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Chapter

How Do Whales See?

Elena Vecino, Xandra Pereiro, Noelia Ruzafa
and Sansar C. Sharma

Abstract

The eyes of two whales *Balaenoptera physalus* and *Baleoptera borealis* were studied by our group. In this chapter, we present the anatomical, histological, immunohisto-chemical and ultrastructural studies of the eyes of both types of whales. Based on the results, we can conclude that at least in these two species, the whales are rod mono-chromat; their resolution is very limited due to the reduced number of retinal gan-glion cells, some of which were giant size (more than 100 micrometers in diameter). The excellent representation of melanopsinic positive retinal ganglion cells suggests an adaptation to the dim light as well as involvement in the circadian rhythms. The large cavernous body located in the back of the eye may provide a mechanism that allows them to move the eye forward and backwords; this may facilitate focusing and provide protection from cold deep-sea temperatures.

Keywords: whales, cetacean, eye, vision, retina, optic nerve, anatomy

1. Introduction

The cetaceans are fully aquatic mammals with 89 species recognized by the Society of Marine Mammalogy Committee on Taxonomy [1]. The artiodactylian ancestors moved to aquatic life about 50 million years ago [2] and at present some relatives, like hippopotamuses, are semi-aquatic.

The adaptation to the new media, under the water, induced several changes in the morphology of the eyes. Although anatomy and functional vision have been studied in the odontocetes like dolphins and orca (cetaceans with teeth), limited studies have been done on mysticete eyes, the larger cetaceans (with baleen). Moreover, very few studies have been done on the molecular distribution and ultrastructure of the retina. In the present chapter, we will summarize the main results of our group on the structure of the eyes of two large fin whales (18 meters large and 20 tons in weight) that beached on the Cantabric coast of Spain; they died a few hours after beaching, but this allowed us to study the eye in perfect morphological details and some bio-chemical analysis. Since the eyes of both fin whales had similar size and the animals were of the same sex, we will discuss both without distinction. Both specimens were adult males; one was *Balaenoptera physalus* (beached on the 4th of February 2019 in Sopelana beach, Biscay Spain) and the other *Baleoptera borealis* (beached on the 20th of January 2021 in Serantes, Asturias Spain).

The results shown in the present chapter are based on anatomical, histologic, immunohistochemical and electron microscopy studies performed during the last 2 years that have partially been published in several articles [3–5]. The methodology was explained in those articles. Here, we will concentrate on explaining the conclusions of how our research has helped us understand how the whales see.

2. Anatomy of the eye

The first anatomical discovery was the size of the eye. Even though it was very small in proportion to the large body size of the animal, the whale eye was huge. When compared with other terrestrial mammals, it weighs 1 kilogram and is almost 13 cm in diameter. The shape of the eyeball was markedly flattened on the anterior segment compared with the spherical shape of the terrestrial mammals. As a result, the axial length of the eyecup was smaller than its diameter is close to a hemisphere. The eyes were located, as in other mysticetes, in the oral commissure. Two very thick eyelids protect the eye. The eyelids lack eyelashes that would not function under water (**Figure 1A–D**). Due to the adaptation to the big body size, and to resist the high pressures, the sclera was very thick, and was 4 cm in the thickest posterior part of the eye. Its composition was mainly collagen indicating that even when its texture is like bone the composition lacks hydroxyapatite [3]. Encapsulated sensory corpuscles were found in the sclera in groups in the proximity of the iridocorneal angle. It has been suggested that this corpuscle within the cetacean eye may function as pressure receptors, possibly to control intraocular pressure [6, 7].

The cornea was an elongation of the sclera that becomes transparent only in the most anterior part of the eye. The thickness of the cornea was not uniform. The cornea was thinner in the centre and thicker at the periphery with a peripheral rim of almost 4 mm thick while the central part was 2 mm. Moreover, the cornea in the central part of the eye was flattened, another adaptation to vision underwater [3]. The cornea in the case of these cetaceans acted as a weak divergent lens and the refractive index is very little different from that of the water (**Figure 1C**). Therefore, in cetaceans, light refraction and focusing of an image on the retina are almost entirely performed by the lens [8]. The intraocular lens, the crystalline, in these mysticetes was almost spherical similar to that in fishes and measured 2 cm in diameter. It was placed in the centre of the eyecup so that light coming from any direction is focused on the retina. The curvature of the lens surface provides sufficient refractive power to focus images on the retina. Thus, the optics of these cetaceans are similar to those of fish, reflecting the adaptation to the common environment and optical properties of the vision under the water. The very viscous vitreous body filled the vitreous chamber and as in fish, this viscosity is an adaptation to equilibrate the refraction.

The adaptation of the cetacean vision, from the deep underwater where the light is very low to a rapid change of brightness at the surface of ocean when the animal dives into the well-lit water surface, is perhaps due to the iris structure and its pupil shape. Most cetaceans have a special pupil with a U-shaped slit, however, the two mysticetes studied had the pupil oval and horizontally elongated with dimensions of 5 x 3 cm (**Figure 1A**). Several studies on the refraction index in the cetacean eyes, and especially in dolphins, had evoked the conclusion that the refractive index between the air and the cornea should make the cetacean eye catastrophically myopic (near-sighted) in air. However, this myopia is countered by the presence of flattened cornea [9]. The constriction of the iris and pupil shape can provide a correction of aerial
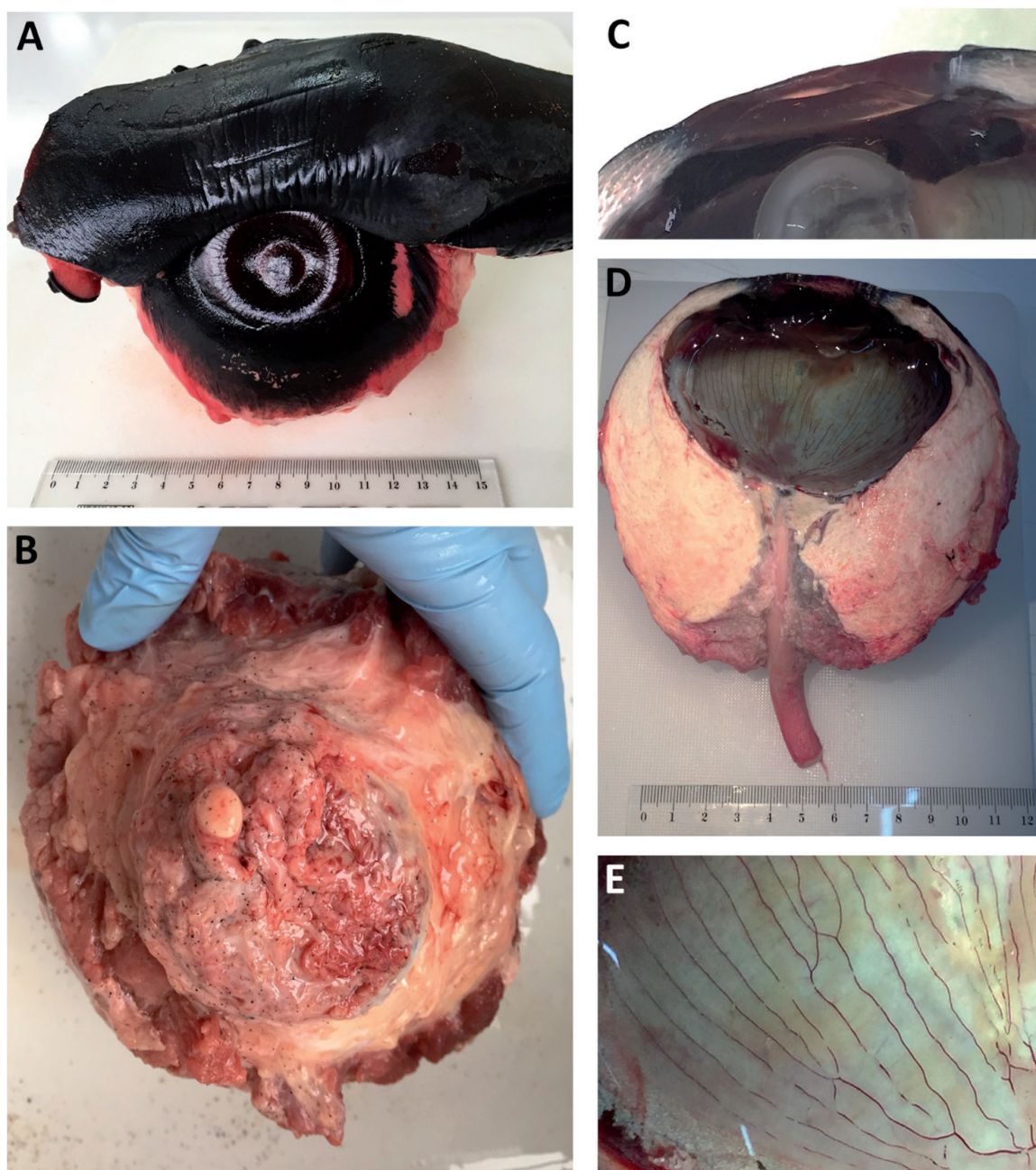
Figure 1.
(A) Eye and upper eyelid. Note the oval shape of the cornea and the round iris. (B) Detailed of the cavernous tissue surrounding the optic nerve. (C) Transversal section of the cornea and location of the round crystalline in the Centre. Note that the cornea is flat and thicker in the periphery than in the Centre. (D) Section of the eye showing the thick sclera, and the hemispheric retina and its vascularization. (E) Detail of the retina vascularization with parallel vessels.

myopia. Another adaptation of the cetacean eyes to conditions of low luminosity is a highly developed reflective layer, the tapetumlucidum, which lies behind the retinal pigment epithelium within the choroid. The tapetum in cetaceans has been described previously by [10]. We found a well-developed tapetum in the present two mysticetes studied. Its tapetum is formed with extracellular collagen fibrils and covers the complete fundus. What is unusual in the terrestrial mammals that live and hunt during the night is that the tapetumlucidum does not usually extend below the horizontal equator of the eye.

The eyes have strong extraocular muscles that cover a large cavernous tissue refilling the space that forms the sclera in the back of the eye and it surrounds the

optic nerve with a conical shape. The cavernous tissue is also named by other authors as vascular plexus, rete ophthalmica and musculus retractor bulbi is speculated to function as a vascular rete to supply both heat and oxygen during dives [11]. A great number of blood vessels were surrounded by elastic fibers, smooth muscle and fat (**Figure 1B**). The function of this tissue could be to protect the optic nerve from the cold water and warm it and propel the eye outwards thereby helping with the focus. The massive musculus retractor bulbi, which produces axial displacements of the globe of the eye within the orbit, has been observed in other animals, mainly non-mammals like amphibians and the whale shark, and other cetaceans. However, the theory purposed by Kröger and Kirschfeld for dolphins in 1989, about the possibility that the focus could be based on shifting the lens backward due to the changes in the intraocular pressure, are very unprovable mechanism for whales, because of the very thick sclera (4 cm), that surrounds the retina, will protect the inner part of the eye from deforming and thus would be impossible to move the lens. We believe that the filling of the rete will increase necessary pressure to move the eyeball outwards. The retractor muscle will accompany the outward movement and when the rete is emptied the eye returns to the interior of the orbit. During this movement, the thick sclera will protect the eyeball from deforming forces. This could provide a mechanism to increase the field of vision when the eye protrudes. However, we do not believe that the lens will modify its position due to the propulsion of the eye.

3. The retina

The macroscopic view of the retina showed a dichotomous vascularization similar to that in a horse but in this case, it was holangiotic (**Figure 1D**, **E**). The vasculature had a radial distribution for the whole extension of the retina as previously described [12]. The shape of the retina is an incomplete hemisphere and a peripheral rim of the retina is bent inward (**Figure 1D**).

The thickness of the retina in cross-sections was not thicker than the human or pig retina. The number of rows of photoreceptors was 6–8 in the outer nuclear layer of the retina, however, the inner layers were thinner with less cellularity especially noticeable were the scarce and larger RGCs that were between 26.5 and 112.9 micrometers in diameter (**Figure 2A**) [4].

A detailed study of the photoreceptors showed that these species of mysticetes do not have cones. We used several antibodies to identify the different opsins, like rhodopsin, M/L opsin and S opsin as well as antibodies against rat and human cone arrestin. The only positive result was with rhodopsin, which specifically was present in rods. We conclude that in our study, the cone opsins that terrestrial animals used were not present in the whale retinas [4]. Previous studies demonstrated the monochromacy in some cetaceans and several mutations in the opsin gene sequences suggesting evolutionary modification of the cone cell function. In some cases, the cone structures have been partially maintained but with the absence of outer and inner segments [13]. Recent studies in other species of cetacean have found that cones have been adapted to other use, and instead of having visual pigments, like cone-opsins, they contain two proteins involved in magneto sensation, suggesting the possibility of an alternative functional role in responding to changes in geomagnetic fields [14].

Once the light impacts the photoreceptors, the next cells responsible for the transmission of the visual impulse within the retina are the bipolar and amacrine cells. We found that even when the cones' opsins were not present, bipolar and
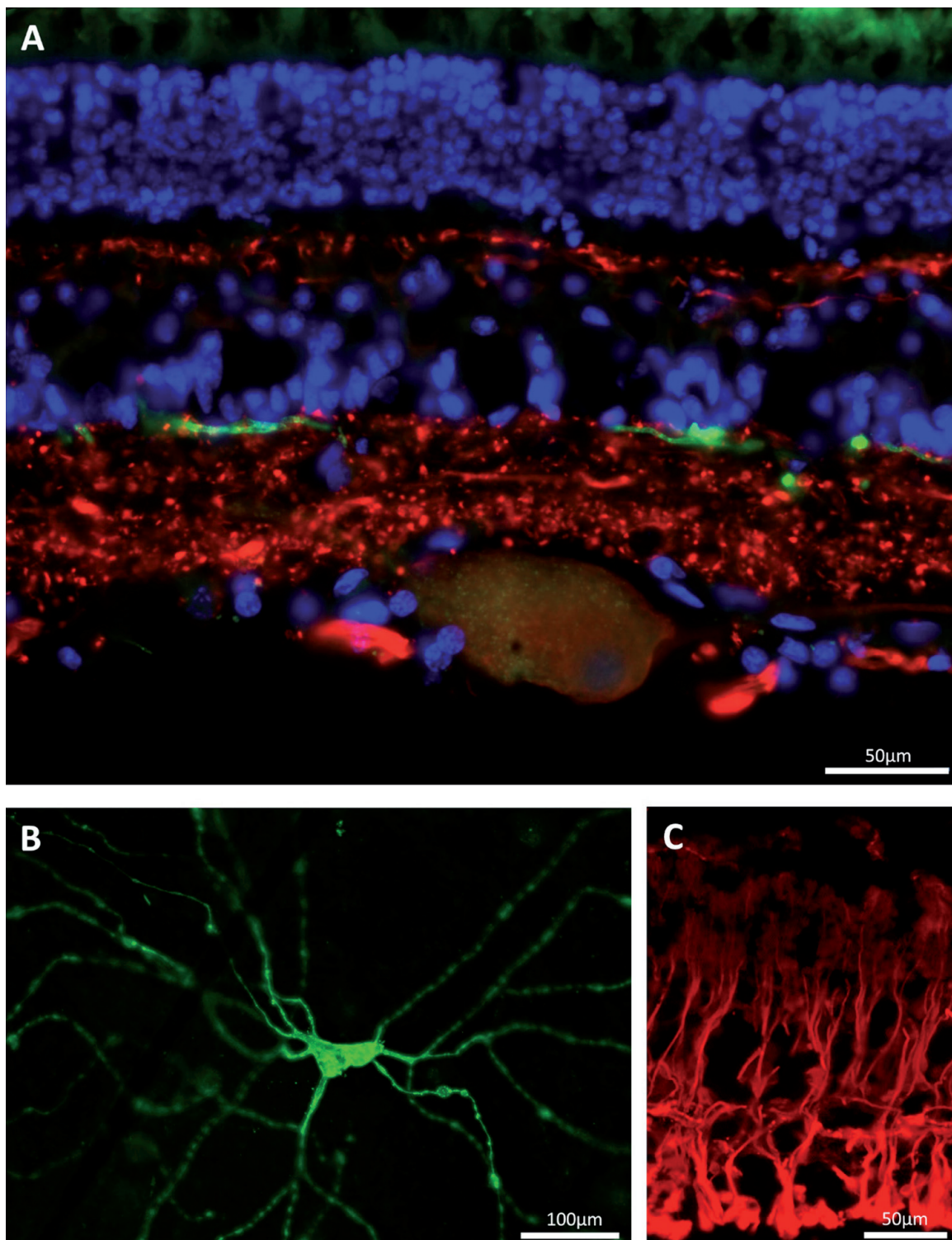
Figure 2.
(A) Immunostaining of a retina section. Red neurofilaments labels the large retinal ganglion cell and their branches. In blue DAPI, staining shows the 6–7 layers of photoreceptors in the upper part of the picture. (B) Flat mount of the retina showing a melanopsin positive retinal ganglion cell. (C) immunostaining of a retina section. In red, the Müller glial cells are stained with antibodies against vimentin.

amacrine cells maintained their molecular signals as well as location. The same results were found using electroretinograms to measure the electrical response to the light of these interneurons. [15] found that the cetaceans rod monochromat has both On and OFF bipolar cell pathways. The next step within the retina is the cells that are responsible to communicate the eye with the brain. These are the

retinal ganglion cells (RGCs). The density of these cells was very low, lower than in any cetacean studied earlier [4], confirming the low resolution of that the whales' retina. It appears that relatively few RGCs may have to integrate the information from a great number of photoreceptors that are abundant. We did not count the number of photoreceptors, however, considering the large size of the eye and the number of rows of rods, the proportion of information that the RGCs have to integrate is massive. Even when the RGCs were scarce in number, the size of the cell bodies was 3 times larger than in humans, with some cells reaching 100 micrometers (**Figure 2A**).

Besides the RGCs that integrate the visual inputs and send this information to the visual centres of the brain for processing, other specific type of cells are located in the retinal ganglion cell layer that does not transmit information to the image forming visual area of the brain. These specific cells only transmit information regarding light intensity to the brain and are areas responsible for controlling the circadian rhythms and pupillary light reflexes. We have been the first research group to describe them in cetaceans. These cells are melanopsinipRGCs [4]. They form a mosaic that covers the complete area of the retina and were more abundant in the centre of the retina and reduce in density toward the periphery (**Figure 2B**). There are at least six types of ipRGCs and in the whale's retinas, we identify three types, the M1, M2 and M3 although the majority of them were M2. As per comparison in rodent retina, the number of M1 is higher than M2 or M3 [16]. In humans, M1d ipRGC is the predominant subtype [17]. These differences between species may be due to the different roles of the ipRGC subtypes. M1 projects to approximately 15 brain targets not involved in image forming activities, projecting predominantly to the suprachiasmatic nucleus (SCN) and to the olivary pretectal nucleus (OPN) to control pupillary light reflex [18, 19]. However, M2 ipRGCs that were the predominant ones in the whales´ retinas project mostly to the OPN and relatively fewer to the SCN suggesting that the control of the pupillary light reflex is very important for the whale [4].

In addition to neurons, there are glial cells in the retina that develop a very important role. The glia cells in cetacean's retinas were slightly different to other mammals. Thus, the astrocytes had a punctate pattern surrounding the large arteries of the retina but due to the very large and strong blood vessels, they were seldom visualized embracing the vessels as they typically do in other mammalian retinas. The Müller glia was very robust and with the same morphology as in other mammalian retinas (**Figure 2C**). They had the capacity to facilitate the elongation of the RGC axons [20] and for that reason, we had immortalized the whale's Müller glia for further study [5]. We also studied the microglial cells, which are the immune cells within the retina. They are present but were larger and more diffused. These differences with the terrestrial mammals could be related to the metabolism of the cetacean retina. For further discussion on the glial cells, see Ref. [4].

4. The optic nerve

The optic nerve was 1 cm in diameter, small in comparison with the large size of the eye. The axons in the optic nerve were mainly 'Giant' (greater than 15micrometres in diameter) corresponding to the very large RGCs found in the retina. The size of the axons and cells is a common plesiomorphic character of cetaceans rather than being related to the large body size of these animals. This interpretation is supported by the comparison with other large terrestrial species. Thus, in elephants there are no

Giant RGCs' despite the large size of the animals [21], indicating that this has been an adaptation to the aquatic environment.

The high astroglial content in the cetacean nerve could be due to the highly developed metabolic support that the central nervous system required to sustain nervous activity during anaerobic and energy-demanding tasks like prolonged apnea [22]. The bigger the diameter of the axons is, the faster the impulse travels [23]. There was considerably more astroglia in the cetacean optic nerve than inland mammals, with astrocyte processes and myelin occupying a higher proportion of the nerve [4].

5. Adaptation to the aquatic vision

Similar characteristics of adaptation to the aquatic vision as described in the present study, have been found in other mysticetes of smaller size humpback and Bryde's whales [24] or in Gray whale [25] aquatic mammals.

The described characteristics of the cornea play a minor role under the water because of its mall curvature and refractive indices of the media in front (seawater) and behind the cornea (aqueous humor). Although some refraction cannot be neglected especially due to the thickness [26]. The spatial resolving power of the cetaceans is very low compared to that of terrestrial mammals. Computing the peak of RGC density values range indicates that it is approximately 1 to 5 cycles/degree [24], compared for example with the horse that is approximately 20 cycles/degree [27], or the giraffe with approximately 20 cycles/degree [28].

Due to the large numbers of rod photoreceptors, and the few RGCs, it seems that for the cetaceans the sensitivity to the light is far more important than the resolution. A rod-vision provides better underwater vision in conditions where light intensity is low and light is scattered with increasing depth and rod dominance animals are more rapid to dark adaptation. Marine mammals use vision primarily in low light levels, where color vision may be of secondary importance. We believe that Peichl's comments are very appropriate in this regard 'the ocean for the whales is not blue' [29]. Moreover, the very well developed melanopsin RGCs network indicates that the sensibility to the changes in light is highly preserved and the control of the pupil is very important to reduce the amount of light that penetrates the retina thus, as a pinhole camera they could see better the object that it wants to see. The mechanism which protrudes the eye with the cavernous tissue together with the retractor bulbils muscle allows them to move the eye forward and backwords. This could facilitate the whales to focus when the eye is protruded outward and be protected from the cold temperatures when in the deep ocean waters where the eye is moved inside the orbit and covered by the eyelids.

6. Conclusions

The large whales' studies have been adapted to the underwater vision by a pupil that regulates the variations in luminosity together with the optic tapetum. The retina is similar to that of nocturnal terrestrial mammals with the absence of cones and large size of ganglion cells, separated by wide intercellular spaces, but a very well developed melanopsin system provides an adaptation for vision in low light environments. Thus, despite their eye large size, the retinal resolving power in cetaceans is

generally weaker than in terrestrial mammals, due primarily to their low density of retinal ganglion cells.

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Conflict of interest

The authors declare no conflict of interest.

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