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Ciliary muscles in the eye of the long-finned pilot whale *Globicephala melaena* (Traill, 1809)

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Abstract

Histological observations on the ciliary body of *Globicephala melaena* indicate both circular and longitudinal fibres and forms the anatomical basis for a mechanism of lenticular accommodation. Its function is discussed in relation to accommodation during underwater vision.

Introduction

Descriptive works on the structure of the odenotocete eye by Pütter (1903) and Rochon-Duvigneaud (1940, 1943) provide limited information on the histology of the ciliary body. Pütter (1903) found ciliary muscle to be present as did Walls (1942) and Slijper (1962), though these authors offered differing interpretations about is development and function. Rochon-Duvigneaud (1940, 1943) stated that ciliary muscle is lacking and other studies also reported its absence (Dral, 1975; Dawson, 1980; Kastelein *et al.*, 1990).

Contradictory evidence about the nature of accommodation in odontocetes is evident in the results of refraction studies of the delphinid eye. Dawson *et al.* (1987a) commented on a surprising degree of refractive stability evident during examination of the eye fundus of *Tursiops truncatus* and *Grampus griseus*. Dral (1972) however noted variations in the refractive state of the *T. truncatus* eye during ophthalmoscopy which could be corrected using weak lenses. Both sets of observations were made using air-water interface devices that allow normal refractive procedures to be used whilst the cornea is bathed in sea water.

Although the *T. truncatus* eye presents high axial myopia in air (Dawson *et al.*, 1972; Dral, 1972), behavioural work shows this cetacean is capable of visual resolution of comparable acuity levels in both air and water (Herman *et al.*, 1975). The latter authors proposed that the optics of the pin-hole pupil accounted for the dioptric compensation occuring as the eye passed between media. However Dawson *et al.* (1979) found that full pupil constriction would not have occurred at ambient light levels reported by Herman *et al.* (1975) during their visual acuity tests.

These findings indicate that a mechanism of accomodation independent of pupil function is present. This report describes the structure and function of ciliary muscles in the eye of *G. melaena*.

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Material and Methods

Eyes were obtained from N. Atlantic pilot whales (*G. melaena*) caught in the Faroe Island commercial drive fishery. Specimen details are given in Table 1. Tissues were fixed in 10% formalin. Segments of the ciliary body and associated sclera were prepared for histology from specimen F78/7 and stained with Haematoxylin and Eosin. Sectioning was facilitated by paring away the outer layers of sclera after wax embedding; vertical and transverse sections of the ciliary body were prepared.

Table 1.

Specimen No.	Total Length (cm)	Sex	Eye side
F78/1	—	—	L, R
F78/5	425.0	—	L, R
F78/6	575.0	—	L, R
F78/7	465.0	♀	R.

Results

The limits of the ciliary body are marked posteriorly by the *linea terminalis retinae* and by a poorly developed iridio-corneal spongium anteriorly. Superficially, a short pars plana lies between the retina and ciliary folds. The ciliary epithelium is two layered and zonular fibres that support the lens are evident on its surface. Beneath it there are numerous pigmented fibroblast cells, pigment cells and blood vessels (Fig. 1) forming the main structural elements

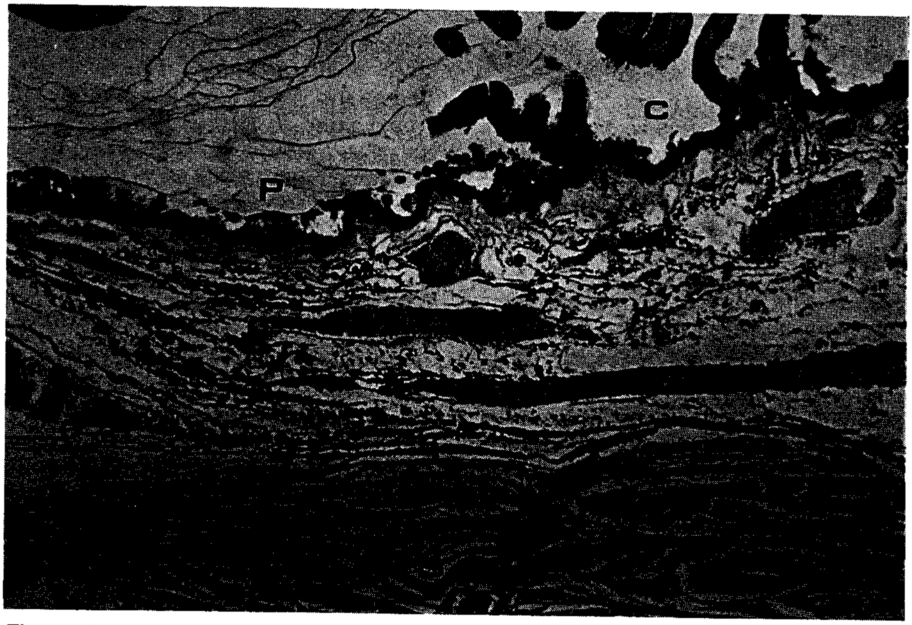

Figure 1. Vertical (meridional) section of the ciliary body of *G. melaena*. P, pars plana. C, pars plicata. S, sclera. × 70

Figure 2. Transverse (equatorial) section of the posterior ciliary body of *G. melaena* showing circular ciliary muscle fibres. S, sclera. × 70

of the ciliary body. Numerous nerve bundles are evident among the fibres of the iridio-corneal spongium. No pectiate ligament or similar structure was observed.

Ciliary muscle fibres are evident in the ciliary body (Fig. 2). Two types of muscle fibres are present: circular muscle fibres run parallel to the equatorial axis of the eye and are found throughout the ciliary body; longitudinal muscle fibres pass through the ciliary body from the region posterior to the ciliary folds towards the iridio-corneal spongium.

The cells in both muscle types are packed together in discrete finely branching strands. Most muscle fibres are found to lie in the posterior regions of the ciliary body in the area marked superficially by the transition between the *pars plana* and *pars plicata*.

Discussion

The anterior segment of the eye of *G. melaena* is dominated by a large, near spherical lens and an inconspicuous ciliary body which appears proportionately small in relation to other structures of the anterior segment. The anterior segment sclera is thin, though it becomes greatly elaborated around the optic nerve. There is clear and consistent evidence of localised scleral thickening of the anterior segment in the eyes examined. This occurs in the region close to the corneal periphery. The cornea itself is also thickened at its edge.

These features apparently function to increase the rigidity of the eye and may be adaptations to rapid external hydrodynamic changes, brought about by swimming or leaping. They may also maintain eye shape against the high intraocular pressure. Dawson (1980) reported values of about 70 mm in the *T. truncatus* eye.

The capacity of the lens to undergo deformation during muscular accommodation depends on the quantity of ciliary muscle present, the physical characteristics of the lens capsule material and the properties of the lens fibres themselves. Little is known about the physical properties of the odontocete lens due to the difficulties of making immediate post mortem examination of this structure. Delphinid lenses fixed in formalin have a hard, mineral-like core but whether this lack of plasticity is a feature of the fresh lens awaits further work.

In *T. truncatus*, histological appearances indicate that an amorphous capsule forms the external boundary of the lens (Waller, 1980). It is of uniform thickness (60 microns) over the whole circumference except the posterior lens face where it is markedly thinner (22 microns). A comparable structure in the human eye surrounds the lens though here the capsule is less thick than in *T. truncatus* and becomes thinner at both anterior and posterior lens faces (Alpern, 1969). If this capsule has an analogous function during accommodation to the human capsule in increasing the curvature of the anterior lens surface and thus its power, then lenticular deformation could only occur at the posterior lens surface in *T. truncatus*. Ciliary muscle of similar form to that described here for *G. melaena* is present in *T. truncatus* (Waller, 1980).

The development of ciliary muscle described here is consistent with lenticular accommodation of relatively small amplitudes. This is of significance in underwater vision. Since any addition in lens power would cause an increased myopia with the eye in air, ciliary muscle activity is likely to be absent in accommodation during aerial vision.

Delphinids appear to see well in air and refraction studies by Dral (1972) indicated the presence of an emmetropic aerial image in the eye of *T. truncatus*. The mechanism that results in this dioptric compensation has been the subject of numerous studies.

Rivamonte (1976) and Dral (1987) suggested that an opercular pupil functioned in combination with a poorly refractive lens periphery to form a restricted aerial image. Waller (1979, 1984) and Dawson (1980) pointed out that asymmetry of the eye chamber is present in the *T. Truncatus* eye. This may function optically in air in a similar way to the ramp retina described in ungulates by Walls (1942). Dral (1972) and Dral & Dudok van Heel (1974) described localised variation in corneal curvature in relation to stereotypic viewing postures, though recent detailed analysis of corneal structure by Dawson *et al.* (1987b) failed to confirm these findings in *T. truncatus*.

The contradictory nature of much of these data clearly demonstrates the need for further studies and the importance of achieving a consensus viewpoint.

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