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Evolution of vertebrate visual pigments

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ABSTRACT

The visual pigments of vertebrates evolved about 500 million years ago, before the major evolutionary step of the development of jaws. Four spectrally distinct classes of cone opsin evolved through gene duplication, followed by the rod opsin class that arose from the duplication of the middle-wave-sensitive cone opsin. All four cone classes are present in many extant teleost fish, reptiles and birds, but one or more classes have been lost in primitive fish, amphibians and mammals. Gene duplication within the cone classes, especially in teleosts, has resulted in multiple opsins being available, both temporally and spatially, during development.

1. Introduction

Vision provides an animal with the ability to detect, almost instantaneously, the environment around it. There is a tendency for humans to have an anthropocentric view of vision in assuming that we have evolved the 'best' visual system, especially in terms of colour discrimination. However, the human retina with rods and just three spectral classes of single cone looks relatively simple when compared to that of say a diurnal bird or turtle, where the retina contains not only rods, but four spectral classes of single cone with an additional class of double cone. These cones are also more complex in possessing in their inner segments an array of colour filters in the form of oil droplets containing high concentrations of carotenoids. What is the evolutionary history behind these differences? In this review, I shall concentrate on the evolution of visual pigments and photoreceptors within vertebrates, but the parallel evolution of the neural complexity of the retina and higher visual centres required to analyse the input signals from the receptors should not be forgotten.

The earliest vertebrates, the jawless fish (agnaths) of the Cambrian and Ordovician periods (about 450–550 million years ago, MYA) lived in shallow lagoons probably feeding by sifting food from the muddy substrate where vision would be of little importance. Their visual sense would be primarily directed at identifying the approach of predators simply by detecting the movement of a sudden shadow or an abrupt change in illumination. Superficially, this could be achieved by a single class of photoreceptor. However, such a detection task in shallow waters, where surface ripples and waves, as well as reflections from the substrate, cause continuously flickering and variable luminance, is not straightforward (McFarland & Loew, 1983; Snyder & Dera, 1970). It would be difficult for a fish to distinguish between relatively intense slow-frequency flickering and potential predators or to detect objects against a background solely on luminance differences, if the brightness of either the object or the background were highly variable. Flicker, on the other hand, will change the luminance, but will not change chromaticity, so that an opponent process between two spectrally different receptors can filter out the flicker, but will have the added advantage of leaving a 'colour' signal enabling the easier detection of objects against the background (Maximov, 2000). Similarly, potential confusion from highly variable luminance can also be overcome by an opponent process providing the ability to detect differences in the spectral composition of the environment, where spectral reflectance (colours) will be independent of luminance.

Although the minimum requirement for colour vision is two spectrally distinct classes of photoreceptors combined with a nervous system that can compare the quantum catch of one class of receptor with the quantum catch of another, this may not give maximum information about wavelength discrimination and colour vision throughout the full 'visible' daylight spectrum, from the near-UV around 300–350 nm to the far-red above 700–750 nm. An effective colour vision system has to contend with the broad spectral sensitivity functions of opsin-based photosensitive pigments, the high energy demands of the receptors and the complexity of the neural mechanisms required for colour perception. Given these constraints, the most efficient number of spectral classes of photoreceptor appears to be four, and adding a fifth spectral class probably provides little or no advantage (Barlow, 1982; Osorio & Vorobyev, 2005). Vertebrate photopic vision is generally mediated by more than one spectral class of cone with dichromacy, trichromacy and tetrachromacy common amongst most lower

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vertebrate groups. It should be emphasised that although there is a considerable database on the number of spectral cone classes possessed by a wide range of species, there is really very little data on the dimensionality of their colour vision. For example, the presence of four cone classes may strongly infer tetrachromacy, but only behavioural studies can establish this, and these data are often sadly lacking.

Rods and cones contain visual pigments that are composed of a protein moiety, opsin, linked to a chromophore, retinal, the aldehyde of Vitamin A. Opsins are members of an extensive family of G-protein-linked membrane receptors that are composed of about 350 amino acids that form a palisade of seven α-helical transmembrane regions enclosing a ligand-binding pocket (Fig. 1). Retinal is bound into the pocket through a Schiff base linkage to a lysine residue in the seventh helix. Since all vertebrate visual pigments contain retinal (either retinal or 3-dehydroretinal), their spectral sensitivity is determined primarily by the structure of the opsin, predominantly by interactions of the chromophore with specific amino acids lining the ligand-binding pocket (Fig. 1).

Comparative studies across all of the major vertebrates groups have established that in addition to the rod class of pigment, there are four spectrally distinct classes of cone pigments encoded by distinct opsin gene families (Fig. 2): a long- to middle-wave class (LWS) maximally sensitive in the red–green spectral region from about 490–570 nm, a middle-wave class (RH2) sensitive in the green from about 480–535 nm, a short-wave class (SWS2) sensitive in the blue–violet from about 410–490 nm and a second short-wave class (SWS1) sensitive in the violet–ultraviolet from about 355–440 nm (for a review, see Yokoyama, 2000). This is a somewhat unhelpful and cumbersome classification of opsin classes, but has become firmly established in the literature. The LWS (sometimes L/M) and SWS notation is intuitive, but the RH2

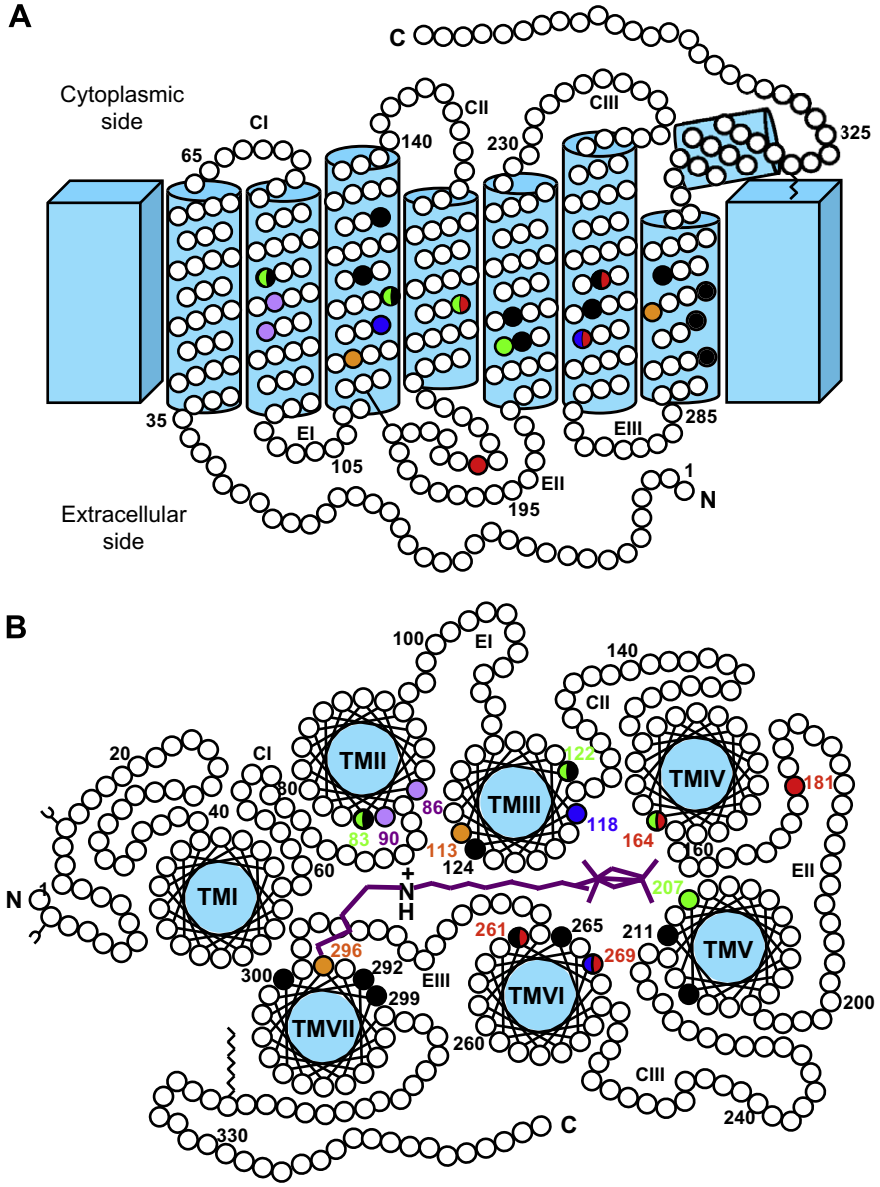

Fig. 1. Schematic diagrams of a visual pigment molecule. (A) Two-dimensional diagram illustrating the seven transmembrane α-helices. (B) View showing the arrangement of the helices around the chromophore, retinal, shown in purple (basic design kindly supplied by W.L. Davies). Although the helices are of different lengths, for simplicity, each helix is shown with only the central 18 amino acids. The numbering is based on mammalian rod opsin. Lysine 296 (orange) is the binding site of retinal and glutamate 113 (orange) provides the Schiff base counter ion. Major sites involved in spectral tuning are colour coded with opsin class: LWS red, RH2 green, SWS2 blue, SWS1 violet and RH1 black. Split colours indicate sites involved in tuning in more than one opsin class. Note how sites tend to cluster around either the Schiff base linkage or the ionone ring of retinal. Figure from Bowmaker and Hunt (2006).

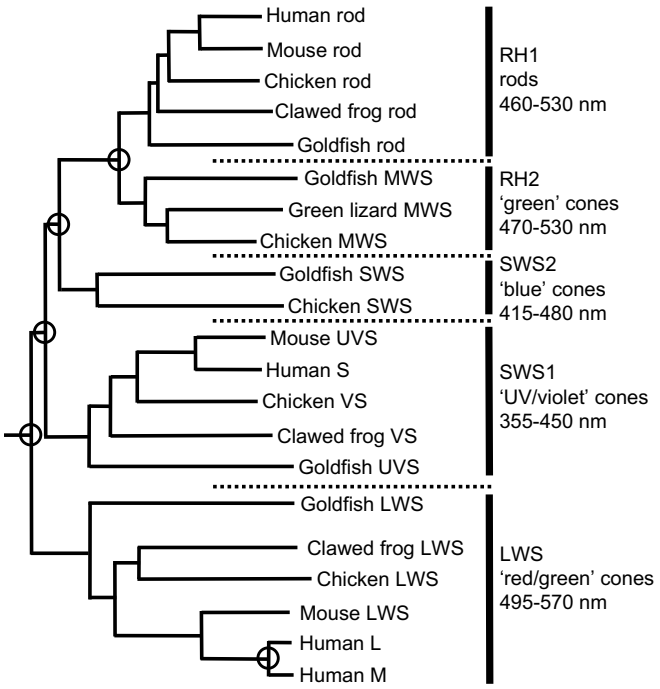

Fig. 2. Generalised phylogenetic scheme of the evolution of the five vertebrate visual pigment opsin gene families. Representatives of the major vertebrate groups are shown. Note the absence of SWS2 and RH2 opsin genes in mammals and the RH2 opsin gene in amphibians. Although only the lizard RH2 gene is shown, all five opsin classes are represented within the reptiles. Circles indicate gene duplications, four occurring early in vertebrate evolution, about 500 MYA with the Old World duplication of the LWS gene occurring relatively recently, about 35 MYA.

terminology for 'green'-sensitive cones derives from the close homology of these opsins with the rod opsins (RH1).

The four cone classes have arisen from an ancestral single opsin gene through a series of gene duplications (Fig. 2). By applying estimates of the rate of gene divergence, it is suggested that the appearance of the four classes occurred very early in vertebrate evolution, by about 450 MYA (Nathans, Thomas, & Hogness, 1986). This is close to the time of one of the major steps in vertebrate evolution, the appearance of jaws. Modern vertebrate groups, most notably diurnal reptiles, birds and shallow water teleosts, express at least one gene from each of the four cone opsin classes. However, animals have evolved their visual sensitivity to match aspects of their photic environment, and it is likely that the primary adaptive selective pressure is the spectral range and intensity of daylight. At the most basic level, nocturnal animals have rod-dominated retinas whereas diurnal species have cone-rich retinas. Nevertheless, visual sensitivity can be adapted, at the receptor level, to specific spectral regions and/or specific visual tasks by spectrally tuning the sensitivity of the visual pigments and/or by varying the number of spectral classes of cone.

These two tuning mechanisms are not mutually exclusive. First, mutations within an opsin gene can lead to a spectral shift in the sensitivity of the pigment. A single nucleotide substitution may lead to the replacement of an amino acid that alters the interaction between the chromophore and opsin, leading to a spectral shift. The change in spectral sensitivity arising from a single amino acid substitution may be only a few nanometres, but can be greater than 60 nm (Wilkie et al., 2000). Additional mutations can lead to further spectral shifts, but there are only a limited number of sites within opsin that can be altered without producing a non-functional pigment. Second, a species may modify the ancestral vertebrate pattern of four spectrally distinct cone classes either by the loss of one or more of the cone classes or by gene duplication, where multiple copies of one or more cone classes may be present. Mutations in the duplicated genes can then lead to the generation of two or more spectrally distinct pigments within a single opsin class.

A further tuning mechanism can be achieved by changing the chromophore of a visual pigment from retinal, the aldehyde of Vitamin A_1, to 3-dehydroretinal derived from Vitamin A_2: switching from a rhodopsin to a porphyropsin. 3-Dehyroretinal has an extra double bond in the terminal ionone ring of the polyene change which has the effect of displacing the maximum absorbance (λ_{max}) of the visual pigment to longer wavelengths. The displacement is wavelength dependent, being much greater with long-wave-sensitive visual pigments. A pigment based on retinal with λ_{max} at 565 nm, will have a 'paired pigment' based on 3-dehydroretinal with λ_{max} close to 615 nm. At wavelengths around 500 nm the spectral difference between pigment pairs is reduced to about 25 nm and at about 440 nm, the difference is just a few nanometres (Hárosi, 1994; Parry & Bowmaker, 2000). As a consequence an animal can make significant changes in its spectral sensitivity and colour vision by simply switching chromophores, a conversion that can occur either during development or seasonally as seen in a number of fish and amphibians (for classical reviews, see Bridges, 1972; Knowles & Dartnall, 1977). As a general rule, though with notable exceptions (see below), porphyropsins are found in freshwater species of fish, amphibians and reptiles, whereas rhodopsins are common in marine and terrestrial environments. Porphyropsins are absent from birds and mammals.

In this review, I have traced the evolution of visual pigments or more specifically of cone visual pigments throughout all the major vertebrate groups from 'primitive' jawless fish to birds and mammals. Much of our understanding of the distribution of visual pigments has come from direct measurements of their absorbance spectra by microspectrophotometry (MSP) or of their spectral sensitivity by electroretinography, but our understanding of their evolution is derived primarily from molecular techniques used to isolate and sequence opsin genes. Obviously, the review cannot be comprehensive, but I have tried to include most of the more recent relevant literature without the text becoming a simple catalogue of papers.

2. Agnatha: Jawless fish

Primitive jawless fish are represented today by two distinct groups: lampreys (Petramyzontiformes) and hagfish (Myxiniformes). Little is known of the nature of the photoreceptors in the degenerate eye of hagfish (Fernholm & Holmberg, 1975; Holmberg, 1970, 1977; Vigh-Teichmann, Vigh, Olsson, & van Veen, 1984), but there was much early debate as to the types of photoreceptor present in lamprey retina (e.g. Crescitelli, 1972), a debate aggravated by the considerable variation in photoreceptors seen across species. Northern hemisphere lampreys (*Petromyzon* and *Lampetra* spp.) appear to contain only two classes of photoreceptor classified as rods, maximally sensitive around 510–525 nm, and a single class of cone maximally sensitive at longer wavelengths above about 550 nm (Govardovskii & Lychakov, 1984; Hárosi & Kleinschmidt, 1993; Ishikawa et al., 1987; Negishi, Teranishi, Kuo, & Miki, 1987). Precise λ_{max} are difficult to determine since a number of lamprey species migrate between marine and riverine environments and change their visual pigments from rhodopsins to porphyropsins during migrations. The classification of the two classes of photoreceptor is also not straightforward since electrophysiological data suggest that the rods have some cone-like features and function at both scotopic and photopic levels (Govardovskii & Lychakov, 1984).

Rod opsin-like genes have been isolated and sequenced for both the river lamprey, *Lampetra japonica* (Hisatomi, Iwasa, Tokunaga, &

Yasui, 1991) and the marine lamprey, *Petromyzon marinus* (Zhang & Yokoyama, 1997). The deduced amino acid sequences show about 92% similarity and have about 80% identity with rod opsins from higher vertebrates. These rod opsins are presumably expressed within the 'short', more rod-like photoreceptor. The gene sequence for the longer-wave visual pigment in Northern hemisphere lampreys has not so far been published, but in *P. marinus* the porphyropsin exhibits an ionochromic spectral displacement from a λ_{max} close to 600 nm to about 550 nm related to the concentration of chloride ions (Hárosi & Kleinschmidt, 1993), a feature common to LWS cone visual pigments (Kleinschmidt & Hárosi, 1992; Wang, Asenjo, & Oprian, 1993; Zak, Ostrovsky, & Bowmaker, 2001).

In the Southern hemisphere species, *Mordacia mordax*, there is apparently only a single class of rod photoreceptor (Collin, Hart, Wallace, Shand, & Potter, 2004), but in marked contrast to lamprey with limited photoreceptor classes, the Southern hemisphere species, *Geotria australis*, has in addition to rods, multiple spectral classes of cone (Collin, Hart, Shand, & Potter, 2003). Microspectrophotometry (MSP) has identified two spectrally distinct classes of cone containing porphyropsins with λ_{max} at about 610 and 515 nm along with rods with λ_{max} at about 505 nm (similar to *P. marinus*). However, study of the genetic complement of visual pigment opsins in *Geotria* has identified five opsin genes (Collin, Knight et al., 2003). Three of these are orthologous to the LWS, SWS2 and SWS1 opsin genes of jawed vertebrates, but the remaining two, RHA and RHB appear to be equally distantly related to the gnathostome RH1 and RH2 gene families. Four of the *Geotria* pigments, SWS1, SWS2, RHB and RHA, have been regenerated with 11-*cis* retinal yielding pigments with λ_{max} at 358, 439, 492 and 497 nm, respectively (Davies et al., 2007b), but the LWS failed to regenerate. The RHA opsin would appear to be that expressed in the rods whereas the RHB is presumably expressed in MWS cones.

Collin, Knight et al. (2003) proposed that the gene duplication that gave rise to the true rod RH1 gene and the middle-wave-sensitive cone RH2 gene of jawed vertebrates occurred after the separation of the gnathostomes from the agnaths. This assertion has been questioned though (Collin & Trezise, 2006; Pisani, Mohun, Harris, McInerney, & Wilkinson, 2006), with further phylogenetic analyses suggesting that the RHA lamprey gene is orthologous to the RH1 gene. The status of the lamprey RHB gene is less clear, but the expressed and regenerated pigment data (Davies et al., 2007b) gives supporting evidence to the rod and cone status of the RHA and RHB opsins. The debate about the evolution of rod opsins and scotopic vision will continue, and it raises the intriguing question as to what defines a rod and a cone. Are these cell types defined by their morphology, opsin content, the isoforms of the proteins involved in visual transduction, or the physiological parameters of excitation and adaptation?

Irrespective of the classification of the two RH opsin genes in lamprey, it is apparent that at least in one species from the Southern hemisphere, functional genes from all four cone opsin classes are present. From this, it is clear that the cone opsin genes originated before the evolution of jaws, perhaps as early as 540 MYA, implying that primitive jawless fish of the shallow late Cambrian and Ordovician seas possessed four spectrally distinct cones classes and thus had the potential for a tetrachromatic colour vision system. Nevertheless, the great variation in photoreceptor classes across species of lamprey illustrates the dangers of making broad generalisation extrapolated from limited data, emphasising the need for extensive comparative studies.

3. Rays and sharks

The elasmobranchs comprise one of the two subclasses of cartilaginous fish in the Class Chondrichthyes, the other being the Holocephali (chimaeras). The phylogenetic position of elasmobranchs, radiating early (about 400 MYA) from the main gnathostome lineage, implies that they have the potential of retaining all of the four vertebrate cone opsin classes, but traditionally they were thought to be primarily adapted for scotopic vision in having an all rod retina (Walls, 1942). Indeed, some skates may have pure rod retinas (Govardovskii & Lychakov, 1977; Ripps & Dowling, 1990) and in two species of *Raja*, the rods function at both scotopic and photopic levels (Dowling & Ripps, 1990; Ripps & Dowling, 1990), superficially similar to the rods of Northern hemisphere lamprey (Govardovskii & Lychakov, 1984). However, it is clear that most, if not all sharks and rays, possess at least a single class of cone (Cohen, 1990; Sillman, Letsinger, Patel, Loew, & Klimley, 1996), as in the guitarfish, *Rhinobatos lentigenosus*, where MSP has identified a single spectral class of cone with a λ_{max} identical to that of the rod (Gruber, Loew, & McFarland, 1990).

In contrast, electroretinography from the retina of the common sting ray, *Dasyatis pastinaca* (Govardovskii & Lychakov, 1977) revealed a spectral sensitivity with three peaks, suggesting cone visual pigments with λ_{max} at 476, 502 and 540 nm. Further, studies of horizontal cells from a related species, the red stingray *Dasyatis akejai* (Toyoda, Saito, & Kondo, 1978) identified three layers of horizontal cells in which the inner most layer consisted of chromatically-coded C-type cells. More recently, MSP studies have demonstrated that two species of shovelnose ray (*Rhinobatos typus* and *Aptychotrema rostrata*) (Hart, Lisney, Marshall, & Collin, 2004) and the blue-spotted maskray, *Dasyatis kuhlii*, (Theiss, Lisney, Collin, & Hart, 2007) possess three spectral classes of single cone with λ_{max} at about 460–480, 490–500 and 550–560 nm. All three species have rods with λ_{max} close to 500 nm. These data clearly demonstrate that some species of ray have the potential for at least a trichromatic colour vision system probably based on LWS, RH2 and SWS2 cone classes, but appear to have lost the short-wave SWS1 class of cone.

4. Chondrosteans/Acipenseriformes

This ancient order of ray-finned fish, radiating about 375 MYA from the main gnathostome lineage, comprises 25 species in two families, the sturgeons (Acipenseridae) and the paddlefish (Polyodontidae). The retinas of all the species of sturgeon and paddlefish so far studied contain rods and single cones, but with the possible exception of the stellate sturgeon which has an all cone retina (Govardovskii & Zueva, 1987). Within a species there is little morphological difference between spectrally distinct cones and generally they all possess a colourless oil droplet (although there is a report of a small cone without a droplet in the Siberian sturgeon Govardovskii, Byzov, Zueva, Polisczuk, & Baburina, 1991). All knowledge of the cone visual pigments in these groups comes from MSP (for a recent review, see Sillman & Dahlin, 2004) which has identified three spectral classes with λ_{max} at about 605–620, 525–540 and 440–470 nm, presumably representing LWS, RH2 and SWS2 opsin genes, respectively. The rods have λ_{max} around 535–540 nm and all the pigments are probably porphyropsins. As with the elasmobranchs, the short-wave SWS1 cone class appears to have been lost. Most adult sturgeon and paddlefish are bottom-feeders living in dim, muddy, highly turbid environments. Because of this, and because of their relatively small eyes and highly developed sense of smell, it is surprising to find that these species have retained such a complex potential colour vision capability.

5. Holosteans

These primitive fish, diverging from the chondrosteans about 250–300 MYA, were dominant in both marine and freshwater environments in the Triassic, some 200 MYA, though there are only

two surviving genera, both inhabiting freshwaters in North America. The Amiidae have a single surviving representative, the bowfin *Amia calva* whereas the Lepisosteidae (gars) consist of seven surviving species.

In *Amia*, Burkhardt, Gottesman, Levine, and MacNichol (1983) identified double cones containing pigments with λ_{max} at 624 and 556 nm and single cones with λ_{max} at 457 nm, porphyropsins spectrally similar to those of the chondrosteans and implying the expression of LWS, RH2 and SWS2 opsin genes. As in the sturgeons, no evidence had been found for ultraviolet-sensitive cones. In marked contrast, the longnose gar, *Lepisosteus osseus* has a more complex complement of opsin gene expression. Previously only two classes of cone pigment had been reported with λ_{max} at about 623 and 535 nm (Burkhardt et al., 1983; Levine & MacNichol, 1979), presumably representing LWS and RH2 opsin classes, but a recent MSP study of adult longnose gar (Loew, personal communication) has identified five cone pigments with λ_{max} at 631, 541, 441, 427 and 365 nm. These most likely represent expression of all four of the opsin cone classes, but of particular interest is the presence of what could be the expression of two SWS2 genes (the 427- and 441-nm pigments) suggesting an early gene duplication in this class (see below).

6. Teleosts

Teleosts perhaps offer within a relatively closely related vertebrate group, the greatest range of visual capacity, extending from pure rod vision in many deep-sea fish species to tetrachromacy in a number of more shallow living species. The teleost radiation began in the Cretaceous about 150 MYA and by the end of the Cretaceous had become the dominant fish in both oceanic and freshwater habitats comprising about 96% of all living fish species. Adult epipelagic teleosts tend to be trichromatic or dichromatic, having lost or no longer expressing either the LWS or the SWS1 opsins or both. In contrast, fish living in highly turbid or deeply stained waters tend to lose or not express the shorter-wave opsins, but retain the LWS and RH2 opsin genes. In more extreme conditions, fish may become cone monochromats expressing only the RH2 or LWS genes.

Unlike most other vertebrate groups, many teleost families have duplicated their cone opsin genes to produce a range of functional opsins within each opsin gene class. There is evidence that the Actinopterygia (ray-finned fish) have more genes than other vertebrate groups and it has been suggested that a whole-genome duplication occurred early in the evolution of ray-finned fish, in the Devonian around 350 MYA, after their divergence from the sarcopterygian lineage (Christoffels et al., 2004; Furutani-Seiki & Wittbrodt, 2004; Meyer & Schartl, 1999). Thus the sarcopterygian fish, which includes coelacanth and lungfish, and all land vertebrates (amphibians, reptiles, birds and mammals), tend to have only half the number of genes compared with actinopterygian fish. However, the evolution of gene families is an active process in which gene duplication (whether by whole-genome duplication or duplication of a limited number of genes) will be accompanied by the subsequent mutation of genes, leading either to the decay of some genes into pseudogenes and eventually junk DNA or to a divergent gene with a new function (neo-funtionalization) (Ohno, 1970). In groups such as cichlids and cyprinids, mutations in the duplicated genes have led to additional functional genes with visual pigments spectrally displaced from one another, most notably within the RH2 gene family (Fig. 3), but also in both the LWS and SWS2 classes.

6.1. RH2 duplication

One of the most striking examples of opsin gene duplication is found in the cichlid populations of the African Great Lakes. Lake Malawi has more than 700 species of cichlids that have evolved from a common ancestor within the last million years (Meyer, 1993; Turner, Seehausen, Knight, Allender, & Robinson, 2001) and are notable for their diversity, particularly in their colour patterns. Most species are sexually dimorphic and visual communication is crucial for mate choice (for reviews see Kocher, 2004; Seehausen, 2000).

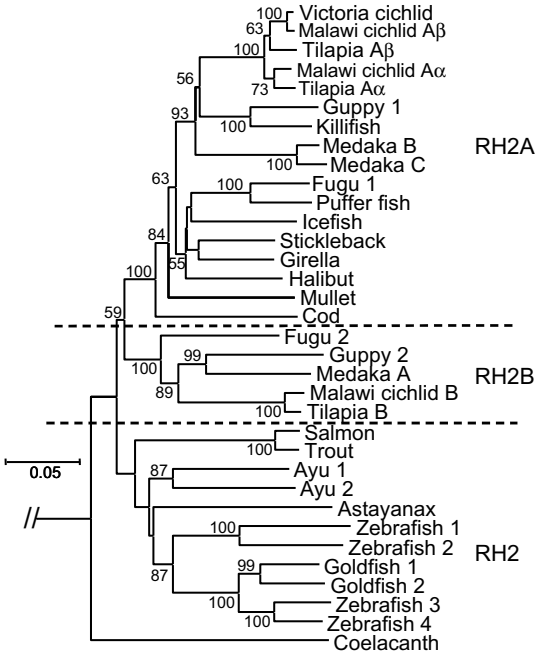

Fig. 3. Phylogeny of teleosts RH2 cone opsin genes. Nucleotide sequences were aligned by Clustal W, and the tree was generated by the neighbour-joining method (Saitou & Nei, 1987). The bootstrap confidence values (1000 replicates) are shown for each branch. The *Drosophila* Rh4 sequence was used as an outgroup (not shown). The scale bar is equal to 0.05 substitutions per site. The dashed lines indicate the divergences of the three major 'classes' of RH2 gene. Note the gene duplication of the RH2A gene in African cichlids (RH2Aα and RH2Aβ) and in medaka (RH2A B and RH2A C). Duplications also occur in the goldfish, zebrafish and ayu RH2 genes. Figure from Bowmaker and Loew (2007).

Adult African cichlids typically possess three cone visual pigments, with non-identical double cones maximally sensitive at longer wavelengths and shorter wavelength-sensitive single cones (Carleton, Hárosi, & Kocher, 2000; Carleton & Kocher, 2001; Fernald & Liebman, 1980; Jordan et al., 2006; Parry et al., 2005; Van der Meer & Bowmaker, 1995). The precise λ_{max} of the cones vary between species, superficially related to the clarity of the water in their specific habitats. Mbuna (rock dwelling) species tend to have double cones with maximum sensitivities at about 535 and 488 nm and ultraviolet- or violet-sensitive single cones with λ_{max} at about 370 or 420 nm (Fig. 4). In contrast, non-Mbuna species that are more sand-dwelling, may be less sensitive to short wavelengths, possessing double cones with maximum sensitivities at about 570 and 535 nm and blue-sensitive single cones with λ_{max} at about 450 nm (Carleton et al., 2000; Jordan et al., 2006; Levine & MacNichol, 1979; Parry et al., 2005).

Remarkably, in some species, rare additional spectrally distinct cones have been identified suggesting that at least seven spectral types of cone pigment are expressed in the retina (Parry et al., 2005). In confirmation of this, analysis of the opsin gene complement of these cichlids has identified seven functional cone opsin genes, three from the RH2 gene class, two from the SWS2 class, with single representatives of the LWS and SWS1 gene classes (Fig. 4) (Parry et al., 2005; Spady et al., 2006).

The three 'green-sensitive' cone pigments suggest that duplication in the RH2 gene has occurred on at least two occasions in the

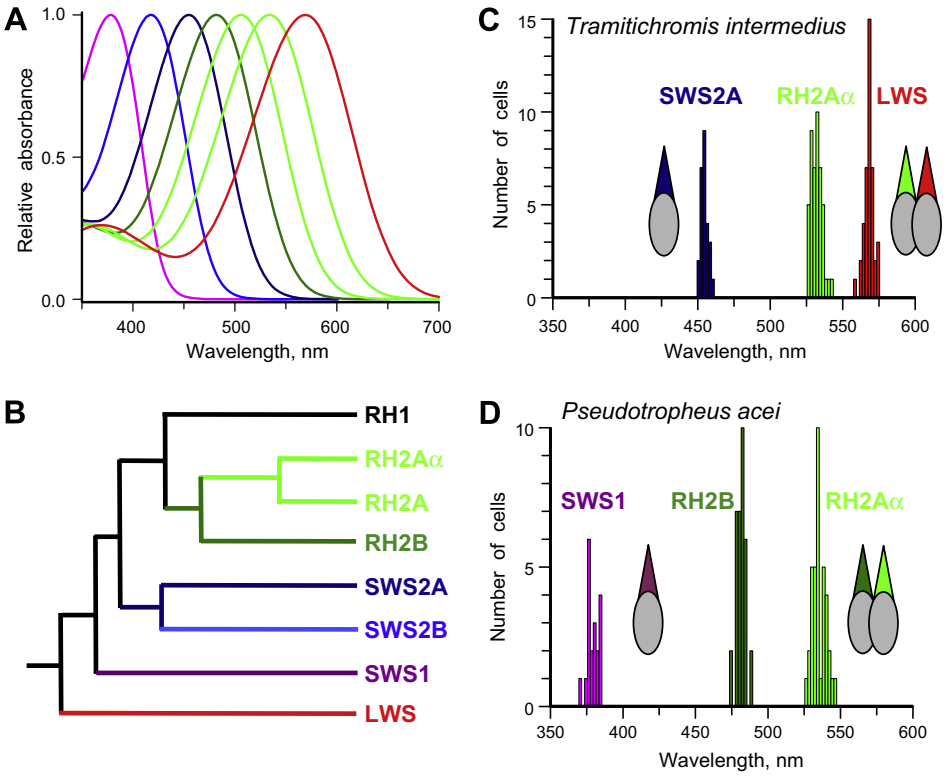

Fig. 4. The organisation of the seven cone opsin genes present in the species flocks of African cichlid fish. (A) Absorbance of the seven cone pigments colour coded with opsin class. (B) Schematic of the phylogenetic arrangement of the opsins illustrating the gene duplications that have occurred within the SWS2 and RH2 opsin classes. The recent duplication within the RH2A class may be restricted to African cichlids. (C,D) The distribution of the dominant spectral cone classes in two different species of Malawi cichlids as measured by microspectrophotometry. The two species illustrate differential expression of three of the seven cone opsins present in the cichlids. Figure from Bowmaker and Hunt (2006).

cichlid lineage (Fig. 4). There was a relatively ancient duplication, leading to RH2A and RH2B genes, which occurred after the divergence of the Acanthopterygii from other teleosts, sometime between about 260 and 150 MYA (Fig. 3) (Furutani-Seiki & Wittbrodt, 2004; Kumazawa, Yamaguchi, & Nishida, 1999). These two genes have diverged such that their expressed cone pigments may be separated by as much as 50 nm. The second, much more recent duplication of the RH2A gene probably occurred within the past 10 MYA only in the intralacustrine cichlid radiation (Kocher, Conroy, McKaye, Stauffer, & Lockwood, 1995). The duplication has led to two spectrally distinct classes, RH2Aα and RH2Aβ, with λ_{max} separated by only about 10–20 nm (Fig. 4) (Parry et al., 2005; Spady et al., 2006).

Since genes that are not expressed would be expected to evolve free of any constraints of selective pressure and would build up random mutations leading to non functionality, what are the functions that maintain the presence of all seven genes? Functional opsins may be differentially expressed either spatially and/or temporally. Regional variations in the distribution of cone pigments across the retina and ontogenetic changes in cone opsin expression are not uncommon, both in teleosts and mammals. In the African cichlids, variations in expression across the retina have not been described, but ontogenetic changes have been established. Larval tilapia express primarily four of the seven opsins: SWS1, RH2B, RH2Aα and LWS at approximately equal levels (Spady et al., 2006) with the inference that the larvae are potentially tetrachromatic. During development though, there is a major switch in expression with a marked down regulation of the SWS1 and RH2B genes and a significant up regulation of the SWS2A and LWS gene. Adult tilapia then express primarily only three opsins, SWS2A, RH2Aα and LWS, with the LWS noticeably dominant, and are presumably limited to trichromacy.

Since the duplication into RH2A and RH2B occurred early in the radiation of teleosts, at least before the divergence of the Paracantopterygii (including gadids) and the Acanthopterygii (including cichlids) (Furutani-Seiki & Wittbrodt, 2004; Kumazawa et al., 1999), all of the orders within the percomorph teleosts should show evidence of both genes (Fig. 3). Indeed, these have been identified in the guppy (*Poecilia retinculata*, Atherinomorpha, Cyrinodontiformes) (Hoffmann et al., 2007) and medaka (*Oryzias latipes*, Atherinomorpha, Beloniformes) (Matsumoto, Fukamach, Mitam, & Kawamura, 2006), which has a very similar pattern of cone opsin genes to the African cichlids. However, in puffer fish (Tetraodontiformes) the orthologue of the RH2B gene has been truncated to a pseudogene (Neafsey & Hartl, 2005) and in other groups may have been lost completely (Fuller, Carleton, Fadool, Spady, & Travis, 2004; Fuller, Fleishman, Leal, Travis, & Loew, 2003; Pointer et al., 2005) (for a detailed review, see Bowmaker & Loew, 2007).

Gene duplication of the RH2 gene has also occurred independently within distantly related teleosts (Fig. 3). In the cyprinids both goldfish and zebrafish express multiple copies of the RH2 gene which, at least during larval development in zebrafish, are expressed both temporally and spatially as spectrally distinct cone pigments (Chinen, Hamaoka, Yamada, & Kawamura, 2003; Chinen, Matsumoto, & Kawamura, 2005a; Johnson et al., 1993; Takechi & Kawamura, 2005), though the functional significance of this is not at all clear. Similarly, the ayu (an osmerid salmonid) expresses two RH2 genes separately, in long single cones and in one half of double cones (Minamoto & Shimizu, 2005).

6.2. SWS2 duplication

Phylogenetic analysis shows that the SWS2 gene also duplicated in the early ancestry of the Acanthopterygii in a similar fashion the

RH2 gene. Subsequent mutations have led to two spectrally distinct sub families, SWS2A opsins having λ_{max} around 440–455 nm and SWS2B opsins with λ_{max} at shorter wavelengths between about 405 and 425 nm (Bowmaker et al., 2006; Carleton & Kocher, 2001; Fuller et al., 2004; Fuller et al., 2003; Matsumoto et al., 2006; Parry et al., 2005).

In teleosts other than Acanthopterygii, although SWS2 gene duplication is not apparent, a similar separation in the spectral location of SWS2 pigments appears to have occurred. For example, in cyprinids a given species may have either an SWS2 cone pigment (based on retinal$_1$) with λ_{max} at about 440–450 nm, such as goldfish (Avery, Bowmaker, Djamgoz, & Downing, 1983; Bowmaker, Thorpe, & Douglas, 1991; Chinen, Matsumoto, & Kawamura, 2005b; Downing, Djamgoz, & Bowmaker, 1986; Hárosi, 1985; Hárosi & MacNichol, 1974; Johnson et al., 1993; Loew & Lythgoe, 1978) or about 405–415 nm, such as zebrafish (Cameron, 2002; Chinen et al., 2003; Hárosi & Hashimoto, 1983; Nawrocki, BreMiller, Streisinger, & Kaplan, 1985; Palacios, Goldsmith, & Bernard, 1996; Robinson, Schmitt, & Dowling, 1995; Whitmore & Bowmaker, 1989). Chinen et al. (2005a, 2005b) have reconstructed the likely ancestral SWS pigment of the goldfish and zebrafish which, when expressed with 11-*cis*-retinal, has a maximum absorbance at 430 nm, indicating that mutations have occurred in both species to displace the pigment to longer and shorter wavelengths respectively.

6.3. SWS1 pigments

Duplication of SWS1 genes appears to be rare within teleosts and all the reported SWS1 pigments are expressed as true UV-sensitive pigments with λ_{max} between 350 and 380 nm (Chinen et al., 2003; Cowing et al., 2002; Matsumoto et al., 2006; Parry & Bowmaker, 2000; Parry et al., 2005; Spady et al., 2006). The exception to this is the smelt, ayu (*Plecoglossus altivelis*) where two SWS1 genes have been identified (Minamoto & Shimizu, 2005), but one of the pair (SWS1-1) is expressed at a very low level and could not be identified by *in situ* hybridization. The spectral sensitivity of the two opsins is not known and it may be that they are spectrally identical. It would appear that the tuning mechanisms that have evolved in other vertebrate groups to tune SWS1 opsins to longer wavelengths above 400 nm (Cowing et al., 2002; Hunt et al., 2004; Parry, Poopalasundaram, Bowmaker, & Hunt, 2004; Shi, Radlwimmer, & Yokoyama, 2001; Shi & Yokoyama, 2003; Wilkie et al., 2000; Yokoyama, Radlwimmer, & Blow, 2000) have not been achieved in teleosts, where violet sensitivity is achieved through SWS2B opsins.

6.4. LWS duplication

Duplication of the LWS gene has been identified in a number of acanthopterygian teleosts including medaka and guppy (Hoffmann et al., 2007; Matsumoto et al., 2006; Miyazaki, Yamauchi, Takami, & Kohbara, 2005). These duplications appear to have occurred independently, but it is possible that they have a common origin, and subsequent gene conversion has removed any trace of long divergence. Outside of the Acanthopterygii, LWS gene duplication also occurs in zebrafish (Chinen et al., 2003), and the cave fish *Astyanax* (Yokoyama & Yokoyama, 1990).

The LWS opsin genes in *Astyanax* provide a classic example of convergent evolution. The cavefish possesses three LWS genes: two have maximum absorbance at about 535 nm, whereas the third has λ_{max} at about 565 with the spectrally different pigments located in the two halves of double cones. Inspection of the amino acid sequences of the opsins demonstrates that exactly the same amino acid substitutions are found tuning between the 535 and 565-nm cone pigments as are found between the L and M cone pigments of primates (see below) (Kleinschmidt & Hárosi, 1992; Parry, Peirson, Wilkens, & Bowmaker, 2003; Yokoyama & Yokoyama, 1990; Yokoyama & Radlwimmer, 2001).

In zebrafish the two LWS genes have been expressed with λ_{max} at 558 and 548 nm (Chinen et al., 2003), but in contrast to *Astyanax*, there is no evidence for two spectrally distinct populations of LWS cones (Cameron, 2002; Nawrocki et al., 1985; Robinson, Schmitt, Hárosi, Reece, & Dowling, 1993). This raises the question as to whether the two pigments are coexpressed in the same cones. A similar possibility arises in goldfish where, although there are two spectrally distinct RH2 cone pigments (Johnson et al., 1993), we have been unable to show in adult fish that the two opsins are expressed in separate classes of cone (unpublished observations). The situation in the guppy is even more confusing where between two and six LWS genes may be present (Hoffmann et al., 2007; Weadick & Chang, 2007), but MSP of cones in adult guppies gives three potential λ_{max} at about 533, 548 and 572 nm (Archer & Lythgoe, 1990). It is possible that the 533-nm pigment may represent an RH2A gene, leaving the two longer cone pigments as candidates for LWS genes. However, Archer and Lythgoe (1990) suggested that the 548-nm cones may be coexpressing the 533- and 572-nm pigments. The precise arrangement of pigments will only be resolved with further work on the expression of the isolated opsin genes.

7. Coelacanth and lungfish

The exact phylogenetic relationship between lungfish (Dipnoi), coelacanths (Crossopterygei, Coelacanthimorpha) and tetrapods remains unclear (e.g. Brinkmann, Venkatesh, Brenner, & Meyer, 2004; Meyer, 1995; Takezaki, Figueroa, Zaleska-Rutczynska, Takahata, & Klein, 2004), but lungfish and coelacanths occupy a unique evolutionary link between terrestrial vertebrates such as reptiles and birds, and aquatic vertebrates such as teleosts and elasmobranchs. These groups diverged in the early Devonian about 350–400 MYA.

There are only three extant species of lungfish, geographically separated in Australia, South American and Africa. The retinal organization of the Australian species, *Neoceratodus forsteri* has recently been studied in some detail. The retina contains, in addition to rods, multiple classes of cones distinguished by brightly coloured oil droplets (Bailes, Robinson, Trezise, & Collin, 2006; Robinson, 1994), a feature common to reptiles and birds. At least three morphologically distinct cone classes can be identified: about 75% with a large red droplet, about 15% with a yellow pigmented ellipsoid region and about 5% with a small clear droplet (Fig. 5). This strongly suggests that *N. forsteri* has the potential for at least trichromatic colour vision and recent analysis of visual pigments by MSP (Marshall, Vorobyev, Collin, Bailes, & Hart, 2006) has identified four spectrally distinct cone pigments in addition to a rod pigment. In adults, three porphyropsin cone pigments are present with λ_{max} at 479, 557 and 620 nm, whereas young fish have an additional UV-sensitive cone pigment with λ_{max} at 374 nm. The Australian lungfish has therefore retained the four vertebrate ancestral cone pigments with the potential for tetrachromatic colour vision, at least at a juvenile stage. Morphologically different cone classes may also be present in the African and South American lungfish (Ali & Anctil, 1973; Walls, 1942), but their spectral properties have not been examined.

In contrast to lungfish that live in shallow freshwater rivers, the two extant species of coelacanth are found in relatively deep waters between 100 and 400 m in the Indian Ocean. Their retinae are more typical of deep-sea fish and are rod dominated with cones comprising only about 1–2% of the photoreceptors (Locket, 1973; Millot & Carasso, 1955). Nonetheless, the cones may possibly be divided into three morphological classes with the rarest class containing a colourless oil droplet (Millot & Carasso, 1955). The extracted rod

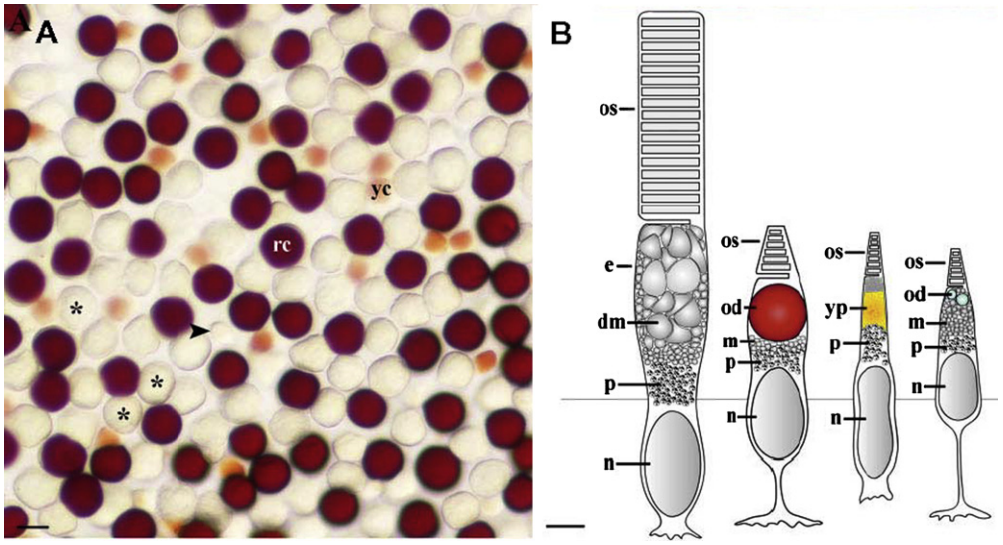

Fig. 5. Photoreceptors of the Australian lungfish, *Neoceratodus forstei*. (A) Retinal wholemount of a fresh retina showing all four morphological photoreceptor types at the level of the ellipsoid. The large, clear photoreceptors (asterisks) are rods; the red (rc) and yellow (yc) cones are easily distinguishable by the colour of their intracellular inclusions. One clear cone (arrowhead) can be identified because it is noticeably smaller than the rod photoreceptors. (B) Schematic summary of photoreceptor types drawn to scale. dm, distended mitochondria; e, ellipsosome; m, mitochondria; n, nucleus; od, oil droplet; os, outer segment; p, paraboloid; yp, yellow pigment. Scale bars, 10 μm. Figure from Bowmaker and Loew (2007), modified from Bailes et al. (2006), with permission of Wiley-Liss, Inc., a subsidiary of John Wiley & Sons, Inc.

pigment with λ_{max} at 473 nm (Dartnall, 1972) is typical of deep-sea fish and its sensitivity may be correlated with the maximum transmission of oceanic water, around 470–480 nm and/or with the maximum emission of bioluminescence. Recently, two opsin genes have been isolated from both species of *Latimeria* (Yokoyama & Tada, 2000; Yokoyama, Zhang, Radlwimmer, & Blow, 1999) which are orthologous to RH1 and RH2 opsins. These genes have been expressed and have λ_{max} at 485 and 478 nm, respectively. Yokoyama et al. (1999) also isolated a pseudogene derived from the SWS1 class, but no evidence was found for either an LWS or SWS2 gene. Yokoyama et al. (1999) suggested that because of their spectral closeness, the 473-nm pigment extracted by Dartnall (1972) was in fact the RH2 pigment, but this cannot be the case. Extraction techniques typically yield only rod pigments and given the very low numbers of cones in the retina of *Latimeria*, the extracted 473-nm pigment must be the RH1 pigment, which, when expressed, has λ_{max} at 485 nm. The 12-nm discrepancy between the two values is surprising, given that extracts of rod pigments from deep-sea fish typically agree with direct measurements of visual pigment absorbance by MSP. It has also been suggested (Yokoyama et al., 1999) that the presence of the RH1 and RH2 pigments could give the coelacanth rod/cone-based colour vision within the narrow spectral window available at depth in the ocean, but given the very low density of cones, this seems an unlikely scenario.

The two extant species of coelacanth are nocturnal piscivorous predators living at depth in the ocean (Fricke & Hissmann, 2000), but their Devonian ancestors probably lived in a coastal wetland environment (Thomson, 1993) and presumably possessed a typical vertebrate polychromatic photopic visual system. Comparisons of the RH1 and RH2 opsin genes from both coelacanth species suggest that the migration to the deep sea occurred about 200 MYA (Yokoyama & Tada, 2000). The change in habitat to the relatively dim monochromatic deep sea presumably resulted in the loss of colour vision along with the loss of function of the other three cone opsin genes.

8. Oil droplets

These data from lungfish and coelacanth highlight an important consideration in the evolution of cone pigments and cone morphology, the presence of oil droplets. These organelles, located in the distal region of the inner segment, are found somewhat spasmodically throughout the vertebrates (Fig. 6). Amongst fish, they are absent from lampreys, elasmobranchs (rays and sharks), holosteans (bowfin and gars) and teleosts (bony fish), but are found in birchir (Brachiopterygii, *Polypterus*), sturgeons and coelacanths as well as lungfish, though only the lungfish have brightly coloured droplets. The presence of oil droplets in these more primitive fish implies that this feature is ancient and may represent the ancestral composition of cones (Robinson, 1994; Walls, 1942). In terrestrial vertebrates they are present in some amphibians, retiles and birds, but are notably absent from placental mammals (Fig. 6). In amphibians, clear droplets are found in anurans (frogs and toads), but are absent from salamanders and caecilians, whereas within reptiles coloured droplets are found in turtles and most lizards, but are absent from snakes and crocodiles. Coloured droplets are ubiquitous in birds and clear droplets are found in the non-eutherian mammals, monotremes and marsupials. The absence of oil droplets in teleosts is somewhat surprising since they are present, albeit uncoloured, in chondrosteans and holosteans, but the absence in eutherian mammals may be more easily explained and has been put down to the nocturnal phase experienced during early mammalian evolution (Walls, 1942).

9. Amphibians

Amphibians fall into three phylogenetic groups, the legless, burrowing caecilians, the caudata (urodeles, salamanders and newts) and the anurans (frogs and toads). The caecilians have small somewhat reduced eyes with pure rod retinas that express typical rod visual pigments, but with their λ_{max} shifted to shorter wavelengths around 488 nm (unpublished observations). In contrast, all other amphibians have a duplex retina with both double and single cones and rods.

A striking feature of the anurans and some salamanders is the presence of two spectral classes of rod described as early as the late 19th Century (see Crescitelli, 1972). In these rod dominated retinas, the majority of rods (about 90–95%) may be described as typical, since they contain a rhodopsin with λ_{max} close to 502 nm (or the paired porphyropsin). The remaining minority of rods are

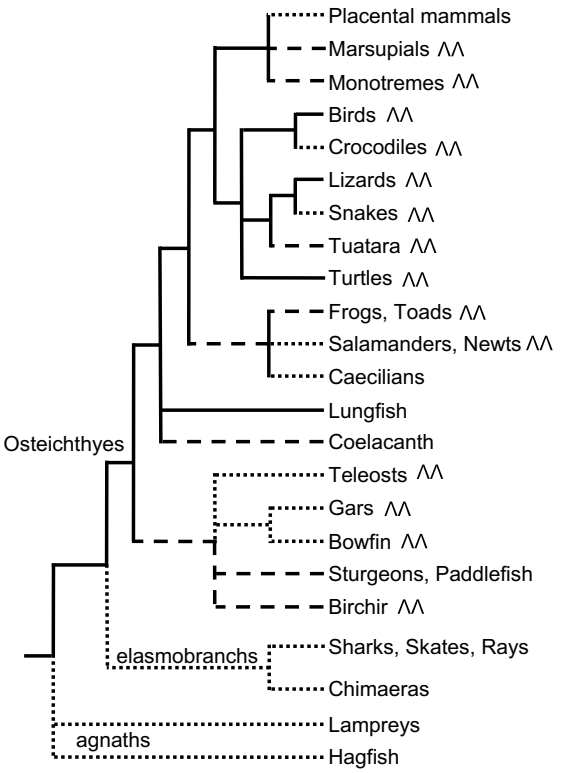

Fig. 6. Phylogenetic scheme of the major vertebrate groups indicating the evolution of oil droplets and double cones. Dotted lines specify the absence of oil droplets, dashed lines the presence of colourless droplets and full lines the presence of coloured droplets. The symbol ΛΛ indicates that presence of double cones. Oil droplets appear after the evolution of the Osteichthyes and are absent from agnaths and elasmobranchs. Coloured oil droplets first appear in lungfish. The phylogeny is based on that from Meyer and Zardoya (2003).

short-wave sensitive with λ_{max} around 435–445 nm. These two classes of rod have been termed, somewhat confusingly, 'red' and 'green' rods, respectively, based on their colour, the 'green'-sensitive 'red' rods containing sufficient visual pigment to appear red under the light microscope, whereas the 'blue'-sensitive rods apparently appear green (Denton & Wyllie, 1955). The visual pigment in the red rods is a typical RH1 pigment, but that of the green rods is an SWS2 'cone' pigment (Darden et al., 2003; Hisatomi, Takahashi, Taniguchi, Tsukahara, & Tokunaga, 1999; Ma et al., 2001b).

In addition to the two classes of rods, anuran and caudatan retinae also contain double cones and probably two spectral classes of single cone. Both members of the unequal double cones are long-wave sensitive expressing a LWS rhodopsin pigment with λ_{max} close to 565 nm or a mixture with the paired porphyropsin (e.g. Makino, Groesbeek, Lugtenburg, & Baylor, 1999; Röhlich & Szél, 2000; Sherry, Bui, & DeGrip, 1998). In anurans the principal member of the double cones contains a clear oil droplet, but this is not found in salamanders and newts. The two classes of single cones contain a UV-sensitive SWS1 cone pigment and a blue-sensitive SWS2 pigment, identical to that found in the green rods (Deutschlander & Phillips, 1995; Hárosi, 1982; Hisatomi et al., 1998; Ma et al., 2001a; Ma et al., 2001b; Yusuke, Hisatomi, Sakakibara, Tokunaga, & Tsukahara, 2001). In the newt, which has no green rods, the SWS2 pigment when regenerated with retinal has λ_{max} at 474 nm, some 40 nm longer than that found in other amphibians (Takahashi & Ebrey, 2003). Somewhat surprisingly, the middle-wave-sensitive RH2 cone opsin has not been identified in any amphibian and was presumably lost early in their evolution.

Clearly both anurans and urodeles, with three spectral classes of cone, have the potential for photopic colour vision (Przyrembel, Keller, & Neumeyer, 1995), (though there is evidence of coexpression of pigments in the UVS cones (Makino & Dodd, 1996)), but the function of the two classes of rods is not so easy to define. Although the green rods and the 'blue'-sensitive cones contain the same visual pigment, they possess different transduction mechanisms with the green rods having a rod transducin (Ma et al., 2001b). However, the different transducins do not appear to markedly affect the photon sensitivity or response kinetics of the two cell types. Presumably, the green rods are involved in wavelength discrimination, probably at mesopic levels and may be involved in the instinctive blue-sensitive, positive phototactic behaviour seen in anurans (Muntz, 1962; Muntz, 1963a; Muntz, 1963b).

10. Reptiles

Modern reptiles include a wide range of groups extending from the relatively ancient crocodilians through the squamates, which includes lizards and snakes, to the testudines (chelonids), the turtles and tortoises. The crocodilians, reptiles most closely related to the dinosaurs and birds (Janke & Arnason, 1997), have remained relatively unchanged for about 200 MY. They have a duplex retina dominated by rods, but also including single and double cones that lack oil droplets. The Mississippi alligator (*Alligator mississippiensis*) possess four spectral classes of cone and thus has the potential for tetrachromatic colour vision. The unequal double cones contain pigments with λ_{max} at about 566 and 503 nm, presumably belonging to the LWS and RH2 opsin classes and two forms of single cone have maxima close to 535 and 443 nm (Sillman, Ronan, & Loew, 1991). Probably the 443-nm pigment has an SWS2 opsin, but the status of the 535-nm pigment is not clear since it could be a second shorter-wavelength LWS pigments or a longer wavelength RH2 pigment. The only other crocodilian to have been studied, the spectacled caiman (*Caiman crocodilus*) (Govardovskii, Chkheidze, & Zueva, 1988), has single cones spectrally similar to those of the alligator, but does not possess the long-wave pigment. In the caiman, the double cones contain either a 535-nm pigment in both halves or a 535/506 nm pigment combination. Both species have rods with λ_{max} close to 500 nm and the opsin sequence from the alligator shows similarities with avian rod opsins (Smith et al., 1995).

As with crocodilians, our knowledge of the visual pigments of turtles is restricted to just a few species, but these follow a basic pattern that is also reflected in birds (see below). The retinas of turtles have a high percentage of a complex array of cone types comprising double cones and four spectral classes of single cone. In the identical double cones, both members contain a long-wave sensitive visual pigment, but the two halves are morphologically distinct with the principal member containing a large coloured oil droplet, usually pale yellow or orange, whereas the accessory member lacks a distinct oil droplet, but may contain low concentrations of carotenoids (Lipetz & MacNichol, 1982; Loew & Govardovskii, 2001; Ohtsuka, 1985a). The two halves will therefore be spectrally different, though optical coupling may negate this, and there is also debate as to whether these double cones are electrically coupled. There has also been confusion as to the visual pigments in the two members of the double cones (Liebman & Granda, 1971; Richter & Simon, 1974), but it is now clear that they both contain a 'red'-sensitive pigment (Loew & Govardovskii, 2001; Ohtsuka, 1985b). In addition to the double cones, there are four spectral classes of single cone that contain brightly coloured oil droplets and are thought to support tetrachromatic colour vision. The details of this arrangement are fully described below for birds.

The evolution of rods and cones and visual pigments within the very diverse group of squamates is complex and far from under-

stood. This extensive group includes true chameleons, iguanid lizards, monitor lizards, geckos, skinks and snakes, with many diurnal, crepuscular and nocturnal members. Possible changes during evolution in the life style of these reptiles from diurnal to nocturnal and back, have led to the idea of the transmutation of cones to rods and a tertiary change back to cones. For classical discussions of the transmutation theory of Walls, see (Crescitelli, 1972; Walls, 1935; Walls, 1942).

The anoline lizards are perhaps the most fully studied. They have a pure cone retina containing both double cones and single cones, all containing coloured oil droplets. There are four spectrally distinct cone classes containing visual pigments with λ_{max} close to 564, 495, 455 and 365 nm providing the potential for tetrachromatic colour vision (Fleishman, Loew, & Leal, 1993; Kawamura & Yokoyama, 1997; Kawamura & Yokoyama, 1998; Loew, Fleishman, Foster, & Provencio, 2002; Provencio, Loew, & Foster, 1992). A broad range of Caribbean anoline lizard known to live in differing photic habitats and having distinctly different dewlap colours have been studied, but the conserved pattern of cone spectral sensitivities across all species suggests that the anoline cone complement is not necessarily adapted to the photic environment or to the colour of significant visual targets such as their prominent dewlaps (Loew et al., 2002). The complete absence of rods in anoline lizards has been questioned recently by the identification of low levels of expression of a rod opsin RH1 gene in the retina (Kawamura & Yokoyama, 1997; McDevitt, Brahma, Jeanny, & Hicks, 1993), but whether this indicates a population of rods not previously identified or co-expression of the RH1 pigment in cones has yet to be established.

A notable feature of *Anoles carolinensis*, probably unique amongst the anoles lizards, is that its visual pigments are porphyropsins, more typical of aquatic species, with the LWS cone being maximal at about 625 nm (Loew et al., 2002; Provencio et al., 1992). Surprisingly, the true chameleons (Chamaelionidea), which have a cone complement very similar to anoline lizards, also contain porphyropsins, but mixed with rhodopsins to form pigment pairs, and show great variation in spectral sensitivity across the retina, exemplified by the LWS cones that have a broad range of λ_{max} extending from about 555 to 610 nm (Fig. 7) (Bowmaker, Loew, & Ott, 2005). The significance of the presence of porphyropsins in these highly terrestrial species and the variation in spectral sensitivity seen in chameleons is difficult to explain on either evolutionary or environmental grounds, since there seems to be no obvious correlation with habitat or significant visual targets.

The transmutation theory of Walls is most often invoked in discussions of the photoreceptors in geckos (Gekkonidae). Walls proposed that geckos evolved from pure cone diurnal lizards, first to nocturnal species, but then followed by the re-evolution of some diurnal species of gecko. This theory was based primarily on the gross morphology of the retina where nocturnal geckos have photoreceptors with large rod-shaped outer segments, including double rods, but diurnal species have much smaller somewhat more cone-like outer segments. Although the outer segments of the photoreceptors of nocturnal geckos are superficially very rod like, more detailed study suggests that 'the visual cells of geckos exhibit characteristics of cones at all levels of their ultrastructure' (Röll, 2000). Another feature of cones in some vertebrate groups is the presence of oil droplets in the inner segment. Colourless oil droplets are common in diurnal geckos, but except for the nocturnal *Aristelliger praesignis*, other nocturnal geckos possess visual cells without droplets (Röll, 2000). The droplets in diurnal geckos perhaps represent the vestiges of coloured oil droplets in the cones of ancestral diurnal lizards. Similarly, visual cells of the nocturnal lizards *Heloderma*and *Sphenodon*also contain apparently colourless oil droplets. The 'tertiary' origin of diurnal species of geckos is also

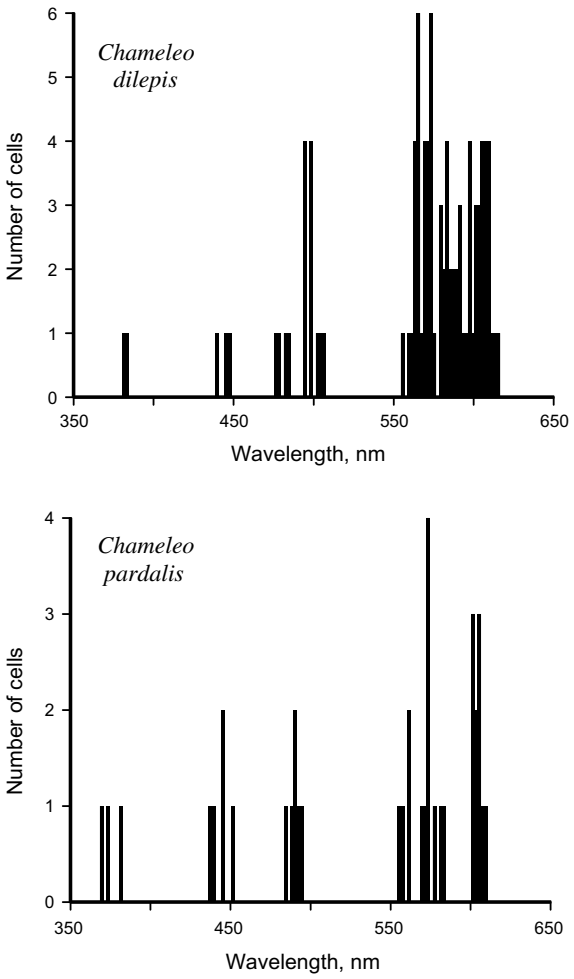

Fig. 7. Spectral distribution of the λmax of individual cones from two species of chameleon as determined by MSP (bin size of 2 nm). The four spectral classes have λ_{max} ranging from 555 to 610 nm (LWS), 480 to 505 nm (RH2), 440 to 455 nm (SWS2) and 370 to 385 nm (SWS1). The visual pigments are variable mixtures of rhodopsins and porphyropsins with a suggestion that the LWS cones may fall into three spectral classes. Data from Bowmaker et al. (2005).

supported by recent analyses of the eye lens crystallins from a wide range of gecko species (Röll, 2001).

The cone like structural similarities of gecko photoreceptors are reflected in the visual pigments of nocturnal geckos which are more cone like than rod like (Crescitelli, 1963; Crescitelli, 1977). The 'rods' contain a longer-wave-sensitive pigment with λ_{max} about 521 nm, a shorter-wave pigment with λ_{max} about 467 nm and a UV-sensitive pigment with λ_{max} about 365 nm (Loew, 1994; Loew, Govardovskii, Röhlich, & Szél, 1996). Molecular evidence confirms that these visual pigments are expressions of opsins belonging to three of the four cone opsin classes, LWS, RH2 and SWS1 respectively (Kojima et al., 1992; Yokoyama & Blow, 2001). These are also present in diurnal geckos (Ellingson, Fleishman, & Loew, 1995; Taniguchi, Hisatomi, Yoshida, & Tokunaga, 1999).

The final reptilian group for which there is some limited data is the snakes. The evolution and phylogenetic relationships of snakes (Serpentes) is clearly beyond the scope of this review (e.g. see Heise, Maxson, Dowling, & Hedges, 1995; Scanlon & Lee, 2000), but the more 'primitive' snakes such as boas and pythons (Henophidia) have a retina dominated by rods, λ_{max} 495 nm, comprising about 90% of the photoreceptors and two classes of single cone, a majority long-wave sensitive cone with λ_{max} about 550 nm and

an ultraviolet-sensitive cone with λ_{max} about 360 nm (Sillman, Carver, & Loew, 1999; Sillman, Johnson, & Loew, 2001). Both boas and pythons are nocturnal and their retina, rod dominated and with reduced dichromatic colour vision with ultraviolet sensitivity, is somewhat reminiscent of some nocturnal rodents (see below).

In contrast some 'advanced' colubrid snakes have pure cone retinas. In the garter snake (*Thamnophis sirtalis*) the retina is dominated by double cones and large single cones with at least two populations of small single cones (Jacobs, Fenwick, Crognale, & Deegan, 1992; Sillman, Govardovskii, Röhlich, Southard, & Loew, 1997). The double and large single cones contain the same long-wave-sensitive pigment, λ_{max} about 554 nm and the small single cones have λ_{max} at either 482 or 360 nm. Garter snakes are highly diurnal and their cone and pigment arrangement is somewhat reminiscent of turtles and birds, though snakes do not possess oil droplets. The sensitivity to ultraviolet is presumably through an SWS1 cone opsin, and to long wavelengths through an LWS cone opsin, though no molecular data are available. In the garter snake the 482-nm pigment is most probably based on an RH2 cone opsin.

11. Birds

The avian photoreceptor array probably represents the culmination of the evolution of cones in terms of the combination of morphological cone types, visual pigments and oil droplets. The retinas of birds appear to be highly conserved across species with the presence of double cones and four spectral classes of single cone subserving tetrachromatic colour vision and is found in almost all species so far studied, though with exceptions in some nocturnal species (for reviews, see Hart, 2001; Hart & Hunt, 2007). Generally in diurnal birds, the double cones comprise about 50% of the cone population with the 'red' LWS and 'green' RH2 single cones in approximately equal numbers adding a further 20% each. The remaining 10% is composed of 'blue' SWS2 and 'violet or ultraviolet' SWS1 single cones. It has been suggested that birds segregate visual mechanisms at the receptor level where double cones appear to be more concerned with achromatic functions such as luminance, form and movement detection, whereas the four spectral classes of single cone are involved primarily in chromatic tasks (Campenhausen & Kirschfeld, 1998; Maier & Bowmaker, 1993; Osorio & Vorobyev, 2005; Osorio, Vorobyev, & Jones, 1999).

The striking feature of avian cones, like that of turtles, is the presence of coloured oil droplets that act as long pass filters cutting off sorter wavelengths (Fig. 8). Double cones contain a red-sensitive LWS cone pigment in both members, with the principal member containing a large pale yellow, P-type droplet that cuts off at about 460 nm and the accessory member having low concentration of carotenoids that may or may not be contained in a small droplet. In the single cones a logical combination of oil droplet type and visual pigment is found. 'Red'-sensitive cones contain a 560- to 570-nm LWS pigment associated with a red R-type droplet that cuts off light at about 560 nm. 'Green'-sensitive cones have a 505- to 515-nm RH2 pigment and a yellow Y-type droplet with a cut off at abut 505 nm, and 'blue'-sensitive cones have a 430- to 450-nm SWS2 pigment and a C-type droplet with a cut-off at about 410–440 nm. There are two varieties of the fourth single cone class, 'violet'-sensitive (VS) with a 400- to 425-nm pigment and 'ultra-violet'-sensitive (UVS) with a 360- to 370-nm SWS1 pigment, both having a transparent T-type droplet that shows no significant absorbance above 350 nm (Fig. 8) (Bowmaker, Heath, Wilkie, & Hunt, 1997; Hart, 2001). Direct measurements of VS and UVS cone pigments suggest that VS pigments are found in Anseriformes (ducks), Ciconiiformes (shearwaters and penguin) and Galliformes (chickens and quail), whereas UVS pigments are common in Passeriformes (perching birds) and Psittaciformes (parrots), but this restricted distribution reflects the limited number of species that have been studied, rather than a comprehensive review.

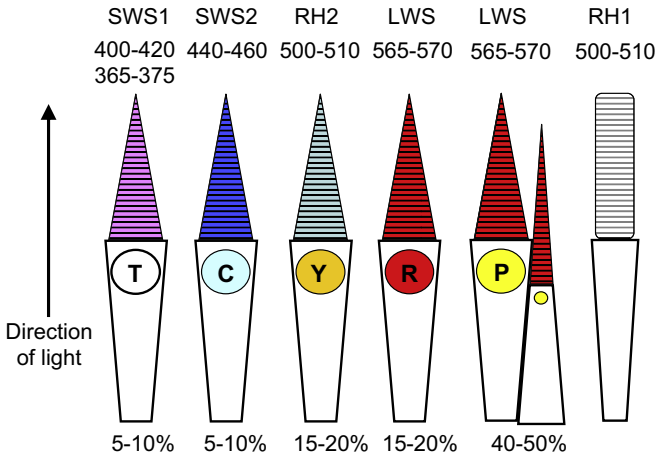

Fig. 8. Schematic diagram of the complement of photoreceptors in the avian retina, as found in many diurnal passerines. The λ_{max} of the visual pigments of the four spectral classes of single cone, double cones and rods are shown above the diagrams. The UV/UVS class have maxima either in the UV close to 370 nm or in the violet between 400 and 420 nm. Both members of the double cones contain the same LWS pigment as the R-type single cones. The oil droplets are Pale (Principal) in double cones and Red, Yellow, Clear and Transparent in single cones. The percentage values are the approximate relative percentages of the different cone types.

Recently a notable exception to this general pattern has been reported in the bobolink (*Dolichonyx orizivorus*) (Beason & Loew, 2008). Although this species is a passeriform, it belongs to the icterids, members of which may be limited to North and South America and which have not been previously studied. Remarkably, and somewhat confusingly, it has double cones that contain a 565-nm pigment in the principal member, but paired with a violet-sensitive 403-nm pigment in the accessory member, which has an oil droplet that cuts off light below about 410 nm. In addition, the species also possesses a typical UVS single cone with a 372-nm pigment, but no evidence was found for a cone class with a 440- to 460-nm pigment. How common this arrangement is amongst bird species will have to wait for further work.

Although the visual pigments of avian retina are highly conserved, the evolution and divergence of the UVS and VS forms of the SWS1 opsins has generated considerable interest. It is most probable that the ancestral vertebrate SWS1 pigment was ultraviolet-sensitive, as found in some lamprey, teleosts, salamander and reptiles, but that the ancestral avian pigment was violet-sensitive (for a recent review, see (Hart & Hunt, 2007). The displacement from UVS to VS appears to be based primarily on a single amino acid change at site 86 in helix II of the opsin (bovine rod opsin numbering), with the ancestral vertebrate UVS pigment having phenylalanine (Phe) at this site (Fig. 1). However, the ancestral avian VS pigment has Phe replaced by Serine (Ser), the single amino acid replacement causing a spectral shift of some 40–60 nm. The avian UVS pigments have then re-evolved independently in a number of different groups, not simply by replacing Ser86, but also by exchanging Serine at site 90 for Cysteine. Both of these sites located in the centre of helix II lie close to the Schiff's base counter ion, Glutamate at site 113 in helix III (Fig. 1).

In all of the avian species studied to date, either by MSP or with molecular genetics, an SWS2 pigment with λ_{max} around 440 nm is paired with an SWS1 pigment with λ_{max} at either about 400–420 nm or 365 nm. But the bobolink is an exception. It is reported to have both a 372-nm and a 403-nm pigment (Beason & Loew,

2008), raising the question as to whether the 403-nm pigment is a second SWS1 pigment or a very short SWS2 pigment. In teleosts the SWS1 opsin appears to be expressed only as a UVS pigment and VS pigments with λ_{max} close to 410 nm are an expression of the SWS2B opsin, so that for the bobolink, both possibilities remain open.

12. Mammals

The class Mammalia includes not only main stream Eutheria, the placental mammals, but also Metatheria, the marsupials, and the more primitive, reptilian-like Prototheria, the egg-laying monotremes. Until relatively recently, it was assumed that all mammals, other than primates, were dichromats, possessing cones only from the two spectrally extreme opsin families, having lost the RH2 and SWS2 classes (Jacobs, 1993). The loss of two cone classes is assumed to be a consequence of the nocturnal phase that ancestral mammals experienced about 150–200 MYA when colour vision would have been severely limited. Nevertheless, it is now becoming clear that some Australian marsupials are trichromatic (Arrese, Hart, Thomas, Beazley, & Shand, 2002) and that the monotremes have retained a different subset of the vertebrate ancestral opsin classes (Davies et al., 2007a). In addition, all marine mammals and a number of nocturnal mammals retain only a functional LWS opsin gene and are cone monochromats (Peichl, 2005).

The monotremes diverged from placental and marsupial mammals around 200 MYA and today are represented by a single species of platypus (*Ornithorhynchus anatinus*), and two genera of echidna, *Zaglossus* and *Tachyglossus* restricted to Australia and New Guinea. Analysis of the platypus genome has identified only two functional cone opsin genes, orthologous to the LWS and SWS2 genes (Fig. 9) (Davies et al., 2007a). These have been expressed *in vitro*, and when reconstituted with 11-*cis*-retinal found to have λ_{max} at 550 and 451 nm, respectively. The rod pigment has λ_{max} at 498 nm. The 451-nm λ_{max} falls well within the range of SWS2 pigments recorded from many lower vertebrate groups and the 550-nm λ_{max} is very similar to many other mammalian LWS pigments. Interestingly, a small fragment (exon 5) of an SWS1 opsin gene was also identified, but presumable the full functional gene has been lost during evolution, along with the RH2 gene. On the assumption that echidna are similar to the platypus, it is quite remarkable that the monotremes maintain a dichromacy based on a different short-wave-sensitive cone opsin from marsupials and eutherian mammals, and suggests that ancestral mammals possessed at least three cone opsins with the potential for trichromacy.

The marsupials, who separated from the placental mammals about 125 MYA, offer yet another fascinating variant on the mammalian theme. Both monotremes and marsupials have double and single cones and in the marsupials and platypus clear oil droplets are present, though absent in echidna (Walls, 1942; Young & Pettigrew, 1991). In contrast to monotremes and most mammals, some Australian marsupials are trichromatic with three spectrally distinct cone classes (Arrese, Beazley, & Neumeyer, 2006; Arrese et al., 2002, 2005). Four species (honey possum (*Tarsipes rostratus*), fat-tailed dunnart (*Sminthopsis crassicaudata*), quokka (*Setonix brachyurus*) and quenda (*Isoodon obesulus*)) possess SWS1 cones with λ_{max} either in the UV around 350–360 nm or in the violet around 420 nm (reminiscent of birds) and LWS cones with λ_{max} at either about 550–560 or 530–540 nm. In addition, all four species possess a third cone with peak sensitivity in the green around 505–510, almost spectrally identical to their rods, again a feature common to birds.

Although the SWS1 and LWS genes have been isolated from these species, along with those of the Tamar wallaby, no candidate gene, either an RH2 or modified LWS gene, has been identified that could correspond to the 505-nm cone pigment (Arrese, Beazley, Ferguson, Odd, & Hunt, 2006; Arrese et al., 2005; Deeb et al., 2003; Strachan, Chang, Wakefield, Graves, & Deeb, 2004). One possible scenario could be that the 505-nm pigment is in fact the rod (RH1) opsin, but expressed in a functional cone. Such a suggestion may not be too heretical, since cone opsins are expressed in the 'green' rods of anurans (Hisatomi et al., 1999; Ma et al., 2001b) and in the 'rods' of nocturnal geckos (Taniguchi et al., 1999; Yokoyama & Blow, 2001).

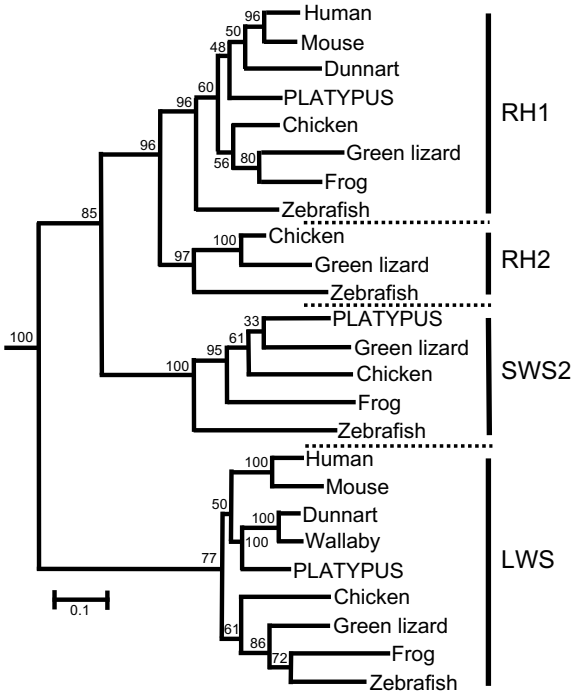

Fig. 9. Visual pigments of the duck-billed platypus. Phylogenetic tree of full-length coding sequences of SWS2, LWS and RH1 opsins. The platypus expresses an SWS2 short-wave opsin and not the SWS1 opsin found in marsupials and placental mammals. The tree was generated by maximum likelihood using the Kimura-2 parameter model. The robustness of each branch point is indicated by the bootstrap values. The scale bar indicates the number of nucleotide substitutions per site. The tree was rooted by using fruit fly *Rh4*as an outgroup (not shown). Figure redrawn from Davies et al. (2007a).

12.1. Eutherian mammals

Although it is probably a reasonable assumption that the majority of eutherian mammals are dichromats, both the long-wave LWS and short wave SWS1 show a wide spectral range in their λ_{max} (for reviews, see Jacobs, 1993; Yokoyama, 2000). The LWS cones can range from about 560 nm, as found in a wide variety of groups such as some canines, tree shrews and racoons, to as short as about 495 nm as found in some rodents. Similarly the SWS1 cones range from blue-sensitive pigments with λ_{max} as long as about 450 nm to UVS pigments with λ_{max} as short as 365 nm. As a general rule it seems that if the LWS pigment is more long-wave sensitive around 550–560 nm, then the SWS1 pigment is also at longer wavelengths around 440–450 nm, as in many canines, but if the LWS is shorter with λ_{max} nearer 500 nm, then the SWS1 is ultraviolet sensitive as in the mouse.

Notably, the SWS1 cone pigments tend to fall into two spectral groups, those that are violet- or blue-sensitive with λ_{max} greater than 400 nm and those that are ultraviolet-sensitive with λ_{max} close to 360 nm. As in avian SWS1 opsins, tuning between UVS

and VS pigments is based primarily on a single amino acid substitution in opsin (Fig. 1). In mammalian pigments, the critical residue is site 86 with Phe being present in UVS pigments, commonly replaced by either Tyr or Leu in VS pigments (Cowing et al., 2002; Fasick, Applebury, & Oprian, 2002). The ancestral mammalian SWS1 pigment was almost certainly UVS, with the shift to longer wavelengths occurring independently in a number of groups (Hunt et al., 2007). UVS pigments are retained in some rodents (e.g. Chavez, Bozinovic, Peichl, & Palacios, 2003; Jacobs, Calderone, Fenwick, Krogh, & Williams, 2003; Jacobs, Neitz, & Deegan, 1991), at least in one insectivore, the European mole (Glösmann, Steiner, Peichl, & Ahnelt, 2008) and in the prosimian, the aye-aye (Hunt et al., 2007).

The presence of two spectral classes of cone strongly implies the presence of dichromatic colour vision, but this can only be demonstrated conclusively by behavioural studies (e.g. Jacobs, Fenwick, & Williams, 2001) and requires that in general the two cone pigments must be expressed predominantly in separate cone classes. Surprisingly, it is now clear that in a number of mammals, principally rodents, the pigments are often coexpressed, at least in a percentage of the cones, and that the two classes of cone are not uniformly distributed across the retina (Ahnelt & Kolb, 2000; Applebury et al., 2000; Röhlich, Van Veen, & Szél, 1994; Szél, Lukats, Fekete, Szepessy, & Röhlich, 2000).

There is considerable debate as to the extent of coexpression both in the percentage of cones that exhibit coexpression and its topographic distribution in different rodent species. In the guinea pig (*Cavia porcellus*), for instance, there are populations of 'green'-sensitive LWS cones (M cones) with λ_{max} at approximately 530 nm and SWS1 cones (S cones) with λ_{max} close to 400 nm (Parry & Bowmaker, 2002; Parry et al., 2004). Using antibody labelling of cone opsins (Röhlich et al., 1994), the distribution of cones across the guinea retina appears highly asymmetric, with the dorsal retina dominated by M cones with approximately 5% S cones, whereas in the ventral region all the cones are labelled strongly for the S pigment but also showed positive for the M pigment. Slightly ventral of the equatorial region is a broad transition zone in which the majority of cones exhibit coexpression. Antibody labelling of opsins is somewhat qualitative and attempts to make direct quantitative measurements by MSP are somewhat contradictory with the antibody labelling (Parry & Bowmaker, 2002). The majority of cones in all regions were M cones with approximately 10% of cones in the transition region coexpressing the M and S cone pigments in a ratio of approximately 4:1. Coexpression was not detected in S cones.

In some other species it is suggested that all cones express both M and S pigments (Applebury et al., 2000; Lukats et al., 2002), but the observed degree of coexpression may at least in part be a consequence of the methods used, whether antibodies (and of what type) or *in situ* hybridisation (Applebury, 2001; Neitz & Neitz, 2001). Nevertheless, although coexpression conflicts with the basic view of colour vision, if there are relatively low levels of coexpression (in terms of the percentage of each pigment), it seems unlikely that this would cause any significant detriment to dichromacy. Indeed, behavioural experiments demonstrate that at least the mouse and rabbit have dichromatic colour discrimination (Jacobs, Williams, & Fenwick, 2004; Nuboer, 1971; Nuboer, 1986).

12.2. Monochromacy in mammals

A notable departure from the general dichromatic mammalian pattern is the loss of SWS1 cone pigments in marine mammals and some nocturnal terrestrial species. These species, including representatives from most major mammalian groups, possess only the LWS cone pigment and are thus cone monochromats, precluding cone-based colour vision (Fig. 10). The SWS1 opsin gene is

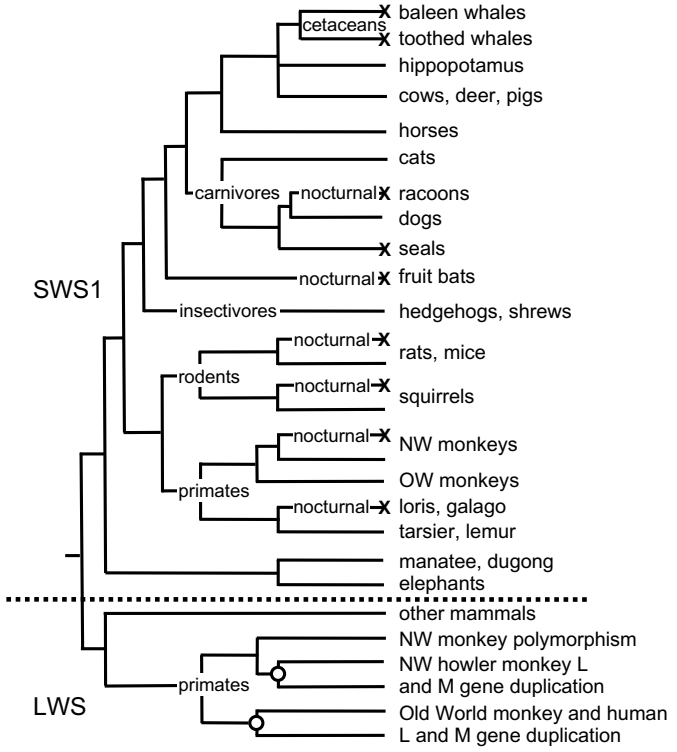

Fig. 10. A highly schematic representation of the distribution of LWS and SWS1 cone opsins in mammals. The phylogenetic tree shows only groups where information of SWS1 loss is available. The LWS opsin is probably expressed in all mammals. Gene duplication in Old World monkeys and New World howler monkeys has led to trichromacy in these species. The SWS1 opsin fails to express as a cone pigment probably in all marine mammals (whales and seals), but is expressed in the aquatic manatees and dugongs. Most of the other mammalian groups in which SWS1 cones are absent tend to be nocturnal. Redrawn from Bowmaker and Hunt (2006).

present, but suffers from amino acid substitutions and/or deletions that render the expressed protein non-functional. Since these genetic alterations have occurred in such a wide range of species, they must have occurred independently, several times during mammalian evolution.

The loss of SWS cone appears to be universal in marine whales (Cetacea) and seals (once classified as Pinnipedia, but now Canifornia). These species have retinas dominated by rods and contain only a very small percentage of LWS cones (Crognale, Levenson, Ponganis, Deegan, & Jacobs, 1998; Peichl, Behrmann, & Kröger, 2001). Molecular analyses in several species of whale, both baleen (Mysticete) and toothed (Odontocete), have identified one or more mutations that indicate that their SWS1 opsin genes are pseudogenes and are unable to code for functional visual pigment proteins (Levenson & Dizon, 2003; Levenson et al., 2006). The phylogenetic distribution of some of these mis-sense mutations indicates that they probably occurred before the divergence of the two groups of whales. The seals, not at all closely related to whales, similarly have lost SWS1 cones (Fig. 10) (Crognale et al., 1998; Newman & Robinson, 2005; Peichl & Moutairou, 1998). In the harp seal a pseudogene has been identified, whereas the harbour seal appears to have an intact SWS1 gene that apparently fails to be transcribed in the retina (Newman & Robinson, 2005).

Since the closest terrestrial relatives of the seals, the carnivores, and whales, the hippopotamus (Artiodactyla) possess both LWS and SWS1 opsin genes (Ahnelt, Fernandez, Martinez, Bolea, & Kubber-Heiss, 2000; Calderone & Jacobs, 2003; Jacobs, Deegan, Crognale, & Fenwick, 1993; Neitz, Geist, & Jacobs, 1989; Peichl et al., 2001), the mutations in the SWS1 gene in these two distinct groups

of marine mammals must have evolved independently, suggesting a common selective pressure. However, it is not clear what that selective pressure was. An attractive suggestion might be that the underwater photic environment is substantially diminished in brightness and relatively monochromatic, thus reducing the value of colour vision. The loss of SWS1 cones though, is somewhat counter intuitive. Water transmits primarily blue/green light and most pelagic fish have retained SWS cones and possess at least the potential for dichromatic colour vision (Bowmaker, 1995; Bowmaker & Loew, 2007). Does the loss of SWS cones in marine mammals preclude any form of wavelength discrimination or colour vision? For obvious practical reasons, there are only limited behavioural data available for some species of seal and dolphin (Busch & Ducker, 1987; Griebel, Konig, & Schmid, 2006; Griebel & Schmid, 1992; Griebel & Schmid, 2002; Wartzok & McCormick, 1978), but these do suggest a limited ability to distinguish some colours independently of luminance (for a detailed review, see Griebel & Peichl, 2003), which is presumably a consequence of rod/cone interactions at mesopic light levels.

In contrast to the whales and seals, the manatee (Sirenia) possesses both LWS and SWS1 cones (Newman & Robinson, 2006) and has been shown to have dichromatic colour vision (Cohen, Tucker, & Odell, 1982; Griebel & Schmid, 1996). The closest terrestrial mammals to the sirenians are the elephants (Proboscidea) and these too have been shown to possess both LWS and SWS1 cone pigments (Yokoyama, Takenaka, Agnew, & Shoshani, 2005). Of course the life styles of whales and seals and the sirenians are very different, the manatees and dugongs being arrhythmic and herbivores living in shallow coastal lagoons.

Cone monochromacy has also been reported in a wide range of nocturnal mammalian groups (Fig. 10) including rodents such as some rats and flying squirrels (Carvalho, Cowing, Wilkie, Bowmaker, & Hunt, 2006; Peichl & Moutairou, 1998), procyonid carnivores such as raccoons and coati (Jacobs & Deegan, 1992), chiropterans such as fruit bats (Müller, Goodman, & Peichl, 2007) and primates, both prosimians such as bush babies and lorises (Deegan & Jacobs, 1996; Kawamura & Kubotera, 2004; Wikler & Rakic, 1990) and New World monkeys such as the owl monkey (Jacobs, Neitz, & Neitz, 1996c). In almost all species, the SWS1 gene is present, but suffers from a deleterious mutation so that it cannot be expressed. In a similar fashion to the cetaceans, the lorises and gulagos have a common ancestral mutation (Kawamura & Kubotera, 2004), but clearly the loss of function of the short-wave opsin gene has occurred independently within each separate group.

Why these losses have occurred is not immediately apparent. Superficially, since these animals are all nocturnal, it could be concluded that colour vision is of little functional significance and that the loss of the SWS1 cones is of little consequence or in fact may even be advantageous. However, although all the species that have been identified as having lost their SWS1 cones are nocturnal, the converse is not true. Many of these species have close relatives that are also nocturnal but retain both LWS and SWS cones and presumably exhibit dichromacy.

Although ancestral mammals were clearly restricted to dichromatic colour vision, trichromacy re-evolved in primates through modifications of the LWS opsin gene: in New World monkeys (Platyrrhini) primarily through a polymorphism of the gene and in Old World monkeys (Catarrhini) through gene duplication. Polymorphism of the LWS gene has resulted in allelic variants that are expressed as cone pigments with different spectral sensitivities, but since the gene is located on the X chromosome, males will be obligate dichromats and it is only in females, heterozygous at the gene locus, who can be trichromatic. This assumes that X chromosome inactivation ensures that only a single allele is expressed in any given L cone and that the visual neural mechanisms are sufficiently plastic to utilise the chromatic information. (Bowmaker, Jacobs, & Mollon, 1987).

Within the prosimians (Strepsirrhini), polymorphism has been identified in two species of lemur and also the closely related Cockerel's sifaka which possess two alleles that are expressed as pigments with λ_{max} around 543 and 558 nm (Tan & Li, 1999). Electrophysiological studies have confirmed the potential for both dichromatic and trichromatic colour vision at least in the sifaka (Jacobs, Deegan, Tan, & Li, 2002). Prosimians then exhibit all three forms of mammalian cone-based vision with some species being cone monochromats, some dichromats and others in which at least a percentage of females have the benefit of trichromacy. It would be a simple solution if trichromacy was found only in diurnal species, whereas all nocturnal prosimians were cone monochromats, but this is certainly not the case.

Polymorphism is more highly developed in New World monkeys, and it may be that allelic variations of the LWS opsin gene occurred before the separation of the Strepsirrhini (prosimians) and the Haplorrhini (tarsiers and simians). However, although tarsiers possess both SWS1 and LWS opsin genes, there is no evidence for polymorphism of the LWS gene within a single species, though the opsin sequences suggest an L pigment in the Western tarsier and an M pigment in the Philippine tarsier, perhaps indicating that their mutual ancestor was polymorphic (Tan & Li, 1999).

In New World monkeys, LWS alleles have been identified in the cebids and it would appear that all marmosets, tamarins, capuchin and squirrel monkeys have the advantage of polymorphism. Usually three alleles are present, but the spectral locations of the pigments differ. In callitrichids the three pigments have λ_{max} close to 563, 556 and 544 nm, whereas in saimirids the maxima are at about 563, 549 and 535 nm (Hunt, Williams, Bowmaker, & Mollon, 1993; Jacobs, 1984; Jacobs & Deegan, 2003; Jacobs & Neitz, 1987; Jacobs, Neitz, & Neitz, 1993; Mollon, Bowmaker, & Jacobs, 1984; Tovée, Bowmaker, & Mollon, 1992; Travis, Bowmaker, & Mollon, 1988). The consequence of three allelic variants is that within a given species there will be six different colour vision phenotypes. All the males, and females homozygous at the LWS gene locus, will be obligate dichromats, but of three different forms, whereas females heterozygous at the locus will be trichromatic, but again three different forms will occur. Three alleles may not be the maximum number present is a given species, since the dusky Titi (Pitheciidae: *Callicebus molochi*) has been reported to possess five, with similar λ_{max} to the five spectral locations found in cebids (Jacobs & Deegan, 2005). This would give the potential for ten forms of colour vision within the species, but the frequency of the different phenotypes would be dependent on the relative frequency of occurrence of the five alleles.

In primates, the LWS cones may then have five spectral locations and tuning to these points is achieved primarily by just three amino acid substitutions at sites 164, 261 and 269 (rod opsin numbering) (Fig. 1) or 180, 277 and 285 (primate LWS opsin numbering). The shortest wavelength pigment with λ_{max} close to 535 nm has alanine, phenylalanine and alanine at the three sites, respectively, whereas the longest with λ_{max} close to 565 nm has these replaced by serine, tyrosine and threonine, all being polar residues containing hydroxyl groups. The spectral effect of each substitution is relatively small and somewhat dependent on the specific opsin background, but additive, so that different combinations of the three substitutions results in the five spectral locations found (Asenjo, Rim, & Oprian, 1994; Chan, Lee, & Sakmar, 1992; Hunt et al., 2006; Merbs & Nathans, 1993; Nathans et al., 1986; Neitz, Neitz, & Jacobs, 1991; Yokoyama, 2000).

Two notable exceptions to polymorphic colour vision are found in New World monkeys. The nocturnal owl or night monkeys (Aotidae) have lost their SWS cones (Wikler & Rakic, 1990), but as with other mammalian groups, the gene can still be identified, but suf-

fers from deleterious mutations and fails to be expressed (Jacobs et al., 1996c). These monkeys are therefore cone monochromats expressing only a single LWS pigment with λ_{max} at about 543 nm (Jacobs, Deegan, Neitz, Crognale, & Neitz, 1993), though behavioural experiments suggest that they have some residual dichromacy, presumably derived from rod/cone interactions (Jacobs, 1977).

The other somewhat surprising divergence from polymorphic colour vision in the New World primates is found in the howler monkeys (Alouatta) (Jacobs, Neitz, Deegan, & Neitz, 1996b). These diurnal frugivorous monkeys are uniformly trichromatic, achieved through the duplication of the LWS gene yielding two spectrally distinct pigments with λ_{max} at about 563 and 535 nm. The duplication ensures that both males and females are able to express the two pigments in separate cone populations. Genetic analyses suggest that the gene duplication in the ancestor of howler monkeys was derived from the incorporation of two alleles that were very similar to the 535- and 563-nm pigment alleles found in the squirrel monkeys and capuchins. This implies that the polymorphism existed before the platyrrhine radiation which began about 20 MYA and is independent of the gene duplication that occurred in Old World monkeys (Boissinot et al., 1997; Dulai, von Dornum, Mollon, & Hunt, 1999; Hunt et al., 1998; Kainz, Neitz, & Neitz, 1998).

The Atelidae family of New World monkeys, which includes howler monkeys, also encompasses spider monkeys (*Ateles*), woolly monkeys (*Lagothrix*) and woolly spider monkeys (*Brachyteles*). These further genera are also diurnal and primarily frugivorous, but in contrast to howler monkeys, retain the LWS gene polymorphism of the cebids. The spider and woolly monkeys may possess only two alleles expressed as pigments with λ_{max} at about 550 and 563 nm (Jacobs & Deegan, 2001), though Brachyletes appears to have three (530, 550 and 563 nm) (Talebi, Pope, Vogel, Neitz, & Dominy, 2006). For a recent fully comprehensive review of colour vision in New World monkeys, see (Jacobs, 2007).

Colour vision in Old World primates (Catarrhini), which includes apes and humans, is uniformly trichromatic across all species, having evolved from a gene duplication of the ancestral LWS gene which occurred presumably after the separation of the Old and New World monkeys about 35 MYA (Hunt et al., 1998; Hunt, Jacobs, & Bowmaker, 2005). All of the species that have been studied possess L and M cones with λ_{max} at about 530 and 563 nm, spectral locations similar to the shortest and longest maxima found in New World monkeys (Bowmaker, Astell, Hunt, & Mollon, 1991; Bowmaker & Dartnall, 1980; Bowmaker, Dartnall, & Mollon, 1980; Dartnall, Bowmaker, & Mollon, 1983; Deeb, Jorgensen, Battisti, Iwasaki, & Motulsky, 1994; Dulai, Bowmaker, Mollon, & Hunt, 1994; Jacobs, Deegan, & Moran, 1996a).

The striking differences between colour vision within the different primate groups raises many questions that are difficult to answer. The marked polymorphism of colour vision seen in the majority of New World monkeys is probably unique to these species and has not been observed in any other vertebrate group. Presumably, the trichromacy achieved in about two thirds of the females is advantageous, since it will allow these individuals increased wavelength discrimination and 'red-green' colour vision. Only in the howler monkeys and in Old World monkeys has full trichromacy been achieved. This raises the somewhat thorny questions as to what the evolutionary forces were which led to the re-establishment of trichromacy amongst primates, both Old and New World, and how the polymorphism in platyrrhines is maintained.

A number of different theories have been put forward for the evolution of trichromacy in primates and for the spectral location of the L and M pigments in Old World primates and howler monkeys. The most prominent theories relate to feeding strategies and the necessity of detecting orange and red fruits against a highly variable background of green foliage, where luminance cues may be effectively absent. These ideas were put forward at least as early as the end of the nineteenth Century and stated explicitly by Polyak (1957). Not only should red/green colour vision make the task straightforward, but it also allows the detection of the ripeness of the fruit. The idea was expanded on with a detailed consideration of the frugivorous diet of some monkeys (Mollon, 1989) and has been tested more rigorously with careful analysis of the task in terms of the spectral location of the L and M pigments and the reflectance spectra of a broad variety of relevant fruit and leaves (Osorio & Vorobyev, 1996; Regan et al., 1998; Sumner & Mollon, 2000a; Sumner & Mollon, 2000b). Much of the argument has been over whether the primary evolutionary force for trichromacy was the task of detecting ripe fruit or of distinguishing young reddish and more nutritious leaves (Dominy & Lucas, 2001; Lucas et al., 2003; Riba-Hernandez, Stoner, & Lucas, 2005), but the two tasks are not necessarily mutually exclusive. The discussion also extends to the advantage of trichromacy over dichromacy and the maintenance of the polymorphism seen in New World monkeys (De Araujo, Lima, & Pessoa, 2006; Smith, Buchanan-Smith, Surridge, & Mundy, 2003; Smith, Buchanan-Smith, Surridge, Osorio, & Mundy, 2003; Stoner, Riba-Hernandez, & Lucas, 2005).

13. Concluding remarks

The appearance of colour vision early in the evolution of vertebrates has to be inferred from the identification of five families of opsin genes in the living relatives of the most ancient vertebrate lineage, the jawless lamprey. Assuming a parallel evolution of the necessary neural mechanism, these primitive fish had the potential for tetrachromatic colour vision at least 540 MYA and although the morphology of cones may have increased in complexity with the inclusion of coloured oil droplets and the development of double cones, four spectral classes of cone still appears to be the maximum number employed.

Gene duplications and mutations have provided a wide spectral range for all of the four cone opsins and the rod opsin, with considerable spectral overlap between cone classes, though there is a clear tendency for the peak sensitivities to cluster. This is exemplified in the two short-wave SWS1 and SWS2 opsin classes. In subgroups of teleosts that diverged over 100 MYA, the SWS2 cone pigments appear to fall into two spectral groups centred around 410–420 and 440–450 nm. Outside of teleosts, the short-wave-sensitive cone pigments of birds also fall into these two spectral locations. The avian 'blue'-sensitive pigment (SWS2) has a λ_{max} close to 450 nm, and birds that lack a true UV-sensitive cone, possess a violet-sensitive pigment with λ_{max} at about 405-420 nm, but this is the expression of an SWS1 opsin and not the product of an SWS2 opsin. Indeed, this would appear to be the case in all vertebrate groups with the exception of teleosts. In mammals, including humans, where the S cones pigment has λ_{max} at about 420 nm, all short-wave sensitive pigments are SWS1 pigments and the SWS2 gene has been completely lost. As yet there appears to be no definite answer to the question as to whether these two spectral locations are driven by ecological factors or determined by structural constraints on opsins.

Although five opsin genes have been identified in lamprey, there is some debate over whether two of the classes are more rod or cone like and this raises the question of the definition of rods and cones. In many species the distinction is clear, but in others this is not the case. In some lamprey and elasmobranchs there are 'rods' that appear to function at both scotopic and photopic levels and the 'green rods' of amphibians and the 'rods' of nocturnal geckos contain cone pigments, but presumably function primarily at scotopic and/or mesopic levels and are most likely involved in

some form of colour vision. Indeed, wavelength discrimination based on rod/cone interactions is all that is available to marine mammals and also possibly to some nocturnal mammals.

The ability to identify and isolate opsin genes from a wide range of animals including rare and protected species has greatly expanded our understanding of the evolution of visual pigments and colour vision in vertebrates. This has produced some unexpected and exciting observations such as the presence of multiple opsins in many teleosts and a functional SWS2 cone opsin in monotremes. There must be further surprises just waiting to be discovered.

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