The Evolution of Vision
Transcript

Date: Wednesday, 21 November 2012 - 6:00PM
Location: Museum of London
I am going to start the talk with an extraordinary image of an eye. This is what we call a compound eye. We have multiple different tiny eyes together, rather that you might see in bees or arthropods today, and you can see that this is indeed an arthropod, segmented – it is a trilobite, and this trilobite lived in the sand, and it just poked its eyes out above the sand to see what was coming along. Throughout this lecture, I am going to try and show you the remarkable diversity of eyes that have come about, and how that might have happened.

So, there are many types of eyes, and eyes are present in 95% of all animal species, which implies that eyes and vision are really, really important and must have a survival advantage in various environments. The question is: did eyes arise once and therefore they are all descended from a single eye, or did eyes evolve many times, or were they made many times?

For example, octopuses and humans, superficially, have very similar eye designs. This is a squid eye; and this is a human eye. They look very, very similar, and they are both camera eyes. In fact, jellyfish also can develop a camera eye, and here is the iris, here is the lens…and also fish. Now, these evolve in a completely different way, from completely different ancestors, using completely different tissues to come to the same solution, which is a camera eye that is useful for those animals to survive in their environments.

Rather similar, that if you want to be an animal that lives in water, you want to be shaped like a torpedo. So, you could be related to a whale, like a dolphin, which is a mammal, you could be a reptile, and here is an ophthalmosaurus, one of the ichthyosaur groups, or you could be a fish, or in fact even indeed a whale, another mammal, and all of these shapes are the same, but, quite clearly, they have come from very, very different ancestry, and this is called convergence. The question that is being asked now is: were these shapes, or indeed the eye, which is a complex organ, were they miraculously designed or is there any evidence that gradual evolution could have led to these amazing, complex organs? The evo-devo versus God argument...

On what basis should I be talking about this? I am not an evolutionary biologist and I am not a molecular biologist; however, I have done quite a lot of work in cell signalling in the past, and I spend my life looking at eyes, and particularly damaged eyes, and trying to work out ways that we can repair them.

This is a multidisciplinary area, and someone who is an expert in evolution may not necessarily be the best person perhaps to talk on the shape of eyes or aspheric aberrations or how the corneas may have developed in different species over the years.

I am also not an expert in God, but I would like to say that those who are should be rather afraid because I bet she is rather angry about what happened last night.

William Paley was the Senior Wrangler at Christ College Cambridge and lectures on Moral Philosophy. Interestingly, he was a supporter of the American colonialists because he was anti-slavery, and Samuel Johnston was against the American colonialists because he was also anti-slavery, which meant that there was obviously a schism occurring in the American colonies at that time, prior to their independence from the British Empire. He wrote a book in 1785, “The Principles of Moral and Political Philosophy”, which was studied by Darwin a couple of generations later when he was a student. Natural Theology tries to explain the evidence using daily things that are around us to explain God, and one of the arguments used – it is actually a very old argument, it was used previously in ancient history as well – says that, if we are walking along the heath and we find a watch, then it must be inevitable that watch must have had a maker, unlike, for example, a stone, which we might not imagine might have had a maker, and therefore there must have existed, at some time and in some place or other, an artificer or artificers who formed it for the purpose with which we find it actually to do.

There were many arguments suggesting that there may be other explanations for finding complex things on the heath, and really going back to Erasmus Darwin, who had formulated already that there may be a process of evolution. James Hutton also – we will talk about him a little bit later – and Lamarck had his own theory about how complex characteristics might arise through generations, and was subsequently disproven by the genetic variation, but actually there are some Lamarckian traits that still need to be explained. William Herbert, John Southwell and William Chilton, all of whom put in theories of evolution, not particularly well-developed and they did vary in their sophistication. Perhaps the most important one was Alfred Russel Wallace on the law which regulated the introduction of new species, and this is the paper that was sent to Darwin that stimulated Darwin to publish his previous unpublished papers, which were presented at the Linnaean Society in that very famous talk, interestingly without the permission of Wallace and in the absence of Darwin.

There are many sources, for those of you who want to read further on this, there is “The Evolution of Phototransduction and Eyes – Philosophical Transactions”. There is a dozen papers in here which are excellent,
beautifully written, and are accessible to the non-specialist. Ned Freeman, Professor of Evolutionary Biology at Harvard, excellent on plant evolution, but generally is a very good writer and very accessible. Wikipedia has been used as a source for many of the photographs that I did not have time to get permission to go to the National History Museum to take for myself. A wonderful book, “Evolution’s Witness” by Ivan Schwab, who also wrote a series of articles over the last twenty years in the British Journal of Ophthalmology; “Animal Eyes” by Michael Land & Dan-Eric Nilsson is now in its second edition – a little bit more turgid, but for those of you who have a particular interest, I cannot recommend this book too highly; finally, Marcel, who kindly took me on long rambles and explained to me the nature of geology, and my father, Roland Ayliffe, who first introduced me to evolution and to the multiple types of animals and plants that are around us and how they may have developed.

Now, Thomas Malthus started this off with his essay on “Principles of Population”, which suggested that, if there were no break on populations, there would be a lack of a food supply and various problems associated with that, including mass starvation. So, three doctors took this on board.

One was William Wells, who was a colonial-born military surgeon. He had to put his affairs in order in North Carolina fairly smartly and leave, before he was tarred and feathered, and came back to Britain, where we then went to work as an officer in the army in Holland, quite a colourful chap, ended up threatening his boss with a duel, it did not actually happen, but he wrote this wonderful essay, which was published after his death, entitled “The Differences in Colour and Form between the White and Negro Races”, and what he proposed was that dark people can live in certain environments because they carry an immunity from tropical diseases, which, as Frank, the former Professor, will tell you, is actually quite true and does form a selective pressure. However, this is really only applying to humans and is not general to other species, but certainly it was the first really sound inking of natural selection, which Darwin himself recognises later.

James Pritchard also spoke about the dividing of human species and how that might have occurred, and Sir William Lawrence, a surgeon and ophthalmologist and a medical reformer – he helped publish “The Lancet” at the time, when it was a rather dangerous organ for the government. He was forced to withdraw his book after fierce criticism by the Lord Chancellor, who ruled it “blasphemous”, and, interestingly, the Court of Chancery in those days not only sat on matters of chancery, it also sat on matters of blasphemy, and that was not reformed until the nineteenth century.

A very important person you will come across is Patrick Matthews, a Scottish landowner and fruit-grower, who complained to Darwin that Darwin had failed to recognise his great work on natural selection. He was talking about the evolution of timbers and how they might be grown to improve naval architecture, at a very important time in Britain. Darwin actually responded in a letter to the “Gardeners’ Chronicle” saying: “I have been much interested by Mr Patrick Matthews’ communication in the number of your paper April 17th. I fully acknowledge that he has anticipated by many years the explanation that I have offered for the origin of species, under the name of natural selection. I think that no one will feel surprised that neither I nor apparently any other naturalist had heard of Mr Matthews’ views, considering how briefly they are given and they appear in an appendix to a work on naval timber and arboriculture. I could do more than offer my sincere apologies to Mr Matthews for my entire ignorance of his publication.”

Darwin himself had a very coherent theory of natural selection, although, as we have seen, many of the people in this period were coming to this idea, that this might be a better explanation of why there are so many different animals and plants out there, rather than actually having separate species individually plonked on Earth by a watchmaker.

After many travels, and many years of work, he published in his notebooks, but did not put them into the general field until he was forced to do so by a letter from Alfred Russel Wallace, who, influenced by Darwin, went on a trip to the Latin American countries, but unfortunately, his collection was entirely lost on the way home by a ship fire, and they were on an open boat and lucky to be rescued themselves on a passing boat to Liverpool. Undisturbed by this, he sets off to Malay, collecting 125,660 specimens, including no more than a thousand of the former Professor, will tell you, is actually quite true and does form a selective pressure. However, this is really only applying to humans and is not general to other species, but certainly it was the first really sound inking of natural selection, which Darwin himself recognises later.

On receiving this letter, Darwin was perplexed as to what to do because he realised that this was entirely his life’s work that had been produced completely independently by someone who was currently residing on the other side of the world, so he asked the leading scientists of his day for advice, and that is why they decided that all the papers should be published together, including the 30-year old data from Darwin’s original voyage.

However, Darwin did realise there was a problem with complex organs, particularly the eye: “To suppose that the eye, with all its contrivances for adjusting the focus to different distances, for admitting different amounts of light, for the correction of spherical and chromatic aberration, could have been formed by natural selection, I fully confess absurd in the highest degree.” However, he does go on to say that, “I however can imagine that very, very small steps could lead to this.”

In a letter to Asa Gray, the American naturalist, he says: “The eye, to this day, gives me a cold shudder, but
when I think of the fine-known gradation, my reason tells me I ought to conquer the odd shudder.” He proposed that the eye could well have evolved many times.

Richard Dawkins, in his book “The Blind Watchmaker”, describes an experiment that he did with a computer. It is often mentioned in public houses across the land that, if you gave a monkey a typewriter – by the way, the last one was manufactured yesterday in Wales as it is closed down, so this may be a historical experiment – that if you gave him long enough, he would be able to publish the complete works of Shakespeare. However, let us make it simpler for the monkey, and what we will do is we will just give him one line, this line here, “Methinks it is like a weasel” that is spoken by Hamlet when he is pretending he is going mad, describing some distant clouds as he is being summoned to his mother.

If that monkey had to write that sentence and was given a typewriter, he would have 27 to the 28, or about 10 to the 40, possible combinations, which would take him about a million, million, million, million years to actually do, which is about a million, million, million times longer than the universe has so far existed. So, it seems unlikely that the typewriter would survive that bashing.

However, if you do a computer programme and you put a random error into the copying, and the computer selects the output of the mutant that most likely represents this phrase, you can get there over a lunchtime, and in generation one, you have the random letters and spaces, generation two, we have selected one mutation here, generation ten, there are more mutations that have been selected, and very, very soon we come to “Methinks it is like a weasel”. Using this, Richard Dawkins was saying this is a model to explain how, if we select for changes that are advantageous, we can end up with quite complex things a thousand, thousand, thousand, thousand, million years earlier than we would do if we waited to do it completely by chance, the analogy being that natural selection is the mechanism, along with variation and genetic changes, that allows for evolution. It is not a complete analogy because, remember, evolution does not start off with “Methinks it’s like a weasel”, i.e. a human eye, and then you have some arcane tadpole waddling around with a couple of photoreceptors and says we are going to go from here to this. Evolution does not work like that, and furthermore, it is well-argued that Richard Dawkins’ programme required a watchmaker, who was Richard Dawkins, to actually do it. But, nevertheless, that is not the point that Dawkins was making. Dawkins was making the point that single, random changes, that are selective, are a mechanism for change.

So, how long, using this model, would it take to evolve an eye? Nilsson & Pelger in 1994 did a calculation that if there was a 0.005% change in each generation, which is a minute change, and often changes are much larger than this, and if that change was selective to improving the visual function of an organism, and that organism needed that improvement because the environment it was either living in was changing or it was trying to inhabit another environment, then it would take about 364,000 generations, which sounds like a lot, but it is the blink of an eye, if you will excuse the phrase, in geological terms.

If we have a patch of pink epithelium but one of the pink epithelium cells has some receptors in it for light, this animal can respond to light – it knows where it is dark, it knows where it is light, it can move under boulders and various other behaviours. If, however, it starts to evolve a cup with some pigment around it here that shields it, it now can see direction of light and it knows where the light is coming from, and it gives it a simple way of detecting direction of prey in early habitats, and as we come up and form a pinhole camera, we can get quite sophisticated vision from this, and this is still used by some ancient cephalopods like nautilus. These are still used by many animals, in part or sometimes in their development, and this is still used by some ancient cephalopods like nautilus. These are still used by many animals, in part or sometimes in their development, and this is still used by many animals that only need to respond to light on the outside of their surface, on their epithelium.

Taking this further, we get more sophistication if we fill in this open cup full of seawater with a gel and we now start to get primitive focusing, and if we start to make that gel a little bit more condensed and into an organism that is called a lens, we can get very sophisticated focusing indeed, and then we can start to develop a rigid outer coat, and then we can come out of the water and have a camera-like eye both in the water and out of the water. This takes a very, very short time to do, so it is very plausible that, if this model is correct, that the eye could have evolved from a very simple mutation in a cell on the surface of a simple organism.

If this is going to happen, what we might want to look at is the tasks that might need to be undertaken by these organisms. We could have a type one task, which I mentioned before, which is just really to monitor the ambient light: is it day, is it dark, and animals have different behaviours in the day and the dark. It has no direction at all, it is useful for circadian rhythm, avoidance of light, and shadow direction, very crude predator detection – if you have got a large shark coming over you, you might want to crawl up into your shell or under a rock somewhere.

Also, it is useful for burrowers – it tells them when they are getting to the top of the burrow, and when they need to go down again. No organ is required, so it is very difficult to identify these in fossil animals, and they need microscopes to identify them in living animals today.

Class two are behaviours based on the direction of light, and these allow us to phototaxis – that means we can move towards the light, we can control our posture relative to light, and we can see the approach of predators. This requires a few modifications: we need to stack the photoreceptors so that we have got a lot of surface area; we need to shield the photoreceptors with some pigment, either in a simple arcane photoreceptor itself or by adding in a separate cell; and then, eventually, we need to add a bunch of photoreceptors together in a little
cup. If we make that cup into a pinhole, or duplicate it and make a multiple pinhole camera, which is done in many arthropods, we can get spatial vision with a low resolution. But if we want high resolution, what we are going to do is to add in a focusing lens, which is a class four task.

So I hope by these two last illustrations I have given you that we can have a big overall of what I am going to talk about for the rest of this lecture.

Now, Arendt’s division of labour model of eye evolution is really rather interesting. We start off by having an ancient cell type that has to have at least three functions: one is light detection, via a photoreceptive organelle; light shading; and movement direction, via a locomotive cilia, and these are very important aspects of surviving as single-cell animals. Now, located around the circumference of zooplankton larvae, we actually do have these cells which can mediate phototaxis because what is happening, phototaxis, the light, you are going towards the light, and what you are doing is linking these photoreceptors directly with cilia that can beat, and we are going to see some examples of that later on.

Now, so, the first thing to evolve, we need the biochemical mechanisms. We need these what are called serpentine proteins that go up and down in the cell membrane. They are used for lots of things. Before sight was ever thought about, these were used for detecting nasty substances, they were used for detecting hormones, and they were used for signalling between different animals. They are linked to a signalling molecule, and that signalling molecule leads to flow of material through pores, which can then affect how the cell behaves. These are more complex assemblies, where we have the photoreceptor shielded by a pigment cell, and now we have a neuron that is going to connect this to other bits of the body that are going to react to the light, and we are starting to develop cells inside the eye, such as a hyalocyte or a vitreous cell, and later on, lens cells and other stretchers and, eventually, we are going to form a complex, sophisticated organ, and the shape of that organ that we are going to form will depend very much on the environment that we are living in, and there are many bad plans for what that shape might be.

We have seen cup eyes before. We have seen multiple cup eyes. These are both the same, and these depend on shadow.

We have this series of eyes, which depend on focusing.

And then this series of eyes depend on reflection.

All of these are used by animals, different animals, to see.

These eyes are simple eyes or chambered eyes, because they just involve one chamber.

These eyes, down here, are compound eyes, and these are generally used by many arthropods and many invertebrates, although some invertebrates will develop camera eyes, as we said in the first slide, and different types of chemicals and chemical reactions are used.

Is this evidence that the eye evolved many times? Well, it might be, because there are so many different types of eyes, but then, Gehring and Quiring in Basel, who were looking at fruit-fly transcription factors, identified a protein that binds to DNA. This is a feature of transcription factors, so they immediately sent it out to a worldwide computer database to see if there were any similar genes that had already been reported, and indeed there were. There was a mouse gene, called PAX-6 and there was a human gene called Aniridia and there was a great deal of similarity between this new gene, and furthermore, identical genes were subsequently found in a whole bunch of different animals.

Now, this gene was very interesting. The location was on a chromosomal site that harboured mutations in flies with developmental eye defects, and if you put these gene in artificially into a developing fly and you turned it on, the animal would develop extra eyes, and sometimes it would develop extra eyes in funny places, like on its antennae or the end of its legs or on its wings, and these were fully functioning eyes. So, the result of this was, it was realised that there was a master control gene that was developing eyes and it did not matter what sort of eye it was, whether it was a simple eye, like a human eye, or a compound eye, like an insect eye. This gene was the master controller that was making these embryonic larvae metamorphose and to metamorphose and grow eyes where there should not have been if any of these master control genes were present. Interestingly, these are very important genes associated with developmental defects.

Now, this gene was very interesting. Long before animals were ever thought of, there were organisms living in the primeval soup, and these organisms diversified into bacteria and into another group of organisms called archaea, and they lived on Earth for a very, very long time, and from archaea, multi complex cells developed with a single nucleus, still a single cell, and this branching tree of life was shown in one of the pages of Darwin’s notebooks, although he was not relating it to ancient organisms, but what we are implying is, is that all life is coming from a common ancestor. We are implying that life may not have evolved many, many times, or at least current life may not have evolved many, many times. We have no data that goes back before the Hadean Age because the Earth’s crust, which had crystallised, was completely melted and subducted. It is possible that there may have been some form of
life, but if we imagine how harsh the conditions were, it seems difficult to imagine that there would have been, but it is possible.

From this, we can start to imagine the evolution of animals. We have a single-cell animal here, which then starts to clump together and starts to have a division of labour, and in fact, there is a group of cells together – called volvox. Then, we have more sophisticated cells developing, with more specialised functions, and these are what are called metazoans, so multi-cellular animals, and they go on to radiate into either sponges, which have no true tissues and are called parazoans, or they come into metazoans, which are animals that do have specialised tissues, and these fall into two great groups: they fall into those that if you cut them down the middle they have two roughly identical halves; and there are those, if you cut them down the middle, that you can cut them down many times and they have what is called radial symmetry. How these animals are put together in their embryonic stage is very different as well, but the great thing about bi-lateral symmetry is it enables you to have a front and a back, a head and a tail, and this is going to be really important in our story talking about the development of eyes.

A couple of things happened as well here: we start to develop tubes for digestion, and we can develop this as a pseudo-tube, we can develop it as a proper body cavity, and if we do develop proper body cavities, we can then develop things like muscles, which we can make into hearts, we can move around our environment, we are not passively swayed by the tides, as animals that do not have true tissues can do.

Eventually, we come on and evolve chordates and these go on to form us.

Using DNA, that relatively simple way of looking at evolution, has been slightly modified and this is the new – it is not that different, and I am not going to go into it in too much detail, except for to show there are some surprising out-groups, like a worm-like creature that is very simple that lives in the silt of Norwegian fjords and turns out to be very closely related to us. So, not all deuterostomes necessarily have backbones, vertebrates, as those of us who work with middle-management know too well. Jellyfish radiate off very early, and they remain pretty much the same as they did in those days, and what is astonishing about that is that they can form eyes, so the mechanism for forming eyes must have been present way back in time. It does not necessarily have to be used all the time, but if you need to develop it, you need to use those genes and bring them together. Now, those genes, so those are the proteins maybe doing something else for much of evolution. For example, the cells that we use to form a human lens are exactly the same proteins that bacteria use to deal with a short sharp shock to stop them dying. Squid use a completely different form for their lenses, and so do octopus, and they use some proteins that are similar to enzymes. Nature is very parsimonious: if it has got a gene that is useful, it will use it, and it will use it in many different ways, as is directed by the environment and the time that is necessary for it to be used.

I am sorry about this, but I have to tell you how light is converted to electricity, and my first lecture I ever gave, this is where I counted the vast majority of people falling to sleep, so I will see if I can do better this time!

It is a complex thing and it does remind us of chemistry at school, which actually is a lot more fun now than it ever used to be. We have light that strikes this cell. This cell, luckily for us, is studded in its membrane with this beautiful purple pigment that is called visual purple, as we remember, described by Franz Christian Boll, who was the man who went on to dissect the eyes of newly hanged criminals to see whether we could find the image on the back of their eyes that might reveal who they had murdered. Of course, this takes milliseconds to decay and he had no chance, but nevertheless, this beautiful visual purple that no ophthalmologist has seen unless he has worked in the lab because it decays so quickly.

Once that light strikes, the vitamin A derivative changes shape, and it causes the serpentine protein to open up, revealing the active part of its molecule, which wakes up a signalling cascade that very rapidly leads to a lot of energy coming into the cell, and this linkage with a G-protein is universal. Now, some of these proteins linked to G-proteins do not see sights and they do lots of other things. It is very useful linking to a G-protein. G-protein can exaggerate a signal very, very quickly, and it is a very powerful way of doing it. So, if you have a receptor that is going to, for example, meet a noxious chemical and you need to make a quick response to it, you will use a G-protein coupling for it. Sometime in the history, when in those metazoan, the multi-cellular animals came together, one of those proteins developed a mutation, and that mutation was a sticky lycene on the seventh part, here, which allowed the vitamin A derivative to stick to it, and that is probably how the light receptor evolved. Light receptors are linked to G-proteins, and G-proteins cause a cascade which magnifies the signal many times.

Now, prokaryotic, which are bacteria and ancient single-cell organisms, which do not have a nucleus, also have opsins, and originally people were very excited by this because they thought, oh, that is the origin of opsins – they have been around forever, and all we had to do was to eat these things and then we had automatically an eye that was present. Unfortunately, there is homology between prokaryotic opsins and nucleated cells’ opsins. There are not even related by chance – they are not related, which is a shame, and then some clever scientists rubbed the back of their necks and then they came up and said, do you know, it is so important to react to light that of course this could evolve separately and we could co-opt a serpentine protein if we were a bacterium to respond to light, because responding to light for a bacterium is also very, very important as well, and they need
it for bacterial photosynthesis, for the phototaxis, the movement towards light, and also, in sensory rhodopsins, inhaler bacteria, which we will talk about presently.

In celled animals, different types of this photo pigment develop, and they are fundamentally different, and they are so fundamentally different that they get packaged in two different types of cells, which I am going to tell you about right now because they are going to come up as the lecture goes on. One of them is on a finger-like stalk that sticks out, and that finger has a little ruffled border to it all the way round, and the reason it does that is to increase its surface area, and this is studded with this molecule here that I have shown you, which is this up and down, seven trans-membrane, serpentine, meaning like a snake, protein. Now, in ciliary photoreceptors it is linked to the G-protein, which then activates PDE, which leads to cyclic GMP. Now, rhabdomeric photoreceptors look like Bart Simpson's head, and he has got this brush haircut, and they are linked through a different G-protein, to a different enzyme, and they respond in a slightly different way. Now, what turns out to be really, really interesting is that there is another bunch of cells in the human eye which were not recognised as photoreceptors, called ganglion cells, and it turns out that ganglion cells also use this mechanism, and we will come onto this fundamental difference in just a moment.

Here is a living fossil, which will illustrate what I have been talking about for the last 34 minutes. Platynereis is a marine annelid or a ragworm. In its larval state, it has two very, very simple structures which see light, and it has a photoreceptor cell and a pigment cell, and this reacts to light, and it sends it down a neural mechanism, down to these hairy cells, that then start to beat, and if you stimulate it on this side, these beat, and it moves, and it can change direction according to the light, which is really rather cool. This is probably one of the simplest eyes that you could imagine and it represents those very early stages that scientists imagine must have existed in the evolution of eyes.

The adult eye is also interesting. It has got a pair of eyes here. It has also got a pair of eyes deep in its brain, and in its brain, it has this ciliary, it has the C-opcin, so the story was that animals with backbones use ciliary opsins to see with, and animals without backbones, invertebrates, use ciliary opsins in their brain, which is important for light and day and circadian rhythms, but use rhabdomeric, or R-opsins, to see with in their eyes. So, there is a fundamental difference between eyes in these two great animal kingdoms.

Then somebody found rhabdomeric receptors in the human, which are those ganglion cells that I told you about, and they have the function of circadian rhythms. So, way back, before we evolved into protostomes and deuterostomes, the very fundamental difference which was going to lead onto insects, arthropods, molluscs and all of those creatures, and fish and us, both of these photoreceptor types must have existed.

What happens is, is that they are in the brain, in the developing vertebrate, and we use the ciliary receptors for seeing and for circadian rhythms in our retinas, because our retinas come from our brains. It turns out that insects and other animals like this use the ciliary receptors in their brains, and they stay in their brains, and the rhabdomeric receptors are in the eyes for vision. There is a little bit of variation on that.

I will just put it here: these are the two different types, ciliary and rhabdomeric, and they are here. Now, what is interesting is they do not go into sponges, so they are after sponges, and over here, the jellyfish evolve their own one. There is a little branch where the ciliary receptor is slightly different when it goes into jellyfish, but they still have a ciliary type of receptor that they actually use, those jellyfish that have eyes and those jellyfish that have sophisticated camera eyes, particularly the box-jellyfish, do use this.

Then this passes on and is used, and here is the big split, when we go into protozoans, they are going to use this for vision, and we are going to use this for vision, and we are going to use that for daily rhythms, and they are going to use that for daily rhythms – quite a switchover.

So how does this all fit in to the panoply of how long things have been on Earth? Well, if this section at the top is the life of the Earth, and one year is a millimetre, that line would be 4,600 kilometres long, so the Earth is very, very old. Dinosaurs would have been about 160 kilometres on it, and humans would have been about 10 metres, and that dot even there is a bit rather large.

You may have heard of some of these words, the Hadean, the Archean, the Proterozoic and the Phanerozoic Era – we live in the Phanerozoic Era now. The Proterozoic is the one immediately preceding ours, where life as we know it and multi-cellular life started. The Archean is the ancient times, and there is even evidence, the first evidence of life in this period, and the Hadean was that hot birth. If we draw it as a clock, we can actually have a look, and we can see the last little bit here is a very, very, very short time period indeed, and I will refer to that as we go along.

Knowing how old the Earth was is a relatively new thing, and the explanation of fossils and various other things and the diversity of animals and life was that just there is a lot of animals – animals were God's way of keeping making meat fresh, and in the days before a fridge, it sounds quite plausible. And then, a Danish Catholic Bishop, Nicolas Steno compares the teeth of a shark head with a fossil tooth and starts to work out that there may be animals that are extinct, that actually did not get onto the boat and survive the flood. Robert Hooke, a former Gresham Professor here, had also argued that, and there is a famous picture of him with his ammonite, which
This is a very important organism, here, which causes these dinoflagellates, and they have quite sophisticated cilia of a ciliated photoreceptor that is engulfed by organisms and go on and form a ciliated cell in, for example, responds to light, and can change their behaviour. Now, the hypothesis may be that this flagellan becomes the letter to the Royal Society, and what is interesting about them is, is they have a little stigmata, a little spot, that A long time ago, looking down his microscope, Antonie van Leeuwenhoek saw these little animalcules and sends found in potatoes, which subsequently can lead to diseases of humans, like starvation, and they cause a number are still with us, they are all around – they are algae, water molds, slime molds. They cause diseases. They can be protists. Multi-cellular eukaryotes are going to go on – we are multi-cellular eukaryotes. But the single-cell ones The advantage of a eukaryote is they love oxygen, and once oxygen develops, they can thrive. Now there are of other fairly horrible things that can go wrong, from diseases in the eyes to the body generally.

James Hutton was a very important geologist, and this is called a Hutton Disconformity, and what it points out is that the processes of Earth that have previously gone on are on-going today, but within unimaginably slow time periods, and that this must have been deposited on this much later in time, and furthermore, this must have been flat and has been pushed up under the Earth to have the next layers deposited on top. He also, amazingly, produces a theory of artificial selection.

Smith, who drew the famous map, enabled us to understand the geology of England and collected various fossils, and this map is pretty similar to what is used today.

I am going to explain some of the terms. Most of them were developed by British geologists who dominated this field. So, the Cambrian period, it is a classical name for Wales, where they were studying – Darwin was actually taking to Wales to study Cambrian rocks. Ordovician and Silurian are names of Welsh tribes. Devonian stands for itself – they found these down in Devon. Carboniferous – that is an adaptation of the coal measures, carbon. Permian – this was defined from strata in perm in Russia by the Scottish geologist, Murchison. Now, there were a couple of foreigners who got in on the act: the Triassic was described by Friedrich Von Alberti; and the Jurassic by Alexandre Brogniart in a marine limestone in the Jura Mountains. It was called Triassic because it has three colours – you can see the red, the white, the black, the red, the white, the black, the red, the white, the black, repeating, so that is how it got its word “Triassic”.

Now, this is this Hadean era when the Earth is born in this appalling heat and unimaginable bombardments. One of these bombardments indirectly led to the formation of the Moon. This is not a place for life. But after a billion or so years, things start to cool down a bit, and some of this bombardment has brought onto the Earth water, which eventually condenses out and forms oceans. In these oceans, eventually life forms, possibly from RNA forming ribosomes, which are little mini, nano, technical machines, and some of these will form these stromatolites, and they still exist today. Here are stromatolites in existence in Australia.

Some of these bacterium form these large mats of single-cell organisms. If we want to imagine what this Archean period might have looked like, we can pop over to America and see these boiling lakes and take a picture from a helicopter, and that is what it meant, and furthermore, we can see them here, in very ancient stones, this evidence of ancient life.

Some of these bacteria are with us today. For example, hala bacteria live in very salty conditions. We also have them in all of our guts – the methanogens are related to these ancient single-cell organisms, and there are two types of them: there is bacteria and there is archaea. This is the beginning of vision, if you like. We would not call it vision, but what it is, is to use the Sun’s energy to change a behaviour, and what it does is it goes through a bacteria rhodopsin, and it turns on an engine and the engine moves, and the bacterium comes towards the light. When there is too much light – remember, ultraviolet light is very dangerous and this is a period where there is a lot of ultraviolet light around, they then need to go out and they go down again into the shade, when the motor switches over.

These organisms are very successful, but they have a waste product, and that waste product is called oxygen, which is extremely toxic to them, and to us as well. It is bound with iron. There is a lot of ferrous iron in the sea, and it is bound to iron for millions of years, and we can see these in these ancient stones, which are basically stones of rust. But eventually, the iron runs out, and then oxygen starts to build up in the sea, and then into the atmosphere, and there is a mass extinction, and countless numbers of these organisms cease to exist.

But, another organism arises, which has a cell membrane and accumulates organs in it, including a nucleus which is self-replicating, and it may have arisen by a simple process, by engulfment of other organisms. Lynn Margulis actually took up the theory of Konstantin Mereschkowski and, although she was considered mad in her lifetime and was extremely unpopular, it has turned out that she was probably right.

The advantage of a eukaryote is they love oxygen, and once oxygen develops, they can thrive. Now there are lots of eukaryotes around. Ernst von Haecckel suggested that we use the term for these single-cell eukaryotes as protists. Multi-cellular eukaryotes are going to go on – we are multi-cellular eukaryotes. But the single-cell ones are still with us, they are all around – they are algae, water molds, slime molds. They cause diseases. They can be found in potatoes, which subsequently can lead to diseases of humans, like starvation, and they cause a number of other fairly horrible things that can go wrong, from diseases in the eyes to the body generally.

A long time ago, looking down his microscope, Antonie van Leeuwenhoek saw these little animalcules and sends a letter to the Royal Society, and what is interesting about them is, is they have a little stigmata, a little spot, that responds to light, and can change their behaviour. Now, the hypothesis may be that this flagellan becomes the cilium of a ciliated photoreceptor that is engulfed by organisms and go on and form a ciliated cell in, for example, a jellyfish.

This is a very important organism, here, which causes these dinoflagellates, and they have quite sophisticated
ways, some of them, of blooming. We know of them because they cause toxic red tides of course. It is a predator, but it is also autotrophic. When there is lots of light, it can be photosynthetic; when there is not any light around, it gets motoring around and it eats other organisms. What is extraordinary is some of these things have what is called an oscilloid. This is a single-cell, but part of that cell has a focusing mechanism, a pigment protective layer, and a little bundle of photoreceptive cells here. So, already, a focusing mechanism… This thing can sit on the bottom of the pond, and if it sees a little thing flying around above it, it can zip up and eat it for breakfast. Lynn Margulis proposes that these may have actually been the source of the very first eyes in the very first organisms, of which we have very little to go by because the Ediacaran biota, all of these animals were soft-shelled, but there are some impressions of these soft-shelled animals here.

We do not exactly know what they were. They may well have been parazoans, meaning they were like sponges or porifera. They are not necessarily related to more complex animals, but the suggestion is that some of these may have had legs and may have moved and may have been the early representatives of jellyfish and cone-jellies. They are probably representatives of mollusca Kimberella and various other even arthropods.

So, if mussels were in existence there, i.e. molluscs, could we see, well, chitons are a very ancient form of mollusc around, and some of these chitons actually have eyes, and we can see these eyes in the shell. What they use for these is aragonite, a crystal, to actually use as a focusing mechanism. They do not use proteins and they do not use calcite, which other animals use to form lenses; they use aragonite, and they can form a pretty sophisticated image and they have got an imagining – and actually, someone has done visual tests on these, and I will talk about testing chiton eyes to see what they can see when I talk about animal eyes next year. They can differentiate between night and day, they can differentiate between predators, and the resolution of these eyes is about twenty times what the image of the Moon would be on our own retinas.

The Paleozoic Era arises, as the end of the early life forms, and the sea starts to warm up and it breaks up the continents, and we get an explosion of life, which is called the Cambrian Explosion, and in the seas – there are no animals on Earth, but in the seas, multiple different plans for different types of animals suddenly come to the fore: we have got different types of worms, we have the trilobites and these are tremendously successful and last throughout the whole of this era, until they finally become extinct, along with nearly everything else, in the Permian, which is the largest mass extinction that the Earth is going to see.

Some of these animals, unfortunately, are no longer with us. Look at this critter here. Look at how many eyes it has got. I bet you that would be one of the tastiest lobsters you have ever had! You see, I love arthropods. Arthropods, although a lot of people think they are ugly and strange, they are absolutely delicious – they are one of my favourite animals, from shrimps to lobster to various other things.

Now, clearly, very complex vision was developing here. Why? Because predators – once you have got a predator, you have got to develop some pretty smart ways of avoiding it, and the smartest way of avoiding it is to see it a long way off before it comes to you. It is better to see a predator than smell it. By the time you can smell, it is often too late. So, there is a big selectionary pressure. And, also, the predators themselves start to develop good eyes, so they can see their prey as well.

This is Anomalocaris, which actually means very, very nasty, big shrimp essentially, or anonymous shrimp, and this is its reconstruction in the Science Museum and it is an absolutely appalling thing. You would not really want to meet that if you were a tiny little animal burrowing around at the bottom of the sea.

Now, did it really exist or not? Well, just recently, they found its eyes, and here are its eyes, which show a very complex compound eye, which must have had amazing resolution.

Trilobites were one of the most successful creatures and these were the first animals that we definitively know had eyes because we can see their eyes on them here, and this is the first simple type of eye they develop, which is called a holochroal eye. It has a single skin over the surface of it, analogous to a cornea, and the reason this is, it is one of these animals that mouls, so it can actually change the size of its eyes as well as its body.

More complex eyes start to develop, and what is interesting about these is that these start to be aspherical eyes. They are starting to have aspheric optics long before we thought about this, with Hubble telescopes and developing laser refractive surgery. And in fact, long before we discovered spherical aberration in telescopes, before Huygens, these animals were already developing multifocal aspheric lenses which were formed by having two different lenses glued together. Now, there was a little bit of argument saying this is not true and that you could actually do this just by different condensation of gradient of calcite crystals, but in fact, they now definitely have shown that, in one of the species at least, dominatina, that there is definitely a doubled up lens, which is astonishing because they have discovered this several hundred million years before humans did, which is really one of those extraordinary things when we think about how clever humans are, we realise how much cleverer biology is.

None of these survived the extinction and they are not going to be used again, so evolution itself tries things out and it can come to a dead-end. Maybe, one day, there will be a marine animal like a trilobite that may need aspheric vision and it will develop aspheric vision, and it will probably use very much the same materials that were
around then as are around now to do that.

Now, why not achromatic vision? It is because these are sea-dwelling animals and there is not any chromatic aberration when you have got a single light source deep down in the sea. The colours of light are taken out very, very quickly as we go down, and that is why they did not need to evolve that, and so they did not.

What we are going to come down now is onto chordates, and if you thought that creepy-crawlies and things were horrible, you are going to see the most horrible animal on Earth that has ever existed ever in a moment, which is actually related a bit to us, unfortunately.

Chordates are things with a chord, at least at some part of their evolution. Now, not all of these are going to look like animals. Some of them actually look like vegetables – the tunicates, for example – but they are little chordates, and tunicates are little tadpoles when they start and then they go on and form these beautiful, static, filter-feeding tubes in their adult life form.

These are the cephalochordates, and interestingly, they have a prototype eye which has the structures that are going to be used as we develop later on.

Now, this is singularly the most disgusting creature that has ever been invented, ever, called the hagfish. It does not have a jaw, but it does have a round mouth with suckers, and it goes onto the outside of its prey, which it burrows into and eats it from the inside out. To stop itself being eaten, it secretes a disgusting slime. Also, its carriion and its various other habits make it very unpopular with fishermen. It actually has an eye, but the eye is underneath a piece of skin, so it is not used for sight; it is used for circadian rhythms, so, behaviourally, it is almost blind. It has got a rudimentary retina, but only two cells, and these cells project to the hypothalamus, a very basal, important part of the brain.

Now, chordates develop. They are a bit more sophisticated animals, and this animal, resembling an eel, had two rather eyes at the front. Large eyes imply two things: either you live in a dark environment or you are moving pretty fast. It seems that rather faster moving animals were developing fish-like characteristics.

Lampreys are very important because these are the oldest group of animals that have eyes similar to our own. I suppose they are important to us if we are looking at it from an anthropomorphic point of view, if we are looking at how our eye might have evolved. Very ancient. They are jawless as well, and here is their mouth, without a jaw. They have got an eye very similar to us, and they have got four types of opsins, and these evolved before the separation, here. So, at this period here, we know that we have a sophisticated opsin, light-gathering, biochemical mechanism.

Henry I of England died actually of eating too many of these. These are also delicious, and he had a surfeit of lampreys.

Lucinius Crassus actually kept one as a pet, and when it died, he cried, and Gnaeus Domitius called him a hypocrite because, actually, these were very, very expensive luxury items, and he responds to this criticism saying, “I wept for the death of my lamprey, yes, I did, but did you not weep for any of your three wives?!” It may not, unfortunately, have been a lamprey, because, along with the Emperors, who also kept pet lampreys, they used to allegedly decorate them with earrings, which would suggest that they were actually eels, not lampreys, which do not have any lateral dorsal fins to hang earrings off, which is a rather sad way to end this slide, as I move onto the next one, and we will talk about shelly animals developing, these warm seas.

There is a little band, right at the end, in the Ordovician period, where there are lots of shells, and shelly things do have lots of eyes. These are clams’ eyes, rather beautiful things, rather clever things. They are reflective, and what happens with reflective is that you can actually gather a lot more light and focus it than you can if you are just using a direct ray of light.

And the old nautilus – here is an old fossil, still around, using the simple camera eye. That is all it needs. It is rather slow-moving, and it does not need to have the sophisticated vision that this clam needs to shut itself down at the first onset of the sight of a predator.

This era slowly comes to an end, but just before the Silurian extinction, the second largest of the five major extinctions, where 60% of all these marine species are going to die off, we develop early fish. At this time, critters crawl out of the sea and start to colonise the land, which, for the first time, has something on it for them to eat, which are these large algal mats, and we develop insects, and this movement requires the development of eyes.

At the very final period, there are these rather bony fish. These were some of the most voracious predators that we could imagine. They would snap a shark in half. A shark would easily fit into that jaw and be chomped up into nice small bits.

We will come onto the Devonian period, which is the age of fish, and this is when we start to really see the
development of eyes that are going to go on to form the land vertebrate eye, and a very sophisticated amount of receptors.

The next slide I am going to show you is a rather complicated one, but what it actually shows is how these genes, which I have shown in the light blue boxes, duplicate, and it turns out that bony fishes have a lot more receptors for different wavelengths of light than we do, as ours die out and we lose them, because we became nocturnal animals to stop dinosaurs eating us, so we did not need all of this mechanism around, and if you do not use it, you lose it, and that is exactly what happened. Then, we re-duplicated it again, as old world monkeys, to develop a medium wave for green, if you like, whereas the new world monkeys that we will discuss later did not, and so they are colour-deficient compared to us.

Animals, particularly insects, take to the air, and when you take to the air, you move fast, and you need very sophisticated vision. This is how big these things would be. They are absolutely enormous! Insects take advantage of this, because there is a lot of oxygen around. The oxygen level starts to come down, and insects never regain this size again, even though oxygen levels subsequently do, and the reason they never grow to this size again is they get a competitor and a predator, called a bird. If you have got birds around and predators around, you do not want to be this size because you are going to make a lovely lunch for a whole family. You want to be as small and inconspicuous as possible.

Our ancestors come out after this massive extinction, when 96% of animals die - 95% of species go. This is an early sort of prototype mammal that is coming through this period and bringing forward this visual witness into the future. We have mentioned how the fish are also developing, but as well as fish, reptiles start to expand, and we have these beautiful Jurassic animals, with their bony scales around their eyes, which enabled us to reconstruct how big they are – the size of footballs or beach-balls, these eyes, rather enormous. Why? You will see that when we discuss the giant octopus, the giant squid size, in a subsequent lecture, but it is to enable them to see scattering of photo-bioluminescence to escape predators.

Then birds, which we mentioned before, develop a very, very sophisticated imaging system, and actually have vision six to eight times better than humans in the predator raptor birds.

In summary, I think I have shown you that as well as imagining that many, many different types of eyes could have evolved or could have been made by a watchmaker, it is also plausible, and more evidence is arising, that they could have also evolved by a series of small minute steps, as imagined by Darwin. We know that these genes are present in ancient life forms, and we know that these genes have been radiated out to their descendants to this day. For example, the ancestral pattern that we saw in platinarius in its form both in the larvae and in the adult. The evolutionary line that leads to vertebrates, we used both of these types of receptors that have developed here and we put them into our eyes.

So, there may have been a common ancestry of all multicellular animal eyes, and I think that the more work that comes out, the more that we see that there is an ancestral toolkit for assembling what is needed, we can imagine how eyes might develop and be evolved. So, there is evidence of evolution. That is not necessarily evidence for the absence of God in this process, and it does remain a very controversial topic, and I am aware of that, but it should still not stop people searching to see and to find how this beautiful and wonderful organ that we take for granted was assembled and how it may have evolved over 3.6 billion years. Thank you.