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Patterns in Palaeontology: A story of vision

by [James Fleming](#)^{*1}

Introduction:

Photoreception, the ability to perceive light, is a sense shared by many living organisms on Earth. However, only some can take the step beyond merely detecting light levels, and generate an image.

Humans are among the animals that have image-forming vision, and are able to see in colour in the day (polychromatic diurnal vision) and in black and white at night (monochromatic nocturnal vision) — the shades of colour that we pick up on an evening out trigger our diurnal receptors at very low levels. However, this is not the only way in which animals can see the world around them. Some species, such as whales and dolphins, can see only monochromatically no matter the time of day, while others see in colour no matter how dark it gets! The elephant hawk-moth, a nocturnal insect, actually sees in the complete reverse — in black and white during the day and colour at night. This helps it to locate the right flowers to feed on at night.

Opsins and vision:

A specific group of proteins in the body, known as opsins, are vital for perceiving light. Opsins come in a variety of types, and they aren't just expressed in the eyes, but also in the brain and skin, where they help to govern a lot of different light-dependent activities, from sight through to the regulation of [circadian rhythms](#), or the body clock. Opsins bind to a specific form of vitamin A known as retinal — carrots are also high in vitamin A, which could contribute to their supposed power to improve eyesight. When the retinal is hit by a particle of light, called a [photon](#), it changes shape, which in turn changes the shape of the opsin around it. This starts a chain reaction known as a signalling cascade that passes information about the opsin deformation to the brain, which results in the perception of light.

[Vertebrates](#) use a system of visual opsins in which, after this initial deformation, the opsin is bleached by the light and needs to be recharged by another protein. Invertebrates, by contrast, have bistable visual opsins — this means that the deformation caused by a photon hitting the retinal is reversed when another photon hits the deformed structure, effectively recharging the opsin.

Different visual opsins respond to different, specific light wavelengths. Some wavelengths of light will stimulate one opsin more than others, whereas other wavelengths will stimulate multiple types of opsin in different ratios. The ability to compare the responses of different types of opsin is what causes colour perception. Humans, for example, have three colour opsins in their eyes for diurnal vision. These mean that a human can see three primary colours — red, green and blue. (That is why computer monitors use an RGB spectrum to make colours.) For example, when a photon of light with a



Figure 1 — The visible spectrum as interpreted by the human eye (bottom) and the dog eye (top). Credit: J. Fleming.

wavelength around 580 nanometres contacts the opsins in the human eye, it triggers a large response from the red opsin, and a lesser response from the green opsin, resulting in the perception of the colour yellow. A dog can perceive only two primary colours, yellow and blue (Fig. 1) — they have an opsin that is intermediate between red and green that responds best to yellow — but it may be able to distinguish between red and green by shade (Figs 2 and 3). By contrast, some species of mantis shrimp have 16 classes of visual opsin, extending into the ultraviolet (UV) and infrared parts of the spectrum and also giving greater definition to what humans consider the ‘visible light’ range. That means that mantis shrimp in effect see new primary colours where we might see shades.

Having multiple different visual opsins doesn’t always mean that you see in colour, though. Some animals instead pair up different visual opsins into the same space in an eye, and use these to tune the wavelengths of light that they can and can’t respond to. It can be especially useful if you really need to pick up a specific band of light wavelengths and don’t want to be tricked by something else. For example, the males of the small white butterfly (*Pieris rapae*) express a blue opsin in some violet-type receptor cells; this helps them to distinguish males from potential mates.

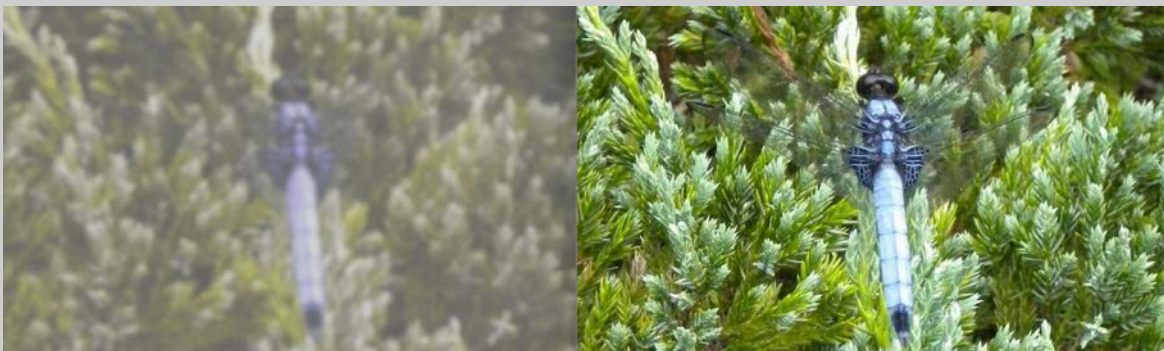


Figure 2 — The dragonfly *Orthetrum albistylum* as interpreted by the human eye (right) and the dog eye (left). Credit: J. Fleming.

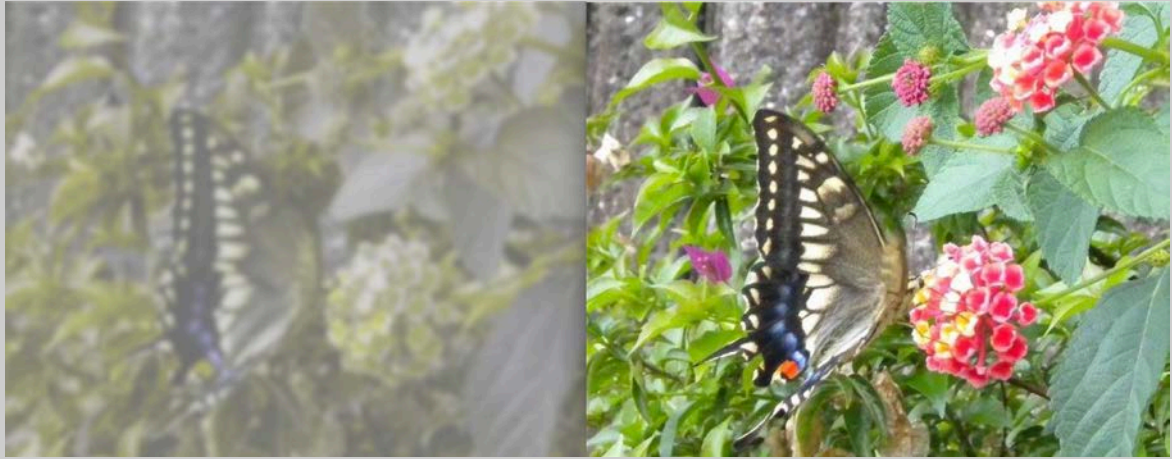


Figure 3 — The butterfly *Pieris machaon* as interpreted by the human eye (right) and the dog eye (left). Credit: J. Fleming.

Fossil evidence of visual systems:

Despite the soft and squishy nature of eyes, we have a surprisingly good understanding of their history in deep time, from the fossil record. To a large extent, this is provided by vertebrate skulls — although blind creatures, like cavefish, may still have eye sockets, for example, they don't have the scars that show that they had the right arrangement of muscles to attach an eye, so we can study fossil skulls to establish whether an eye was present in life even if it was not preserved in the fossilized remains. Many vertebrate modifications to the complex camera eye (Called such because the lens in the vertebrate eye focuses light on to the back of the light-sensitive retina, like a camera on to film) involve tuning to specific colours — for example, birds express coloured oil droplets in some of their opsins to shift the responses of their eyes towards certain colours. These alterations do not tend to appear in even the best-preserved fossils. However, we can gain an understanding of the acuity and sensitivity of the vertebrate eye, provided that we have 3D preserved fossils. Two measurements can allow us to compare the vision of extinct vertebrates with that of modern ones. These are: the size of the [sclerotic ring](#), a ring of bone in the eyes of certain animal groups; and the [depth of the orbit](#), or eye socket. Sensitive eyes — ones that work under small amounts of light energy — are more likely to be found in nocturnal animals. These eyes have a large [cornea](#) diameter relative to the eye length. Diurnal animals more often have acute eyes, good at discerning detail. These have a long eye length relative to the cornea diameter.

Of great importance in our understanding of the history of vision are lagerstätten — sites of exceptional fossils scattered across the world that can even preserve soft tissues, such as eyes, allowing for a more thorough understanding of the anatomy and evolution of this structure in different groups. The earliest known eyes come from the [Cambrian](#) Chengjiang biota in China, which is around 515 million years old. Fossils from this period show staggering variation in eye shape and complexity, suggesting that the first eyes may have evolved considerably earlier. Some researchers have suggested that the evolution of the eye may have caused an evolutionary arms race: when predators can use light to perceive prey, prey must perceive light or deceive sight to avoid predators, meaning that predators must become better at discerning prey, and so on. This is one hypothesized cause of the Cambrian explosion — the apparently sudden appearance of diverse animal forms during the Cambrian period, starting around 542 million years ago. It is known as the light-switch theory.

The iconic Cambrian predatory [arthropod](#) *Anomalocaris* provides an early insight into the complexity of arthropod eyes (Fig. 4). Some of the oldest fossilized remains of this animal preserve a pair of large, stalked eyes, which are covered in thousands of tiny lenses — compound eyes. Each eye is thought to have been made up of around 16,000 lenses, giving it a resolution of around 3,000 pixels. The human eye has a resolution of about 576 million pixels, which is much bigger; however, the compound eye of *Anomalocaris* and other arthropods is more concerned with predicting speed and motion than with building a full and detailed image of its surroundings, so for it to have a resolution as high as it does is truly exceptional. The complexity and size of the eyes of *Anomalocaris* strongly support the idea that it was one of Earth's first visual predators. It could probably track down and hunt prey by sight before going in for the kill with its powerful frontal appendages.

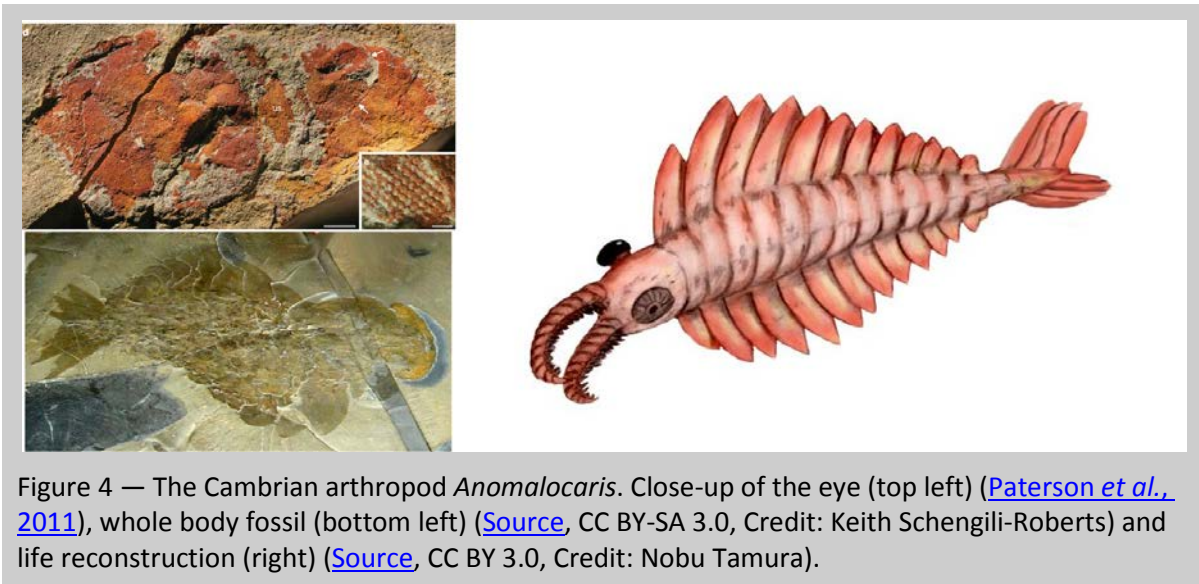


Figure 4 — The Cambrian arthropod *Anomalocaris*. Close-up of the eye (top left) ([Paterson *et al.*, 2011](#)), whole body fossil (bottom left) ([Source](#), CC BY-SA 3.0, Credit: Keith Schengili-Roberts) and life reconstruction (right) ([Source](#), CC BY 3.0, Credit: Nobu Tamura).

Molecular palaeobiology of vision:

One of the most interesting frontiers in palaeontological research involves using what we know about the [molecular biology](#) of modern organisms to find out about past ones. For example, comparing the [DNA](#), [RNA](#) and protein sequences of living species informs our knowledge of [palaeogenomics](#), which can provide insights into the evolutionary history of systems such as eyes and vision.

One of the biggest ongoing debates regarding arthropod eyes concerns the group that includes centipedes and millipedes, called the Myriapoda. Millipedes don't have a compound eye; instead, their eyes have a series of simple, flat lenses. Centipedes, by contrast, have a variation on the compound eye. It has been suggested that the eye of this group's shared common ancestor was relatively simple, more like that of living millipedes, and that the compound eye evolved again in centipedes.

Alternatively, some have proposed that the common ancestor had a compound eye, which millipedes independently lost and centipedes modified. Studies of genomic data might help to address this question, but the debate will probably remain unresolved until the fossil record surrounding these charismatic creatures is better understood.

Just as scientists construct trees that depict the relationships between different species of animals, it is also possible to make trees of the relationships between proteins — indeed, over long periods of time

(millions of years), proteins are much better at establishing these relationships than DNA, because they are less subject to change. A vital protein, tinkered with in the wrong way, is almost sure to result in an animal becoming less well adapted to its environment, making it less likely that the protein will be passed on to the next generation. Proteins also have a layer of redundancy — multiple different codons (potential variations of three nucleotide bases) code for the same amino acid, and opsins, for example, are 300 amino acids long. In addition, the fact that there is a 20-letter alphabet of amino acids, as opposed to the 4-letter nucleotide alphabet of DNA and RNA, means that there is less chance for random change to create a false signal — in a nucleotide sequence where every nucleotide has an equal chance of occurring at any site, there is a 25% chance it will be a particular one, as opposed to the 5% chance of a particular amino acid occurring in the protein sequence that those nucleotides code for. New opsins are mainly created by [gene-duplication](#) events, and when we try to track the evolution of colour vision, we are on the hunt for when and where these duplications occurred.

When constructing protein trees, we are interested in whether particular proteins are more closely related to others of the same type from different animals, or others of different types from the same animal. In other words, we want to know whether opsins are more closely related by colour or by species. If they are related by species — for example, if a moth's red and blue opsins are more closely related to each other than the moth's red opsin is to a grasshopper's red opsin — then it suggests that colour vision evolved in that species independently of other species. If the opsins are more closely related by colour — a moth's red more closely related to the grasshopper's red than it is to a moth's blue — then it suggests that the gene-duplication event occurred before these species diverged.

In the case of arthropod visual opsins, the latter is true. It seems that the gene-duplication events that fuelled colour vision in the arthropods occurred before the origin of even the earliest living group: the [Chelicerata](#), which contains the arachnids, horseshoe crabs, ticks and extinct eurypterids. Indeed, extinct arthropods such as the trilobites are likely to have had at least four visual-type opsins: those for seeing UV light, blue light and green/red light, plus one more called Rh7. No one really knows what Rh7 is used for, and it is hotly debated.

We can also tell a lot about the ecology of early arthropods, and the reasons that they developed colour vision, from trees depicting the evolutionary history of visual opsins (Fig. 5). The earliest arthropod visual opsins responded to UV light (shown in violet in Fig. 5), and the next colour receptors that emerged were sensitive to blue wavelengths. The ability to discern UV light is useful in water for working out how deep you are — UV light is stronger near the surface. This suggests that the first arthropods that could see were probably mainly concerned with ascertaining their height in the water column, rather than perceiving other objects or individuals. Blue light is also very useful in water, because it allows the perceiver to pick objects out from the background. The wavelengths of light that correspond to the colour blue penetrate the deepest into water, persisting even when many other wavelengths have been absorbed (Fig. 6). Some arthropods have extra duplications of the blue opsins, tuned to different wavelengths of blue. This could be an adaptation to distinguish between different depths and/or to help them to colonize deeper waters. That the ability to see red and green arose next is not surprising, either: it would have been useful when the arthropods started to colonize shallower water, because dirty, sediment-filled water at the coasts tends to be redder than deep oceanic water, so a perceiver must be able to pick out that colour to make things out against the background.

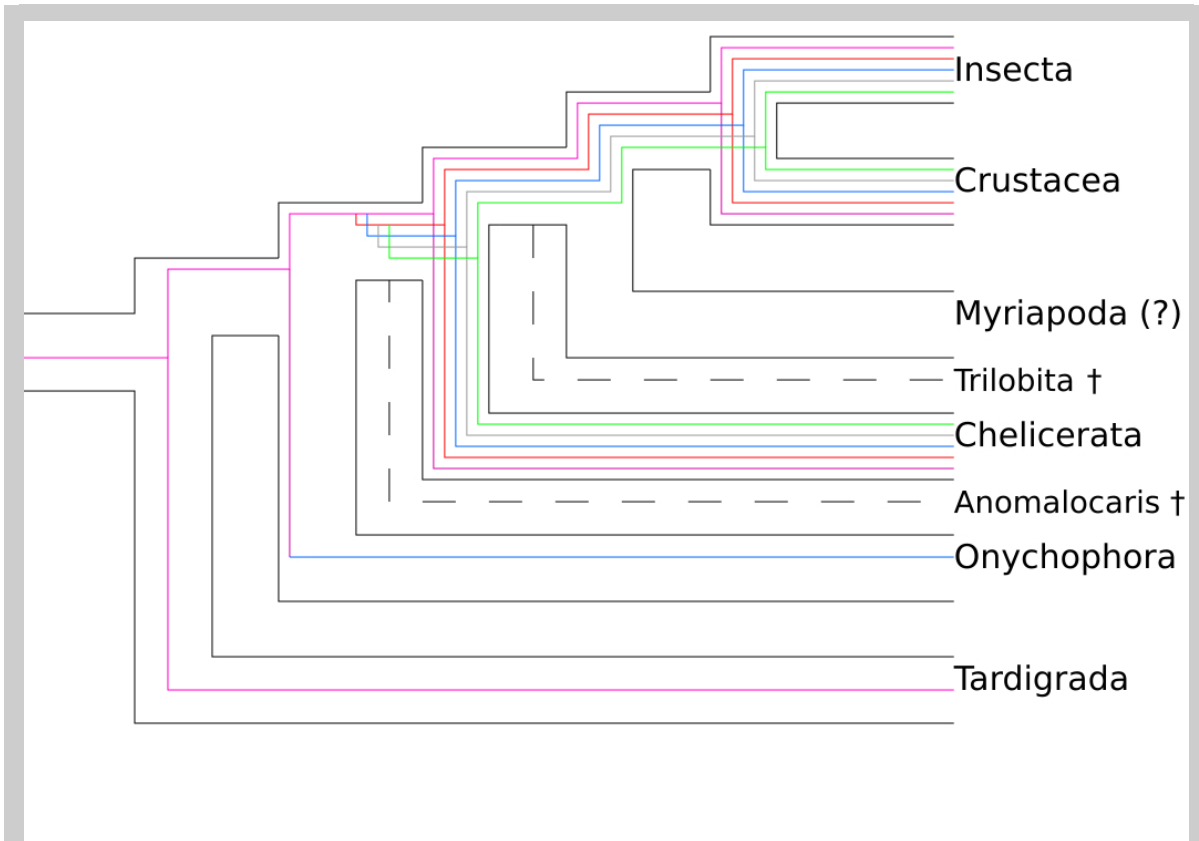
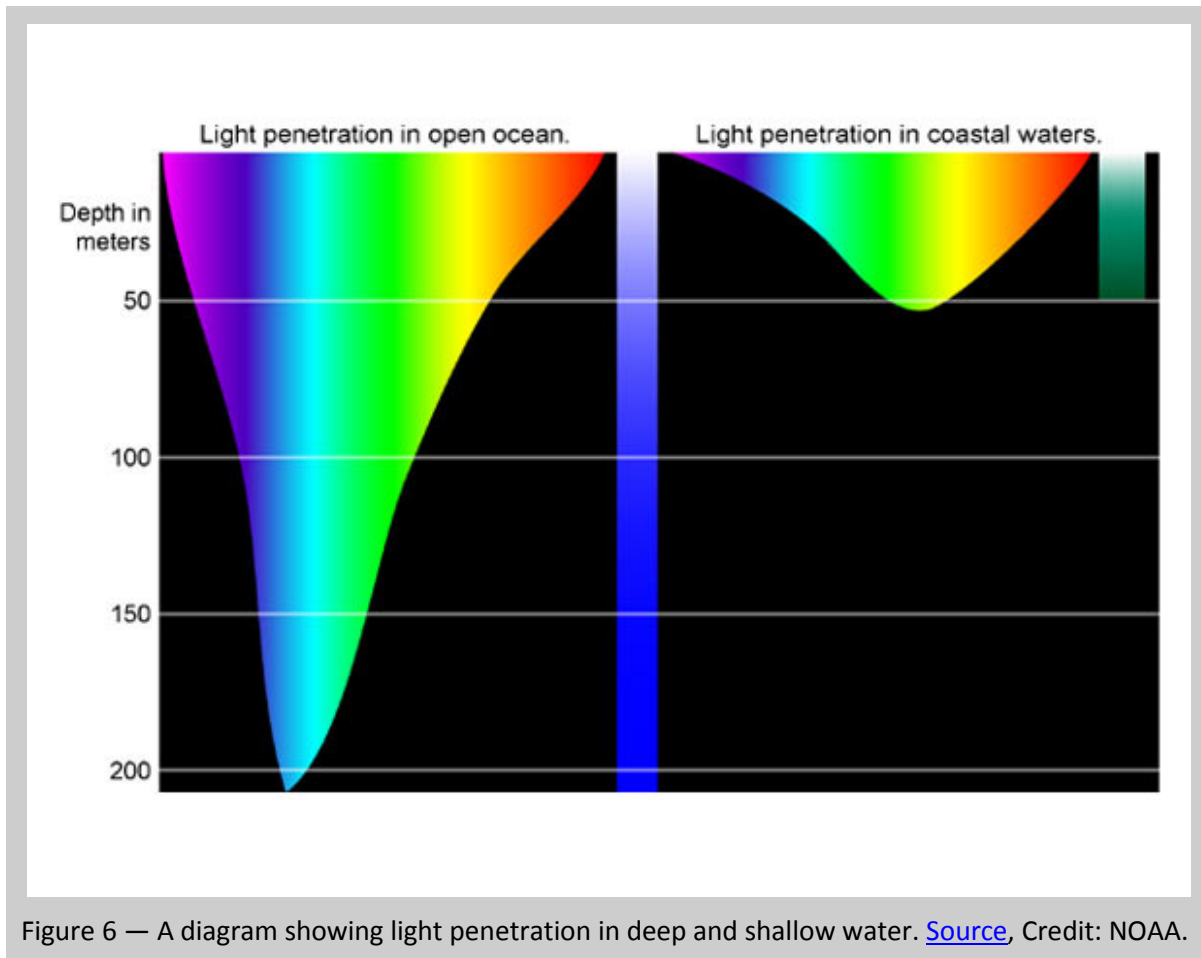


Figure 5 — An evolutionary tree showing the relationships of arthropods and onychophorans. Extinct taxa are marked with dotted lines. Within the species tree are gene trees; each coloured branch represents the capability to detect a particular wavelength of light. UV receptors are shown in violet for readability. The grey line represents an opsin called Rh7 — there is debate as to its function. The visual opsins of the Myriapoda have yet to be properly characterized, and so a ‘?’ is placed on the figure. Credit: J. Fleming.

Summary:

Unfortunately, such protein trees don't give us the whole picture. For instance, the fossil record shows that many trilobites independently lost their eyes, so it seems plausible that opsins might have been independently recruited or lost in different trilobite lineages, as has occurred in mantis shrimp and dragonflies. We also have to use a technique called [phylogenetic bracketing](#) — which involves comparing animals with others closely related to them — to make inferences about vision. *Anomalocaris* certainly had immense eyes, which seem to suggest that it hunted by sight, but we cannot tell what colours it saw in; on the evolutionary tree, it first arose before the origin of the modern groups of arthropods, but after the origin of extant creatures called onychophorans, or velvet worms (Fig. 5), which have monochromatic vision (and are probably highly modified from the ancestor that they shared with all arthropods). Such research is also relatively recent, and barely any work has been done on colour vision in centipedes and millipedes, even though we know that they have eyes and some species could potentially see in colour.

In the future, as we gather more data on living organisms, we will have ever-clearer understanding of the relationships between the proteins that underlie animal visual systems and, consequently, of the visual systems themselves. Some groups have considered, and even tried, resurrecting ancestral



proteins by using statistical methods to work out the most likely ancestral sequence at a point on a tree, and then reconstructing the protein from amino acids in the lab. However, before this can be done reliably, we must have a much greater understanding of the structure and interactions of the molecules, as well as a greater ability to predict likely sequences. A combination of such biochemical techniques with an understanding of taxonomy and an eye for fossil visual systems will light the way forward.

Knowledge about the evolution of colour vision — that it has occurred only twice, in the arthropods and the vertebrates, and that it existed in the very early arthropods and so predates the Cambrian explosion — opens up whole new worlds of ecology. Understanding the past requires learning how ancient creatures made sense of their world, and understanding the history of these proteins, and studying the fossils left behind, is one of the surest ways to do this.

Suggestions for further reading:

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