

## HYPOTHESES

## Insights &amp; Perspectives

# The glow of the night: The tapetum lucidum as a co-adaptation for the inverted retina

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## Abstract

The vertebrate retina is said to be inverted because the photoreceptors are oriented in the posterior direction and are thus unable to maximize photodetection under conditions of low illumination. The tapetum lucidum is a photoreflexive structure located posterior to the photoreceptors in the eyes of some fish and terrestrial animals. The tapetum reflects light forward, giving incident photons a “second chance” to collide with a photoreceptor, substantially enhancing retinal photosensitivity in dim light. Across vertebrates (and arthropods), there are a wide variety of tapeta that vary in structure, chemical composition, and even tissue architecture, indicating repeated convergent evolution. To date, the tapetum has not been observed in any cephalopod, however, which also possess a camera-like eye, but with the retinal photoreceptors oriented in the anterior direction. We therefore hypothesize that the tapetum lucidum is a compensatory adaptation for the suboptimal design of the inverted retina of vertebrates.

## KEYWORDS

cephalopods, evolution, photoreceptors, retina, tapetum lucidum, vertebrates

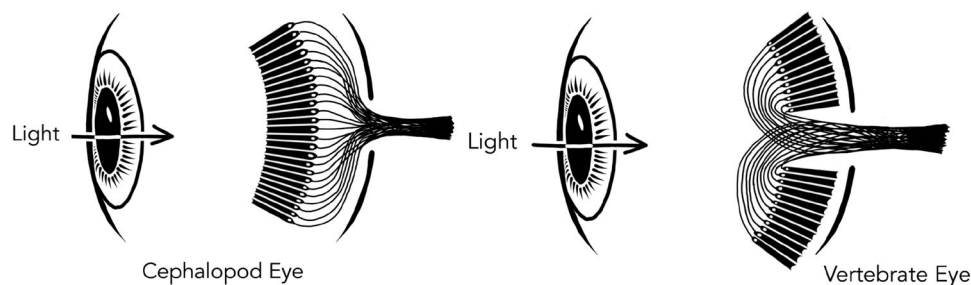
## INTRODUCTION

In the animal world, there are a wide variety of eye types that have evolved independently in at least ten separate clades.<sup>[1]</sup> The eyes of vertebrates, however, are all descended from a common ancestor proto-eye that first appeared during the Cambrian diversification some 540 million years ago. The first proto-eyes were flat eyespots on the outer surface of the body which later invaginated to multicellular eye cups, bringing the ability to detect directionality, rather than just vague ambient light conditions. The light-sensing organs then evolved and developed rapidly, driven by the enormous selective advantage brought by this unique form of sensation-perception.<sup>[2]</sup> The impressive power of animal visual systems was likely the result of an evolutionary arms race among predators and prey.<sup>[3]</sup>

The most sophisticated and powerful type of eye is the camera-style eye of vertebrates and cephalopods (squids, octopi, and nautiloids) complete with an aperture, lens, and a two-dimensional photosensitive surface in which visual information is conveyed to the central

nervous system via an optic nerve. In a remarkable example of convergent evolution, the camera eye evolved independently in these two lineages. This homoplasy is obvious because, while the two eye types are almost identical in concept, they harbor profound structural, biochemical, and genetic differences that reveal their independent origins. Nevertheless, recent work has shed light, so to speak, on the parallel genetic mechanisms involved in the evolution of these two eye types.<sup>[4]</sup>

One of the gross structural differences between the vertebrate and the cephalopod eye is the orientation of the photoreceptors within the retina.<sup>[5]</sup> While the cephalopod photoreceptors are oriented toward the aperture, vertebrate photoreceptors are pointed *away* from the incoming light, which is why the vertebrate retina is often called *inverted* (Figure 1). This odd arrangement requires histological accommodation to allow photons to travel through several tissue layers in order to reach the receptors. Worse, the inverted retina necessitates the existence of the *optic disc*, where the axons of the photoreceptors converge into a bundle – the optic nerve – causing a blind spot



**FIGURE 1** The retinas of cephalopods and vertebrates. This cartoon shows how the inverted nature of the photoreceptor cells within the vertebrate retina makes the optic disc necessary and the resulting blind spot unavoidable. Image by Donald Ganley, from *Human Errors* (Lents, 2018),<sup>[6]</sup> used with permission.

that vexes all vertebrates to this day. The *verted* retina of cephalopods has no optic disc, no blind spot, and the photoreceptors can pack together more tightly, allowing maximal absorption of incident light. Some ophthalmologists believe that the inversion of the retina contributes to retinal detachment in vertebrates, a condition that has not been observed in cephalopods.<sup>[6]</sup>

Some vertebrates have a structure known as the *tapetum lucidum* behind their retinas. This crystalline structure reflects light back towards the front of the eye and is responsible for the “eye shine” that is observed in some animals when their eyes are illuminated at night.<sup>[7]</sup> This adaptation is found in a variety of mostly nocturnal land animals and aquatic animals found in murky or deep waters, as the reflection of light forward aids visual perception under conditions of low illumination. Interestingly, there are several types of tapeta lucida, which vary markedly in their structure and chemical composition, indicating, yet again, convergent evolution of this highly adaptive structure.<sup>[8]</sup> On the other hand, the tapetum lucidum has never evolved in any cephalopod species despite the fact that they are heavily reliant on vision for hunting, predator detection, and reproductive success, and many species occupy the same dimly lit habitats as aquatic vertebrates that have evolved this adaptation.<sup>[9]</sup>

## The hypothesis

We therefore present the hypothesis that the tapetum lucidum is a co-adaptation that compensates for the inverted nature of the vertebrate retina in animal lineages in which visual detection under low levels of illumination presents a strong selective pressure. Conversely, the *verted* cephalopod retina requires no such compensation, explaining the lack of this co-adaptation in squids, octopi, and nautiloids.

## Evolution of the vertebrate eye

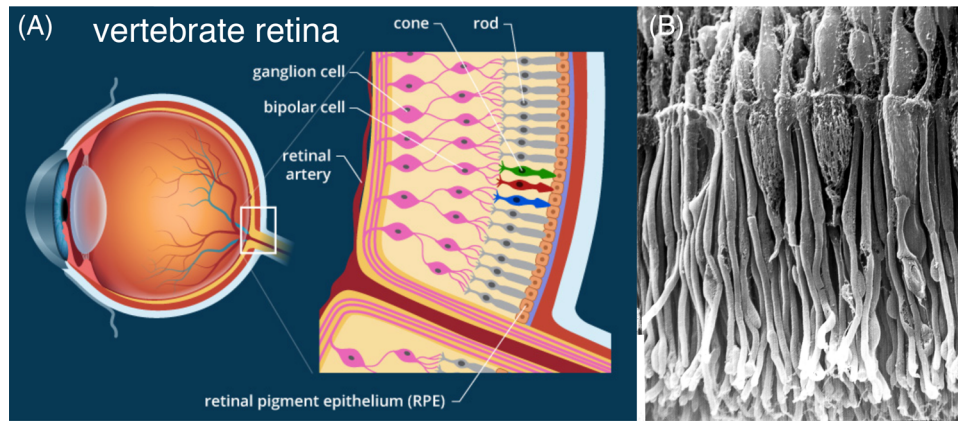
The evolution of the eye was a crucial step in the lives of early vertebrates, allowing them to meet the challenges of surviving in the ancient aquatic landscape.<sup>[10]</sup> Though initially crude in their functionality, early eyes established a structural chassis that was continually improved upon in various ways throughout the sprawling tree of verte-

brate biodiversity. The fossil record shows that the evolution of jawed and jawless fishes, including lampreys, hagfish, cartilaginous fishes, and lungfish, occupy critical stages in the evolution of the vertebrate body plan. As such, these evolutionary-developmental milestones also provide insight into the evolution of vertebrate photoreception.<sup>[11]</sup>

The ability to detect and identify prey and predators was one of the major drivers of speciation among animals in the Early Cambrian period.<sup>[3]</sup> This put tremendous selective pressure on the image-forming eye to evolve the ability to discriminate colors and strike an optical balance between resolution and sensitivity in the murky waters of the Cambrian ocean. Many of the ocular features that evolved in this period are retained in extant animals. Millions of years later, some vertebrate lineages transitioned from dim, low-light underwater environments to terrestrial habitats with light exposure in a broader wavelength spectrum and much higher intensity, and the eye adapted in turn.

The vertebrate retina is located on the inner rear surface of the eye and contains specialized cells known as photoreceptors that respond to photon bombardment<sup>[12]</sup> (Figure 2). The two types of photoreceptors in the retina are rods and cones, which work independently during the phototransduction phase of visual sensation.<sup>[13]</sup> Structurally, these photoreceptors are distinguished by their shape: the outer segments of rods are cylindrical while those of cones are tapered, hence their names. Rods detect changes in brightness, shape, and movement and only contain a single type of light-sensitive pigment. Cones can have separate pigments for responding to photons in the red, green, and blue ranges of the visible wavelength spectrum, but are less sensitive, which explains why color vision is mostly or completely impaired during conditions of low illumination.

The overall process of capturing a photon and transforming it into a biochemical signal in order to produce an image involves a variety of chemical reactions that are similar in all eye types due to both homology and homoplasy. The spectral sensitivity of rod versus cone photoreceptors reveals that color vision was an early adaptation in vertebrates and an effective means to manage the tradeoff between resolution and sensitivity.<sup>[14]</sup> This evolutionary event likely occurred near the origin of jawed vertebrates, as the eyes of lampreys and other jawless fishes possess only cone-type receptors. Gene duplication and diversification drove the emergence of rod and cone photoreceptors found in jawed fishes and their tetrapod descendants.



**FIGURE 2** Placement of the photoreceptor cells within the vertebrate retina. (A) Cartoon of the cell layers of the human retina. Image courtesy of All About Vision. (B) Scanning electron micrograph of a primate photoreceptor cells. Image courtesy of Dr. Ralph C. Eagle, Jr.

## Verted and inverted retinas

In the camera-type eye of both vertebrates and cephalopods, light passes through an aperture known as the pupil, is focused by a crystalline lens, and is directed onto the retina, where rods and cones translate visual information to electrical signals. The optic nerve sends this information to the brain, which then produces an image by a process called bottom-up visual processing. The retina plays a major role in this process and functions similarly across both cephalopod and vertebrate species.<sup>[15]</sup>

In the inverted retina of vertebrates, the light-sensitive photoreceptor cells are oriented toward the posterior direction while the axons of these neurons protrude in the anterior direction and synapse with bipolar neurons or with the ganglion cells directly (Figure 3A).<sup>[16]</sup> In this architecture, light must pass through two distinct layers of transparent cells including bipolar, horizontal, amacrine, and ganglion cells, along with associated capillaries and extracellular matrix, before reaching the photoreceptors (Figure 3C). This leads to a considerable amount of light scattering, which must be compensated for by sophisticated signal modulation that is not yet fully understood. Further, the ganglion cells, the axons of which converge and bundle to form the optic nerve, form the most anterior tissue layer, forcing the optic nerve to cross through the retina as it heads toward the brain. This forms a structure called the optic disk, which results in a “blind spot” in which the retina cannot respond to light.

On the other hand, verted retinas place their photoreceptors in the most anterior position and the processing neurons and capillaries are located in posterior tissue layers. This eliminates the optic disk and its associated blind spot altogether (Figure 3C). In addition, the anterior placement of the photoreceptors allows them to capture light before it passes through layers of cells, preventing any light scattering by tissue and microvasculature in the retina (Figure 3D). The neuronal network of cephalopods, located posterior to the photoreceptor cells, is thinner and lacks bipolar neurons and ganglion cells, as shown in the circuitry diagrams in Figure 3A,B. While the tissue architecture of the vertebrate retina is more complex, it may very well be that the greater sophistication is necessary to compensate for the inverted orientation of the photoreceptors. The verted cephalopod retina exhibits a more

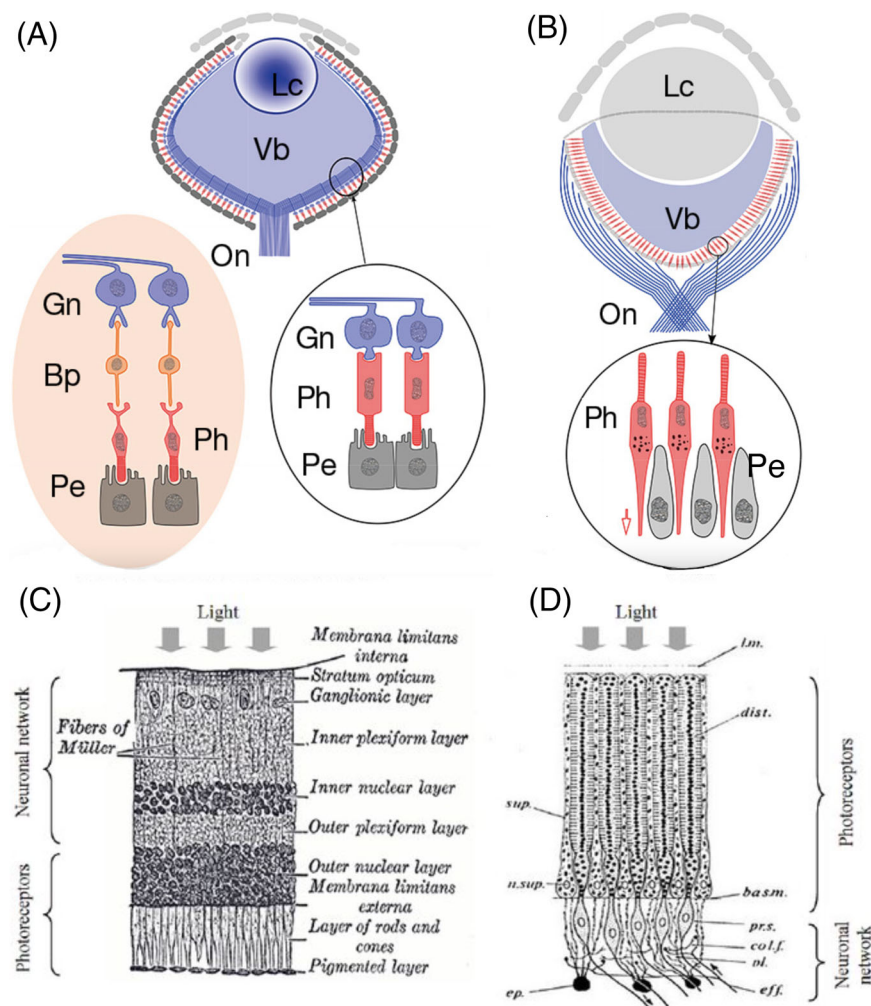
streamlined tissue architecture with fewer cell layers and yet still achieves a high degree of visual acuity. Despite their conceptual similarities, the structures of the verted and inverted retinas are wholly different.

## Function of the tapetum lucidum

The vertebrate retina harbors a variety of accessory adaptations to maximize the capturing of light, particularly in species endemic to poorly illuminated environments. Among these is the tapetum lucidum, an acellular crystalline layer located posterior to the photoreceptor cells. The TL, or simply the tapetum, serves as a retroreflector of light that passes through the tissue layers of the retina, bouncing it back in the anterior direction.<sup>[7]</sup> This reflection creates a “second chance” for photons that slip past the photoreceptors in their initial pass to successfully collide with a photoreceptor, substantially enhancing the overall photosensitivity of the retina. Therefore, the tapetum is responsible for the “eye-shine” phenomenon seen in some animals. Because light is bounced back along the same path from which it originated (retroreflection), there is minimal loss of optical contrast and sharpness, that is, the incident and reflected light are precisely matched. Tapeta have been shown to enhance light capture by nearly 50% in very low levels of illumination, making clear the advantage conveyed by these structures.<sup>[9]</sup>

Throughout vertebrates, there are a variety of tapeta that differ substantially in structure, organization, and chemical composition. As discussed in the seminal work on the tapetum lucidum in mammals,<sup>[18]</sup> this structure exhibits a striking amount of diversity throughout vertebrates. While all tapeta function to increase retinal sensitivity, each type does so through a distinct mechanism. In fact, it appears that the TL of some species has adapted to maximally reflect the wavelengths of light most relevant to the respective ecological niche.<sup>[9]</sup> This argues that the structure has been subject to intense selection and refinement and thus confers considerable survival advantage.

This is reflected in the differences in chromatic quality of the TL between species, particularly those with pigment-reflecting crystals.<sup>[9]</sup> For example, Arctic reindeer may cope with extreme changes in



**FIGURE 3** Structural comparison of verted and inverted retinas. A and B) Drawing (Carreras, 2018)<sup>[16]</sup> of the neurons within the (A) inverted retinas of vertebrates and (B) verted retinas of cephalopods. Lc, lens cells; Vb, vitreous body; Ph, retinal cells; Pe, pigment epithelium; On, optic nerve; Bp, bipolar; Gn, ganglion cell. (C and D) Drawing of the histology of (C) the inverted retinas of vertebrates (Gray, 1878)<sup>[17]</sup> and (D) the verted retinas of cephalopods.<sup>[5]</sup> Images used with permission or are in the public domain.

light conditions between the summer and winter by changing the wavelength reflection of their TL.<sup>[19]</sup> In the summer, their TL shines golden-yellow, with more light reflected back through the retina. In the winter, however, their TL shines predominantly blue and boosts retinal sensitivity. In fact, most mammals appear to share this chromatic quality in their TL, with blue areas surrounding a golden interior. Due to this configuration, the central retina becomes saturated with long wavelengths to which rods are less sensitive, while the exterior regions of the TL appear more blue, are more sensitive to low light conditions, and can capture more light.

The vertebrate tapetum lucidum first evolved in fish, allowing them to better detect prey and predators as they navigate through the low light conditions in murky waters.<sup>[20]</sup> Remarkably, some fish may be able to communicate with their tapeta lucida. For example, it is believed that flashlight fish use eye-shine to detect and communicate with conspecifics. On the other hand, TL-mediated eye shine may also have negative consequences as it draws attention from predators, especially in dark environments. Thus, the migration of retinal epithelial pigments within the tapeta lucida may have evolved in some fish species to limit the exposure of eye shine, even at the cost of reducing the effectiveness of the photoreflexion. This type of tapetum is said to be occlusible.<sup>[7]</sup> The conspicuous nature of eye-shine may also help explain why the

tapetum has been lost in many lineages in which it does not directly enhance survival. On the other hand, the black dragon fish (*Malacosteus niger*) is capable of bioluminescence and possess photophores that emit red light unrecognized by other deep-sea animals. In conjunction with a diffused and red-pigmented tapetum, these fish can visualize prey and communicate with conspecifics, while evading detection from predators.<sup>[21]</sup>

Among terrestrial vertebrates, the TL is found mostly in nocturnal species, and much less commonly in diurnal or crepuscular ones, for obvious reasons.<sup>[9]</sup> Perhaps the most striking and well developed tapeta in the Animal Kingdom are those of crocodilians. While crocodilians also have a very well developed sense of smell, they employ a stalking hunting strategy that is highly reliant on vision. Further, most crocodilians pinch their nostrils shut while underwater, cutting off olfaction entirely. Thus, their niche of nocturnal hunting in murky waters makes night vision a key adaptation for crocodilians, a function that is aided significantly by their tapeta.

Besides crocodilians, the only other class of terrestrial vertebrates that harbor tapeta are the mammals. This is not surprising because night vision may have been a key adaptation early in their evolutionary history.<sup>[9]</sup> In fact, many diurnal mammals appear to have vision that is better adapted for night vision than daytime vision, leading



some scientists to propose that nocturnal adaptations were an evolutionary bottleneck in early mammals as they survived mostly in the shadow of the Mesozoic megafauna, the dinosaurs.<sup>[22]</sup> It is further speculated that the impressive olfactory and auditory senses of many mammal taxa were compensatory adaptations in the face of poor visual acuity (a phenomenon that was reversed in the primate lineage). Within mammals, tapeta are generally restricted to nocturnal carnivores, underscoring the principle that night vision is more crucial to carnivores than to herbivores. Indeed, one of the visual specializations that is vital for many herbivores is precise wavelength discrimination, that is, color vision, which tends to operate only under conditions of abundant illumination, owing to the fact that color-sensitive cones experience more “noise” in their signal transduction pathways, forcing most vertebrates to switch to color-insensitive rods under conditions of low illumination.<sup>[23]</sup>

## Types of tapeta

The two basic morphotypes of the tapetum lucidum in vertebrates are the retinal tapetum and the choroidal tapetum. The choroidal TL is located within the choroid layer found behind the retina. The choroidal TL can be further differentiated into three structural subtypes: guanine, cellulose, and fibrous.<sup>[7]</sup> Guanine tapeta consist of a palisade of cells containing stacks of guanine crystals within the choroid. Cellulose tapeta contain rectangular shaped cells stacked into layers of varying thickness that contain organized and highly refractive crystals that vary in shape and composition. Fibrous tapeta are acellular and contain stacked extracellular collagen fibrils that are weakly reflective. As shown in Figure 4, these three sub-types are structurally distinct and bear no signs of structural or chemical homology.

In contrast, the retinal TL is embedded within the retina layer itself. The tapetal layer of cells are located immediately posterior to, but often projecting directly into, the retinal pigment epithelium, which is a cellular monolayer that consists mainly of cuboidal cells adjoined to the outer segments of the photoreceptor cells.<sup>[24]</sup> The tapetal cells within the retina lack light-absorbing pigments and instead contain the reflective structures and stain darkly in micrographs, as shown in Figure 4B,C. Retinal tapeta can be composed of various substances, with guanine crystals being the most common.<sup>[9]</sup>

Tapeta can be further differentiated based on whether the tapetum is occludible or non-occludible.<sup>[7]</sup> A non-occludible tapetum consists of the otherwise nondescript semicircular zone of unpigmented reflective cells that are not regulated in any form, and the tapetal area contains little to no melanosomes, while peripheral epithelial cells contain both reflecting materials and pigmented cells.<sup>[30]</sup> On the other hand, occludible tapeta can be regulated to adjust the degree of reflection through several possible mechanisms. For example, in teleosts (most ray-finned bony fishes), migration of melanin within the retinal pigment epithelium can effectively mask the reflective surfaces, thus maximizing light absorption and inhibiting reflection.<sup>[7]</sup> Cartilaginous fishes (sharks, rays, and skates), however, use an entirely different mechanism for occluding the TL involving the migration of the retinal pigment

cells themselves. It is believed that occludible tapeta function to dial down reflection and therefore reduce eye shine that would impair concealment from potential predators or prey.

All variations of tapeta lucida have some degree of reflectivity due to the presence of several alternative layers of material with high to low reflective index.<sup>[7]</sup> Although the structural differences are pronounced, there are some similarities that are likely due to convergent evolution. For example, the hexagonal packing observed in the extracellular structures in both the choroidal fibrous TL and the choroidal cellulose TL are nearly identical in their spatial arrangement within the endocellular structures of the retinal tapetum. The precise geometry of these reflective structures coincides with the optimal wavelength of reflection for the species.

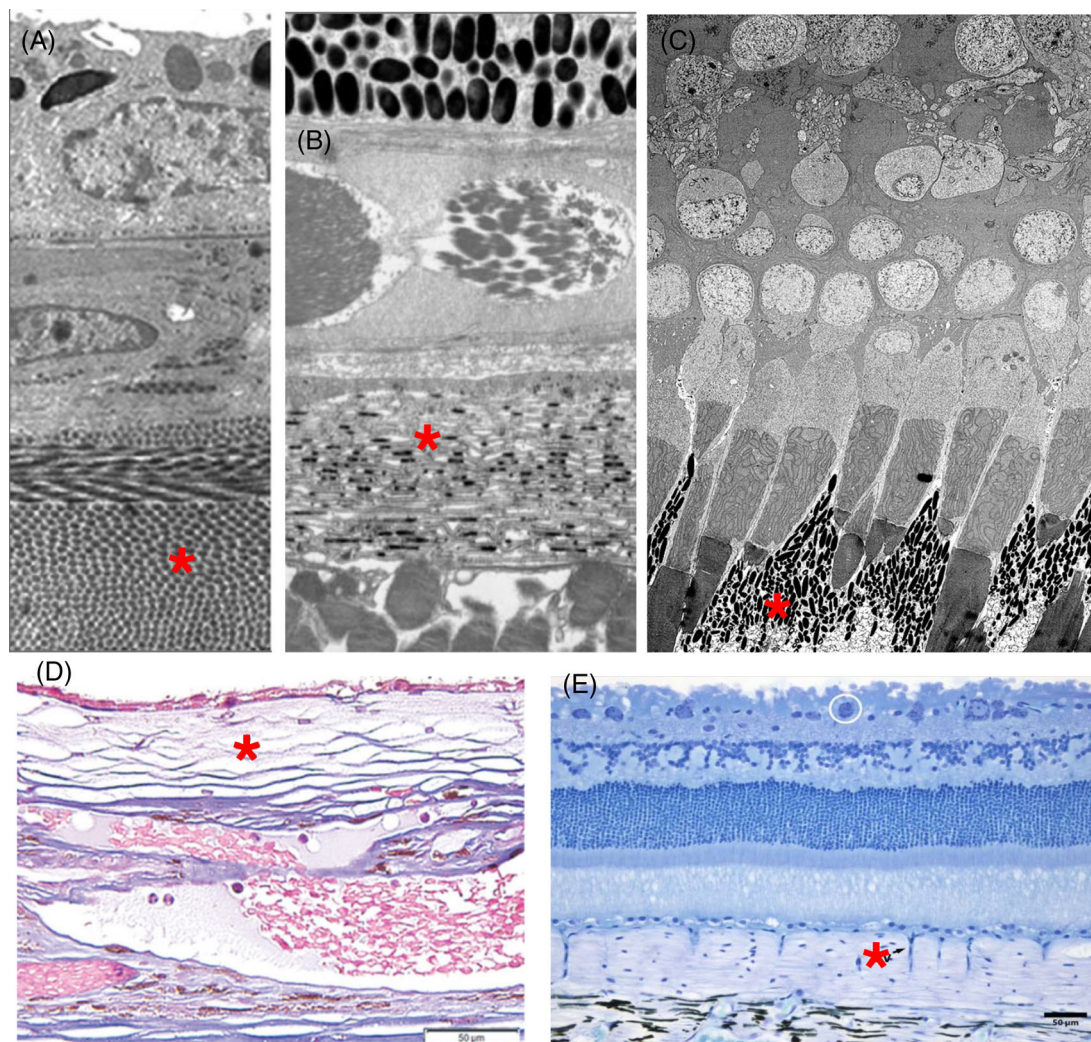
## The diversity of vertebrate tapeta

Throughout the vertebrate clade, tapeta lucida vary considerably in structure, microanatomical arrangement, and chemical composition. This diversity is especially striking considering how strongly conserved most other components of the eye are. This supports the hypothesis that the tapetum evolved independently many times in the evolutionary history of vertebrates, an hypothesis first formulated 12 decades ago.<sup>[18]</sup> Indeed, cladistic analysis supports this notion, as major classes and orders of animals have similar tapeta, while more distantly related taxa harbor entirely different ones. Even within a specific type of tapeta, for example, the retinal type, distantly related organisms exhibit analogous, not homologous, tapetal histology.

Extant fishes display considerable diversity of TL types. Jawless fish (lampreys and hagfishes) do not have tapeta lucida at all, likely placing an upper limit on the first appearance of the tapetum at around 440 million years ago coincident with the emergence of jaws.<sup>[11,31]</sup> Many species of the oldest group of jawed fishes – the cartilaginous fishes (*Chondrichthyes*) – do have tapeta, indicating that this is the clade in which this structure likely first appeared. The tapeta of cartilaginous fishes all have the guanine subtype of choroidal cellulose TL.<sup>[9,31]</sup> This tapetum contains sheets of superimposed guanine crystals in the choroid and is found exclusively in *Chondrichthyes*. Interestingly, some sharks exhibit an occludible version of the guanine choroidal cellulose TL, a feature that is not found in any other choroidal tapeta.<sup>[9,32]</sup>

Among the bony fishes (*Osteichthyes*), the lobe-finned fishes (*Sarcopterygii*) also have the guanine sub-type of choroidal cellulose TL.<sup>[9,33]</sup> However, the vast majority of bony fishes are ray-finned fishes and have an entirely different type of tapetum: the retinal type.<sup>[7,9,20]</sup> Among them, some are occludible and others are not. It is curious that the lobe-finned fishes – from which terrestrial tetrapods are descended – possess the guanine-based choroidal cellulose tapetum, which is not found in any species outside of fishes. This argues that the tapetum of tetrapod vertebrates evolved entirely separate from the tapetum of their lobe-finned ancestors.

As early aquatic vertebrates transitioned onto land, most ocular features were retained and the terrestrial vertebrate eye is not substantially divergent from the marine one. To date, the tapetum lucidum



**FIGURE 4** Diverse Tapeta Among Vertebrates. (A) The choroidal fibrosum type tapetum of horses.<sup>[25]</sup> (B) The retinal type tapetum of laternfish.<sup>[26]</sup> (C) The guanine-retinal type tapetum from crocodilians.<sup>[27]</sup> (D–E) The choroidal cellulsum type tapetum of (D) dogs<sup>[28]</sup> and (E) seals.<sup>[29]</sup> In all panels, the tapetal layer is labeled with an asterisk (\*). Images republished under creative commons license or with permission from publisher.

has not been observed in any extant amphibians or reptiles, with the notable exception of the crocodilians,<sup>[9]</sup> and, to date, only one bird species has been definitively found to harbor a tapetum: the Japanese Nightjars, a nocturnal species.<sup>[9,34]</sup> One explanation for the lack of TL across most major terrestrial vertebrate clades is that the tapetum was lost as early tetrapods found themselves in the much more brightly illuminated environment of land. Because the first terrestrial animals were herbivores, it is believed that the terrestrial niche was not initially rich with the vertebrate predator-prey relationships that eventually led to temporal partitioning into nocturnal, diurnal, and crepuscular lifestyles. Therefore, the tapetum may not have contributed to the fitness of early terrestrial vertebrates and disappeared.

Bolstering the notion that the TL was lost in early tetrapods, the tapeta of crocodilians and mammals are structurally and materially distinct from each other *and* from those of all fishes. Crocodilians possess a retinal type TL that is similar to that of ray-finned fish but with reflective crystals composed of guanine.<sup>[9,27,35]</sup> Thus, the crocodilian

tapetum is *anatomically* similar to that of ray-finned fishes, *chemically* similar to those of cartilaginous fishes, but *structurally* distinct altogether. The crocodilian TL, therefore, appears to have evolved independently. Further, because most clades of tetrapods – the amphibians, birds, and reptiles other than crocodilians – lack tapeta entirely, it is most likely that this feature remained absent in these clades and then emerged again in crocodilians and, later, mammals.

Likely owing to how common the nocturnal lifestyle is throughout this order, mammals possess a wide variety of diverse tapeta spread across the entire clade.<sup>[9]</sup> Most modern mammals, including species that are strictly diurnal, display visual adaptations to nocturnal activity that is similar to those seen in nocturnal reptiles and birds. The tapetum lucidum is one of the features seen in extant mammalian sensory systems that likely evolved in their early history. Evidence from the mammal fossil record suggests that these visual adaptations, which may include the TL, may be the result of a prolonged nocturnal “bottleneck” during their early evolutionary history.<sup>[19]</sup> Nocturnality likely

allowed mammals to avoid predation from diurnal dinosaurs that dominated the Mesozoic Era and diurnal activity likely evolved following the extinction of dinosaurs before the Cenozoic Era.<sup>[36]</sup>

Monotremes and most marsupials lack tapeta but the two extant marsupial taxa that do possess a TL have substantially different types. While Tasmanian wolves possess the more common choroidal fibrosum sub-type of tapetum made of collagen fibers, opossums have the retinal type tapetum.<sup>[9,30]</sup> While it is structurally similar to the retinal tapetum of crocodilians and ray-finned fishes, it is not likely to be homologous, since all other tetrapods possess the choroidal type, as do the lobe-finned fishes, the clade from which tetrapods evolved.<sup>[7,9]</sup> Further, the retinal tapetum of opossums is made of lipids, while that of crocodilians is made of guanine crystals.<sup>[30,33]</sup>

Placental mammals, on the other hand, possess only the choroidal type TL, with several sub-types throughout the clade as well as various constituent chemicals that comprise the reflective surface.<sup>[9]</sup> For example, most carnivorous mammals, including cats, dogs, ferrets, mink, and all pinnipeds (seals, sea lions, and walruses) have the cellulose sub-type of choroidal TL. It is worth noting that the felid tapetum – perhaps the most exquisitely adapted of all terrestrial tapeta – is built with riboflavin while all others in *Carnivora* are made of zinc cysteine. Ungulates that have tapeta, including cetaceans, possess the fibrosum sub-type of choroidal TL, made of collagen fibers, as does one rodent species, the paca. All other rodents, however, lack tapeta.

Most primates, including humans, lack tapeta.<sup>[7,37]</sup> However, there are species of bushbabies and lemurs that do possess a TL.<sup>[38,39]</sup> These prosimian species exhibit the cellulose sub-type of choroidal TL composed of riboflavin, similar to that of cats but almost certainly evolved independently given the phylogenetic distance between the clades. The stark differences in tapetal structures throughout tetrapods, and especially within mammals, make it exceedingly unlikely that the TL is homologous and more likely the result of convergent evolution. Figure 5 shows this apparent homoplasy.

## DISCUSSION: THE EVOLUTION OF THE TAPETUM

The tapetum lucidum is a highly efficient structure for maximizing the absorption of photons by the vertebrate retina through the reflection of light that passes through without striking a photoreceptor in the first pass, creating a second chance for a collision and increasing the effective photosensitivity of the retina.<sup>[7]</sup> In certain ecological niches, photosensitivity in conditions of minimal illumination brings considerable advantages to both predators and prey animals. The most obvious such habitats are murky waters, for fish and aquatic tetrapods, and nocturnal lifestyles for terrestrial vertebrates.<sup>[9]</sup> Crocodilians are semiaquatic and therefore occupy both of these niches. They hunt in murky waters and are most active at night when they can capitalize on their superior photosensitivity. The tapetum appears to be highly advantageous for these animals.

What is perhaps most striking about the TL throughout vertebrates is its diversity throughout the clade. The tapeta of crocodilians, nocturnal mammals, and fish have much in common functionally, but

differences in their structural organization and chemical composition make it unlikely that they are homologous. Even within these clades – especially the fish and the mammals – the diversity of tapeta is greater than expected. In most other respects, the eyes of all mammals are highly conserved in their structure, organization, and composition. The tapetum may be the ocular structure with the most divergence across the clade.

The existence of so many diverse types of TL throughout *Vertebrata* argues that this structure has evolved independently many times throughout evolutionary history. As animal lineages moved in and out of various habitats (e.g., murky waters or nocturnal lifestyles), it seems likely that the tapetum disappeared and then evolved once again. The phylogenetic tree below shows the frequent re-appearance of the tapetum throughout vertebrates, emphasizing the convergent nature of its evolution (Figure 6).

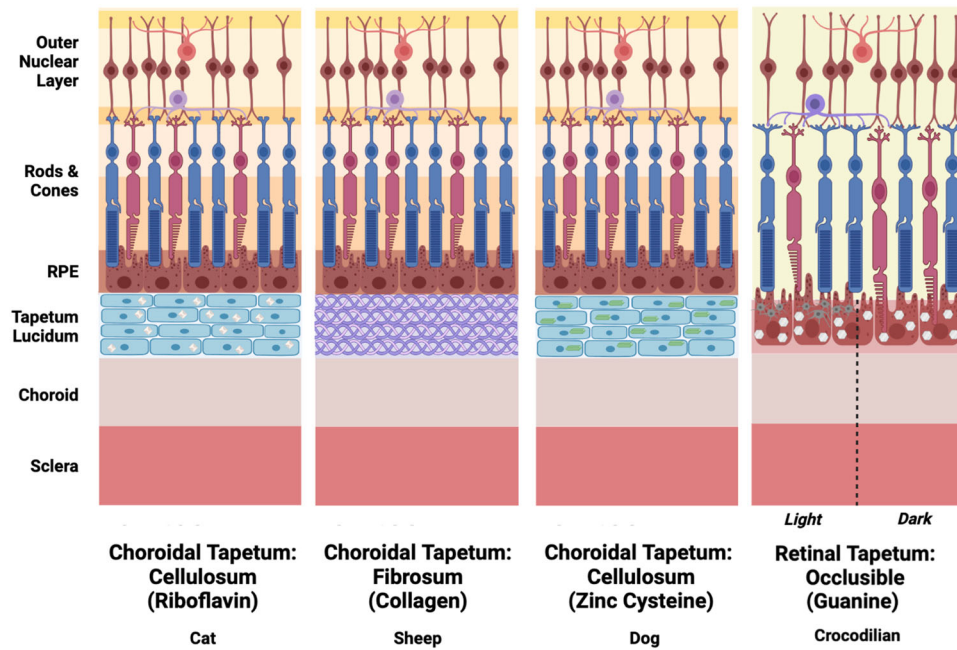
Interestingly, many moths and arachnids also possess a tapetum.<sup>[40]</sup> As the vertebrate eye evolved independently from invertebrate eyes, there is no homology and the invertebrate eyes are altogether divergent in structure and function. Yet, at least three distinct types of tapeta have evolved among spiders alone, all of which function similarly to that of vertebrates. This argues that, yet again, the strong advantage that the tapetum confers establishes a selective pressure favoring the evolution of this structure. As others have noted, the visual system is rife for exaptation and the large number of times that photodetection has independently evolved underscores this.<sup>[41]</sup>

It is our hypothesis that the tapetum evolved as a compensatory mechanism for the poor design of the inverted retina of vertebrates, rather than simply an enhancing co-adaptation. The best evidence for this hypothesis is the complete lack of tapetum in any known cephalopods.<sup>[9]</sup> The strong advantage conferred by the TL in vertebrates and arthropods has led to its evolution multiple times. And, since this structure does not fossilize, examples in extant animals probably significantly undercount the number of separate lineages in which this structure has emerged. And yet, cephalopods occupy the same murky water niches as fishes and aquatic tetrapods,<sup>[42]</sup> but have never, as far as we know, evolved the tapetum. It is worth noting that the cephalopod lineage is older than the vertebrate clade, originating in the Cambrian. By the mid-Paleozoic, near the origin of vertebrates, cephalopods had already diversified into the four known subclasses including squids and octopuses (*Coleoidea*), and the nautiloids.<sup>[43]</sup>

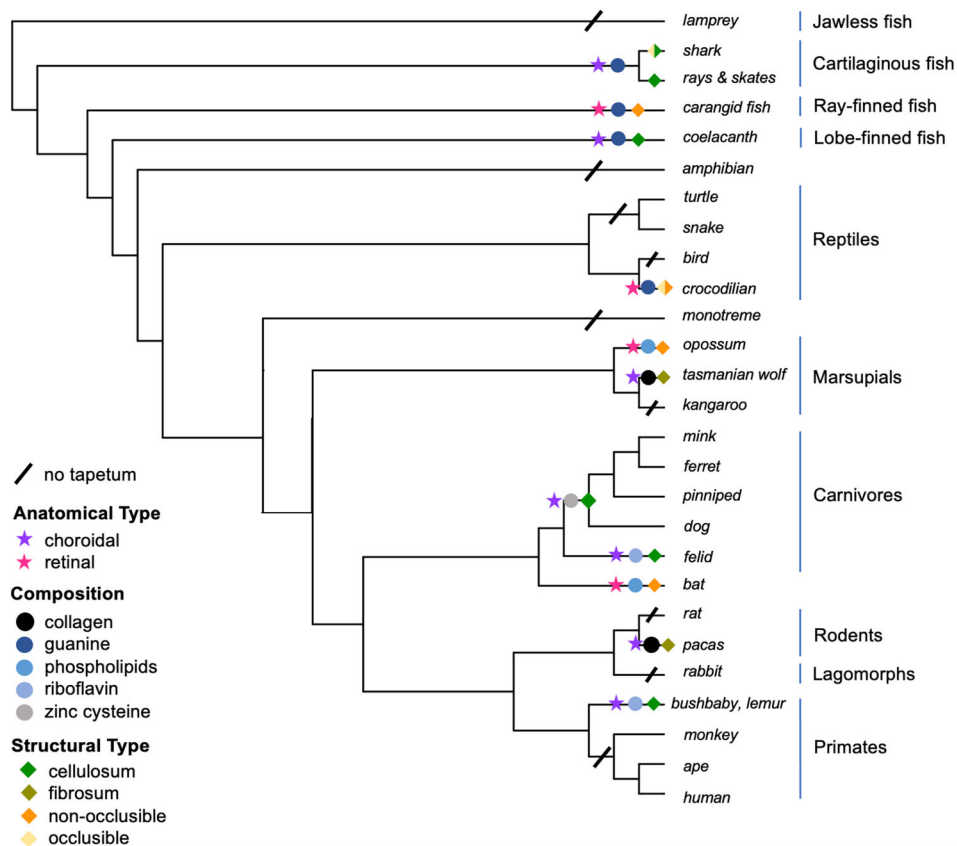
The cephalopod eye is remarkably similar to the vertebrate eye in terms of function and the overall camera-like structural chassis. However, any appearance of homology breaks down upon close inspection of the microanatomy, most conspicuously in the arrangement of the photoreceptors within the retina. In fact, the functional similarity of the cephalopod and vertebrate eyes, and their pointed difference from all invertebrate eyes, is among the most prominent examples of convergent evolution among animals. Even the retinal layers themselves evolved striking similarities in vertebrates and cephalopods, with the key difference between the inverted histological architecture relative to one another.<sup>[44]</sup>

Because the cephalopod retina is verted, with the photoreceptors placed into the most anterior cell layer, these receptors are densely





**FIGURE 5** Convergent Evolution of the Tapetum. While most retinal structures are strongly conserved across vertebrates, the tapetum lucidum shows a striking amount of chemical, structural, and histological variation, evidence of homoplasy, rather than homology (Figure created with BioRender.com).



**FIGURE 6** Phylogeny of the vertebrate tapetum lucidum. Phylogenetic tree showing evolutionary relationships among example vertebrate species with a variety of tapetal types and compositions



packed into an unbroken sheet with no optic disc. It is therefore possible that these retinas are as photosensitive as they can possibly be, and a tapetum would be of little or no value. It is also possible that the structure of the cephalopod retina precludes the evolution of a posteriorly located retroreflective structure. There could be histological, genetic, or functional barriers to the evolution of a tapetum, though it is not clear what those might be and the sheer number of times that the tapetum has evolved in vertebrates and arthropods argues against this. Thus, the more likely explanation is that the orientation of the cephalopod retina is already optimized for the maximum absorption of light in conditions of minimal illumination. Indeed, both squid and octopus retinas are impressively photosensitive and, while a direct comparison has not been made, appear to be on par with those of felines, the most sensitive vertebrate retinas known.<sup>[42,43]</sup>

We therefore present the hypothesis that the tapetum lucidum evolved in vertebrates as a compensatory co-adaptation for the suboptimal photosensitivity of the inverted retina. Although this hypothesis is centered on vertebrate histology, the experimental work that could support or disprove this notion would mostly focus on the cephalopod retina because the function and value of the tapetum in vertebrates is already well established. It would, therefore, be interesting to demonstrate if tapetum-like enhancements would be of any value to cephalopod retinas.

A correlate to our hypothesis is that the verted nature of the cephalopod retina allows an unbroken tissue layer of photoreceptors packed tightly enough to capture as many photons as possible under conditions of low illumination. Further, with the receptors positioned as anteriorly as possible, scattering of photons by the neuronal network layer is avoided, scattering that must be corrected with various co-adaptations in vertebrates. For this reason, the vertebrate retina has been described as more complex. It may be, rather, that the cephalopod retina is more streamlined, efficient, and more maximally optimized for the capture of photons without the need for a compensatory structure such as the tapetum.

Experiments with *ex vivo* cephalopod retinas could yield support for this hypothesis. For example, reflective structures could be placed behind the cephalopod retina to determine if they enhance photon capture by the photoreceptor layer. Both synthetic photoreflectors and isolated vertebrate tapeta could be used, although such an *in vitro* reconstruction of an *in vivo* tissue would be daunting. Importantly, these experiments would also require careful controls. One such control would be an isolated retina from a vertebrate that possesses a tapetum, both with and without the tapetal layer left intact. If the addition of a tapetum to a vertebrate retina, but not a cephalopod retina, enhances photodetection, this would constitute evidence for the hypothesis. These are complicated experiments but technically feasible.

Simpler direct comparisons would also be illuminating, if less definitive. Measuring the passage of small numbers of photons through verted and inverted retinas, with and without tapeta, and as measured from both posterior and anterior positions, would be informative, as would measurement of photo scattering in both kinds of retinas under various experimental conditions. While these measurements

have been made in a variety of retinas in isolation, there are no recent studies that attempt to make direct comparisons between verted and inverted under controlled laboratory conditions. Such comparisons could form the foundation for additional experiments aimed at dissecting the precise role of the tapetum and its potential value, or lack thereof, for cephalopods. It is our hope that our analysis here will inspire such research in the vision community so that the hypothesis may be examined. Regardless of the outcome, a deeper understanding of the mechanisms and evolutionary history of vision would be the result of such research.

## CONFLICT OF INTEREST

The authors do not have a conflict of interest.

## DATA AVAILABILITY STATEMENT

Data sharing not applicable – no new data generated.

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