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Research Article

# Squid as a Model Organism - Part 3: Ocular Morphology and its Implications in Biomimicry for Human Ophthalmology

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## Abstract

The distinctive feature of cephalopods is their lack of scales, possession of eight arms and two long tentacles, with considerable diversity in shape, size, and habitat. Giant and colossal squids represent some of the largest marine creatures. Giant squids, in particular, are exceptionally captivating beings with unique characteristics that allow them to thrive in the incredibly dark depths of the oceans. Despite their large size, these cephalopods are agile swimmers, capable of sudden changes in direction. Vision is the primary sense for cephalopods, enabling them to perform these rapid movements. The giant squid (Architeuthis) has the largest eyes among marine and terrestrial animals, constituting a significant percentage of its weight and volume. These large eyes have captured the attention of biologists, leading to investigations into the anatomy, physiology, and histology of the cephalopod eye. It is noteworthy that the highest concentration of neural cells in the brain is found in the optic lobes of the giant squid, emphasizing the importance of vision in its life in dark and formidable habitats. In this review, we delve into the evolution, histology, structure, and physiology of the giant squid's vision, followed by a comparative analysis with human optics.

**Keywords:** eye evolution, optics, giant squid

## 1. Introduction

On Earth, the largest recognized animal in terms of weight and structure is the blue whale, measuring about 35 m in length and weighing approximately 1 ton. However, it is interesting to note that in terms of body length, the colossal squid (giant and colossal species) ranks among the longest creatures on the planet. The giant squid (Architeuthis)

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reaches a weight of approximately 400 to 700 kilograms and a body length of about 15 to 25 m, with tentacles extending up to 10 m. The accidental discovery of a giant squid in the stomach of a sperm whale in 1925 by Robson led to its documentation in the WRMS [1]. Geographically, giant squids are predominantly found in the Pacific Ocean, the Atlantic Ocean, and the Mediterranean Sea. The exact depth at which giant squids inhabit the ocean column is uncertain, but their estimated depth range is from 300 to 1200 m below the sea surface [1].

Cephalopods, including giant squids, are classified as mollusks, specifically from the order Octopoda and the family Architeuthidae. These soft-bodied creatures, belonging to the octopus family, venture to shallower waters during the night for feeding while residing in the ocean depths during the day. Over 700 known species of living cephalopods have been identified on Earth. This species diversity is largely due to their adaptability to environmental changes, even though, in general, most cephalopods have relatively short lifespans. The body length of giant squids varies significantly, ranging from the smallest to the largest animals in the oceans. Typically, these creatures have eight robust arms with suckers and two long tentacles used for hunting. When feeling threatened, many cephalopods release a dark ink, like the giant squid, to confuse predators.

As mentioned earlier, the giant squid, like other cephalopods, possesses eight arms and two very long tentacles, utilizing fin-like structures for movement. Water is drawn into the mantle or the main part of the body, then forcefully expelled. The pressure created by the expulsion of water results in jet-like movement, contrary to the direction of water exit. This rapid movement, coupled with sudden changes in direction and acceleration, is an effective defense mechanism against predators, requiring comprehensive and rapid vision.

One prominent feature that distinguishes giant squids, making them highly formidable for defense or predation, is their large eyes and telescopic vision. Giant squids have the largest eyes in the animal kingdom, with each eye nearly the size of a basketball (approximately 27 cm). This characteristic enables these creatures to have an extensive field of vision, equivalent to a football field, in the depths of the ocean, where other animals lack this capability due to absolute darkness. In fact, the size of the eyes of giant squids ranks first and second, respectively, among the largest eyes of animals. Giant squids have exceptional vision specialized for rapid directional changes, the detection of specific colors, and distinctive patterns, enhancing their defensive and predatory capabilities. In the following sections, we will delve into the unique and fascinating aspects of the eyes and vision of the giant squid.

## 2. Evolution and Development of Eyes in Organisms: From a Light-Sensitive Spot to a Complex Eye

The simplest description of the concept of vision can be expressed through multiple light-sensing cells in a multicellular organism that can only detect the presence or absence of light. The evolutionary journey of the eye began with the emergence of this light-sensitive spot [2–4]. Following the appearance of light-sensitive molecules, the evolution of light-receptive cells ensued, aiming for improved and more precise vision. Indeed, after approximately 35,000 generations from the appearance of the light spot, the necessity for creating a cup-shaped structure to dominate visual information about the surrounding spatial and environmental details led to the development of the eye organ [5]. In this process, two types of light-sensitive cells emerged in animals, utilizing microvilli and ciliary cellular structures to enhance light absorption. Subsequently, the organization of these light-sensitive cells formed the retina within the inner part of the cup-shaped eye structure. The lens focused light at a specific point in the eye, enabling the perception of distant and nearby objects by altering its curvature. In the final stage of evolution, advanced camera-like eyes with cornea and iris were perfected. The cornea protected the eye structure, while the iris regulated the incoming light intensity. This complex and intricate structure is present in many organisms, including soft-bodied fish, colossal squid, and humans [6].

Evolutionary overview of the eye life first evolved approximately 3.7 billion years ago, acquiring the ability to perceive light [5]. At that time, organisms needed to absorb light for various functions such as energy production and finding suitable living conditions. Therefore, over countless years, light-absorbing sensors, known as eyes, evolved in various shapes and sizes, ranging from simple light spots to camera-like eyes. The evolution of the eye can be divided into four main stages, which will be discussed in order [4].

### 2.1. Evolution of Light-Receptive Molecules

Opsins are organic molecules capable of light absorption. In multicellular eukaryotic animals, the amino acid sequence of the opsin protein has twisted seven times across the cell membrane, forming two segments: a and b. Each opsin protein requires the association with a light-sensitive protein called chromophore or retinal for light absorption. Retinal, a derivative of vitamin A, binds covalently to opsin, creating the opsin-retinal compound. In this compound, when retinal is exposed to light, its spatial conformation changes, initiating a chemical cascade that conveys the visual signal to the light-receptive cell and eventually sends the visual message to the brain [4].

## 2.2. Evolution of Light-Receptive Cells

Proteins sensitive to light (opsin-retinal compounds) are proteins that reside in the membrane of light-receptive cells. Based on this, two unique membrane structures, microvilli and ciliary, evolved to accommodate light-sensitive proteins in the membrane of light-receptive cells. Light-receptive cells in most invertebrates are of the microvillar type, while in vertebrates and chordates, they are of the ciliary type. Each type of light-receptive cell contains a specific subgroup of light-sensitive proteins, leading to different signaling pathways. In microvillar-type light-receptive cells, the light beam is absorbed by the rhodopsin protein, resulting in the opening of sodium channels and cell depolarization. Meanwhile, in ciliary-type light-receptive cells, light is absorbed by the cone opsins, leading to the closure of sodium channels and cell hyperpolarization [4].

## 2.3. Evolution of Different Types of Light-Receptive Cells

The bodies of animals consist of various cell types, each specialized for a unique function. It appears that during the evolution of these multicellular organisms, specialized cell types were created by dividing tasks among different cells. According to the division of labor theory, during the evolution of the eye, an ancestral multi-functional light-receptive cell with opsins, microvilli, and pigment granules, performing more than three functions, existed years ago (Figure ??). Subsequently, this mother cell proliferated, giving rise to various sister cells, each specialized in one of the functions of the ancestral light-receptive cell. This process led to the emergence of light-receptive cells, ciliated cells with motile cilia, and cells containing pigment granules separately (Figure ??).

## 2.4. Evolution of Vision Organs

Roughly, the first stage in eye evolution is the creation of a light spot. The light spot consists of a small number of light-receptive cells alongside pigment cells. These eyes can only detect light and darkness in the surrounding environment and are incapable of discerning details. If we consider the eye as an organ evolved for spatial information

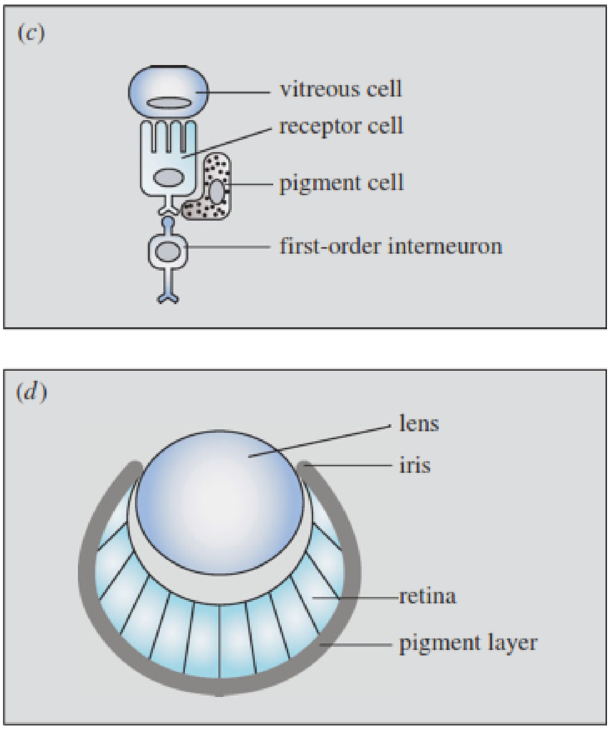

**Figure 1**: Overview of the four main stages in eye evolution: (a) evolution of light-receptive molecules, (b) evolution of light-receptive cells, (c) evolution of different types of light-receptive cells, and (d) evolution of vision organs [4].

transmission, the curvature of the eye structure was necessary for expanding light-sensitive cells in a cup-shaped manner. The created curvature reduces the amount of incoming light, increases image clarity, and widens the field of view. In the continued evolution towards more advanced eyes, the cup edges came so close together that only a small aperture remained for light entry into the eye. This type of eye, known as the pinhole eye, is observed in the ancient chambered Nautilus. Despite its large diameter, the pinhole eye is considered weak because the reduction in pupil diameter to enhance image clarity and the entry of water into the eye reduces the incoming light to the retina. In the next stage, to increase image clarity and quality, cells containing crystals were added to the eye structure, and eyes with primitive lenses took shape. Finally, camera-like eyes composed of cornea, iris, lens, external eye muscles, and retina formed, representing the most complete type of eyes (Figure **1**) [5].

## 2.5. Evolution of the Eye in Squid

The complexity of the eye has been a subject of evolutionary investigation for a long time. Astonishing diversity in eye anatomy and the structure of Salwanian Plaun and Ernst Mayer’s light receptor cells has convinced scientists in the field of evolution that

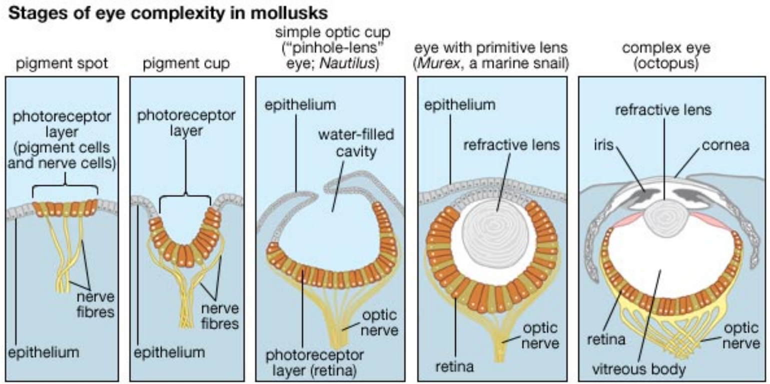

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**Figure 2**: Types of eyes from simple light spot to complex camera-like eyes in invertebrates. Various stages of eye evolution, from simple to advanced, can be observed in soft-bodied organisms (The New Encyclopaedia Britannica).

the origin of animal eyes was not singular, and eyes have independently evolved 40 to 65 times throughout the evolution of various animals [7]. A notable example of this convergent evolution theory is the emergence of large spherical eyes resembling a camera in the colossal squid. The colossal squid, belonging to the soft-bodied group and the cephalopod family, resides in the depths of the ocean. Its eyes exhibit remarkable structural and visual similarity to the eyes of vertebrates, particularly humans, and possess sensitivity and visual discrimination capabilities. Additionally, significant genetic similarities have been observed in crystallin proteins, responsible for lens formation, between the colossal squid and vertebrates [8]. In summary, the theory of convergent evolution suggests that there is an optimal design in nature for providing the most sophisticated eyes using biological materials, and this design has been repeated in the evolutionary process of different organisms.

On the other hand, with the advancement of molecular and genetic science, researchers have proposed the idea that eyes in various animal species evolve from a conserved mechanism dependent on the Pax-6 protein. Pax-6 plays a crucial role in the evolution of vertebrate eyes, and based on this, the theory of parallel evolution of animal eyes has been introduced. Evidence supporting this theory includes heterozygous mutations in the Pax-6 gene of vertebrates leading to various eye diseases in humans and the development of smaller-than-normal eyes in rodents. Furthermore, homozygous mutations in Pax-6 result in the complete loss of eyes, nose, and severe defects in brain formation. The eyeless protein in the fruit fly, Drosophila, also bears structural and functional similarities to the Pax-6 protein in vertebrates, contributing to the evolution of eyes in these organisms. Interestingly, any reduction in the expression of the eyeless gene in vinegar flies leads to eye malformation. Based on these findings regarding Pax6 and eyeless, these genes have been considered as key genes controlling eye evolution. Overall, these findings indicate that advanced eyes in vertebrates and simple eyes in arthropods have followed similar evolutionary pathways [9].

According to this theory, the evolution of the compound eyes of the colossal squid, as a classic example of convergent evolution with vertebrates, has been questioned and remains uncertain. Although the structure and physiology of vision in this specific group of invertebrates are considerably similar to vertebrates, the process of their evolution differs in many details. For instance, in the colossal squid, eyes originate from epidermal folds, whereas in vertebrates, eyes develop from neural plates [8,10]. Nevertheless, evidence indicates that the Pax-6 gene is expressed in the eyes, brain, and olfactory organs of colossal squid embryos. Moreover, the Pax-6 gene in the colossal squid can induce the formation of external eyes in vinegar flies [9, 10]. Therefore, it can be speculated that the Pax-6 homologous protein in the colossal squid, similar to eyeless in vinegar flies and Pax-6 in vertebrates, plays a role in the evolution of eyes. These results suggest a common evolutionary origin of eyes in invertebrates and vertebrates, indicating parallel evolution rather than convergent evolution [9]. Given the existing ambiguities in both convergent and parallel evolution theories, the study of the evolution of the compound eyes of the colossal squid, which shares significant molecular, cellular, and tissue similarities with vertebrate eyes, can potentially unveil the secrets of eye evolution.

## 2.6. Anatomy of the Giant Squid's Eye

The squid has two large eyes on either side of its head, depicting a quadrilateral eye arrangement in the skull. These eyes establish communication with the squid's brain through optic lobes. From an anatomical perspective, the axons of ganglion cells exit from the back of each eye, traverse the posterior-ventral chiasm, and terminate in the optic lobes on the same side [8, 11]. Notably, a structure called the "white body" is positioned between each eye and its associated optic lobe (Figure **2**), encompassing the posterior-lateral aspect of the respective optic lobe. The presence of the white body likely serves an anatomical role, acting as a cushion to protect the optic lobe and nerves exiting from this large eye cup [6, 8]. Additionally, cartilaginous structures are present to stabilize these elongated axons as they journey towards the brain [12, 13]. The distance between the optic lobes in the giant squid is short, allowing messages to directly transmit from the eyes to other parts of the brain with minimal intermediaries.

The diameter of eyes varies across different aquatic animals, ranging from less than 1 mm for instance in the lanternfish [15], to the size of a football in the giant squid

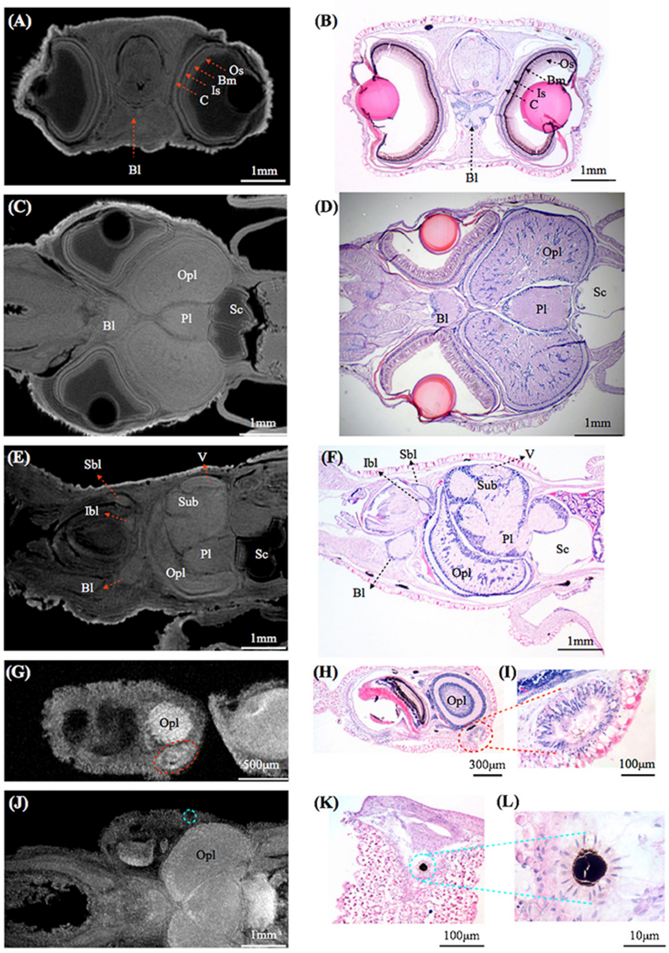
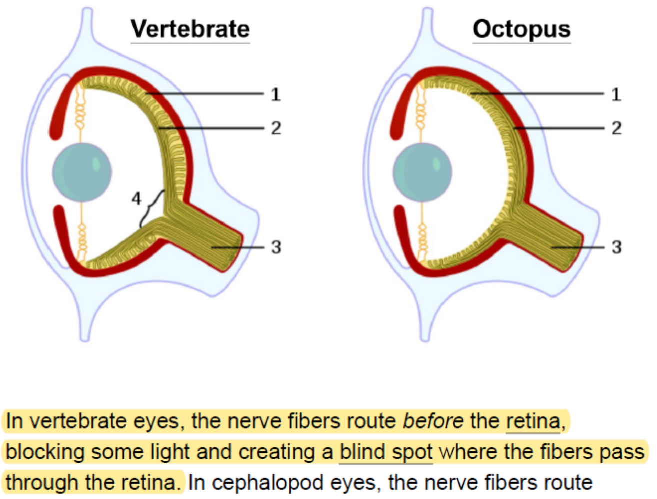


**Figure 3**: Comparison between magnetic resonance histology and traditional histology of the squid, *Idiosepius notoides* [14]. (A, B) Cross-sectional views of the squid's head, revealing four distinct retinal layers: the outer segment layer (Os), basal membrane (Bm), inner segment layer (Is), and cartilaginous eye cap (C). (C, D) Horizontal sections of the squid's head. (E, F) Sagittal sections of the squid's head. (G–I) Rhinophore. (J–L) Chromatophore. (E) denotes the eye, while other labeled features include gill (G), liver (L), ventral lobe (V), brachial lobe (Bl), statocyst (Sc), inferior buccal lobe (Ibl), optic lobe (Opl), pedal lobe (Pl), superior buccal lobe (Sbl), subesophageal mass (Sub), supraesophageal mass (Sup). The MRI slice resolution at 16.4T closely approximates that of standard histology. However, unlike histological sections that provide cellular details allowing individual cell identification, MRI images lack such cellular resolution. Voxel resolution: 9 $\mu$m.

[7]. The anatomical size of the eye is a crucial factor in determining the visual range. The eye diameter in vertebrates like the blue whale, sperm whale, and humpback whale is relatively 109, 61, and 55 mm, respectively [16, 17]. Even in large fish, eye size typically does not exceed 90 mm [7], while in the vertebrate giant squid, eye sizes from 250 to 400 mm have been reported [12, 18, 19]. Corresponding to its large eyes, the anatomical size of the lens in the giant squid ranges from approximately 8 to 10 cm. The lens structure is specially adapted to enable effective focusing at both near and far distances. The central region of the lens has high cellular density, while the peripheral regions have fewer cells [8]. A cornea, composed of skin, forms the outer layer, having a distinct ectodermal origin from other eye parts. The initial eyelid is either

fully closed or connected to the anterior chamber of the eye by a small aperture. This primary eyelid closes with the contraction of the front edge muscles over the eye [8]. The iris, situated in front of the lens, has radial muscles that contract or expand based on ambient light intensity. With the contraction or expansion of the iris muscles, the pupil, ranging from approximately 3 to 9 cm, adjusts its opening and closing, regulating the amount of light entering the eye. Specialized muscle cells called statocytes are located on both sides of the lens and iris, contributing to the stability and balance of the giant squid's large lens and iris in their respective positions [20]. The vitreous humor inside the eye occupies a substantial volume of this large eye.

The retina structure in the giant squid's eye is much simpler compared to humans, with fewer layers and less cell diversity. Generally, in giant squids, the blind spot and yellow spot have not been observed [21]. Studies have shown that the eyes of giant squids have a structurally simple retina, consisting of rod-type photoreceptor cells [22] and, in fact, lacking cone cells for color image detection [21]. Unlike the eyes of vertebrates, in giant squids, the nerve fibers of photoreceptor cells are located behind the retina. Therefore, there is no neural blind spot in this structure (Figure **3**).



In vertebrate eyes, the nerve fibers route *before* the retina, blocking some light and creating a blind spot where the fibers pass through the retina. In cephalopod eyes, the nerve fibers route

**Figure 4**: In the eyes of vertebrates, nerve fibers pass in front of the retina, obstructing certain light and resulting in a blind spot where these fibers traverse the retina. In contrast, cephalopod eyes exhibit a different arrangement, with the nerve fibers running behind the retina, avoiding the obstruction of light and maintaining the integrity of the retina. In the diagram, 1 represents the retina, 2 depicts the nerve fibers, and 3 signifies the optic nerve. Additionally, 4 illustrates the blind spot characteristic of vertebrate eyes.

In the colossal squid, besides having the largest eye and lens size among all terrestrial creatures, specialized visual organs have evolved to improve its vision. Each eye of the colossal squid has a visual organ located on the outermost part of the lens. These light-emitting organs, arranged in two elongated structures on the ventral surface of each eye, emit a specific and constant light to enhance the vision of the colossal squid in its surroundings [9]. When the eyes rotate inward to focus directly on the colossal squid's arms, these specialized light-emitting organs provide sufficient and acceptable light to improve the colossal squid's vision, enabling it to detect prey, spot predators, escape, and survey its overall environment [18].

## 2.7. Physiology of Vision in the Colossal Squid

Remarkably, the large eyes of the colossal squid are proportionate to its 25-m body, providing nearly 360-degree vision [23]. While vision is the primary sensory perception in the colossal squid, the compelling reason for the oversized eyes remains elusive [20, 24]. The maintenance of large eyes in biological systems is costly and may disrupt an animal's stealth [24]. This suggests that the colossal squid requires its large eyes for a specific, unique vision, offering distinct advantages. The extensive field of view in the colossal squid, facilitated by its large eyes, is comparable to a telescope, expanding with size.

The deep-sea habitat, with its unique visual characteristics due to bioluminescent light, presents a world where objects in the background appear uniformly visible. Due to light absorption and scattering in water, contrast between objects and the background significantly decreases, creating a visual challenge. For inhabitants of this habitat, any object seen in this visual field becomes crucial, whether as a threat/food or a mating opportunity. The colossal squid's large eyes can be justified by its need to detect objects in the vast distances of the ocean, allowing it to respond appropriately to behavioral cues such as fleeing, attacking, etc. Thus, the colossal squid's large eyes contribute to its adaptability as a highly skilled predator in the ocean depths [12, 13, 25].

These colossal compound fish have the largest eye size in the animal kingdom throughout the history [12]. Their vision is monocular or stereoscopic, capable of distinguishing between two different visual fields with their two eyes [12]. The eyes are positioned on either side of their head, allowing them to see in front and behind, though lacking binocular vision necessary for depth perception [12]. In essence, the large eye and monocular vision help eliminate blind spots, allowing the colossal squid to see more space around its body.

## 3. Optical Structure of the Colossal Squid's Eye and Comparison with the Human Eye

The optical structure of the colossal squid's eye, like that of the human eye, utilizes a camera-like design. This structure includes the cornea, spherical lens, vitreous, and light-receptive cells. Images are formed by the lens on the retina. The role of receptors involves transmitting light signals from the retina and converting them into neural signals directed towards the brain. While the human eye can see up to a depth of 500-600 m underwater, the colossal squid's eye, with its large size, can see depths of up to 1,000 m underwater, leveraging the advantage of its substantial eyes [13].

In the human eye, muscle movements connected to the lens and changes in its diameter adjust its focal point. Conversely, in the colossal squid's eye, direct movement of the lens achieves the adjustment of its focal point. This structure bears a significant resemblance to how a camera adjusts its image focal point with a movable lens. Colossal squid species often have monocular vision, where their eyes are independent of each other, although monocular vision's drawback lies in the inability to perceive volume [13].

The lens of the colossal squid's eye is optimized for underwater vision, being biased towards a camera-like structure. This adaptation ensures accurate functionality for the eye in the dominant blue color of deep waters, while other colors are somewhat involved in color aberration [1]. Numerically, the refractive index of the colossal squid's eye cornea ranges from 1.376, and the lens refractive index ranges from 1.441 to 1.485 [1]. In contrast, the refractive index of ocean water is approximately 1.39. The difference in refractive indices between water and the lens leads to the focusing of the image on the retina. The colossal squid's eye lens has a slightly convex shape and is not entirely spherical, which influences the effective focal length for image focusing.

Unlike the human eye, which cannot detect the polarization of light, the colossal squid's eye is sensitive to polarization direction. Polarization of light represents the direction of vibration of the light field perpendicular to the direction of propagation. Their eyes can identify the vertical and horizontal polarization of light. This sensitivity to polarization results in increased image contrast in underwater depths [3]. Additionally, this capability enhances the power of vision at the edges and margins of objects in low-contrast aquatic environments [4]. Compound eyes, in general, are not sensitive to polarization since the opsins of the cylindrical and cone cells are randomly arranged. However, the colossal squid's eye is polarization-sensitive due to the perpendicular arrangement of adjacent sensor regions, known as rhabdoms. The presence of polarization-sensitive receptors in physiological studies has been confirmed [3].

## 4. Conclusion

In delving into the intricate world of the colossal squid's eye, we uncover a marvel of evolution and adaptation that has enabled these deep-sea dwellers to navigate the abyss with unparalleled precision. The optical architecture of their eyes, resembling a sophisticated camera system, showcases a unique set of features finely tuned to the challenges of the ocean's depths.

The colossal squid's eye, with its large size and intricate design, extends the boundaries of underwater vision, surpassing the capabilities of the human eye. This adaptation allows them to explore depths of up to 1,000 m, a feat beyond the reach of most marine creatures. The utilization of monocular vision, while presenting limitations in perceiving volume, underscores the efficiency of their ocular structure in addressing the demands of their environment.

A standout feature is the lens's optimization for underwater vision, emphasizing functionality in the dominant blue hues of the deep sea. The sensitivity to polarization adds an extra layer to their visual acuity, enhancing image contrast and allowing for a more nuanced perception of their surroundings. These adaptations, coupled with the colossal squid's ability to detect bioluminescent signals in the dark ocean depths, paint a picture of a highly specialized and efficient visual system.

As we draw parallels between the colossal squid's eye and the human eye, we appreciate the diversity of evolutionary solutions to the common challenge of sight. While the colossal squid's eye excels in the specific conditions of the deep sea, the human eye showcases its own remarkable adaptability to the varied demands of the terrestrial environment.

In conclusion, the colossal squid's eye stands as a testament to the wonders of nature's ingenuity. Unraveling the mysteries of their vision not only deepens our understanding of marine life but also inspires awe for the intricate adaptations that enable these enigmatic creatures to thrive in the depths of our planet's oceans.

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