

## INFERRING THE RETINAL ANATOMY AND VISUAL CAPACITIES OF EXTINCT VERTEBRATES

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### ABSTRACT

One goal of contemporary paleontology is the restoration of extinct creatures with all the complexity of form, function, and interaction that characterize extant animals of our direct experience. Toward that end, much can be inferred about the visual capabilities of various extinct animals based on the anatomy and molecular biology of their closest living relatives. In particular, confident deductions about color vision in extinct animals can be made by analyzing a small number of genes in a variety of species. The evidence indicates that basal tetrapods had a color vision system that was in some ways more sophisticated than our own. Humans are in a poor position to understand the perceptual worlds of

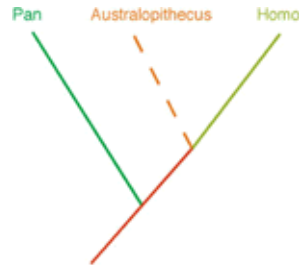
other terrestrial vertebrates because of the loss of anatomical specializations still retained by members of most all tetrapod lineages except eutherian mammals. Consequently, the largest barrier to understanding vision in extinct animals is not necessarily the nonpreservation of relevant structures, but rather our deep and largely unrecognized ignorance of visual function in modern animals.

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## PLAIN LANGUAGE SUMMARY:

We can deduce that extinct animals had particular soft tissues or behaviors via extant phylogenetic bracketing (EPB, Witmer 1995). Application of EPB entails the recognition of two extant lineages that diverged earlier and later, respectively, from the extinct organisms' lineage (Figure 1). Parsimony indicates that a character or character-state shared by each of two lineages existed in their most recent common ancestor (MRCA). Thus, unless subsequently lost in particular lineages, the character or state was also present in all other descendants of the MRCA including those whose extinction left no direct evidence of the character. The EPB method can be applied using DNA sequences as proxies for the proteins that those sequences encoded. Results of the search for genes that code for opsins - the proteins that signal the detection of light in retinal photoreceptors - suggest that the MRCA of the two major bony fish radiations had four different opsin genes (Bowmaker 1998). Many tetrapods retained all four genes whereas the basal eutherian mammals apparently retained only two (Jacobs 1993). By newly deriving a third opsin, our ancestors endowed us with a color vision system approaching, but not equaling, the system probably retained by most Mesozoic tetrapods. Many animals also have oil droplets screening the light-sensitive parts of their photoreceptors (Walls 1942). Again eutherian mammals are aberrant in showing no trace of these structures which



**Figure 1.**

(in animals that have them) probably sharpen the spectral tuning of photoreceptors and thus enhance perceived color contrasts (Bowmaker et al. 1997). Eutherian mammals also lack double cones and the mosaics of these structures found in a variety of other vertebrates (Walls 1942). Double cones and their mosaics have been known for roughly 100 years, but no compelling theory explains the utility of such anatomical arrangements. Comparative anatomy and EPB allow reasonable inferences about which extinct animals had double cones and mosaics, but these inferences do not help us to understand these animals because we do not know how double cones are used by living animals.

Much of our perceptual world is built upon what our eyes report to us. Indeed, much of the primate cerebral cortex is devoted to deciphering signals from the retina (Felleman and Van Essen 1991). However, the primate visual system evolved from one that was secondarily simplified from a more complex state (as indicated by the apparent loss of oil droplets, double cones, and some opsins). Hence our visual worlds are probably very different from those of animals that never underwent this simplification. Psychologists have recognized for some time that what we perceive is a reconstruction of the world around us. This reconstruction strongly depends upon the characteristics of our sense organs. Biologists are only beginning to appreciate the significance of this insight when studying the behavior of other animals (Bennett, et al. 1994). Hopefully, paleobiologists will not lag behind neobiologists in reaching this understanding.

## INTRODUCTION

As a historical science, paleontology readily presents questions that cannot be answered via empirical methods. For instance, paleobiologists wishing to understand how an extinct animal viewed its surroundings have infrequent access to tissues that mediated visual perception. Soft tissue preservation is a rare occurrence even within the set of rare occurrences in which anything at all is preserved from an animal that lived long ago. Needless to say, even when fragments of fossilized soft tissue are found they are non-functional.

On the other hand, the fossil record has been relatively generous to those pursuing answers to particular questions about perception. Farlow (1994) addressed questions about tyrannosaur lifestyle with simple geometrical considerations about the position of their eyes relative to the ground. Similarly, an animal's total field

of view and area of stereoscopic overlap can be determined from physical measurements of its skull (Stevens 1997, Coates 1998). Preservation of the lenses of trilobite eyes provides enough detail to indicate the acuity of their bearers' vision (Fordyce and Cronin 1989, Fordyce and Cronin 1993), and a few cranial endocasts provide detail on the relative sizes of different brain regions in skulls that have been particularly well preserved (e.g., Stensiö 1927 in Gould 1988; Rogers 1998; Brochu, personal commun., 1999; and *Paleoneurology: the Study of Brain Endocasts of Extinct Vertebrates on the University of Wisconsin site Comparative Mammalian Brain Collections*).

Here I follow a different approach. I wish to explore the visual capacities of extinct animals via extant phylogenetic bracketing (EPB, Witmer, 1995) the method

described in Figure 1. Whereas Witmer (1995) inferred that *Tyrannosaurus rex* had eyeballs, I will go further out on the limb and infer what sorts of receptors it had within those eyeballs.

Gordon Walls (1942) compiled much of what we know about comparative visual anatomy in vertebrates almost 60 years ago. In many areas Walls' treatise still represents the envelope of our knowledge, but revolutions in some areas of science - particularly molecular

## FUNDAMENTALS OF VISION

The production of a neural image of the light converging upon an animal begins with the focusing of that light onto a sheet of receptors. Figure 2 depicts a generalized bird eye. In terrestrial animals most of the focusing power of the eye is at the air/cornea interface. In aquatic vertebrates the refractive index of the cornea is similar to that of the water in which it is immersed, and hence most of the focussing power is provided by the lens. In either case, light impinging upon the eye from particular directions is redirected to particular locations on the retina, the tissue lining the inside of the eye. Within the retina are photoreceptors, cells specialized for transducing relative light intensities into neurochemical signals that can be passed along to the central nervous system.

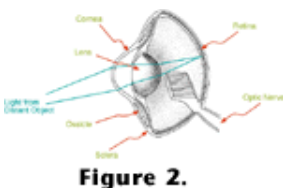


Figure 2.

### The Molecular Basis of Phototransduction

Figure 3 contains a drawing of a cross-section of a human retina showing the position and orientation of the photoreceptors. Figure 4 diagrams the photoreceptor outer segments, where light is absorbed and transduced in vertebrates.

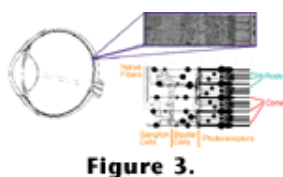


Figure 3.

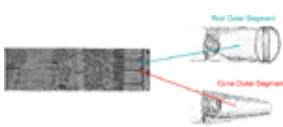


Figure 4.

The outer segments consist of sets of disks stacked like pancakes and constructed of lipid bilayers. Embedded in the disk membranes are large numbers of photopigment molecules. Each photopigment consists of a chromophore covalently bound to a protein called an opsin. In all known visual photoreceptors the chromophore is a vitamin A derivative such as the retinal diagrammed in Figure 5. Aside from minor differences in casting, the phototransduction processes described here are the same in all animals with eyes. When a photopigment is cre-

ated, the retinal is in a configuration named 11-cis to denote the orientation of the bonds around the eleventh carbon atom (Figure 5).

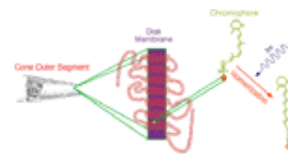


Figure 5.

When the chromophore absorbs a photon, an electronic rearrangement may occur, which results in a rotation of the constituent atoms around the eleventh carbon bond. This isomerization of the chromophore causes a change in the shape of the opsin, and in its new configuration, the opsin behaves as an enzyme.

The rate at which the reaction catalyzed by the opsin occurs sets the rate at which the photoreceptor releases neurotransmitters to other retinal neurons. Figure 6 shows the absorption probability of a typical vertebrate photopigment as a function of wavelength and, essentially, the absorption spectrum of a photoreceptor as well, since in most cases, all of the opsin molecules within a given photoreceptor are chemically identical. Neglecting some nuances such as adaptation processes (that are quite important for visual function but are not important for the arguments presented here) the rate at which opsins are catalyzing within a photoreceptor can be determined by integrating the product of the quantal flux through the photoreceptor's outer segment and the photopigment's absorption spectrum as shown in Figure 6B.

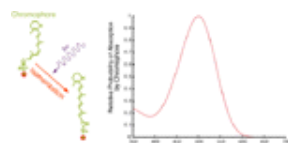


Figure 6A.

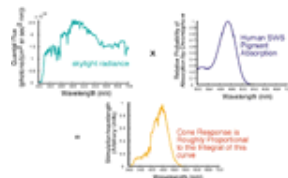


Figure 6B.

Embedded in this description is an attribute of visual function that is so essential it has been given a name - the principle of univariance. This principle states that once a photon has been absorbed by a photoreceptor, all information about the wavelength of the photon is lost.

This is because the photopigment's activation is like a switch. Either the photopigment is acting as a catalyst or it is not. Isomerization of the chromophore caused by the absorption of one photon is identical to the isomerization caused by the absorption of any other photon irrespective of the photon's wavelength. Consequently, a single photoreceptor cannot convey any information about the spectral energy distribution (read color) of the light passing through it.

### Color is in the Brain of the Beholder

Animals extract information about the spectrum of light striking different regions of their retinas by contrasting the responses of photoreceptors containing different photopigments. Animals generate different photopigments by expressing different opsins. Opsins with different amino acid sequences may have drastically different absorption spectra. However, the shapes of the absorption spectra vary in regular ways such that almost any photopigment absorption spectrum can be adequately described by knowing only the structure of the chromophore, and the wavelength at which the photopigment's absorption peaks (Stavenga et al. 1993; Palacios et al. 1998). Figure 7A depicts the absorption spectra of the three types of photopigment that mediate human color vision and the four types of photopigment that mediate color vision in the European starling.

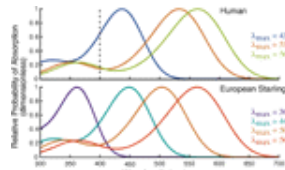


Figure 7A.

Figure 7B depicts the transformation from an incident spectrum of light to the relative responses that each of these photopigments would generate. The numbers inset in the plots are the integrals of the correspondingly-colored curves. Note that since starlings have four cone photopigments, there are four different outputs, and note that none are identical to any of the three outputs of the human cones. Because these photoreceptor outputs are all that nervous systems retain for the analysis of color, the colors we see are different from the colors seen by a starling (or indeed any other animal). It, therefore, makes little sense to talk of color in the vernacular sense as a property of objects or lights. Such nomenclature works well when the subjects of discussion are all humans because the vast majority of us have essentially the same photopigments. However, when the subjects of a visual study are animals other than humans great care must be taken. Objects having the same hue to the experimenter may have drastically different hues to an animal and vice versa (Bennett et al. 1994, Fleishman et al. 1998).

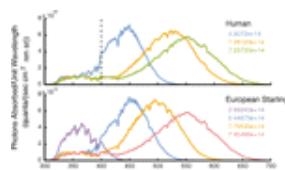


Figure 7B.

### Visual Pigment Diversity

Absorption spectra from a large variety of animal photopigments have been determined since microspectrophotometry (a technique for measuring spectral absorption in individual photoreceptors) was developed 35 years ago (Leibman and Entine 1964). Consequently we know that many animals not only have photopigments that differ from our own, but, like the starling, many have more than three (Goldsmith 1990). Furthermore, recent analyses of the cloned sequences of a variety of opsin genes indicate that the MRCA of sarcopterygians and actinopterygians had four opsins mediating light-adapted vision (Hisatomi et al. 1996, Heath et al. 1997, Wilkie et al. 1998, Yokoyama et al. 1998).

With such data we can reasonably conclude that the starling's photopigment complement has been handed down through every generation since before its ancestors became terrestrial; that is, the starling's four cone pigments are likely orthologs of the four cone pigments of the common ancestor of a starling and a goldfish. Figure 8 contains a cladogram of visual pigment genes from a subset of those that have been sequenced. Molecular biologists have been disproportionately sequencing the pigment genes of eutherian mammals. To date, at least partial sequence data have been collected for about 50 different cone pigments, and half of these come from eutherians. Consequently the groupings depicted in Figure 8 should be viewed cautiously. However, if the groupings withstand analysis after the addition of more sequences, several fascinating conclusions may be drawn about evolution in tetrapod vision.

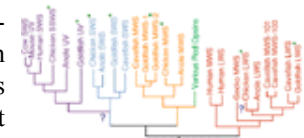


Figure 8.

Walls (1942) provided the first serious attempt at mapping the evolution of vertebrate color vision. Using Walls' analysis, Gauthier (1994) proposed that "excellent hue discrimination" is a reptilian apomorphy. Opsin sequence data suggest instead that tetrachromatic color vision was the plesiomorphic condition for sarcopterygians (and hence tetrapods). Indeed, although opsin sequence data are not yet available to establish the homology of tetrachromacy among all reptiles, at least four visual pigments are known to mediate light-adapted vision in turtles (Bowmaker 1991) and alligators (Sillman et al. (1991) as well as the lizards (Kawamura and Yokoyama 1997) and birds (Vorobyev et al. 1998) for which sequence data do suggest homology as indicated in Figure 8. Since the opsin genes do not necessarily cluster together on purely functional grounds the apparent homology of tetrachromacy is not likely due to convergence. That is, the nearest neighbors in the tree are not generally the genes that code for the pigments with the most similar absorption spectra, so the position of

the pigment genes on the tree is substantially determined by the sequences of segments that preserve adaptively neutral phylogenetic signals rather than sequences convergently selected for particular spectral tunings. Upon finding four cone pigments in *Alligator*, Sillman et al. (1991) suggested that dinosaurs, which (like alligators) were large reptiles, had color vision. At present the Sillman et al. suggestion appears too tenuous. Since modern reptiles bracket most dinosaurian lineages we can argue that dinosaurs not only had color vision, but actually had color vision that was, in at least some ways, better than ours.

Walls (1942) suspected that mammalian color vision arose *de novo* because either mammals secondarily lost their capacity for color vision during the Mesozoic Era, or their pre-Mesozoic ancestors never acquired it. In a thorough review, Jacobs (1993) demonstrated that the most parsimonious view of more recently acquired data is that the MRCA of eutherian mammals had two opsins. This conclusion is strongly supported by the phylogenetic analyses of opsin sequence data, but another rather interesting twist is suggested by the results of these analyses. The chicken, goldfish, and American anole, all have opsins similar in spectral sensitivity to the short wave sensitive pigment found in

most orders of mammals (e.g., see the human visual pigment absorption spectra in Figure 7A). However, instead of clustering with those opsin genes, the genes coding for the short wave sensitive pigments of human, marmoset, squirrel monkey, talapoin monkey, and cow, as well as the UV sensitive pigments of mouse and rat, cluster with the UV sensitive pigments of goldfish, parakeet, and anole and the almost UV sensitive pigments of chicken, pigeon and clawed frog (Hisatomi et al. 1996, Yokoyama and Yokoyama 1996, Heath et al. 1997, Wilkie et al. 1998, Yokoyama et al. 1998), suggesting these pigments are all orthologs. Therefore, the short-wave sensitive pigment retained by eutherian mammals was likely a UV pigment ancestrally. Prior to the discovery of UV sensitivity in rodents (Jacobs et al. 1991), it seemed implausible that any mammals had visual sensitivity to UV light (Goldsmith 1990). Ironically it is now a defensible position that ancestrally all eutherians were UV-sensitive. That possibility raises intriguing questions about why this particular pigment was retained whereas two others were lost, and why the pigment's absorption spectrum was shifted toward longer wavelengths for most eutherians other than a subset of murid rodents.

## OTHER DETERMINANTS OF VISION

### Striking Oil in the Retina

Color vision in animals is sculpted by filters that modify the spectrum of light before it reaches the photoreceptor outer segments. In humans (Goldsmith 1990) and some fish (Thorpe et al. 1993) the lens and other structures absorb a fair amount of light, particularly at short wavelengths. This absorption makes us insensitive to UV light (Stark and Tan 1982). Of greater potential interest are pigments contained in oil droplets within individual photoreceptors.

Because different photoreceptors may have different oil droplets, these droplets provide another mechanism by which animals could have modified the absorption spectra of photoreceptors to extract spectral information from the light striking their eyes (see Figure 9A-Figure 9B). However, animal evolution appears not to have taken this pathway in the develop-

ment of color vision. Instead, oil droplets sharpen the tuning of photoreceptors reducing the window of the receptor's spectral responses (Goldsmith 1990, Bowmaker et al. 1997, Vorobyev et al. 1998). This sharpening is graphically depicted in Figure 9C.

Oil droplets are known to exist in the retinas of a wide variety of animals, primarily terrestrial tetrapods (Robinson 1994). Walls (1942) and later Robinson (1994) suggested that the presence of pigmented oil droplets in distantly-related groups of animals implies that they first appeared in basal sarcopterygians, approximately 400 million years ago. The patchy distribution of oil droplets and, more particularly, pigmented oil droplets was explained by Walls as an indication that when animals with oil droplets evolve nocturnal lifestyles they lose their oil droplets (or at least their droplets' pigmentation). Once lost the oil droplets (or their sequestered pigments) cannot be reacquired.

The homology of oil droplets among various clades cannot currently be supported with any firm data, though Figure 10 depicts reasonable hypothetical relationships. Unlike that of the opsins, the

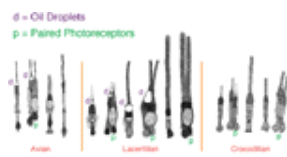


Figure 9A.

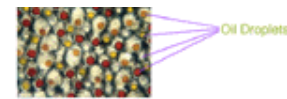


Figure 9B.

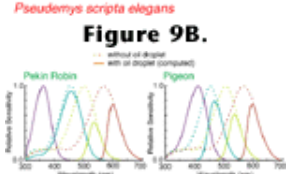


Figure 9C.

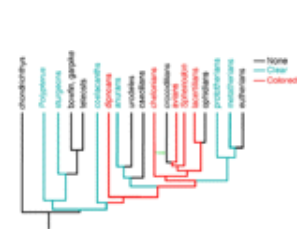


Figure 10.

molecular biology underlying the production of oil droplets is unknown, so we cannot evaluate Walls' suggestion that lost oil droplets are difficult to recover. If Walls was correct, though, his supposition suggests many interesting paleobiological conclusions. For instance, the MRCA of all tetrapods would have to have been diurnal, and metatherian and prototherian mammals must have been more active under the Mesozoic sunlight than their eutherian cousins who were apparently forced to spend their days sequestered in shaded hideouts. Similarly - particularly if the recent claim of a close relationship between chelonians and crocodylians (Hedges and Poling, 1999) is correct - we could safely infer that most if not all dinosaurian lineages were well-endowed with brightly colored oil droplets in their cones.

## Double Vision

In 1942, Walls wrote (p. 103):

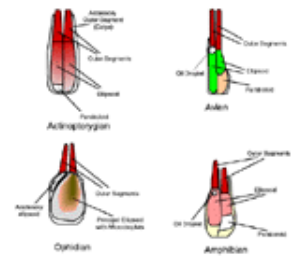
In truth, the working out of the photochemical system of the cone may long continue to seem the most difficult branch of the physiology of the eye. [...] with the most careful methods, we can succeed in seeing living cones only as completely colorless structures, whose bland innocence conceals invisible traces of three important somethings - to our utter exasperation.

On this topic, much has changed in the intervening years. As discussed above, we now have a fairly-detailed understanding of the photochemistry of retinal cells and its relation to color vision. We also know that despite his comparative genius, Walls was too parochial in presuming that other animals would, like us, be restricted to having only three visual pigments. In the hopes of stimulating further research in a particular direction, I would like to contrast what we've learned since Walls wrote the above quote to what we've learned since he wrote the following (p. 58-59):

...the puzzle [double cones] represent is particularly irritating to the curious investigator because they are so very widespread among vertebrates. If they occurred in only one or two animals, we might dismiss them as a curiosity. Perhaps if they occurred in the human retina we would before now have gained some clue to their role in visual processes; but their functional significance, their exact mode of formation in the developing retina, and the probable time and manner of their evolutionary origin have yet to be determined. Next to amacrine cells, the double cones are physiologically the most obscure elements in any and all retinae. They have unfortunately not greatly interested

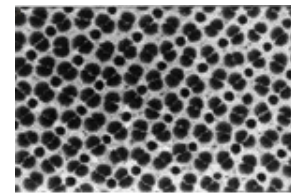
visual physiologists, since the latter have their attention focused upon the human retina, in which double cones are lacking.

Little to no editing would be required to make these statements an accurate reflection of our current state of knowledge about "double cones". In addition to those of Figure 9A, Figure 11 contains schematic drawings of these structures in a variety of vertebrates to show some of their diversity as well as their common features. Whether or not all double cones - or more generally, paired photoreceptors - are homologous, and whether or not they serve similar functions are open questions.



**Figure 11.**

One potential clue about the function of paired photoreceptors is that they frequently inhabit retinas in the form of regular mosaics. Figure 12 is a photomicrograph of the retina from a sunfish (*Lepomis cyanellus*). Clicking on the image highlights the orderliness of the orientations of the double cones. Such mosaics are common among fish (Ali and Anctil 1976), and qualitatively similar patterns have been demonstrated in one bird (Engström 1958) and one lizard (Dunn 1966). Most tetrapods that have double cones *appear* to have irregular mosaics (i.e., no pattern), but close inspection of the chicken retina indicates that its double cones are not randomly oriented (Morris 1970). It is possible that some semblance of order will be found upon close examination in all retinas containing double cones.



**Figure 12.**

A few hypotheses have been put forward to explain the functional significance of paired photoreceptors and their mosaics. Many explanations revolve around electrical connections between the two constituent photoreceptors of each double cone (e.g., Richter and Simon 1974). Such explanations are not compelling given that electrical coupling between photoreceptors can be accomplished with a much smaller areal contact via gap junctions near the synapses of the cells. Many nonpaired photoreceptors are electrically coupled via such junctions, and at least sometimes double cones do not have any demonstrable electrical connections between their constituent photoreceptors (Mariani 1986). Others have argued that double cone mosaics somehow aid the detection of movement (Lyll 1957, Wagner 1972, Wagner 1978). Acceptance of this explanation suffers from the fact that the two halves of double cones appear to be optically coupled in such a way that absorption in one of



turnal or (like us) the descendent of a lineage that had gone through a nocturnal phase.

We can thus draw a line from the first terrestrial tetrapod to almost any extant bird, turtle or lizard and see an unbroken chain of animals that retained all of the features associated with the retinas of such animals today - four or more classes of cones (note this argument is independent of the argument presented above based on gene sequences), colored oil droplets, and probably double cones. Similarly we can conclude that many extinct side branches (e.g., ichthyosaurs, pterosaurs and most extinct dinosaurs) were also

so endowed. Figure 16 depicts some of the perceptual consequences we might predict from this endowment. In Witmer's (1995) parlance, it is a Level I

inference to say that, for example, *Deinonychus* had four cone classes, oil droplets and double cones in its retina. That is, we are justified in making a decisive and positive assertion that *Deinonychus* had these soft tissue features because they are present in birds and turtles, and they are associated with scleral ossicles that *Deinonychus* also retained (see: the Tree of Life, Chordata section). Dinosaurs are generally restored as having been diurnal creatures. To the best of my knowledge, the above chain of reasoning is the first attempt at providing positive evidence that such a restoration is reasonable for essentially all lineages of reptiles (extinct or extant) other than modern crocodiles and snakes.

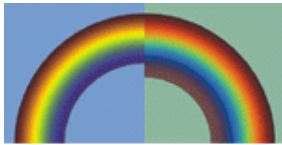


Figure 16.

### Potential Bones of Contention

Two cautionary notes must be raised in regard to the chain of logic linking scleral ossicles and circadian patterns of activity. First, it is possible to erroneously conclude that a structure did not exist in a lineage merely because it has not been found. For instance, ossicles are almost never found in large theropod dinosaurs, so one might deduce that in order for a theropod to grow to a large size it had to become nocturnal. However, scleral ossicles have been found in one specimen of *Tyrannosaurus bataar* (Sabath, personal commun., 1999). Ossicles likely existed in all theropods and are only missing in many forms due to preservation and/or preparation artifacts. The conclusion that the structures did not exist in an animal will always be more tentative than the conclusion that they did in forms for which positive evidence is known. On the other hand, when living forms do not have the structures it is reasonable to infer that the last animals *known* to have them may well have been the last animals in that lineage to have actually had them.

One group of extant animals that does not have scleral ossicles is mammals. Scleral ossicles have been found in the remains of some early synapsids (T. Rowe 1988), so their absence in extant mammals represents a secondary loss. This is consistent with Walls' view that Mesozoic mammals were nocturnal. Using the argument from the previous paragraph, we can infer that scleral ossicles were lost from synapsid lineages at some point in the Late Triassic, since tritylodonts had them (T. Rowe, personal commun., 1999), but they are not known from later mammal or mammal-like forms. We thus have a basis for reasoned speculation about the precise ecological forces which led to nocturnality in our ancestors. For instance, what were the exact competitors, predators and sources of food for Late Triassic mammals? Or conversely, what flora and fauna permitted (if not encouraged) diurnality in Early Triassic mammalian ancestors? Similar arguments can be made for amphibians, crocodylians and any other group of animals that have lost or reduced their scleral ossicles.

The claim that it is a Level I inference that the retina of *Deinonychus* had four cone classes, double cones and oil droplets rests on the correlation between these structures and scleral ossicles. However, it is not necessarily true that all "scleral ossicles" are homologous, and it is certainly not true that all structures named "scleral ossicles" perform the same function. Included in Figure 15 is a photo of the skull of a specimen of *Dunkleosteus*. This and other fish dating back to at least the Silurian had small plates of bones in (or at least closely associated with) their eyes. Walls (1942) argued, based upon his understanding of the structures from which the ossicles evolved in the two lineages, that the ossicles of such actinopterygian fish could not be homologous with those of reptiles. It has been generally believed that the ossicles of modern fish form via ossification of scleral cartilages, which in reptiles coexist with the ossicles that form by direct ossification (Hall and Miyake 1992, Canavese et al. 1994). However, Andrews (1996) examined ossicular development in turtles and concluded that it was more like that of fish than that of birds. Whether or not the ossicles are homologous in birds and fish, they cannot perform the same functions in both groups - as mentioned previously, the corneas of aquatic animals do not aid in focussing light. Thus, unlike birds, fish cannot (and of course, do not) accommodate by changing the shape of their corneas. Extant fish also do not squeeze their lenses as do reptiles, so the ossicles would not help them to accommodate in that fashion. Finally, in modern fish, there is no corneal-scleral sulcus as there is in reptilian eyes. However, this condition is similar to that of penguins which have well-developed ossicles in spite of their lack of a corneal-scleral sulcus (Suburo and Scolaro 1990). Frequently the corneas of fish are flattened probably to improve streamlining around the eye, so the junction between the cornea and sclera is



convex. In extant actinopterygians, scleral ossicles are most prominently associated with large, swift-swimming scombrids, which may have retained them as supports for their relatively large extraocular muscles (Nakamura and Yamaguchi 1991).

If it could be established that (contra Walls 1942) fish and reptile scleral ossicles are, in fact, homologous then some of the previous conclusions would have to be modified pending the establishment that the ossicles of reptiles took on their present functions prior to the timing of the split between the lineages leading to the various major tetrapod groups. Consequently, further examinations of the nature of these structures in both extinct and extant forms are probably warranted. However, to put this objection into perspective, if we ultimately reject the logical linkage between scleral ossicles and diurnal activity patterns - and hence the retinal char-

acteristics that appear linked to diurnality in reptiles - then my inferences about *Deinonychus*' retina merely become Level I' in Witmer's (1995) terminology. That is, we would still have good reason to infer that dinosaurs had retinas more similar to those of modern birds than those of say, modern mammals, but our confidence in the inference would not be quite as strong. If scleral ossicles are not reliable osteological correlates of double cones, oil droplets and four visual pigments it would be harder to argue against the hypothesis that some or all of these features were secondarily lost in particular lineages. Such secondary losses would be evolutionary changes for which we have no direct evidence in most lineages, though, and in such instances (e.g., for *Deinonychus*), it would be more parsimonious to conclude that the ancestral features were retained.

## CONCLUSIONS

Many facets of the biology of extinct animals will likely remain forever outside of the domain of empirical verification. However, with EPB it is possible to reach conclusions with varying degrees of certainty about anatomy, physiology and behavior in animals that we could never actually observe. In hypothesizing about the visual systems of extinct animals we are fortunate that much of retinal anatomy appears to have been conserved in many lineages over the last 300 to 400 million years of evolution. We are unfortunate in that we are not among the lineages in which this preservation occurred, so our own visual systems are not good models for the visual systems of most other animals. This review has

focused upon the photoreceptors, the most peripheral part of the visual system. A similar review could be written to address comparisons of more central visual structures and how EPB could be applied for them. Interesting contrasts have already been drawn between cortical processing of visual signals in birds vs. mammals (Shimizu and Karten 1991). Ultimately, we can draw some strong conclusions about particular aspects of visual function in a number of extinct animals. However, we are currently scratching only the surface of the wealth of knowledge that we can in principle obtain from extant animals and apply to their extinct relatives.

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## GLOSSARY

**Accommodation** Adjusting the focal length of the eyes.

**Actinopterygian** From the Greek for “ray winged.” Ray-finned fish, a taxonomic group comprising most of the animals today referred to as “fish.” See: Tree of Life, Actinopterygii section.

**Apomorphic** The derived state of a character in an evolutionary analysis. For instance, bipedal walking is apomorphic in humans relative to the quadrupedal locomotion of our ancestors. See plesiomorphic.

**Apomorphy** A derived character (see Apomorphic).

**Catalyst** A molecule that facilitates a chemical reaction without actually being modified by that reaction. Most physiological reactions proceed toward equilibrium. However, the rates of these reactions may be greatly increased by the action of catalysts produced by the organism. See enzyme and phototransduction.

**Chromophore** From the Greek for “color bringer”, a chromophore is generally a molecule that acts as a pigment that gives an object color by selectively absorbing light at particular wavelengths. In the context of this article, a chromophore is a retinal (vitamin A) derivative that forms part of a photopigment. See opsin, photopigment, retinal and retinol.

**Clade** A monophyletic group of organisms.

**Cladistics** A method of inferring evolutionary ancestry by methodically comparing possible evolutionary relationships between organisms and selecting as most likely the relationships which require, for instance, the fewest number of evolutionary transformations between character states.

**Cone** A vertebrate photoreceptor that is primarily sensitive to lights with high intensity (e.g., daylight).

**Cornea** The transparent covering on the front surface of the eye. The cornea and sclera together form the outer surface of the entire eyeball. See sclera.

**Dichromatic** From the Greek for “two colored.” Strictly speaking, an animal for which only two independent lights are required in order to represent all colors visible to the animal. *Independence* here means that it is not possible to adjust the intensity of one of the lights in such a way as to make it appear like the other light (provided that the lights are intense enough to be

visible to the animal and not so intense as to saturate its photoreceptors). Loosely speaking an animal that has only two photopigments operating at a given time is considered to be dichromatic. See monochromatic, trichromatic, and tetrachromatic.

**Double Cone** A pair of cones that are directly apposed to each other over the length of their inner segments.

**Enzyme** A protein that catalyzes a chemical reaction. See protein and catalyst.

**Eutheria** From the Greek for “true beast.” In phylogenetic taxonomy it has been defined as placental mammals and all animals more closely related to them than to marsupials. See: Tree of Life, Eutheria section.

**Fossorial** A reference to an underground lifestyle such as that lead by moles.

**Homologous** Derived from the same ancestral structure.

**Inner Segment** One of the constituent regions of a photoreceptor. In all vertebrates the inner segment contains the ellipsoid, a volume filled with mitochondria that serve not only as the site of oxidative phosphorylation but also as a region of high refractive index. The latter property causes the inner segment to act as a waveguide that channels light to the outer segment. Some inner segments contain oil droplets and/or parabolooids. The latter is made up of carbohydrates that are believed to fuel the photoreceptor; the former apparently function as filters of the light impinging upon the photoreceptor.

**Isomerization** A change in the organization of the atoms in a molecule with no change in the constituency of the molecule. In the context of vision, isomerization usually refers to the rotation around a particular carbon (the 11<sup>th</sup> carbon in the traditional numbering system) of the chromophore. Because this isomerization is caused by light, it is frequently referred to as photoisomerization.

**Light** Radiation with wavelengths which can be perceived by the eyes of animals. For humans this wavelength range is generally considered to be 400 to 700 nm. Absorption by the human lens provides a fairly sharp cutoff at 400 nm, but radiation with wavelengths as long as 1000 nm can be perceived as light if the inten-

sity is high enough relative to the background at shorter wavelengths. Many animals can perceive light with wavelengths both longer and shorter than that perceivable by humans, so a more general definition might include as light electromagnetic radiation with wavelengths ranging from 300 nm to 800 nm (natural sources which would allow for the visual detection of longer wavelengths by any animal are essentially nonexistent).

**Metatheria** From the Greek for “later beast.” A stem clade of mammals represented today by marsupials (e.g., kangaroo and opossum).

**Monochromatic** From the Greek for “one colored.” (1) For an animal, the state of having only one functional photopigment at a particular time. See dichromatic, trichromatic, and tetrachromatic.

(2) For radiation, the state of having all energy concentrated around a narrow range of wavelengths (generally, a monochromatic light is one for which a plot of energy or quantal flux vs. wavelength will have one sharp peak, and the difference in the wavelengths at which the intensity is one-half the value of the maximum on either side of the peak is 10 nm or less).

**Monophyletic** Pertaining to a set of organisms consisting of one species and all of that species' descendants.

**Oil Droplet** A structure found in the inner segments of some photoreceptors. Oil droplets generally have a high refractive index, and thus may play some role in sculpting the quantity and polarization of the light passing through them to the light-sensitive part of the photoreceptor. They also frequently contain pigments such as carotenoids, which absorb light, particularly light having relatively short wavelengths.

**Opsin** A protein that when combined with a chromophore to form a photopigment is converted into an active enzyme by the absorption of light. Photoreceptors contain large numbers of (generally only) one type of opsin. The rate of photon absorption by photopigments within a cell sets the rate at which the chemical reaction catalyzed by the opsin occurs. This reaction is the first link in a cascade of reactions that ultimately leads to the regulation of neurotransmitter release from the photoreceptor to other neurons in the retina; hence modulation in the rate of photon absorption is causally linked to modulations in the rate of neurotransmitter release. See photopigment and phototransduction.

**Orthologous** Similar to the term homologous, but applied only to molecules (i.e., genes and proteins). The term is also more restrictive than homologous in that it entails a similarity in function. See Figure 17 and paralogous.

**Outer Segment** One of the constituent regions of a photoreceptor. Specifically, it is the last part of the photoreceptor that light passes through on its first pass (i.e., prior to any reflections) through the retina. Outer segments are composed of stacked disks flattened in planes perpendicular to the path of the light. The photopigments are bound to the membranes of the outer segment disks.

**Paralogous** A term describing the relationship between two genes that arose via duplication within a single phyletic lineage. See Figure 17 and orthologous.

**Photon** A quantum of light; the smallest (nonzero) amount of energy which can be transferred via radiation at a given wavelength.

**Photoreceptor** A cell that is specialized for converting the rate at which it absorbs photons to the magnitude of a signal, which can be relayed to and interpreted by the organism's central nervous system.

**Photopigment** The combination of a chromophore and an opsin. Photons are absorbed by the chromophore with a probability that depends upon the chemical structure of both the chromophore and the opsin as well as the wavelength of the photon. Vertebrate photopigments use almost exclusively one of two particular chromophores, so most of the differences in spectral sensitivity between photopigments are established by the amino acid compositions of the opsins.

**Phototransduction** The process of converting the intensity of light to a neural signal. It is a series of chemical steps that begins with the absorption of light by a chromophore and ends with a change in the rate of neurotransmitter release by the cell that absorbed the light. When a chromophore absorbs a photon, the chromophore may isomerize and in turn cause an isomerization of the opsin. The opsin then behaves as an enzyme catalyzing the conversion of another protein, transducin, to its enzymatic form. In vertebrates, activated transducin catalyzes the activation of a phosphodiesterase. The phosphodiesterase catalyzes the conversion of cyclic guanosine monophosphate (cGMP) to 3'-5' GMP, thus reducing the amount of cGMP inside the photoreceptor. Cyclic GMP binds to an ion channel in the cell membrane, and when bound it holds the channel in an open state. As the phosphodiesterase decreases the cell's concentration of cGMP, cGMP molecules bound to ion channels become unbound causing those channels to close. The resultant change in permeability of the cell membrane causes the cell's electrical potential to become more inwardly negative. This change in the voltage across the cell membrane results in a decrease in the rate at which neurotransmitter molecules are released at the base of the cell. Since the

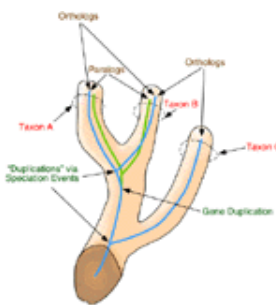


Figure 17.

absorption of one photon can cause the opsin to convert many transducin molecules to their active form, and each activated transducin molecule can convert the activation of many phosphodiesterase molecules, and each phosphodiesterase molecule can isomerize many cGMP molecules, photon absorption is said to be amplified by the phototransduction process. For additional information about phototransduction and other aspects of retinal function, see the Webvision page, particularly the section on phototransduction.

**Phylogenetic Taxonomy** A system of naming only monophyletic groups of organisms. The hierarchical structure of the names devised by such a system, in principle, accurately reflects the evolutionary relationships of all the named groups of organisms.

**Plesiomorphic** The ancestral state of a character in an evolutionary analysis. Plesiomorphic is the antonym of apomorphic.

**Plesiomorphy** An ancestral character. See plesiomorphic.

**Protein** A molecule made up of amino acids (also called peptides and hence proteins may be called polypeptides), members of a class of compounds that contain both a carboxylic acid and an amine group in a particular combination. There are 20 amino acids used in the construction of most proteins, which may be composed of thousands of amino acids strung together in a single chain. The chains are folded into a variety of shapes, which allow the proteins to act as catalysts (enzymes) or as structural components of cells and their surrounding media.

**Prototheria** From the Greek for “first beast.” A stem clade of mammals whose only living descendants are the monotremes (platypus and echidna).

**Quantal flux** The rate at which quanta (plural of quantum) pass through a given region of space.

**Quantum** The smallest physically realizable unit of something. A quantum of light has the special name of photon.

**Radiation** (1) A propagating disturbance in the electromagnetic field; see light. (2) The evolutionary diversification of a group of organisms from a smaller number of closely related ancestral organisms.

**Reptiles** Animals whose ancestry can be traced back (at least in principle) to the most recent common ancestor of snakes and crocodiles. Note that this definition includes birds. See Tree of Life, Reptilia in the Amniota section.

**Retinal** (adj). Pertaining to the retina, the thin sheet of cells lining the inside of the eye. (n.) The aldehyde form of vitamin A, which is synthesized in animals from carotenoids extracted from ingested plants. Also called

retinaldehyde, retinal is one of the molecules primarily responsible for light sensitivity. See phototransduction.

**Retinol** The alcohol form of vitamin A. See retinal.

**Rod** A vertebrate photoreceptor that is primarily sensitive to light at low levels of intensity. Electrophysiology and human psychophysical experiments indicate that rods can reliably respond to the absorption of a single photon. Rods predominate in the retinas of nocturnal animals.

**Sarcopterygian** From the Greek for “flesh-wing.” Lobe-finned fishes and tetrapods. See tetrapod and Terrestrial vertebrates, Stegocephalians: Tetrapods section of the Tree of Life pages, particularly the note about the node T.

**Scleral Ossicles** A ring of bones embedded in the sclera and surrounding the irises of the eyes of many animals particularly reptiles.

**Sclera** The fibrous covering on the posterior part of the vertebrate eye. See cornea.

**Spectrum** (1) A range of wavelengths (as in, “the visible region of the electromagnetic spectrum”). (2) The variation of some function over a range of wavelengths. Examples of such functions might be power or number of photons passing through an area per unit time, or percentage of light reflected or absorbed by an object or substance.

**Tetrachromatic** From the Greek for “four colored.” Strictly speaking, a tetrachromatic animal is one for which four independent light sources are required for the simulation of all visible colors. *Independence* here means that no combination of intensities of a subset of the lights can be made to appear identical to any combination of intensities of the remaining lights in the set. More loosely tetrachromatic is taken to mean that an animal has four different photopigments functioning in its retina all at the same time since an animal that is so endowed may possibly meet the stricter definition. See monochromatic, dichromatic, and trichromatic.

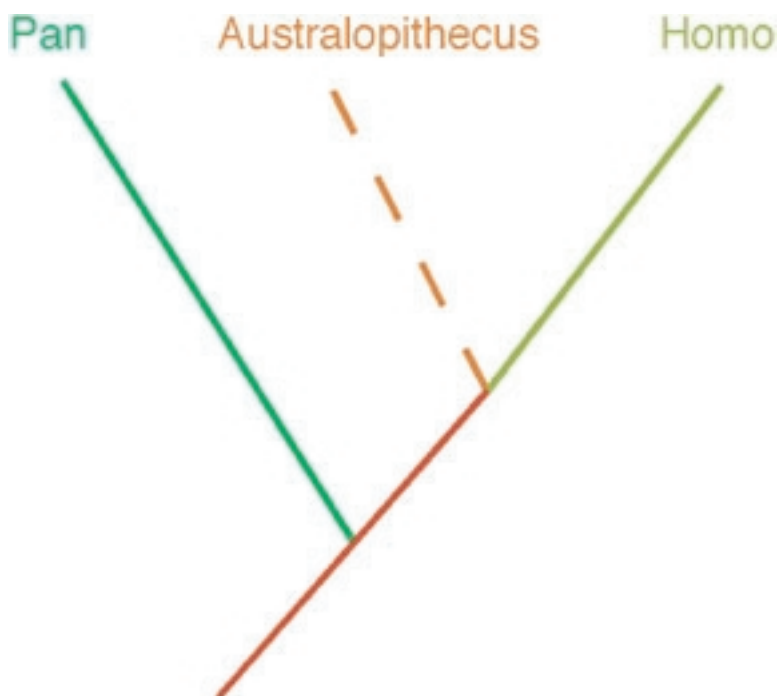
**Tetrapod** From the Greek for “four foot.” In phylogenetic taxonomy, tetrapod has been defined as all of the descendants of the most recent common ancestor of amphibians and amniotes. Note that this definition includes many animals (e.g., snakes) that do not have four feet. See: the Tree of Life, Classification of Terrestrial Vertebrates.

**Trichromatic** From the Greek for “three colored.” Strictly speaking, an animal for which any visible color can be simulated with the linear combination of intensities from three independent light sources. *Independent* here means that no combination of intensities of two of the lights can be made to appear the same as the third light at any intensity. Light-adapted humans with “nor-

mal" color vision are trichromatic over much of their visual field, which is why television sets and computer monitors require only three phosphors to do a reasonably good job of representing colors for humans.

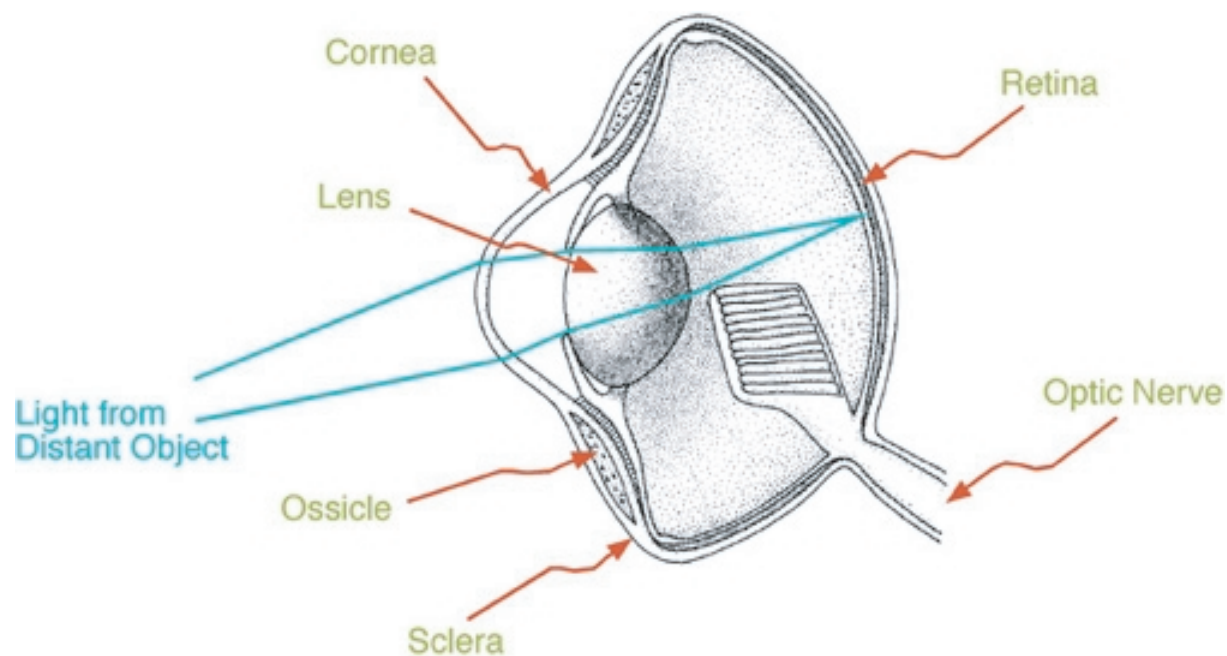
Loosely speaking trichromacy is the state of having three photopigments operative at the same time. See monochromatic, dichromatic, and tetrachromatic.

**Figure 1.** The extant phylogenetic bracket (EPB) method. In order to infer properties of the soft-tissue anatomy of an animal such as *Australopithecus*, one can study the soft tissues of two extant relatives with reasonably well established phylogenetic relationships. Human's (*Homo*) and chimpanzee's (*Pan*) respective lineages diverged from each other before *Homo*'s lineage diverged from *Australopithecus*. Therefore, soft-tissue features inherited by *Homo* and *Pan* from their most recent common ancestor will have existed ancestrally in *Australopithecus* as well. Consequently *Australopithecus* would have also had those features unless they were secondarily lost after *Australopithecus* diverged from *Homo*. For instance, it is safe to infer that *Australopithecus* had a four-chambered heart since both humans and chimpanzees have four-chambered hearts. We can reasonably conclude this even though the fossils of *Australopithecus* do not provide unambiguous evidence documenting the presence of such a structure.

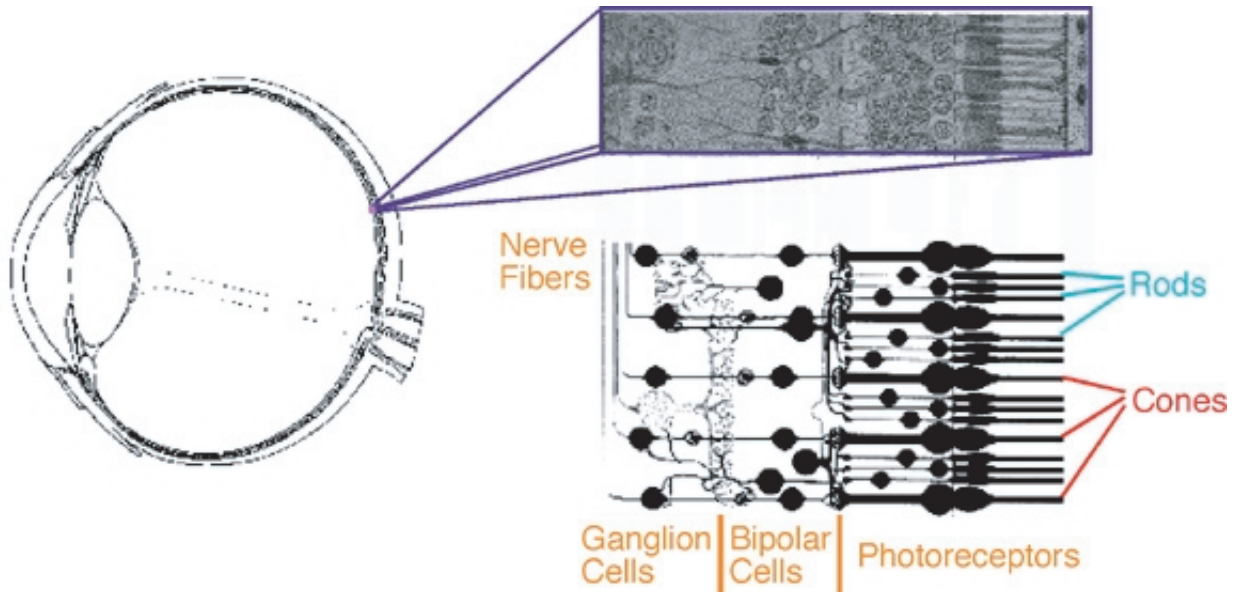




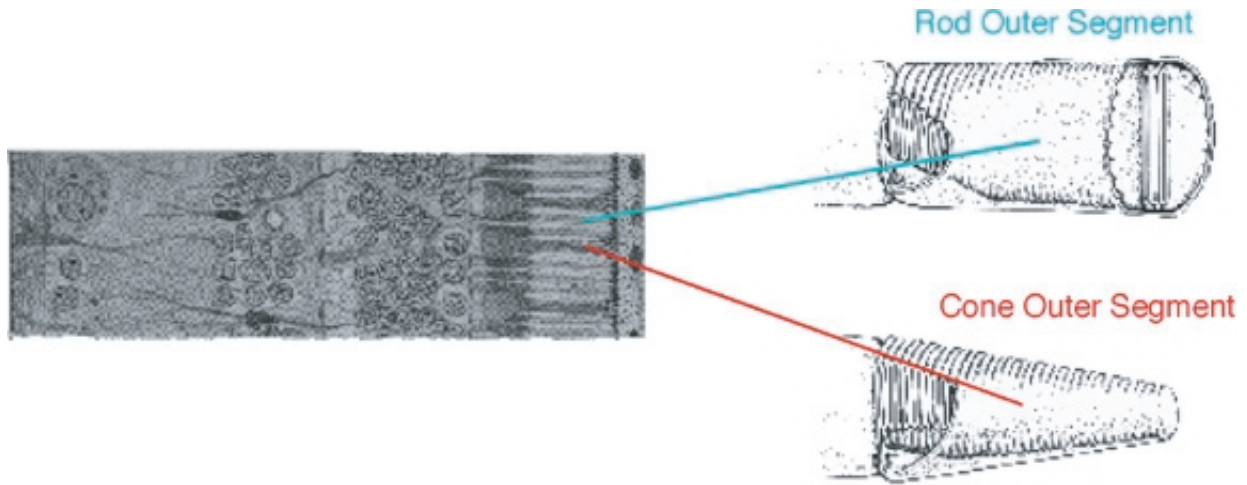
**Figure 2.** A vertebrate eye. Although there is considerable diversity among the eyes of various vertebrates, they all share some common features. In particular they have optical elements such as the cornea and lens which focus light in order to form an image on the retina. See Figure 14 for more on scleral ossicles such as are evident in this cross-section. (Drawing from Waldvogel, 1990, originally created by Virge Kask for Meyer 1977).



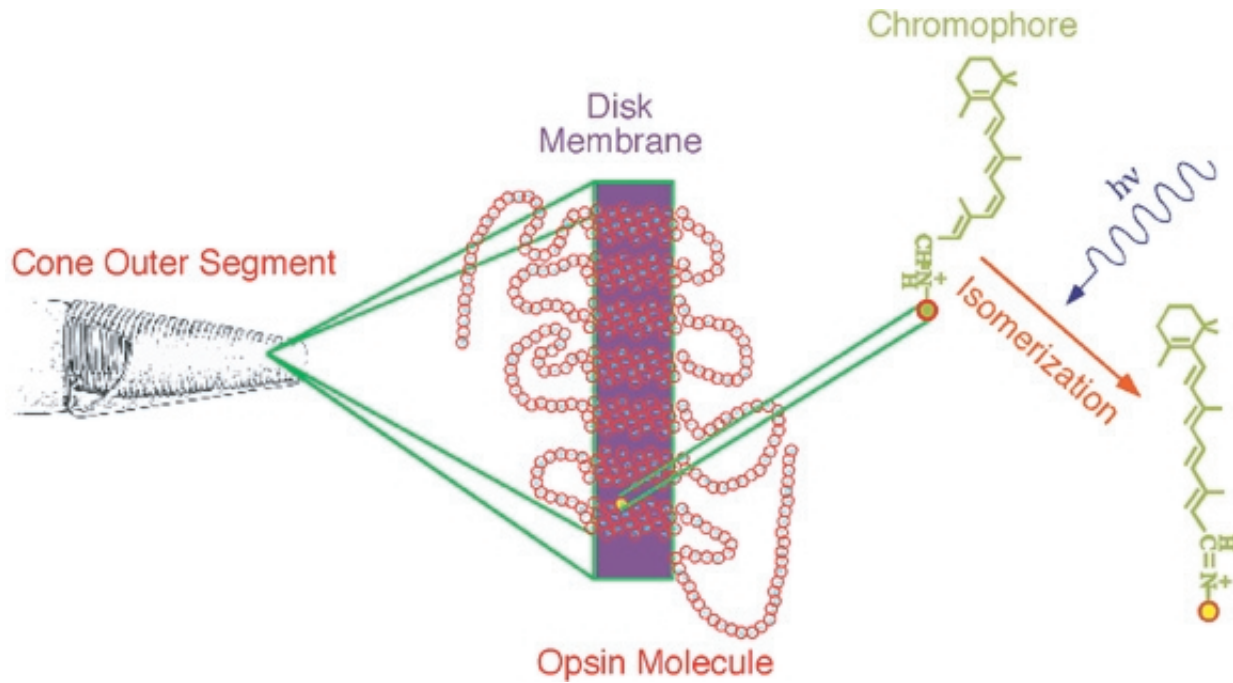
**Figure 3.** The vertebrate retina. The retina is the thin set of tissue layers lining the inside of the vertebrate eye. The drawing to the left is a cross-section of a human eye. The drawings to the right indicate the position and orientation of the three layers of cell bodies in the neural portion of the retina. The last layer -- sometimes referred to as the bacillary layer or the photoreceptor layer -- contains the cells which convert the absorption of light into an electrochemical signal. Almost all vertebrate retinas contain two major populations of photoreceptors, rods and cones. Although originally so named because of their shapes in many animals, modern usage generally discriminates between the two populations on functional grounds. Rods are active at low light levels, and are thus saturated and useless during the day. Conversely, cones are less sensitive, and thus operate almost exclusively during the day (or for modern humans under artificial sources of illumination). Cones can usually be further subdivided into a small number of classes based upon their spectral sensitivity. (Drawings adapted from Walls 1942)



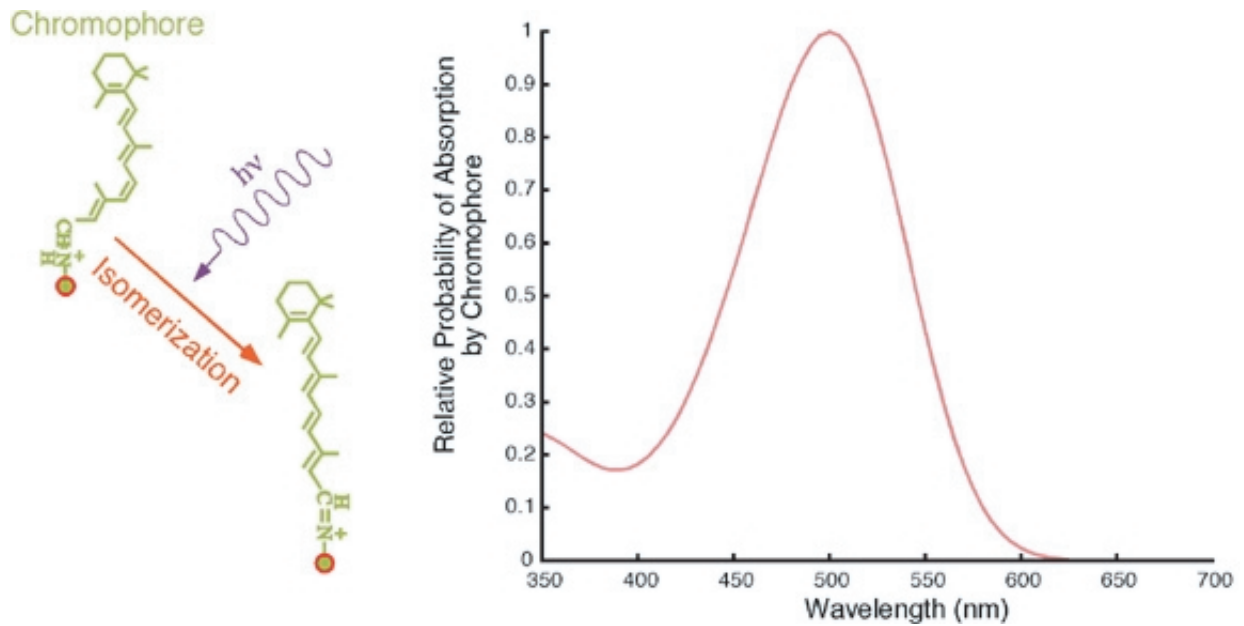
**Figure 4.** Photoreceptor outer segments. The left part of the figure is reproduced from Figure 3. The detail on the right depicts some of the finer structures of the outer segments of the photoreceptors. The outer segment is the last part of the cell that light passes through as it travels through the living retina, although in some animals a reflective layer behind the retina causes a significant quantity of light to pass back through the retina in the opposite direction. In any case, the outer segments contain the molecules which absorb light and convert that absorption into a biochemical signal. The outer segments are comprised of a series of disks, probably to increase the amount of membrane and hence photopigment -- which is bound to these membranes -- in the cell. The drawings of the outer segments have been partially cut away to reveal the cross-sections of the disks. (Drawings after Walls 1942, and Bailey and Gouras 1985).



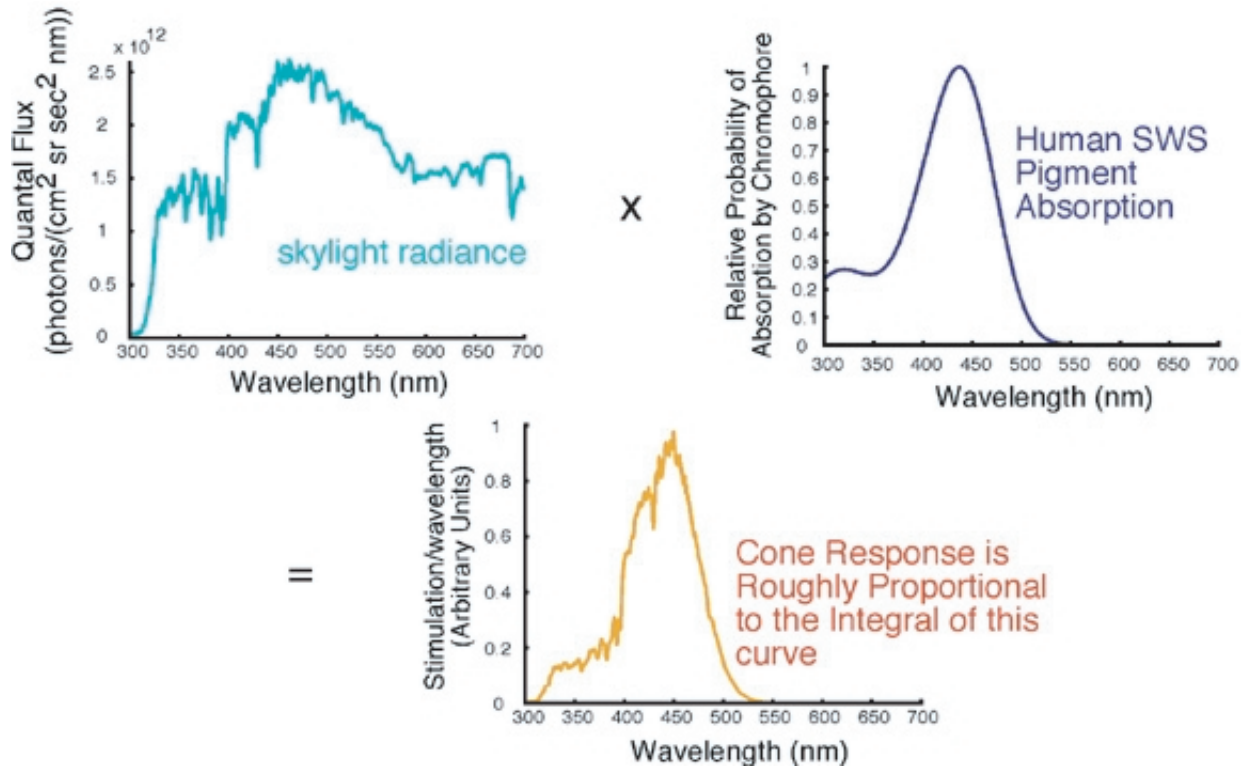
**Figure 5.** Phototransduction. The drawing to the left is reproduced from Figure 4. The diagram in the center schematically depicts how a photopigment is embedded within a disk membrane of a photoreceptor outer segment. Each circle represents an individual amino acid. The filled yellow circle is a lysine to which is attached the chromophore, the molecule schematically represented on the right. The chromophore is a vitamin A derivative which can exist in two stable configurations. The absorption of a photon may cause the chromophore to convert from the 11-cis form to the all trans form as shown by the chemical reaction. This conformational change in the chromophore causes a change in the shape of the opsin molecule. The opsin's change in shape converts it from an inactive to an activated enzyme, and thus is light absorption converted to a biochemical signal in a photoreceptor. (Opsin sequence adapted from Wilkie et al. 1988).



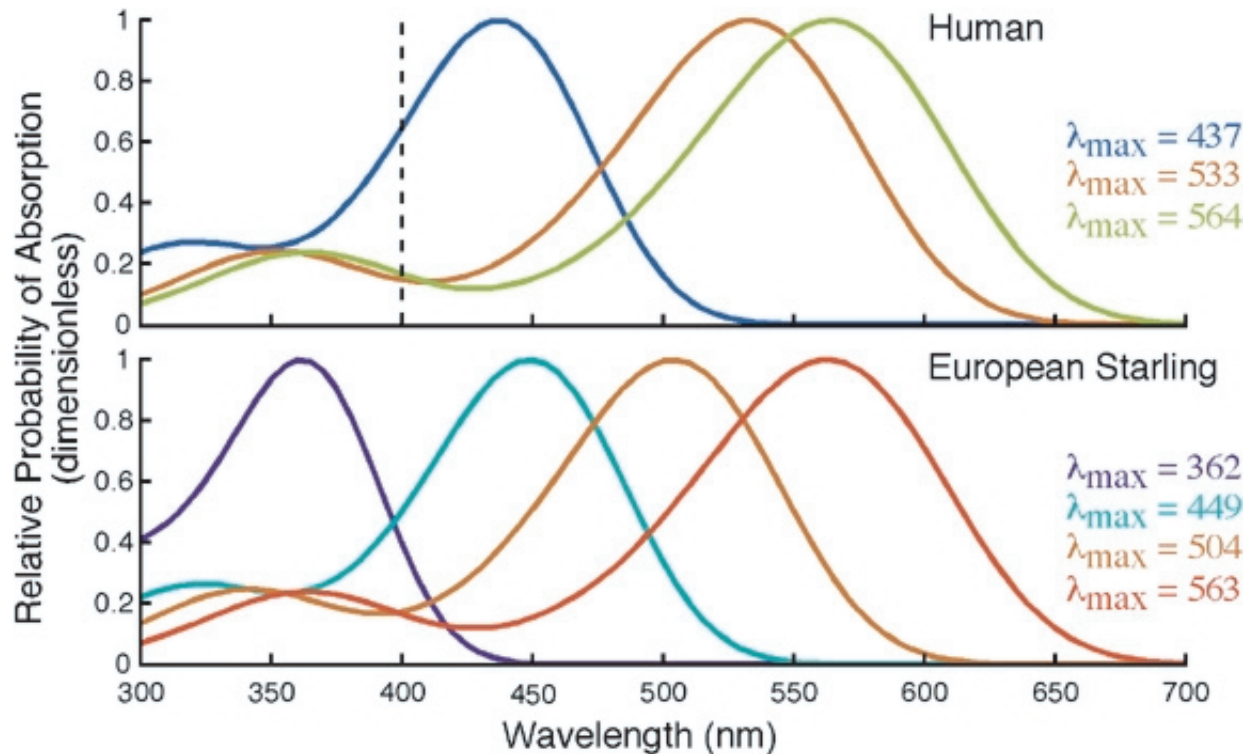
**Figure 6A.** Wavelength dependence of phototransduction. The reaction on the left is reproduced from Figure 5. The plot on the right shows how the probability that a chromophore will absorb a photon with a given wavelength depends upon that wavelength. The absorption spectrum in this case is that of a human rod. At night we are most sensitive to light with wavelengths around 500 nm. See Figure 6B.



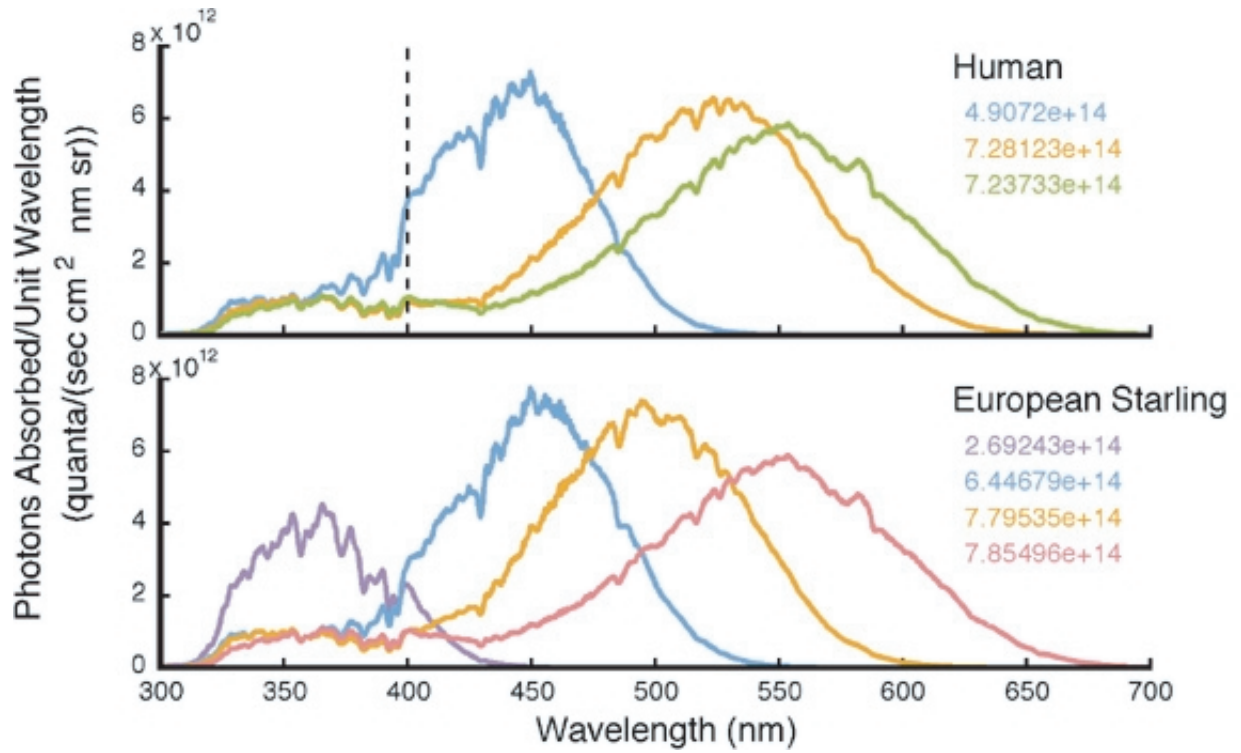
**Figure 6B.** Conversion of light intensity to cone response. Typical light sources are broad-band - they radiate photons having many different wavelengths. The plot on the left is a quantal flux distribution from a small patch of blue sky overhead near dusk. The plot on the right is an absorption spectrum like that of Figure 6A, only it is for the human short-wave sensitive cone rather than the rod. The final plot is merely the data from the first two plots multiplied together. The response of the short-wave sensitive cone is essentially proportional to the integral of the data in this plot (after correcting for other effects such as the absorption by pre-retinal media; for example, the human lens strongly absorbs most light with wavelengths shorter than 400 nm).



**Figure 7A.** Extracting color from sets of one-dimensional signals. The operations in Figure 6B convert an incident spectrum to one number at each point in time (and space on the retina). In order to retain some information about the spectrum of incident light, animals use cones which have different absorption spectra. The top plot shows the spectra of the three cones found in humans. The bottom plot shows the absorption spectra of the outer segments of the four cone types in the retina of the European starling. The shapes of the curves vary slightly in systematic ways as a function of the wavelength where the absorption peaks. Therefore, the cones can be characterized by that peak wavelength. The absorption peaks for each of the seven pigments are inset in the two plots. See Figure 7B.

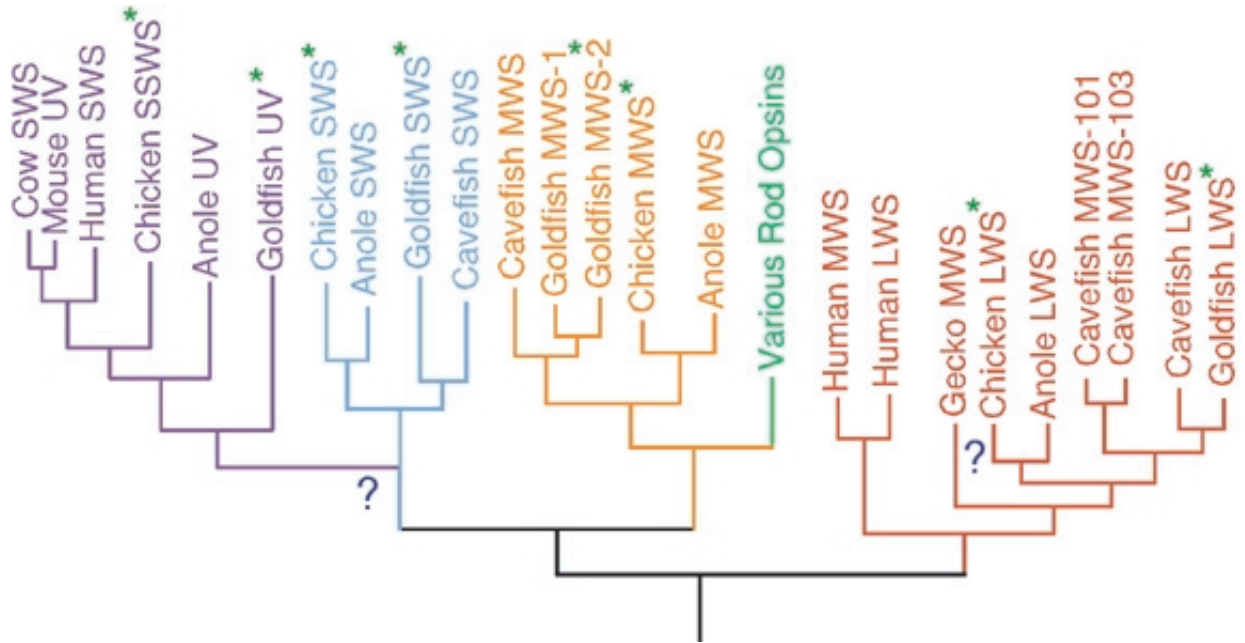


**Figure 7B.** Cone signals. Analogous to the operations shown in Figure 6B, these seven curves represent the product of a skylight spectrum and the seven absorption spectra of Figure 7A. The inset numbers are the integrals of the seven curves. These numbers represent essentially all the information that the nervous system retains about the average and spectral intensity of the skylight's radiance.





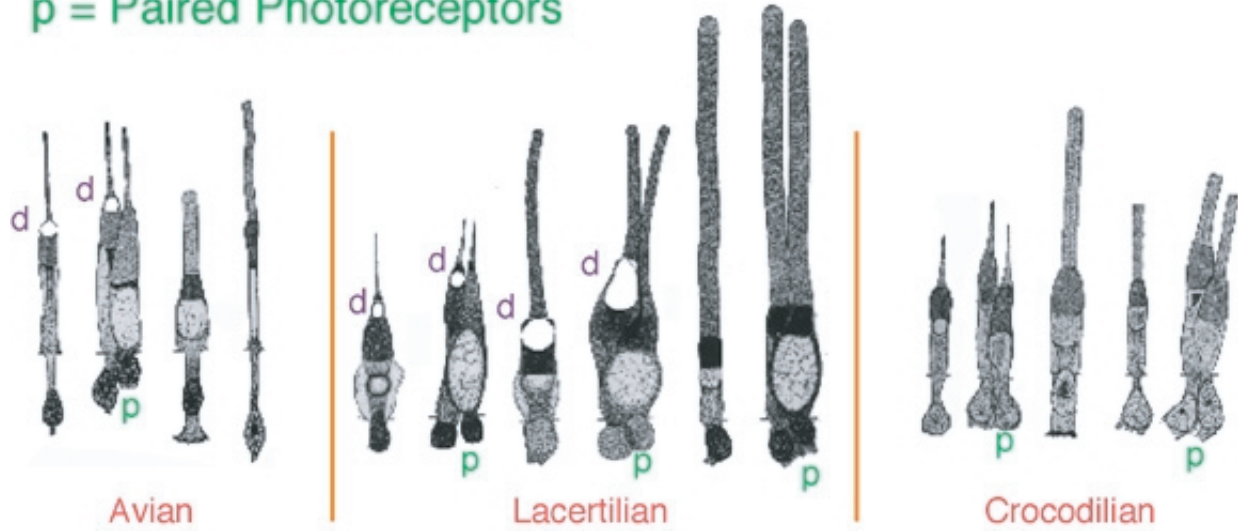
**Figure 8.** Distribution of photoreceptor opsins. Opsins have been at least partially sequenced for approximately 50 different cone photopigments. The diagram here is consistent with the topology derived from cladistic analyses of these genes (Hisatomi et al. 1996, Heath et al. 1997, Wilkie et al. 1998, Yokoyama et al. 1998), with question marks indicating relatively uncertain branch points. Note that the four reptilian cone opsins (represented here primarily by sequences from the domestic chicken, *Gallus gallus*, and the American anole, *Anolis carolinensis*) cluster together with four Teleost cone opsins (represented here primarily by the goldfish, *Carassius auratus*). This particular clustering (highlighted with asterisks on the chicken and goldfish opsins) indicates that the four opsins of reptiles are orthologous to four opsins of actinopterygian fish. Thus basal tetrapods bracketed by these two groups must also have had four opsins barring secondary losses. Also of note is the clustering of mammalian short-wave sensitive pigments with reptilian UV-sensitive pigments (the chicken SSWS cone has a peak sensitivity that is intermediate between the human SWS cone and the UV cones found in many other animals). The SWS/UV clustering suggests that despite the apparent paucity of UV-sensitivity in mammals, mammals were ancestrally sensitive to UV light.



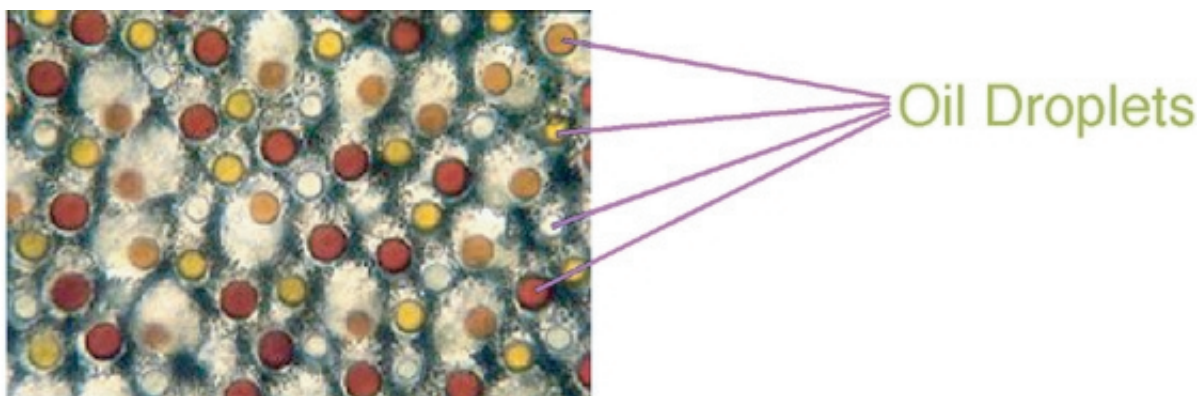
**Figure 9A.** Position of oil droplets in photoreceptors. These drawings represent some of the diversity of reptilian photoreceptor anatomy. The orientation of these cells is such that the outer segments are at the top, and light from the lens would enter from the bottom. The “d’s” show the positions of oil droplets in the photoreceptors which have them. The “p’s” indicate which receptors are paired (see text and Figure 11). Oil droplets are situated immediately prior to the light-sensitive outer segments in the photoreceptors that have such droplets. They thus act as a screen of the light prior to its absorption by these photoreceptors. (Adapted from Walls 1942). See Figure 9B, Figure 9C.

d = Oil Droplets

p = Paired Photoreceptors

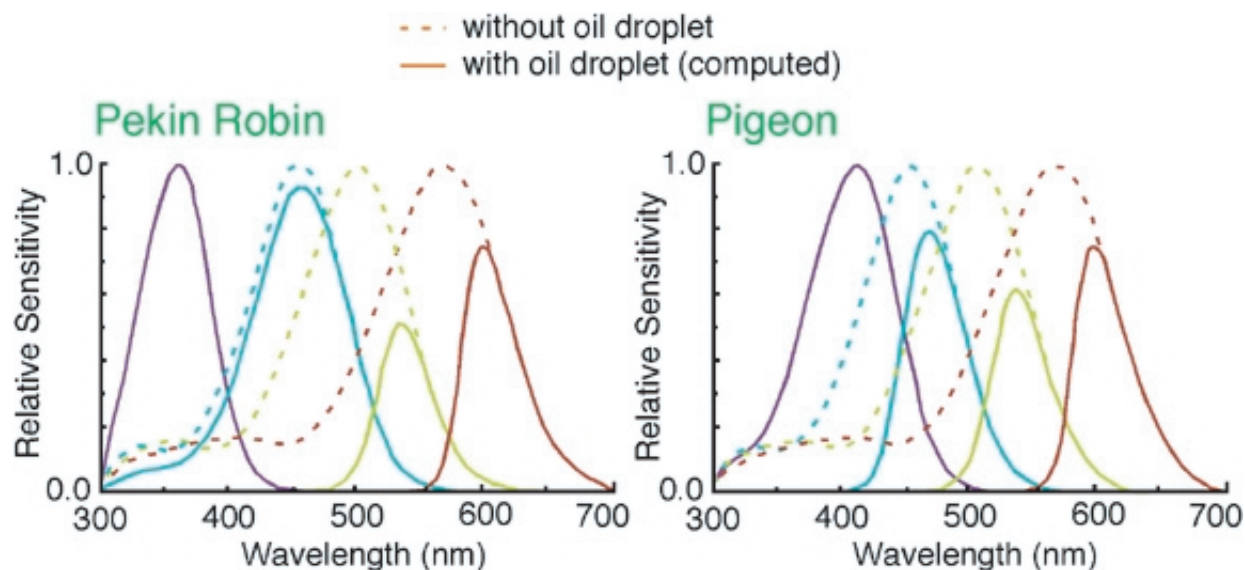


**Figure 9B.** Pigments in oil droplets. Oil droplets such as these from the retina of a Red-eared Slider (*Pseudemys scripta elegans*), frequently contain pigments so that light at particular wavelengths is strongly attenuated. In this case there are five types of oil droplet, four of which are easily discriminated visually (the “clear” droplets actually form two different spectral classes). The retina is whole-mounted here, and the light used to generate the image passed through the photoreceptors in the normal direction. Figure from Ahnelt et al. (2000). See Figure 9A, Figure 9C.

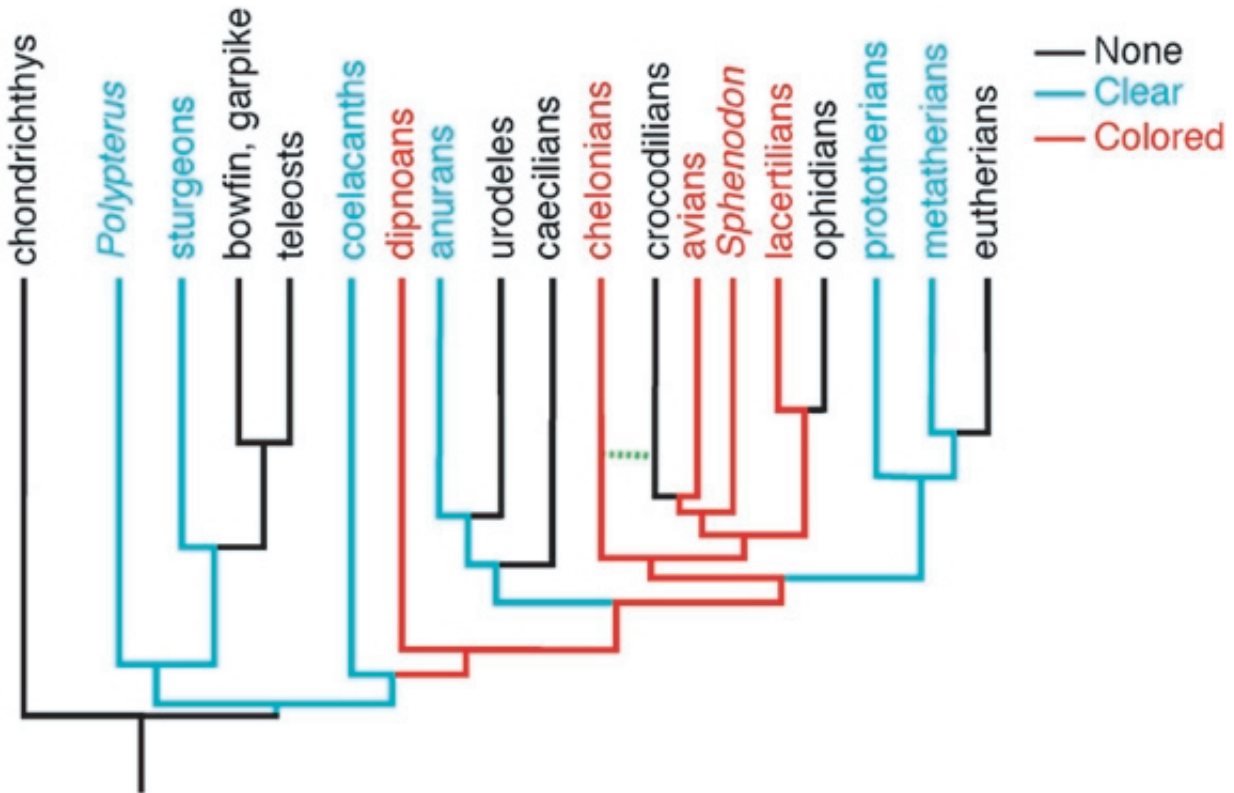


Whole mount of retina from:  
*Pseudemys scripta elegans*

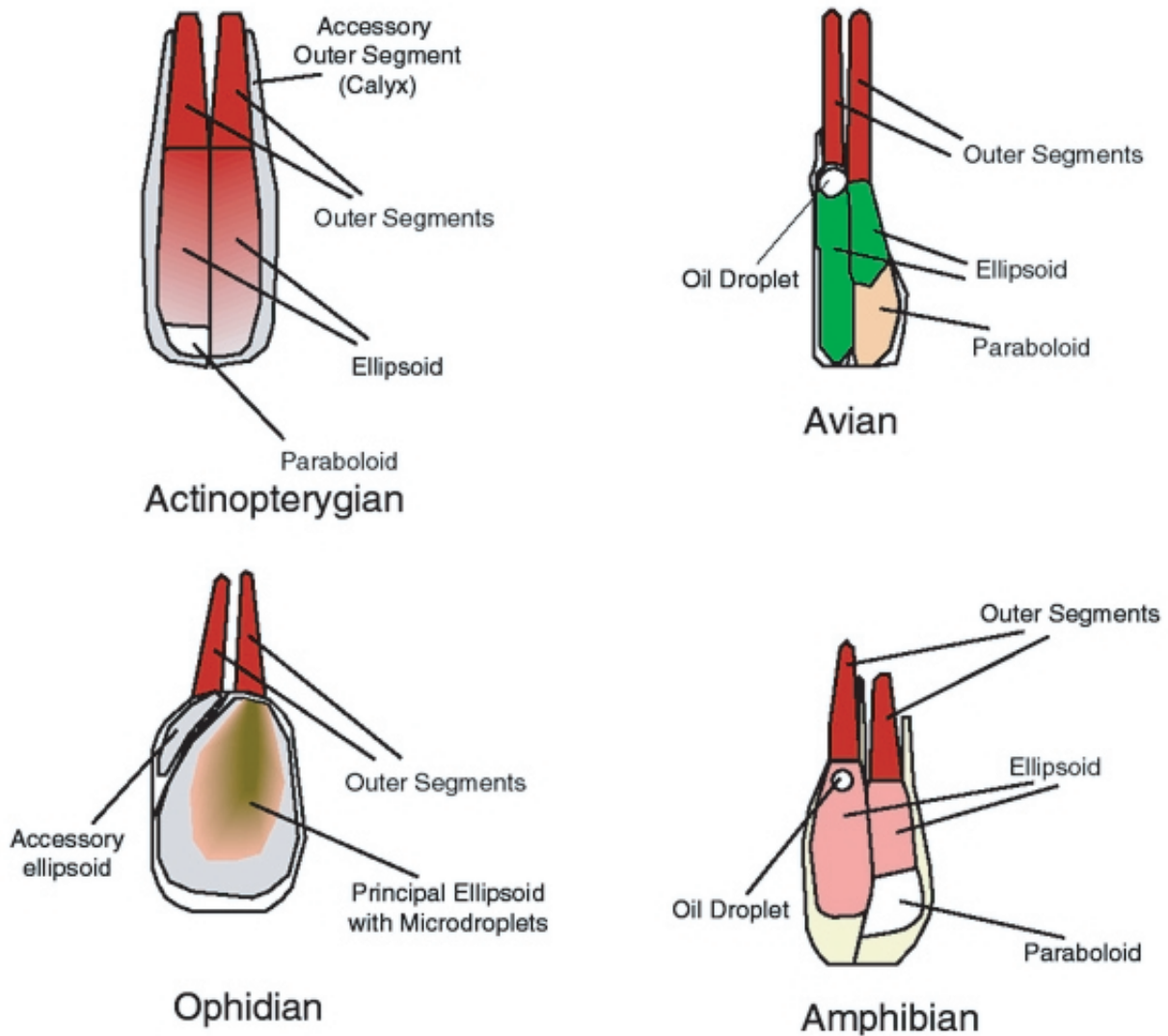
**Figure 9C.** The effect of oil droplets on photoreceptor sensitivity. Pigmented oil droplets generally absorb light at the short-wave end of the spectrum. As such they shift the photoreceptor's peak absorption toward longer wavelengths. The dashed curves in these plots indicate the absorption spectra of the outer segments when measured from the side (i.e., ignoring absorption by any other structures within the photoreceptor). These eight curves for the Pekin robin (*Leothrix lutea*) and the rock dove (i.e., the pigeon, *Columba livia*) are similar to the starling absorptions shown in Figure 7B (where the effect of oil droplets was similarly ignored). The solid curves show the effect that the oil droplets associated with these outer segments have upon the photoreceptors' actual absorption spectra. Note that the solid curves have much less overlap with each other than do the dashed curves. That is, the oil droplets reduce the redundancy in the sampling of different wavelength regions. For example, without oil droplets all four of the cones from each bird would be substantially sensitive to lights with wavelengths between 300 and 400 nm. With the oil droplets in place, only one of the pigeon's and two of the robin's photoreceptors are appreciably responsive to these wavelengths. (Adapted from Vorobyev et al. 1998). See Figure 9A, Figure 9B.



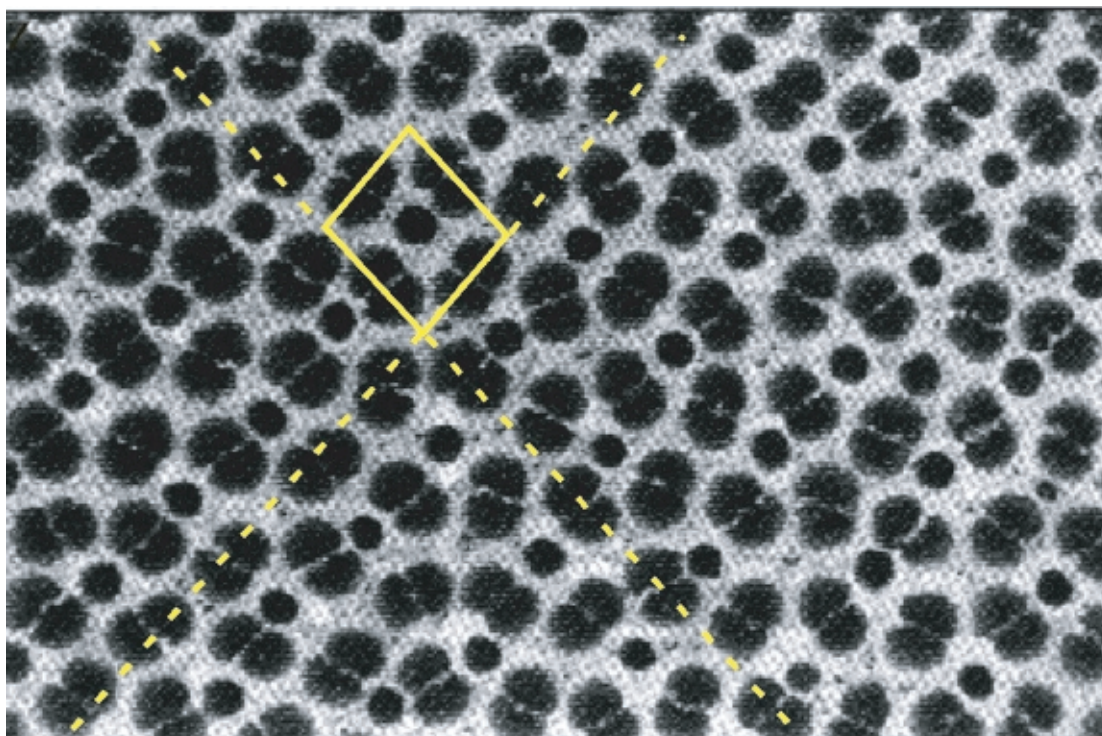
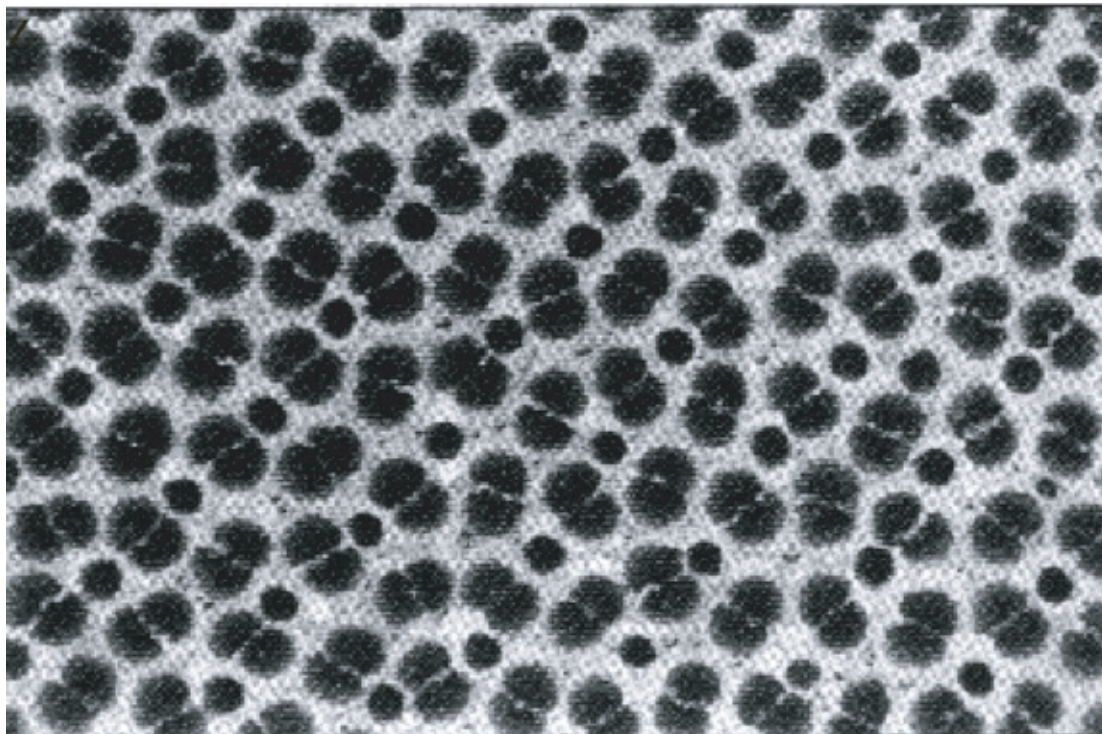
**Figure 10.** Distribution of oil droplet types within vertebrates. Taxa in black are not known to have any members with oil droplets in their photoreceptors. Those in cyan have members with photoreceptors with oil droplets which do not appear to have any color when viewed with a light microscope. Those in red have members with colored oil droplets such as those depicted for the turtle in Figure 9B. The homology of oil droplets and their pigments is presumed here, so conclusions which might be drawn from this figure (e.g., pigmentation in oil droplets arose only once and was subsequently lost in mammalian and amphibian lineages) should be accepted with caution. However, the presence of pigmented oil droplets in nearly all major reptilian taxa does suggest that such droplets are basal to at least that group. The dashed green line suggests an alternative branching for Chelonians as recently suggested by Hedges and Poling (1999). This figure is meant to show the branching pattern only; no significance should be accorded the relative lengths of the branches. (Adapted from Robinson 1994).



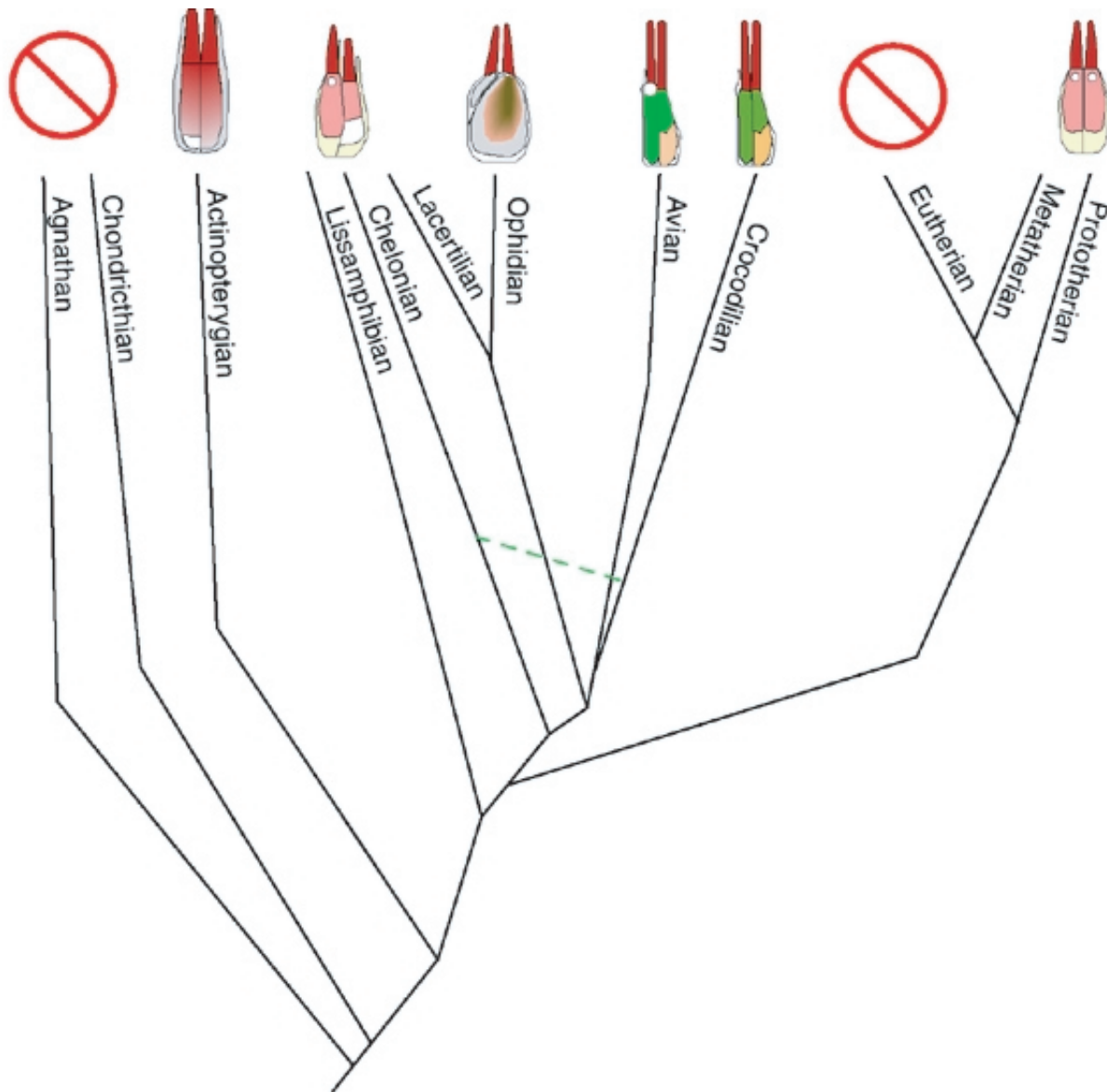
**Figure 11.** Double cone morphologies. These schematized drawings depict some of the variety in constitution of double cones. Diagrams only show inner and outer segments of photoreceptors (the cells also contain myoids and nuclear regions). Inner segment organelles generally provide metabolic and/or optical functions. For instance, the ellipsoids are comprised of dense aggregations of mitochondria, which not only serve as sites for the conversion of sugars to other fuels useful to the cells, but also have a high refractive index and thus tend to guide light into the outer segments. One feature commonly shared among double cones is the direct apposition of the ellipsoids against the membranes which unite the two constituent photoreceptors of a given double cone. This suggests that the doubling of photoreceptors arose as a means to optically couple the joined photoreceptors. Exactly what benefit such coupling might serve is presently unknown. Microdroplets in snake cones may be descended from oil droplets more similar to those currently found in other reptilian retinas. (Avian cones derived from images in Walls 1942, and Morris and Shorrey 1967; amphibian derived from Nilsson 1964; ophidian after Walls 1942, and Wong 1989).



**Figure 12.** Double cone mosaic. When viewed as a whole mount looking through the retina in the direction light would normally travel in an intact eye, double cones can be seen to form regular patterns in some animals, particularly teleosts. This image is of fixed and stained tissue from a green sunfish (*Lepomis cyanellus*) focused at the level of the inner segments. The mosaic is typically described as “square” because the long axes of double cones are arranged like the sides of squares around a central single cone, although careful analyses of sunfish retinas suggest that the mosaic might more accurately be described as rhombic (Cameron and Easter 1993). Clicking on the image will cause a square and a pair of dashed lines to appear as highlights of the regularity of this particular mosaic. (Photo prepared by D.A. Cameron and S.S. Easter, Jr.)

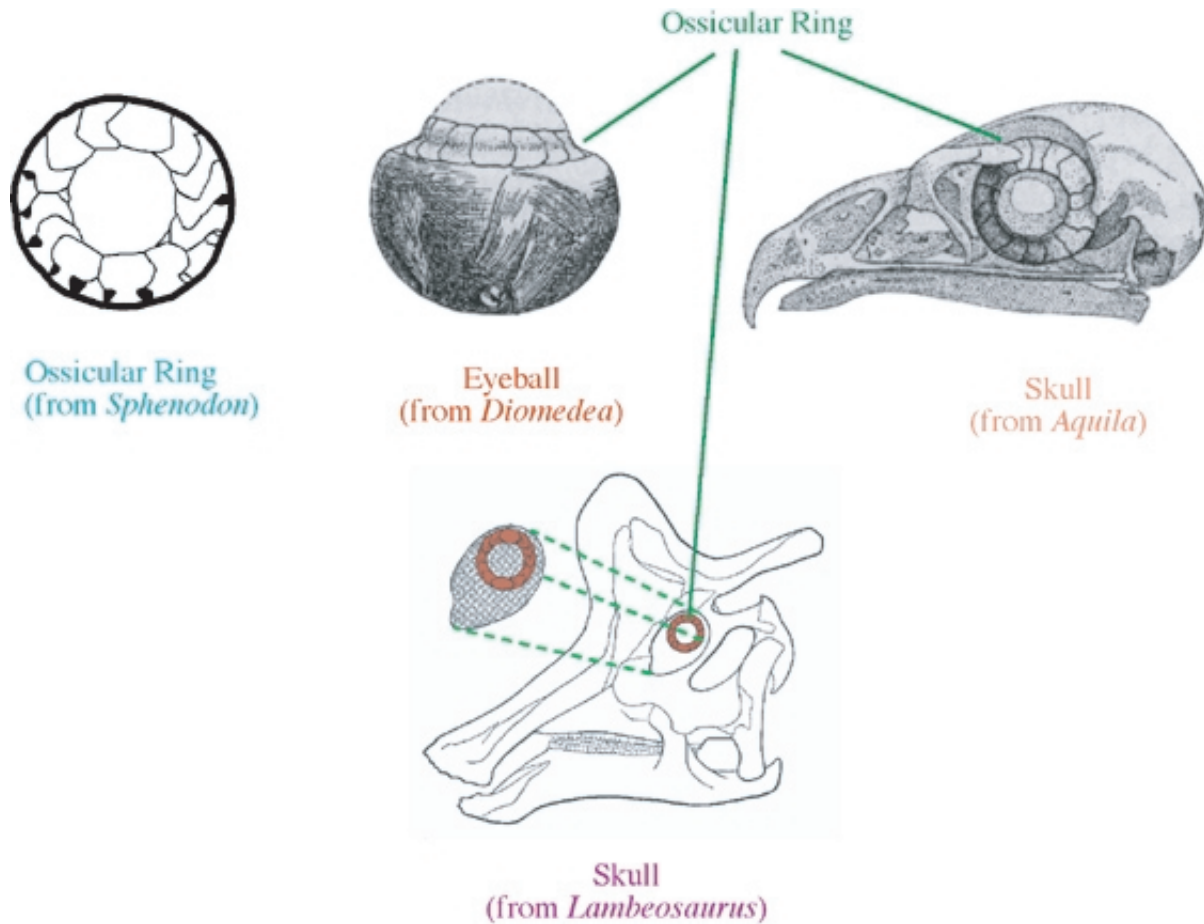


**Figure 13.** Distribution of double cones among vertebrates. Given their widespread abundance among vertebrates, it appears double cones initially arose around the same time as calcified skeletons. Oil droplets probably arose shortly thereafter. Although double cones have been reduced in number and complexity in other lineages, eutherian mammals appear to be unique in having completely discarded the structures once they were acquired. The dashed line indicates the uncertainty in the phylogenetic positioning of “Chelonia”. This diagram is intended to hint at a broad pattern of photoreceptor evolution; beware that it masks much diversity within the lineages depicted.





**Figure 14.** The structure and placement of ossicular rings. Rings of bony plates surrounding the iris of the eye are present in most reptiles. On the left is a drawing of the arrangement of the plates, variously referred to as sclerotic or scleral ossicles, ossicular rings etc. from the eye of a tuatara. The eyeball is that of an albatross depicted from the side in order to show how the ossicles shape the junction between the cornea and the sclera. To the right and bottom are depictions of the skull of an eagle and a *Lambeosaurus*, respectively, showing the positioning of the ossicles within the orbit. The primary purpose of the ossicles appears to be to reinforce the corneal scleral junction. In birds, the ossicles allow the animals to adjust the shape of the cornea during accommodation. (Top 3 drawings adapted from Walls 1942; lambeosaur adapted from Colbert 1961).



**Figure 15A.** Some representative fossils with scleral ossicles. **A-D** demonstrate that scleral ossicles were widespread throughout the Dinosauria; **E-G** demonstrate their existence in pliosaurs, mosasaurs and ichthyosaurs as well. Although none are shown here, scleral ossicles also existed in the eyes of pterosaurs; **H** shows the scleral “ossicles” of a Late Devonian placoderm. Whether or not the ossicles of fish were and are homologous or even functionally similar to those of reptiles remains to be resolved. *Dunkleosteus*, like actinopterygian fish, contained only four ossicles per eye. Reptiles generally have 14. (Photographs courtesy of K. Carpenter except for *Tylosaurus* which was supplied by M. Everhart, see Figure 15B.).



**Figure 15B.** Some representative fossils with scleral ossicles. **A-D** demonstrate that scleral ossicles were widespread throughout the Dinosauria; **E-G** demonstrate their existence in pliosaurs, mosasaurs and ichthyosaurs as well. Although none are shown here, scleral ossicles also existed in the eyes of pterosaurs; **H** shows the scleral “ossicles” of a Late Devonian placoderm. Whether or not the ossicles of fish were and are homologous or even functionally similar to those of reptiles remains to be resolved. *Dunkleosteus*, like actinopterygian fish, contained only four ossicles per eye. Reptiles generally have 14. (Photographs courtesy of K. Carpenter except for *Tylosaurus* which was supplied by M. Everhart, see Figure 15C.)



**Figure 15C.** Some representative fossils with scleral ossicles. **A-D** demonstrate that scleral ossicles were widespread throughout the Dinosauria; **E-G** demonstrate their existence in pliosaurs, mosasaurs and ichthyosaurs as well. Although none are shown here, scleral ossicles also existed in the eyes of pterosaurs; **H** shows the scleral “ossicles” of a Late Devonian placoderm. Whether or not the ossicles of fish were and are homologous or even functionally similar to those of reptiles remains to be resolved. *Dunkleosteus*, like actinopterygian fish, contained only four ossicles per eye. Reptiles generally have 14. (Photographs courtesy of K. Carpenter except for *Tylosaurus* which was supplied by M. Everhart, see Figure 15D.)



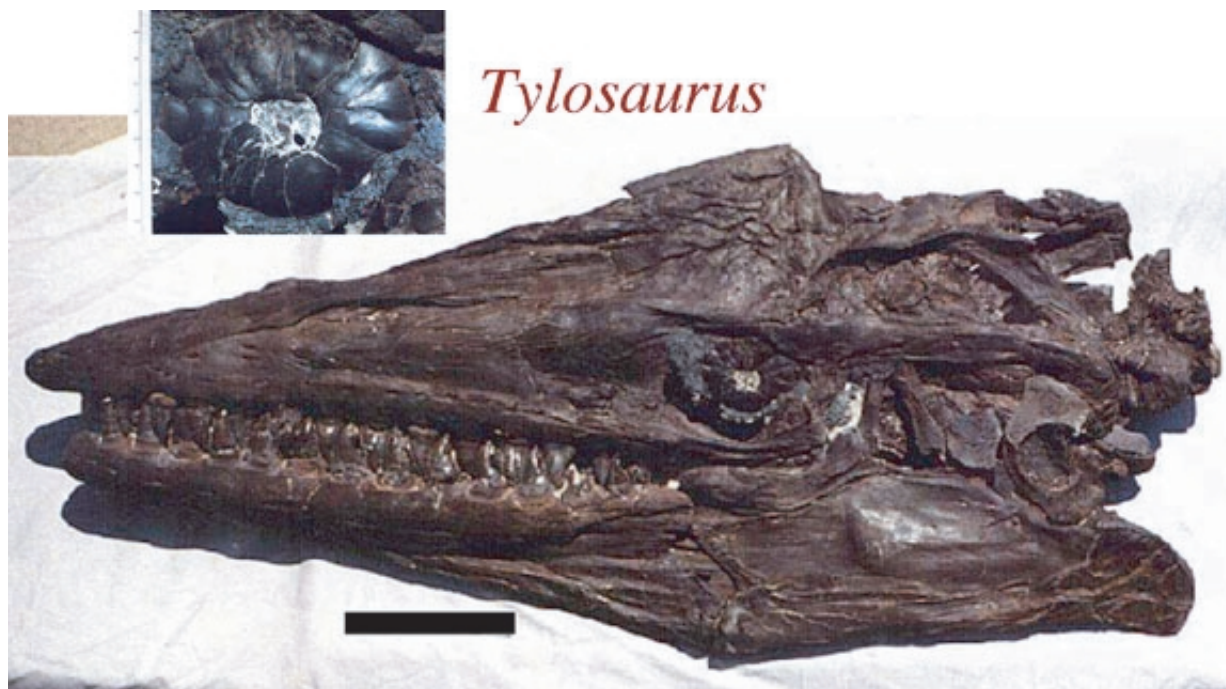
**Figure 15D.** Some representative fossils with scleral ossicles. **A-D** demonstrate that scleral ossicles were widespread throughout the Dinosauria; **E-G** demonstrate their existence in pliosaurs, mosasaurs and ichthyosaurs as well. Although none are shown here, scleral ossicles also existed in the eyes of pterosaurs; **H** shows the scleral “ossicles” of a Late Devonian placoderm. Whether or not the ossicles of fish were and are homologous or even functionally similar to those of reptiles remains to be resolved. *Dunkleosteus*, like actinopterygian fish, contained only four ossicles per eye. Reptiles generally have 14. (Photographs courtesy of K. Carpenter except for *Tylosaurus* which was supplied by M. Everhart, see Figure 15E.)



**Figure 15E.** Some representative fossils with scleral ossicles. **A-D** demonstrate that scleral ossicles were widespread throughout the Dinosauria; **E-G** demonstrate their existence in pliosaurs, mosasaurs and ichthyosaurs as well. Although none are shown here, scleral ossicles also existed in the eyes of pterosaurs; **H** shows the scleral “ossicles” of a Late Devonian placoderm. Whether or not the ossicles of fish were and are homologous or even functionally similar to those of reptiles remains to be resolved. *Dunkleosteus*, like actinopterygian fish, contained only four ossicles per eye. Reptiles generally have 14. (Photographs courtesy of K. Carpenter except for *Tylosaurus* which was supplied by M. Everhart, see Figure 15F.)



**Figure 15F.** Some representative fossils with scleral ossicles. **A-D** demonstrate that scleral ossicles were widespread throughout the Dinosauria; **E-G** demonstrate their existence in pliosaurs, mosasaurs and ichthyosaurs as well. Although none are shown here, scleral ossicles also existed in the eyes of pterosaurs; **H** shows the scleral “ossicles” of a Late Devonian placoderm. Whether or not the ossicles of fish were and are homologous or even functionally similar to those of reptiles remains to be resolved. *Dunkleosteus*, like actinopterygian fish, contained only four ossicles per eye. Reptiles generally have 14. (Photographs courtesy of K. Carpenter except for *Tylosaurus* which was supplied by M. Everhart, see Figure 15G.)



**Figure 15G.** Some representative fossils with scleral ossicles. **A-D** demonstrate that scleral ossicles were widespread throughout the Dinosauria; **E-G** demonstrate their existence in pliosaurs, mosasaurs and ichthyosaurs as well. Although none are shown here, scleral ossicles also existed in the eyes of pterosaurs; **H** shows the scleral “ossicles” of a Late Devonian placoderm. Whether or not the ossicles of fish were and are homologous or even functionally similar to those of reptiles remains to be resolved. *Dunkleosteus*, like actinopterygian fish, contained only four ossicles per eye. Reptiles generally have 14. (Photographs courtesy of K. Carpenter except for *Tylosaurus* which was supplied by M. Everhart, see Figure 15H.)

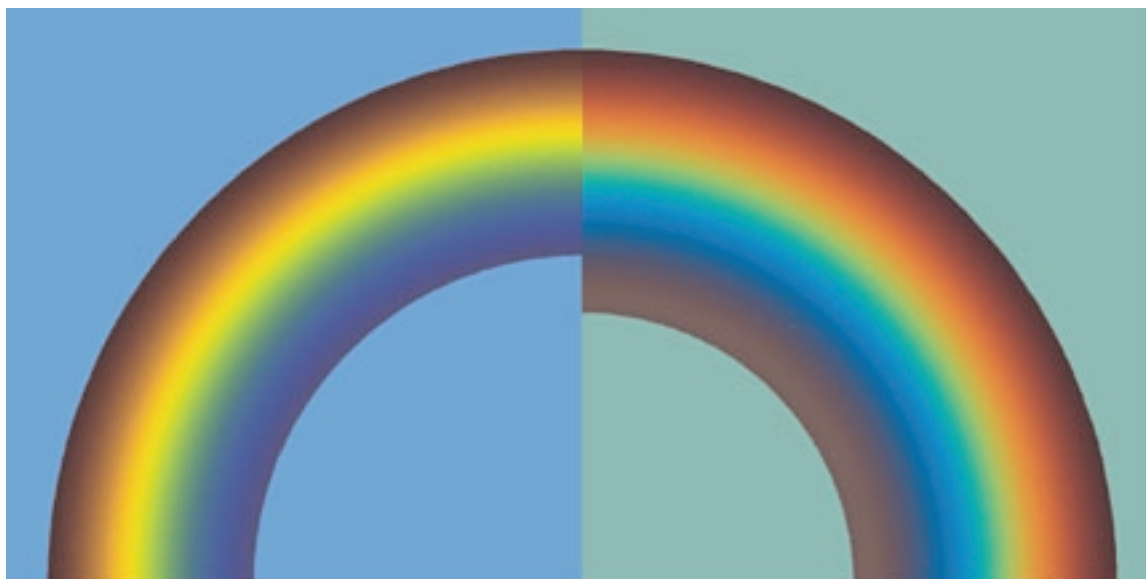




**Figure 15H.** Some representative fossils with scleral ossicles. **A-D** demonstrate that scleral ossicles were widespread throughout the Dinosauria; **E-G** demonstrate their existence in pliosaurs, mosasaurs and ichthyosaurs as well. Although none are shown here, scleral ossicles also existed in the eyes of pterosaurs; **H** shows the scleral “ossicles” of a Late Devonian placoderm. Whether or not the ossicles of fish were and are homologous or even functionally similar to those of reptiles remains to be resolved. *Dunkleosteus*, like actinopterygian fish, contained only four ossicles per eye. Reptiles generally have 14. (Photographs courtesy of K. Carpenter except for *Tylosaurus* which was supplied by M. Everhart.



**Figure 16.** Two views of a rainbow. It is not possible to see the world as another animal sees it since any attempted depiction would necessarily be viewed through the sensory system of the human perceiver. However, it is possible to depict some of the features which might appear different to non-human animals than they do to us. The left half of this figure is intended to look somewhat like a “normal” rainbow. To the right is the other half of the rainbow modified such as to capture some of the features that a dinosaur might have seen. In particular, note that dinosaurs probably saw shorter wavelengths (the extension beyond the violet), and a larger number of bands of distinct hues. The hues were also probably more vivid as a consequence of the isolation of photoreceptor responses by the screening oil droplets (see Figure 9C). Finally, the color of the sky would not match the short-wave end of the spectrum as well as it would wavelengths closer to the middle of the rainbow seen by a dinosaur.



**Figure 17.** Definitions for ortholog, paralog and gene duplication. The solid object in this figure represents the phylogenetic relationship between three monophyletic taxa, A, B, and C; the blue and green lines within the object represent the phylogenetic relationships among the genes in a subset of the genomes of individuals from the three taxa. The most recent common ancestor of the three taxa had one copy of a gene that was duplicated after taxon C diverged from the line leading to taxa A and B, but before taxa A and B diverged from each other. This is the only true duplication here in the sense that the word “duplication” is used in the context of molecular evolution -- in that sense, a gene is duplicated only when additional copies accrue within a single lineage. There are three *apparent* duplications, the two indicated for the blue gene lineages and an additional one for the green gene lineage, which are due to the two speciation events in the diagram. Note that by virtue of their common ancestry at the root of this branch, all of the genes are homologous to each other. However, after the gene duplication event, genes in the green lineages may evolve independently of genes in the blue lineage both within a taxon and between taxa. Consequently the phylogeny of the genes is different from the phylogeny of the taxa. The terms paralogous and orthologous were coined (Fitch and Margoliash 1970) to make distinctions between different types of phylogenetic relationship between genes. A gene in one taxon is orthologous to a gene in another taxon if the only duplications (in the colloquial sense) leading to differentiation between them were consequences of speciation events. Two genes are paralogous to each other if they differ (at least in part) due to a duplication event (in the more restricted sense). Note that this means that the gene in the blue lineage of taxon A is paralogous to the gene in the green lineage of taxon A (as per the original definition of the word -- Fitch and Margoliash 1970) as well as to the gene in the green lineage of taxon B (only the latter relationship is indicated in the figure). The green gene of taxon A is orthologous to the green gene of taxon B because any differences between them arose merely due to their independent evolution within their respective lineages. Similarly, the blue gene of taxon A is an ortholog of the blue gene of taxon B. According to the original definitions, the blue gene of taxon C is neither an ortholog nor a paralog of any of the genes in taxa A and B. However, retained similarity of function between the blue gene of taxon C and the blue genes of taxa A and B could be construed to make all of them orthologs of each other, and that is how the term is used in this manuscript. For a more thorough treatment of various related terms and the theoretical issues in which they are involved, see Patterson 1988.

