1. I keep on my desk a fossilized trilobite named Gerald. He used to live in Morocco, belonged to the species *Coltraneia oufatenensis* and he is around 300 million years old, give or take a few million years. I bought him during a late-night essay crisis to give me a sense of perspective. Whilst I am fussing about whether to use this word or that word, it helps me to remember that Gerald was grubbing around in the mud before birds existed. His magnificent schizochroal eyes are perfectly preserved, since the lenses were made of calcite. You can clearly see each lens on the eye turrets.

2. I wonder what Gerald saw? Did he cower in terror from *Anomalocaris*? Did he frolic with his fellow trilobites, or was he solitary? I wonder whether in 300 million years, my skull may lie on the desk of some creature whose intelligence is to mine as mine is to Gerald's. And will that creature dream of what light passed through my blank sockets?

3. I first became fascinated by eyes in a documentary by David Attenborough, in a section where he discusses what trilobite eyes can tell us about their lives. He shows us a trilobite with flanges on its eye turrets, which must have lived in bright, shallow water, where it could have been dazzled. A trilobite with eyes on stalks, which buried itself in the mud. A trilobite with almost non-existent eyes, which probably lived in gloomier, deeper waters. And a trilobite with 360 degree vision, whose eyes were wrapped in a band right around its body, which probably swam in the water column, and needed to detect predators.

3b. We know so much about trilobite eyes because the lenses fossilized, as they were made of calcite, a crystal of calcium carbonate. The trilobite's eyes were grown from its mineralized exoskeleton. Today, the chiton has a similar solution, with lenses made of aragonite.

3c. Aragonite is 'birefringent' – it has two different refractive indices, depending on light polarisation and propagation direction, meaning that these chitons have lenses with two focal lengths. They live in the intertidal zone, and this miraculous material gives them 'good' sight in both water and air.

4. This essay is an attempt to pass on my sense of wonder at the many weird and wonderful ways in which visual organs have evolved in the animal kingdom.

5. Light-detecting organs have evolved multiple times, a prime example of convergent evolution, where good solutions to common problems evolve multiple times. Other examples include the wing, the shape of the fish, the doughnut, and the chromatic scale. I am fascinated by convergent evolution, but I don't want to get diverted by that now.

6. They say that eyes are the window of the soul. If the soul is in the brain, then there is some truth to this, as when you look into a person's pupil, the darkness that you see is the retina, the outermost reaches of their brain. This is the only 'external' point on the body where one could say that.

6b. It would not be true to say that an octopus's eyes are the window of its soul. The human retina is generated by the neural epithelium – it is a part of the brain. But remarkably, an octopus eye is generated entirely by the epidermal epithelium – it is a part of their skin. Most people would argue that the concept of a centralised ‘brain’ is a bit vertebrate-centric, and that the octopus ‘brain’ is distributed throughout its body, including in its tentacles. So maybe an octopus’s skin is the window of its soul.

7. It’s a near-impossible job to categorise the enormous variety of eyes that we can see in the animal kingdom. But if you had to start, you would probably do so by dividing eyes into the compound eyes, and the simple eyes. Compound eyes are convex, with many image-forming structures, and are used by the insects and the crustaceans. I suspect that, like me, you will find the image produced by compound eyes near-impossible to conceptualise. Gerald’s eyes are compound. The simple eye is the more familiar, common or garden eye, with a single image-forming structure, something like a camera. Within each of these broad categories, we can find a baffling and awe-inspiring array of specialisations. If you can imagine a solution to an optical problem, odds are that Nature has found it.

8. My plan in this essay is to try and render the miracle of sight in understandable language. I have trawled through the textbooks on animal vision, and extracted the most exciting and interesting examples. Rather like penguins regurgitate food for their young, I have done all the hard work, catching the fish, and digesting them, and I am giving you a readily-digestible version, with all the bones removed.

9. The evolution of visual systems is a topic of complete and utter wonder, great complexity and ineffable mystery. At the start of the Cambrian explosion, about 540 million years ago, something developed an ‘eye’ that gave them a competitive advantage, thus triggering the greatest arms race the planet has ever seen. From the start of the Cambrian Explosion, we see a huge number of new and brilliantly strange body plans preserved in the fossil record. I don’t want to write anything about phyla, as it will be out of date by the time the next person reads this. But you can think of the interesting part of the story as having begun about 540 million years ago.

9b. It has been demonstrated through computer modelling that a patch of light-sensitive epithelium (skin) can evolve into a perfectly-focused camera-type eye (like ours), in around 364,000 generations, with a 0.005% change each generation. This is remarkably speedy, and it’s also a very beautiful process. As a child, I was shown the usual creationist videos about how the eye couldn’t possibly evolve, and when Darwin considered the refined form and function of the human eye, he supposedly experienced a cold shudder. But with one little diagram, it’s perfectly possible to see how the human eye could have evolved. The lens, which is the bit I struggled to imagine evolving, could form from tissue with a non-optical function, such as a protective layer of epithelium.

9c. We can see some examples of compound eyes evolving into simple eyes. This appears to have happened in some of the Chelicerata (scorpions), and we can see it in the unique compound superposition eye of the shallow-water shrimp *Dioptromysis paucispinosa*. Although all the mechanics are those of a compound eye, it only has one large facet (compared to a dragonfly, which has 30,000 facets). The fascinating thing is that because it is a superposition eye, it produces an erect, rather than an inverse image.

9d. It’s not entirely surprising that we might see compound eyes evolving into simple eyes, as compound eyes are a bit of an evolutionary blind alley, despite being by far the most numerous visual system in the animal kingdom. The trouble is that there is a fundamental conflict between sensitivity and resolution in compound eyes, which can’t be resolved without excessive eye size. This is obviously not a viable solution for insects, whose size is limited by their breathing apparatus and the concentration of oxygen in the atmosphere.

9e. Superposition eyes are a more complex case, and it remains a bit of an enigma how they evolved. It must have been from typical apposition compound eyes, and butterflies seem to be a part of the answer, as their eye function in both ways. But the evolutionary pathway is still unclear – how did those butterfly eyes with a dual functionality evolve?

10. Among animals, there is simple directional photoreception in nearly all phyla. One has to feel some sympathy for *Porifera, Placozoa* and *Ctenophora*, who don’t even have that. ‘Sophisticated’ visual systems have only evolved a few times – in arthropods, cephalopods (octopuses and squids) and vertebrates.

11. In this essay, I will only really be discussing animal eyes. I have been wondering recently whether a leaf could be considered as a kind of eye. It provides directional photoreception, and some plants are able to act on the basis of that information (*phototaxis*). To be honest, I’m having enough difficulty covering the diversity of animal eyes, without discussing plants, fungi, bacteria and archaea. So we might just park that thought here.

12. The function of the eye is simple; to detect light. Light carries with it a great deal of information, and different eyes can harvest different types of information from this light. We can harvest colour (wavelength), intensity (number of photons), and direction, from which we can extract spatial information about the world around us. By contrast, if you were a planarian flatworm, you might only be able to say whether there was some light, or no light. And this might be enough for you. You don’t have a brain to do any of the necessary processing, so what would be the point of having an eye that could harvest wavelengths? We can consider that in most cases, eyes are optimally evolved for the needs of the species.

13. If we were the product of a designer, there is no way that they would have wired our eye the way that it is wired. The wiring of the nerves sits *in front* of the light-detecting rods and cones, and all the wiring has to pass back through the eyeball to reach the brain, creating a blind spot in each eye. This ridiculous situation is reversed in the octopus eye (which is otherwise nearly identical). Although it doesn’t actually have much of an impact on our sight (the wiring is relatively transparent), it’s certainly not an elegant solution, and no self-respecting creator would have been satisfied with it. We can console ourselves in the knowledge that the planarian flatworm’s eye has an even uglier wiring system. The nerves literally go back out of the pigment cup, as if our nerves came out of the front of our eyes, and thence into the brain.

14. Our eyes have evolved to tell us *what* things are, and *where* they are. These are two very useful pieces of information.

15. But there is more information in light that our eyes can't harvest. For instance, polarization – in which direction is the light wave oscillating? You might not think this ability is very useful, but I suspect that is because you don't have it. Organisms that can 'see' polarisation have some superpowers. Some are able to find water more easily (*Notonecta sp.*, the backswimmers), as light reflected from water is polarised. If you can see polarised light, you can see where the sun is, even if it is hidden behind clouds, because the atmosphere polarises light as it scatters it. This could come in very handy if you wanted to navigate by the sun on a cloudy day. Similarly, male mantis shrimps in the genus *Odontodactylus* have parts of their bodies that differentially reflect polarised light. It's thought that this is used in a sexual displays, as a private communication channel with the female mantis shrimps. Rather like we used Pig Latin at school. Except there were no females. Only teachers. And I'm pretty sure they understood what we were saying.

16. An example of some other information we can't harvest is spectroscopic information. In 1835, August Comte asserted that we would never know about the chemical composition of stars, as the only information we received from them came by light. Thanks to the discoveries of Bunsen and Kirchhoff, we found that when the light from stars was decomposed into its component wavelengths, distinct black bars formed on the spectrum. By analysing these (spectral analysis), we could find out what elements were present in stars, and in which quantities. This in turn has enabled us to unlock the secrets of stellar fusion. Light is the gift that keeps on giving!

17. Whilst we're on the topic of light, it is worth pointing out that photons, whilst massless, do have momentum. This is the principle behind solar sails, which is one of the proposed methods of interstellar travel. I have always wondered whether it would be possible to knock somebody over with a really **really** bright flash of light.

18. Because animals have evolved to occupy as many available niches as possible, there is a tremendous diversity of eyes, evolved to deliver many different kinds of information in many different environments. There are eyes for the night-time, eyes for the desert in the day-time, there are eyes for the deep sea, and there are eyes for hunting from high up in the sky. You name it, Nature has evolved it. Except for the Fresnel lens. This type of lens was developed for use in lighthouses, and focuses light using concentric circles. This is the one optical trick that humans have discovered that we haven't yet found in Nature.

19. The basic component of the eye is a molecule that is sensitive to light. The protein used for all visual systems we know about is called opsin, and is derived from vitamin A. There is a space in the protein that can capture a photon, between the 11^{th} and the 12^{th} carbon atoms, and capturing a photon causes the protein to change shape slightly. This mechanical information is then converted to electrical information, and transmitted to the brain.

20. From thereon out, the world is your oyster. Your eye can be refined by the addition of more components. If you want any spatial information, then you're going to need some form of shading, so that light only arrives from a particular angle. A lens will help to focus the light onto a particular point in the eye, an iris and associated muscles can control the amount of light that gets into the eye, and so on and so forth.

21. It's not universal, but eyes tend to be located at the front of the organism, because they're generally involved in steering. I have a somewhat Victorian sensibility, and I have always felt that it is indecent that the mouth is located on the face. It also stresses me out that the oesophagus and the trachea share the same entry way. If I were given a blank slate, I would move the mouth down onto the chest, out of sight, out of mind. The nostrils would remain on the face, and become adapted so that we could use them for speaking. Thus the noble pursuits of listening, breathing, communicating and seeing would remain on display, and the all-too biological function of eating would be moved to somewhere more discrete

22. Size matters. The Giant Squid has the largest eyes of any living animal, expect perhaps the colossal squid. Its eyes are up to at least (nice double qualifying prepositions) 27cm in diameter, with a 9cm pupil. Icthyosaurs (which were reptiles) had bigger eyes, up to 30cm in diameter. On land, apparently it's the ostrich, whose eyes are bigger than its brain. The tarsier has the largest ratio of eye size to body size. My mother always said that my eyes were bigger than my tummy.

23. Size matters for a variety of reasons, as neatly illustrated in this extract from my forthcoming eye-focused retelling of classic fairytales. This is an extract from Little Red Riding Hood:

GIRL

My, Grandma, what big eyes you have!

WOLF

All the better for obtaining a low minimum resolvable angle and a high retinal sampling frequency, reducing diffraction and ensuring a high optical cut-off frequency, giving a wide aperture, ensuring adequate photon numbers, and good contrast detection in dim light.

24. The smallest eye with a spherical lens, which because of Matthiessen's law, looks almost identical to the squid's, belongs to another mollusc. The pond snail *Lymnea* has a perfect spherical lens in an eye only 0.15mm across.

24b. A perfectly spherical lens does not bring incident light rays to a focused point, which is a problem for vision. This is so-called 'spherical aberration'. There are two solutions to this problem: either make your lens non-spherical (as in humans), or have a refractive gradient across your spherical lens. This is a so-called Mathiessen lens, and it is shared by many creatures, including the giant squid, and the pond snail *Lymnia*.

25. If you asked the man on the street what the best eyes in the animal kingdom were, he would probably think for a moment, and tell you it was a hawk's eyes. We will tell him that 'ignorance is opportunity', and make a mental note to give him this essay for Christmas.

26. In terms of outward appearance, though, we could probably credit his answer. Who has not marvelled at the blood-red iris of the Goshawk, or the bright yellow of an eagle owl? You are staring death in its implacable face. I think that may be a cliché, but I'll leave it in anyway.

27. The iris contains what is surely one of the best-named pieces of the human anatomy: the Crypts of Fuchs. It sounds like a novel by Edgar Allan Poe. The Crypts bathe the Iris in aqueous humour.

28. I always think that the iris looks like something dead. I think this is because there is no epithelium, so you see the fibrous stuff that is usually kept hidden away under the skin. The dilator muscles pull the iris in folds to open the pupil. This summons up for me visions of a beautiful curtain being drawn, or the awning of the Colosseum.

29. Most falcons dive in a spiral path, with one eye locked on to their prey. I have written in my notes that an American Kestrel can see a 2mm insect from an 18m tall tree, and that birds can see the slow shifting of the sun and the stars. But neither of these facts is attributed, so we will never know whether they are true or not.

30. A hawk's resolution is almost double that of a human. It can see objects that are twice as fine as we can. Resolution in the hawk eye is improved using three factors; pupil size, a sneaky trick involving a foveal pit, and the size/packing of the photoreceptors. In humans, our photoreceptors are 2μm across, and the smallest receptors in vertebrates are 1μm across. For contrast, a human hair is about 50μm.

31. Theoretically, if you could get a thinner receptor, your resolving power would also increase. But this is where things start to get trippy. Any smaller than 1μm, and the receptors start to 'leak'. Up to that point, light bounces quite happily off the edges of the receptor, a phenomenon called total internal reflection. When the receptor becomes too thin, the light can be thought of as travelling down the receptor in the form of a wave, in which the edges of the wave have spread out into the next-door receptors. This is obviously no good for resolution.

32. The fovea (point of greatest receptor density) of raptors is in the form of a steep-edged pit, and it has been suggested that this acts as a negative lens, shifting the image backwards, giving a longer overall focal length and therefore a better image. A similar system is used for telephoto lenses, and in the jumping spider *Portia fimbriata*.

33. Many birds and some lizards have a nictitating membrane, something like a cross between an eyelid and a windscreen wiper. It lubricates the eye, protects it from damage, and even acts as a contact lens in some diving species.

33b. Using their very powerful ciliary muscle, some diving birds can squeeze their lens through the iris, forming a small bulge at the front of their eye. This tiny lens-pimple has an incredible curvature, effectively solving the problem of sight underwater. But it's a nasty thought – imagine if they squeezed so hard that their lens burst.

34. A prominent eyeridge gives raptors their distinctive stare. I was once in St Peter's Square in Rome, watching a group of gulls tear apart a pigeon, and I began to think about the prominent eyeridge in predatory birds. The function of this ridge of bone is to protect the soft eyeball from damage. But by God it looks evil, and never more so than on these vicious gulls.

35. As a child, when I wanted to make the faces I had drawn look angry (or demonic), this was achieved by the simple addition of two slanting lines above the eyes, meeting in the middle. In other words, a very prominent and slanted eyeridge. Are we programmed to think of predatory birds as the embodiment of violence, anger and evil? Or are they the unfortunate victims of an as-yet unexplained correlation?

36. Whichever it is, there is something unnerving about the unflinching stare of a raptor. Does the gaze have power in and of itself?

37. Unless I have misunderstood, Jesus certainly thought so. He told us that 'whoever looks at a woman to lust for her has already committed adultery with her in his heart', and that 'if your eye causes you to sin, pluck it out and cast it from you. It is better for you to enter into life with one eye, rather than having two eyes, to be cast into hell fire.'

38. In all four Gospels, Jesus heals a blind man, and this is surely significant. John, ever insightful, prefaces the miracle with a helpful reminder that Jesus is the light of the world. Jesus spits on the ground, makes a paste of clay, and anoints the eyes of the blind man. In Mark, there is a passage that I have never understood, but always found deeply evocative. The healing proceeds in two stages, and after the first, Jesus asks the man whether he can see. The man replies 'I see men as trees, walking'.

39. Presumably this means simply that his vision is a little blurry still. But I think I would rather have stuck with 'I see men as trees, walking', rather than 20:20 vision. It's deeply poetic. I'm sure it made perfect sense in the original, but that's the charm of the Bible in translation.

40. The cuttlefish has a very distinctive, w-shaped pupil. I think it is my favourite pupil. Other candidates are the gecko, with a notched slit pupil, and the household cat, whose pupil reminds me of the famous fourteenth-century scissor arches in Wells Cathedral.

40b. Pupil shape matters greatly for a variety of reasons. One of the challenges faced by a spherical lens eye is chromatic aberration, where the lens does not focus all colours to the same point, since the refractive index of the lens depends on the wavelength of light – the colour. This results in an image that appears blurred, with colour separation. The solution is to have a lens with a refractive gradient. But if you had a circular pupil, as you shut off certain parts of the lens, certain colours would come out of focus. The slit pupil avoids this problem.

40c. The batoid fishes, such as the shovel-nosed ray (Aptychotrema rostrata), have a very unusual flap of iris with fingerlike projections hanging down into the pupil, called the pupillary operculum. It performs many mystical functions, but the easiest to grasp is that of a sunshade.

41. A contractable pupil is very useful, because it can be used to strike a compromise between the problems of diffraction (wide pupil) and aberrations (small pupil). If, like the Nautilus, you don't have a lens, pupil diameter also reflects a compromise between sensitivity (wide pupil) and resolution (small pupil). The ideal compromise in both cases varies depending on the light level, hence the need to adjust the pupil.

42. This fact is neatly illustrated in this extract from my forthcoming eye-focused retelling of classic fairytales: The tale of Nautilocks (*Nautilus pompilius)* and the three pupil diameters.

At first, Nautilocks opened her pupil to a diameter of 2.8mm.

"It's far too blurry" said Nautilocks.

Then she shut it down to a diameter of 0.4mm

"It's far too dim" groaned Nautilocks.

She found a compromise point, but it was honestly still pretty rubbish.

"If only, in my 500 million years of evolution" thought Nautilocks, "I had been able to evolve a lens, which would sharpen the image by focusing rather than shading."

43. Unfortunately, unlike all the other cephalopods, the Nautiluses never evolved a lens, and are stuck with a pinhole-camera type eye. It also seems like they are not as intelligent as the other cephalopods. They are the Ugly Duckling of the cephalopods.

45. Gecko pupils can cut down light a thousandfold by closing to a series of notches, allowing them to hunt in the daytime without bleaching their retina. This is compared to a measly 10-fold change in humans.

46. My friend Gordon lives on the Isle of Skye. Last year, a whale skeleton washed up on his beach. His neighbour analysed the DNA, and declared it to be Cuvier's Beaked Whale. These are the deepest diving creatures known, able to dive from the surface down to nearly 3000m.

47. Down in the darkness, the whale's eyes are useless. They can see only through the magic of echolocation. This ability has developed several times, in birds, toothed whales, bats, shrews, and humans. In the toothed whales, *Odontocetes*, it may have evolved to enable them to hunt beyond the photic zone, pursuing diurnal vertical migrating animals, like squid, down into the darkness. I cannot think of anything more frightening.

47b. Toothed whales emit a focused beam of high-frequency clicks in the direction that their head is pointing. Sounds are generated by passing air through the phonic lips, which are a bit like our vocal cords. The focused beam of sound is modulated by a large fatty organ known as the 'melon'. This acts like an acoustic lens because it is composed of lipids of differing densities. This is analogous to a Matthiesen lens. The lens is a focusing organ, and is useful for focusing sound as well as light; it channels information in the right direction. I suppose a teacher is a bit like a lens. And an author.

48. The poor Cuvier's Beaked Whale which washed up on Gordon's beach was most likely hunting down in the darkness when it was disturbed by the sonar from one of the military exercises that are common in the Scottish Isles. This fearless predator, which could hunt for hours in the blackness, thousands of metres below the surface, was most likely spooked by the noise (or even 'blinded'), and bolted for the surface. It died of decompression sickness as a result, and washed up on Gordon's beach.

49. *Galleria mellonella,* the greater wax moth, has evolved some remarkable mechanisms to confuse pursuing bats. When it hears the bat's clicks with its sensitive tympanic membrane, it can literally drop out of the sky in order to evade the bat. The spinning hindwing tails of silk moths (*Saturniidae*) can divert bat attack by reflecting sonar to create a misleading echoic target.

50. I suppose that, for much of our lives, we only look at the echoes of light. The one exception would be sunrise and sunset, and at night, when we are able to look directly at the stars.

51. Echolocation is a way of 'seeing' that doesn't involve light. Frustrated by the size-limit of the light microscope, humans developed some alternative ways of 'seeing', such as electron microscopy, and scanning probe microscopy.

52. Snakes and melanophilia (beetles which rely on recently-burned wood as food for their larvae) can 'see' into the infra-red using specialised nerve cells.

53. There was once a small Zebra jumping spider, *Salticus scenicus*, on the windowsill in my room at Cambridge. They have four eyes, in two pairs, one very large pair at the front of the head, and a slightly smaller pair to the side. They use these eyes to fix on their prey before they jump, and they are generally said to have excellent vision.

54. The strangest thing was that I had the distinct impression that I had locked eyes with this tiny spider. I was absolutely certain that it was looking into my eyes, just like the feeling that you have where paintings follow you around the room. It was probably assessing whether I was a prey item or not, but I choose not to dwell on that. When I looked up this phenomenon, I read that it was relatively common.

55. Annie Dillard famously had the same experience with a weasel.

56. A friend of mine told me that she once had a very similar experience with the stars, where she was suddenly and briefly struck with the absolute certainty that they were watching her. As Neil Gaiman says in *Stardust*: "A philosopher once asked, "Are we human because we gaze at

the stars, or do we gaze at them because we are human?" Pointless, really..."Do the stars gaze back?" Now, that's a question.”

57. Most people’s immediate response would probably be to say it’s impossible that the stars are watching us. But my response is rather that I wish it would happen to me.

58. The spiders have evolved a very opulent visual system. The true spiders generally have 8 eyes, giving them an enormous field of vision. Each of the four pairs of eyes is arranged according to the ecological niche of the spider and its needs, and the arrangement varies greatly from species to species. It’s possible that these eyes are compound eyes that have, by a process of evolution, become simple eyes, and that would explain the numbers. Generally, there is one very large pair, and lots of tiny ones, all of which perform different functions.

59. You may think that having eight eyes is overkill but consider the box jellyfish; it has 24 eyes, of 4 different types. Unfortunately, the biggest ones, the lower lens eyes, look **through** the jellyfish’s body, which seems to be quite a serious design flaw, if you ask me.

60. The box jellyfish has nothing on Argos Panoptes, whom Hera set to guard the sacred cow Io from her husband Zeus. He had 100 eyes, so that he could see in all directions at once. The reason that he needed 100 eyes was so that he would be ever watchful, as his eyes would all sleep at different times. Honestly, Hera could have saved herself the bother, and used a dolphin, as they sleep with one eye open.

61. The ‘best’ spider eyes belong to the jumping spiders, the wolf spiders, crab spiders, huntsmen and ogre-faced spiders. These are not passive predators, but active ones, and they need to see what they are doing.

62. Spiders in the genus *Deinopis*, also known as gladiator spiders, hunt at night using a net of silk which they drop onto unsuspecting prey from above. The extraordinary feature of these eyes is that the spiders resorb the light-sensing microvilli during the day time, and then grow them again each night, in order to protect the photopigment from bleaching. Imagine if we digested our eyes each night, and grew them again in the morning! It would make it harder to get to the bathroom in the middle of the night.

63. Some web-building spiders have strange, unfocused lens/mirror combinations. It’s thought that they’re celestial eyes, involved in navigation. But maybe they can see ghosts.

64. The reason that cat’s eyes glow is because of a layer of tissue called the *tapetum lucidum*. Literally translated, this means a ‘silvery carpet’. These iridescent layers are startlingly beautiful, like opals. In the poetic words of Land and Nilsson, the function of the tapetum is to ‘double the light path [back] through the photoreceptors and so improve their photon catch’. Some of that light bounces back directly out of the eye without being absorbed, giving the characteristic eyeshine.

65. The Tapetum lucidum is made out of many different materials in different animals: guanine in most fish; riboflavin in bush-babies; the zinc salt of cysteine in cats; tiny spheres of fat or melanin in teleost fish; collagen in ruminants like cows.

66. Light reflecting out of the eyes is actually a bit of a problem for many animals. About 4% of incident light bounces straight off our cornea. If you are hiding from a predator, you don’t want your eyeshine to give you away. The surface of our eyes does reflect some light, but not very much, except in the case of my friend Ben. He has the most gorgeously reflective eyes, and there is consequently always a twinkle in them. This was a huge advantage when he worked in music theatre, and he was perfectly cast in *My Fair Lady*. As as I pointed out to him grimly, he wouldn’t last long in the jungle.

67. Humans solve this problem in their optical instruments by coating the glass with magnesium fluoride. It’s not to protect their instruments from predators; there is little danger of a microscope being stalked by a tiger. It’s just to increase the light available for looking.

68. The reason that seals look so irresistible, with their great limpid eyes, is that they have a flattened cornea, the front surface of their eye. The flat surface reflects more light than a curved surface like ours.

68b. This helps them to see in both air and water. This solution is seen also in diving birds like penguins and in some rock-pool fish. The rock-pool fish *Mnierpes macrocephalus* has incredibly flat corneas, which would restrict the field of view, and cause serious distortion at the edges. Its solution? Two separate corneas, pointing in two different directions!

69. Moths and butterflies have a so-called ‘nipple array’ on their eyes. These nipples interfere with the light waves, reducing reflectivity to near-zero. The taller the nipples, the less light reflects from the eyes.

70. In my textbook, there is a reference to a rather charming portrait taken by H.E. Eltringham of his friend Sir Edward Poulton ‘through the eye of a glow-worm’. At first glance, this seems like standard imagery from a Romantic poet, but the more one considers, the more nightmarish it becomes.

71. The brownsnout spookfish, *Dolichopteryx longipes,* is very famous, as it has two eyes, one using a lens, and the other a mirror, to focus light. It looks upwards for silhouettes with a lens, and simultaneously downwards with a mirror, for bioluminescent flashes.

71b. The remarkable thing about this mirror is that it is not one single surface, but a whole sequence of discrete mirrors, arranged along a concave surface. Each one is a stack of guanine crystals, and they are arranged at increasing angles along the backing membrane. This is a very clever solution – one single curved surface over such a wide angle (48 degrees) without a lens would result in severe spherical aberration (the light rays would all converge in different places). By having a whole sequence of tiny mirrors arranged in this way, the spookfish gets the top bang for its buck – an excellent image over a very wide angle.

72. The humble lobster also uses mirrors, rather than lenses, in its superposition eyes as a focusing device. It has a whole series of tapered boxes, which are coated with mirrors. By a fiendishly clever mechanism, the light is reflected out of the mirror boxes in the same direction it entered, only much deeper in the lobster's head.

72b. Superposition eyes are very special compound eyes. Unlike all the other compound eyes, they don't produce multiple inverse images, but one single erect image, which lies relatively deep within the eye. Sigmund Exner suggested in 1891 that the only way this could be achieved was with a two-lens system, which could 'dog-leg' the light beam effectively. Dog-legging means to pass the beam back across the imaginary central access of the optical system – ie a sharp angle of reflection.

72c. When scientists armed with interference microscopes set out to probe his theory in the 1950s, they made the unfortunate decision to look at crayfish eyes, and could find no lenses, only jelly with a disappointingly low refractive index. What was going on?

72d. It turns out that crayfish use mirrors, not lenses, to achieve the dog-leg. Exner was correct, and with the exception of crayfish and their relatives, almost all other species use a two-lens system, with the exception of some crabs.

72e. Exner predicted that the lenses he actually saw in Nature would not have enough refractive power to achieve the dog-leg, given their refractive indices and curvature. He proposed that the lenses must have a variable refractive index from the periphery to the centre, and indeed, this is exactly what we see in Nature. The horshoe crab, *Limulus*, uses a series of inward-pointing conical projections with a refractive index gradient, which direct the light down towards the rhabdom by ray-bending. Think of it as a person walking a dog – the further the dog goes from the direction of travel, the harder the person pulls on the lead, until the dog points in the right direction again.

72f. The long-bodied decapod crustaceans have my favourite solution of all. Their eyes are made up of tapered mirror boxes. They are exactly the right length to ensure that the light will reflect off the mirrored walls twice as it travels down the box, and this has the remarkable result that the light ray exits the box travelling in the same direction that it entered. Whatever their angle of incidence, the rays are reflected through two right angles, and thus emerge in the direction they came from, preserving the directional information of the light ray.

72g. There is another type of eye, discovered in 1988 in a swimming crab. It's called a parabolic superposition eye, and it's a little bit like an intermediary between an apposition eye and a superposition eye, using both lenses and mirrors. But I just can't face trying to describe it at the moment.

73. In the benthic fish genus *Ipnops*, the eyes are reduced to flattened, bony photosensitive plates. The glasshead barreleye has a transparent dome-shaped head, to allow the eyes to look directly upwards. The surface-feeding fish *Aplocheilus* has two separate visual streaks, which are able to provide it with two different views of the prey item in the same eye – one from below,

and one from just *above* the water surface. You may not think this is feasible, but refraction makes all things possible!

74. *Anableps anableps*, a fish from South America that cruises with half of its eye above the water, and half below, has evolved a double pupil system, with two associated retinas, one for the air, and one for the water. Truly remarkable. I was first told about this fish at breakfast in St John's one Sunday morning, by Dr David Williams.

75. I suppose the solution is a bit like bifocal glasses.

76. The scallop also uses mirrors in its eyes. You may not know that a scallop has eyes, but they are very beautiful, like tiny blue pearls scattered along the mantle. At the back of the eye is a hemispherical mirror, the argentea, which focuses the incoming light onto the receptors which sit in front of it. Thus, if you look into a scallop's eyes, you will see yourself reflected. How poetic.

77. We can find mirror eyes in the deep-sea ostracods *Gigantocypris* and the amphipod *Scypholanceloa*. But in both cases, the mirrors and the retinae are strangely shaped. In *Scypholanceloa*, the upper mirror is highly curved, and looks more like a rabbit's ear than an eye. It's sight Jim, but not as we know it.

78. The mirrors in animal eyes are generally constructed to take advantage of the same physical effects that give a soap bubble its colours. The colours in a soap bubble result from interference between the light waves reflected off the top of the bubble's skin, and the light waves reflected off the bottom of the skin. The colour is all to do with the relationship between the thickness of the bubble and the wavelength of the incoming light.

79. A single film will only reflect a few percent of incident light, but if you stack a whole load of layers, each a quarter wavelength thick, and a quarter wavelength apart, you can get close to complete reflection. This is how animal mirrors work, and it's very different from the mirror on your bathroom wall, which probably uses one sheet of very flat aluminium.

80. By varying the distance between the layers and the thickness of the layers, you can also produce colours, which are described as structural, rather than pigmentary.

81. These structural colours are very common in nature: peacocks, butterflies and many fish. The birds of paradise inflate little rodlets of melanin with nitrogen, turning them into flattened plates. The blue stripe of the neon tetra is produced in a similar way. It can be 'turned off' at night by a mysterious mechanism that changes the spacing between its plates, moving the reflectance peak into the ultraviolet spectrum.

82. The Greeks believed in the so-called 'emission theory' of sight. I probably shouldn't tar all the Greeks with that brush, but that's history for you. The idea was that Aphrodite kindled a fire in our eyes, and that fire shone out of the eyes and illuminated objects. It's pretty hard for me to put myself in their shoes – I can't quite see how they thought it worked, but hindsight is a wonderful thing. Plato believed in it, apparently Euclid questioned it, and good old Lucretius

actually got things bang-right (literally describing Einstein's 1905 paper on the photoelectric effect).

83. Hasan Ibn al-Haytham was supposedly the first one to suggest in his manual on optics, *Kitab al-Manazir*, how sight actually works. I don't mean to boast, but I'm fairly sure if I had been around in Ancient Greece, I would have been **very** dubious about emission theory. The trouble with living in the 21st century is that all the low-hanging intellectual fruit has been taken. There are no easy thoughts left to have. If you don't have a hadron collider to hand, all you can do is point out the parallels. I went through a maddening period where every time I thought I had had a new idea, it turned out that Max Weber had thought it about a hundred years before. Now I have completely given up on having any original ideas.

84. The Greek Philosopher Diogenes supposedly lived in a barrel. He had this in common with *Phronima sedentaria*, a deep-sea amphipod which has extraordinary 5mm long light guides, which convey light from the lens to the distant retina. Its barrel is gruesome. It takes a salp or a pyrosome, and hollows out the inside, scraping away all the soft tissue until just the barrel is left. It then lives and raises its young in the barrel. If you think this is monstrous, I refer you to your own leather shoes, or the Kiribati helmets made of pufferfish – it's really not that different.

85. The salp is a tunicate, like the sea squirt. Sea squirts have eyes as larvae, and then, in a cruel trick of mother nature, lose them when they settle down as adults. But if you can't move, there's not much point having eyes.

86. That seems as good a place as any to stop. Thank you for reading!