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Morphology of the Eyeball From the Humpback Whale (*Megaptera novaeangliae*)

FERNANDA M. RODRIGUES,[1,2] FERNANDA M.O. SILVA,[3] ANA CAROLINA TROMPIERI-SILVEIRA,[4] JOCIERY E. VERGARA-PARENTE,[2] MARIA ANGÉLICA MIGLINO,[3] AND JULIANA P. GUIMARÃES[2,3]*
[1]*Faculdade Pio Décimo, Campus III, Av. Tancredo Neves, 5655, Bairro Jabotiana, Aracaju, Sergipe, Brasil*
[2]*Núcleo de Estudo dos Efeitos Antropogênicos nos Recursos Marinhos/Fundação Mamíferos Aquáticos, Av. Tancredo Neves, 5655, Bairro Jabotiana, Aracaju, Sergipe, Brasil*
[3]*Departamento de Cirurgia, Setor de Anatomia dos Animais Domésticos e Silvestres, Faculdade de Medicina Veterinária e Zootecnia, Universidade de São Paulo, Av. Prof. Dr. Orlando Marques de Paiva, 87, Cidade Universitária, São Paulo, São Paulo, Brasil*
[4]*Universidade Federal de Sergipe, Av. Marechal Rondon, s/n, Rosa Elze, São Cristovão, Sergipe, Brasil*

KEY WORDS eye; *Megaptera novaeangliae*; aquatic mammals; ultrastructure

ABSTRACT Aquatic mammals underwent morphological and physiological adaptations due to the transition from terrestrial to aquatic environment. One of the morphological changes regards their vision since cetaceans' eyes are able to withstand mechanical, chemical, osmotic, and optical water conditions. Due to insufficient information about these animals, especially regarding their sense organs, this study aimed to describe the morphology of the Humpback whale (*Megaptera novaeangliae)* eyeball. Three newborn females, stranded dead on the coast of Sergipe and Bahia, Brazil, were used. Samples were fixed in a 10% formalin solution, dissected, photographed, collected, and evaluated through light and electron microscopy techniques. The Humpback whale sclera was thick and had an irregular surface with mechanoreceptors in its lamina propria. Lens was dense, transparent, and ellipsoidal, consisting of three layers, and the vascularized choroid contains melanocytes, mechanoreceptors, and a fibrous tapetum lucidum. The Humpback whale eyeball is similar to other cetaceans and suggests an adaptation to diving and migration, contributing to the perception of differences in temperature, pressure, and lighting. *Microsc. Res. Tech. 77:348–355, 2014.* © 2014 Wiley Periodicals, Inc.

INTRODUCTION

Studies indicate that three groups of marine mammals (cetaceans, pinnipeds, and sirenians) evolved from terrestrial ancestors and underwent several environmental challenges throughout their evolution (Flynn and Nedbal, 1998; Gatesy and O'Leary 2001; Lavergne et al., 1996). The adaptation from a terrestrial to a marine environment caused morphological and physiological changes in several body systems, including vision (Griebel and Peichl, 2003).

Cetaceans' eyes are able to withstand mechanical, chemical, optical, and osmotic water conditions (Griebel and Peichl, 2003), and due to low light levels, their tapetum lucidum is well developed and increases visibility into the aquatic environment (Mass and Supin, 2007). Compared to other mammals, their cornea, sclera, and choroid are thicker, assisting in protecting the eye against mechanical damage by diving and underwater cooling (Mass and Supin, 2007).

Although whales' echolocation contributes to orientation in their natural habitat, the vision also plays important biological functions (Mass et al., 1986), assisting in the detection and capture of prey, identification of conspecifics, and guidance during migration (Griebel and Peichl, 2003; Madsen and Herman, 1988).

The Humpback whale (*Megaptera novaeangliae*) is commonly sighted in coastal regions, close to islands or coral reef systems in the winter and in tropical areas in the spring (Lodi and Borobia, 2013), approaching the Brazilian coast to start their reproductive season early winter (Pinedo et al. 1992).

Although there are studies with the Humpback whale in Brazil, these are focused on research population through photo-identification and genetics (Pomilla and Rosenbaum, 2006; Portela, 2013); however, studies on the morphology of this species and even other whales are scarce (Hetzel and Lodi, 1993). Knowing that vision is important for aquatic mammals' adaptation to their habitat, this study aimed to describe the morphology of the Humpback whale eyeball, enabling its comparison to other species of whales and aquatic mammals.

MATERIALS AND METHODS

Both eyeballs from three female Humpback whales, in good state of preservation, were used. All animals were calves, stranded dead on the beaches of the northeast coast of Brazil (Bahia and Sergipe State).

*Correspondence to: Ms. Juliana Guimarães, Departamento de Cirurgia, Setor de Anatomia dos Animais Domésticos e Silvestres, Faculdade de Medicina Veterinária e Zootecnia, Universidade de São Paulo, Av. Prof. Dr. Orlando Marques de Paiva, 87, Cidade Universitária, São Paulo, São Paulo, Brasil.E-mail: jpgrbm@yahoo.com.br

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Fig. 1. Positioning of the Humpback whale left eye (arrow), adjacent to the buccal commissure (BC). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

After being removed from the orbit, eyeballs were dissected and photo documented.

For light microscopy, tunics and lenses fragments were collected and fixed in a 10% formalin solution. Then, they were dehydrated in an increasing series of alcohols (70 to 100%), cleared in xylene, and embedded in histologic paraffin (Paraplast®). Five-micrometer sections were obtained and stained for hematoxylin-eosin (visualization of cell nuclei and connective tissue), Masson's Trichrome (connective tissue identification), and Picrosirius (collagen fibers identification). Slides were analyzed and images are captured using a light microscope (Nikon Eclipse E-800).

For scanning electron microscopy (SEM), samples were fixed in 10% formalin solution at collection. Upon arriving at the laboratory, samples were washed and fixed in a 2.5% glutaraldehyde solution. Posteriorly, samples were washed in distilled water, dehydrated in increasing series of alcohols (70% to absolute), dried, mounted on metal bases, and coated with gold. Samples were examined and photographed in a SEM (LEO 435VP).

RESULTS

General Morphology of the Eyeball

Humpback whale eyes were positioned on both sides of the head, adjacent to the oral commissure (Fig. 1). The eyeball (Figs. 2A and 2B) was located within the orbit and has anteroposterior and dorsoventral

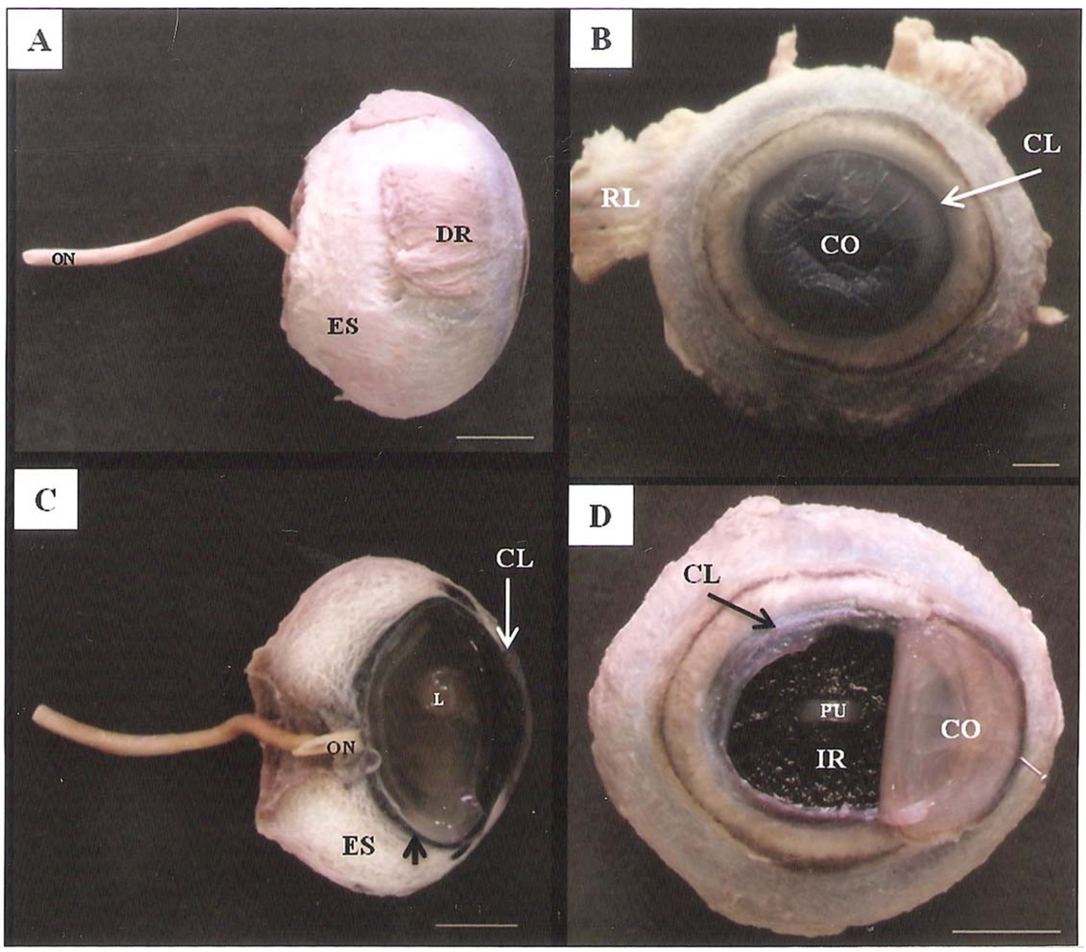

Fig. 2. Humpback whale right eye. (**A**) Lateral view. (**B**) Anterior view. (**C**) Mid-section for visualization of internal structures. (**D**) Anterior surface of the Iris, visualized by partial incision along the corneal limbus. IR, Iris; L, Lens; ON, optic nerve; ES, sclera; CO, cornea; CL, Corneal limbus; PU, pupil; DR, dorsal rectus; LR, lateral rectus muscle; Black arrow, choroid. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

TABLE 1. Average dimensions of the eyeball.

Structure	ML	DV	AP
Eyeball	4.52	6.40	6.92
Cornea	–	3.92	4.36
Lens	0.70	1.12	1.12

Cornea and lens measured in centimetres. ML = Mediolateral; DV = Dorsoventral; AP = Anteroposterior.

dimensions greater than the mediolateral, making the eye bulb flat in this direction (Table 1).

Cornea

The cornea, oval in its mediolateral direction (4.36 × 3.92 cm^2) (Fig. 2B), was located in the anterior pole of the eyeball, had a convex anterior surface (Fig. 2C) and a greater thickness in its periphery (0.22 cm) when compared to its center (0.10 cm). Histologically, the stroma was thicker at the periphery and consisted of multiple layers of collagen fibers oriented in parallel, which changed their direction from one layer to another. The anterior lamina consisted of a homogeneous and thick outer layer (Figs. 3A and 3B).

Sclera

The sclera had a smaller thickness anteriorly, accompanying the corneal limbus (0.10 cm), than posteriorly, in the region of the cribriform plate, through which the optic nerve passed by (1.56 cm) (Figs. 2A and 2C). A vascular network that fed the internal structures of the eye penetrated the sclera and two vessels in the median section of the bulb were identified.

The outermost layer of the anterior sclera was formed by a stratified squamous epithelium, corresponding to the bulbar conjunctiva (Fig. 4E) and receded as it approached the posterior sclera (Fig. 4C). In the lamina propria, loose connective tissue and blood mechanoreceptors (Fig. 4E) vessels were present. The stroma was composed of dense collagenous fibers interlaced (Figs. 4A and 4B) and melanocytes were present in the lamina fusca (Fig. 5D).

Through SEM it was possible to observe the arrangement of the sclera layers in its anterior region (Fig. 4F) and irregularities in its surface (Fig. 4D). In the transition zone of the cornea to the sclera (corneal limbus; Fig. 2B), the corneal epithelium gradually became a prismatic stratified epithelium of the bulbar conjunctiva (Fig. 5A).

Choroid

The choroid extended from the optic nerve to the ciliary body (Fig. 2C). The suprachoroid lamina contained numerous melanocytes distributed in a network of connective tissue, adjacent to the choroid vascular lamina (Fig. 5D). The capillary lamina of the choroid or choriocapillari contained capillaries distributed in a single plane. The tapetum lucidum, a green-blue colored fibrous structure rich in collagenous fibers (Fig. 5G) covering two thirds of the ocular fundus, was located between the choriocapillari and the choroid vascular lamina. In some regions of the choroid, it was possible to observe the presence of mechanoreceptors (Fig. 5F).

Ciliary Body

The ciliary body, located between the iris and choroid, projected ciliary processes arranged radially as short and long folds. Its basic component was loose connective tissue rich in pigment cells (Fig. 5C) and blood capillaries. There were nerve fibers peripherally to the inner vascular region (Fig. 5B) and the ciliary muscle, consisting of bundles of smooth muscle fibers arranged longitudinally (Fig. 5D).

Iris

The iris was a dark and flat ring, located between the cornea and the lens (Fig. 2D). Its anterior surface was lined by a simple columnar epithelium adjacent to a layer of pigmented cells (iris pigment epithelium) and its interior consisted of blood vessels embedded in loose connective tissue (Fig. 6A). Unlike the anterior surface, the posterior surface was covered by the iris pigment epithelium and had spaces of iridocorneal angle (Fig. 6B). The dilator muscle of the iris was not found. The pupillary aperture, horizontally oval, was located in the iris center (Fig. 2D).

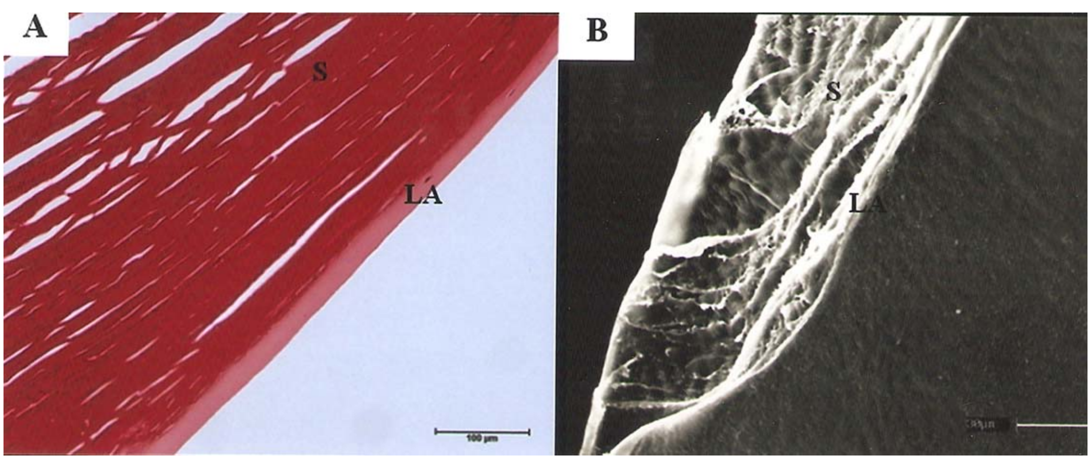

Fig. 3. (**A**) and (**B**): Photomicrograph of anterior limiting lamina (AL) and stroma (S) of the cornea. Picrosirius and SEM, respectively. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

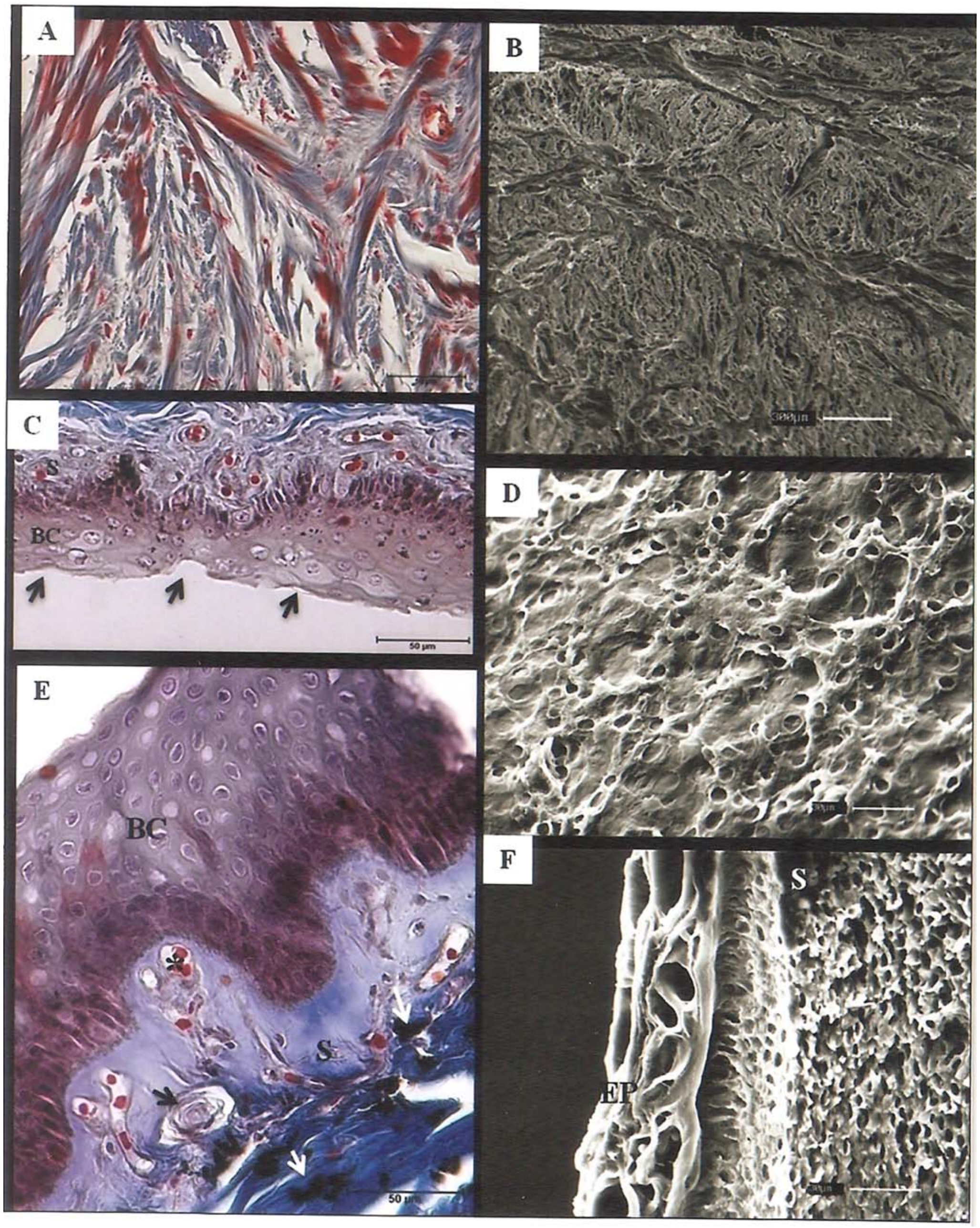

Fig. 4. Photomicrographs of the Humpback whale sclera. (**A**) and (**B**) Stromal sclera. Masson's Trichrome (MT) and SEM, respectively. (**C**) Stroma (S) and irregular surface (arrows) of the bulbar conjunctiva (BC). MT. (**D**) Irregular surface of the bulbar conjunctiva (SEM). (**E**) Anterior layers of the sclera. Bulbar conjunctiva (BC) and vascularized (*) stroma (S) with the presence of mechanoreceptors (black arrow) and melanocytes (white arrow). MT. (**F**) Layers of the anterior sclera (SEM): epithelium (EP) and stroma (S). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Retina

The retina formed the inner layer of the eyeball and extended from the optic disc to the iris, irradiating blood vessels.

Ten layers of photosensitive retina were observed: pigment epithelium (Fig. 5G), rods and cones, outer limiting membrane, outer nuclear, outer plexiform, inner nuclear, inner plexiform, ganglion cell, nerve fiber, and internal limiting membrane (Fig. 6C).

Lens

The lens was transparent and dense, suspended posteriorly to the iris and anteriorly to the vitreous camera (Figs. 2C and 2D). Although nearly spherical, its anteroposterior direction indicated that its shape was ellipsoidal (Table 1). Histologically it consisted of three layers: capsule, lens epithelium, and lens fibers (Fig. 6D).

The lens capsule was a homogeneous acellular and hyaline coating. The lens epithelium was composed of a single layer of cuboidal epithelial cells. Lens fibers were long and had thin prismatic elements that lost their nuclei as they were positioned at the center of the lens.

Anterior and Posterior Chambers

Anterior (between the cornea and iris) and posterior (between the iris and the lens) chambers communicated through the pupil and were filled by the aqueous humor. The vitreous chamber was located between the lens and retina and was filled by the vitreous humor.

Optic Nerve

The optic nerve (Fig. 2A) was surrounded by an anastomosis network submerged in connective and adipose tissues. A reduction of the optic nerve diameter was observed in the optic disk area (0.46 cm) (Fig. 2C). Microscopically, there was the presence of myelinated fibers (Fig. 7).

DISCUSSIONS

Despite their large size compared to terrestrial mammals (Mass and Supin, 2007), cetaceans' eyes are not designed for high visual acuity (Supin et al., 2001). The eyeball size and cornea disposition in the Humpback whale are similar to the reported in other aquatic mammals (Buono et al., 2012; Dawson, 1988; Mass et al., 2007; Mass and Supin, 2002; Zhu et al., 2001).

With the exception of some freshwater dolphins (Kroger and Kirschfeld, 1994), the greatest thickening of the peripheral cornea was found in all cetacean species studied (Hanke et al., 2008; Kroger and Kirschfeld, 1994; Mann, 1946; Mass and Supin, 1997, 1999, 2002; Pütter, 1903; Welsch et al., 2001; Zhu et al., 2000). Different thickness and rigidity of the ocular tissue minimize the eye distortion during the pressure exerted by aquatic maneuvers, providing resistance to intraocular pressure, and acting as diverging lenses in underwater viewing conditions (Dawson, 1988; Kroger and Kirschfeld, 1994).

In river dolphins and manatees (*Trichechus manatus latirostris*), corneal vascularization aids in protecting the body against pathogens (Bauer et al., 2003; Molina, 2007). However, studies indicate that the presence of these blood vessels can impair vision, which may clarify discussions on the different visual capabilities of aquatic mammals (Samuelson et al., 1994, 1997).

The anterior limiting lamina found in the Humpback whale is also present in the California sea lion (*Zalophus californianus*) (Miller et al., 2010), and according to Dawson (1988), their presence contributes to ocular thermal insulation. However, the epithelial layer and posterior lamina was neither identified in our study nor in the Southern Right whale (*Eubalaena australis*) (Buono et al., 2012). Such fact does not state the absence of these layers in the cornea, which may have been lost before fixation. These structures are sensitive to autolysis in a few hours postmortem or during histological processing.

The sclera of the Humpback whale is thick which can assist in cornea mechanical protection and thermal insulation of the eye under different pressures (Bjerager et al., 2003; Buono et al., 2012; Dawson, 1988; Kastelein et al., 1990; Mass and Supin, 1999,

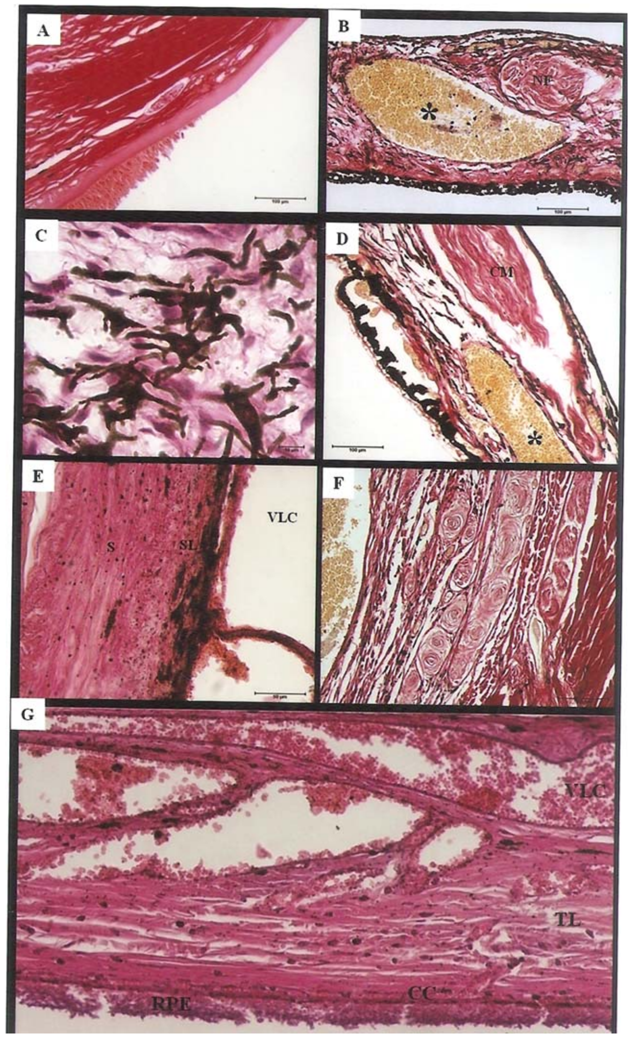

Fig. 5. Photomicrographs of the fibrous, vascular, and internal tunic of the Humpback whale eyeball from different regions. (**A**) Corneal limbus. (**B**) Internal vascular region (*) and nerve fiber (NF) of the ciliary body. Picrosirius (PS). (**C**) Pigment cells distributed in the ciliary body stroma. Hematoxylin-Eosin (HE). (**D**) Ciliary muscle (CM) and internal vascular area (*) of the ciliary body. PS. (**E**) Scleral stroma (S), vascular lamina of the choroid (VLC), and suprachoroid lamina (SL). HE. (**F**) Mechanoreceptors arranged in the suprachoroid lamina. PS. (**G**) Vascular lamina of the choroid (VLC), Tapetum lucidum (TL), choriocapillari (CC), and retinal pigment epithelium (RPE). HE. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

2002; Zhu et al., 2001). The bulbar conjunctiva epithelium and the scleral stroma in this study correspond to those observed in terrestrial and aquatic mammals (Bacha and Bacha, 2003; Buono et al., 2012; Zhu et al., 2001).

The presence of mechanoreceptors differs from the observed in other animals (terrestrial and aquatic) and it is suggested that these nerve endings may be sensitive to temperature variations during migration (Wheater et al., 1987), in which it changes considerably according to region (Rasmussen et al., 2007). Knowing that Humpback whales have sensory structures in their head called tubercles, connected to a vast network of nerves (Clapham, 1996), it is possible

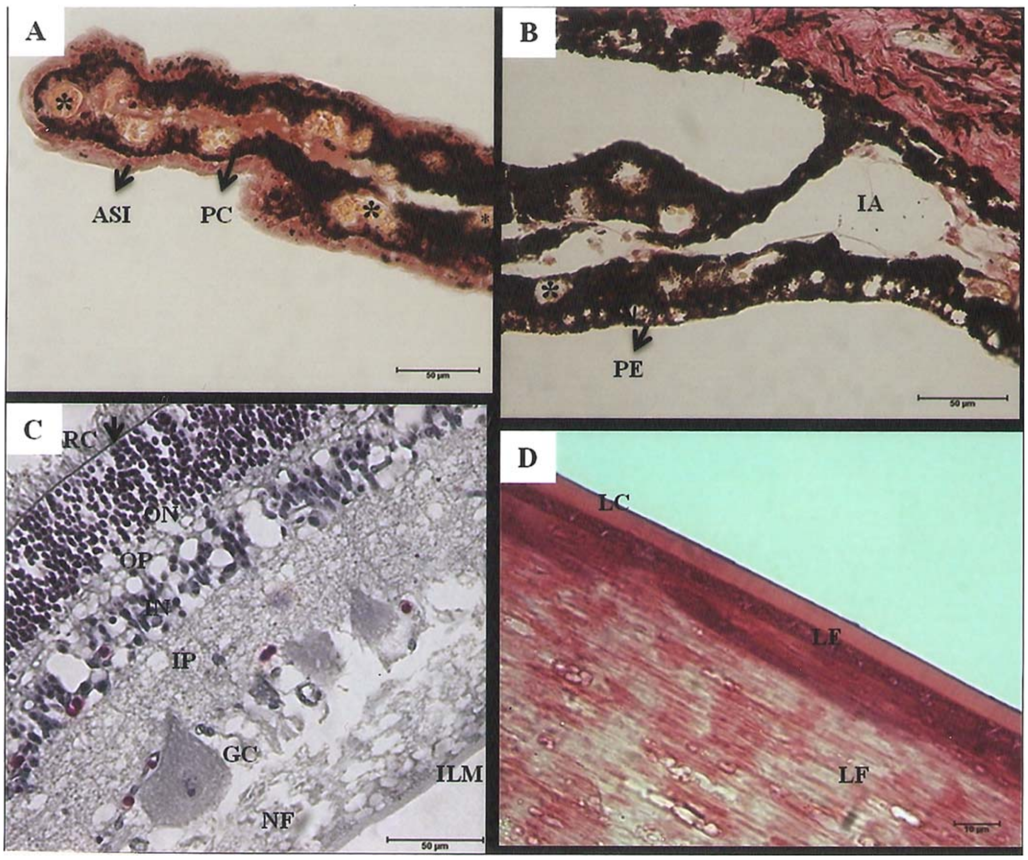

Fig. 6. Photomicrographs of the Humpback whale eyeball. (**A**) Vascularized stroma (*) and epithelium of the anterior surface of the iris (ASI), adjacent to the pigmented cell layer (PC). Picrosirius (PS). (**B**) Double pigmented epithelium (PE), spaces of iridocorneal angle (IA) and blood vessels (*) of the posterior iris. PS. (**C**) Retinal layers: rods and cones (RC), external limiting membrane (arrow), outer nuclear (ON), outer plexiform (OP), inner nuclear (IN), inner plexiform (IP), ganglion cells (GC), nerve fibers (NF), and internal limiting membrane (ILM). Masson's Trichrome. (**D**) Lens capsule (LC), lens epithelium (LE), and lens fibers (LF). Hematoxylin-Eosin. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

to suggest that these animals develop a differentiated sensory function, also assisted by the sclera and choroid mechanoreceptors.

Mass and Supin (2007) assert that the tapetum lucidum is present in all cetaceans and represents a reflective layer that operates at low light levels. This layer may be distributed throughout the back of the eye (Waller, 1984) or only in two thirds (Dawson, 1988). Unlike the Humpback whale, the tapetum lucidum covers the entire ocular fundus of the Greenland whale (*Balaena mysticetus*) (Zhu et al., 2001), having a blue-gray coloration in the Southern Right whale (*Eubalaena australis*) (Buono et al., 2012). In Belugas (*Delphinapterus leuca*) the tapetum lucidum was not observed in the dorsal region of the choroid (Mass and Supin, 2002) and in the California sea lion (*Z. californianus*) its green color does not cover the periphery (Miller et al., 2010).

According to Griebel and Peichl (2003), the full distribution of the tapetum lucidum in the back of the eye indicates high sensitivity to light and Supin and Mass (2007) suggest that numerous layers of fibrils result in multiple reflection of light to the retina.

Based on amino acid analysis, Murayama et al. (1995) reported that the tapetum lucidum in the Dall's porpoise (*Phocoenoides dalli*) contains collagen and is thicker at the posterior end of the eye. The distribution of this structure in the Tucuxi (*Sotalia fluviatilis*)

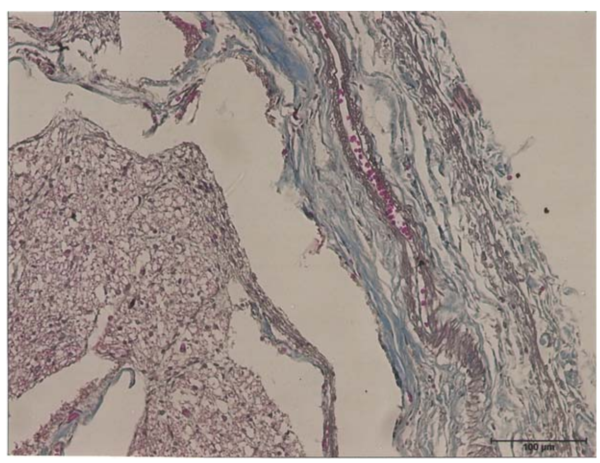

Fig. 7. Photomicrograph of the Humpback whale optic nerve, with the presence of myelinated fibers. Masson's Trichrome. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

(Mass and Supin, 1999) is similar to the observed in the present study.

According to Mass and Supin (2002), the Beluga choroid is more developed than in dolphins. In the Humpback whale, the suprachoroid lamina is similar to the observed in the Southern Right whale (Buono et al., 2012). Ninomiya et al. (2014) reported that choroid and retina arteries are derived from the rete mirabile.

As described by other authors (Buono et al., 2012; Zhu et al., 2001), ciliary processes of the Humpback whale are arranged radially as short and long folds. The epithelium of the ciliary body has two layers and a zonula of fibers which holds the lens of the Pilot whale (Waller, 1992). The loose connective tissue in pigmentary cells, reported by this author, was also observed in this study and in the Southern Right whale (Buono et al., 2012). Nerves of the ciliary body were also present in the Humpback whale, as well as in the Pilot whale (Waller, 1992).

Although the ciliary muscle is absent in most baleens (Bjerager et al., 2003; Waller, 1984; West et al., 1991) and toothed whales (Dawson, 1988; Draw 1975; Kastelein, 1990), it was observed in our study. This structure is poorly developed in the Weddell seal (*Leptonychotes weddellii*) (Welsch et al., 2001) and evident in the bottlenose dolphin (Waller, 1980), and the Pilot whale (Waller, 1992).

Blood vessels embedded in loose connective tissue and the iris layout in the Humpback whales was similar to the observed in other baleens (Buono et al., 2012; Zhu et al., 2001). Several authors reported the presence of an operculum in cetaceans, which constricts the iris structure and changes the shape of the pupil during dives at different lighting levels (Dawson, 1988; Miller et al., 2010; Mass and Supin de 1997; 1999; 2007; Reidenberg, 2007; Waller, 1992; Zhu et al., 2000), but this structure was not observed in the present study. Similar to the Beluga (Mass and Supin, 2002) and the Tucuxi (Mass and Supin, 1999), the pupil of the Humpback whale is elongated horizontally.

The retina composition in cetaceans is similar to terrestrial nocturnal mammals since both are exposed to low light levels (Reidenberg, 2007). Although rods and cones are present, there is no evidence that cetaceans have color vision (IBAMA, 2005). Studies indicate that the presence of two types of cones in manatees' retina differentiates their dichromatic vision from the monochromatic vision of pinnipeds and cetaceans (Ahnelt and Kolb, 2000).

According to Dehnhardt (2002) and Supin and Popov et al. (2001), the architecture and morphology of the retina in pinnipeds contribute to a better eye functioning at low light levels. Moreover some researchers deny the need for nonvisual explanations for underwater orientation of these animals (Levenson and Schusterman, 1999).

The retina of the Humpback whale, manatees (Mass et al., 1997), California sea lion (Miller et al., 2010) and other aquatic mammals (Mass et al., 1997) is characterized by scattered large neurons called ganglion cells. Retinal layers present in Humpback whales were the same observed in the Beluga (Mass and Supin, 2002) and different from those found by Buono et al. (2012), who identified only seven layers in the Southern Right whale.

The ellipsoidal shape and morphological characteristics of the lens were also observed in the Tucuxi (Mass and Supin, 1999), Beluga (Mass and Supin, 2002), Southern Right whale (Buono et al., 2012), and Greenland whale (Zhu et al., 2001). However, some authors claim that the lens is spherical in cetaceans (Bjerager et al., 2003; Waller, 1984; West et al., 1991) and compensates the refractive power of the cornea underneath water (Jamieson and Fisher, 1972; Mass and Supin, 2002).

Similar to the observed in the Southern Right whale (Buono et al., 2012), the optic nerve diameter is approximately 0.45 cm. At this point, the vascular tissue (permeating the connective and adipose tissue) is similar to the ophthalmic rete mirabile in ruminants (Dyce et al., 1997) and other baleens (Buono et al., 2012; Zhu et al., 2001). Unlike the California sea lion, the optic nerve of the Humpback whale has myelinated fibers (Miller et al., 2010).

This study showed that the morphology of the Humpback whale eye is similar to the other cetaceans and suggests an adaptation to diving and migration, thus contributing to the perception of the difference in temperature, pressure, and lighting in different regions.

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