Feature Article

The Night Begins to Shine: The Tapetum Lucidum and Our Backward Retinas

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The “argument from poor design” as evidence for evolution dates back to Charles Darwin himself. The dysteleological argument, as it is formally known, goes something like this: If the world and everything in it were created by an omniscient and omnipotent creator, why are there such clear examples of quirks and glitches in living organisms, including humans? The argument is seldom used as evidence against the *existence* of God but rather as evidence against creationism as the explanation for how life unfolded on the planet.

On the other hand, if we accept universal common descent, as all the available evidence supports, we understand that the randomness of mutation, gene duplication, horizontal transfer, and other unguided molecular tinkering is the source of all variation. Further, we appreciate how natural selection, genetic drift, etc., have shaped the history of all species, and we fully expect instances of suboptimal design at all levels of life—from molecules to ecosystems. Evolution is aimless, clumsy, and cruel.

The vertebrate retina has often been held as a prime example of poor design in nature because it appears as though the photoreceptors are wired in backward—that is, they face in the backward direction rather than facing toward the incoming light (Miller 2005; Novella 2008). Many evolutionary theorists have mused about this curious arrangement (Dawkins 1986; Lents 2018). It would be strange enough that the photoreceptors are nestled behind several layers of tissue with vasculature interspersed, which prevents a clean capture of incoming light and reduces sensitivity. But what makes this even more strange is that cephalopods have the same type of retina but with the photoreceptors facing forward in the logical way (Figure 1).

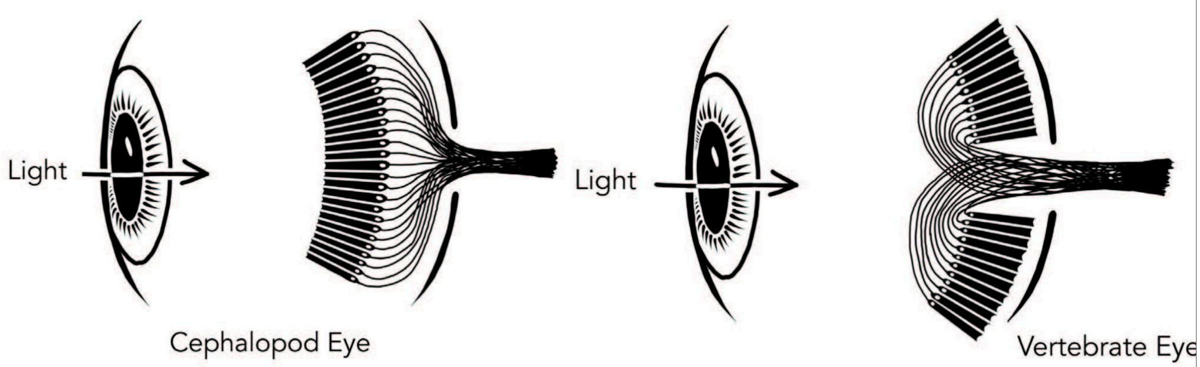

Figure 1. The inverted orientation of vertebrate photoreceptors. Image by Donald Ganley from Human Errors (Lents 2018).

Cephalopods (squids, octopi, and nautiloids) have the same type of camera-like eye that vertebrates have, a striking example of convergent evolution (Serb and Eernisse 2008). But there are several profound differences, including the genetic and developmental programming, that reveal the separate origins of the vertebrate and cephalopod eyes. The inverted nature of the photoreceptor cells relative to one another is another striking difference between them.

The more straightforward arrangement found in cephalopods allows an unbroken sheet of photosensitive neurons with their axons projecting backward and collecting into the optic nerve. The inverted arrangement found in vertebrates, however, means that the axons project forward. This adds to the tissue that stands between the light and the receptors and, worse, forces the axons to converge *in front* of the retinal layer and then plunge back through the retina in the posterior direction to head to the brain (Ramachandran 1992).

The point at which the photoreceptor axons bundle together in vertebrates is called the optic disc, which creates a blind spot not far from the center of the visual field. In humans, this blind spot is rarely noticeable because of how much the visual fields of our two eyes overlap, but in animals with a wider field of vision, whose eyes face more to the sides of their heads, such as most birds and mammals other than primates, the blind spot is a real hinderance (D'Ombrain 1936). (For a good demonstration of how to find your own blind spot, see Lohner and Science Buddies 2020.) This is why scientists have called the vertebrate retina an example of poor design. There is no reason the photoreceptors must be oriented backward, and it comes with real costs that they are.

Creationists, of course, take umbrage with this claim. Intelligent design proponents in particular have mounted a rigorous defense of the design of the vertebrate retina, noting several adaptations in vertebrates that enhance the visual acuity and maximize photodetection that are not present in cephalopods—though they have not managed to get their arguments published in peer-reviewed scientific journals (Bergman and Calkins 2005). Examples include the matching of blood vessels with metabolic demand and neural circuitry that compensates for the light scattering that occurs when photons pass through tissue to reach the photoreceptors (Figure 2).

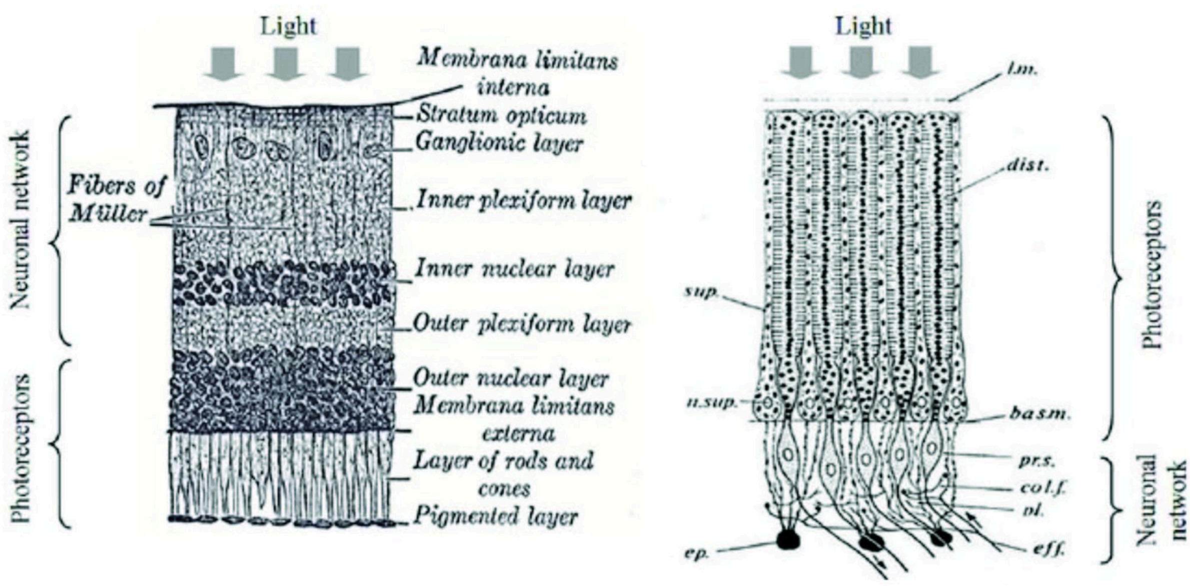

Figure 2. Tissue layers in the vertebrate retina (left from Gray 1878) and the cephalopod retina (right from Young 1962). The latter is far simpler and more streamlined.

This completely misses the point. These adaptations are only necessary because the retina is inverted to begin with. These are compensatory co-adaptions to *make up for* the inverted nature of the vertebrate retina. And that's why they aren't found in cephalopods.

In a paper published in the October 2022 issue of *Bioessays*, Gerald Barclay, Sam Vee, and I argued that the tapetum lucidum is another such compensatory adaption (Vee et al. 2022). The tapetum is a structure in some vertebrates that lies just behind the photoreceptors and reflects incident light back toward the front of the eye, leading to the phenomenon of *eye shine*. This photoreflection creates a second chance for photons that initially slip past the photoreceptors to collide with them as they make their second pass though the retina. As such, the tapetum considerably boosts detection of light in dim conditions (Hesse and Willemse 2012).

Not all vertebrates have tapeta. They are found almost exclusively in nocturnal land animals and fish that live in murky or deep waters. This makes sense because only in such environments would the tapetum offer much value. However, what is most surprising about the tapeta is the incredible amount of diversity there is among the various species that have it. There are many kinds of tapetum that display totally different physical structures, cellular organization, locations within the retina, and even the materials with which they are constructed. For example, some tapeta are made of coiled collagen fibers, others are made of stacked zync cysteine crystals, while still others are made of guanine or riboflavin (Ollivier et al. 2004).

We performed a phylogenetic analysis and found that the many types, histological arrangements, and chemical compositions of the tapetum are the result of numerous instances of convergent evolution. The tapetum appears to have evolved, disappeared, and evolved again countless times throughout the vertebrate clade (Figure 3).

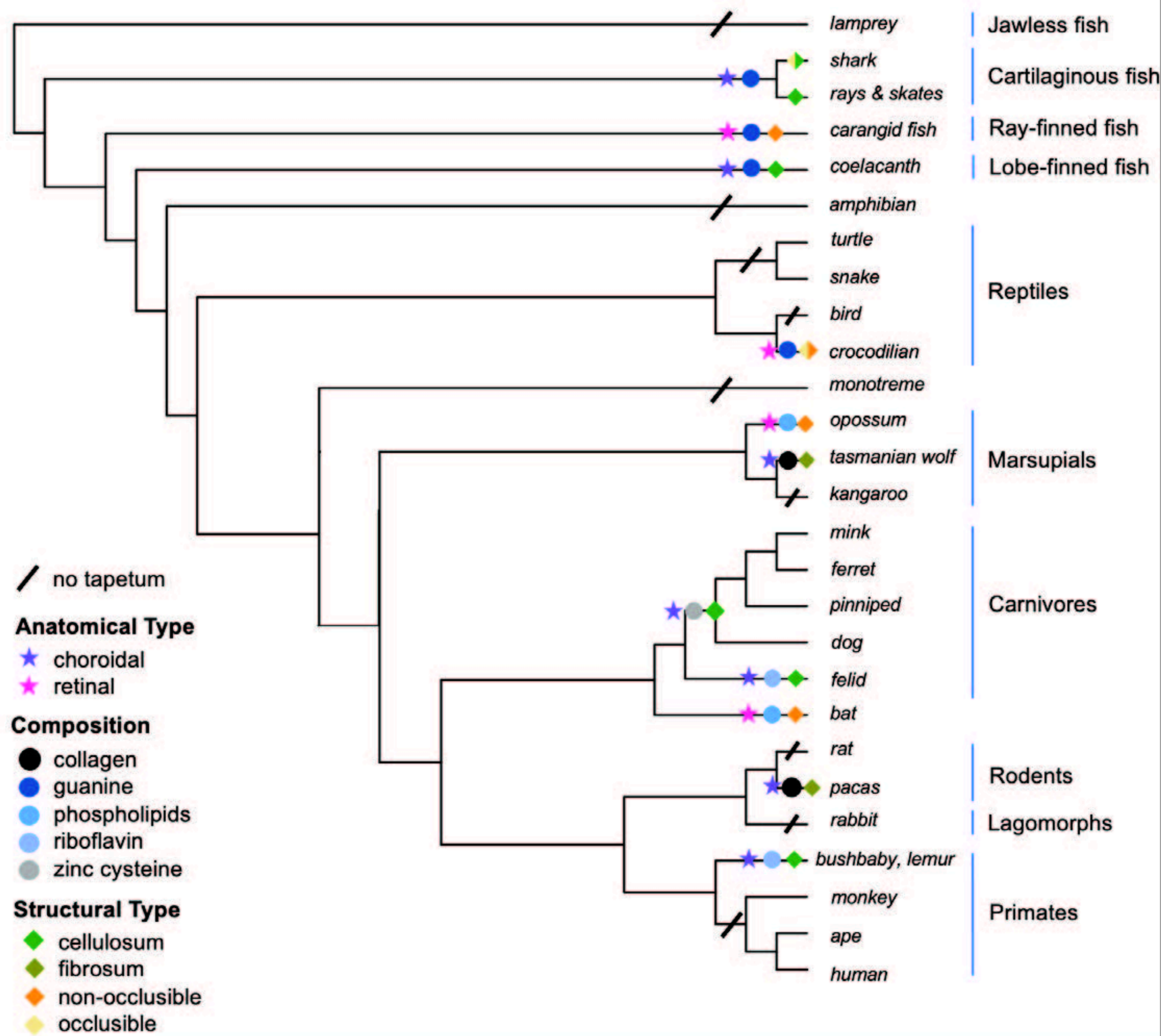

Figure 3. Phylogenetic tree of the many types, structures, and compositions of the tapetum lucidum in vertebrates (Vee et al. 2022; used with permission)

However, cephalopods do not have a tapetum. This is telling because cephalopods have the same type of eyes and occupy the same murky waters as many of the fish species that do have tapeta. And cephalopods have an even older evolutionary origin than vertebrates, so they have had more time to evolve this highly advantageous structure. And yet, as far as we know, they never have.

The reason we propose that cephalopods have not evolved a tapetum is the cephalopod retina, with its forward-facing photoreceptors, is already as optimized as it can possibly be for the capture of photons under conditions of dim light. Indeed, while direct comparisons have not been made, experiments with isolated retinas have revealed that octopus retinas rival the photosensitivity of felines, the most sensitive known vertebrate retinas (Wood et al. 1987). And they do so without a tapetum. With their axons projecting backward, the cephalopod photoreceptors can pack together tightly and form an unbroken sheet of photosensitive tissue, which, besides being simpler, is also more efficient, allowing a more streamlined retinal architecture (see Figure 2). In vertebrates, however, a tapetum is required to capture every last photon because so many of them slip past the photoreceptors on their first pass.

It may also be possible that there are some genetic or microanatomical constraints in the cephalopod retina that preclude the emergence of the tapetum. However, the sheer number of ways that the tapetum evolved in vertebrates argues against this.

Further, tapeta have also been discovered in spiders, insects, and crustaceans, which have an entirely different kind of eye (Benson and Suter 2013). And, again, the presence and absence of the tapetum throughout the various clades of arthropods argues for repeated instances of convergent evolution. Within the compound eyes of spiders, there are two distinct retinas. The primary one has its photoreceptors oriented in the verted arrangement, like cephalopods, while the secondary retina is inverted, reminiscent of the vertebrate retina. In some spiders, these inverted secondary retinas have tapeta, while the primary retinas do not have tapeta (Morehouse et al. 2017). Yet again, we see a correlation between the inverted retina and the necessity of a tapetum to assist in photosensitivity.

We therefore offer the hypothesis that the tapetum lucidum is a compensatory co-adaptation in the vertebrate retina made necessary by the inverted arrangement of the photoreceptors.

Experiments to test this hypothesis are challenging but possible. For example, scientists could make direct comparisons of the photosensitivity of isolated cephalopod and vertebrate retinas *in situ*, with and without tapeta, followed by the grafting of a tapetum onto a cephalopod retina to observe if photodetection is enhanced. These types of experiments require a great deal of care and many controls, but it should be possible to test this hypothesis. The testing of predictions made by hypotheses is the hallmark of science and a key feature that separates scientific ideas from pseudoscientific ones such as intelligent design.

It is our hope that this hypothesis will provoke robust discussion and future research that will either refute or lend support to this idea. Even if it is proven incorrect, the theoretical and experimental work that this hypothesis inspires will help to *illuminate* the function and evolution of the vertebrate and cephalopod retinas. If you'll pardon the pun.

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