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**STRUCTURE AND OPTICS  
OF THE  
ANTERIOR SEGMENT  
OF THE  
CETACEAN EYE**

A Thesis presented in fulfilment of the requirements for the degree of  
Master of Philosophy  
at  
Massey University

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## ABSTRACT

The anterior segment of the mammalian eye is concerned with the function and maintenance of its optical components, the most important of these being the maintenance of transparency and stable intraocular pressure. The structures of the eye change throughout life. Continuous growth occurs in the lens, and a number of other changes associated with aging also occur, many of which reduce visual capacity. Many of these manifest in humans because of their long life span but have very little relevance in terms of survival. However, other long lived animals such as some birds, reptiles and whales, could be severely compromised by complete or partial blindness associated with aging. The aims of this study were to evaluate the importance of vision as a sense in whales by observation of the structure and optics of the anterior segment, and compare the findings with other species whose visual functions are well known. Pathological changes were recorded where appropriate.

The findings in this thesis are based on a three year survey of eyes from 45 whales in which i) differences between species in the size of the globe, lens, and cornea are described ii) the unique histological structure of the uveal tract is demonstrated and defined iii) evidence of emmetropia in both air and water from NMR images of two eyes is given iv) lens shape and capsular features which indicate that there could be a capacity for accommodation, are described, and v) lens pathology (four cataracts and one case of phacolysis) is described in five animals.

The largest whales (baleen and sperm) had the largest eyes, but this was mainly due to the thickness of sclera. Internal dimensions showed little variation with respect to body size, suggesting that there is an upper limit on internal size which is dependant on the focal length of the lens, a structure which enlarges only slightly with age. Corneal and lens sizes were especially large in the baleen whales, and particularly small in the sperm whale.

The uveal tract was found to be very vascular when compared to other species, and particularly well innervated with specialised nerve endings which are thought to be unique to cetaceans. Although the findings are not conclusive, evidence from this study suggests that the whales' unique uveal vasculature and aqueous drainage methods may be instrumental in modifying the dioptric strength of the eye. The abundance of specialised pressure-receptors in the ciliary body indirectly supports a proposed mechanism for this, whereby the engorged ciliary body raises intraocular pressure causing increased corneal curvature, and releases tension on the zonule to allow 'rounding up' of the lens.

Optically, the study showed that eyes from two long-finned pilot whales were

emmetropic by virtue of a cornea with only a very small amount of optical power in both air and water, and a very powerful lens (about 72D in water). Emmetropia was thus not affected unduly by transition from air to water as it is in most mammals, where the cornea is optically very significant in air but neutral in water. Lenses in both animals showed an unusual 'bump' on the central posterior surface, and the increased radius of curvature in this area was responsible for the very high dioptric strength of the lenses.

The prevalence of lens pathology, particularly cataracts in young animals, was high, but in all cases the cause was unknown.



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The study lasted for three years, and eyes from 45 dead stranded cetaceans were examined. The work would not have been possible without the cooperation of the Department of Conservation (DOC) and its staff who have helped to develop a network of communication which enables tissues to be collected and distributed as soon as possible *post mortem*.

I am indebted to the late Professor David Blackmore for so willingly giving his time in discussions for the planning of this study. His wisdom, knowledge, and breadth of vision were a source of inspiration; his enthusiasm a source of energy; and his advice, to 'follow your passion', has been invaluable.

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## ADDENDUM

PAGE 11.

A rete is a body of convoluted blood vessels, commonly found in mammals, connecting arteries to veins, arteries to arteries, and veins to veins. They are believed to store blood and regulate its flow.

PAGES 25, 56, 107, 109, 111, 114, 115.

There are significant limitations involved in measurement of material in these cases for the following reasons;

i] many of the specimens were suffering from some degree of autolysis. This may have affected subsequent dimensions. In addition, lens and cornea increase in thickness with *post mortem* imbibition of water.

ii] formalin fixation can also alter the dimensions of structures. Although this was investigated prior to the study and found not to be a significant factor for structures measured to the nearest millimetre, it may have been a significant factor for microscopic techniques with measurements in microns.

This has not been taken into account when presenting data.

iii] artefactual changes associated with tissue processing may have affected the sizes of structures in histological studies. Where these changes were obvious, the sites were avoided for measurement.

iv] some of the variations in size may have been attributable to the age and size of the animal. Lenses enlarge throughout life, and capsular thickness varies with age.

PAGE 54.

An unequivocal conclusion that whales lack pectinate ligaments could only be made using more sophisticated techniques, such as scanning electron microscopy or photographs taken with a dissecting microscope of the '*en face*' view of the ciliary cleft. This study merely reports that the pectinate ligament was not evident in any of the histological sections examined in these whales.

PAGE 56.

Dimensions of the ciliary body would have been better expressed as a percentage of overall ocular size.

PAGES 59, 62.

There are some limitations involved in the use of indian ink to trace aqueous outflow pathways using in vitro specimens; there is no possibility of active transport mechanisms operating; autolysis may damage the permeability of membranes and affect the resistance to flow of molecules; in addition, fixation will contract all membranes, valves and tissue spaces, and coagulate all proteinaceous substances within them. Better results would have been obtained using more sophisticated techniques, such as tracing the passage of latex microspheres or radioactively labelled substances in live animals.

PAGES 130-141

The study documents a small number of lesions in moderately autolysed specimens. Cataract was diagnosed on the basis of gross, rather than histological findings. However, strictly speaking, *post mortem* diagnosis of cataract should meet very specific histological criteria. The value of this chapter is to highlight the need to examine whales' eyes for cataracts with an ophthalmoscope at every possible opportunity, particularly at *post mortem* of by-catch or stranded animals.



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## INTRODUCTION

The order cetacea demonstrates extreme diversity between its 78 species. Morphologically, size can vary from the small Hector's dolphin at 1.3m in length to the 30m blue whale (Dawson 1985). Habitats can range from polar to tropical seas, with a few freshwater species. Some species, such as some of the beaked whales, are seen rarely. This could be due to their pelagic habits and relatively short periods spent at the surface, or could indicate a genuinely small population. Other species, such as many dolphins, are seen frequently because they have a coastal habit and spend large periods of time near the surface.

Whales evolved in the late eocene period around 53 million years ago (Dawson 1985). Both mysticetes and odontocetes are believed to have evolved from land based artiodactyls (even toed ungulates).

The ancient Greek philosopher Aristotle (384-322 BC) described dolphins as having lungs, and as being like humans in their behaviour, growth, and reproduction, but still referred to them as fish (Dawson 1985). Similarly in biblical times, the whale was considered to be a fish (Jonah, Old Testament). However, by 1776AD Linnaeus had devised a theory for the classification of animals which is still in use to day, in which he states;

“I hereby separate the whales from the fish....  
 .... On account of their warm bilocular heart,  
           their lungs, their movable eyelids,  
           their hollow ears, penem intrantum  
           feminam mammis lactentem”.

Even in 1851, the claim that the whale is a mammal and not a fish, was disputed. In Moby Dick (Herman Melville 1851) the description is given;

“to be short then, the whale is a spouting fish  
           with a horizontal tail”.

Melville's problem with the mammal theory was probably that it was inconceivable that the inhospitable and alien environment of the deep ocean could be inhabited by anything other than fish. The very fact that this 'fish' had a horizontal tail, unlike any other fish, and a body motion in a corresponding plane, should have indicated its mammalian rather than piscine nature. Earliest investigations of the cetacean eye were in the sixteenth century (Pierre Belon, 1517 - 1564, and Guillaume Ronderkelt 1507 - 1566, cited by Waller 1984). In 1719 Anton van Leewenhoek dissected a whale's eye that had been preserved in wine by the captain of a Greenland whaling boat, and noted the thick sclera.

Leewenhoek, who was famous for his invention of the light microscope, was able to put this instrument to good use in identifying and describing the ophthalmic rete mirabile, and the lamellar construction of the lens (Waller 1984).

Walls in 1942 and Prince in 1956 produced texts on comparative anatomy which were mainly descriptive in orientation. They included small amounts of information on cetacean eyes.

Since 1972, further innovative and original study of the cetacean eye has occurred, covering many aspects of anatomy, histology and optics.

## **1.1 ADAPTATIONS TO A MARINE ENVIRONMENT**

### **1.1i Body Adaptations**

Massive evolutionary adaptations have been necessary for whales to maintain themselves in an environment which is extremely hostile to a class that originally evolved for land living.

The ocean environment represents a challenge because it presents extremes of pressure, temperature and light intensity.

Pressure increases by one atmosphere for about every 10m increase in depth (Kooyman and Ponganis 1998). A shallow dive of this depth would therefore be equivalent to 2 atmospheres (202.6kPa or 30psi). During dives, the flexible ribs collapse to reduce lung volume and gas becomes compressed into the upper airways (Kooyman and Ponganis 1998). Heart rate slows, and blood is diverted to muscle and the central nervous system (CNS). Although cardiac output reduces, stroke volume and blood pressure are maintained (Kooyman 1989). Air filled compressible areas become filled with engorged rete vessels. In addition to mechanical effects on anatomical structures, pressure affects proteins at a molecular level, which could affect muscular contraction and nerve conduction (Schmidt-Nielson 1990) so special adaptations to alleviate this effect must exist. Water temperature can be variable, but more importantly the thermal conductivity of water is so much higher than that of air that there is a significant need to maintain body temperature. Fur and feather insulation have been replaced by a thick layer of blubber.

Light intensity decreases with depth so that depending on the quality of the water, 90% of light may be absent at 9m and 99% at 35m (Walls 1942).

There is a constant potential for drowning, and the whale has developed mechanisms to reduce the threat of this in the form of specific diving adaptations, such as an extremely high oxygen carrying capacity by virtue of a high haematocrit during dives and high mean corpuscular haemoglobin content



(MCHC). The circulating and stored blood volumes are similarly increased, and much more oxygen is stored as myoglobin than in humans (Schmidt-Nielson 1990). The animal is always alert by virtue of the brain's arrangement that only one cerebral hemisphere shuts down at a time during sleep (Ridgway 1988).

### 1.1ii Ocular Adaptations

The cetacean eye has also adapted dramatically to meet the needs of wide variations in light intensity, temperature, pressure, osmotic effects and the loss of corneal power underwater. Hydrostatic pressure adaptations are complex. If an analogous plastic bag full of water is taken underwater to a pressure of 10 atmospheres, it will not suffer deformation. Compressive forces only exist where there is an air interface, such as around the thorax, sinuses and middle ear, and this is where the most profound adaptation occurs. There is a distinction between a compressive force, and hydrostatic pressure. It is not known what adaptations to increased hydrostatic pressure the eye has made, particularly with respect to the protection of nerve function. "High pressure nervous syndrome" has been described in several species (not cetaceans) as a direct mechanical effect of pressure on nerves, but the mechanism remains unexplained (Kooyman 1989).

The osmotic gradient imposed by seawater affects mainly the cornea. A thick layer of viscous jelly protects the corneal surface (Prince 1956). This layer is not thought to contribute to the dioptric strength of the eye (Dawson 1980). The jelly also provides protection from suspended particulate matter, since eyelashes are absent, as they are of little use in this medium.

The loss of dioptric power by the cornea when the eye is immersed in water occurs because the refractive indices of the cornea and water are similar (Walls 1942; Prince 1957; Dawson 1972). In land animals, the cornea is the main refractive device contributing about 2/3 of the dioptric strength of the eye while the lens contributes 1/3 (Spooner 1957). When the eye is submerged and the effect of the cornea is lost, the lens has sole responsibility for refraction. Land animals are therefore longsighted (hyperopic) underwater. Cetaceans have adopted the fish model of a powerful, spherical lens to combat this effect. However, unlike the fish whose vision is entirely aquatic, some whales, such as dolphins and orca (*Delphinidae sp.*) also need good aerial vision. Another problem arises when the whale eye with its powerful lens is taken out of water and into air. It is believed that if the cornea is reinstated as an important refractive element, when coupled with a powerful lens the system becomes hopelessly myopic. However, in reality we know that dolphins have good eyesight in air from their displays in dolphinariums. Visual acuity in *Delphinidae sp.* has been tested and found to be similar to that of a cat in daylight (Spong *et al.* 1971; White *et al.* 1971; Herman *et al.* 1975).

## 1.2                    IMPORTANCE OF VISION AS A SENSE

Whales are "top feeders" (ie. they are at the top of the food chain consuming an energy rich, carnivorous diet of plankton, krill, fish or squid) and are therefore reliant on their intuitive and acquired skills as predators.

When the anatomy of the ungulate eye and the cetacean eye are compared it is obvious that the cetacean eye differs in a number of ways, suggesting that vision has become highly adapted and is therefore a sense of some significance.

If eyesight is important to cetaceans, it is possibly more important to some species than to others. In the Ganges River Dolphin, which is reputed to be sightless, the eye is small and the optic nerve is a mere thread (Tinker 1988; Waller 1983).

Madsen and Herman (1980) have suggested that vision has many important functions in cetacean life, including navigation, group movements, prey detection and capture, predator defence, and for identification and communication of behavioural state.

Visual problems may be a relevant consideration in the question of why whales 'actively' strand. It is noteworthy that strandings occur mainly in a few odontocete species and all are deep diving whales with non-coastal habits. In New Zealand, the commonest stranders are pilot whales, false killer whales and sperm whales, and these are responsible for 84% of individual and a high proportion of mass strandings (Brabyn 1992).

It is not known how migration in whales is accomplished, but magnetite has been found in the dura mater of *Delphinus delphis* which suggests that magnetic information may be used for orientation (Zoeger *et al.* 1981). In addition, a relationship between magnetic minima and mass strandings has been demonstrated (Klinowska 1985; Kirschvink 1986) and also between magnetic storms and strandings (Klinowska 1985).

Other methods of orientation or 'homing' such as chemotaxis, the ability to detect vibrations with a lateral line system or electric fields using electroreceptors, detection of polarised, infra red or ultraviolet light have not been demonstrated in cetaceans. Local orientation is achieved by echolocation in toothed whales. Spatial orientation is assumed to be achieved, like other mammals, by a series of proprioceptive and vestibular reflexes. These may be of more significance in aquatic environments because these animals may need to be able to orientate without the aid of fixed visual topographical cues such as a horizon, sky, or ground. The effect of gravity may be small, even zero, depending on the buoyancy of the body. Without light, reference points, and in neither positive nor negative buoyancy it can be possible to suffer from spatial disorientation until proprioceptive mechanisms stabilise. Although downwelling light may be absent as a navigational cue in the deep sea, sensitive vision is necessary to perceive light produced by marine organisms, either from photophores, or from



bioluminescent organisms in the gut.

When considering the cranial nerves, their comparative sizes are often used as indicators of their relative importance. The optic nerve is the third largest cranial nerve in whales although this is variable between species. This adds further support to the statement that vision is a significant sense in cetaceans. The largest cranial nerve in mysticetes is trigeminal five and in odontocetes is auditory eight. Odontocetes have well developed echolocation skills, hence the size and importance of this nerve. The second largest is auditory eight in mysticetes and trigeminal five (supplying the melon) in odontocetes (Tinker 1988).

The facial nerve is relatively large in both families. Other nerves associated with the eye such as oculomotor three, abducens six, and trochlea four, vary according to the mobility of the eye. Hypoglossal, olfactory and glossopharyngeal nerves are small, reflecting the relative unimportance of these senses (Tinker 1988). This information indicates that the importance of vision has often been severely underrated as a special sense in whales.

The aims of the present study were to examine the anterior segments of several species of whale to determine their anatomical and histological features and correlate these with a range of possible functions, but particularly accommodative capacity; to determine the refractive state of one or more whales to establish whether there is a refractive error in air; and to record any pathological changes observed.

From these observations, some hypotheses can be formulated about the importance of vision as a sense, and how this, or its pathology, may contribute to the stranding phenomenon.