Anatomia, Histologia, Embryologia

WILEY

ORIGINAL ARTICLE OPEN ACCESS

Adaptations of the Vertebrate Retina to Low-Light Conditions: A Review

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Received: 16 December 2024 | **Accepted:** 6 May 2025

Keywords: dim-light environments | nocturnal vision | photoreceptors | retine | spectral tuning | visual adaptations

ABSTRACT

Vision is a critical sensory modality in vertebrates, enabling diverse adaptations to environmental challenges. This review explores the remarkable adaptations of vertebrate eyes to low-light environments, such as nocturnal habitats, deep-sea ecosystems and subterranean niches. Key structural and functional modifications include enhanced eye size, rod-dominated retinas, reflective tapetal layers and photopigment spectral tuning. The role of photoreceptor specialisation and retinomotor movements in optimising photon capture and minimising light scatter is examined, alongside evolutionary trade-offs that prioritise sensitivity over resolution. Furthermore, adaptations such as bioluminescence detection in deep-sea fish and the regressive evolution of vision in subterranean species highlight the intricate relationship between ecological demands and visual evolution. By synthesising current research, this review provides insights into the evolution in vertebrate visual systems and offers future perspectives on the molecular and ecological drivers of these adaptations.

1 | Introduction

Vision is one of the most versatile and vital sensory modalities, allowing organisms to perceive and respond to their surroundings with remarkable precision. Essentially, vision depends on the interaction between light, specialised ocular structures and neural processing, which together transform physical stimuli into meaningful perceptions. This interplay has driven the evolution of an extraordinary diversity of visual systems, adapted to the ecological demands of specific environments. Among vertebrates, the eye is a remarkably adaptable organ, capable of notable modifications to meet the challenges posed by diverse habitats (Walls 1942; Lamb 2013).

In environments with abundant light, such as terrestrial ecosystems during the day, vision emphasises high resolution, colour perception and rapid processing. However, in low-light habitats—whether the perpetual darkness of deep oceans, the intermittent dimness of nocturnal landscapes or the obscurity of caves—visual systems are under entirely different evolutionary pressures. Here, the ability to capture scarce photons becomes critical, driving adaptations that prioritise light sensitivity over sharpness, monochromatic perception over vibrant colour and reflexive responses over conscious visual experience (Walls 1942; Warrant and Johnsen 2013; Musilova et al. 2019). These adjustments illustrate the adaptability of the eye as a sensory organ and the selective pressures shaping its evolution.

Vision in such conditions is not merely about light detection; it involves interpreting subtle cues, such as gradients of shadow or the faint bioluminescent glows of deep-sea organisms. These tasks demand an intricate coordination of structure and function, where features such as enlarged eyes, highly sensitive photoreceptors and reflective tapetal layers work in concert to optimise photon capture. This dynamic system demonstrates that vision, far from being a universal experience, is an ecological solution to specific challenges. For some species, the eye acts as a precise instrument for forming images, while for others it primarily facilitates immediate and survival-critical reflexes (Ollivier et al. 2004; Walls 1942).

The diversity of ocular adaptations reflects the evolutionary pressures imposed by low-light environments. Whether by enlarging the eye, increasing the sensitivity of the retina, or fine-tuning the spectral properties of photopigments, vertebrates have developed ingenious strategies to overcome the limitations of light scarcity. These innovations emphasise the importance of vision not just as a biological function but as a driving force in the evolutionary history of vertebrates (Cronin and Porter 2014; Fröhlich et al. 2024; Gai et al. 2023; Lamb and Pugh 2008; Zhao et al. 2009).

This review examines the structural and functional adaptations of vertebrate eyes to low-light environments (Table 1). By synthesising current research and exploring these modifications across diverse habitats, we aim to illuminate the evolution that has enabled vertebrates to thrive under such challenging conditions. From anatomical refinements to ecological implications, the study of these adaptations offers a window into the complex relationship between sensory biology and environmental constraints.

2 | Eye Adaptations

2.1 | Ocular Morphology

Relative eye size, particularly in proportion to body size, serves as a critical distinction between nocturnal and diurnal vertebrates (Potier et al. 2020). For instance, Strigiformes (owls), such as eurasian eagle-owl (*Bubo bubo*) (Figure 1; Alix et al. 2017), the barn owl (*Tyto alba*) and the great horned owl (*Bubo virginianus*), exhibit exceptionally large eyes relative to their body size, a feature that significantly enhances their ability to capture light and navigate effectively in dim conditions (Lisney et al. 2012; Martin 2014; Hall and Ross 2007). Similarly, nocturnal teleost fish such as squirrelfish and cardinalfish optimise light intake through large eyes, while diurnal species often prioritise smaller eye sizes for sharper visual acuity in bright environments. Nocturnal animals typically exhibit proportionally larger eyes, an adaptation enhancing light capture in dim environments. Studies on nocturnal birds, such as barn owls (*T. alba*) and great horned owls (*B. virginianus*), and reef fishes, including squirrelfish (Holocentridae) and cardinalfish (Apogonidae), have demonstrated that larger corneal diameters, which facilitate wider pupils, significantly enhance light intake, enabling these species to thrive in dimly lit environments (Fishelson et al. 2004; Hall and Ross 2007; Lisney et al. 2012; Fogg et al. 2022; Schmitz and Wainwright 2011). For example, Strigiformes display significantly larger corneal diameters and shorter axial lengths compared to diurnal birds, optimising light sensitivity (Hall and Ross 2007).

However, larger eyes also impose constraints. In reef-dwelling teleosts, increased eye size reduces depth of focus and optical diversity, as seen in squirrelfish (Holocentridae) and cardinalfish (Apogonidae) (Schmitz and Wainwright 2011).

Eye shape and pupil morphology are closely tied to environmental light conditions and behaviour. Nocturnal species often exhibit round or vertically slit pupils, which enhance light regulation. For instance, vertical pupils in domestic cats (*Felis catus*) (Hammond et al. 1985), as well as reptiles such as geckos (*Gekkonidae*) (Roth et al. 2009), balance nocturnal sensitivity with daytime light control. This adaptation enables these species to efficiently exploit diverse ecological niches by modulating light intake under varying conditions (Lisney et al. 2012; Hall and Ross 2007). In contrast, nocturnal birds such as owls have large, round pupils that maximise light capture without the distortions associated with slit pupils (Hall and Ross 2007).

Increased pupil size and rod-dominated retinas, common in nocturnal species, favour sensitivity at the cost of fine detail perception (Walls 1942; Schmitz and Wainwright 2011). By contrast, diurnal eyes prioritise resolution through high cone densities and greater axial lengths, producing sharper retinal images. For example, hawks such as the red-tailed hawk (*Buteo jamaicensis*) and falcons such as the peregrine falcon (*Falco peregrinus*) achieve exceptional visual acuity due to specialised retinal configurations and elongated axial lengths, allowing them to spot prey from great distances (Lisney et al. 2012; Hall and Ross 2007).

2.2 | The Retina

The retina is a multilayered structure that transduces photons to electrical impulses that travel over the optic nerve to the optic tectum of the brain. The structure of the retina is illustrated in Figure 2. The innermost layer consists of ganglion cells (GCL), which give rise to the optic nerve. The outermost layer consists of rod and cone photoreceptor cells (PL). Between these two layers are several others that vary in number depending on the species, but which always include an inner nuclear layer (INL) next to the ganglion cells and an outer nuclear layer closer to the photoreceptors. The outer nuclear layer (ONL) is actually that portion of the rods and cones where their nuclei reside. The inner nuclear layer contains horizontal, bipolar and amacrine cells that relay impulses from the photoreceptors to the ganglion cells. The synapses made between the photoreceptors in the outer nuclear layer and the bipolar cells of the inner nuclear layer show up in sections as the outer plexiform layer (OPL). A similar inner plexiform layer (IPL) is created by the synapses between the neurons of the inner nuclear layer and the ganglion cell layer (GCL). The ends of the photoreceptors are embedded in the epithelial cells of the pigmented layer of the retina. Outside the retina is the retina pigmented epithelium (RPE) and outside the RPE is the choroid, a layer of heavily vascularised connective tissue (Figure 3).

Specialised adaptations are apparent in animals active under scotopic conditions, such as deep-sea fish and nocturnal mammals. These species exhibit retinas dominated by rods, which are highly sensitive to low light and optimised for photon capture. Additionally, in species such as owls and tarsiers, the retina often lacks a well-developed cone system, prioritising scotopic vision over photopic acuity (Warrant and Locket 2004). The trade-off in these adaptations reflects the necessity to maximise light sensitivity at the expense of colour discrimination and fine spatial resolution.

TABLE 1 | Summary of scotopic adaptations in the retina of different vertebrate groups.

Adaptation	Fish	Amphibian	Reptile	Bird	Mammal	References
Retinomotor movements	+++	++	+	+	–	Burnside (2001), Braekevelt and Young (1994), Falcón et al. (2010) and Solessio and Engbretson (1993)
Retinal tapetum lucidum	+++	–	+	–	+	García et al. (2017), Ollivier et al. (2004), Braekevelt and Young 1994 and Douglas et al. (1998)
Choroidal tapetum lucidum (guanine)	++	–	–	–	–	Ollivier et al. (2004) and Braekevelt and Young (1994)
Cellulosic tapetum lucidum	–	–	–	+	++	Ollivier et al. (2004) and Shinozaki et al. (2013)
Fibrous tapetum lucidum	–	–	–	–	++	Shinozaki et al. (2013)
High rod-to-cone ratio	+++	+++	+++	+++	+++	Finlay et al. (2005), Ingram et al. (2016) and Reichenbach and Bringmann (2010)
Spatial summation	+++	+++	+++	+++	+++	Warrant (2008) and O'Carroll and Warrant (2017)
Temporal summation	+++	+++	+++	+++	+++	Warrant (1999), Warrant (2008) and O'Carroll and Warrant (2017)
Rods stacked in rows	+++	–	–	+	–	Wagner et al. (1998) and Rojas et al. (2004)
Reflective cups (tapetal grouping)	+++	–	–	–	–	Francke et al. (2014) and Kreysing et al. (2012)
Photopigment spatial adjustment	+++	+++	+++	+++	+++	Douglas et al. (1998) and Veilleux and Cummings (2012)
Homogeneous ganglion cell topography	++	+++	+++	+++	+++	Silveira et al. (1996), Lisney et al. (2012) and Litherland and Collin (2008)
Scotopic colour vision	–	+	+	–	–	Kelber et al. (2017) and Roth and Kelber (2004)
Retinal filter	++	–	–	–	–	Busserolles et al. (2015), Crescitelli et al. (1985), Douglas et al. (1998), (Douglas et al. 2016), Kelber and Roth (2006), Warrant (2000) and Warrant and Locket (2004)
MLS	+	–	–	–	–	Busserolles et al. (2014)
Fundal pigmentation	+	–	–	–	–	Busserolles et al. (2014)

Note: (–), not prevalent or absent; (+), limited prevalence; (++), moderately prevalent adaptation; (+++), highly prevalent adaptation.

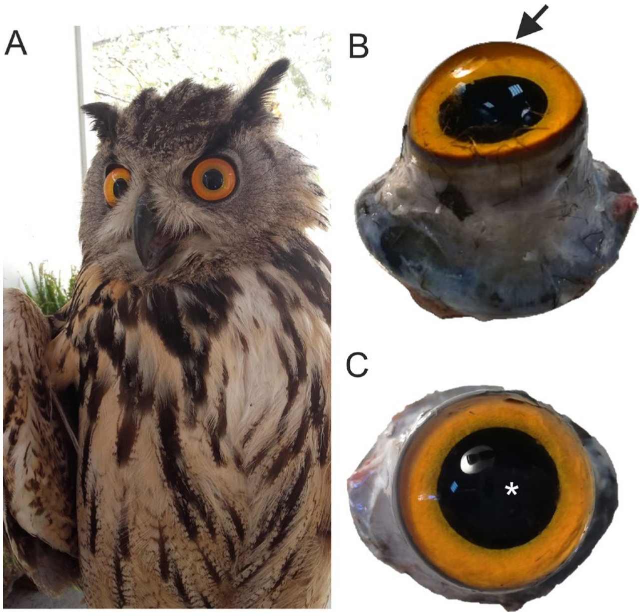

FIGURE 1 | Nocturnal eye shape. The figure includes an image of *Bubo bubo* in a frontal view (A), illustrating the arrangement of its eyes. The dissected eyes (B) display the typical tubular morphology characteristic of nocturnal adaptation, with large corneas (arrow). The pupils (C, asterisk) further enhance light capture, maximising lux intake in low-light environments.

2.2.1 | Photoreceptor Specialisations

Rod-dominated retinas are supported by structural features such as a reflective tapetum lucidum, enhancing photon capture by reflecting light back onto the photoreceptor layer. Furthermore, the neural organisation of the retina facilitates efficient signal processing, ensuring that critical visual information is preserved and relayed even under minimal light conditions (Finlay et al. 2005; Schmitz and Wainwright 2011).

In nocturnal and deep-sea species, retinas are dominated by rods, which can constitute 98%–100% of photoreceptors, while cones are sparse or absent (Reichenbach and Bringmann 2010). Rods, evolved from cones, are more sensitive to light, allowing scotopic vision. This adaptation supports functionality in dim and bright conditions through duplex retinas (Ingram et al. 2016). In mesopelagic fish such as *Nezumia sclerorhynchus* (Figure 3; García et al. 2017), the inner nuclear layer contains significantly fewer interneurons compared to the outer nuclear layer, reflecting an emphasis on light sensitivity over detailed image processing (Reichenbach and Bringmann 2010). Nocturnal animals also show increased rod density due to prolonged proliferation of progenitor cells during retinal development, enhancing sensitivity but reducing visual acuity and colour discrimination (Finlay et al. 2005).

Many deep-sea fishes stack rods in rows to maximise photon absorption (Fogg et al. 2023). This arrangement is also found in nocturnal birds such as *Steatornis caripensis*. Nightjars exhibit fewer rods, but their outer segments are longer and thicker, enhancing sensitivity (Wagner et al. 1998; Rojas et al. 2004).

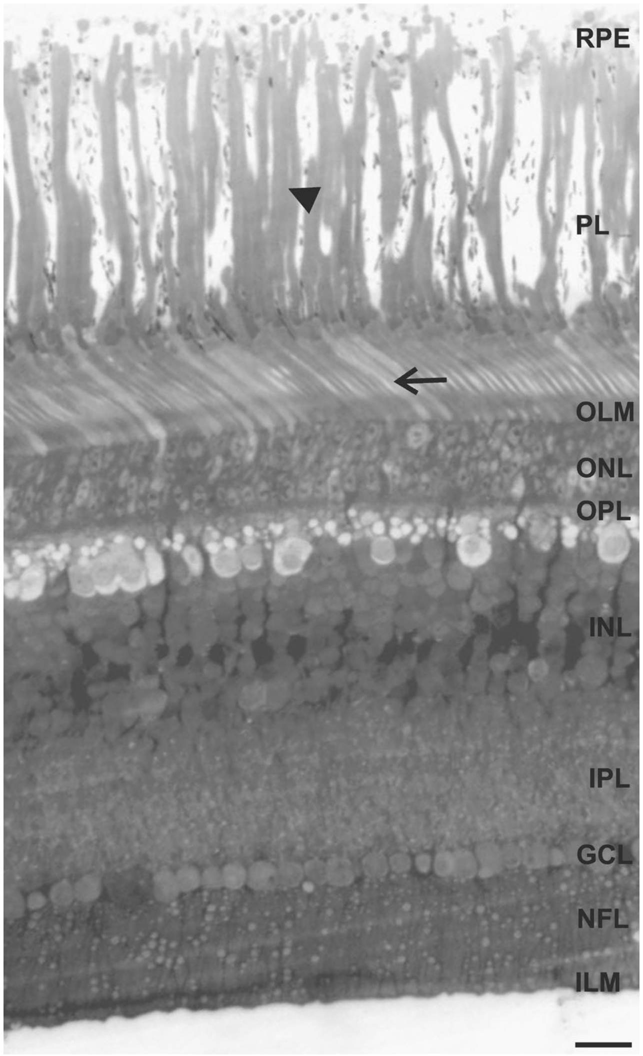

FIGURE 2 | Microscopic section of the central retina from *Bubo bubo hispanicus*, showing its stratified architecture. The labelled layers include the retinal pigment epithelium (RPE), photoreceptor layer (PL) outer limiting membrane (OLM), outer nuclear layer (ONL), outer plexiform layer (OPL), inner nuclear layer (INL), inner plexiform layer (IPL), ganglion cell layer (GCL), optic nerve fibre layer (NFL), and inner limiting membrane (ILM). An arrowhead denotes the outer segments of the photoreceptors, while the arrow identifies their inner segments. This complex organisation underpins the retina's role in capturing and processing light signals. Scale bar: 15 µm.

In 17 fish families, photoreceptors are organised into reflective cups formed by epithelial cells containing crystals. This structure amplifies light capture, as seen in *Gnathonemus petersii*, where cones in these cups increase incident light by 500% (Kreysing et al. 2012; Francke et al. 2014).

2.2.2 | Ganglion Cells

The size and distribution of ganglion cells in vertebrate retinas demonstrate significant adaptations to dark environments, reflecting ecological demands for optimised visual processing. In nocturnal species such as owls, ganglion cells are distributed concentrically, prioritising high spatial

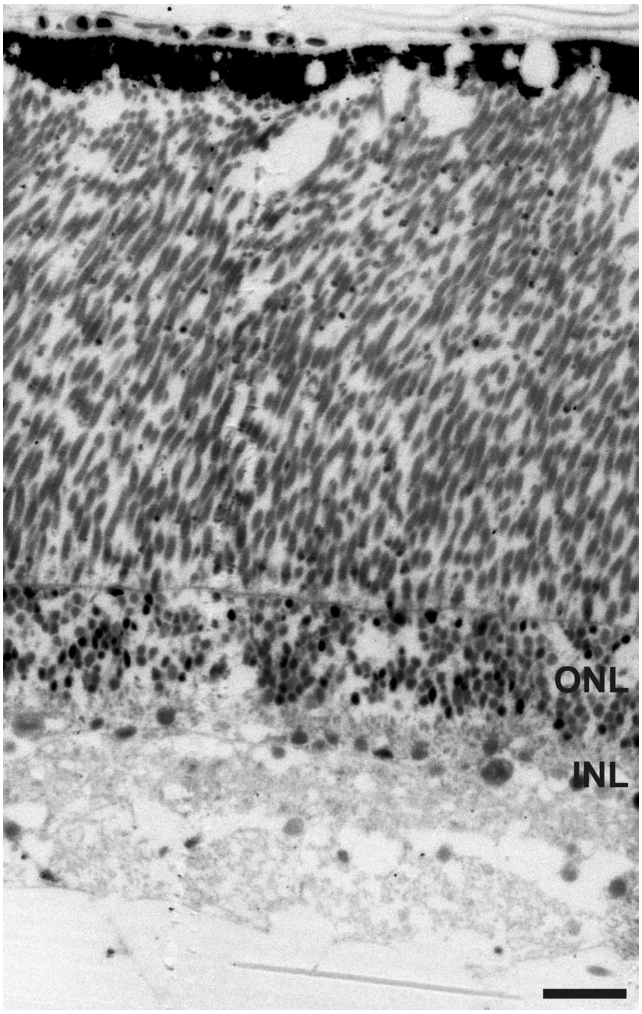

FIGURE 3 | General morphology of the retina of the deep-water fish *Nezumia sclerorhynchus*. The thick outer nuclear layer (ONL) is characterised by the abundance nucleus of rod photoreceptors, while the inner nuclear layer of the retina (INL) contains markedly fewer bipolar and ganglion cells. This retinal structure reflects a high degree of convergence, optimising photon capture but limiting spatial resolution, a common adaptation to deep-sea environments. Scale bar = 20 µm.

resolution in low-light conditions, which supports precise central vision crucial for nocturnal predation (Lisney et al. 2012). Similarly, mesopelagic fish display regions of elevated ganglion cell density aligned with high rod convergence, enabling enhanced detection of bioluminescent cues in their dimly lit habitats (De Busserolles et al. 2014). In deep-sea environments, the convergence of multiple rods onto single ganglion cells amplifies visual sensitivity by pooling faint light signals, while specialised adaptations such as the reflective tapetum lucidum further augment photon utilisation (Douglas and Cronin 2016; Douglas et al. 2016; Warrant and Locket 2004). Additionally, these adaptations often involve morphological changes, including the enlargement of ganglion cells, which increases their capacity to integrate dim-light signals effectively (Schmitz and Wainwright 2011).

2.2.3 | Retinomotor Movements

Retinomotor movements in vertebrate retinas are essential adaptations that allow dynamic responses to changes in ambient light, ensuring optimal visual performance and photoprotection. These movements involve the repositioning of photoreceptor cells and the migration of melanin granules within the retinal pigment epithelium (RPE). In scotopic (low-light) conditions, cones elongate, rods contract and melanin granules aggregate at the base of the RPE cells, enabling increased rod-mediated photon capture. Conversely, under photopic (bright-light) conditions, cones contract, rods elongate and melanin granules move into the apical processes of the RPE, shielding photoreceptors from excessive light exposure. Such movements have been observed in teleost fishes such as *Carassius auratus* (goldfish), amphibians such as *Xenopus laevis* (Anderson and Green 2000), birds such as great blue heron (*Ardea herodias*) (Braekevelt and Young 1994) or emu (*Dromaius novaehollandiae*) (Braekevelt 1998) and reptiles including *Anolis carolinensis* (Burnside 2001; Solessio and Engbretson 1993).

These movements are primarily regulated by intracellular signalling pathways modulated by environmental light and

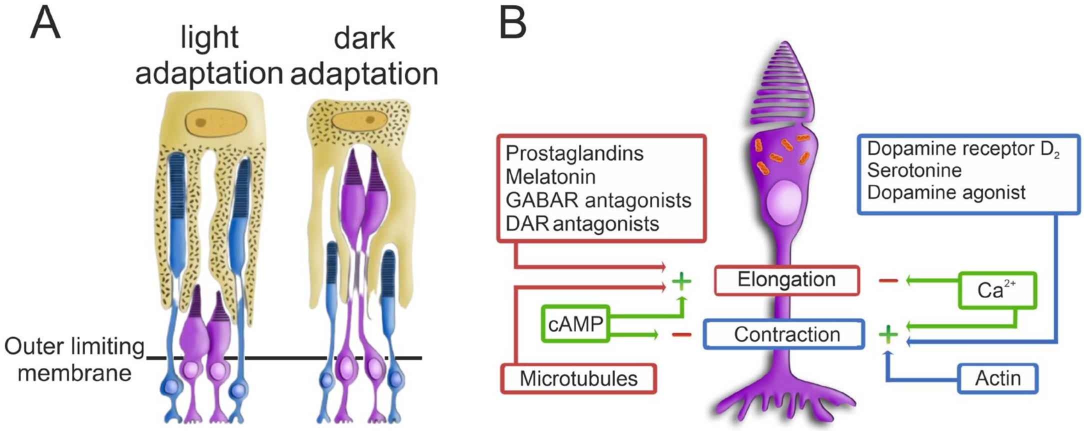

FIGURE 4 | Schematic representation of retinomotor movements in vertebrate retinas (A). Under low-light (scotopic) conditions, rods contract towards the pigment epithelium to optimise light capture, while cones elongate. In bright-light (photopic) conditions, the reverse occurs: Cones contract to protect against excess light, and rods elongate. (B) molecular basis of retinomotor movements. DAR, dopamine receptors; GABAR, gamma-aminobutyric acid receptors.

circadian rhythms (Figure 4). Cyclic adenosine monophosphate (cAMP) acts as a key signal for darkness, promoting the elongation of photoreceptors and the aggregation of melanin granules. Light exposure suppresses cAMP levels, triggering the reverse movements. Additionally, dopamine released from retinal interplexiform cells supports light adaptation by acting through D2-like receptors. These mechanisms demonstrate the functional and evolutionary importance of retinomotor responses in light-sensitive environments (Anderson and Green 2000; Burnside 2001).

Circadian control plays a central role in retinomotor responses, ensuring that retinal adaptations align with predictable light–dark cycles. For instance, in *Xenopus laevis*, intrinsic retinal clocks maintain photoreceptor and pigment movements even in constant darkness, emphasising the robustness of this adaptation across taxa. The persistence of these movements under circadian control suggests evolutionary conservation and underscores their importance for optimising vision in dynamic lighting conditions (Anderson and Green 2000).

In addition to facilitating photoprotection, retinomotor movements enhance visual sensitivity under dim-light conditions. In species such as *Carassius auratus* and *Oncorhynchus mykiss* (rainbow trout), melanin migration within the RPE reduces photobleaching and complements photoreceptor adjustments to maximise sensitivity. This dual functionality is particularly critical for species inhabiting environments with rapid or extreme light changes, such as aquatic habitats and twilight zones (Ali and Klyne 1985; Solessio and Engbretson 1993). Moreover, in amphibians such as *Rana pipiens* (northern leopard frog), these movements provide additional light regulation in the absence of pupil dilation, illustrating their significance in non-mammalian vertebrates (Ali and Klyne 1985; Falcón et al. 2010).

2.2.4 | Tapetum Lucidum

The tapetum lucidum is a reflective retinal structure that enhances visual sensitivity by doubling photon capture. This adaptation is particularly prevalent in nocturnal animals and certain fish species, enabling vision in dimly lit environments (Ollivier et al. 2004). Despite its functional consistency, the morphology, location and composition of the tapetum vary significantly across taxa, reflecting evolutionary adaptations to diverse ecological niches.

In teleost fish, such as *Siganus luridus*, the tapetum lucidum is integrated into the retinal pigment epithelium and consists of densely packed reflective crystals, often guanine. This structure produces the characteristic ‘eye-shine’ effect and supports visual sensitivity in low-light conditions. Additionally, *Siganus luridus* has a choroidal gland, or rete mirabile, which facilitates oxygen delivery to the retina—an adaptation critical for nocturnal or dim-light activity, even in species living in shallow waters (Derbalah et al. 2024). These findings suggest that herbivorous and diurnal species may also rely on similar adaptations under specific ecological constraints. Similarly, in deep-sea teleost fish such as *Nezumia sclerorhynchus*, the tapetum lucidum (Figure 5) consists of reflective platelet-like crystals that are adapted for extreme dim-light conditions, a feature that highlights the morphological plasticity of this structure in response to environmental pressures (García et al. 2017). The combination of reflective efficiency and strategic location ensures maximum photon capture, enabling survival in environments with extremely limited light availability. Among elasmobranchs, such as sharks, the choroidal tapetum lucidum alternates between reflective tapetal cells and melanocytes, which retract in darkness to maximise reflectivity (Braekevelt and Young 1994). In other fish, such as *Malacosteus niger*, the tapetum is integrated with unique bioluminescent adaptations, allowing the species to detect prey and communicate in the deep sea (Derbalah et al. 2024).

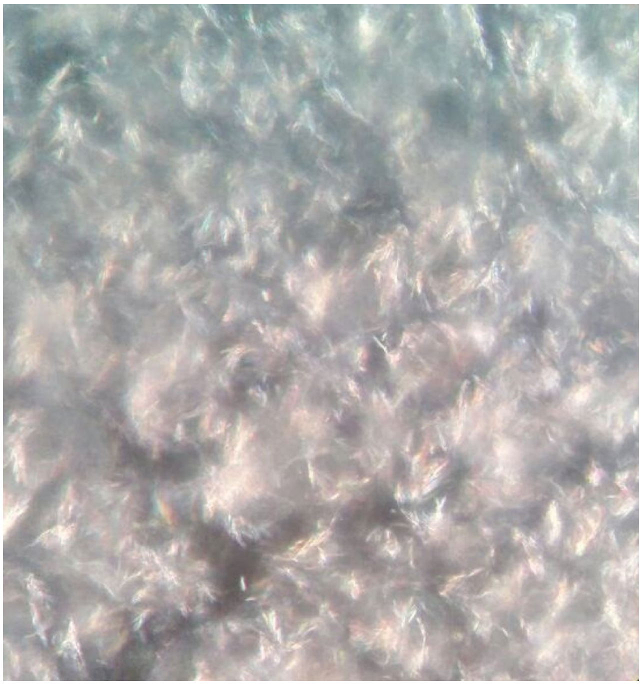

FIGURE 5 | The stratum argenteum of *Nezumia sclerorhynchus*, located in the choroid, contains iridescent crystals that enhance retinal sensitivity. Light passing through the retina is reflected by this layer, directing unabsorbed photons back onto the photoreceptors. This reflective mechanism significantly increases the efficiency of photon capture, contributing to improved visual sensitivity under low-light conditions.

In mammals, the tapetum lucidum demonstrates considerable variation. Predatory species, such as felines, possess a reflective riboflavin-based tapetum lucidum, optimising vision for nocturnal hunting. Ungulates, however, feature an acellular fibrous tapetum made of collagen fibrils, facilitating vision in dim twilight conditions (Shinozaki et al. 2013). Seasonal adaptations have also been documented in species such as the arctic reindeer, where the tapetum changes from yellow in summer to blue in winter, maximising light capture in varying illumination levels (Ollivier et al. 2004).

Interestingly, the degeneration of the tapetum lucidum in some taxa reflects its variable evolutionary utility. In the southern two-toed sloth (*Choloepus didactylus*), histological analysis shows a choroidal *tapetum lucidum cellulosum* with signs of degeneration, aligning with its diminished reliance on nocturnal vision (Klećkowska-Nawrot et al. 2024). Similar patterns are observed in other species, potentially linked to ecological or dietary shifts (Ollivier et al. 2004).

The evolutionary trajectory of the tapetum lucidum highlights its role as a convergent adaptation, arising independently in diverse lineages to enhance photon capture and vision in low-light conditions. Its absence in cephalopods underscores its significance as a compensatory mechanism for the inverted vertebrate retina, demonstrating its unique role within vertebrate evolution (Vee et al. 2022).

2.2.5 | Visual Photopigments

The visual environment exerts selective pressure on photopigments to adjust their absorbance to the available wavelengths, a process known as 'spectral tuning'. This manifests as a shift in the spectral sensitivity peak of photopigments.

The variation in light in diurnal habitats is well-documented but less so in nocturnal ones. The intensity of nocturnal light varies depending on the openness of the habitat (open or wooded), the lunar phase or cloud cover. In nocturnal forests, the light has a yellow-green spectral dominance with a maximum peak at 560 nm. The spectral sensitivity of the cones of nocturnal animals, tuned to 560 nm, coincides with the maximum flow of nocturnal forest light, optimising the perception of the environment. Additionally, diet can influence the spectral sensitivity of S cones, tuned to detect food sources such as flowers and fruits (Veilleux and Cummings 2012). Environmental elements can exert selective pressure on photopigments to adjust their spectral sensitivity when their wavelength has biological relevance.

In terrestrial habitats, nocturnal light conditions, influenced by factors such as lunar phase, cloud cover and vegetation density, predominantly feature yellow-green spectral light peaking at approximately 560 nm. The cones of nocturnal vertebrates, such as certain mammals and amphibians, exhibit peak sensitivities tuned to this spectrum, optimising their ability to detect environmental cues under limited illumination (Veilleux and Cummings 2012). In nocturnal forests, this spectral alignment facilitates improved perception of foliage and other ecologically relevant objects.

Marine environments demonstrate more pronounced spectral tuning due to the rapid attenuation of light as depth increases. Within mesopelagic zones (150–1000 m), light is monochromatic and dominated by blue wavelengths (Kaartvedt et al. 2019). Animals inhabiting these zones, such as bioluminescent sharks *Etmopterus lucifer*, *E. splendidus*, *E. spinax and Trigonognathus kabeyai*, adapt their rhodopsin pigments to absorb light within the 450–500 nm range, maximising photon capture under dim conditions (Douglas et al. 1998). For instance, dragonfish (*Malacosteus niger*) utilises chlorophyll-derived photosensitisers to extend their sensitivity into the far-red spectrum, enabling efficient use of their own bioluminescence (Douglas et al. 1999). This adaptation is critical for detecting bioluminescent signals, which serve as key visual cues in these depths (Warrant and Locket 2004). Beyond 1000 m in the bathypelagic zone, sunlight is absent, and bioluminescence becomes the primary light source, necessitating further specialisation in visual systems (Robison 2004).

The rhodopsins of deep-sea vertebrates exhibit peak spectral sensitivity shifts towards the blue, an adaptation driven by habitat depth and the spectral composition of ambient light. Cetaceans, such as dolphins, have blue-shifted rhodopsins sensitive around 488 nm due to amino acid substitutions at key sites, optimising vision in their aquatic environments (Fasick and Robinson 2000; Hunt et al. 2009). Similarly, mysid shrimp populations demonstrate spectral sensitivity shifts driven by chromophore changes, reflecting rapid adaptation to local light environments (Ostrovsky 2024).

Spectral tuning is not limited to aquatic species. Some nocturnal terrestrial vertebrates exhibit unique adaptations, such as the aye-aye (*Daubentonia madagascariensis*), which retains functional SWS1 and LWS opsins to enhance dichromatic vision under low-light conditions (Hunt et al. 2009). Additionally, bats and marsupials with UV-sensitive SWS1 opsins demonstrate convergent evolution of spectral tuning to accommodate nocturnal activity (Hagen et al. 2023).

Environmental factors strongly influence spectral tuning across habitats. Fish species inhabiting turbid waters exhibit red-shifted sensitivities compared to those in clear waters due to the attenuation of shorter wavelengths by suspended particles. For instance, anchovies and species such as *Gnathonemus petersii* enhance photon capture through reflective retinal structures, amplifying light efficiency by up to 500% (Francke et al. 2014; Kreysing et al. 2012). Terrestrial examples include moths, which adjust their spectral sensitivity through pigment migration, optimising detection of floral cues (Satoh et al. 2017).

The adaptation of spectral sensitivity also aligns with specific visual tasks. Nocturnal predators, for instance, rely on enhanced long-wavelength photoreceptor sensitivity to detect prey or navigate complex environments. Examples include the modifications in retinal architecture of nocturnal birds and deep-sea fish that optimise detection of dim or bioluminescent stimuli (Warrant and Johnsen 2013; Margetts et al. 2024).

Overall, spectral tuning underscores the evolutionary versatility of visual systems in adapting to diverse light environments. From the open oceans to dense forests, these modifications optimise visual performance under varying ecological constraints and offer valuable insights into the interplay between environment and sensory evolution.

2.2.6 | Cone Photopigments

In dimly lit environments, the proportion of cones to rods in the retina is significantly reduced, reflecting a reliance on scotopic vision. Despite this, most mammals retain dichromatic vision, mediated by two cone types: S cones, sensitive to short wavelengths (blue), and M cones, responsive to medium wavelengths (green). However, nocturnal mammals often exhibit reduced diversity in cone pigments, with some species, such as the owl monkey (*Aotus trivirgatus*), entirely lacking S cones (Jacobs et al.

1993). This loss appears to result from evolutionary changes prioritising rod function, as no mammals have been found to lack L-opsin, critical for luminance and acuity under non-scotopic conditions (Peichl 2005).

UV sensitivity is an adaptation observed in certain nocturnal rodents, such as the fat-tailed gerbil (*Pachyuromys duprasi*) and the house mouse (*Mus musculus*), which utilise S cones for detecting ultraviolet light. This sensitivity supports behaviours such as predator avoidance and resource localisation during twilight hours. UV sensitivity has also been documented in nocturnal birds such as the scops owl (*Otus scops*), where UV reflectance in chicks' beaks serves as a signal for parental feeding strategies (Müller et al. 2009; Parejo et al. 2010).

In marine mammals, adaptations in cone photopigments align with environmental light constraints. Pinnipeds such as the harbour seal (*Phoca vitulina*) display dichromatic vision, while many cetaceans, including the sperm whale (*Physeter macrocephalus*), exhibit monochromacy, retaining only M cones. These adaptations correspond to the spectral properties of their habitats, as blue light dominates at oceanic depths. Amino acid substitutions in opsins are linked to spectral tuning, enabling these species to optimise light absorption in aquatic environments (Fasick and Robinson 2000; Newman and Robinson 2005).

Deep-sea fish also demonstrate remarkable cone adaptations. In species such as *Gnathonemus petersii*, cones are embedded in reflective retinal structures, which amplify photon capture, enhancing vision in turbid waters. Dragonfish (*Malacosteus niger*), notable for their far-red bioluminescence, utilise specialised photopigments to detect these unique signals, providing an advantage in prey detection (Douglas et al. 1999; Kreysing et al. 2012).

2.2.7 | Colour Vision in Scotopic Environments

Colour vision under low-light conditions is highly limited. The threshold for colour detection is imposed by dark noise in the cones. Vertebrates with a duplex retina rely on rod-based vision when noisy signals from the cones become unreliable, a transition marked by the Purkinje effect. Interactions between cones and rods only contribute to colour vision at mesopic light intensities (Kelber et al. 2017).

The retina of animals in scotopic environments compensates for the lack of cone functionality by increasing the proportion of rods and neuronal convergence. Although visual acuity and colour vision are generally sacrificed for sensitivity, some species can distinguish colours at extremely low-light intensities, sacrificing spatial and temporal resolution in favour of spectral resolution. Colour vision is more reliable than greyscale vision (Kelber and Roth 2006).

In nocturnal birds such as the Eurasian Eagle-Owl (*B. bubo hispanicus*), cone oil droplets (Figure 6) play a role in enhancing visual sensitivity by focussing light onto the outer segments of photoreceptors. These droplets, which include yellow and colourless types, act as filters that reduce chromatic aberration and optimise light transmission to the visual pigments (Alix et al. 2017). This adaptation reflects the owl's ability to balance sensitivity and acuity, allowing it to function effectively in both crepuscular and low-light conditions.

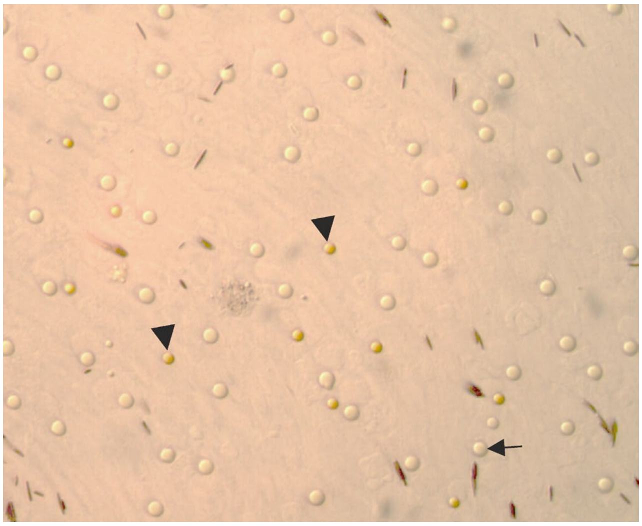

FIGURE 6 | Light micrograph of a flat-mounted retina from *Bubo bubo*, highlighting the presence of lipid oil droplets. Brilliantly yellow-coloured oil droplets (arrowhead) and colourless oil droplets (arrow) are visible.

Diurnal lizards have lost their duplex retina and only have cones, but geckos, adapted to nocturnal life, have widened their pupils and reduced their focal length, with elongated cones that exhibit rod-like characteristics (Roth and Kelber 2004). In contrast, the garter snake Thamnophis sp. has functional rhodopsin in its cones, suggesting that its rods have been modified to function as cones. The photoreceptor transmutation theory (Walls 1942) explains these evolutionary transitions, shaped by environmental constraints and evolutionary pressures (Schott et al. 2016).

Frogs and toads have two spectral types of rods with opposing signals (Kelber et al. 2017). ‘Green’ rods are sensitive to blue and yellow-red light, using a cone opsin that provides colour sensitivity. ‘Red’ rods with rhodopsin contribute to brightness sensitivity. Together, these rods maximise absolute sensitivity, visual acuity, and colour sensitivity (King et al. 1993). In species such as *Hyla arborea*, nocturnal colour vision is crucial for mate selection, as sexual dimorphism based on the colour of the vocal sac, related to carotenoids, indicates the health and quality of the male (Gomez et al. 2009).

2.2.8 | Bioluminescence Detection

Bioluminescence is a key ecological feature in the mesopelagic ocean, serving diverse functions such as communication, predation and defence (Johnsen et al. 2012). Beyond 1000 m depth, where sunlight ceases to penetrate, point bioluminescent sources become the primary illumination, driving specialised adaptations in deep-sea fish to detect specific wavelengths. Species such as *Malacosteus niger* and *Aristostomias scintillans* (family

Stomiidae) exemplify these adaptations, possessing photopigments attuned to long-wavelength red bioluminescence, a capability rare among deep-sea fish, which typically absorb short wavelengths (Douglas et al. 1998; Crescitelli et al. 1985). This unique sensitivity enables predatory strategies that rely on detecting prey without being seen, as their red bioluminescence remains invisible to other organisms.

Malacosteus niger highlights the interplay between bioluminescent emission and photoreceptor adaptation. Its tapetum lucidum, containing astaxanthin and bacteriochlorophyll-based photosensitisers, emits fluorescence at 680 nm, aligning with the spectral sensitivity of its long-wavelength photopigments (Douglas et al. 2016; Douglas and Cronin 2016). This adaptation underscores the evolutionary pressure to balance stealth and detection in an environment dominated by bioluminescent signals.

To enhance spatial resolution and improve the detection of bioluminescent cues, some deep-sea species have developed specialised retinal structures. For instance, *Rouleina attrita*, a fish inhabiting depths of 1.4–2 km, exhibits a temporal fovea with a high density of ganglion cells, facilitating precise localisation of bioluminescent signals over significant distances (Warrant 2000). Similarly, lanternfish (Myctophidae) exhibit retinal topographies that enhance visual acuity in specific regions, complemented by a high proportion of displaced amacrine cells (70%–80%) in their ganglion cell layer, likely of the AII type. These cells are hypothesised to improve the detection of small bioluminescent flashes against the mesopelagic background (Busserolles et al. 2015).

2.2.9 | Other Adaptations

Lanternfish are one of the most abundant groups of mesopelagic fish in the world. They exhibit multiple visual adaptations to dim light, such as large eyes relative to body size, aphakic aperture, tapetum lucidum and a retina dominated by long rods. Recently, two new specialisations have been discovered (Musilova et al. 2019).

One of these is the aggregation of extracellular microtubular structures (MLS) in the inner nuclear layer. These structures, different from classical microtubules, are not intracellular, are larger, and are closely associated with cell membranes. In some species, MLS surround horizontal cells, suggesting a possible relationship and interconnection between them. However, this topic requires more extensive studies to be confirmed (Busserolles et al. 2014).

The other adaptation is the pigment epithelium of lanternfish, which is thin and lacks melanin except in the central part, where large aggregations of melanosomes are found. This adaptation may reduce the scattering effect caused by the myelin of optic nerve axons, differing from the reflection of the tapetum lucidum. It is speculated that this pigmentation, called fundal pigmentation, could be a larval vestige that protected the photoreceptors from photobleaching during their epipelagic stage before migrating to deep waters, where the pigment epithelium does not grow at the same rate as the retina (Busserolles et al. 2014).

Additionally, some species of lanternfish have yellow pigmentation that acts as a filter for short wavelengths. This shifts the sensitivity peak of photoreceptors to longer wavelengths, improving contrast and the detection of bioluminescent signals in specific parts of the visual field (Busserolles et al. 2015). This adaptation is like the yellow lenses found in other fish (Douglas et al. 1998).

2.2.10 | Regressive Evolution

Regressive evolution involves the degeneration of previously useful structures in a lineage over time. Vestigialisation occurs when organisms occupy a new niche, and one or more traits degenerate due to relaxed selection or direct selection against maladaptive characteristics (Jeffery 2009). This occurs in the eyes of organisms inhabiting environments with little or no light, such as caves, subterranean areas, deep oceans, and nocturnal environments. Vision declines in these settings, while other senses, such as touch and smell, compensate for the lack of vision (Jeffery 2009).

Organisms with vestigialisation accumulate mutations in their opsin genes, rendering them non-functional, although they maintain retinal organisation associated with their lifestyle (Emerling and Springer 2014). In the Iberian mole *Talpa occidentalis*, a normal prenatal eye develops, but after birth, lens anomalies and other severe defects occur. Ganglion cells with melanopsin mediate photoperiodicity, retaining their function.

The giant mole-rat (Spalax) undergoes severe ocular degeneration that prevents image formation but retains classical retinal layers, L-M cones, and ganglion cells with melanopsin for photoperiodicity (Esquiva et al. 2016). Many subterranean rodents display a diurnal dichromatic pattern, although Spalax has lost the SWS cone. In these rodents, the lack of selective pressure allows mutations to accumulate in opsin genes, resulting in non-functional opsins (Peichl et al. 2004).

Cryptomys anselli occupies an intermediate position, with a well-stratified but thinner retina in adults. It has a higher population of short rods with functional rhodopsin and retains S cones, although with fewer ganglion cells (Cernuda-Cernuda et al. 2003).

Most African mole-rats have a typical retina for forming low-resolution images due to the reduced size of their eyes. The retina is dominated by rods but contains a significant population of cones, exceeding 10% of photoreceptors, and retains cones for both low and high wavelengths. This suggests an adaptation to bright light, despite living in dark environments. The outer nuclear layer and inner plexiform layer are thinner than in nocturnal rodents. Additionally, midbrain structures that coordinate visual reflexes are severely reduced, indicating less reliance on visual signals, although they maintain functional circadian cycles (Němec et al. 2008).

Spalacopus cyanus retains normal-sized eyes for its species, with a duplex retina and two types of cones (S-UV and L-M), suggesting an adaptation to short periods of surface activity, such as food foraging (Peichl et al. 2005). In the uco-tuco (Ctenomys), a neotropical rodent, the eye is normal with a low density of photoreceptors but retains a significant population of cones, primarily L-M, and some S-UV. Surface expeditions exert evolutionary pressure to conserve its retina, important for avoiding predators and selecting food (Schleich et al. 2010).

The retina of *Thomomys bottae* also has a normal visual organisation like other rodents, with rod density typical of a nocturnal vertebrate and two types of cones that allow for dichromatic vision (Williams et al. 2005).

The conservation of a diurnal retina in some subterranean rodents may indicate (1) daylight expeditions, (2) insufficient geological time in the subterranean environment to accumulate degenerative mutations and/or (3) useful adaptation for locating gaps through which predators might enter.

3 | Future Perspectives

While substantial progress has been made, further research is needed to address gaps in our understanding of vertebrate visual systems. Investigating the molecular underpinnings of adaptations, such as the genetic mechanisms driving spectral tuning and opsin diversity, could reveal the evolutionary pathways of photoreceptor specialisation. Additionally, field studies combining ecological data and advanced imaging techniques could clarify the functional significance of specific adaptations, such as UV sensitivity in nocturnal rodents or bioluminescence detection in deep-sea fish. As climate change and habitat degradation alter environmental light conditions, studying how visual systems respond to these pressures is crucial for predicting species resilience. Collaborative efforts integrating molecular biology, ecological modelling, and behavioural studies will provide a holistic understanding of vision's role in survival and adaptation. These insights will not only deepen our appreciation of sensory evolution but also inform conservation strategies for species reliant on specialised visual systems.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

No new data were created or analysed in this study. Data sharing is not applicable to this article.

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