usually characterised by 3 absorbance maxima around 425, 450 and 480 nm (Figure 1, curve v), suggesting these pigments are carotenoids. However, in some species, both intact corneal absorbance spectra (Thorpe 1991) and methanol extracts (Dunlap *et al.*, 1989) indicate the presence of mycosporine-like amino acids (MAAs), identical to those acting as short-wave absorbing filters in the fish lens (see 4.2.3) (Figure 1, curve iii). In several, both carotenoid pigments and MAAs are observed in the same cornea; the MAAs being uniformly distributed throughout and the carotenoid forming the dorsal eye-shade (Thorpe 1991), thus effectively screening all wavelengths below 500 nm; the carotenoid-like pigments absorbing light between 400 – 500 nm, and the MAAs absorbing below 400 nm.

Usually, corneal pigments, if present in sufficient quantities, confer a yellow colouration on the cornea. The occlusable corneas (see below) of a small number of species, such as *Hexagrammos octogrammus*, however, have both a yellow

carotenoid pigment, and a second red pigment, probably astaxanthin, contained within a separate group of chromatophores (Orlov and Gamburtseva 1976a&b, Gamburtseva *et al.*, 1979). The orange corneal dorsal eye shade of the goldfish also contains a pigment absorbing maximally around 460 – 480 nm (Figure 14), which is likely to be astaxanthin (Douglas 1989). Astaxanthin is also one of the major pigments in the goldfish skin (Hata and Hata 1971). Similarly in puffer fish, the pigments extracted from the cornea and the skin are indistinguishable (Appleby and Muntz 1979). Thus, there seems to be a close relationship between dermal and corneal pigmentation (Walls and Judd 1933b).

Although having a cornea absorbing significant amounts of light below 500 nm potentially has several advantages in photopic conditions (section 4.2.7), it results in an inevitable, and undesirable, loss of sensitivity in low light levels. Consequently, the levels of pigmentation observed in most fish corneas (usually an optical density of less than 1.0 at wavelengths 400 – 500 nm) probably represent a compromise. However, some fish have overcome this problem and can tolerate much higher levels of corneal pigmentation, by developing 'occlusable' corneas, in which pigment distribution depends on ambient light levels (Orlov and Gamburtseva 1976a&b, Appleby and Muntz 1979, Muntz 1982, Gamburtseva *et al.*, 1979, Shand 1988). In dim light pigment is aggregated in chromatophore cell bodies arranged around the periphery of the cornea. On exposure to higher light levels, the pigment migrates into the central cornea through chromatophore processes, conferring a yellow/orange colouration to the whole cornea. These pigment migrations are produced, as in skin melanophores, using microtubules (Orlov and Gamburtseva 1976a) and are regulated locally within the eye (Appleby and Muntz 1979, Kondrashev and Khodtsev 1984).

Another method of selectively reducing the amount of radiation entering the eye, rather than absorbing it, is to reflect it. Consequently, the corneas of many fish, like those of several invertebrates (section 4.3.1a), contain a variety of reflective structures causing corneal iridescence (Lythgoe 1971, 1975, 1976; Locket 1972; Best and Nicol 1980; Collin and Collin 1996; Figure 2). This is the result of constructive interference of light reflected from multilayer stacks of different refractive index (see section 4.3.1a for explanation) arranged so as to preferentially reflect oblique rays coming from above the animal. As a result, like the dorsal pigmentation described above, they will only reduce the bright downwelling light and do not greatly compromise on-axis vision (Lythgoe 1976). Furthermore, again as in some pigmented corneas and presumably for similar reasons, the iridescence changes with ambient illumination, either completely disappearing, reducing in degree or shifting towards shorter wavelengths during dark adaptation (Shand and Lythgoe 1987; Shand 1988; Lythgoe and Shand 1989; Figure 2). Such short term changes in iridescence are likely to be the result of varying the degree of corneal hydration through the use of epithelial ionic pumps (Ashcroft and Lythgoe 1991).

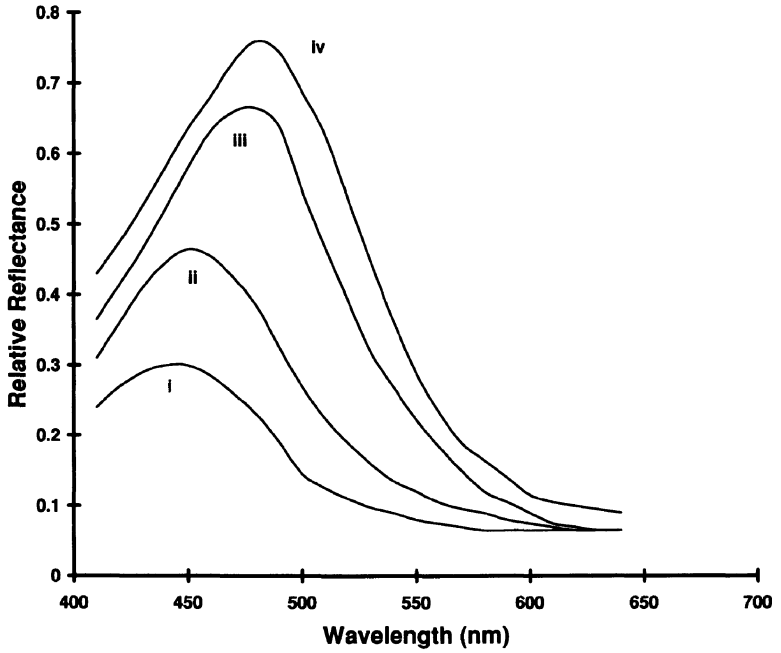


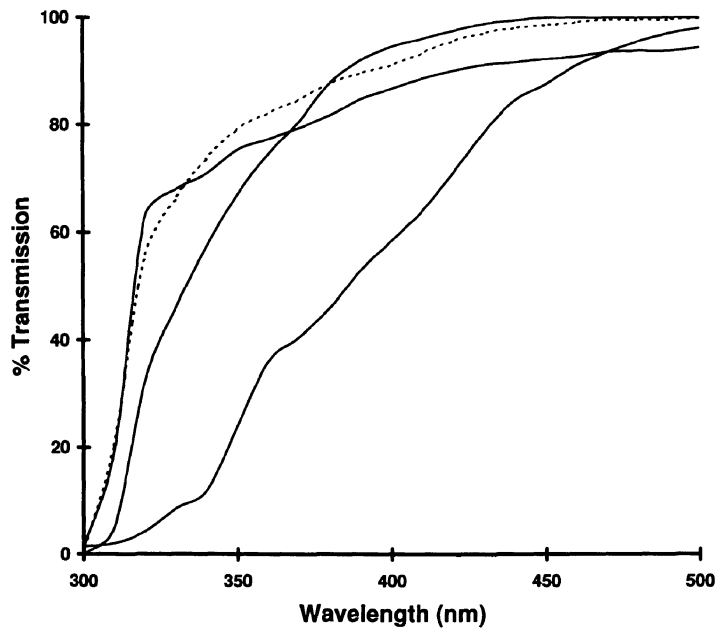
Figure 2 Spectral reflectance from the cornea of the sand goby (*Pomatoschistus minutus*) after (i) 1, (ii) 5, (iii) 20 and (iv) 30 min light exposure following 2 hrs in darkness. (Lythgoe & Shand 1989)

4.2.3 Lens

The lens is the most common vertebrate ocular filter and, with the exception of some pigmented fish corneas, usually determines the spectral absorption of the whole eye. Although, many species have lenses containing no detectable amounts of pigment and hence transmit short wavelengths well (e.g. *Mammals* – Gorgels & van Norren 1992, Brainard *et al.*, 1994; *Birds* – Emmerton *et al.*, 1980; Maier 1994; *Fish* – McCandless *et al.*, 1969; Douglas and McGuigan 1989; Thorpe *et al.*, 1993; *Amphibia and Reptiles* – Thorpe 1991; Figure 3), many animals have lenses with varying degrees of pigmentation. Pigmented lenses are common in fish (Heinermann 1984; Douglas and McGuigan 1989; Thorpe *et al.*, 1993 for reviews; Plate 1e), as well as primates (Boettner and Wolter 1962; Dartnall *et al.*, 1965; Cooper and Robson 1969b, Thorpe 1991) and Sciurid mammals (Walls and Judd 1933b; Cooper and Robson 1969a; Jacobs and Yolton 1972; Yolton *et al.*, 1974; Chou and Cullen 1984; Zigman *et al.*, 1985b), but also occur in some other mammals (Thorpe 1991), amphibia (Merker 1934, Denton 1955; Kennedy and Milkman 1956), and reptiles (Walls and Judd 1933b; Ellingson *et al.*, 1995) (Figure 3). Highly pigmented lenses have never been described in birds, although the ocular media of some species of duck do absorb strongly at wavelengths below 370 nm, suggesting the presence of some lenticular pigmentation (Jane & Bowmaker, 1988).

The identity of the short-wave absorbing lens pigments is known for only a few species. In some animals, these are a number of freely diffusible, water soluble, closely related tryptophan derivatives with absorbance maxima in the UV at 365 – 375 nm and 260 – 265 nm (Cooper & Robson 1969a&b; Thorpe 1991; Figure 4a). In young primates, the major lens pigment is 3-hydroxy-kynurenine-O-β-glucoside, which is found in the human lens together with lower levels of kynurenine and 3-hydroxy-kynurenine (van Heyningen 1971a&b, 1973a; Bando *et al.* 1981; Thorpe 1991; Wood & Truscott 1993). Human lenses, especially those from older individuals, contain, in addition to their tryptophan derived pigments, a number of other chromophores (Zigman 1985; Sen *et al.*, 1992), including low concentrations of the same two carotenoids that make up the primate macular pigment (section 4.2.5b); lutein and zeaxanthin (Yeum *et al.*, 1995). Tryptophan-derived kynurenine pigments are also found in the grey squirrel (van Heyningen 1971b, 1973a; Zigman *et al.*, 1985b; Zigman and Phaxia 1988; Nie *et al.*, 1990; Figure 5) and some species of fish (Thorpe *et al.*, 1992, 1993; Truscott *et al.*, 1992; Figure 4a).

Not all lens pigments are tryptophan-derived, however. Although their absorption spectra often resemble those of the tryptophan-related pigments (Zigman *et al.*, 1985a; Zigman 1991), most fish pigments are in fact a series of dietary-derived MAAs (Dunlap *et al.*, 1989; Thorpe *et al.* 1993; Figure 4b). Spectrally distinct short-wave absorbing pigments, that are probably neither MAAs nor derived from tryptophan, have also been extracted from a variety of other



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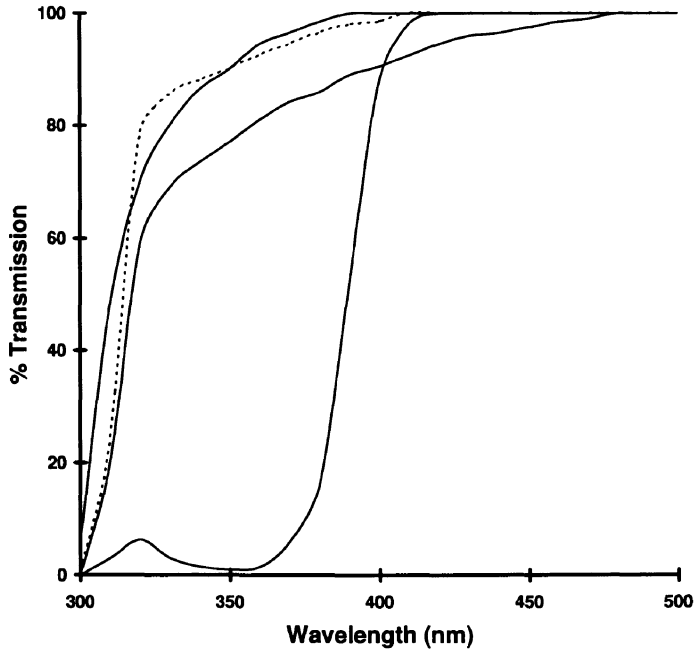

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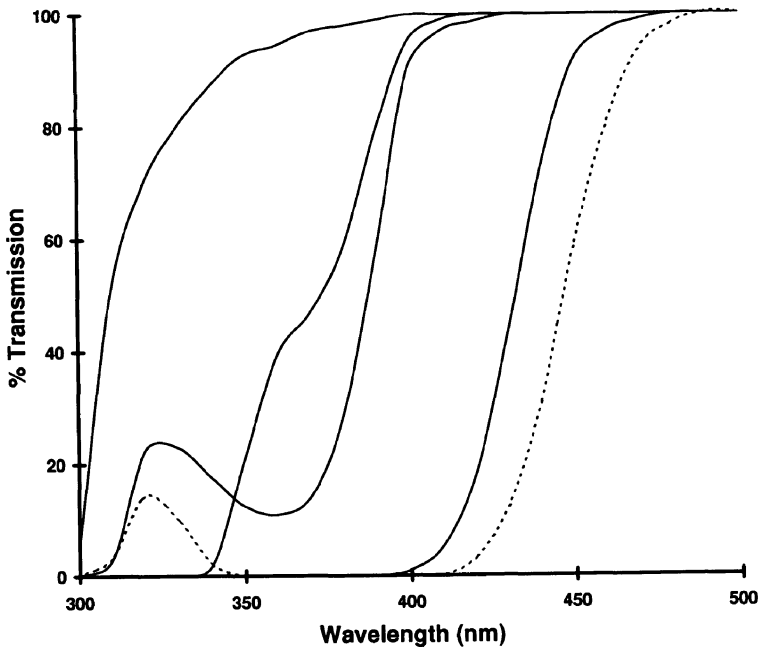

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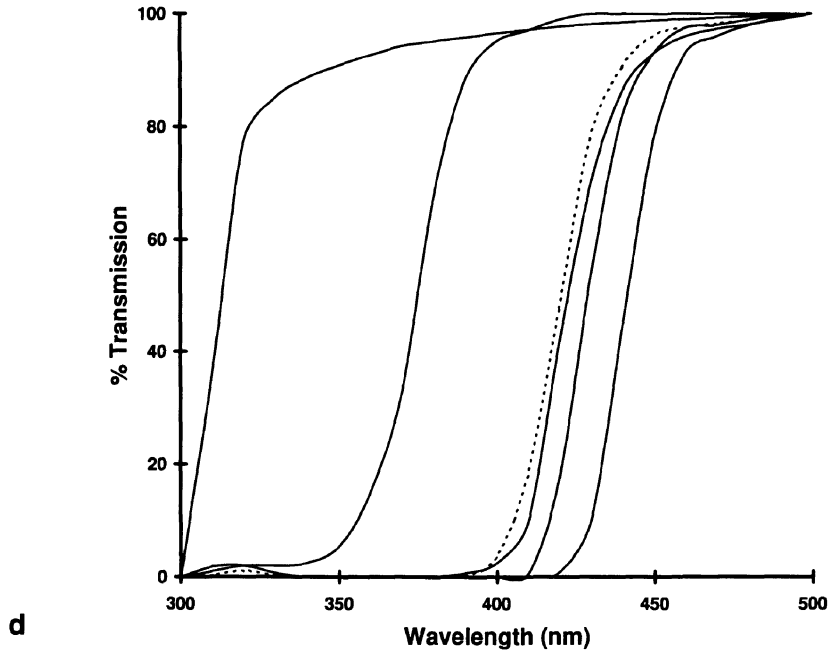
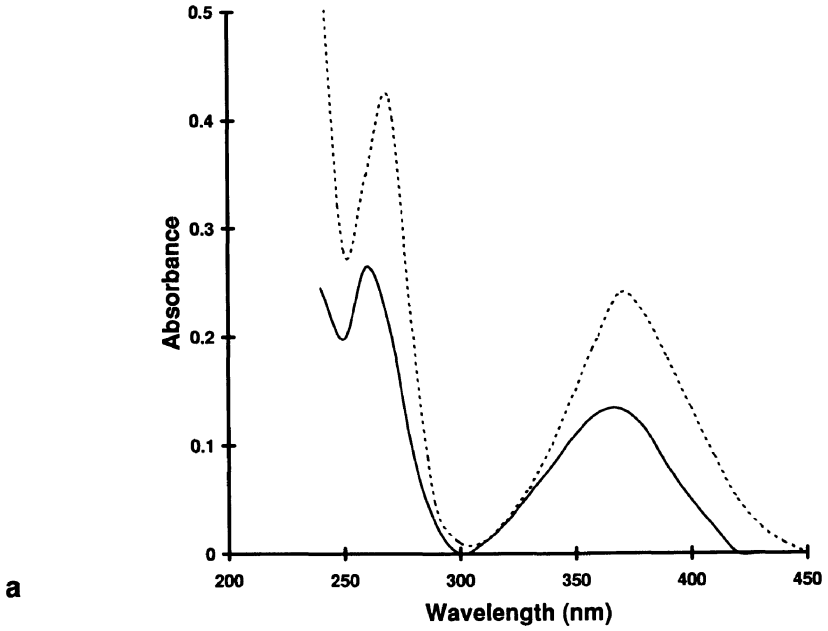


Figure 3 Spectral transmission of vertebrate lenses. (**a**) Birds and reptiles (left to right); i – Robin (*Erithacus rubecula*, 2.6 mm, Douglas unpubl), ii – Water dragon (*Physignathus leseueri*, dotted line, 2.52 mm), iii – average of 10 chicken lenses (*Gallus gallus*, av 4.79 mm), iv – Rat snake (*Elaphe guttata*, 2.89 mm) (**b**) Amphibia (left to right); i – Salamander (*Salamandra salamandra*, dotted line, 2.01 mm), ii – newt (*Cynops pyrrhogaster*, 0.88 mm), iii – Axolotl (*Ambystoma mexicanum*, 1.63 mm) , iv - Frog (*Rana pipiens*, 3.22 mm) (**c**) Fish (left to right); i – *Leuciscus idus* (1.80 mm), ii – *Platytaenoidus degeni* (1.61 mm), iii – *Merlangius merlangus* (3.98 mm), iv – *Herotilapia multispinosa* (2.08 mm), v – *Aequidens maronii* (1.58 mm) (**d**) Mammals (left to right); i – Golden hamster (*Mesocricetus auratus*, Brainard *et al.* 1994), ii – Guinea pig (*Cavia porcellus*, 3.70 mm), iii – Macaque (*Macaca fascicularis*, dotted line, 2.79 mm), iv – Marmoset (*Callithrix jacchus*, 2.97), v – Capuchin (Cebus appelus, 3.92 mm), vi – Grey squirrel (*Sciurus carolinensis*, 3.60 mm). All data are from Thorpe 1991, unless otherwise indicated. The numbers in brackets represent lens diameters along the optic axis

vertebrates. Aqueous extracts of the frog, *Rana pipiens*, lens reveal a pigment unlike that of primates or fish, with a λ_{max} at 347 nm (Kennedy and Milkman 1956; Thorpe 1991, Figure 5). Guinea pig lenses, on the other hand, contain small amounts of a pigment absorbing maximally around 325 nm (Thorpe 1991; Figure 5). As yet unidentified pigments have also been observed in ground squirrel and chipmunk lenses (Nie *et al.*, 1990). The large variety of chemically distinct short-wave absorbing pigments within the vertebrate lens is a clear testament to their importance and indicates that this trait has evolved separately on many occasions.

The vertebrate lens grows continually throughout life. Therefore the path-length the light has to traverse will increase, leading to an inevitable reduction in short-wave transmission in older animals. This accounts for the age related decrease in lens transmission reported in several fish (Douglas 1989; Thorpe and



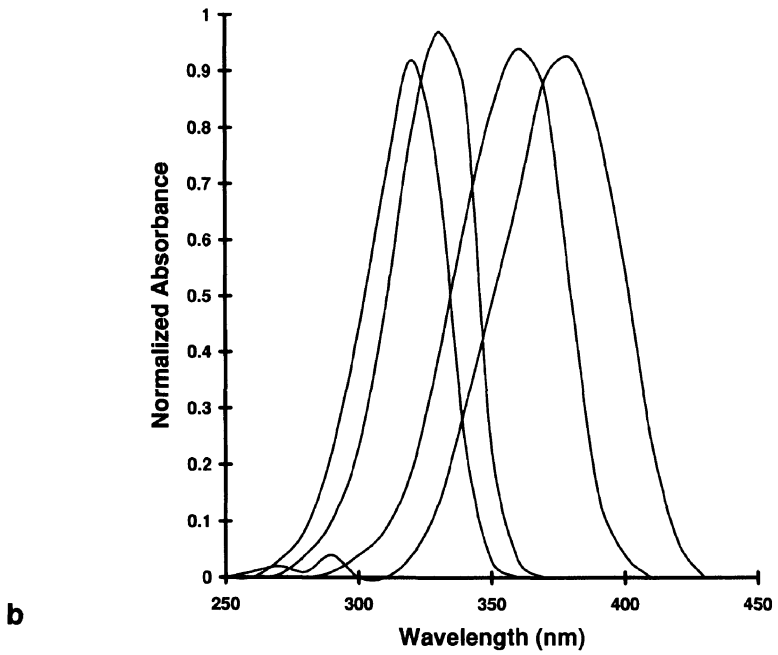


Figure 4 Absorbance spectra of HPLC purified lens pigments. (**a**) Monkey (*Macaca fascicularis*, solid line, Thorpe 1991) and Gourami (*Trichogaster trichopterus*, dotted line, Truscott *et al.* 1992). Both pigments had an HPLC retention time and an absorbance spectrum identical to that of authentic 3-hydroxykynurenine. Absolute absorbance differences between the curves are arbitrary. (**b**) Four mycosporine-related pigments extracted from the lenses of various species of fish (left to right); i – Palythine (λ_{max} 320 nm) from *Oreochromis niloticus*, ii – Asterina-330 (λ_{max} 330 nm) from *Chaetodon* sp., iii – Palythene (λ_{max} 360 nm) from *Clupea harengus*, iv – an unidentified mycosporine-like compound (λ_{max} 385 nm) from *Exocoetus obtusirostris*. (Thorpe *et al.* 1993)

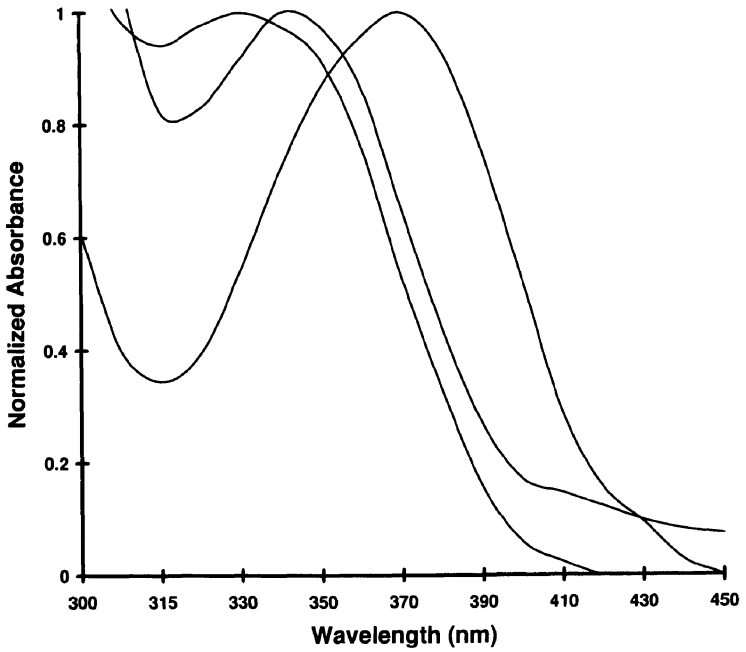
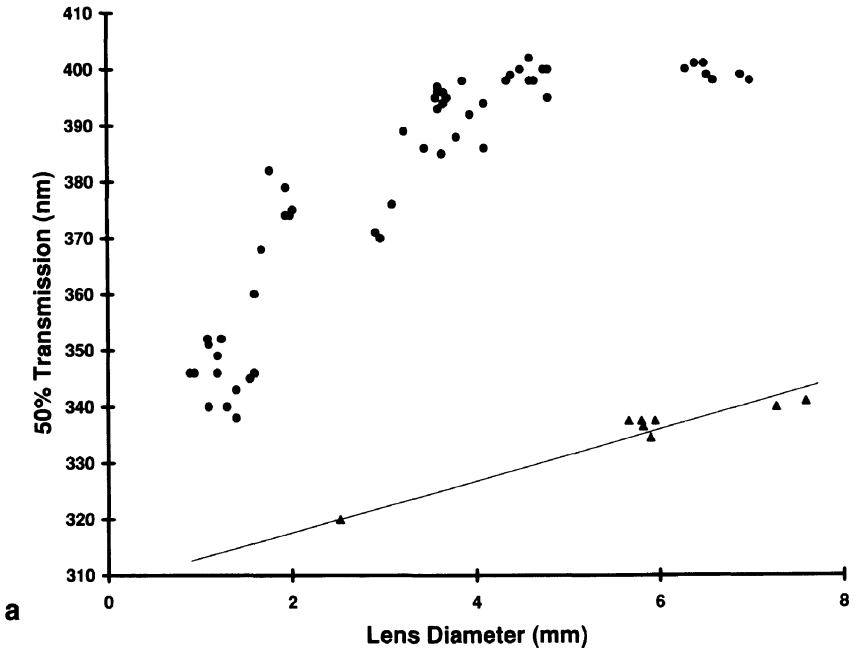


Figure 5 Absorbance spectra of crude water soluble pigments extracted from vertebrate lenses. (left to right); i - Guinea pig (*Cavia porcellus*), ii - Frog (*Rana pipiens*), iii - Grey squirrel (*Sciurus carolinensis*). Extracts have not been purified making a detailed analysis of absorbance below 300 nm impossible. (Thorpe 1991)

Douglas 1993; Figure 6a triangles) and may explain similar phenomena noted in cats (Dodt and Walther 1958) and cows (Merker 1934), and will occur in all species with unpigmented lenses. In pigmented lenses, however, a number of things can happen during ageing depending on the rate of pigment production, resulting in a variety of ageing patterns, all of which can be found in various species of fish (Thorpe and Douglas 1993 for review). In some species, for instance, there is a steady increase in pigment production with age, resulting in decreased short-wave transmission in older lenses (Figure 6b). In others, an initial rapid rise in pigment production is followed by a levelling off (Figure 6a circles) or even a decrease in the amount of UV removed (Figure 6c). Furthermore, some species are born with highly pigmented lenses, that then become more transparent to short wavelengths as they age (Figure 6d). These surprising increases in UV transmission with age in several species (Figures 6c&d) indicate that pigment accumulation has ceased in older animals, and that the inevitable increases in lens volume effectively dilute the freely diffusible lens pigments (Thorpe and Douglas 1993). Why fish should display such a wide variety of ageing patterns is unclear, but may relate to factors such as changes in diet and habitat (Thorpe and Douglas 1993) and possibly exposure to UV radiation (see section 4.2.7d).


410
400
390
380
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360
350
340
330
320
310
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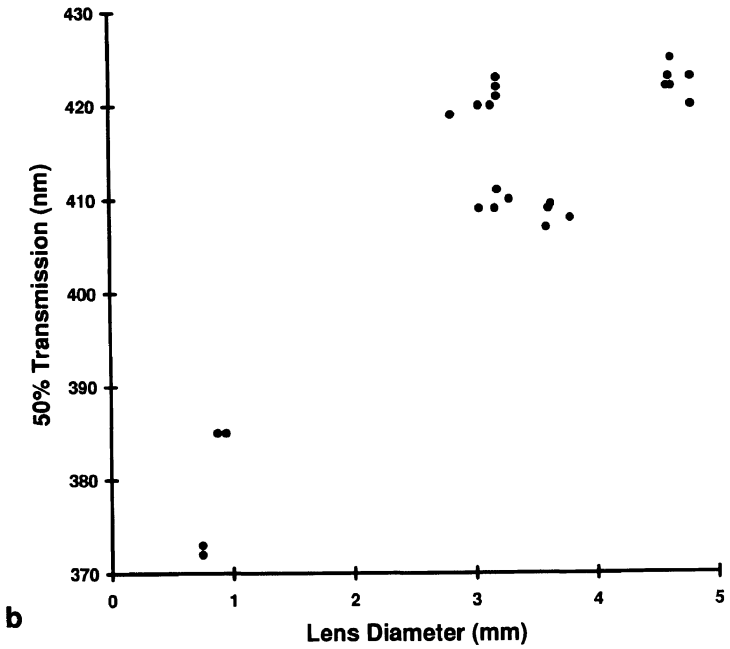
0
2
4
6
8
Lens Diameter (mm)

a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50% Transmission (nm)
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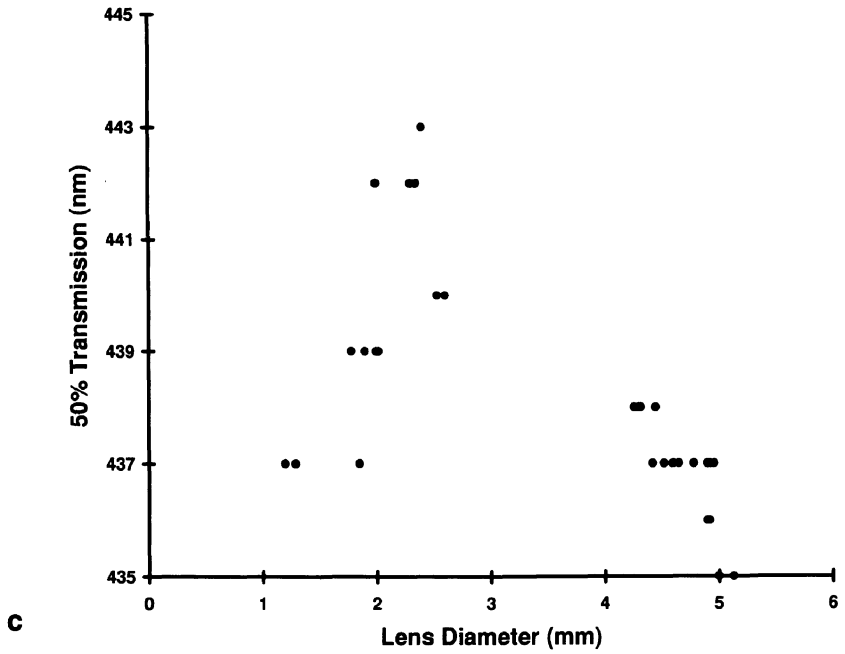
Lens Diameter (mm)

b



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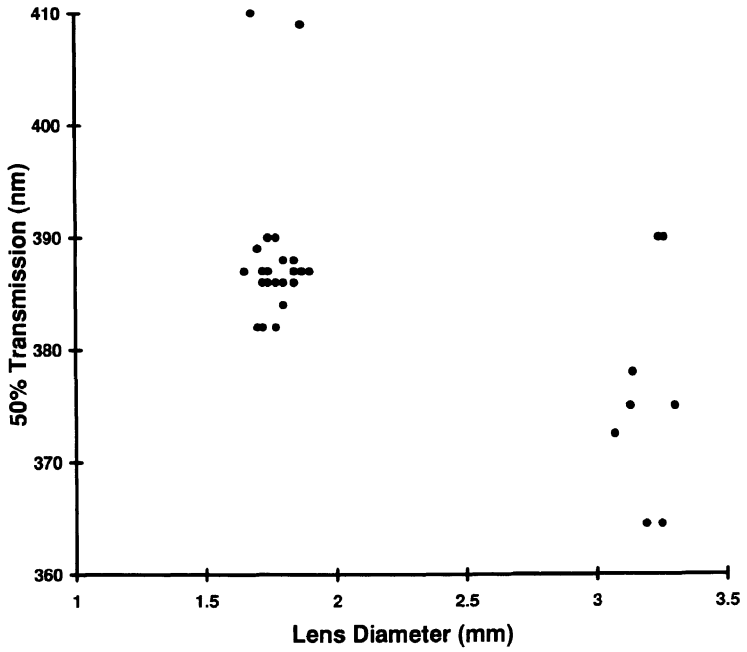

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Figure 6 Wavelength of 50% transmission as a function of lens diameter for various species of fish. The wavelength of 50% transmission indicates the amount of UV removed by the lens, while the lens diameter is a reliable indicator of fish age (Douglas 1987). (**a**) i – Unpigmented lenses of the Hake, *Merluccius merluccius* (triangles, the line, which fits the data well, is the expected relationship if lens transmission were determined solely by an increase in lens diameter without the accumulation of a specific short-wave absorbing pigment), ii – pigmented lenses of Tilapia, *Oreochromis niloticus*. (**b**) Pigmented lenses of Herring, *Clupea harengus*. (**c**) Pigmented lenses of Flying fish, *Exocoetus obtusirostris*. (**d**) Pigmented lenses of Kissing gourami, *Helostoma temmincki*. (Thorpe & Douglas 1993)

Not surprisingly, the most studied lenticular ageing is the reduced short-wave transmission of older human lenses (e.g. Said and Weale 1959; Boettner and Wolter 1962; Grover and Zigman 1972; Weale 1988). Such increased 'yellowing' with age has a marked effect on short-wave colour perception (Ruddock 1972; Werner 1982), and Monet's increased use of blue colours as he aged is, for instance, blamed on lenticular ageing. The mechanisms responsible for this process are complex, beyond the scope of this review and still not completely resolved, but it is clear that the human lens proteins undergo considerable modifications with age, often characterised by changes in fluorescence, which, at least in part, result from exposure to short-wave radiation (e.g. Lerman 1980, 1987; Zigman 1983, 1985; Sen *et al.,* 1992), although it is unlikely that all the pigmentary changes in the ageing human lens are related to prolonged exposure to light (Yu *et al.,* 1988). Perhaps surprisingly, the concentrations of all 3 tryptophan-derived short-wave filtering pigments so far described in the human lens, appear to decrease with age (Cooper and Robson 1969b; van Heyningen 1973b; Bando *et al.,* 1981; Wood and Truscott 1993, 1994). Consequently, the diminished age-related short-wave transmission of the human lens is probably attributable to the accumulation of one or more additional pigments, probably bound to lens proteins within the lens nucleus (e.g. Cooper and Robson 1969b; Zigman 1985; Yu *et al.,* 1989; Weale 1995).

Although, lens pigments are usually associated with animals living in relatively high light levels, a striking exception to this general trend are the large variety of pigments observed in several species of fish inhabiting the deep ocean, an environment with comparatively low levels of illumination (Plate 1e). Of the over 150 deep-sea fish examined to date 27 contain detectable amounts of pigmentation in their lens (Douglas and Thorpe, 1992; Douglas *et al.* 1995 for reviews). These pigments, as in the lenses and corneas of shallow water species, are either carotenoids, kynurenine derivatives, MAAs, or a variety of as yet unidentified substances (Douglas and Thorpe 1992 for review; Figure 7 and section 4.2.7e).

4.2.4 Humours

Dalton incorrectly attributed his own colour blindness to a blue tinted vitreous (Hunt *et al.,* 1995) and in general, there is little evidence for specific light-absorbing filters in either the aqueous or vitreous humour (e.g. *Fish* – McCandless *et al.,* 1969; *Mammals* – Merker 1934; Ambach *et al.,* 1994; *Birds* – Emmerton *et al.,* 1980, Govardovskii and Zueva 1977; Figure 8). The only exceptions are qualitative reports of a yellow vitreous in 2 species of fish (Lythgoe 1971; van Heyningen and Linklater 1976). Experience suggests, however, that these may be *post mortem* artefacts.

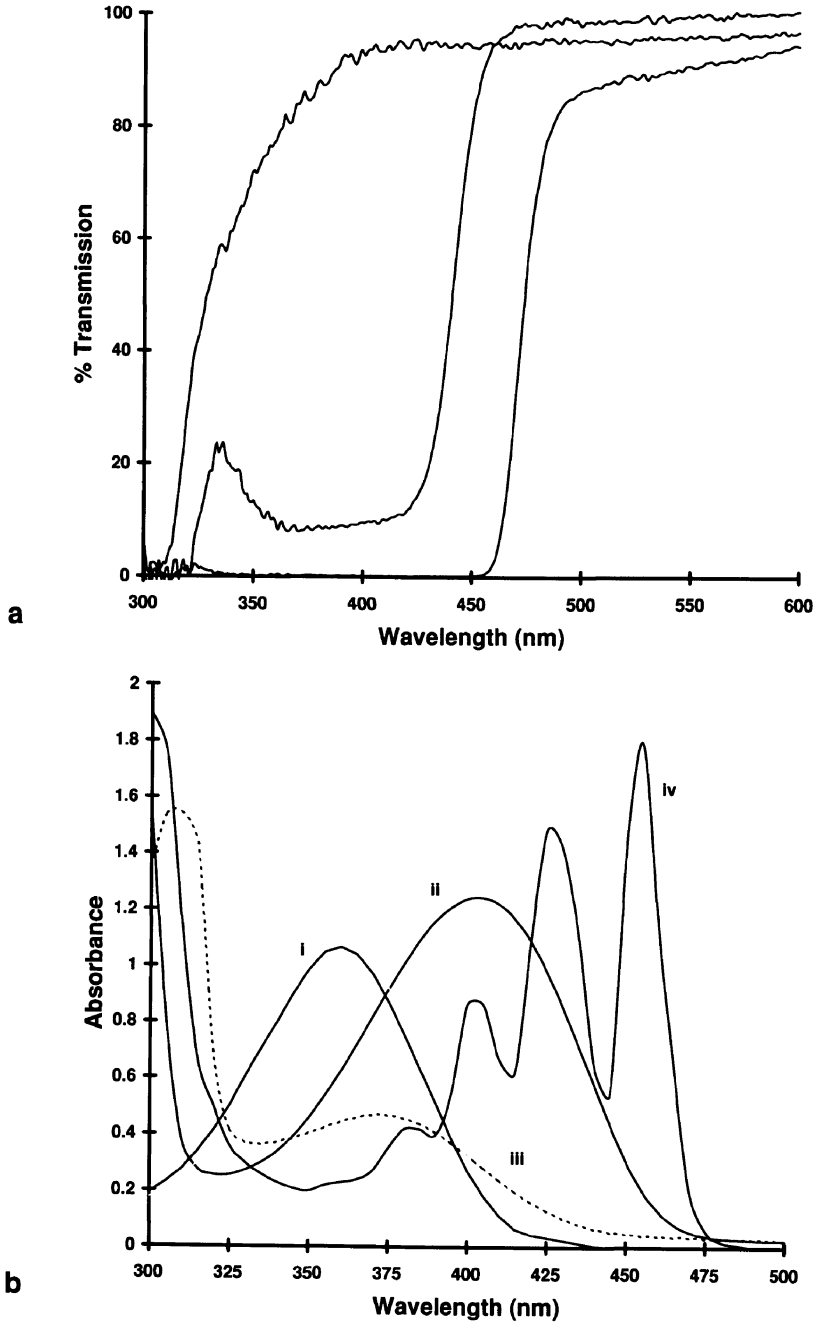


Figure 7 Spectral characteristics of some deep-sea fish lenses (**a**) Transmission spectra through the intact lenses of (left to right); i – *Diretmus argenteus* (diameter 4.0 mm), ii – *Evermanella balbo* (3.6 mm), iii – *Scopelarchus analis* (4.8 mm) (**b**) Absorbance spectra of pigments extracted from the lenses of; i – *Stylephorus chordatus* (λ_{max} 365nm, identified as kynurenine, Thorpe *et al.* 1992), ii – *Scopelarchus analis* (λ_{max} 403.5 mm, unidentified), iii – *Evermanella balbo* (λ_{max} 373 nm, unidentified, dotted line), iv – Intact lens of *Argyropelecus sladeni* displaying a profile typical of a carotenoid (Douglas & Thorpe 1992). All data are from Douglas (unpublished observations), except where indicated

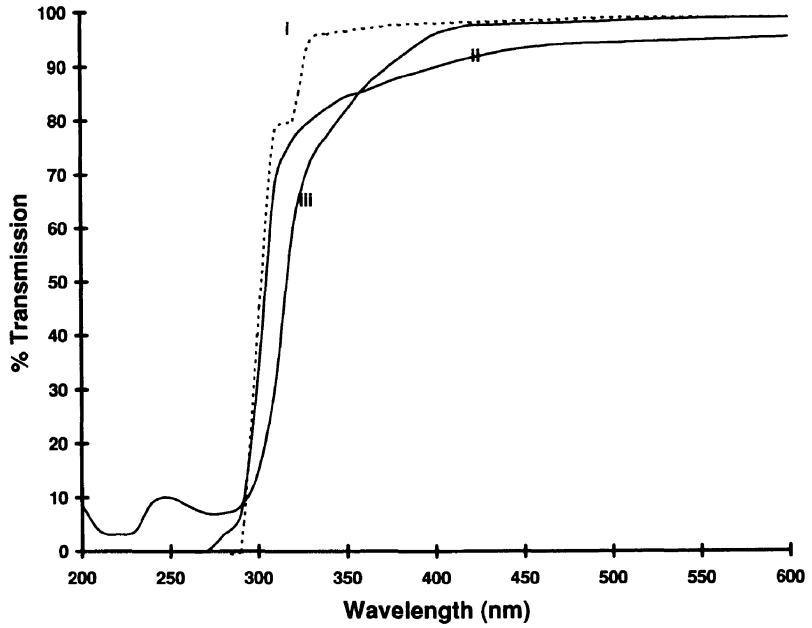


Figure 8 Spectral transmission of vertebrate humours. i – Ground squirrel aqueous humour (Chou & Cullen 1984, dotted line), ii – Human aqueous humour (Boettner & Wolter 1962), iii – Goldfish vitreous humour (Thorpe 1991)

4.2.5 Retina

(a) Blood Vessels The vascular supply to the retina differs markedly between species, ranging from an extensive capillary network throughout most of the retina to the complete absence of an intraretinal circulation (François and Neetens 1974). In animals with extensive retinal capillaries, such as many mammals, the blood, which has a pronounced absorbance maximum at around 420 nm, will inevitably act to some degree as a short-wave absorbing filter as it overlies the retina (Muntz 1972, Sivak and Roth 1978). Such filtering is likely to be uniform, as the vessels will be out of focus (Walls and Judd 1933a), and, due to the small amount of blood in the capillaries, its effect will be slight in comparison to the animal's overall dynamic range. Significant UV absorption by larger vessels has, however, been shown to protect the underlying retina from light induced damage (Collier *et al.*, 1989).

(b) Macular Pigment The central retina of diurnal primates, including man, contains a yellow region centred around the fovea, known as the *macula lutea* (Nussbaum *et al.*, 1981). The yellow colouration is due to a diffuse photostable short-wave absorbing pigment, located mainly within the Henle fibres and to a lesser extent in the inner plexiform layer (Snodderly *et al.*, 1984a,b).

Pigmentation is densest in the central fovea and declines towards the periphery (Snodderly *et al.*, 1984a,b, 1991; Weiter *et al.*, 1988; Abadi and Cox 1992).

Although there is some debate as to the exact form of the macular pigment absorption spectrum (Pease *et al.*, 1987; Stark 1987; Bone *et al.*, 1992), determined both spectroscopically and by psychophysical means, it is typical of a carotenoid (Figure 9, dotted line) and is thought to be a mixture of the xanthophylls, lutein & zeaxanthin (Bone *et al.*, 1985, 1988, 1992, 1993; Handelman *et al.*, 1988, 1991, 1992). As for other carotenoid-based pigments, such as retinal oil droplets (4.2.5c), it is possible to manipulate the level of macular pigmentation by dietary means (Malinow *et al.*, 1980). However, the frequently cited individual variation in the macular pigment density, is explained by both genetic and dietary factors (Hammond *et al.*, 1995). Absolute optical densities reported for humans range from 0 to 1.22, with average densities from 0.13 to 0.77 (Pease *et al.*, 1987 for review, also Werner *et al.*, 1987; Abadi and Cox 1992; Hammond and Fuld 1992; Wild and Hudson 1995).

A somewhat surprising feature of the macular pigment is that it is dichroic, possibly due to its close association with tubulin (Bernstein *et al.*, 1997), thereby causing the entoptic phenomena of Haidinger's brushes and Maxwell's spot (Nussbaum *et al.*, 1981; Bone and Landrum 1984; Snodderly *et al.*, 1984b), and possibly making it a more effective filter (Handelman *et al.*, 1991). The macular

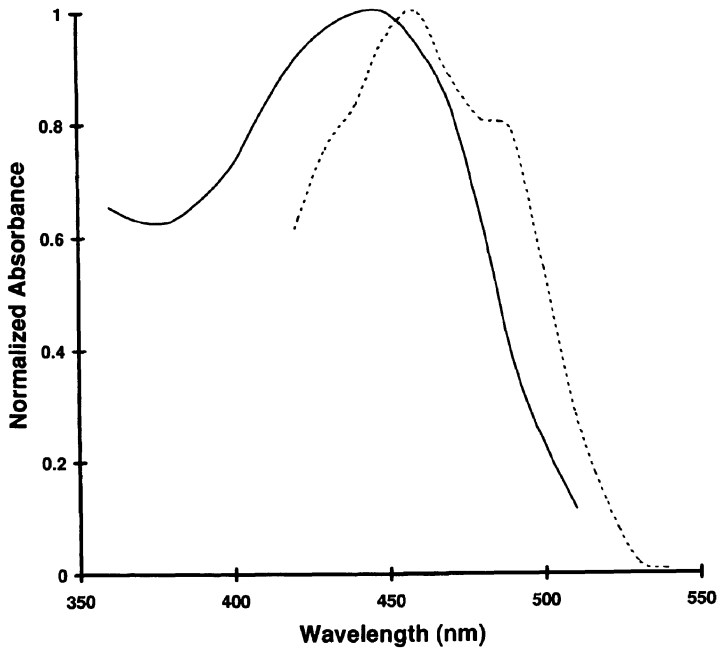


Figure 9 Absorbance spectra of photostable retinal pigments. i – yellow pigment extracted from the fish *Crenicichla lenticulata* (Muntz 1973, solid line), ii – human macular pigment (Vos 1972, in Bone *et al.*, 1992, dotted line)

pigment has two probable functions; the improvement of visual acuity by reducing the amount of chromatic aberration and atmospherically scattered light (section 4.2.7b), and the protection of the retina by both removing short wavelengths, which are those most likely to cause retinal damage, and by acting as a scavenger for cytotoxic free radicals (section 4.2.7a)

Although true macular pigment is restricted to primates, the retinae of some shallow (Muntz 1973, 1976a, 1982) as well as deep-water (Denton & Locket 1989) fish appear visibly yellow, due to the presence, possibly in the outer segments, of high concentrations of photostable short-wave absorbing pigments (Figure 9, solid line). As is the case for oil droplets (section 4.2.5c), the advantage of having the photostable pigment in the outer segment, is that it can act locally on individual receptors. Thus, in the deep-sea fish *Diretmus argenteus*, in a manner reminiscent of corneal eyeshade pigmentation (section 4.2.2), it is only the rods in the ventral retina, which receive the relatively brighter downwelling sunlight, that contain the photostable yellow pigment (Denton & Locket 1989).

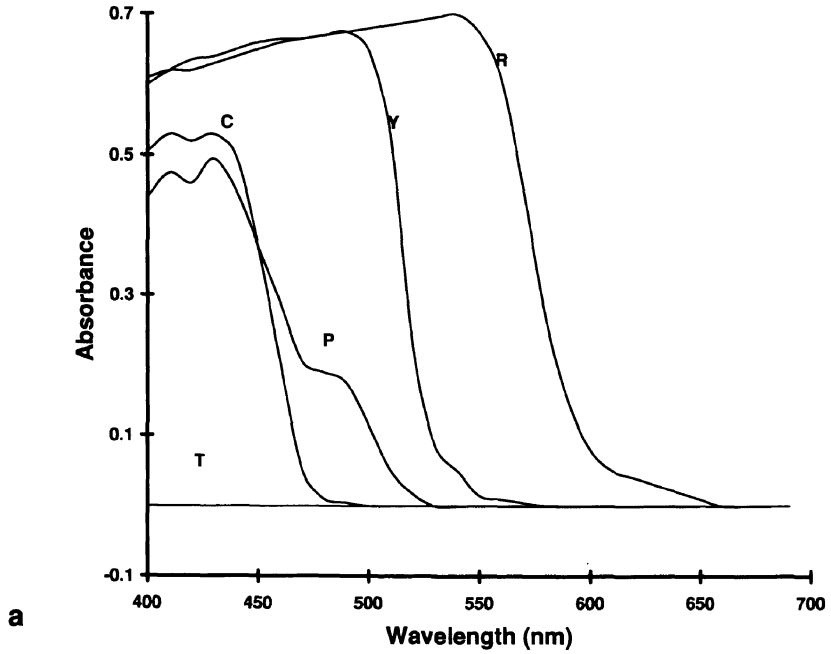
The outer segments of another species of deep-sea fish, *Malacosteus niger*, also contain a photostable pigment (Bowmaker *et al.*, 1988; Partridge *et al.*, 1989). However, this absorbs maximally at 670 nm, which is at significantly longer wavelengths than the visual pigments of this species. Its function therefore, is not as a selective filter and it probably serves as a photosensitiser, enabling these animals to see their own far-red bioluminescence (Bowmaker *et al.*, 1988; Douglas *et al.*, 1998; see also section 4.2.6b).

(c) Oil droplets The ellipsoids of cone inner segments of many birds (e.g. Goldsmith *et al.*, 1984; Partridge 1989; Plate 1i), and reptiles (e.g. Liebman and Granda 1975; Ohtsuka 1985; Lipetz 1984b), as well as some amphibia (Hailman 1976), monotreme mammals (Ahnelt *et al.*, 1995), and 'primitive' (Chondrostei and Dipnoi) fish (Govardovskii *et al.*, 1992; Robinson 1994), contain clear or coloured oil droplets (Muntz 1972; Young and Pettigrew 1991; Bowmaker 1991b for reviews). Oil droplets are absent in placental mammals and teleost fish. Since this structure is situated immediately in front of the light absorbing outer segment, most light absorbed by the visual pigments (> 90% – Wortel and Nuboer 1986; 60% – Schneeweis and Green 1995) will pass through it, inevitably altering the spectral sensitivity of the photoreceptor. Oil droplets usually occur as a single large structure filling the whole outer part of the ellipsoid, but more rarely can be composed of several smaller droplets (Pedler and Boyle 1969). The accessory members of the double cones of some birds and reptiles, as well as the inner segment of some lungfish cones, do not contain an oil droplet as such, yet the ellipsoid region nevertheless contains a similar short-wave absorbing pigment (Bowmaker and Knowles 1977: Jane and Bowmaker 1988; Maier and Bowmaker 1993; Kolb and Jones 1982; Figure 10b). Oil droplets generally act as edge filters transmitting long wavelengths and absorbing short-wave radiation, with a sharp cut-off at some intermediate wavelength that determines the colour of the oil droplet (Figure 10a).

The flat top of most published oil droplet absorbance spectra (Figure 10a) results either from the limited sensitivity of the measurement system or from light leaking around the oil droplets. In turtles, for example, peak optical densities of intact droplets may be as high as 90 (Liebman and Granda 1975). However, thin layers or dilute extracts of oil droplets have absorption spectra typical of carotenoids (Liebman and Granda 1975; Lipetz 1984b; Goldsmith *et al.,* 1984; Figure 10b), as do the relatively lightly pigmented oil droplets and the droplet-free ellipsoids of some species (Bowmaker and Knowles 1977; Jane and Bowmaker 1988; Maier and Bowmaker 1993; Figure 10b). Thus, oil droplets are composed almost entirely of neutral lipids (Johnston and Hudson 1976) and dietary derived carotenoids such as zeaxanthin, astaxanthin and galloxanthin (Wallman 1979; Goldsmith *et al.,* 1984; Schiedt *et al.,* 1991; Bowmaker *et al.,* 1993).

Early workers attributed a variety of functions to oil droplets (Walls and Judd 1933a&b, Walls 1963, Muntz 1972, Wolbarsht 1976 for reviews), most notably perhaps that they were a means by which animals, assumed to have only a single visual pigment, could produce a system for colour vision (e.g. King-Smith 1969). However, many factors have since made this suggestion untenable, most obviously the discovery of more than one cone visual pigment in most animals, including those with coloured oil droplets, and the maintenance of colour vision following dietary oil droplet pigment depletion (Wallman 1979). Consequently, numerous other roles have been assigned to oil droplets. They might, for instance, perform some of the functions attributed to other intraocular short-wave filters (sections 4.2.7a&b), such as reducing chromatic aberration, increasing contrast and protecting the retina. Rather like the filtering pigments found in some fish outer segments (section 4.2.5b), they have an advantage over more global filters, such as the lens, as they act on individual photoreceptors. In general, the longer the λ_{max} of a cone's visual pigment, the more short-wave radiation is removed by the oil droplet associated with it (Ohtsuka 1985; Jane and Bowmaker 1988; Bowmaker 1991a&b; Bowmaker *et al.,* 1993; Maier and Bowmaker 1993). Thus, long-wave sensitive cones often have red coloured oil droplets, thereby exposing their outer segments only to 'optically advantageous' long wavelengths. UV-sensitive cones, on the other hand, have completely unpigmented oil droplets. Consequently, within a single retina, oil droplets are tuned to remove as much 'harmful' short-wave radiation from each cone type as possible, yet still allow an overall broad retinal spectral sensitivity.

Oil droplets, especially those that are transparent to UV and which therefore cannot perform a filtering role, could also act as microlenses to enhance outer segment photon capture (Walls and Judd 1933a; Young and Martin 1984). Alternatively it has been suggested that they contribute to polarisation sensitivity (Young and Martin 1984), and function as chemical storage organs (Hailman 1976). The most attractive function of coloured oil droplets, however, is that they enhance colour vision either by increasing the available number of spectrally



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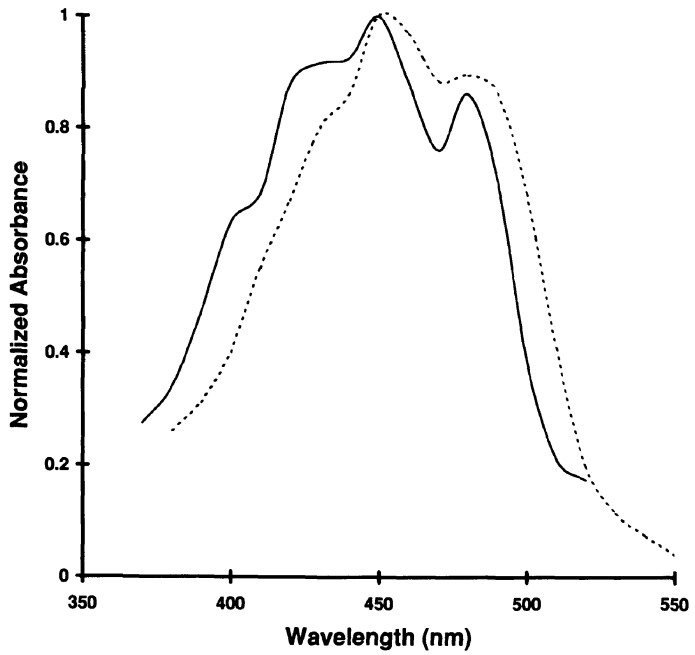

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Figure 10 Spectral characteristics of oil droplets (**a**) Absorbance spectra of Duck (*Anas platyrhynchos*) retinal oil droplets; T – translucent, C – clear, P – pale, Y – yellow, R – red (Jane & Bowmaker 1988). (**b**) Absorbance spectra of; i – 'thinned' yellow oil droplets from the retina of the Turtle (*Emydoidea blandingii*) (Lipetz 1984b, dotted line), ii – the pigment from the oil droplet free accessory cone ellipsoid of the Peking robin (*Leiothrix lutea*) (Maier & Bowmaker 1993, solid line)

distinct photoreceptor types or by sharpening/tuning the response of existing spectral channels. Classically, the pigeon retina, for example, was described as containing 3 different cone visual pigments and 5 oil droplet types, which combined to form 6 spectrally distinct cone types (Bowmaker 1977, 1980). Similarly, the three visual pigments of the turtle that have been described by microspectrophotometry could combine with a variety of oil droplets to give at least six spectrally distinct cones (Schneeweis and Green 1995 for review). Recently, however, the picture, as far as the pigeon is concerned at least, has become somewhat more complex, since pigeons most likely have 5 cone visual pigments (λ_{max}s ca366 nm, 409 nm, 453 nm, 507 nm and 568 nm; Bowmaker *pers com*; Vos *et al.*, 1994). Furthermore, it is probable that not all the possible 7 cone/oil droplet combinations are used in colour vision. It is likely that only single cones, which contain their own exclusive oil droplet types, are involved in chromatic vision, with the double cones possibly coding for luminosity (Maier and Bowmaker 1993). Thus, the most likely function for oil droplets in this situation is not to increase the number of spectral channels available but to narrow existing spectral sensitivities of visual pigments. Such spectral 'tuning' has been shown both theoretically (Bowmaker and Knowles 1977; Bowmaker 1977, 1980; Govardovskii 1983; Jane and Bowmaker 1988) and practically (Martin and Muntz 1979; Neumeyer and Jäger 1985; Maier and Bowmaker 1993) and is accompanied by a shift in wavelength of peak absorption towards longer wavelengths, and a reduction in its overall sensitivity and may serve to enhance hue discrimination (Barlow 1982; Govardovskii 1983; Bowmaker 1991a). A modulatory role for oil droplets in colour vision is supported by the observation that colour vision is altered in birds whose oil droplets have been depleted of carotenoids (Wallman 1979), while visual pigments are unaffected by similar treatment (Bowmaker *et al.*, 1993).

Oil droplets in some (Muntz 1972, Lythgoe 1979), but not all (Jane and Bowmaker 1988) retinae, are unevenly distributed. The pigeon and a number of other herbivorous birds have a posterior dorsal retinal area (the region for looking forward and downward) dominated by single cones associated with red oil droplets (Pedler and Boyle 1969; Bowmaker 1977). The resulting regional variation in spectral sensitivity potentially allows fine spectral discrimination of green foliage (Bowmaker 1979; Martin and Muntz 1978, 1979; Remy and Emmerton 1989; Lythgoe 1979).

Light coloured sea-birds have a general abundance of red and orange oil drops in their retinae. It is argued that this enables them to cut through atmospheric haze and detect other light coloured birds, which may be forming feeding clusters, a long way off (Lythgoe 1979). For birds feeding from the surface red oil drops may also help to filter the scattered light from the surface, enabling them to see further into the water to detect prey (Muntz 1972). Other diving birds and birds which feed underwater possess relatively fewer long-wave filtering oil drops which may reduce sensitivity to the short wavelengths needed for prey

detection beneath the surface (Lythgoe 1979 and see section 4.2.7). However, such ecological explanations for inter-specific variation in oil droplet content may not always be applicable (Begin & Handford 1987).

(d) Ellipsosomes Several teleost fish possess structures which superficially resemble the oil droplets of other animals (e.g. Berger 1966; MacNichol *et al.*, 1978; Nag 1995). Like oil droplets, these ellipsosomes are positioned within the outer segment of some cone types immediately before the outer segment. Although these structures resemble classical oil droplets in certain ways, they are in fact quite distinct organelles since they have, for instance, different staining properties (Kunz and Regan 1973, Nag and Bhattacharjee 1995), develop later (Kunz and Wise 1973, Nag and Bhattacharjee 1995), and possess certain components such as cristae-like structures (Kunz and Wise 1973; Borwein and Hollenberg 1973; Anctil and Ali 1976), which oil droplets do not. Ellipsosomes almost certainly have a mitochondrial origin and contain a pigment similar in its spectral absorbance characteristics to reduced cytochrome c (λ_{max} 415 nm) (MacNichol *et al.*, 1978; Avery and Bowmaker 1982; Figure 11). Since this pigment can have a peak optical density of 0.5 or more, it appears visibly pink in fresh preparations and will prevent much of the incident short-wave (400 – 430 nm) radiation impinging on the outer segments of cones possessing ellipsosomes. Thus, like oil droplets, ellipsosomes will alter the spectral sensitivity functions of the different cone types and possibly enhance wavelength discrimination (Avery and Bowmaker 1982; Bowmaker 1990). Although, true ellipsosomes, containing high densities of cytochrome c are restricted to the cones of teleost fish, primate photoreceptor inner segments have also been found to contain smaller amounts of similar photostable pigments (Snodderly *et al.*, 1984a; Bowmaker *et al.*, 1991).

(e) Visual pigments The visual pigments themselves and their photoproducts could act as selective chromatic filters, as light has to pass through them in order to get to the more scleral parts of the outer segments (Goldstein and Williams 1966, Muntz 1972; Alpern *et al.*, 1987). Although, photoproducts are probably too short-lived to have a significant influence in vertebrate receptors, the longer lasting invertebrate photoproducts may have a greater role to play (section 4.3.3). Self screening by the visual pigment, however, may be of some importance in vertebrates, especially if the optical density of the pigment is high and the outer segments are long. It may, for instance, play a significant role in some species of deep-sea fish which are known to have several layers of rod outer segments. Such animals, could theoretically have a form of colour vision based on just a single photopigment, as the spectral sensitivity of each layer of rods will be significantly different because of modification of the incident light by more vitread layers (Denton and Locket 1989).

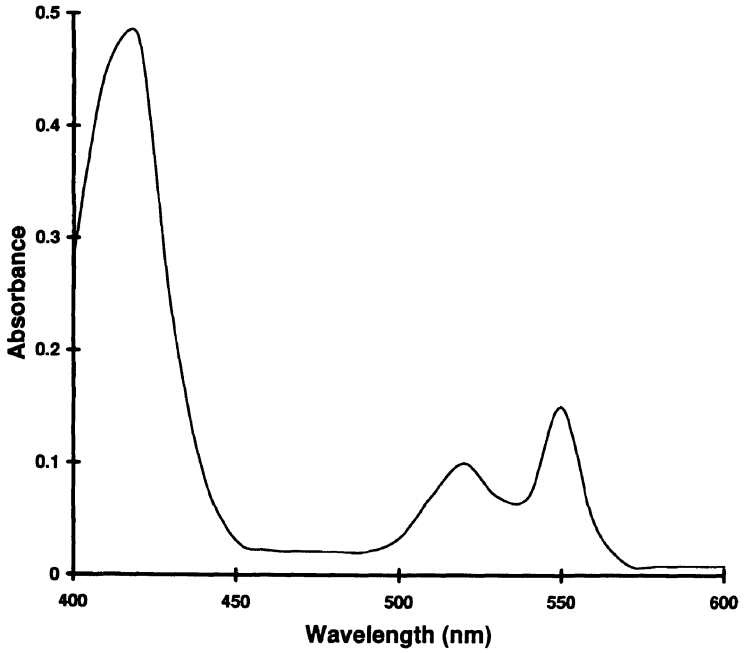


Figure 11 Mean absorbance spectrum of six *Anableps anableps* ellipsosomes. (Avery & Bowmaker 1982)

4.2.6 Postreceptoral filters

Much of the light that reaches the level of the retinal photoreceptors is not absorbed by the photopigments but passes beyond the rods and cones and strikes the retinal pigment epithelium (RPE). In most animals the RPE contains the pigment melanin, which absorbs most of this stray light. However, some species living in low light levels, have highly reflective tapeta, either within the RPE or choroid, that direct this light back towards the photoreceptors. Even in animals with no tapetum, a small amount of light will be reflected from the RPE onto the photoreceptors. As neither melanin nor tapetal reflecting pigments are spectrally neutral, they will act as wavelength selective filters.

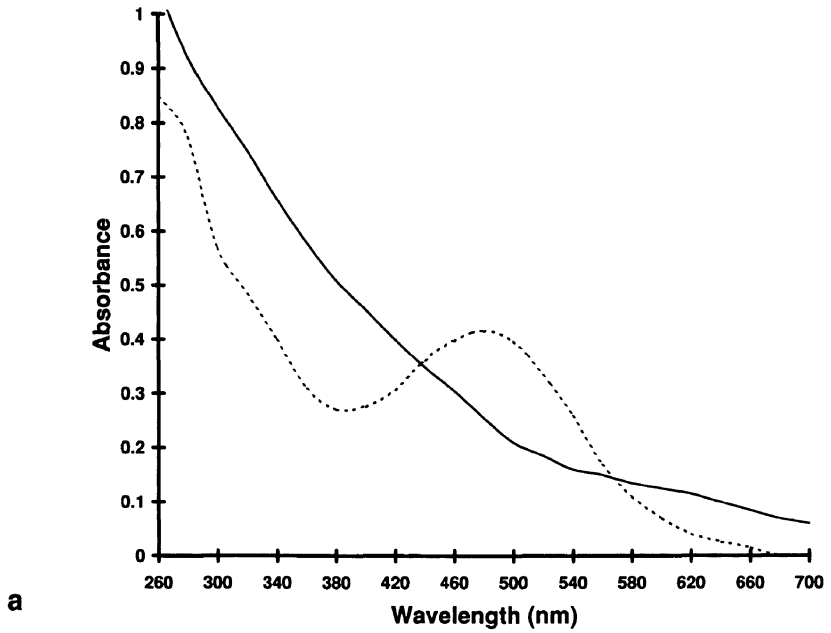
(a) Melanin The main function of the melanin within the RPE is usually thought to be for the absorbtion of stray light, thereby, along with similar pigments in the choroid, ciliary body and iris, contributing to the eye's black box effect, thus enhancing image quality. However, melanin almost certainly also protects the retina from light damage, either by simply decreasing the amount of scattered light or, in a way analogous to the macular pigment, acting as a lipid anti-oxidant by scavenging free radicals and singlet oxygen (section 4.2.7a), although there is some suggestion that melanin might also actually contribute to retinal damage by being a cause of oxidative free radical stress (Sarna 1992 for review).

In 'lower' vertebrates, such as fish and amphibia, the melanin within the RPE, along with the photoreceptors, undertakes diurnal migrations, aggregating near the choroid in dark adapted conditions and expanding to fill most of the rod and cone layer, thereby completely covering the rod outer segments, during light adaptation (Wagner *et al.*, 1992 for review). These 'retinomotor' movements serve both to position the rods and cones optimally for respectively scotopic and photopic vision, and to protect the rods from excessive bleaching in daytime light levels (Douglas 1982).

The absorbance spectrum of RPE melanin has been measured for a number of vertebrates, most commonly humans, and generally absorbance increases with decreasing wavelengths (Geeraets and Berry 1968; Hunold and Malessa 1974; Boulton *et al.*, 1990; Figure 12a) contributing to greater reflection at longer wavelengths (Figure 12b). Although the predominant pigment in the RPE of most species is melanin, in some fish it is replaced by a red pigment (Ito *et al.*, 1975; Best and Nicol 1984; Figure 12a) leading to enhanced long-wave reflectance (Figure 12b).

(b) Tapetum lucidum Tapeta are widespread among nocturnal animals and those inhabiting dimly lit environments (Walls 1963; Nicol 1981). The most commonly held view is that tapeta serve to reflect light back through the retina, giving the photoreceptors a second chance of absorbing the light, thereby enhancing overall retinal sensitivity, often at the expense of image quality. However, in many cases the improvement in sensitivity is surprisingly small (Muntz 1990). Furthermore, Denton and Nicol (1964) showed that in deep-sea fish, the photoreceptors of species with tapeta had approximately half the visual pigment density of non-tapetal animals, resulting in a similar quantum capture in all species. The advantage of a tapetum in these animals is therefore not a simple increase in the number of photons absorbed, but might arise from a reduction in the amount of thermal noise resulting from lower visual pigment densities.

There are a variety of structural types of tapeta both within the RPE and the choroid (Walls 1963; Muntz 1972; Nicol 1981 for reviews) containing a number of different reflecting materials, most commonly guanine. Retinal tapeta are composed of either small densely packed reflective particles or stacks of thin reflective plates within the RPE. Choroidal tapeta are of two types; the tapetum cellulosum composed of tiers of reflecting cells, and the tapetum fibrosum, which is made up of densely packed connective tissue fibres, such as collagen. Tapeta are often restricted to the dorsal half of the eye, which receives the lowest intensity radiation. Some form of reflecting layer has been described in most vertebrate groups (Walls 1963), but specialised tapeta are particularly well developed in most classes of fish (Denton and Nicol 1964; Nicol and Arnott 1973; Locket 1977; Best and Nicol 1980; Somiya 1980; Nicol 1989 for reviews), many mammals (e.g. Dartnall *et al.*, 1965; Braekevelt 1993; Wen *et al.*, 1985) and some reptiles (Laurens and Detwiler 1921) and birds (Nicol and Arnott 1974). Since



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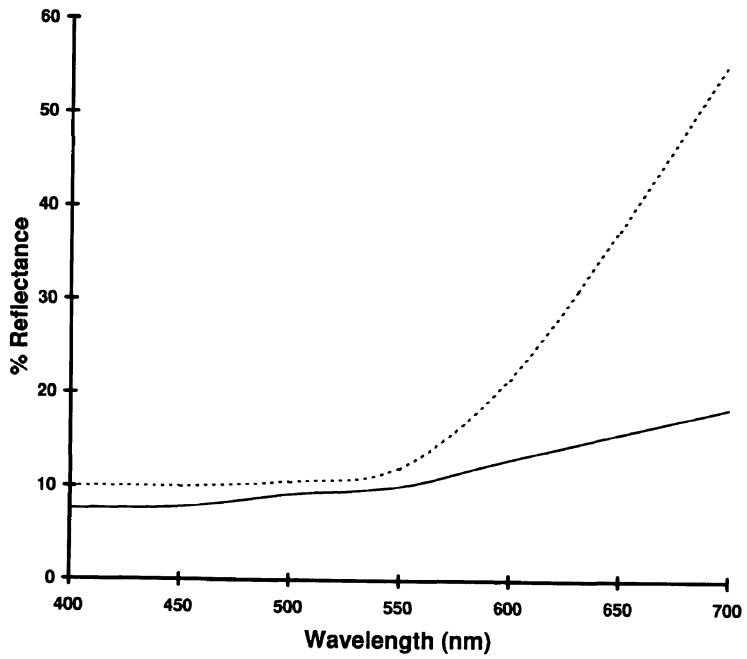

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Figure 12 Spectral characteristics of retinal pigment epithelium (**a**) Absorbance spectra of; i – dissolved RPE melanin from humans aged 30 – 49 years (Boulton *et al.* 1990, solid line), ii – red pigment extracted from the RPE of the cunner (Best & Nicol 1984, dotted line), (**b**) Spectral reflectance of; i – human RPE and choroid (Geeraets & Berry 1968, solid line), ii - RPE of the chain pickerel (Best & Nicol 1984, dotted line)

tapeta are usually only beneficial in low light levels and may cause image degradation in brighter light, some fish have developed occlusable tapeta in which melanin migrates to cover the reflective material during light adaptation (Denton and Nicol 1964; Heath and Hindman 1988).

Surprisingly, given the wealth of structural and biochemical data, information on spectral reflectance characteristics of vertebrate tapeta are relatively sparse. However, it is clear, given the large range in colours of observable eyeshine, that spectra will differ between species (Figure 13 and see Nicol 1981 for review). Furthermore, significant differences between the eyeshine of members of the same species (Weale 1953) and even regional differences within a single retina (Wang *et al.,* 1980), are not uncommon. Spectral reflection curves, which can range from a wide spectral bandwidth, usually indicated by a white/silvery tapetum (Figure 13, curve i), to more narrowly defined spectra, giving rise to specific colours such as blue, green or red, have been obtained from; cat (Weale 1953), bush baby (Dartnall *et al.,* 1965), and various species of fish (Denton and Nicol 1964; Arnott *et al.,* 1974; Wang and Nicol 1974; Nicol *et al.,* 1975; Wang *et al.,* 1980, 1981; Figure 13).

It seems probable that the wavelengths reflected by a selective tapetum are those that are in some way most relevant to the animal. For example, in cartilaginous fishes, deep-water species have shorter wavelength reflecting tapeta than shallow water animals, which matches both the predominant wavelengths in the deep-sea and the shorter-wave absorbing visual pigments of the fish living there (Denton and Nicol 1964). Similarly, tapeta of fish living in freshwater, in which long wavelengths usually predominate, often reflect red light most efficiently (e.g. Wang and Nicol 1974). However, such simple relationships are far from universal (Nicol 1981), and in general, correlating an animal's environment with its visual system is fraught with difficulties, primarily because the environmental factors most relevant to an animal are usually not known in enough detail.

The deep-sea is optically a relatively simple environment, with a narrow spectral band of downwelling illumination centred around 470 – 490 nm and bioluminescent emissions which are often well characterised (section 4.2.7e). Furthermore, many deep-sea fish have comparatively simple visual systems using just a single visual pigment (e.g. Douglas *et al.,* 1995). Consequently, the spectral characteristics of deep-sea fish tapeta provide good examples of adaptations to specific functions. *Malacosteus niger*, for example, is unusual in having far-red bioluminescent emissions peaking around 706 nm, which are invisible to most animals in the deep-sea (Widder *et al.,* 1984; Denton *et al.,* 1985). To facilitate the detection of its own red bioluminescence, it has both long-wave-shifted visual pigments in comparison to most other deep-sea fish (Bowmaker *et al.,* 1988; Partridge *et al.,* 1989) which may be linked to a long-wave photosensitising pigment (section 4.2.5b), and a bright red, astaxanthin-based, long-wave reflecting tapetum (Denton and Herring 1971; Locket 1977; Somiya 1982; Bowmaker *et al.,* 1988; Figure 13 curve iii). A 'normal' deep-sea

fish, such as *Diaphus rafinesquei*, on the other hand, has a tapetum, which appears blue, reflecting maximally around 460 nm (Figure 13 curve ii), that both matches the predominant wavelength of the remaining downwelling illumination, and the emission maxima of most bioluminescent stimuli (section 4.2.7e) and is similar to the absorption spectrum of this animal's single visual pigment (λ_{max} 488 nm, Partridge *et al.*, 1988).

4.2.7 Function of short-wave absorbing filters

As many vertebrate filters act primarily as short-wave absorbing filters, they probably have similar functions (Walls & Judd 1933a; Muntz 1972; Wolbarsht 1976; Kirschfeld 1982; for reviews). Unfortunately, many of the proposed functions remain speculative as they are difficult to prove experimentally. Furthermore, the various theories should not be seen as mutually exclusive, and many short-wave absorbing filters probably perform more than one function.

Most proposed functions for short-wave absorbing filters relate to the fact that, with the obvious exception of deep-sea species, animals with such filters tend to be diurnal, inhabiting relatively high light level environments. Furthermore, if a pigment is unevenly distributed, such as is the case in many fish corneas (section 4.2.2), it is the dorsal area receiving most illumination that is most heavily pigmented. Thus, if animals are exposed to high light levels, there seems to be some benefit derived from decreasing the intensity of short-wave radiation

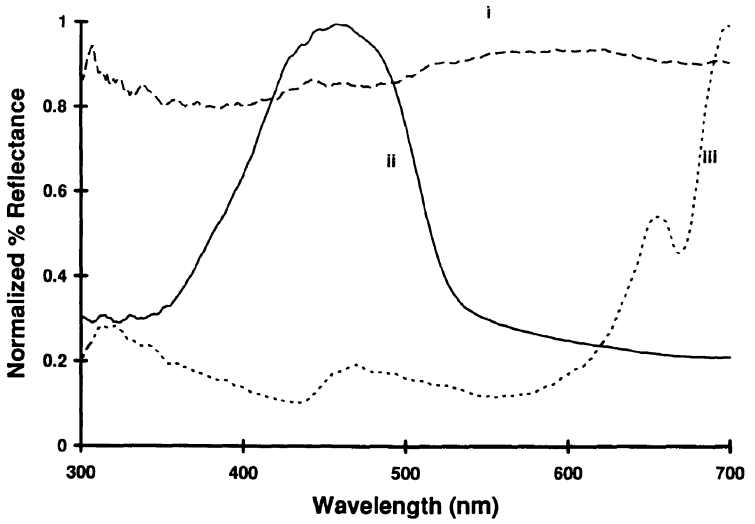


Figure 13 Examples of tapetal reflectance curves from some deep-sea teleosts. i – *Rinoctes sp.*, ii – *Diaphus rafinesquei* and iii – *Malacosteus niger*. All data from Marshall (unpublished observations). Data were obtained using intact eyes measured through aphakic gaps so include any corneal but not lens absorbance. Measurements were made with 'Sub-Spec' an Oriel Instruments/Andor Technology reflectance meter, a Xenon arc lamp and a 'Spectralon' white standard

reaching the retina. Nocturnal animals, or animals living in low light levels, on the other hand, generally do not have short-wave absorbing filters in their eyes, presumably because they would derive no benefit from doing so and would be severely disadvantaged by the inevitable reduction in sensitivity.

It should also be stressed that although short-wave filters are common in diurnal animals, many such species do not possess them, potentially enabling them to perceive UV wavelengths (Douglas and McGuigan 1989; Jacobs 1992). In general, the ocular media set the short wavelength limit to vision. For example, the human 'blue' cones could absorb significant amounts of radiation in the UV (Dartnall *et al.,* 1983). However, they are prevented from doing so by the absorption of these wavelengths by the lens. If the lens is removed, UV becomes perceptible to humans (Stark 1987; Griswold and Stark 1992). Surprisingly however, the possession of intraocular short-wave absorbing filters and UV vision are not always mutually exclusive since a species of diurnal gecko has both a yellow lens and a UV-sensitive retina (Ellingson *et al.,* 1995). In this case, the relatively low optical density of the pigment (1.3) probably represents a compromise, being low enough to allow sufficient UV to reach the retina to enable short-wave sensitivity, yet high enough to bestow on the retina the benefits of diminished levels of short-wave radiation.

(a) Protection Light is potentially damaging to the eye. The degree of actinic photochemical retinal damage in vertebrates, which is probably mediated through photoxidative processes (Ham *et al.,* 1984; Gerster 1991), is related to the wavelength of the incident illumination. In mammals, the incidence of retinal damage rises dramatically at wavelengths below 500 nm and can be particularly severe in the UV (Ham *et al.,* 1976, 1979, 1982; Organisciak and Winkler 1994 for review). UV has also been shown to have similar deleterious effects on the non-primate retina (Zigman and Bagley 1971; van Norren and Schellekens 1990; van Norren 1991). Any short-wave absorbing pigment, regardless of where it is located in the eye, will protect the retina from these potentially damaging wavelengths.

Both light and oxygen can be toxic to cells. Together their toxicity is enhanced (Ham *et al.,* 1984). Thus, the retina, more so than any other tissue, is very susceptible to such photoxidative damage, as light is focused on highly oxygenated cells. This light, apart from being absorbed by the visual pigment, will interact with various photosensitisers such as porphyrins, which are abundant within the retina, resulting in the production of free radicals and excited molecules, such as singlet oxygen, which can cause extensive cellular damage (Krinsky 1979; Kirschfeld 1982; Ham *et al.,* 1984; Handleman and Dratz 1986; Gerster 1991; Schalch 1992).

Carotenoids, such as β-carotene, are known to be highly effective quenchers of various stages of the photoxidative reaction and can prevent harmful reactions such as lipid peroxidation (Krinsky 1979; Burton and Ingold 1984). It is therefore

likely that retinal carotenoids, such as the macular pigment, apart from simply absorbing the most damaging wavelengths, also protect the retina against photoxidative damage by acting as free radical and singlet oxygen scavengers (Kirschfeld 1982; Ham *et al.,* 1984; Handleman and Dratz 1986; Gerster 1991; Schalch 1992). Apart from the macular pigment, other carotenoids, such as those found in the oil droplets of many vertebrates (section 4.2.5c), and in some invertebrate retinae (section 4.3.3b), may have a similar protective role. Furthermore, it is possible, that the carotenoids in the corneas of some species (section 4.2.2) and in the human lens (Yeum *et al.,* 1995) could also help to protect these structures from photoxidative damage.

Although most of the proposed functions for short-wave absorbing filters are difficult to prove experimentally, there is some evidence supporting a protective role. Such a function for the primate macular pigment, for instance, is indicated by the observation that the loss of short-wave sensitivity normally associated with human ageing is higher in the relatively unpigmented periphery than in the pigmented foveola (Haegstrom-Portnoy 1988) and that the macular area is less prone to phototoxic damage than the periphery (Ham *et al.,* 1978; Jaffe and Wood 1988; Weiter *et al.,* 1988). Dietary manipulation of carotenoid levels also supports a protective role for the macular pigment (Snodderly 1995). When monkeys are deprived of carotenoids, their retinae show degenerative changes possibly related to the lack of macular pigmentation (Malinow *et al.,* 1980), while the experimental administration of carotenoids protects the mammalian retina to some extent from photochemical damage (Ham *et al.,* 1984; Tso 1989). A protective role for lens pigments is indicated by the observation that retinae of squirrel eyes which have had their highly pigmented lens removed, suffer considerable damage following exposure to UV radiation, while the retinae of intact companion eyes remain unaffected (Collier *et al.,* 1989).

(b) Enhancement of image quality Short wavelengths are not only potentially harmful to the retina, but they also degrade the retinal image in comparison to longer wavelengths. Their removal should therefore result in increased image quality.

The refractive index of an optical structure, which determines its focal length, will vary with the wavelength of incident light. Different wavelengths will therefore be focused at different levels within the retina. As short wavelengths are most prone to such chromatic aberration, their removal will increase image quality (Walls and Judd 1933a; Reading and Weale 1974; Muntz 1976a; Sivak and Bobier 1978).

Short wavelengths are also more prone to some forms of scatter than longer wavelengths. Scattering caused by small particles (Rayleigh scattering) is greatly increased at short wavelengths, while scattering from large particles is wavelength independent (Muntz 1976a). Light can be scattered by both substances within the eye and in the environment. While environmental wavelength-

dependent Rayleigh scatter is widespread, the majority of intraocular scatter, at least in humans, probably arises from wavelength-independent scatter (Wooten and Geri 1987; van den Berg and Ijspeert 1995).

Short-wave absorbing filters will reduce the amount of Rayleigh scatter. This can have several beneficial effects. Firstly, the overall image quality will be enhanced. Secondly, in bright light, scatter will result in 'glare' and 'dazzle', which will be reduced by short-wave filters. Yellow intraocular filters can also increase the contrast and hence the distance at which objects become visible, by reducing the 'blue haze', caused by short-wave environmental scatter, intervening between an object and the observer (Walls and Judd 1933a; Walls 1963; Muntz 1972, 1976a).

Scattered light is a special problem for animals living underwater, as it can be caused both by the water molecules themselves and by small particles, such as plankton, suspended in the water column. This scattered light, will reduce the range at which objects will be visible underwater (Lythgoe 1975, 1976; Muntz 1976a) and might account for the widespread occurrence of short-wave filters in fish.

As well as enhancing the contrast of objects by removing the scattered 'veiling brightness', short-wave absorbing filters can also decrease the intensity of blue backgrounds, such as the sky and oceanic waters. This increases the contrast of light objects seen against such backgrounds and therefore improves their visibility (Walls and Judd 1933a; Walls 1963; Muntz 1972). A special case of such contrast enhancement is provided by deep-sea animals (section 4.2.7e).

(c) Functions unrelated to spectral filtering Just because a structure in the eye is not spectrally neutral in its absorption one cannot *a priori* assume that its primary purpose is to act as a wavelength selective filter. Vertebrate oil droplets, for example, might act as microlenses or serve as nutritive stores (section 4.2.5c), while carotenoids, such as the macular pigment, are scavengers of free radicals and singlet oxygen (section 4.4.1b), functions quite unrelated to their absorbance spectra. Furthermore, the corneal iridescence of some fish (section 4.2.2; Lythgoe 1976) and invertebrates (4.3.1a), might be primarily a device for camouflaging the eye and it has been suggested that the macular pigment could be a secondary oxygen carrying mechanism for the avascular fovea (Nussbaum *et al.*, 1981). Similarly, although retinal blood vessels will inevitably filter out some light (4.2.5a), this is obviously not their primary function. Cytochromes are also primarily involved in respiration, although they will filter light to some extent (4.2.5d). However, there is likely to be great selective pressure against any structure that significantly impairs visual performance and it is therefore likely that the wavelength-selective effect of these filters is either small or their filtering effect is beneficial to the system even if it is not their primary function.

(d) Functionless result of light exposure It is conceivable that some ocular filters serve no direct function and are simply the inevitable by-product of some

other process. For example, since ocular filters are usually found in animals living in high light levels, it is possible that they are the direct result of light exposure. The age-related 'yellowing' of the mammalian lens, for instance, is probably a consequence, at least in part, of prolonged exposure to short-wave radiation resulting in the accumulation of short-wave absorbing waste products which cannot be disposed of (section 4.2.3). It is certainly difficult to imagine a function for such decreased short-wave transmission with age. Similarly, a direct effect of light on goldfish corneal transmission is likely, since fish raised in high light levels have significantly more skin colouration and greater levels of corneal pigmentation than animals raised in lower light levels (Figure 14). Interestingly, Muntz (1973) also noted that the corneas of fish kept in captivity were much paler than those of fish caught in the wild.

Although light can have a direct effect on ocular media transmission, it is unlikely that short-wave absorbing pigments in general are a direct response to high light levels. For instance, it cannot account for the fact that some fish are born with highly pigmented lenses (section 4.2.3) and that primate macular pigment density changes little with age (Bone *et al.*, 1988). It is also inconsistent

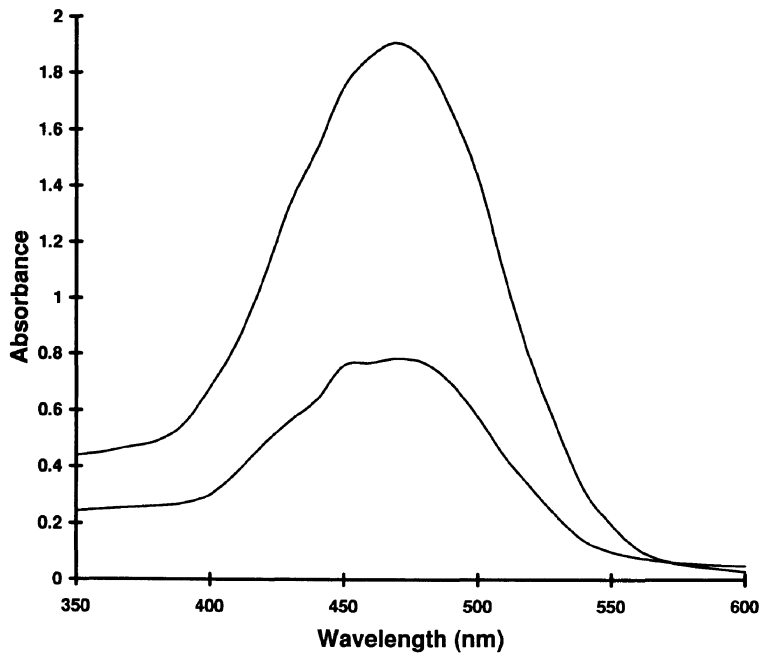


Figure 14 Relative spectral absorbance of acetone extracts of the corneal dorsal eye-shade pigment from *Carassius auratus* raised in different light levels; i – high light (1660 lux for 22 hrs out of every 24 hrs for 11 months, upper curve) and ii – low light (0.94 lux for 2 hrs out of every 24 hrs for 11 months, lower curve) levels. Traces are corrected for differences in extract volume and number of corneas in each sample. Although the degree of dorsal carotenoid eye shade pigmentation varied with rearing conditions, the MAA pigment (λ_{max} 325nm) present throughout the cornea was unaffected (Thorpe 1991)

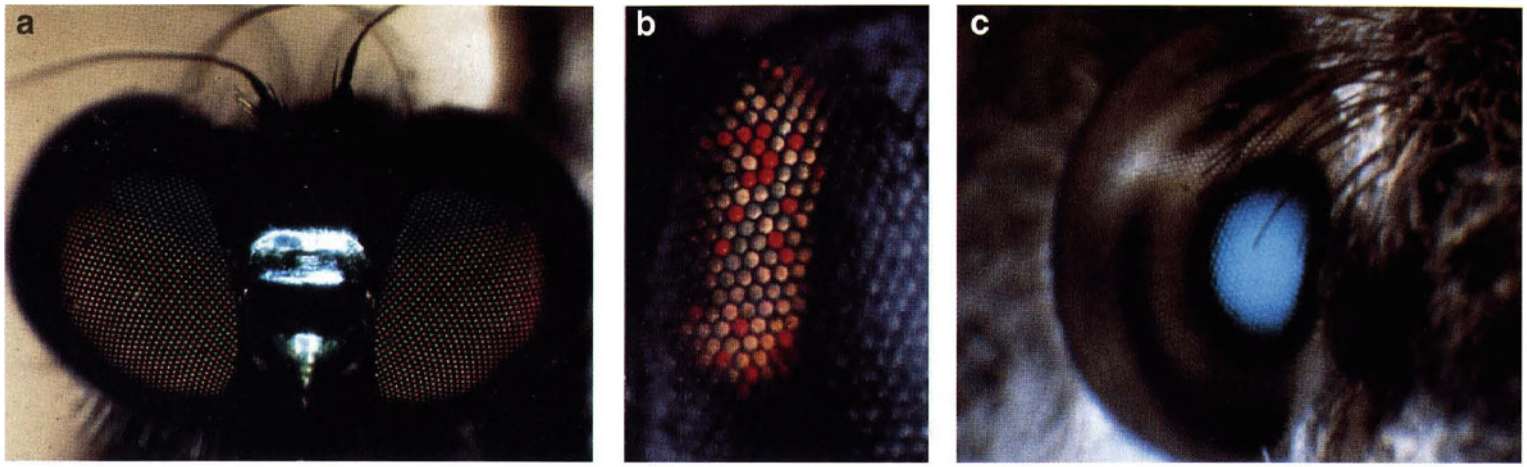
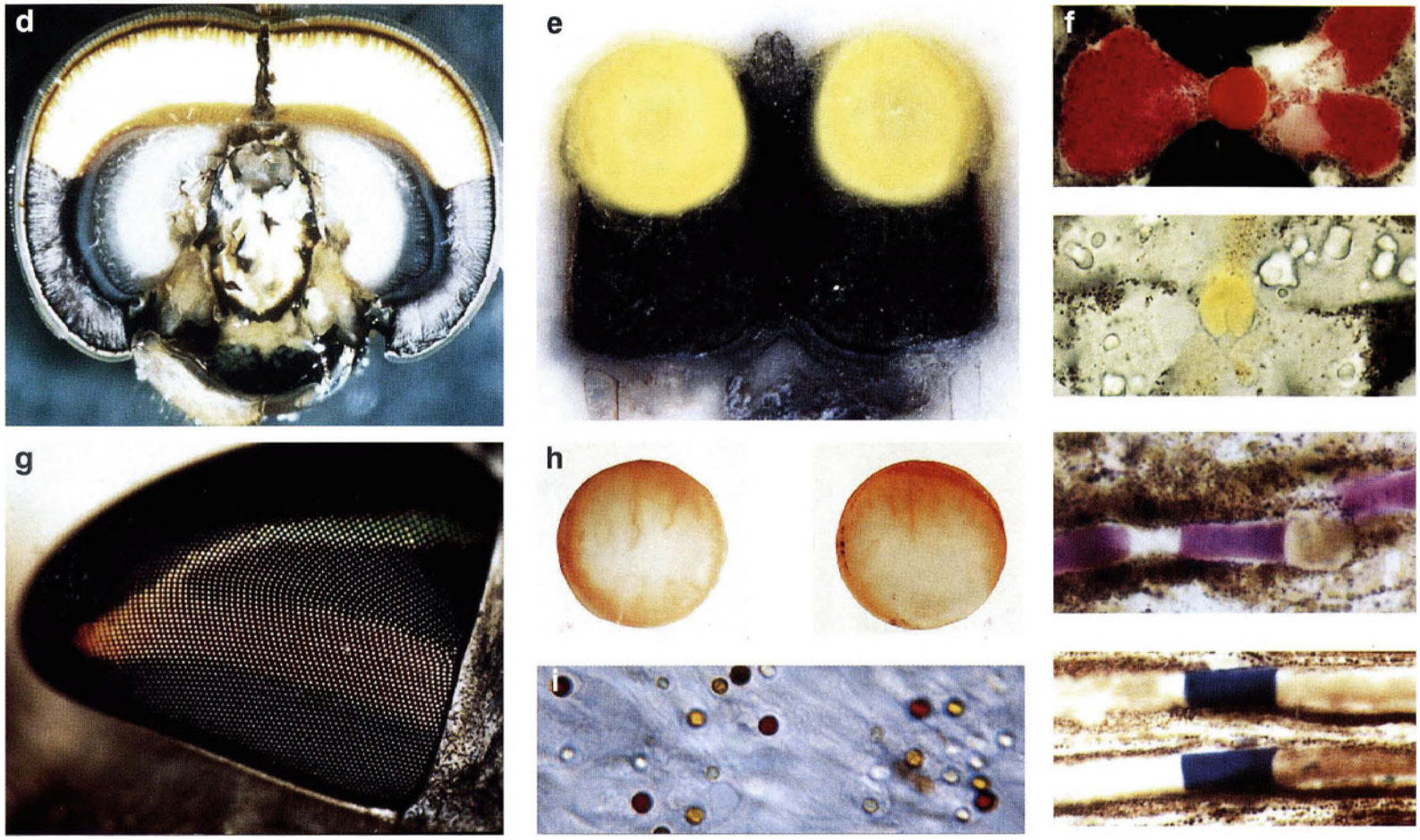


Plate 1 (**a**) Alternate rows of green and yellow facets in the eye of the dolichopodid fly *Condylostylus mundus*. These colours are produced by 1/4λ interference and may influence visual mechanisms in the retina beneath in a number of ways (Photograph – Gary Bernard). (**b**) Intensely coloured light re-emerging from the facets of the eye of the Carolina Satyr butterfly. This is a result of reflection from individual 1/4λ tracheal tapeta at the base of each photoreceptor (Photograph – Gary Bernard and see Figure 23). (**c**) Frontal aspects of the right eye of the diurnal hawkmoth *Macroglossum stellatarum* showing broad-band, sky blue tapetal eye glow (Photograph – Justin Marshall & Claudia Gunther). (**d**) Hemisected head of the dragonfly *Sympetrum* showing yellow pigment in the 'dorsal eye' for photoreconversion of metarhodopsin (Photograph Tom Labhart and see Labhart & Nilsson 1995). (**e**) The yellow lenses of the tube eyed deep-sea fish *Scopelarchus analis*, a possible adaptation for breaking ventral bioluminescent camouflage (Photograph – Justin Marshall). (**f**) Intrarhabdomal filters from the mid-band retina of stomatopod crustaceans, top two in transverse section and bottom two longitudinal section (Photographs – Justin Marshall). (**g**) The head of the tabanid fly *Tabanus lineola*. Alternate bands of colour are the result of 1/4λ interference filters situated in the cornea (Photograph – Gary Bernard). (**h**) Pigmented dorsal corneas in the eyes of two goldfish (Photograph –Ron Douglas). (**i**) Oil drops overlying cone outer segments in the retina of the starling *Sturnus vulgaris* (Photograph – Nathan Hart)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with the decreased levels of pigmentation observed in some older fish lenses (Figure 6). We have also tried raising several species of fish in different light levels, and while we have been able to influence both corneal pigmentation (see above) and retinal structure (Thorpe 1991), we have been unable to affect the level of lens pigmentation.

(e) Deep-sea animals; a special case The spectral region of highest intensity downwelling light in the deep sea is a narrow band between 470 and 480 nm (Jerlov 1976). Not only is the spectral bandwidth of light available for vision severely restricted, but its intensity also decreases rapidly with depth, until at around 1000 m insufficient sunlight penetrates to allow vision in even the most sensitive fish (Denton 1990). The yellow filters in the lenses (section 4.2.3) and retina (section 4.2.5b) of some deep-sea fish and cephalopods (section 4.3.1d) are therefore surprising, since they decrease both the spectral bandwidth and the intensity of the already restricted illumination even further, removing up to 80% of all downwelling light (Douglas and Thorpe 1992). They must therefore confer a significant adaptive advantage. Given the low level of illumination in the deep-sea and the high degree of convergence in the pure rod retinae of most deep-sea fish, it is unlikely that these filters serve to either protect the retina from excessive short-wave radiation or to enhance the quality of the image.

Many deep-sea animals produce their own light, and below about 1000 m this bioluminescence is the only visual stimulus available. In the mesopelagic zone (200 –1000 m), where both bioluminescence and downwelling sunlight are present, there is a potential conflict in tuning visual systems to the perception of these two sources. Although the wavelength of peak emission of most bioluminescent photophores lies between 450 – 500 nm, matching the wavelengths that most readily penetrate the water column, there are several exceptions to this and peak emissions at longer wavelengths are not uncommon (Herring 1983; Widder *et al.*, 1983, 1984). Furthermore, the emission spectra of the bioluminescence often contain more long-wave radiation than the surrounding spacelight. Short-wave absorbing filters will therefore decrease the intensity of downwelling sunlight more than that of the relatively long-wave rich bioluminescence, thereby enhancing the contrast of the bioluminescence and making it more visible (Somiya 1976; Muntz 1976b; Douglas and Thorpe 1992). The absence of significant amounts of intraocular pigmentation in the lenses of fish living deeper than 1000 m, where insufficient sunlight penetrates to provide a visible background (Denton 1990), is consistent with such a function (Douglas *et al.*, 1995).

Bioluminescence in the deep-ocean has a variety of potential uses, probably acting as; an intra and inter-specific signal, a means of startling predators, an attractant to prey, and as a means of simply illuminating their darkened world. Of all the proposed functions, however, perhaps the most interesting is the counter-illumination camouflage employed by many animals. A dark animal observed

from below by a potential predator will inevitably cast a silhouette against the residual sunlight. Consequently, many animals have photophores on their ventral surface matching the intensity of the downwelling illumination, thereby obliterating this shadow. Yellow lenses would effectively break this counterillumination camouflage by removing much of the background light thereby enhancing the visibility of the bioluminescence and making the animal an easy and well illuminated target (Muntz 1976b).

4.3 Invertebrate ocular filters

Eye design in the invertebrates is more diverse than the standard pattern found in vertebrates and this gives rise to a larger variety of filter types. Simple eyes, similar in plan to the vertebrate eye, are found in cephalopods, spiders, some crustaceans and a variety of worms. Many crustaceans and insects, possess compound eyes made up of many units called ommatidia. These have two basic designs: a) The apposition compound eye where each ommatidium acts as an isolated optical unit and the cornea is assigned the job of focusing light on the photoreceptors beneath, b) The superposition eye where the dioptric parts of neighbouring ommatidia are shared in order to form a single image on the retina, either by reflection or refraction of light rays (Land 1981; Nilsson 1990).

At an even simpler level, filters may be found in eyes of unicells and the worm-like animals, often forming eye-cups to give the photoreceptors directionality. For many unicells, especially the phytoflagellates, the basic function of 'vision' is to enable phototaxes away from light to avoid damage or towards it for photosynthesis. Not surprisingly therefore the most complex unicell 'eyes' are found in the phytoflagellates. At their most complex these structures include cornea, lens, humour, retina, pigment cup and tapetum and may contain filters constructed from carotenoids, $1/4\lambda$ interference reflectors and other substances similar to those found in the higher organisms (Couillard 1984). Ocular filters have therefore probably been present since the moment vision evolved.

4.3.1 Cornea and lens

(a) Corneal interference filters In the hard bodied invertebrates, a cornea made of modified chitin is the first structure light passes through on its way to the photoreceptors. Though, like many vertebrates, often clear down to just above 300 nm (Figure 15), corneas of some dipteran insects, for instance, are spectacularly coloured (Plate 1g; Bernard and Miller 1968). Ommatidial facets may be coloured individually or more commonly grouped in clusters or stripes which may be red, orange, yellow, green or blue. Examples are known from 23 of the 60 families of diptera, most notably in the tabanids which, as with the example in Plate 1, generally have alternating stripes of coloured facets (Bernard and Miller 1968).

In common with the iridescent corneas found in some vertebrates (section 4.2.2), these intense colours are the result of thin film interference. Several alternating layers of high and low refractive index cuticle, whose thickness is close to the wavelength of light, are found just below the corneal surface. At every interface a certain fraction of the incident light is reflected back and undergoes constructive or destructive interference with light from other layers. The colour of the reflected light depends on the *optical* thickness of the layers (thickness × refractive index), the wavelength in question and the angle of viewing or illumination. For any wavelength (λ), the most efficient constructive interference, and therefore rejection of the colour, occurs when the thickness of the layers is $1/4\lambda$ (Land 1972). Only a fraction of light of the chosen wavelength is reflected at each layer, however, and a total of around 10 layers are needed for almost 100% reflection. This ideal situation of $1/4\lambda$ layer thickness and 6 –12 layers is often found in nature (Land 1972; Bernard and Miller 1968) and such coloured regions are commonly called $1/4\lambda$ reflectors.

Dipteran flies achieve a variety of corneal colours by adjusting the layer thickness to reject different wavelengths of light. Light not reflected by corneal interference filters is transmitted to the retina beneath and it has been postulated that one or more such wavelength selective filters could enhance colour contrast, photoreconvert metarhodopsins (see section 4.3.2) or even directly mediate colour vision (Lunau & Knüttel 1995). This function has yet to be positively demonstrated and critically depends on the photoreceptors beneath and their neural interconnections. Diptera possess 'open rhabdoms' with a central pair of photoreceptors surrounded by 6 others arranged in a trapezium. These six rhabdomeres (R1-6) are used for spatial vision (Hardie 1986) and in *Musca, Drosophila* and a variety of other species contain a single visual pigment with maximum sensitivity typically around 490 nm. The central two photoreceptors (R7 and R8) are usually more complex, containing different visual pigments that constitute the fly's colour vision system (Hardie 1986; section 4.3.3b). Any one of these photoreceptor types in flies with coloured corneas would have their spectral sensitivity altered by overlying filters, the different colours possibly increasing the number of spectral channels or tuning existing ones. As the photoreceptor spectral sensitivities of any dipteran with a coloured cornea have not been determined, this possibility has not been fully investigated. Alternatively, as the colours in a variety of compound eyes are often arranged in stripes or other patterns, they may simply be for camouflage or display (Stavenga 1979; Lunau and Knüttel 1995; Figure 21b and Plate 1g).

One example is known in which the underlying retinal structure is different depending on the colour of the overlying cornea, strongly suggesting a real visual function for the colour filters. The 'long-legged', Dolichopodid flies possess rows of facets alternately coloured red and yellow/green (Bernard and Miller 1970; Trujillo-Cenóz and Bernard 1972; Plate 1a). In ommatidia with red facets the R7 cells of the central pair of photoreceptors have microvilli oriented

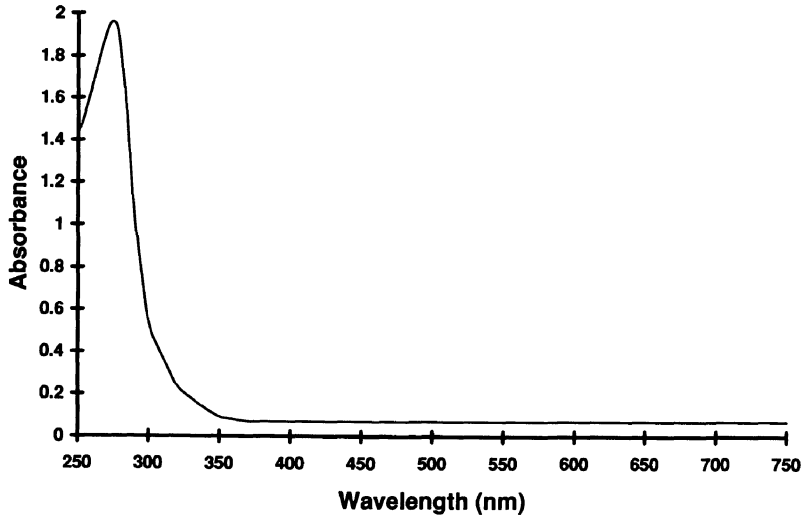


Figure 15 Spectral absorbance of the cornea of a moth showing good transmission to 300 nm (after Miller 1979)

vertically and those beneath yellow/green facets are oriented horizontally (Trujillo-Cenóz and Bernard 1972). The exact spectral sensitivities of these cells are not known, but two plausible suggestions for the function of this filter/ photoreceptor combination have been made.

Trujillo-Cenóz and Bernard (1972) suggest these are the first elements of a colour enhancement system and that red facets with vertical microvilli would be good for prey detection against shiny, horizontally polarized surfaces (and see Land 1993a). Photoreceptors with vertical microvilli are less sensitive to horizontally polarized surfaces such as ponds or shiny leaves, due to the intrinsic dichroism of the microvilli, such that maximum photopigment absorption occurs when light is polarised parallel to the microvilli. Alternatively, Land (1993b) suggests, that the eyes of *Poecilobothrus nobilitatus* are specialized Dolichopodid detectors and aid their elaborate sexual and territorial displays. *P. nobilitatus* bodies are coloured with shiny metallic interference colours which also polarize the light reflected from their surface. As the colour seen on the body depends on the angle of view (as it does with all interference colours), different colours will also be polarized to various degrees, depending on the reflection angle. A set of photoreceptors which combine a colour difference signal with a polarization difference signal may be ideal for spotting bodies reflecting different colours and E-vector intensities.

(b) Corneal nipple arrays The corneal surface of the compound eyes of many nocturnal or crepuscular moths and some diurnal butterflies is studded with thick forests of small nipples (Bernard 1967; Figure 16). The dimensions of these

structures are around $1/2\lambda$ of light in the middle of the spectrum and they render the eyes non-reflective. Man-made lenses and eyes with smooth corneas, exhibit specular reflection of light due to the sudden interphase between air and the higher refractive index glass or chitin. One way round this is to graduate the change in refractive index from outside to inside and this is exactly what the conically-shaped corneal nipples do. The small size of corneal nipples relative to the wavelength of light is critical, as this means they do not interfere with the image-forming action of the lens (Bernard *et al.,* 1965). A gradual refractive index change is hard to achieve in photographic and optical lenses, so lens coating is used as a compromise. A $1/4\lambda$ layer of material, whose refractive index is between that of air and glass, is used to create reflections at the air/coating, coating/glass interfaces, which eliminate each other by constructive interference and cause improved transmission.

The function of the nipple arrays seems to be twofold: sensitivity increase and camouflage (Bernard 1967). The presence of nipple arrays mainly on the corneas of nocturnal insects such as moths (Lepidoptera) and netwings (Neuroptera) suggests they may help in dim light vision. Light, which would be reflected by a smooth cornea, is absorbed by these eyes. Although this is only around 4 – 5% of the total light incident on the eye (Bernard 1967; Muntz 1972), for an insect working at the threshold of vision this is a real advantage.

The shiny eyes of diurnal insects such as dragonflies and bees are conspicuous and may become relatively more so in dim light. Many lepidoptera hide themselves on coming to rest by folding their wings to reveal a camouflaged pattern. A large shiny eye would ruin this camouflage and therefore lusterless eyes will no doubt help when hiding from possible predators. Camouflage is probably the main function of corneal nipples where present in diurnal lepidoptera, as any relative sensitivity increase for these species would be negligible.

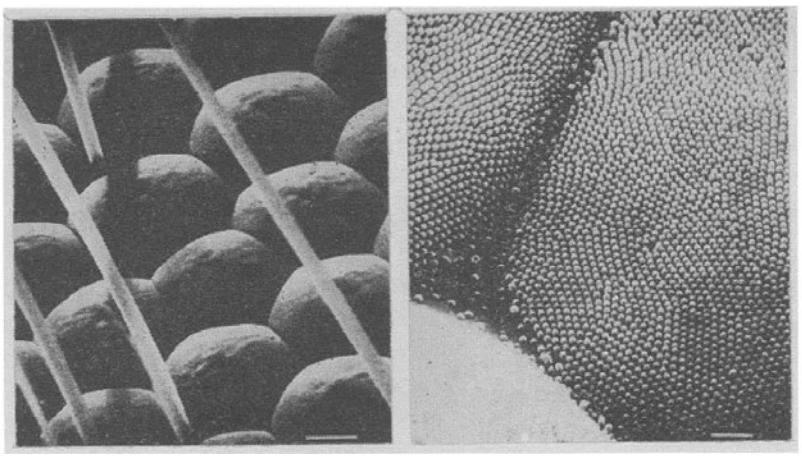


Figure 16 Scanning electron micrographs (SEM) of the eye of a night moth. (**a**) The hexagonal facet array (scale 10 μm). (**b**) Detail of two facets showing corneal nipples (After W.H. Miller *et al.* 1966)

(c) Scattering filters for polarisation vision This category of corneal filters is found associated with areas of compound eyes specialized for the detection of polarized light. These are the 'dorsal rim' areas found in many hymenopteran and a variety of other insects (Rossel and Wehner 1984; Labhart *et al.,* 1992). Ommatidia from this region bear microvilli specifically arrayed for efficient absorption of polarised light, an inherent property of microvillar receptors (Snyder *et al.,* 1973; section 4.3.1a). Along the dorsal rim, microvillar direction varies in a fan-like pattern and this can be matched directly to the pattern of polarised light in the sky at various times of the day (Rossel and Wehner 1984). In this way insects such as ants and bees, for instance, navigate over long distances from home to food sources and back.

The corneal facets of the dorsal rim in the cockchafer, for example, are cloudy or grey in appearance (Labhart *et al.,* 1992). This is due to the presence of small air bubbles or inhomogeneities in the cornea, which scatter light, making the facets seem opalescent. As a result the acceptance angle of the underlying ommatidia is increased in a manner similar to the action of cosine receivers found on some light meters. The function of this, and other adaptations which increase acceptance angle in the dorsal rim ommatidia, seems to be to extend the field of view of the receptors over much of the available sky, rather than increase sensitivity (Labhart *et al.,* 1992). In this way more of the available polarised sky pattern is analysed, and localised disturbances in the pattern, such as clouds or tree branches, are integrated out of the final signal. Fine resolution in this eye area is unimportant.

(d) Lens filters of cephalopod simple eyes Short-wave absorbing pigments are common in various parts of the vertebrate eye (section 4.2). Since the simple eyes of cephalopods (squid, cuttlefish and octopus) are remarkably convergent with the vertebrate design (Packard 1972), the presence of varying degrees of pigmentation in the lenses of cephalopod eyes resulting, as in vertebrates, in widely differing UV transmission between species (Figure 17a), is perhaps no surprise.

It has been suggested (Denton and Warren 1968) that, as for fish (4.2.3), deeper living squid usually have less pigmentation in their lenses than those living nearer the surface. However, in a manner also reminiscent of some deep-sea fish (section 4.2.3), and presumably for similar reasons (section 4.2.7e), the most pigmented lens belongs to *Histiotheuthis meleagroteuthis*, a mesopelagic animal living at depths of 500 –1000 m (Denton and Warren 1968; Muntz 1976b). This species is unusual in having eyes of differing size; a large eye, with a more heavily pigmented lens, that may be orientated in an upward pointing direction and could therefore be involved in breaking bioluminescent camouflage (section 4.2.7e), and a smaller, less heavily pigmented, downward facing eye.

The cephalopod lens splits easily into three different regions; an anterior and a posterior cortex and a central nucleus. In *Histiotheuthis meleagroteuthis*, pigmentation is densest in the posterior portion of the lens (Muntz 1976b), while in

Sepia officinalis and *Loligo forbesi* pigmentation is most intense anteriorly (Thorpe 1991).

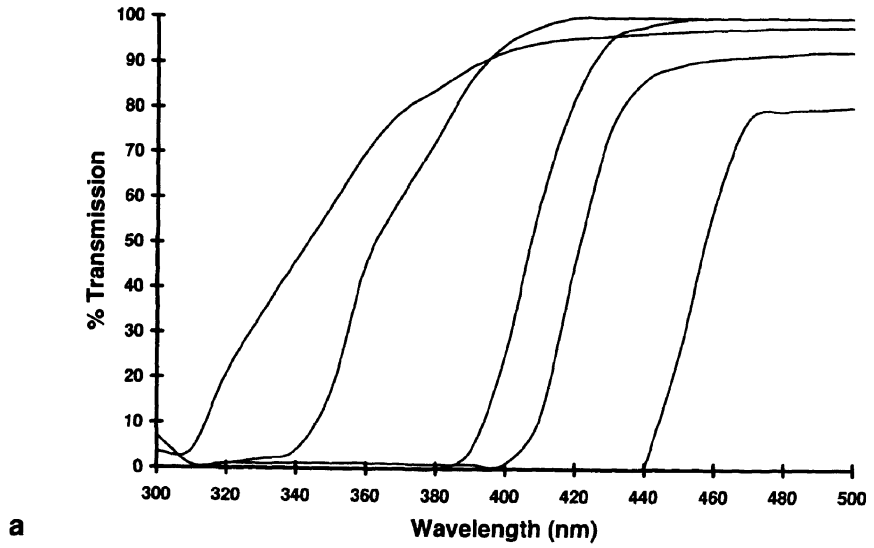
Thin sections of *Histiotheuthis meleagroteuthis* lens indicate that the heavily pigmented posterior portion of the large lens contains a pigment absorbing maximally at just over 400 nm, while the more anterior areas of the large eye and all of the less pigmented small eye, contain a pigment with λ_{max} at 385 nm (Muntz 1976b) (Figure 17b). Extracts reveal that most areas of the *Sepia officinalis* lens, on the other hand, contain a pigment with λ_{max} around 360nm (Figure 17b), although the anterior cortex may contain one or more additional pigments. HPLC purified extracts of all parts of the *Loligo forbesi* lens show a more complex absorption profile with a main peak at 320 nm (Figure 17b). The identity of all these pigments is unknown. There is some evidence that the pigment in *Histiotheuthis meleagrotheuthis* accumulates as a function of age (Denton and Warren 1968; Muntz 1976b). Similar increases in lens pigmentation have been observed in *Sepia officinalis* (Thorpe 1991).

4.3.2 Filters between the crystalline cones

In many apposition compound eyes, such as those in crabs or bees, pigment is found between the crystalline cones, housed in the primary (distal) pigment cells. Its main function is to help optically isolate ommatidia and thus maintain image quality. Its colour and broad absorbance has a similar function to melanin in the vertebrate eye (section 4.2.6a), however invertebrates generally use the dark brown ommachrome pigments for this job (Figure 18; Hallberg and Elofsson 1989; Stavenga 1979). This is what gives the eyes of bees, crabs and other invertebrates their dark brown or black appearance. Pigment between the cornea and retina in superposition eyes may directly adjust image brightness over 2 – 3 log units by varying the extent to which they curtain off individual ommatidia (Nilsson 1990; Warrant and McIntyre 1996).

Primary pigment in a number of insects and crustaceans may be coloured and arranged in spots or stripes over the eye. A possible function for these patterns is camouflage or display (Stavenga 1979). Examples of this can be found in various grasshoppers, flowerflies, some praying mantids, porcellainid crabs and mantis shrimps (Figure 21b). It is not known if these colour patterns have any real visual function as is supposed for corneal interference colours (section 3.3.2). Some incomplete evidence does exist for the clear and brown striped eye of the grasshopper *Phlaeoba* in which lateral filtering by this pigment may differentiate photoreceptors into two types (Kong *et al.,* 1980; section 4.3.3).

In a few instances, brown ommochrome pigments between the crystalline cones have been replaced by a more selective filter which leaks light beyond 550 nm, giving the eye a yellow or orange hue. This apparently poorly designed filter is actually part of an elegant strategy to increase sensitivity in these ommatidia. Pigments like these are found only in specialised dorsal regions of



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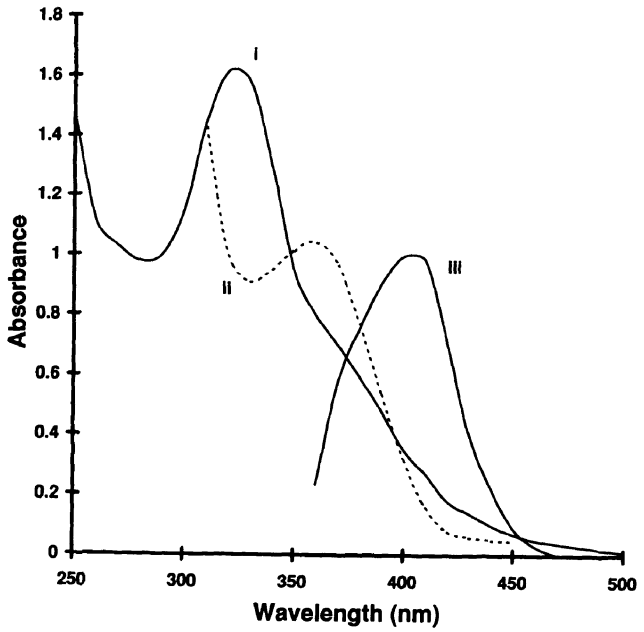


b

Figure 17 Spectral characteristics of intact cephalopod lenses. (**a**) Whole lens transmission spectra. (left to right); i – *Pyroteuthis* sp. (lens diameter along optical axis 5.26 mm; Douglas unpubl), ii – *Alloteuthis subulata* (3.38 mm; Thorpe 1991), iii – *Sepia officinalis* (9.05 mm; Thorpe 1991), iv – *Todarodes sagittatus* (13.6 mm; Douglas unpubl), v – Large eye of *Histioteuthis meleagroteuthis* (ca 10 mm; Muntz 1976b). (**b**) Absorbance spectra of lens pigments; i – HPLC purified lens pigment of *Loligo forbesi* (Thopre 1991), ii – unpurified extract of posterior cortex of *Sepia officinalis* lenses (Thorpe 1991), iii – thin slice of the posterior cortex of a *Histioteuthis meleagroteuthis* lens (Muntz 1976b). Differences between curves in absolute absorbance are arbitrary

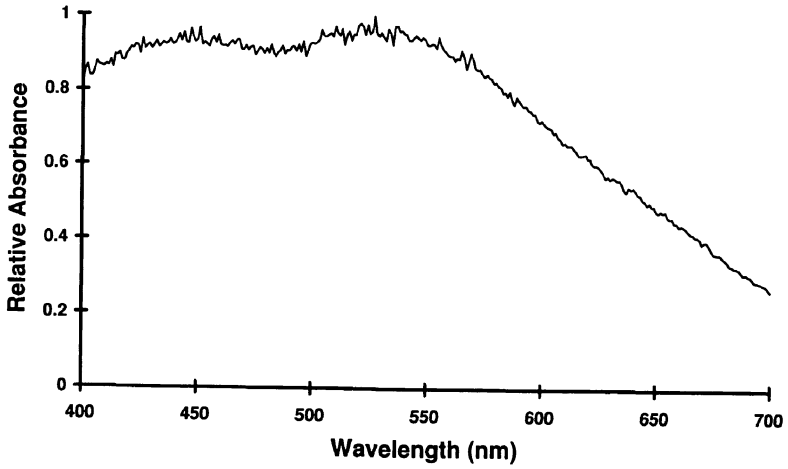


Figure 18 Broad-band absorbance of ommachrome, the dark screening pigment found in many invertebrate eyes (Cronin & Marshall 1989b)

compound eyes which may exist only in the male of the species. The dorsal regions consist of enlarged ommatidia, sometimes entirely separate to the rest of the eye, and are used for the difficult task of detecting small flying objects such as prey or mates against the sky (Figure 21c). Prominent examples are found in mayflies (Ephemeroptera – Horridge 1976; Horridge and McLean 1978), dragonflies (Odonata – Labhart and Nilsson 1995; Figure 19; Plate 1d), owlflies (Neuroptera – Schneider and Langer 1975), simuliids (Diptera – Kirschfeld & Wenk 1976), bibionids (Diptera – Zeil 1983) and drone honey bees where the pigment is red but performs the same function (Hymenoptera – Bertrand *et al.*, 1979; for reviews see Wehner 1981; Land 1989).

For good image detection against the predominantly blue sky, the photoreceptors of dorsal eye regions contain visual pigments with blue or UV sensitivity. All invertebrates have bistable visual pigments: when a molecule of visual pigment (rhodopsin) absorbs a photon, it is converted to a thermostable metarhodopsin which can in turn be reconverted back to rhodopsin by the absorption of another photon. Visual pigments with a short wavelength maximum sensitivity (λ_{max}) usually have metarhodopsins whose λ_{max} is shifted to longer wavelengths (Labhart and Nilsson 1995; Figure 19). For instance in the drone honey bee, the λ_{max} of the dorsal eyes rhodopsin is 446 nm and it's metarhodopsin peak absorption is at 505 nm (Menzel *et al.*, 1991). For the owlfly the equivalent rhodopsin/metarhodopsin λ_{max} values are 345 nm and 475 nm (Hamdorf *et al.*, 1973). Metarhodopsin is 'deactivated' in the sense that it has no affinity for molecules in the phototransduction cascade which convert light to nervous energy.

For light to be seen, as much rhodopsin as possible is needed in the photoreceptors. The yellow, orange or red screening pigments are used in order to 'leak' long wavelengths throughout the dioptric system, and indeed the rest of the eye including the retina (section 4.3.3a describes similar pigments in the retinular cells). This light is absorbed by the long λ_{max} sensitive metarhodopsin, reconverting it to rhodopsin, and is at the same time not visible to the short λ_{max} rhodopsin (Figure 19). The eyes' optical resolution is not degraded, as the yellow/red pigment is an effective screen for the short wavelength sensitive rhodopsin and simultaneously the rhodopsin/metarhodopsin equilibrium is driven almost 100% towards the rhodopsin side under natural conditions. For the dragonfly *Sympetrum*, this increases the sensitivity of the eye by about 0.4 Log units, a critical advantage for an eye straining to see small dark objects against the sky (Labhart and Nilsson 1995).

4.3.3 Retina

Invertebrate photoreceptors (rhabdoms) are typically constructed from relatively long 'rods' of microvilli, contributed to by several retinular cells. These may be fused together in one unit (crustaceans, cephalopods and insects such as bees, butterflies and dragonflies) or exist as separate entities (dipteran insects and a few crustaceans such as the isopod *Ligia*). Once light enters the rhabdom it is kept from leaving the photoreceptor by its inherent light guiding properties (Snyder 1975; Snyder and Horridge 1972) or by retinular cell pigment, usually ommochrome, drawn close to the rhabdom. As well as preventing light entering neighbouring photoreceptors, retinular cell pigment 'bleeds' light from the rhabdom and regulates light flux within it. This longitudinal pupil mechanism contributes to the adaptation of photoreceptors which may be required to respond to intensity ranges of as much as 5 log units over the course of the day (Land 1981).

By replacing the broad-band ommachrome sheath with coloured pigments, light travelling down photoreceptors can be spectrally modified. The pigment acts as a lateral filter, absorbing some wavelengths preferentially and reflecting others back into the rhabdom, thus modifying the spectral sensitivity of the photoreceptor itself. This is a relatively inefficient filter, as only a small proportion of the light within the rhabdom is filtered. In rhabdoms less than 5 μm in diameter, however, waveguide effects mean a substantial fraction of light travels outside the central photoreceptor (Snyder *et al.*, 1973; Snyder 1975). This places the light within the lateral screen itself, making lateral filtering more pronounced, especially if the rhabdom is long, and effectively like a serial filter.

To maximise sensitivity, many invertebrate photoreceptors are long. This however introduces the potential problem of self screening, where the rhodopsin and metarhodopsin of distal regions, filters light reaching the more proximal zone. In a single long photoreceptor, this invariably means the overall sensitivity

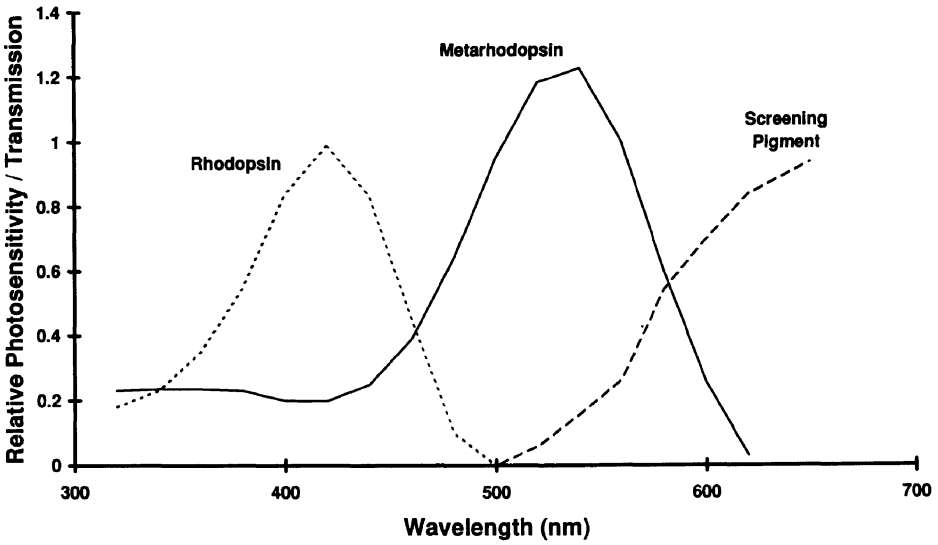


Figure 19 Comparison of rhodopsin and metarhodopsin sensitivities and the transmission of the 'leaky' screening pigment in the Dragonfly *Sympetrum*. The light let through by this yellow pigment (see Plate 1) reconverts metarhodopsin to rhodopsin, while still acting as an effective screening pigment for the rhodopsin, and increases photoreceptor sensitivity (After Labhart & Nilsson 1995)

broadens considerably (and may be modulated by the different peak absorption of metarhodopsin – see section 4.3.2), a desirable feature perhaps for a system seeking general sensitivity but undesirable if spectral sensitivities must be preserved (Snyder *et al.*, 1973).

Much of the remainder of this section examines serial and lateral filters that tune the spectral sensitivity of invertebrate photoreceptors. Firstly however, it may be recalled from section 4.3.2 that a variety of compound eyes, such as the dorsal eye of male owlflies, are specifically adapted for the reconversion of metarhodopsin to rhodopsin in order to increase sensitivity. This adaptation requires yellow, orange or red distal pigments to leak long wavelength light throughout the eye. The same pigments are present in retinular cells, extending the extent of leakage throughout the whole eye including the retina, accelerating photoreconversion (Stavenga 1996).

(a) Lateral screens The fly (Vogt *et al.*, 1982), pierid butterflies (Ribi 1979), the digger wasp *Sphex cognatus* (Ribi 1978), fireflies (Lall *et al.*, 1982, 1987), stomatopods (Marshall *et al.*, 1991b) and a variety of crabs (Leggett 1979; Stowe 1980; Lall and Cronin 1987) have all been shown to possess coloured pigment in close apposition to their rhabdoms and may use these to alter the spectral sensitivity of their photoreceptors. In crabs it has been implied that different coloured lateral screens could work in conjunction with a single visual pigment

to construct colour vision (Leggett 1979; Hyatt 1975; Stowe 1980). This has yet to be convincingly demonstrated and it seems more likely that the job of lateral filters is to tune already existing spectral sensitivities derived from different visual pigment types.

Fireflies present a particularly interesting example, where the colour of lateral screening pigments varies from yellow through pink, magenta and red in different species. Pigment colour is correlated with the species peak activity time around dusk (Lall *et al.,* 1982, 1987). The filter colours sharpen the spectral absorption characteristics of an existing green photoreceptor (λ_{max} 550 nm), maximising the individual species' sensitivity to the bioluminescent emissions of their conspecifics. The absorption profile of the yellow pigment, which is present in the night active *Photinus* sp, is strongly indicative of a carotenoid pigment, while the chemical identity of the red pigments remains unknown (Lall *et al.,* 1987).

The retinular cell pigment in the mid-band photoreceptors of the mantis shrimps (stomatopods) are often coloured differently and provide a good example of how such spectral sharpening works (Marshall *et al.,* 1991b). This highly specialized compound eye region contains more than ten visual pigments, and in concert with a variety of filter types, constructs many sharply tuned spectral sensitivities for colour vision (Marshall 1988; Cronin and Marshall 1989a & b; Marshall 1994; for further explanation see section 4.3.3b). Coloured lateral screens are made from retinular pigment or oil droplets which may be yellow or red in different mid-band rows. Stomatopod photoreceptors in the mid-band are long to increase sensitivity (Marshall and Land 1994). A penalty paid by long photoreceptors is broadening of the photoreceptors spectral sensitivity through self screening (Snyder *et al.,* 1973), an undesirable quality in a chromatic system with many colour channels to fit within the spectrum (Bowmaker 1983). One way to counteract this is to couple optically the photoreceptor to a structure, such as a lateral filter sheath, which absorbs wavelengths offset from the visual pigment λ_{max} and which therefore 'extracts' the broadening wavelengths from light in the photoreceptor. There may also be a shift in the λ_{max} position of the photoreceptor, as occurs in the firefly, depending on the spectral absorption of the filter and the visual pigment it combines with (Marshall *et al.* 1991b). Section 4.3.3b details why such precise spectral sensitivity positioning is critical for stomatopods.

The longitudinally fused rhabdoms in bees or butterflies (Menzel 1981) result in a similar spectral sharpening of their photoreceptors by using visual pigments in place of inert coloured absorbing pigments. Their photoreceptors abut each other along their entire length and are therefore optically coupled. They contain visual pigments of different spectral sensitivity (the bee has a UV (340 nm), blue (440 nm) and green (540 nm) receptor for example) which behave as lateral colour filters for each other. The broad spectral sensitivities expected if these long rhabdoms were separate become three sharply tuned responses with far less

spectral overlap and redundancy (Figure 20a). Both here, and where coloured screening sheaths are used, photoreceptors maintain high absolute sensitivity while sharp individual spectral identity is retained for good colour contrast (Snyder *et al.,* 1973).

(b) Photoreceptor tiering, intrarhabdomal and other serial filters The λ_{max} of photoreceptors can be both sharpened and shifted by serial filters, again largely in order to tune for increased colour contrast rather than create colour vision systems. The penalty paid for this arrangement is a loss of sensitivity in proximal areas due to the light absorbed by the filter above. For animals operating in plenty of light, however, this may not be a problem (Snyder *et al.,* 1973; Marshall *et al.,* 1991b; Cronin and Marshall 1989b). The filter may consist of only the overlying visual pigment in tiered photoreceptors, photostable pigments or both. Where photostable coloured pigments are used, they may be discrete filter units, similar to the coloured oil drops in vertebrate eyes (section 4.2.5c), or dispersed throughout the photoreceptor membrane.

The central photoreceptors of the open rhabdoms of fly eyes (R7 and R8) are tiered and in some instances contain a photostable pigment. This pair of photoreceptors are not a homogenous population throughout the eye but come in 4 different types assigned a variety of functions such as colour vision (two types), sensitivity to polarized light and mate detection (Hardie 1986). R7 overlies R8 so light entering R8 is filtered by whatever is found in R7.

In one of the four R7R8 variants, called R7yR8y due to the yellow colour of light they transmit, R7y contains a remarkably complex cocktail of pigments consisting of two rhodopsins (λ_{max}s at 430 nm and 340 nm) and a blue absorbing photostable pigment dispersed throughout the photoreceptor microvilli (Kirschfeld *et al.,* 1978, 1988). The measured sensitivity of R7y at 355nm is the result of an interaction between all three pigments. Direct absorption of light by the blue sensitive 430 nm visual pigment is largely blocked by the filtering action of the photostable C_{40} – carotenoid pigment (zeaxanthin and/or lutein) the same pigments found in the macula lutea of vertebrate eyes (section 4.2.5b). The high UV sensitivity of the cell (Figure 20b) therefore comes from the 340 nm visual pigment which transfers its absorbed energy to the 430 nm pigment. It is argued that this antennal mechanism increases the sensitivity of the photoreceptor by broadening its spectral sensitivity slightly (Kirschfeld *et al.,* 1988). The carotenoid pigment may also protect the R7y cell from damaging UV radiation (Zhu and Kirschfeld 1984), an important function suggested for similar pigments in vertebrate and cephalopod eyes (section 4.2.7a).

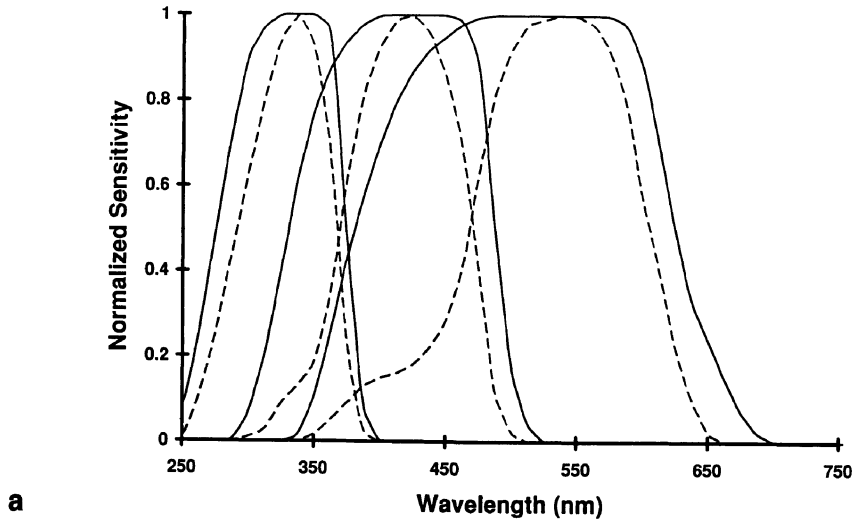
The spectral sensitivity of the R8y photoreceptor is the result of filtering by both visual pigments and to a large extent the carotenoid in R7y, which changes the wide R8 rhodopsin peak at 520 nm to a narrow one at 530 nm (Figure 20b). This, and R7pR8p cells (p stands for pale – the transmission characteristics of these rhabdoms), which have relatively simple sensitivities based only on visual

pigments with λ_{max} values at 335 nm and 460 nm respectively, provide the basis of colour vision in the fly (Troje 1993). R8p is filtered by the R7p visual pigment, but only on its short wavelength limb, resulting in little change.

Stomatopods from the gonodactyloid and lysiosquilloid superfamilies also possess tiered photoreceptors in a specialised zone of 'mid-band' ommatidia (Marshall 1988; Figure 21a). Many crustaceans have a two tiered retina with a single short-wave sensitive retinular cell (R8 – λ_{max} around 400 nm) overlying a rhabdom contributed to by 7 green sensitive cells (R1-7 – λ_{max} around 500 nm and Chapter 9 of this book). Generally the R8 cell possesses a rather short rhabdom, so its filtering effect on the underlying cells is negligible (see Gaten *et al.,* 1992 and below for exceptions to this). The mid-band may contain 6 rows of enlarged ommatidia and in 4 of these rows (numbers 1– 4 counting from the top down; Figure 21a) the rhabdom is divided into three tiers. This is achieved by dividing the R1-7 cells into two tiers of 3 or 4 cells underneath the R8 cell (Figure 22a). Rows 2 & 3 of the mid-band contain remarkable intrarhabdomal colour filters of purple, blue, yellow, orange or red blocks of membrane bound vesicles (Figure 22; Plate 1f). There may be up to four of these in each species situated between the photoreceptor tiers and almost all are at least partially constructed from carotenoid pigments (Marshall 1988; Cronin *et al.,* 1994a; Marshall *et al.,* 1991b).

With one or more colour filter types, theoretically a 'one (visual) pigment screened' colour vision system could be constructed. In practise however, as with the analogous oil droplet structures in vertebrates (section 4.2.5c), and elsewhere in the invertebrates, this does not happen. Intrarhabdomal filters help tune and sharpen photoreceptors, containing different visual pigments, to certain spectral loci (Cronin and Marshall 1989b). Astonishingly, stomatopod species with 6 row mid-bands possess at least 12 different visual pigments, 8 of these in the various R1-7 rhabdomeric portions of rows 1– 4. Although all different in λ_{max}, the sensitivity functions of even the theoretical rhodopsins, not accounting for broadening through self screening, overlap heavily (Figure 22d&e). By an elegant system of sequential serial filtering, utilising the long-pass colour filters of rows 2 and 3 and the filtering properties of the rhabdom tiers themselves, a series of very sharply tuned photoreceptors is constructed (Cronin and Marshall 1989a). This gives the potential for extremely fine spectral discrimination over the whole spectrum, not just a part of it (Troje 1993) and is good for maintaining colour constancy with varying illumination.

The sensitivity loss in this sequential filtering mechanism is enormous. In row 3, for instance, less than 1% of incident light reaches PR1-7 cells in some species and in light limited circumstances, such a photoreceptor would not work. Stomatopods with six-row mid-bands are found in murky, coastal waters and deep waters (10 –100 m, where the spectrum of light is attenuated particularly at short and long wavelengths – Jerlov 1976) and this heavy filtering could present a problem. However species like *Odontodactylus scyllarus* or *Lysiosquilla*



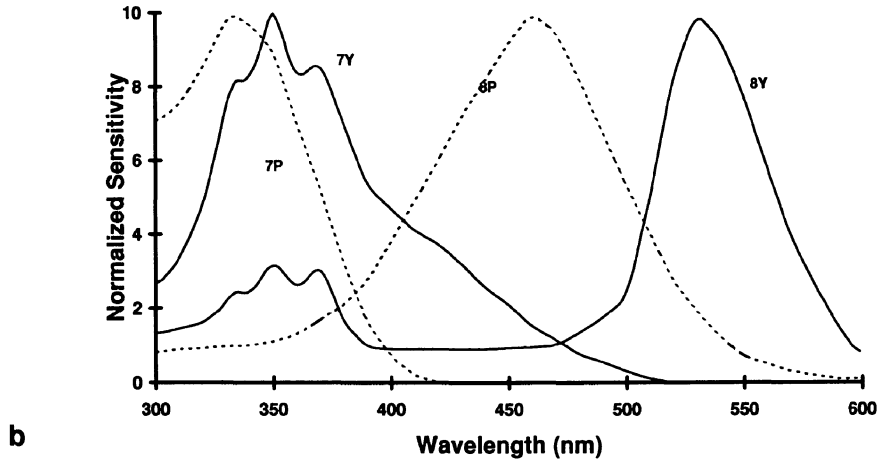


Figure 20 Serial and lateral filtering in the eyes of insects. (**a**) Lateral filtering in three optically coupled photoreceptors in the eye of the bee keeps the spectral sensitivities of photoreceptors narrow (dotted curves) which if not coupled have broad sensitivities (solid curves) and poor spectral resolution due to self screening (After Snyder *et al.* 1973). (**b**) Serial filtering in the central two-tiered rhabdoms (7 and 8) of the fly eye. The 'yellow' (y) and 'pale' (p) photoreceptor populations are found scattered throughout the eye. The relatively narrow spectral sensitivities in the underlying R8 cells are the result of the filtering effect of the R7 cells (After Hardie 1986)

sulcata, which live in these spectrally limited photic environments, restrict their spectral coverage to match the ambient illumination (Cronin *et al.*, 1994b&c). This is achieved by using visual pigments with λ_{maxs} closer to the wavelength of light best transmitted in sea water (475 nm), tuning filter transmission to allow through more light, or even 'removal' of filters.

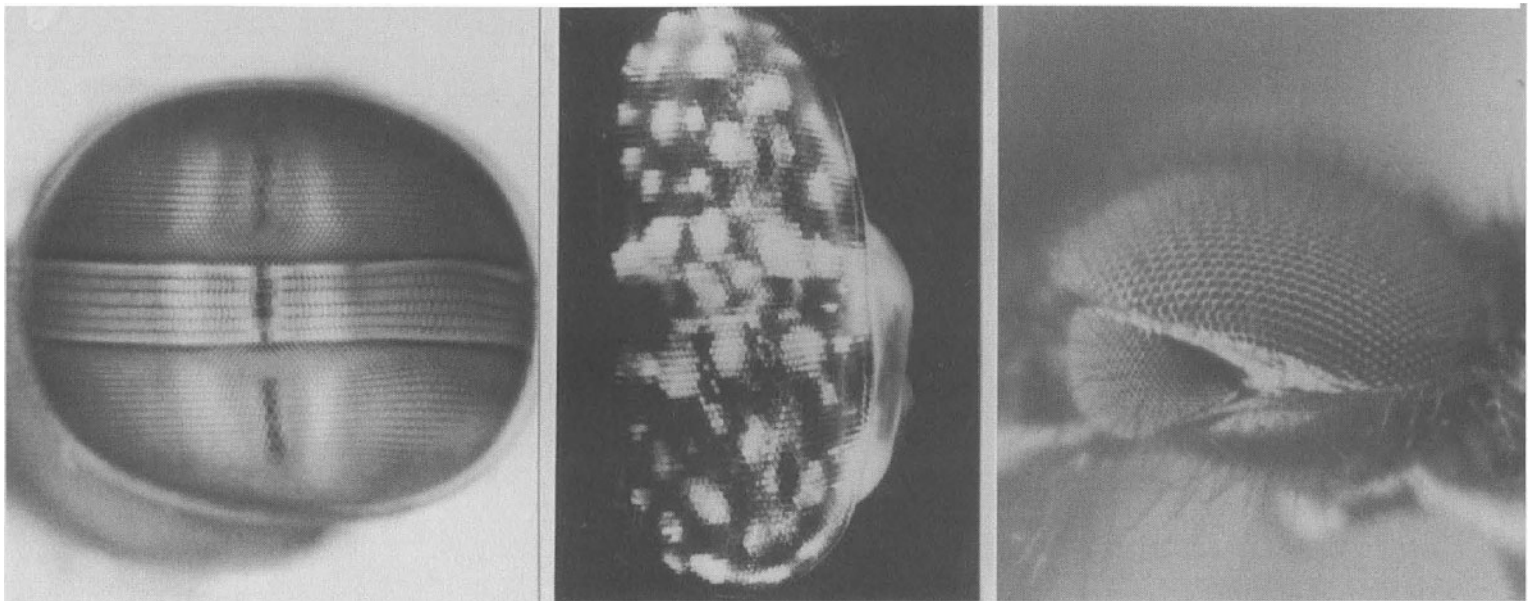
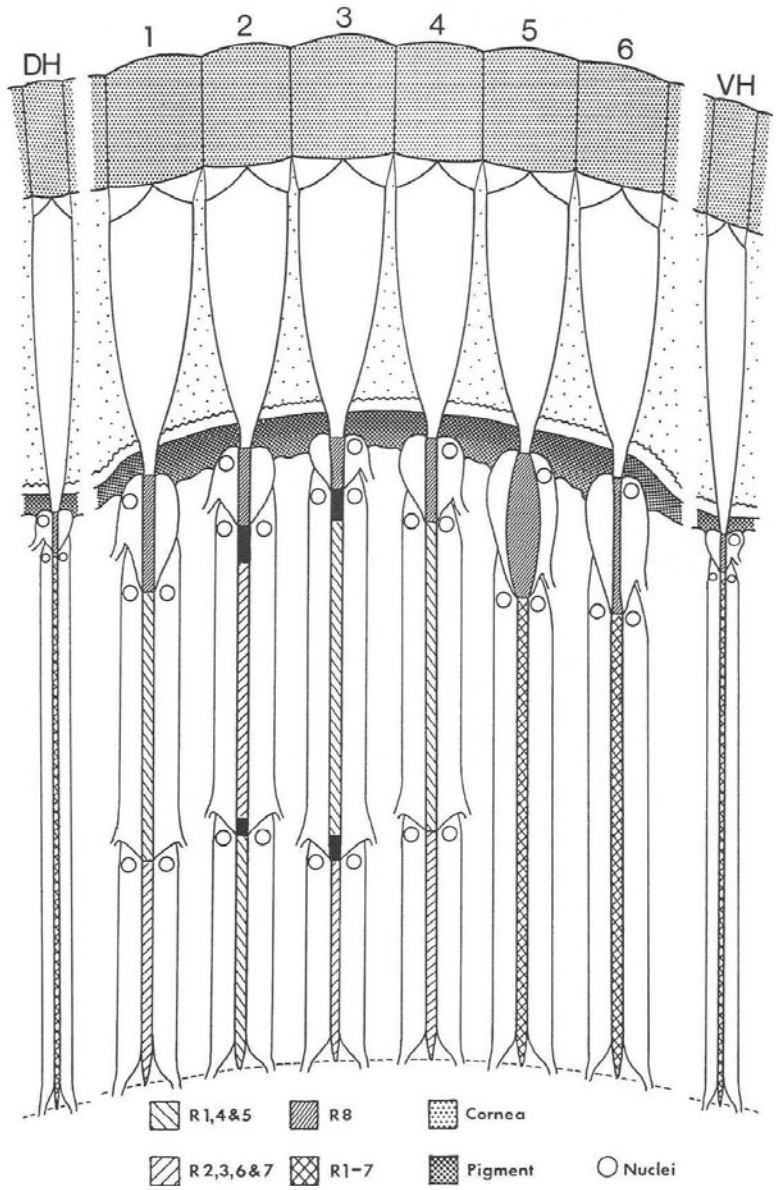
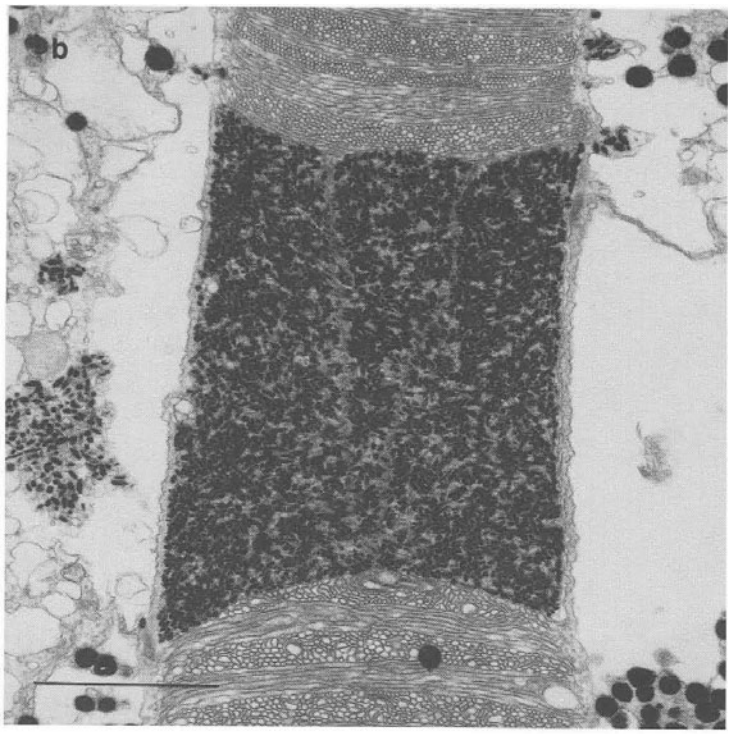


Figure 21 Compound eyes showing various adaptations involving filters. (**a**) The eye of the stomatopod *Odontodactylus scyllarus* showing the enlarged mid-band ommatidia. It is this modified eye region which contains the colour filters and tiered photoreceptors of the stomatopod multispectral colour vision system (Figure 22 and Plate 1). (**b**) The mottled appearance of the eye of the stomatopod *Lysiosquilla maculata*. Although these distally placed pigments may have a function in filtering light reaching the photoreceptors below, it is more likely they camouflage the eyes, which are the only part of the animal protruding through a hole in their sandy burrow as it waits to ambush prey (see also Stavenga 1979). (**c**) The head of a male Bibionid fly in lateral aspect. Each eye is split into a small ventrally directed region and a massively expanded dorsal region used for hunting females (Zeil 1983). These dorsal 'eyes' contain leaky filter screens for metarhodopsin reconversion to gain sensitivity (Photograph J. Zeil and M.F. Land see also Plate 1)

a

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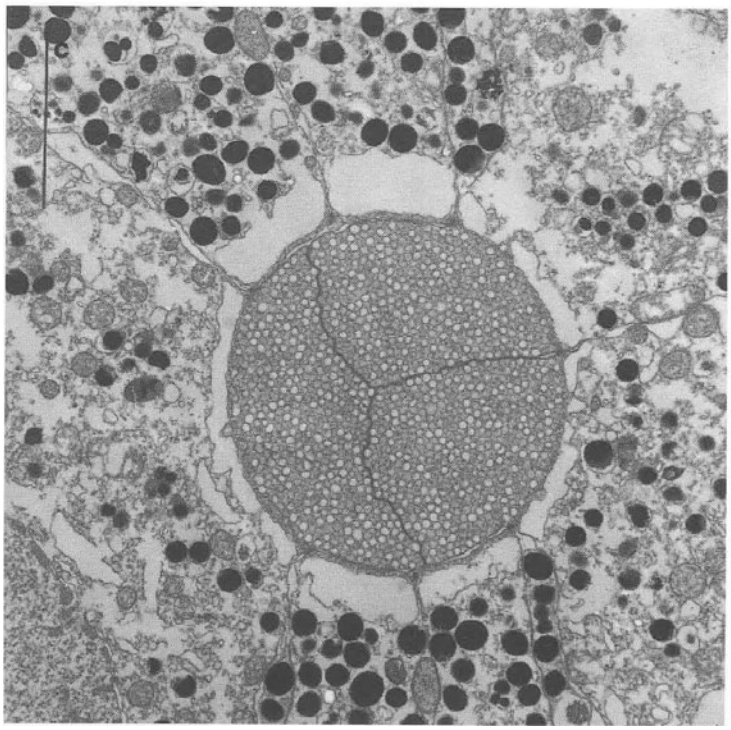
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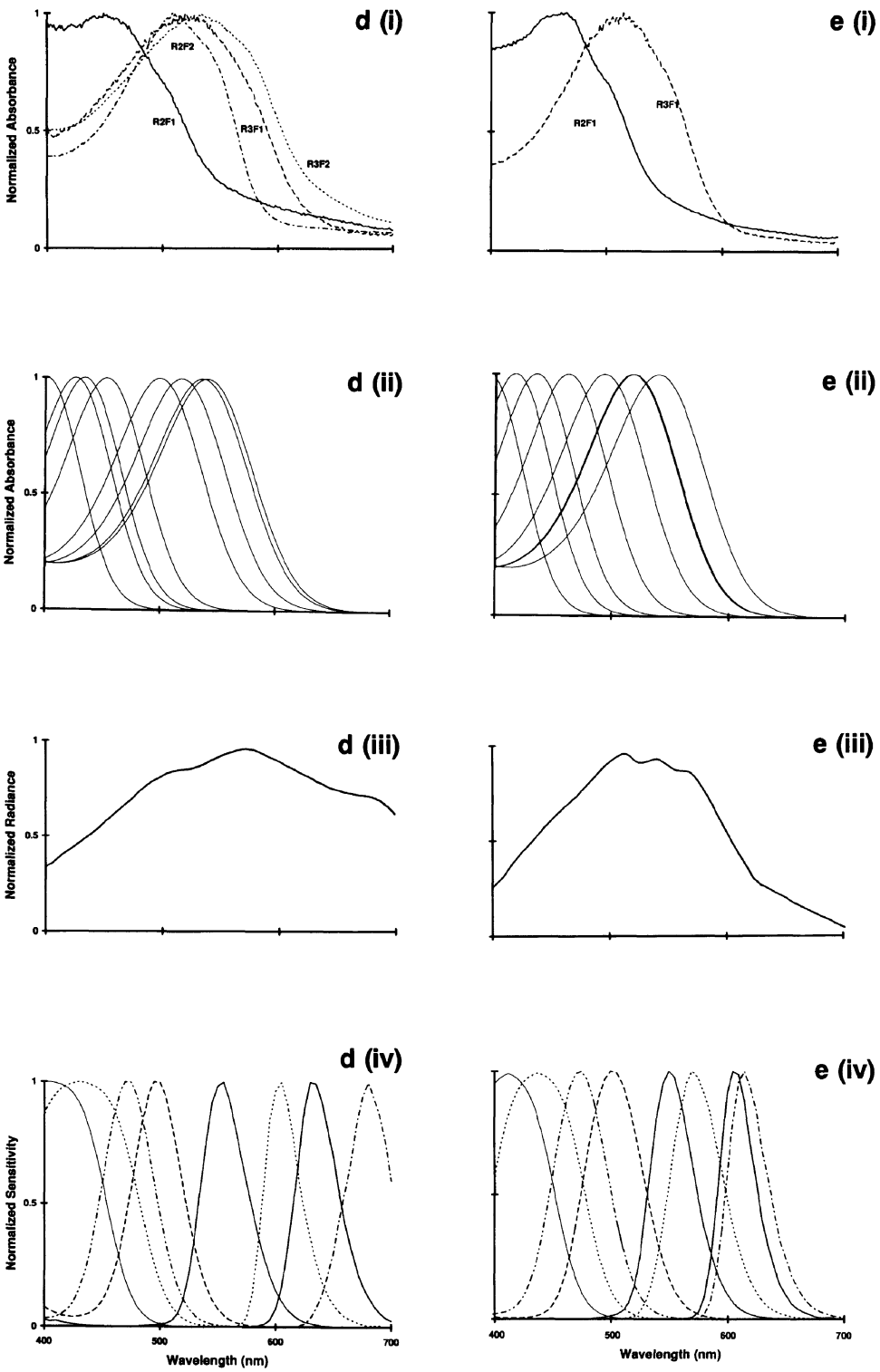
d (i)
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e (iii)
Normalized Radiance
d (iv)
e (iv)
Normalized Sensitivity
400
500
600
700
Wavelength (nm)

Figure 22 (previous pages) Serial filtering in the eyes of stomatopod crustaceans. (**a**) Diagrammatic representation of the specialised ommatidia of the mid-band. Rows 1– 4 compose the colour vision system. They are triple tiered and between the tiers in rows 2 and 3 intrarhabdomal carotenoid filter blocks may be present (Plate 1f). (R1,4&5, R8, R1–7, R2,3,6&7 – retinular cells; after Marshall *et al.* 1991a). (**b** and **c**) TEMs of blue and yellow coloured filters in longitudinal and transverse section respectively. The small vesicles which may be round or oval shaped contain carotenoid pigment (Marshall *et al.*, 1991b, Cronin *et al.*, 1994a). (**d**) *Pseudosquilla ciliata*. Four panels show, from the top down: normalised absorbances of the four filters present in rows 2 and 3 of the mid-band (each acts as a cut-off filter passing long wavelengths Cronin *et al.*, 1994a), nomograms (G.D. Bernard unpublished) of the 8 visual pigments found in the proximal (non R8) regions of rows 1– 4 (Cronin *et al.*, 1994c), normalised radiance conditions in typical *P. ciliata* habitat at 1 m (Cronin *et al.*, 1994c) and calculated sensitivities of the 8 retinal regions based on sequential serial filtering of visual pigments and intrarhabdomal filters (for details of calculations see Cronin & Marshall 1989b). This stomatopod dwells near the surface and therefore has the full spectrum of light available to it. Apparently as a result it 'spreads' its sensitivities across the whole spectrum – bottom panel. (**e**) *Lysiosquilla sulcata*. Four panels equivalent to (**d**). This stomatopod species lives in slightly deeper, murkier water as can be seen in the decreased radiance where it lives at long and short wavelengths. To compensate for this and to boost sensitivity the two proximally placed filters are 'lost' and the visual pigments are clustered more around the middle of the spectrum where light is available. Resulting sensitivities, bottom panel, cover this centralised spectral region and not the red or UV end where light is limited (and see Cronin *et al.*, 1994c)

Tiered retinae nearly always contain photoreceptors with different spectral sensitivities (see section 4.2.5e for an exception to this in vertebrates), the short wavelengths sampled by the distal tiers and progressively longer wavelengths by more proximal layers. Other examples of this are found in jumping spiders (Salticidae), where a 4 layered retina exists with spectral sensitivities at 360 nm, 480 – 500 nm and 580 nm (Yamashita and Tateda 1976) and a variety of insects, other than the diptera discussed above. The layering of the salticid retina, with short wavelength receptors placed closer to the lens, may be arranged to counteract chromatic aberration in which short wavelength rays are brought to a focus in front of longer wavelengths. Although constructed from fused rhabdoms, such as those found in bees, in some lepidopterans (the moths *Dielephila* and *Spodoptera* – Schlecht *et al.*, 1978; Langer *et al.*, 1979: and butterflies – Bandai *et al.*, 1992; Arikawa and Uchiyama 1996), dragonflies (Laughlin and McGuinness 1978; Yang and Osorio 1996), mayflies (Horridge and McLean 1978; Horridge 1976) and the lacewing *Chrysopa* (Horridge 1976), the rhabdoms contribute differing amounts of microvilli at different levels. This effectively makes the photoreceptors tiered and capable of serial sharpening of spectral sensitivity using the visual pigment of distally placed rhabdom portions.

A tiered rhabdom design and multiple visual pigments are found in some members of the enoploteuthid squid family such as *Watasenia scintillans* (Matsui *et al.*, 1988). *Watasenia* has five photoreceptor types in its eyes and three visual pigments with λ_{max} values at 470, 484 and 500 nm (Michinomae *et al.*, 1994). The ventral, upward looking, retinal region is tiered and also possesses yellow and red pigment granules. The sensitivity of the proximal region has been

modelled and is sharpened and shifted from 500 nm to 550 nm by the filtering action of the overlying retina (Michinomae *et al.*, 1994). This is a particularly remarkable finding as all other cephalopods are probably monochromats, possessing only a single visual pigment housed in a monomorphic population of photoreceptors. Stranger still, *Watasenia* and its relatives are deep-sea squid, living below 250 m in the daytime, where the spectral range of light is restricted largely to short wavelengths only. *Watasenia* does however come to surface waters for communal spawning in spring and emits two colours of intense bioluminesce from organs on its arms and body (Tsuji 1985). For this reason it is known as the firefly squid. These bioluminescent displays are particularly notable during surface water spawning, clearly an important event for the survival of these animals. Perhaps this vital group behaviour and whatever spectral discrimination it requires, is enough to explain the unusual retinal complexity of this cephalopod.

(c) Tiered polarizing filters For many arthropods, polarization vision may be as important as colour vision, and there are a variety of adaptations in their eyes which can be classified as polarising filters. The corneal light scattering filters found in the dorsal rim of some dipteran eyes is one example and is discussed in section 4.3.1c. There are also a variety of retinal adaptations which enhance polarisation vision. Photoreceptors constructed from microvilli are intrinsically dichroic, such that they are maximally sensitive to E-vectors of light parallel to the microvilli they carry. Cells with regular arrays of microvilli therefore have high polarisation sensitivity (PS). Where tiered photoreceptors exist the PS of the upper rhabdom may increase the PS of the lower photoreceptor by acting as a polarising filter (Snyder 1975). This filtering effect is exploited in the dorsal rim area of the compound eyes of many insects. Recall that this region of ommatidia are specifically adapted for navigation using the natural pattern of polarised light in the sky (section 4.3.1c; Rossel and Wehner 1984).

Crustaceans often possess rather long photoreceptors which might tend to lose PS through self screening (Snyder 1975). They have therefore adopted an interdigitating arrangement of narrow microvillar layers which exploits the E-vector filtering properties of microvilli to overcome this problem (also note that lateral filtering in optically coupled fused rhabdoms may have the same effect - Snyder *et al.*, 1973; Snyder 1975; Waterman 1981). Alternate layers carry microvilli that are perpendicular to each other, so light passing from one layer to another on its journey down the rhabdom is alternately switched from having vertical to horizontal E-vectors extracted, and therefore remains multidirectional to the bottom of the photoreceptor. While the photoreceptors extract the E-vector information needed for polarisation vision (Bernard and Wehner 1977), the PS reducing self screening, found in long rhabdoms of unidirectional microvilli, is minimised (Snyder 1975).

4.3.4 Postreceptoral filters

A variety of reflective structures exist at the base of invertebrate photoreceptors which increase photon capture by redirecting light back up the rhabdom. In common with the vertebrate tapeta (section 4.2.6b), the primary aim here is to increase sensitivity in the eye without increasing receptor length. It is not surprising therefore, that such adaptations are mostly found in nocturnal or crepuscular invertebrates and in those animals living in the depths of the sea. Beautifully coloured, spectrally narrow, tapeta are also found in the ommatidia of certain diurnal butterflies (Miller and Bernard 1968). Tapeta can be functionally divided into two different types: light coloured scattering pigments and those using thin film interference.

(a) Pigmentary tapeta The eyes of a variety of crustaceans, in particular those from the deep-sea like the *Penaeid* shrimps, exhibit spectacular eyeshine when illuminated (Zyznar and Nicol 1971; Shelton *et al.,* 1992; Gaten *et al.,* 1992). Superposition optics are used in such low-light environments (Land 1981) and the light seen is the 'luminous pseudopupil' (Exner 1891; Stavenga 1979) emerging from the facets involved in forming the superposition image. Light is reflected back through the rhabdom by white or light coloured pigments, generally purines (guanine is one, often used in vertebrate and spider tapeta – section 4.2.6b and below) and/or pteridines, situated round the base of the rhabdom. The reflection, although less efficient at short wavelengths (Miller 1979), is effective over much of the spectrum and can almost double light capture in superposition eyes, clearly an asset for night vision or vision in deep-ocean environments.

Curiously, the cells that form the tapetum in mid-water decapods are not always evenly distributed over the eye. There may be holes in the tapetum or gradations in reflecting efficiency around the eye (Shelton *et al.,* 1992). Typically, the part of the eye which looks into the lightless depths, where ambient brightness is 2 log units less than downwelling light (Denton 1970, 1990), has a thicker tapetum and brighter eyeshine than the regions looking up. The tapetum is in fact matched to the oceanic irradiance distribution with eye regions requiring greater sensitivity served by a thicker tapetum. The gradient is formed relative to the shrimps' natural body position in life. Oplophorid species, such as *Systelaspis debilis*, which swim with their body near horizontal most of the time, have dorso-ventral gradients of bright to dimly reflecting tapeta. Conversely, the sergestid *Sergestes henseni* swims with the body oriented vertically and its bright to dim tapetal gradient is rostro-caudal (Shelton *et al.,* 1992).

(b) Thin film interference tapeta The physics behind thin film interference was explained earlier (section 4.3.1a) and this mechanism is used in a number of invertebrates to construct reflective tapeta. Simple eyed invertebrates known to possess tapeta of this design include lycosid (wolf) spiders (Land 1981, 1985),

some copepod crustaceans (Fahrenbach 1964; Vaissière 1961), rotifers (Eakin 1972), ostracod crustaceans (Land 1981), scallops (Land 1966), and another bivalve mollusc, the cockle *Cardium edule* (Barber and Wright 1969). In two of these examples the tapetum is actually used instead of a lens to image light on the retina. This allows resolution of spatial detail in the scallop *Pecten*, while in the deep-sea ostracod *Gigantocypris*, it is for increasing sensitivity (to around 6000 × that of the human eye! – M.F. Land, pers. comm), an important requirement of life below 600 m in the ocean (Land 1981).

The lycosid spiders also require sensitive vision, as they hunt moving prey at twilight, pouncing on them in a single well executed jump. In common with many vertebrates, spider tapeta are made from thin-layered stacks of guanine crystals. Also like the vertebrates, those spider eyes containing tapeta (each spider has 8 eyes of two different designs – Land 1985) often arrange their retinae in an inverted manner with the receptors pointing inwards, towards the tapetum. This makes the absorption of reflected light more efficient and, as vertebrate eyes evolved in nocturnal animals which probably possessed tapeta, suggests one reason for the curious inverted arrangement of vertebrate eyes left today (Miller 1979).

The lepidoptera construct tapetal reflectors of a quite unique design by modifying part of their tracheal (air breathing) system. This allows them to use air spaces as the low refractive index layers, interspersed with chitinous cytoplasmic plates, giving the highest attainable refractive index change for light passing between layers. This results in the maximum possible percentage reflection of light at each interface. The tapetum in nocturnal moths is a relatively disorganised blanket of tracheal tissue reflecting green or bluish tinted light, relatively broad-band in its spectral characteristics, but possibly matched to the photoreceptors λ_{max}, for maximum photon reflux (Miller 1979). This may be achieved by combining several narrow-band reflector stacks, or by simply constructing multilayers with varying thicknesses and separations.

Surprisingly for day-time active animals, butterflies and some diurnal moths also possess tracheal tapeta consisting of exquisitely regular chitin plates (Figure 23). The result is a distinctively monochromatic or saturated looking colour reflection (Plate 1b). Each rhabdom has its own private tapetum and these may reject different eyeshine colours depending on the actual $1/4\lambda$ thickness of the layers and may also change with position round the eye. Although there is much variation and a number of patterns, dorsal eye facets usually emit blue and those in the ventral eye region, red (Miller and Bernard 1968; Bernard and Miller 1970). Occasionally there is a complete gradation with ommatidia in between these two extremes emitting green, yellow and orange (Miller 1979).

The presumed function of the narrow-band tracheal tapeta, like lateral or serial filtering, is tuning of photoreceptor sensitivity. The tapetal method has the disadvantage that all wavelengths of light enter the rhabdom at the top and are partially absorbed on their way down the photoreceptor, before being colour tinted and returned up the rhabdom by the tapetum. Nevertheless, light of the

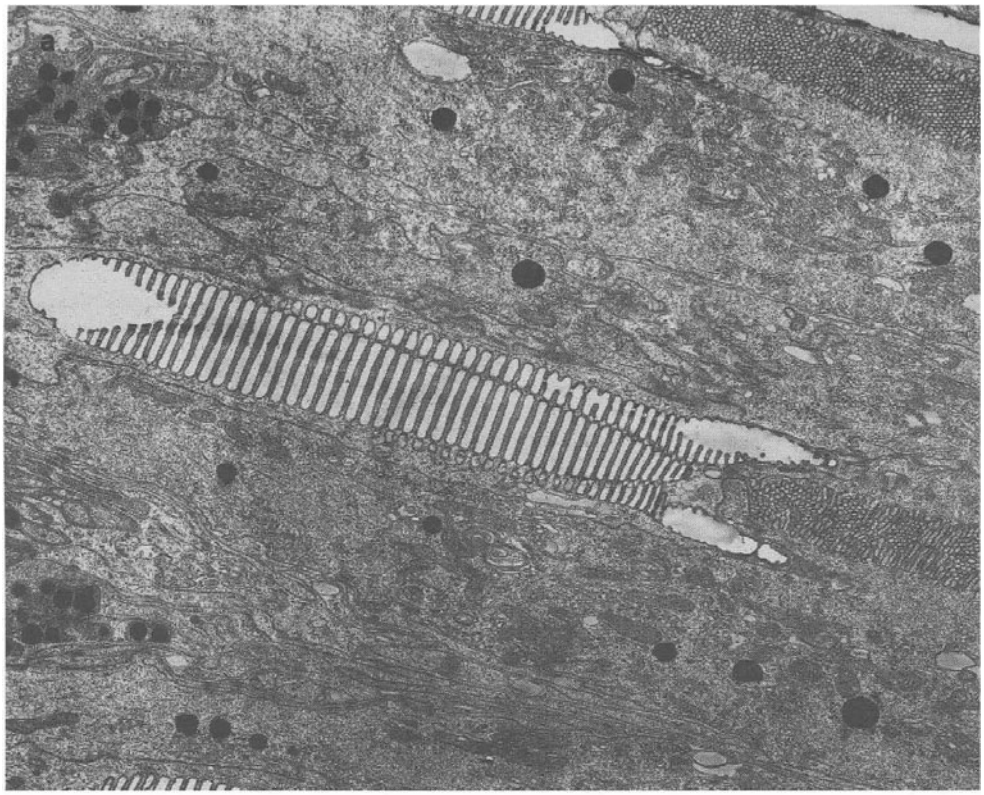

Figure 23 (**a**) Transmission electon micrograph (TEM) of the individual tracheal tapeta of the skipper butterfly. The very regular layering of material of different refractive indices (in this case, chitin and air) and spacing of layers at 1/4λ intervals mean that narrow band colour is reflected back up the photoreceptor. Such colours can be seen emerging from the eye in Plate 1b. (air space thickness between tracheal plates is 0.123 μm) (**b**) Normalised reflectance of a different 1/4λ reflector, in this case the alternating green and yellow corneal facets in the eyes of Dolichopodid flies (Plate 1a). The light not reflected here is transmitted to the photoreceptors below and may help in spectral sensitivity tuning (After Miller 1979)

wavelength reflected by the tracheal interference filter passes twice through the rhabdom, and this may be enough to render ommatidia with different eye glow colours spectrally distinct. Whether this directly affects colour vision or simply enhances colour contrast remains an enigma.

Interestingly red oil drop filters predominate in the ventrally directed dorsal region of bird retinae (Muntz 1972; section 4.2.5c). One explanation for this is that such filtering increases object contrast in a background of green foliage (Lythgoe 1979), the sort of visual signal experienced by flying or perched birds. The same hypothesis could be extended for the red filtered facets in the ventral eye of butterflies and enlarged to include the blue tint of the dorsal facets which possibly increases their efficiency at viewing things in a predominantly blue sky. The tracheal filter distribution is therefore matched to the butterflies' visual world.

One further complication to this story is that not all red eye glow is due to the tapetum alone. Some facets in the eyes of pierid butterflies look red when illuminated but this is the combined result of broad-band light reflected from a tracheal tapetum (which changes the spacing of its plates along its length to reject more than one wavelength – Miller 1979) and specialised laterally placed red retinular cell pigment. The red pigment granules are drawn in so close towards the rhabdom that some actually enter the microvilli, greatly influencing the colour emerging from the facet (Ribi 1978, 1979). The reasons for using a combination filter rather than relying on one method are obscure.

4.4 Conclusions

The importance of intraocular filters is indicated by their widespread occurrence. Some form of filter is, for instance, found in almost every anatomical region of both vertebrate and invertebrate eyes. Furthermore, many structures, such as the lenses of a variety of vertebrates, contain a plethora of spectrally, and hence functionally, similar pigments which are biochemically quite distinct, suggesting such filters have evolved independently on a number of occasions. Finally, even the most phylogentically ancient eyes contain filters, suggesting they have been present since vision first evolved.

This widespread occurrence of intraocular filters, and the fact that they deprive animals of potentially useful spectral information, implies that they must have one or more important functions. Not surprisingly when one considers the greater diversity of eye design in the invertebrates compared to vertebrates, there are some filters whose functions are unique to invertebrates. The functions proposed for intraocular filters in both groups include:

1. *Protection from light damage and the enhancement of image quality*: These are assumed to be the most widespread functions of both corneal and lens filters in vertebrates since most such filters remove short wavelengths, which

are those most prone to optical degradation and most likely to cause structural damage. Similar functions are probably performed by the vertebrate macular pigment, invertebrate corneal nipple arrays and a variety of other coloured retinal inclusions in both vertebrates and invertebrates. The seemingly greater involvement of vertebrate filters in protection against the damaging effects of short wavelengths compared to invertebrates is perhaps due to the generally superior photon capture of most vertebrate eyes, the result of the larger apertures and generally larger sizes of simple eyes.

2. *Enhancement of colour vision/spectral sensitivity modification*: Individual photoreceptors, or groups of photoreceptors, in invertebrates and vertebrates may have their spectral sensitivities tuned by coloured pigments, in or next to the photoreceptors, or by interference filters positioned before or after the retina. In both groups such colour filters exist primarily to narrow existing spectral sensitivities rather than increase the number of spectral channels. Sharpened spectral sensitivities provide a basis for enhanced colour vision (Govardovskii 1983; Cronin and Marshall 1989a; Marshall *et al.*, 1991b). It should be noted that several of these mechanisms, especially in the insects, are still only hypothetical.
3. *Maintenance of photoreceptor isolation to preserve spatial resolution*; is performed by the melanin and ommachrome within the vertebrate and invertebrate retina and by sheaths of pigment round crystalline cones in invertebrate eyes.
4. *Dynamic control of light flux*; using corneal pigment migration and RPE retinomotor movements in vertebrates, and by radial movement of retinular cell pigment and longitudinal pigment migration in invertebrates.
5. *Sensitivity increase/photoreceptor noise reduction*: This is achieved through the use of broad and narrow band reflecting tapeta in both vertebrates and invertebrates. In addition to this, invertebrates have developed a series of measures that also serve to increase sensitivity; photo-reconversion of metarhodopsin to rhodopsin, corneal nipple arrays, and sensitising pigments (such a pigment may also exist in one fish retina). The number of filter mechanisms displayed only by invertebrates to increase sensitivity may be explained by their generally poor light capturing abilities noted above. It should not be forgotten however, that the most sensitive eye belongs to an invertebrate (section 4.3.4), the result of exploiting image formation by mirror optics, a mechanism not found in the vertebrates (Land 1981).
6. *Filters associated with polarisation vision*; such as corneal dispersion and coloured corneal filters are only found in invertebrates. Oil drops in bird eyes may be involved in this visual capability.
7. *Increasing the visibility of bioluminescence*; is probably the main function of yellow filters in the lens, and sometimes the retina, of many deep-sea fish and cephalopods.

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