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Unique iris and pupil morphology in lamnid sharks

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Research Article

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Abstract

Documentation of the iris concentrating on color, pupillary shape, and orientation has been reported in a number of elasmobranch species, but has not been documented in lamnid sharks. This study examined the eyes of three lamnid sharks, white shark (Carcharodon carcharias), mako shark (Isurus oxyrinchus), and porbeagle shark (Lamna nasus) to characterize the iris color and pupil shape. All three species possess a brown color iris circling a horizontal slit pupil. A blue limbal ring of color circles the iris caused by the sclera and cartilage from the limbus which extends into the anterior chamber of the eye. The unique characteristics of the iris and pupil shape are described and implications of these findings on future research are discussed.

Introduction

The family Lamnidae consists of the white shark (Carcharodon carcharias), two species of mako shark, the longfin mako (Isurus paucus), and the shortfin mako, (Isurus oxyrinchus), two species of mackerel, the porbeagle shark (Lamna nasus), and the salmon shark (Lamna ditropis). Lamnid sharks inhabit tropical to cold temperate waters worldwide and share many of the same physical and anatomical traits.

Sharks of the family Lamnidae are active, efficient predators convergent with tuna for “thunniform” body shapes (Bernal et al. 2003a; Donley at al. 2004; Shadwick, 2005; Gemballa et al. 2006; Perry at al. 2007), and posses vascular counter-current heat exchangers giving them the ability to maintain the temperature of specific tissues elevated above ambient water temperature (reviewed in Brill et al. 1994; Dickson and Graham 2004; Goldman et al. 2004). They rely heavily on their sensory system, including vision, for survival and are generally described as having large eyes with round, black, or dark colored pupils (Species At Risk Public Registry, Canada; Dewar, Eguchi, Hyde, Kinzey, Kohin, Moore, Taylor and Vetter, 2013; Helfman and Burgess, 2012, Alexis L. Morris, Elisa J. Livengood, Frank A. Chapman, 2018; Pelagic Shark Research Foundation, www.pelagic.org). Various web-related ecotourism and anatomy sites often refer to the iris of the white shark (Carcharodon carcharias) as being the color blue (www.sharkcagediving.net, www.adventuresportsnetwork.com, www.quora.com, nautiluslivaboards.com). These theories generally stem from photographs and videos of these sharks, as physiological and anatomical research is limited due to worldwide protective status (Carcharodon carcharias), the inability to attain tissue, and the overall difficulties of being able to safely examine an apex predator in the wild.

Among species, including elasmobranchs, a variety of pupil shapes occur, including circular, slit shaped in a horizontal, vertical, or oblique slit, and multiple pinhole pupillary apertures (Hart, Lisney, and Collin, 2006).

Each pupil shape has evolved to provide certain benefits; for example, an advantage of a slit pupil over a circular pupil is the more complete closure that can occur under very bright illumination (Walls, 1942). A disadvantage to slit pupils however, is asymmetry in the transfer of spatial details to the retina, such that linear detail perpendicular to the slit is blurred (Hart, Lisney, and Collin, 2006;Charman, 1991). A shark

with a vertical slit pupil will be able to resolve detail in the vertical plane much better than in the horizontal plane depending on the spatial resolving power of the retina and the amount of other aberrations of the eye (Collin, 2018). Horizontal slit pupils are likely to sacrifice sharpness with the advantage of having a wide field of vision for spotting vertical moving prey. In terrestrial animals, there has been a correlation made between pupil shape and the environment/time of day in which the animal hunts determining that ambush predators (snakes, dogs, cats) tend to have vertical slit pupils, and prey animals (goats, horses, deer) tend to have horizontal slit pupils (Banks, Sprague, Schmoll, Parnell, Love, 2015). Establishing different retinal specializations in conjunction with lens structure and pupil shape can better clarify how a shark may process an image. Retinal mapping has only been performed on one Lamnid species (Carcharodon carcharias) prior to its protective status, which identified diurnal vision based on identification, counts, and measurements of retinal neurons. The presence of a retinal ventro-temporally located *area centralis* was also identified (Gruber and Cohen, 1985). Overall, pupil shape plays several important roles in functional vision.

Studies on visual behavior has offered us glimpses into a shark's visual environment and is readily observed and researched in Carcharodon carcharias. Visual shape discrimination tests have been performed (Strong, 1996), along with predator-prey interactions between seals or seal decoys (Fallows, Aidan Hammerschlag 2011). One study determined that, during low-light conditions, Carcharodon carcharias success rate of capture exceeds 55%, but drops below 40% during bright light conditions. (Martin and Hammerschlag, 2012; Vermeij, 1982). Carcharodon carcharias have been known to attack with the sun at their backs and find ways to use it to their advantage when seeking prey. (Huveneers, Holman, and Robbins, 2015). Many of these field investigations have proved that the visual system in Carcharodon carcharias is highly developed and they have learned to adapt to predator avoidance, prey capture, and environmental changes.

Pupil shape and iris color have not been officially recorded in lamnid sharks. Determining pupil shape could provide more insight on convergent evolution and may play a significant role in determining visual capabilities and behaviors.

Materials And Methods

Subjects:

Six sets of white shark globes were harvested by one of the authors (GS) from sharks that had either washed ashore deceased or had died after beaching themselves in the shallow water off Cape Cod, Massachusetts (MA). Additionally, eyes from a mako and a porbeagle shark were also examined, obtained from fisherman in Rhode Island.

The first set of white shark eyes were from a beached adult male white shark that died on shore in Wellfleet, MA, in 2015. The head of the shark was placed in a freezer shortly after the time of death. In

early 2018, the shark was thawed and both eyes were enucleated and placed in 10% Buffered Formaldehyde.

Four juvenile white shark eyes were obtained from sharks that washed ashore in New York (NY) in June, 2018. The sharks were initially fixed in an ethanol bath for 6 days. Subsequently, the eyes were enucleated and placed in 10% Buffered Formaldehyde.

Two white shark globes were obtained from a juvenile female in Scituate, MA in July 2018 and 2 more globes from a from a juvenile male white shark were obtained in Truro, MA in August 2018. The eyes on these sharks were enucleated immediately on site and placed in 10% Buffered Formaldehyde.

Two globes were obtained from an adult porbeagle shark and an adult mako shark in Rhode Island, in August, 2018 after being caught by fisherman in a net. All globes were fixed in 10% Buffered Formaldehyde.

Two white shark globes were obtained from a juvenile white shark that beached itself in Cape Cod, Massachusetts (MA) in July of 2019.

Methods of Evaluation:

One set of white shark globes was dissected, photographed, and examined under a Zeiss optics operating microscope in a surgical suite at Port City Veterinary Referral Hospital.

Underwater GoPro photographs and videos of white sharks in their natural environment were taken by one of the authors (GS) in conjunction with his white shark population study with the Massachusetts Division of Fisheries. Additionally, photographs of white sharks were obtained with permission from George Probst, underwater photographer. These photos were taken with a Nikon camera in Guadalupe, Mexico.

Photographs of salmon sharks were obtained with permission from Ron Watkins, underwater photographer. These photos were taken with a Nikon camera in Alaska.

Photographs of mako sharks were obtained with permission from underwater photographer Joe Romerio. These photos were taken with a Nikon camera in Rhode Island.

A total of 10 white shark, 2 porbeagle, and 2 mako shark globes were submitted to Dr. Richard Dubielzig, DVM, DACVP, DACVO at the Comparative Ocular Pathology Laboratory of Wisconsin (COPLOW) for histopathological evaluation. Gross photographs were obtained of all globes using a Canon DSLR. An MRI was performed on one of the juvenile white shark eyes that was placed in 10% buffered formaldehyde immediately following enucleation. All globes were sectioned in the vertical plane based on the horizontal position of the pupil and hematoxylin & eosin and alcian blue PAS stains were performed.

Results

On initial exam of the first set of eyes received from the previously frozen adult white shark eyes, cataracts were immediately noticeable likely caused by freezing. The pupil in both eyes was in a horizontal slit position with iris adhesions (due to freezing), and the iris color was noticeably brown with a slight blue hue in the limbus. These findings were confirmed with the use of a Zeiss ophthalmic surgical microscope at Port City Veterinary Referral Hospital in Portsmouth, NH. Globe measurement on both globes were 4 x 4.5in with one of the pupils in a horizontal slit position broken up by an iris adhesion. Pupil diameter on one side of the adhesion was irregular and measured from 1–2 x 4mm and the opposite pupil margin measured 1 x 3mm. The adhesion was 2mm long. The other pupil was also in a horizontal slit position with irregularities measuring 1–2 x 8mm. The corneas measured 22 x 25mm.

Two of the juvenile white shark eyes from New York in June, 2018 were measured. Globes were 1 x 1.5in, pupils were in a horizontal slit position at 1 x 10mm, and corneas measured 20 x 20mm.

Only one set of white shark globes, the juvenile female caught in Scituate, MA displayed bilaterally dilated pupils. This shark was discovered deceased by fisherman in less than 24 hours after they deployed the net. The globes on this shark measured 2 x 3in and the corneas were 20 x 23mm. Full dilation of the pupils were present with iris irregularities. The amount of visible iris measured anywhere from 1-3mm.

One of the globes from the juvenile white shark in 2019 measured 2.5 x 3in, pupil was in a horizontal slit position at 1 x 10mm, and cornea was 20 x 22mm.

The adult Porbeagle globes measured 4.5 x 5in. One of the pupils was slightly irregular in a horizontal position measuring anywhere from 2–3 x 7mm. The other pupil was also in a horizontal slit position measuring 2 x 5mm on one side of an iris adhesion and 2 x 3mm on the other side. The adhesion measured 2mm long.

The Mako shark globes measured 2 x 3in with the pupils in a horizontal slit position measuring 1 x 10mm. The corneas measured 20 x 22mm.

All online and personal photographs of white sharks examined after magnification confirmed a small, elongated horizontal slit pupil and dark brown iris with the ring of blue around the limbus of the iris. No visible cataracts, operculum, or iris adhesions are visibly noted in any of the photographs.

Even though we were not able to secure globes of the salmon shark (Lamna ditropis), ocular photographs confirmed a horizontal slit pupil.

Pathology report confirmed a horizontal slit pupil in the white shark, mako, and porbeagle shark along with a brown iris (Fig. 2, 5, 6, 7, 8). The blue ring mistakenly believed to be the iris, is in fact not the iris, but a section of sclera and cartilage from the limbus that extends into the anterior chamber of the eye (Fig. 4). The white shark globes that were thought to be the best preserved was evaluated by MRI prior to cutting. That showed that the inner structure was uninterpretable, and when the globe was sectioned, it was clear there was advanced autolysis making it impossible to recognize the internal structures of the globe (Fig. 1). The sphincter muscle of the iris was best sampled histologically in the porbeagle shark. A

robust smooth muscle sphincter of the iris circles the horizontal pupil. A dilator muscle was hard to make out (Fig. 3).

Discussion

In conclusion, this research reveals that the lamnid sharks, more specifically Carcharodon carcharias, Isurus oxyrinchus, and Lamna nasus, have a horizontal slit pupil in the light adapted state. The one female white shark with dilated pupils could potentially be the result of a “fight or flight” situation getting caught in a gill net. None of the photographs and video examined showed any evidence of pupils in a dilated state. Due to the robust smooth muscle found within the iris, it is believed that either the incoming light from the sun at the surface of the ocean, and/or the camera and video lights are enough to stimulate the pupil to quickly constrict. Further investigation of pupillary dilation and constriction in these species is warranted.

With Carcharodon carcharias having a specialized retinal *area centralis*, it therefore requires a greater degree of eye movement to locate prey vs other species of shark that have a dorsal or ventral *streak* (Collin, 2018). The retinal variation of Carcharodon carcharias could very well be related to the habitat and hunting methods it possesses, or it could simply be a part of how this species has evolved. Knowing that Carcharodon carcharias possesses a horizontal slit pupil in conjunction with an *area centralis*, there is also reason to believe that they must experience chromatic blurring based on the direction of how the light hits the axis of the pupil. Knowing that this family of shark have a horizontal slit pupil, further studies and tests could potentially lead to a better understanding of certain behaviors, and evolution within this species. Determining the retinal specializations of Isurus oxyrinchus, Lamna nasus, and Lamna ditropis will be helpful in further studies of convergent evolution. Because the Lamnid sharks rely so heavily on vision for survival, understanding their complete visual anatomy will help paint a better picture of migration, navigation, and habitat techniques, and could also help in understanding how Climate Change may be altering these habits.

Declarations

Competing interests:

The authors declare no competing interests.

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Figures

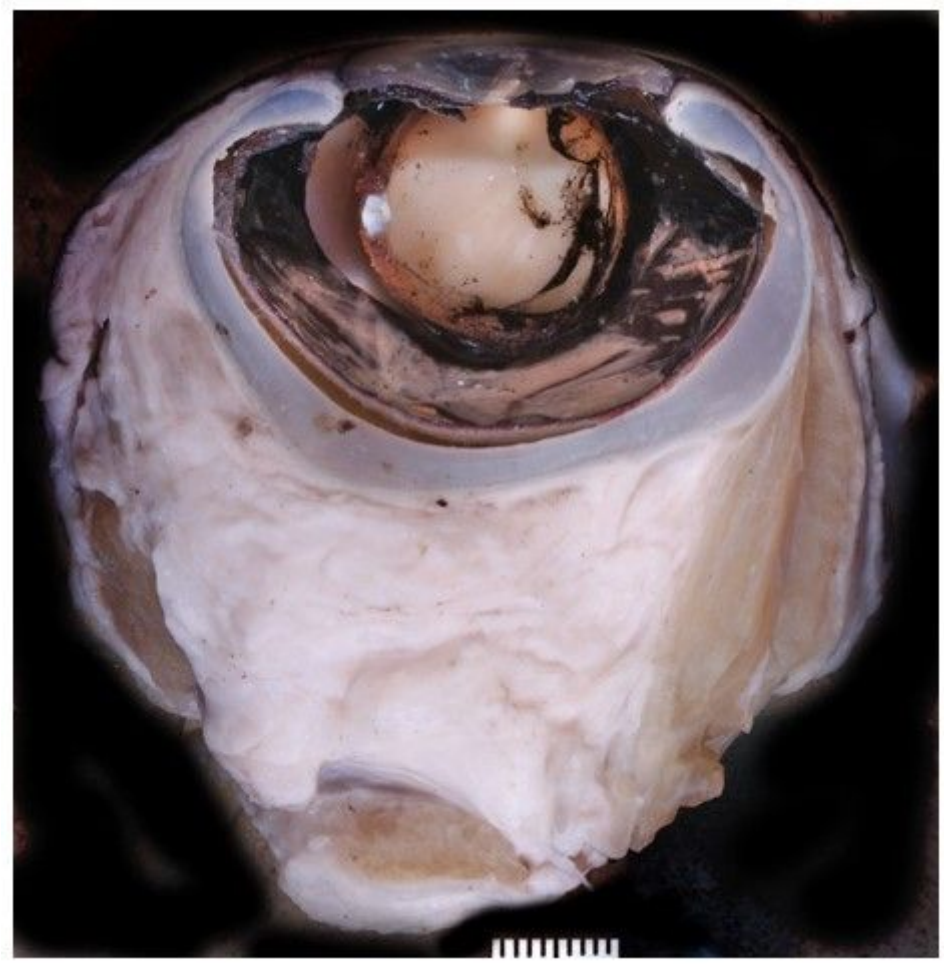

Figure 1

Cross section of the adult white shark globe.

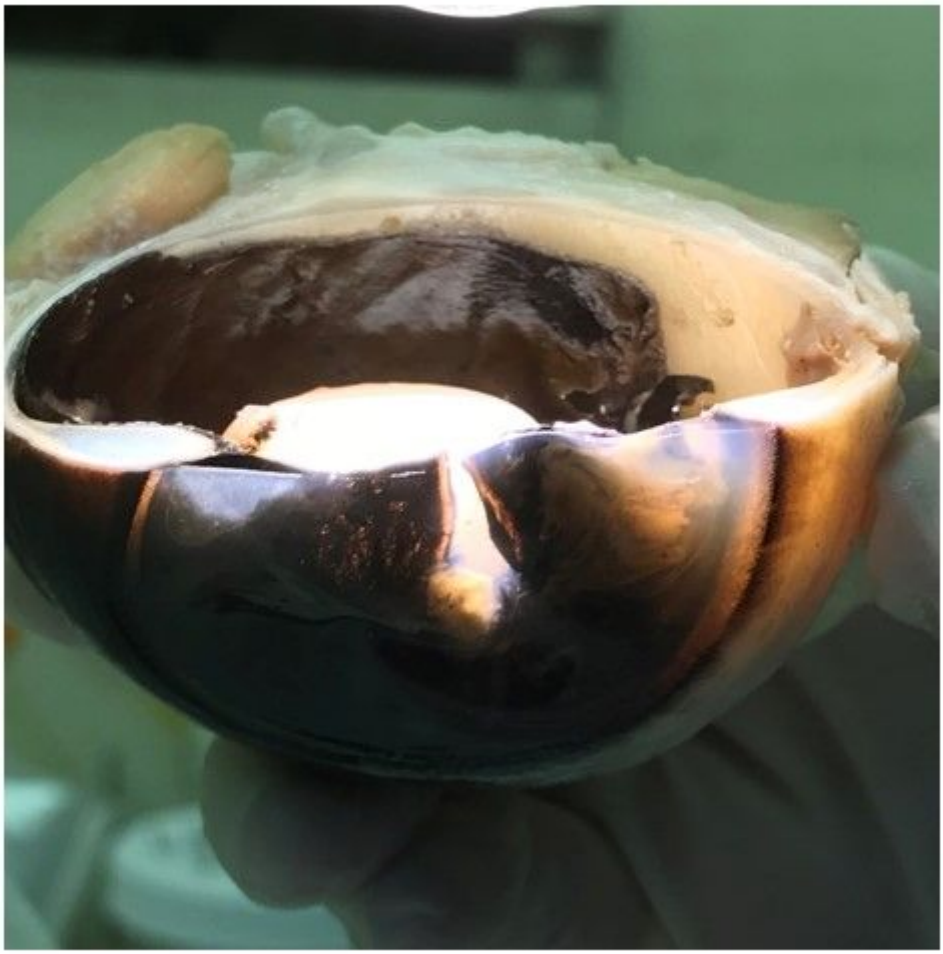

Figure 2

Illuminating the horizontal slit pupil in the adult white shark globe.

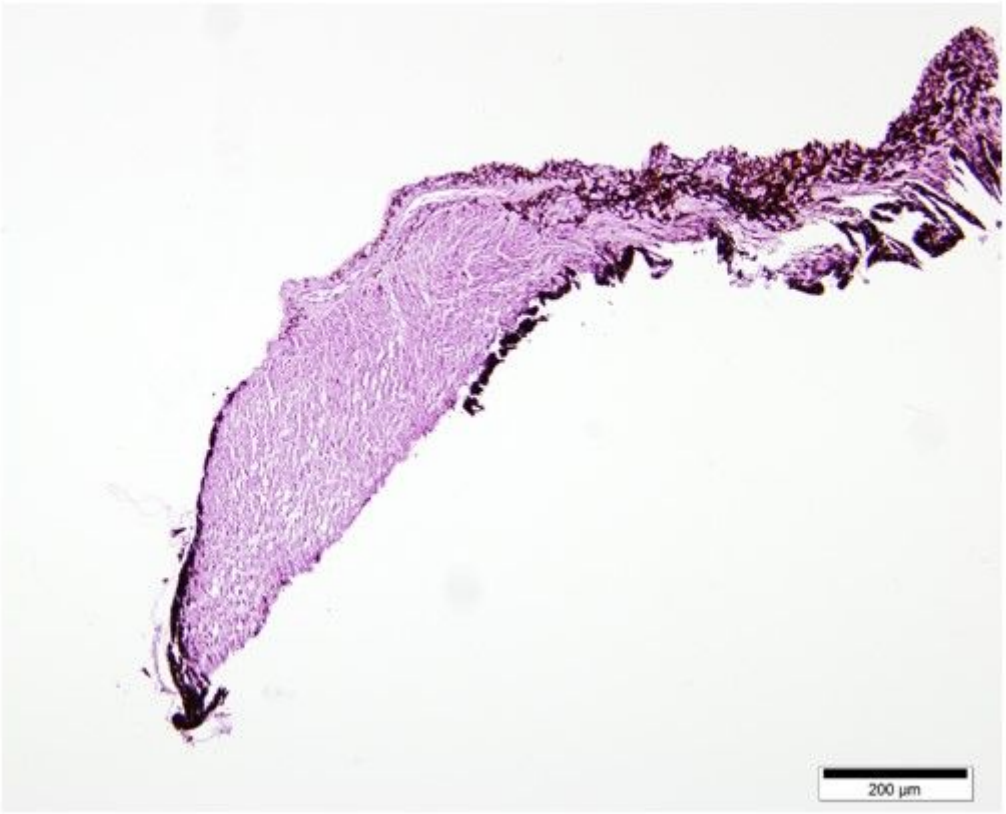

Figure 3

Magnification of the pupillary margin of the iris comprised of smooth muscle.

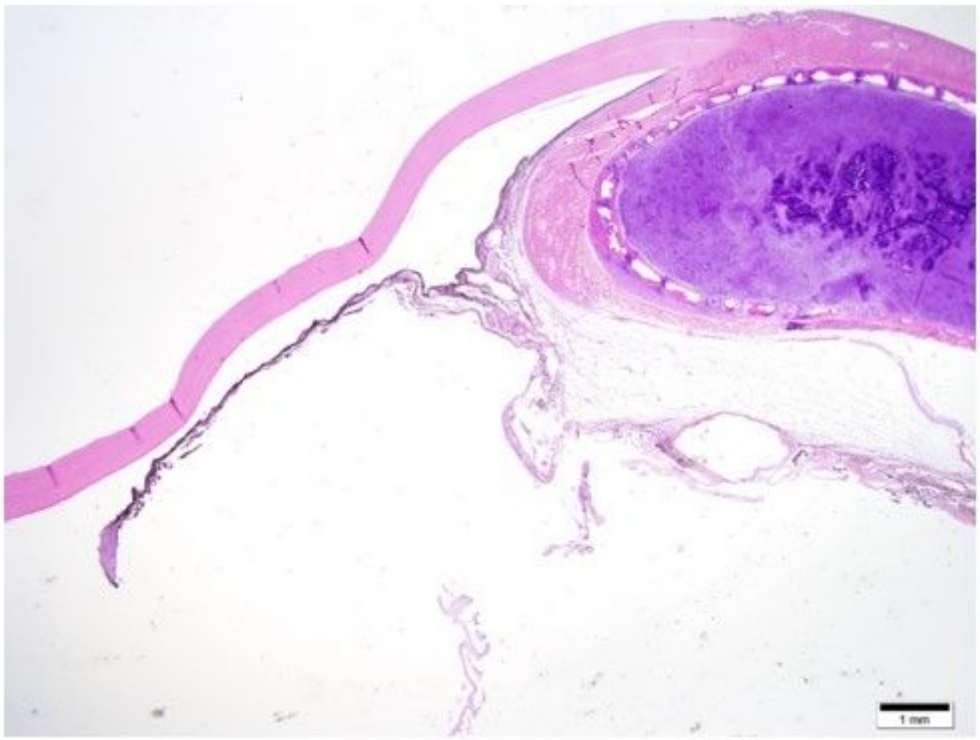

Figure 4

Magnification of the sclera and cartilage extending into the anterior chamber of the eye causing the apparent “blue ring”.

Figure 5

GoPro Footage of Carcharodon carcharias from Dr. Greg Skomal and the Massachusetts Division of Fisheries.

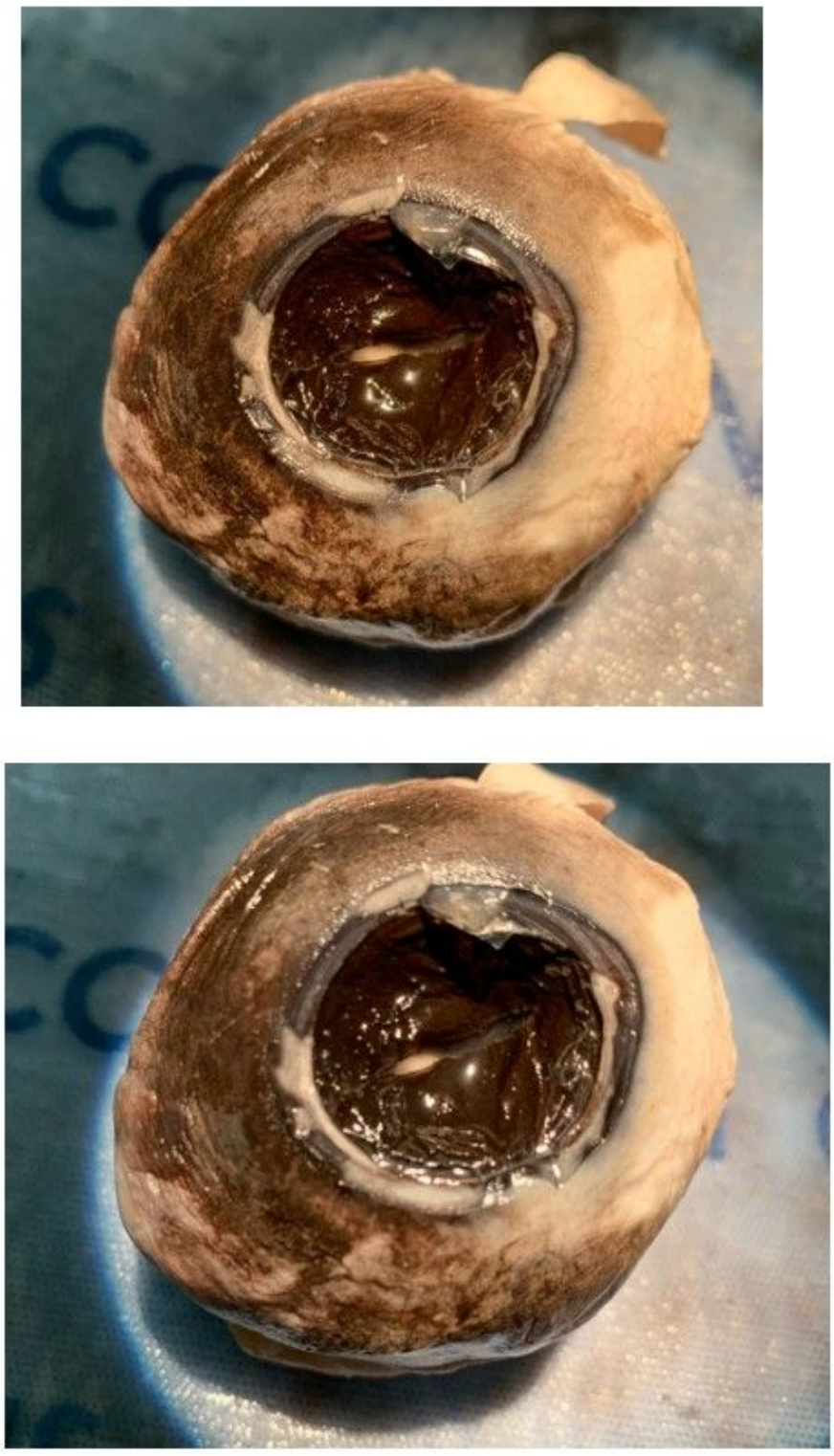

Figure 6

Carcharodon carcharias globe dissection 3/11/2020. Photos taken by Megan Burt

Figure 7

Carcharodon carcharias from underwater photographer George Probst.

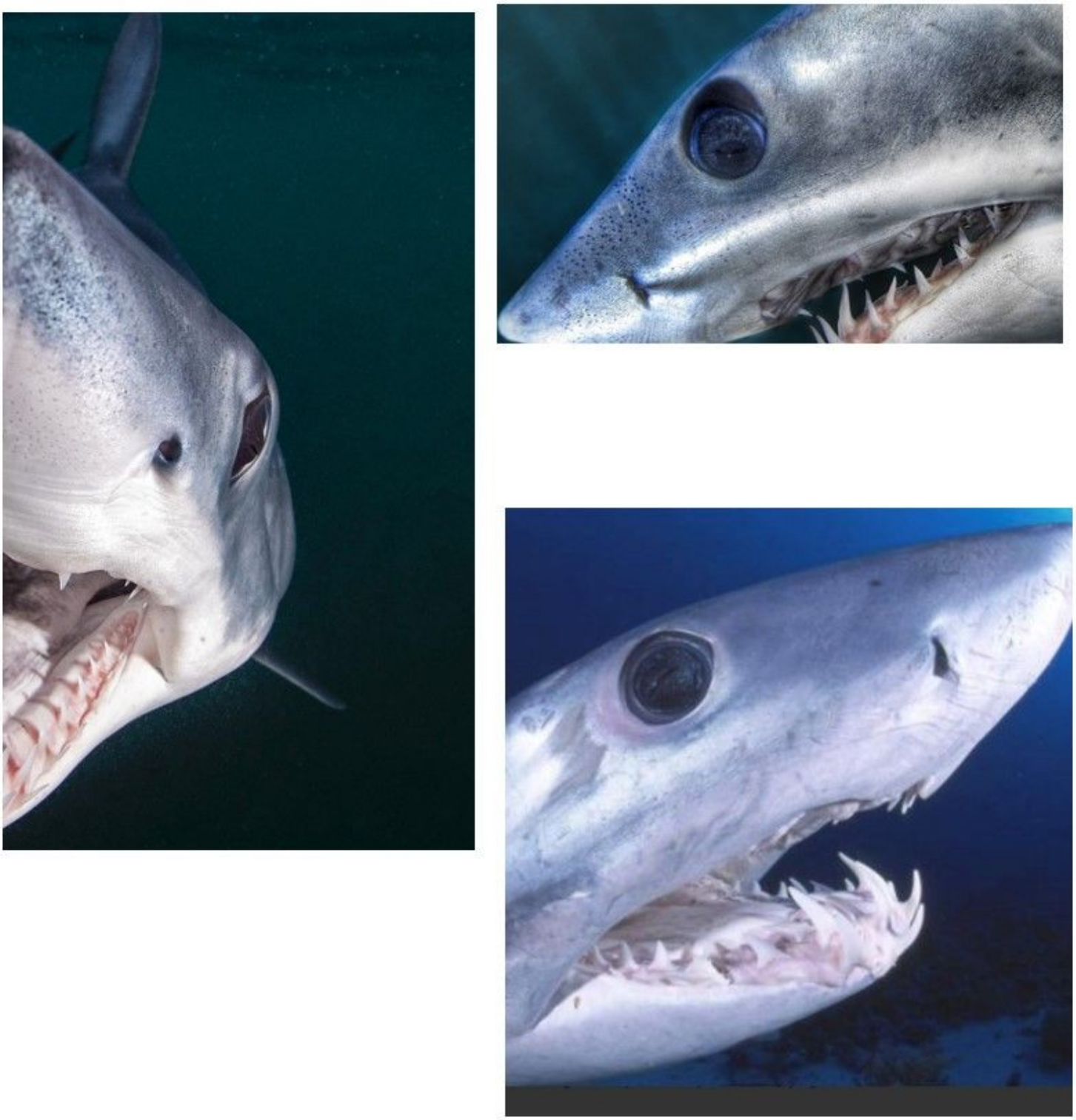

Figure 8

Photos of Isurus oxyrinchus obtained from underwater photographer, Joe Romerio.

Figure 9

Photos of Lamna ditropis obtained via underwater photographer, Ron Watkins.

Lamna nasus globe. Horizontal slit pupil with iris adhesion.

Juvenile Carcharodon carcharias globe illuminating the slit pupil.

Isurus oxyrinchus globe cross sections.

Figure 10

Globes