

Anatomy of the eye of the sperm whale (*Physeter macrocephalus* L.)

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Abstract

Eyes of five sperm whales (*Physeter macrocephalus*) were investigated macro- and microscopically. The general anatomy corresponded well with previous reports on other cetacean species, as well as previous reports on the sperm whale eye. The sperm whale eye does not differ in any great respect from other odontocete eyes, except for the obvious larger size. The most prominent structures were a very thick sclera encapsulating the bulbus, a large, vascularized *rete ophthalmica* surrounding the optic nerve, and a massive *musculus retractor bulbi*. Lack of ciliary muscles was also noted as well as the presence of a choroid tapetum and giant ganglion cells in the retina. It is suggested that the anatomy of the sclera, ophthalmic rete and retractor muscle is linked to the ability of cetaceans to protrude and retract their eyes. The eye is retracted into the orbit by the retractor muscle with the thick sclera providing a firm basis for attachment as well as protection from deformation. Space for the eye in the orbit is provided by drainage of the rete for blood. Protrusion could be facilitated by relaxation of the retractor and eyelid muscles and a refilling of the rete with blood.

Key words: Cetacea, odontocetes, vision, retraction, rete ophthalmica, retractor muscle, eye muscles, *Physeter*.

Introduction

Cetacean eyes deviate from the general mammalian eye in a number of ways. Some of these are clearly adaptations to the aquatic medium and low-light conditions of the ocean. This includes a near-spherical lens, well-developed *tapetum lucidum* and a very high density of rods in the retina (Peich *et al.*,

2001). Few cetacean eyes are well-studied. The majority of recent works are on eyes of smaller odontocetes, such as the bottlenosed dolphin (*Tursiops truncatus*) and harbour porpoise (*Phocoena phocoena*). For reviews see Dawson (1980) and Supin *et al.* (2001). The difficulties in obtaining fresh material limit the possibilities for systematic examination of cetacean eyes mainly to species kept in captivity. For the remaining species one must rely on the unpredictable strandings of live or recently dead animals, as well as by-caught animals.

The eye of the sperm whale (*Physeter macrocephalus*), the largest of the odontocetes and one of the deepest diving whales, has been described by Rochon-Duvigneaud (1940), who provides a general description of the eye and by Hosokawa (1951), who mainly focuses on the innervation of the ocular muscles.

In connection with a recent mass stranding, we had the opportunity to obtain fresh material to study the sperm whale eye. Although we had no *a priori* reasons to believe the sperm whale eye to differ to any large degree from other odontocetes, the sheer size difference to the rest of odontocetes as well as the unique taxonomical position of the sperm whales alone makes it worthwhile to revisit the anatomy of the sperm whale eye.

Materials and methods

On 27 March 1996, 16 male sperm whales (length 11–13 m) stranded on the northwest coast of the Danish Island of Rømø. Five days post-mortem, five eyes and surrounding tissue were removed from five of the stranded whales and fixed in formaldehyde. Due to low temperatures of air and water the eyes were still in good condition and were usable for light microscopy.

The eyes were dissected macroscopically and selected sections were embedded in paraffin,

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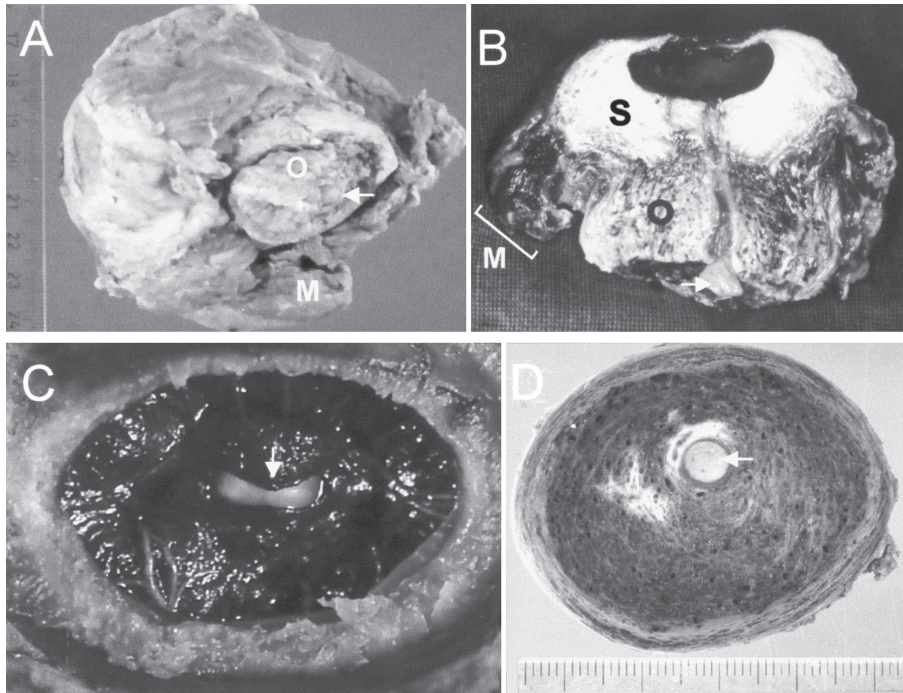


Figure 1. Macroanatomy of the sperm whale eye. (A) The eye seen from the side (anterior to the left) showing the optic nerve (arrow), *rete ophthalmica* (O) and *retractor muscle* (M). Scale in cm. (B) Longitudinal section, showing the thick sclera (S), *rete ophthalmica* (O) surrounding the optic nerve (arrow) and the massive *retractor muscle* (M) surrounding the rete and attaching to the sclera. The lens was lost in preparation. (C) Cornea removed to show the slit-formed pupil. Note the operculum along the dorsal edge of the pupil (arrow). (D) Cross-section of the *rete ophthalmica* surrounding the optic nerve (arrow). Scale bar in mm.

sectioned and stained routinely for histopathological examination.

Results

Macroscopic appearance

The eye slit was 4 cm long and the thickness of the eyelids 2 cm. *Fornix superior* and *inferior* were both 2–3 cm deep. A *membrana nictitans* could not be identified. The eyes were not spherical, but compressed along the visual axis as is normal for cetacean eyes and had average dimensions of $7 \times 7 \times 3$ cm. Average weight of the eye was 170 g. The cornea was ellipsoid with a horizontal axis of 2 cm and a vertical axis of 3 cm. The eyes were somewhat autolytic and the corneas dehydrated. The pupil was horizontally slit-formed, with an operculum on the dorsal edge (Fig. 1C). A thick and very hard sclera encapsulating the eye was very characteristic as was a large 2 cm thick muscle (*musculus retractor bulbi*) attached all the way around the eye at the equator (Fig. 1A, B). The muscle extended at least 30 cm into the deep orbit.

It was difficult to differentiate the very thin extraocular muscles from the massive circular *retractor muscle*.

Microscopic appearance

The epithelium of the cornea was lost due to autolysis. Bowman's layer could be found sporadically. The stroma thinned towards the centre of the cornea where it measured 250 μ m. Descemet's membrane and endothelial cells could also be identified. Pigmentation of the basal epithelial cells was seen in the perilimbal tissue as well as in the deeper stroma.

Sclera was comprised of densely packed collagenous fibres, and had the shape of a bowel with a very thick bottom. The anterior portion of the sclera was thin (1 mm) and increased markedly in thickness towards the posterior pole reaching a maximal thickness of 3 cm (Fig. 1B).

The anterior chamber was narrow, being only 6 mm deep centrally and with an open chamber angle. The iris was highly vascularized on the anterior side (Fig. 2B) and a well-developed muscle

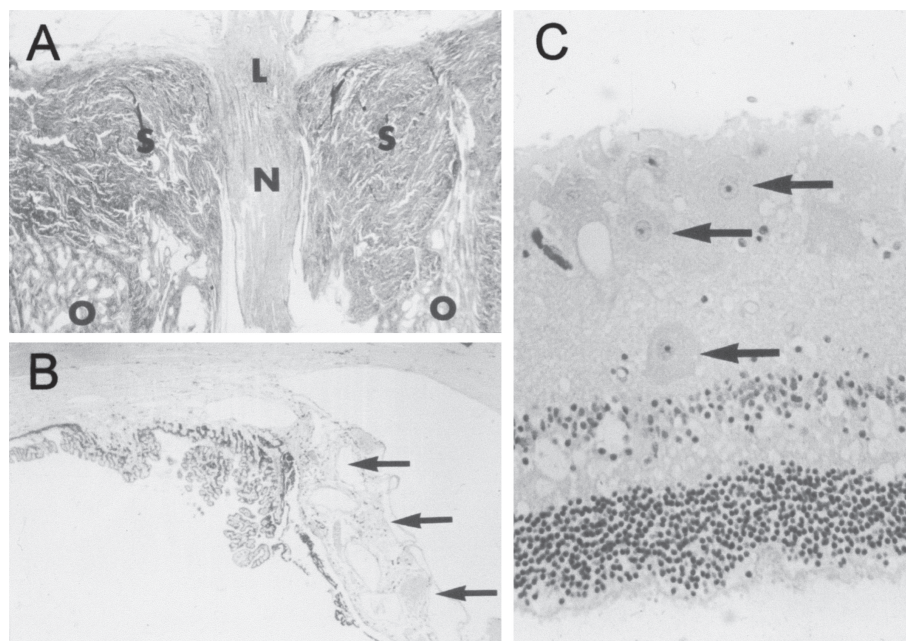


Figure 2. Microanatomy of the sperm whale eye. (A) Longitudinal section of the eye (anterior direction is upwards) with the optic nerve (N) and lamina cribrosa (L). The nerve passes through the thick sclera (S) and is surrounded by *rete ophthalmica* (O). $\times 3.5$. (B) Iris and *corpus ciliare* with numerous blood vessels on the anterior side (arrows). Ciliary muscles are absent. $\times 10$. (C) Retina, with giant ganglion cells (arrows).

(*musculus sphincter pupillae*) was observed. *Corpus ciliare* likewise contained vascularized tissue beneath the ciliary processes. The connection between *corpus ciliare* and sclera appeared weak and a *musculus ciliaris* could not be identified (Fig. 2B).

The lens was spherical, 1 cm in diameter, and with a thick capsule. The posterior chamber measured 1.5×3 cm.

The choroid was very thick, mainly due to the presence of a choroidal tapetum and relatively large blood vessels. The tapetum consisted of a collagenous tapetum fibrosum beneath Bruch's membrane and choriocapillaris. Under the tapetum was the choroidal large vessel layer and an outer collagen layer which was continuous with the sclera.

The retina showed many necrotic areas and the photoreceptors could thus not be evaluated. Many giant ganglion cells were identified (Fig. 2C).

The diameter of the optic nerve was 4 mm, with a thin *lamina cribrosa* when compared to the thick sclera (Fig. 2A). In the orbit, the optic nerve was surrounded by an accessory sheath, which contained a highly vascularized layer (*rete ophthalmica*), surrounded by a fibrous layer (Fig. 1D). The

diameter of the *rete ophthalmica* and the optic nerve was 4 cm.

Discussion

The sperm whale eye generally resembles that of other cetaceans, especially Odontocetes (e.g., Rochon-Duvigneaud, 1940; Dawson, 1980; Kastelein *et al.*, 1990; Supin *et al.*, 2001). Typical features include spherical lens, pupil with operculum, massive sclera, absence of ciliary muscles, well-developed retractor muscle, large ophthalmic rete, presence of tapetum and giant ganglion cells in the retina.

Absence of ciliary muscles is reported from harbour porpoise, *Phocoena phocoena* (Kastelein *et al.*, 1990), beluga, *Delphinapterus leucas* (West *et al.*, 1991) and rudimentary ciliary muscles were reported from the narwhal, *Monodon monoceros* (West *et al.*, 1991). This indicates a lack of ability to change the curvature of the lens which is otherwise the typical mammalian way of accommodation and is consistent with a recent study (Litweiler & Cronin, 2001), which found no evidence of

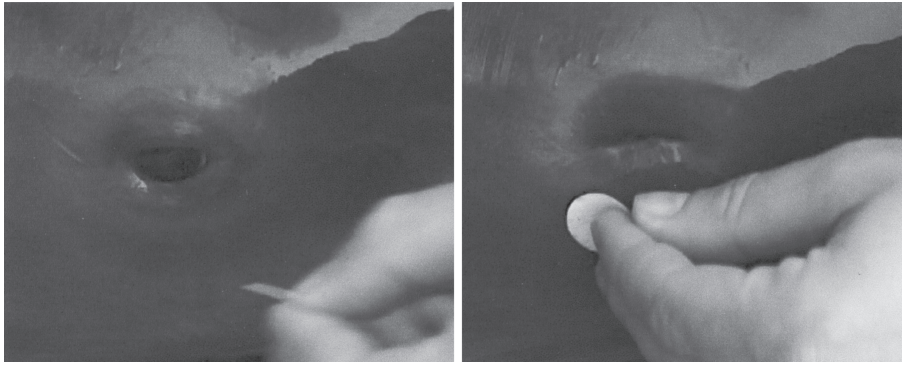


Figure 3. Retraction of the right eye in a harbour porpoise. Left: The eye in normal position. Eye in level with skin surface. Right: Closed eye. Note how the eyelids bulge inwards due to the retraction. Video recording of a female harbour porpoise from Fjord and Belt, Kerteminde, while taken on land for routine medical examination.

accommodation under water in bottlenose dolphins, *Tursiops truncatus*.

The sperm whale tapetum is of the fibrous type, common to other cetaceans (Young *et al.*, 1988) as well as terrestrial mammals such as sheep (Bellais *et al.*, 1975). The presence of the same tapetum in an artiodactyle suggests that this type of tapetum is a synapomorphy of the artiodactyle-cetacean clade (Shimamura *et al.*, 1997) and not an aquatic specialization unique to whales.

The sperm whale retina contained many giant ganglion cells. These cells are well known from a number of other odontocetes (Dawson & Perez, 1973; Kastelein *et al.*, 1990; Mass *et al.*, 1986; Mass & Supin, 1995; Murayama *et al.*, 1995), but their role is unknown. It is interesting to note that the giant ganglion cells in the sperm whale seems to form multiple layers instead of being aligned in a single layer below the inner plexiform layer as seen in other cetaceans (Dral *et al.*, 1975; Dawson *et al.*, 1982; Kastelein *et al.*, 1990; Murayama *et al.*, 1995).

Typical for all cetaceans investigated so far and in correspondence with previous reports on the sperm whale (Rochon-Duvigneaud, 1940; Hosokawa, 1951) are the very well-developed *rete ophthalmica* and *musculus retractor bulbi*. Weakly-developed rectus and oblique muscles resemble what is seen in harbour porpoise (Kastelein *et al.*, 1990), and long-finned pilot whale, *Globicephala melas* (Hosokawa, 1951) and is probably general for odontocetes. The lack of well-developed eye muscles results in a reduced ability to move the eye, except along the longitudinal axis (Hosokawa, 1951). The small rectus and oblique muscles is in contrast to what is seen in the bowhead whale, *Balaena mysticetus* and probably Mysticetes in

general, where all eye muscles are well developed (Zhu *et al.*, 2000).

Eye retraction and protrusion

Probably the most striking features of the cetacean eye are the extremely thick sclera, the massive retractor muscle, and the large intraorbital blood sinus (*rete ophthalmica*) surrounding the optic nerve.

The function of the sclera is probably to retain the shape of the eye bulb and help withstand deformation by external forces. It has been suggested that the thick sclera of cetaceans serves the purpose of withstanding pressure to the eye during fast swimming (Kastelein *et al.*, 1990). This, however, does not seem to fit well with the observation that the sclera is thickest in the posterior part of the eye and thinnest towards the anterior part. The shape of the sclera suggests to us that its primary function is to withstand deforming forces acting from behind, such as the action of the retractor muscle.

The role of the ophthalmic rete is unclear. Retes around the body of marine mammals have been linked to many functions, such as oxygen stores and temperature regulation, but with the exception of the countercurrent heat-exchangers in the skin and of the male testes (Pabst *et al.*, 1995) the exact function of these retes is still largely unknown. It has been suggested that the role of the ophthalmic rete is to maintain a high temperature of the optic nerve and the retina (Dawson, 1980), but it is unclear if a massive rete is needed for this. Seals, some of which dive deeper and longer than most cetaceans do not possess an optic rete and are thus apparently able to maintain retinal temperature by

other means. Another suggestion is a role of the rete in visual accommodation. Without functional ciliary muscles the form of the lens cannot be changed as in terrestrial mammals, but instead it has been suggested that either the lens is moved (Supin *et al.*, 2001) or the curvature of the cornea is changed (Kröger, 1989) by contraction of the retractor muscle, which in turn squeeze the rete and cause a raise in intraocular pressure. This idea, however, is not consistent with the lack of accommodation observed in dolphins by Litweiler & Cronin (2001).

The retractor muscle, which is very large compared to what is seen in other mammals, has the function of retracting the eye into the orbit. When present, the muscle is innervated by the sixth cranial nerve and a strong retraction of the bulbus was observed in the cat upon electric stimulation of this muscle (Hosokawa, 1951). It is commonly known that cetaceans can retract and protrude the eye (Dawson *et al.*, 1972; Supin *et al.*, 2001), but it has not been well documented in the literature. Figure 3 illustrates closing of the eye of a harbour porpoise, *Phocoena phocoena* including a retraction of the eye bulb. When the eye is retracted, the rete is probably drained for blood in order to make room for the bulbus in the orbit. Closing of the eyelids is aided by a contraction of *musculus orbicularis* surrounding the eye slit.

The eye can be protruded beyond the resting state, presumably to increase the field of vision (Dawson *et al.*, 1972), but it is not clear how this protrusion is accomplished. We suggest that a filling of the rete could supply the pressure needed and thus play a role in moving the eyeball outwards. The massive sclera probably plays an important role in protecting the shape of the eyeball from the deforming forces of the retractor muscle, especially in the partially retracted state, where the eyelids are still open and vision is still possible.

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