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The anatomy of the Walrus head (*Odobenus rosmarus*). Part 3: The eyes and their function in Walrus ecology

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Summary

The walrus eye is small in comparison to that of other pinnipeds and the extrinsic eye muscles are well-developed. The strong palpebral muscles can open the eyelids and probably protrude the eye by thickening during contraction. The protrusion and mobility of the eyes enlarges the monocular visual field. The recti muscles can roll the eyes to look laterally, dorsally or frontally. In the latter 2 positions binocular vision is possible. Binocular vision seems a requirement for walrus stereoscopic vision, a property which has not been tested yet. Supraorbital processes are not found in the walrus but, for protection, the eyes can be retracted deep into the orbital cavity and the lids can be closed by the strong *M. orbicularis oculi*. Retraction of the eyeball deep into the orbital cavity may also keep the eye warm and functional. The thick layer of blood vessels between the sclera and the retina probably also has an important thermoregulatory function. Insulating fat-rich connective tissue and many blood vessels are found around the eye. Under low light conditions the pupil is a vertical oval, during moderate light conditions keyhole-shaped, and during high light conditions pinhole-shaped. A *tapetum lucidum* makes the eye more light sensitive. Cones are found in the retina, suggesting colour vision. Based on behavioural observations, anatomical findings and histological investigation of the retina, visual acuity in walruses is judged to be less than in the other investigated pinnipeds and seems specialized for short range use underwater. The role of vision in social interactions, navigation, selection of haul-out areas, detection of predators, and foraging is discussed.

Key words: Walrus, *Odobenus*, eye, vision, colour vision, stereoscopy, extrinsic eyeball muscles, ecology, anatomy, visual acuity.

Introduction

Walruses occur along the high Arctic coasts. They are stenophagous, feeding mainly on bottom-dwelling molluscs in shallow waters (Fay, 1982). Walruses are hunted for subsistence purposes in Alaska, the Russian Federation, Canada and Greenland (Born, 1992). In order to establish a rational management strategy it is necessary to have information about all aspects of the biology of walruses. A series of studies on the anatomy of the walrus head and the relation with aspects of its behaviour and ecology have been designed. Part 1 described the cranial bones (Kastelein and Gerrits, 1990) and part 2 described the head muscles and their function (Kastelein *et al.*, 1991*a*). As it is also important to know how walruses experience their environment, most of the following studies focus on the sensory organs. Knowledge is needed about the sensitivity of the different sensory modalities, and about the role they play in walrus ecology. The only two previous studies on vision in walruses are primarily anatomical investigations by Pütter (1903) and Mass (1992). This paper also mainly deals with the anatomy of the eye, but includes aspects of the behaviour of the animals and considers the use of vision in walrus ecology.

Materials and Methods

The eyes and the surrounding tissues were investigated using the preserved heads of 2 approximately 8-year-old female Atlantic walruses, *Odobenus rosmarus rosmarus* (KFHB#19 and KFHB#20). The heads were obtained from Inuit people in the Hudson Bay area of Canada, in June 1988, frozen immediately after death, and kept in this condition during shipment. One frozen head (#19) was mounted upside-down on a wooden board by means of straps. The tusks were removed from just below the gums and, while frozen, the head was cut in 28 approximately 1 cm thick transverse sections with a band saw. Before each slice was removed it was labelled and a photograph was taken from the side of the head. Each slice was washed, photographed from both sides against a 2 cm grid background and stored in fixative. The other frozen head (#20) was cut in half along the longitudinal axis, and put into fixative (2 Phenoxy Ethanol, 1% solution). After fixation, the tissues around the eyes were removed, and the eye muscles were examined.

For anatomical and histological investigations, additional eyes were obtained from two 11-year-old, male Atlantic walruses (GF#448 and 462), which were killed during an Inuit people's subsistence hunt in the Thule area (NW Greenland) on 19 May 1989. Individual ages were obtained from reading annual layering in the molariform teeth according to Mansfield (1958). The eyes were enucleated within 1 hour after death and preserved in Peters' fixative (0.1 M cacodylate buffered containing 1.25% paraformaldehyde and 1% glutaraldehyde, pH 7.4). Several characteristics of the eyes were examined using light microscopy and scanning and transmission electron microscopy. For light microscopy the eyes were embedded in nitrocellulose. Sections were stained with hematoxylin-eosin. For electron microscopy, samples of the eye were dissected under a biomicroscope. After thorough rinsing in cacodylate buffer, the samples were postfixed for two hours with OsO_4, dehydrated and embedded in Epon 812. Sections of 70 nm were post stained with uranyle acetate and lead citrate.

The eyes from 2 male Pacific walruses, *Odobenus rosmarus divergens* (code A1758, age: 15–20 years; code A1759, age: >25 years), which died of natural causes near Cape Pierce, Alaska, in August and September 1990 were used for anatomical investigations. The eyes were enucleated several hours after death and preserved in 10% formalin. The nomenclature adopted in the present paper is from the Nomina Anatomica Veterinaria (ICVAN, 1983).

A 16-year-old female (OrZH002) and an 8-year-old male (OrZH003) Pacific walrus at the Harderwijk Marine Mammal Park were trained to perform eye and eyelid movements which were photographed. This was done to illustrate the capabilities of the eyelid and extrinsic muscles of the eyeball.

Walruses in the wild and in several zoological parks were examined for the presence and size of the superciliary vibrissae.

An eye of a live 9-year-old male Pacific walrus (OrZH003) was subjected to different light levels which were measured with a light level indicator (Metrawatt, Metrux K) next to the eye. The shape of the pupil was observed and drawn at different light levels.

For a rough test to determine visual acuity, an 18-year-old female Pacific walrus (OrZH002) was trained to discriminate between 2 ways at which a fish (mackerel) was presented. When the fish was presented with the arm of the trainer extended horizontally the animal was taught to shake her head. When the fish was presented with the arm of the trainer extended vertically, the walrus had to nod. Training was done at a distance of about 2 m between the walrus and the trainer until the 90% correct response criterion was reached. Over time, the trainer increased the distance between herself and the walrus. The discrimination threshold was determined as the distance at which she started to make mistakes on more than 10% of the trials in identifying the two ways of presentation. The presentations were done in a random order. The tests were done under different light levels. Light levels were measured with a light level meter (Metrawatt, Metrux K) near the trainer, while pointing the light sensor towards the walrus. Testing was done on 15 days in January and February 1992 at Harderwijk.

Results

Location and movements of the eyes

The orbital cavity is located dorso-laterally in the skull and is oblique to the longitudinal axis of the body. The orbital perimeter is enclosed for two-thirds of its circumference by the maxilla, jugal and frontal bones, and is open only at the dorsal side, as the walrus has no supraorbital processes (Fig. 1).

The eyes of a walrus can rotate parallel to each other, but sometimes the axes of the eyeballs are not parallel (Fig. 2). Whether they can move their eyes independently, still has to be investigated. Most of the time the walrus seems to use monocular vision, but in special circumstances the eyes can be rolled in such a way that they both look forwards (Fig. 3), or dorsally (Fig. 4). Binocular vision would then be possible.

Extrinsic eye muscles and eyelid muscles

The attachment sites of the 6 extrinsic eye muscles on the sclera are shown in Figure 5, and their location in the orbital cavity in Figure 6. The attachment sites of the extrinsic eye muscles found in the present study deviate slightly from those described by Pütter (1903; see his Fig. L). In both studies the eyes of only one animal were investigated, and the differences could be the result of individual variation within the species. Rotation

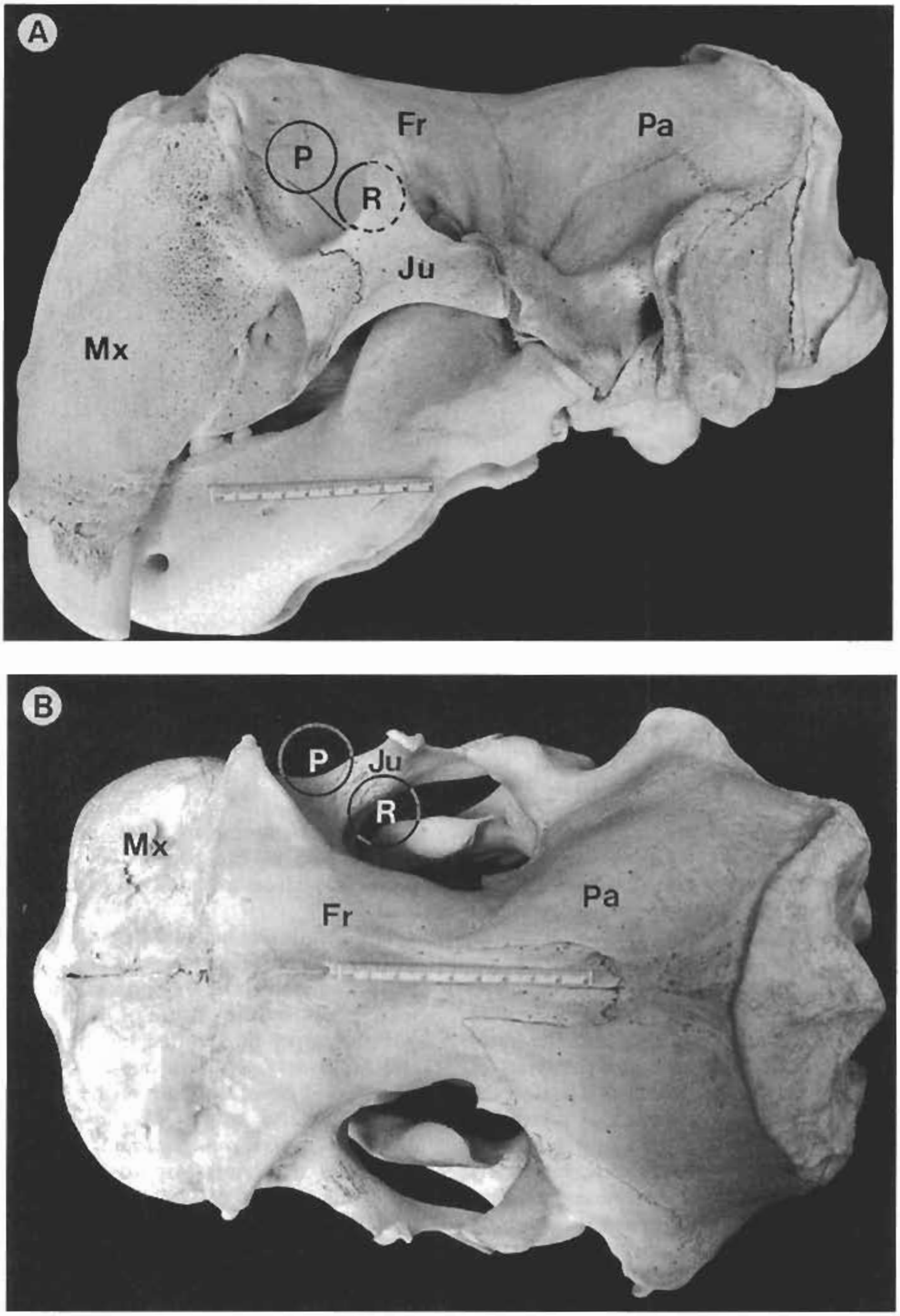

Figure 1. The position of the walrus eye when retracted (R) and protruded (P) in relation to the cranial bones. (A) Side view, and (B) Dorsal view. Bones: Mx=Maxilla, Fr=Frontal, Ju=Jugal, Pa=Parietal (Photos: Henk Merjenburgh).

of the eyeball around the axis through its poles is achieved by contraction of the *M. obliquus ventralis* and the *M. obliquus dorsalis*. The eye is moved in the horizontal plane (Fig. 7) by contraction of the *M. rectus lateralis* and the *M. rectus medialis*. Movements in the vertical plane (Fig. 8) are

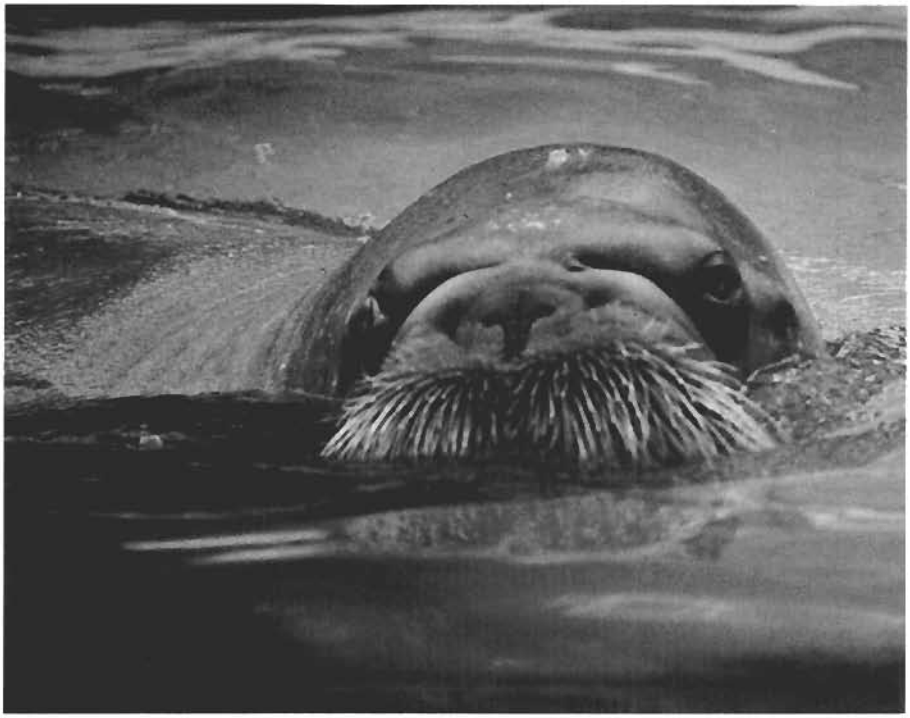

Figure 2. A 16-year-old female Pacific walrus with her head just above water. Note the asymmetrical positioning of the eyes (Photo: Henk Merjenburgh).

achieved by contraction of the *M. rectus dorsalis* and the *M. rectus ventralis*. By contraction of the well-developed *M. retractor bulbi externus* and the *M. retractor bulbi internus* the eye can be retracted deep into the orbital cavity (Fig. 1).

The eye and the extrinsic eye muscles are surrounded by a cone-shaped muscular envelope which consists of 2 muscle layers with muscle fibre directions perpendicular to one another. The fibres of the thick inner layer run from the perimeter of the optic canal to the eyelids. The dorsal part of the inner layer is the *M. levator palpebrae superioris*, the ventral side is the *M. depressor palpebrae inferioris* (Fig. 9A). Both muscles are intimately interwoven with the *Mm. recti superior* and *inferior*, and open the upper and lower eyelids and retract these partly into the orbital cavity. They do not only function in opening the eye but, the contraction, and thus the thickening, of both palpebral muscles probably also plays a role in the protrusion of the eyes. Unequal contraction of the two muscles creates different routes in which the eyeball can be protruded. The thin outer layer of the cone-shaped envelope consists of circular muscle fibres interwoven with fibrous connective tissue which are concentric with the eyeball and the optic nerve (Fig. 9B). This outer muscle layer is called the *M. orbitalis* (Pütter, 1903) and may also play a role in the protrusion of the eye. This protrusion causes a significant increase of the visual field.

The eyelids can be closed tightly by means of the well-developed *M. orbicularis oculi* (Figs. 6A–F & 10A). The eye is probably pressed into the orbita to some extent by the closure of the lids. To open the eye, the upper lid is lifted by the *M. superciliaris* and *M. levator palpebrae superioris*, and the lower lid is pulled down by a slip of the *M. sphincter colli profundus* (also called *M. malaris*) and the *M. depressor palpebrae inferioris* which is well-developed in comparison to that of most other mammals (Figs. 6 & 10B). For the location of the superficial facial muscles, see Fig. 2 in Kastelein *et al.* (1991*a*). In addition to the eyelids, the walrus has a third eyelid or *membrana nicticans* which lies obliquely over the eye. It can be depressed by one of the smooth muscles of Müller (see Miller, 1964) (Fig. 6D-H).

The optic nerve is very long, allowing for extensive eye movements; it is coiled when the eye is retracted. A large amount of fat-rich connective tissue is found between the *Mm. recti* and the *M. retractor bulbi* (Fig. 6). This tissue is richly provided with blood vessels. It may insulate the eyes and

Figure 3. Front view of a 16-year-old female Pacific walrus showing the eyes in a forward position, probably allowing for binocular vision in the rostral direction (Photo: Henk Merjenburgh).

allow individual muscle movements, but also the combined action of the eye muscles by volume displacement due to the thickening of the contracted muscles. More fat-rich connective tissue with many blood vessels surround the optic nerve (Fig. 6).

Eye glands

The Harderian gland (*glandula lacrimalis accessoria*) produces an oily mucus and lies rostro-ventral to the eyeball (Fig. 6B & C). There is no nasal duct.

Eye dimensions

A cross section of a walrus eye is shown in Fig. 11. Dimensions of several parts of eyes from four walruses are presented in Table 1. The walrus eye is extremely small both in absolute size and in relative size to the body compared to other pinnipeds. The diameter in the dorso-ventral plane is larger than the axial length. The sclera is at maximal thickness near the optic nerve. The cornea is thicker near the chamber angle than in the centre of the iris. The lens is almost spherical (indicating use in underwater vision) and very rigid. Unless this rigidity is a fixation artifact, its shape can probably not be changed to form a clear image on the retina. Some dimensions reported in Table 1 vary considerably between the four animals. Apart from age, individual and sub-species differences, this may be due to the different fixation methods and different periods between the death of animals and the fixation of their eyes.

Anterior—and posterior eye chamber

The anterior eye chamber (*camera anterior bulbi*) is enclosed by the cornea on one side and the lens and iris on the other side (Fig. 12). The posterior eye chamber (*camera posterior bulbi*) is located on the posterior side of the iris. In the posterior eye chamber the aqueous humor is secreted by the ciliary body, which is situated at the attachment of the iris. The ciliary body consists of strongly folded processes. Each fold consists of numerous capillaries covered with two layers of epithelial cells. At the capillaries the epithelial cells are pigmented (Fig. 13). This layer is covered with non-pigmented epithelial cells with numerous villi. The villi contain numerous secretive vesicles (Fig. 14). The ciliary cleft is the lateral part of the anterior eye chamber. It is enclosed by the iris and the cornea and the *ligamentum pectinatus*. The *ligamentum pectinatus* runs from the stroma of the iris to the cornea and has gaps on the corneal side to facilitate the flow of aqueous humor to the ciliary cleft (Fig. 11). The ciliary cleft is filled with thick and thin collagen fibres covered with endothelium. The thick fibres are situated near the ligamentum while the thin fibres run from the trabeculum fan-wise to the

Figure 4. An underwater photograph of a 16-year-old female Pacific walrus. Note that the eyes are rolled in a dorsal position, probably allowing binocular vision in the dorsal direction (Photo: Jurgen Foortjes).

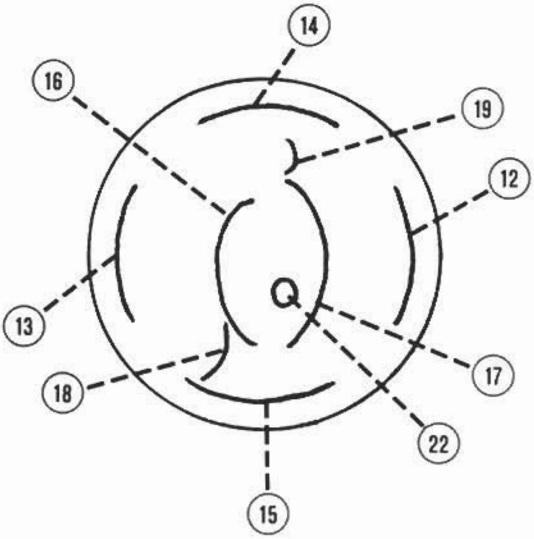

Figure 5. View of the back side of the right eye of an 8-year-old female Atlantic walrus, showing the attachment sites of the extrinsic eye muscles. (12) *M. rectus lateralis*, (13) *M. rectus medialis*, (14) *M. rectus dorsalis*, (15) *M. rectus ventralis*, (16) *M. retractor bulbi internus*, (17) *M. retractor bulbi externus*, (18) *M. obliquus ventralis*, (19) *M. obliquus dorsalis*, (22) Optic nerve (Drawing: Ron Kastelein).

ligamentum. These threads serve as a filter system. Finally the aqueous humor is drained by the trabecular meshwork, situated at the *corneascleral limbus*, the transition zone between the cornea and the sclera (Fig. 12).

Iris

The iris consists of an anterior *stroma* (Fig. 12) of rather loose connective tissue containing many chromatophores and thick-walled blood vessels and a posterior pigmented epithelium. Most walrus irises appear dark brown from a distance, and amber from nearby (Hills, 1990). However, some animals have light blue or greyish irises. The iris functions as a diaphragm, operated by, compared to the human eye, a well-developed *M. sphincter pupillae* (Fig. 12) and a strong *M. dilator pupillae*. The sphincter muscle consists of bundles of smooth muscle fibres, while the dilator consists of myoepithelium cells which are often pigmented.

Pupil

In contrast to that of many mammals but similar to other marine mammals, the walrus pupil is not circular, but oval during low light conditions (Fig. 15A & B). When the light level increases the pupil becomes ventrally narrower, making it keyhole-shaped (Figs. 15C, D & 16). In high light levels the pupil is reduced to a pinhole (stenopaic aperture) (Fig. 15E). This finding is in contrast with Walls (1963) who describes the walrus pupil as a broad horizontal oval under all ambient light levels.

Retina

The retina pigment epithelial cells above the *tapetum lucidum* cells contain small pigment granules which can be seen with electron microscopy (Figs. 17 & 18). Outside the tapetum, the granules are clearly visible in light microscopy (Fig. 19). The outer nuclear layer is quite thick (Fig. 20), and consists of up to 12 cell rows. The outer row contains bigger, less stained nuclei than the other 11 rows, which probably belong to rods. Rod pedicles show only one synaptic ribbon (Fig. 21). In the outer plexiform row, numerous pedicles occur with several ribbons, showing that the nuclei belong to cones (Fig. 22). The cones seem to be evenly distributed over the retina. The ellipsoid of the cones looks similar to rods with long mitochondria (Figs. 23 & 24). The outer segments of cones could not be seen well in the material available.

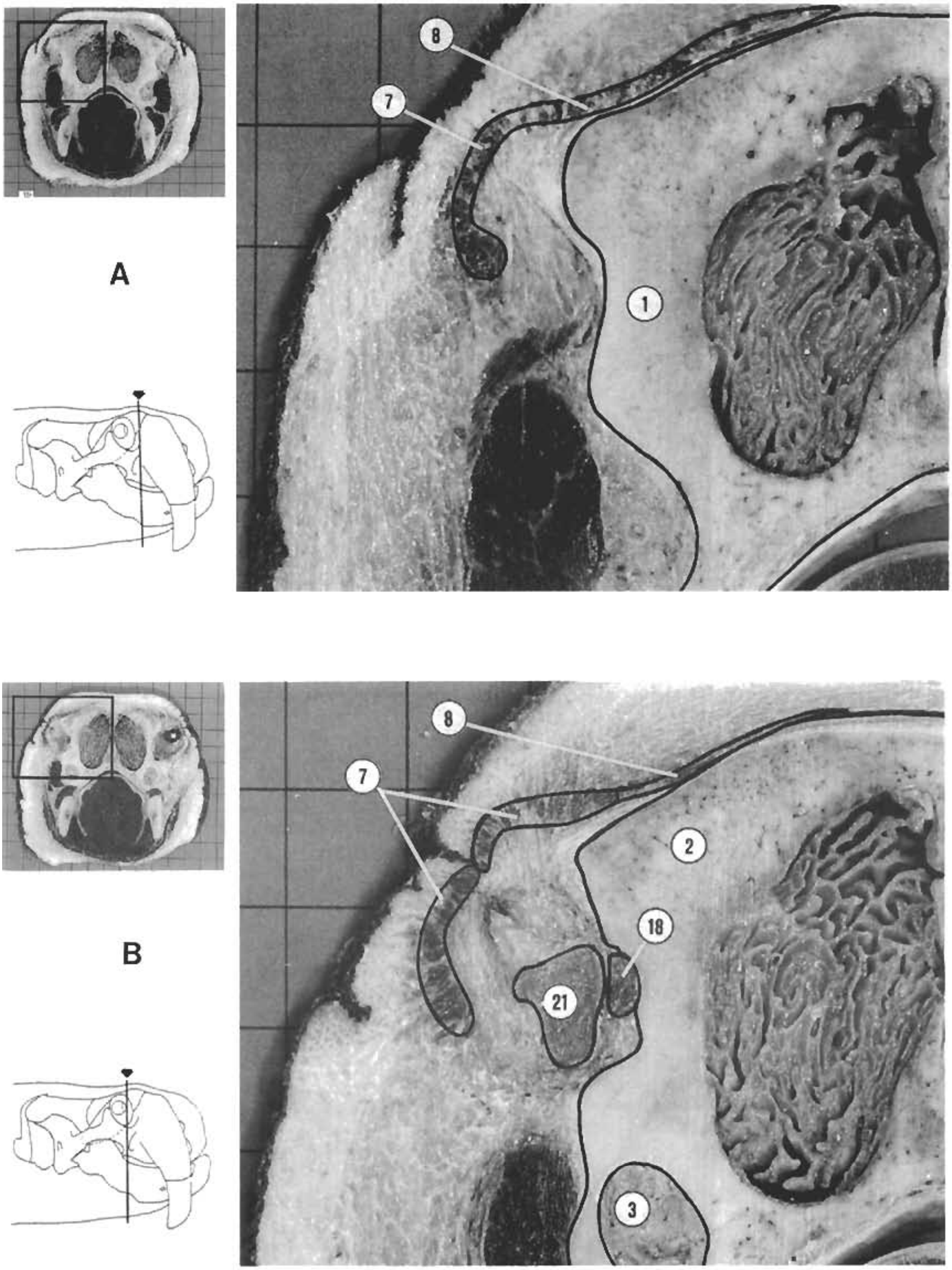

Figure 6A, B.

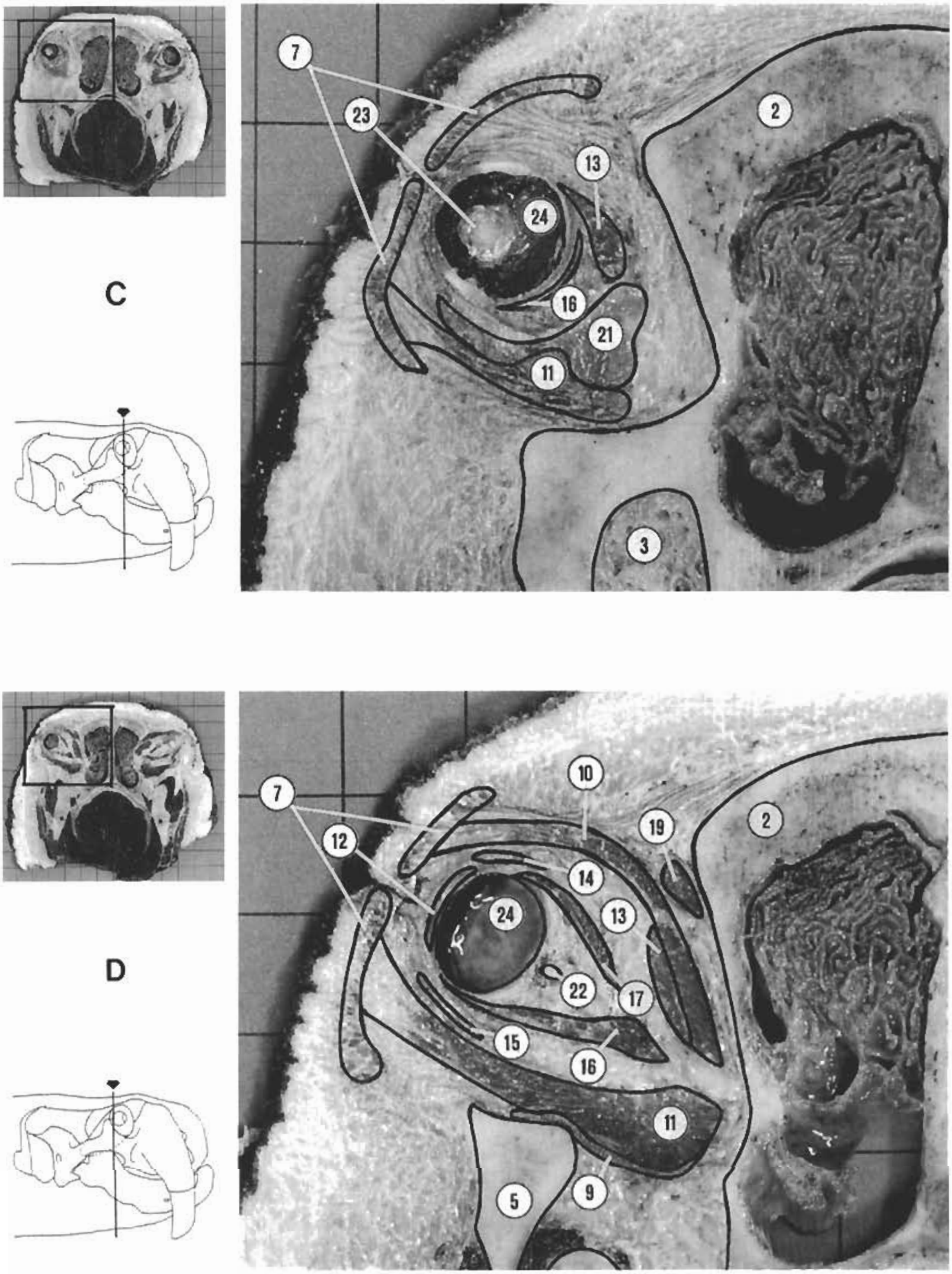

Figure 6C, D.

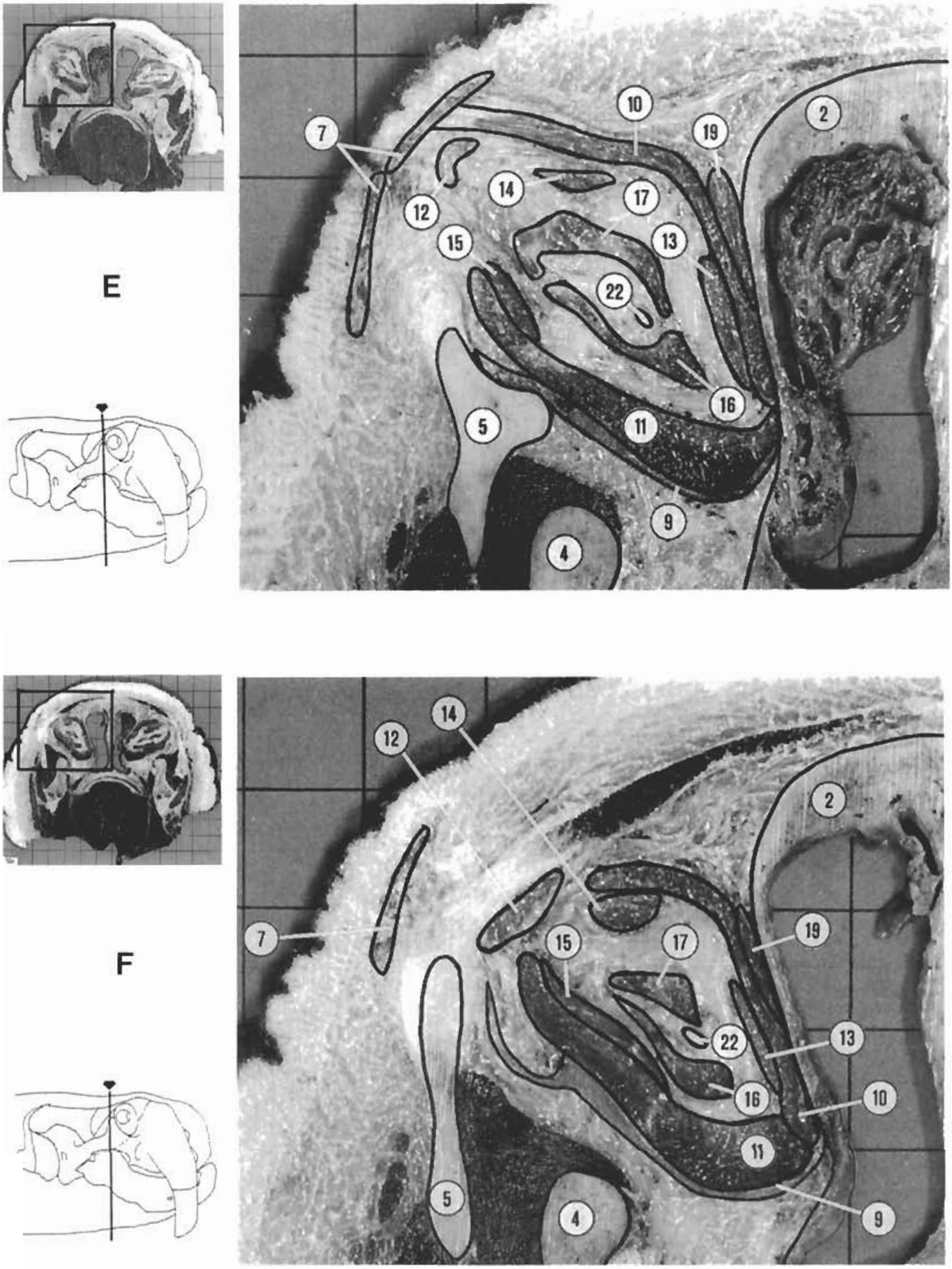
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Figure 6E, F.

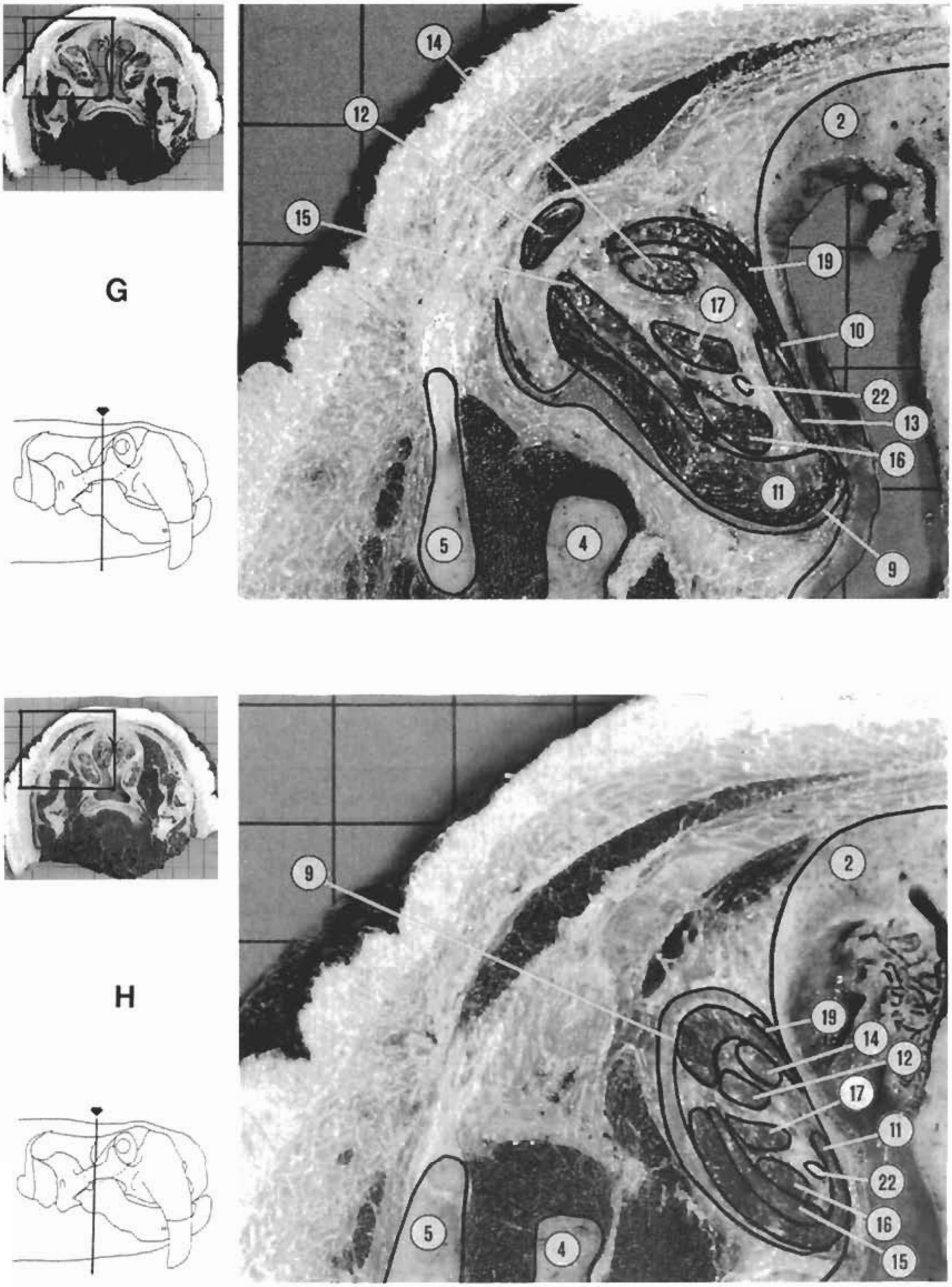


Figure 6G, H.

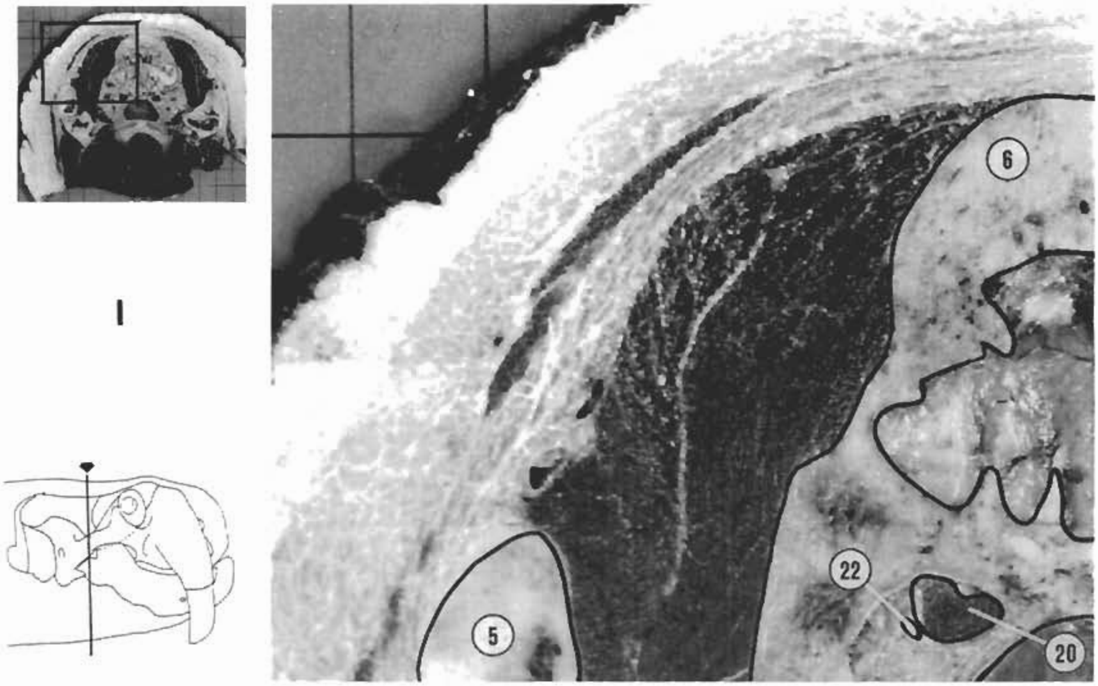


Figure 6. A–I. Frontal views of transverse sections through the right side of the head of an 8-year-old female Atlantic walrus. The arrow indicates the location of the cross-sections. (1) Maxilla, (2) Frontal bone, (3) Infraorbital foramen, (4) Mandible, (5) Zygomatic arch, (6) Parietal bone, (7) *M. orbicularis oculi*, (8) *M. superciliaris*, (9) One of the muscles of Müller related to the functioning of the nictitating membrane, (10) *M. levator palpebrae superioris*, (11) *M. depressor palpebrae inferioris*, (12) *M. rectus lateralis*, (13) *M. rectus medialis*, (14) *M. rectus dorsalis*, (15) *M. rectus ventralis*, (16) *M. retractor bulbi internus*, (17) *M. retractor bulbi externus*, (18) *M. obliquus ventralis*, (19) *M. obliquus dorsalis*, (20) Attachment site of the extrinsic eye muscles, (21) Harderian gland, (22) Optic nerve, (23) Lens, (24) Eyeball. The white between the eye muscles is fat-rich connective tissue. Due to a reduction in pressure in the eyeball after death, the eye is smaller than when the animal was alive. Background grid: 2 × 2 cm (Photos: Henk Merjenburgh).

Choroid and tapetum lucidum

Between the sclera and the retina is an unusually thick layer of blood vessels (Fig. 26). These vessels are separated from the retina by the *tapetum lucidum*. The *tapetum lucidum* is traversed by small vessels connecting the choroid vessels with the *lamina choroidocapillaris* (Fig. 25). Small vessels of the choroidocapillaris lie between the retinal pigment epithelial cells (Figs. 17 & 20). Optically the *tapetum lucidum* acts as a mirror, and reflects the light so that it traverses the visual elements twice. In the walrus, the tapetum occupies the entire posterior area of the fundus up to the equator and beyond the temporal side. It consists of closely set layers of thin, flat endothelial cells (Fig. 25). Each cell is packed with rod-like double refracting crystals (Fig. 27).

Superciliary vibrissae

Two closely examined anaesthetized wild adult male Atlantic walruses at Svalbard, Norway, with 62 and 48 cm long tusks had no superciliary vibrissae. Four of 12 Pacific walruses examined in zoological parks had superciliary vibrissae; always 1 above each eye. In a 15-year-old female at the Hannover Zoo they were 2.5 cm long, in a 13-year-old female at Sea World of Florida 1 cm, and in a 5-year-old male and 7-year-old female at the Brookfield Zoo 3 mm.

Visual acuity test

With light levels between 6000–5 Lux (i.e. between a sunny noon and dusk) the walrus was able to distinguish the two ways arms were presented at a distance of 11 m. With a light level of 2 Lux at 8 m, and at around 0 Lux at 4 m (Fig. 28).

Discussion and Conclusions

Visual acuity

Incidental observations

When considering the following anecdotes, contributions from other sensory channels should not be

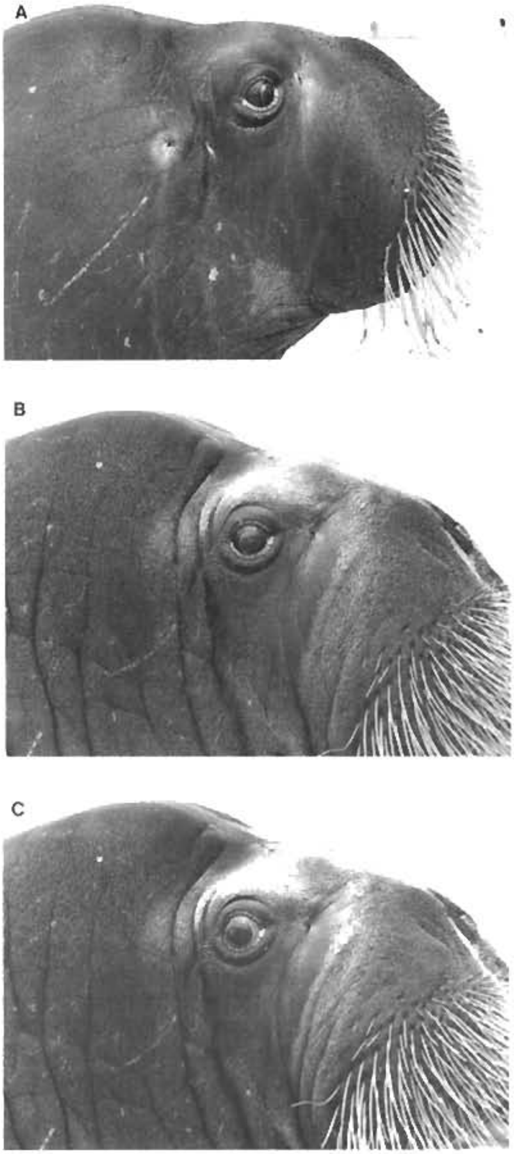


Figure 7. Side view of the head of an 8-year-old male Pacific walrus showing the eye movements in the horizontal plane. (A) Eye rolled forwards, (B) Eye in neutral lateral position, and (C) Eye rolled backwards (Photos: Henk Merjenburgh).

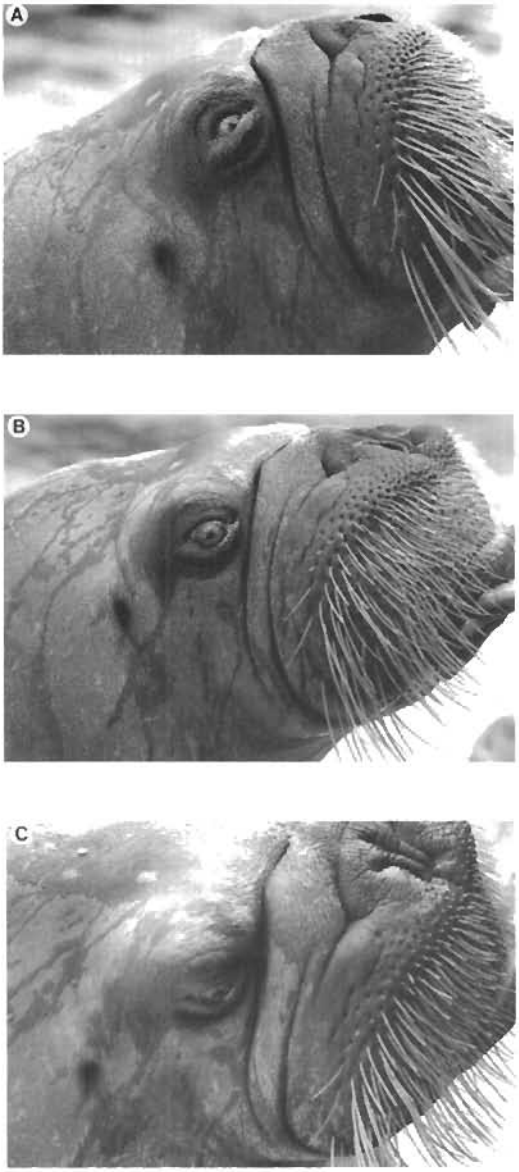


Figure 8. Side view of the head of a 16-year-old female Pacific walrus showing eye movements in the vertical plane. (A) Eye rolled upwards, (B) Eye in neutral lateral position, and (C) Eye rolled downwards (Photos: Henk Merjenburgh).

overlooked. Often, multimodal stimuli influence the behaviour of animals (Evans and Bastian, 1969).

Several authors suggest that walruses have poor vision without giving a reason for their belief (Shuldham, 1775 (in Allan, 1880); Lamont, 1861; Elliot, 1875; Arsen'ev, 1927; Bel'kovich and Yablokov, 1961; Ognev, 1962). Pedersen (1962), Loughrey (1959) and Kibal'chich and Lisitsina (1979) suspected that walruses are short-sighted, and observed that they noticed moving objects sooner than stationary ones. In NE Greenland, a crawling person, who slowly approached a hauled out herd of walruses up wind, apparently was not observed by the walruses until he was about 10 m away (Born pers. obs.).

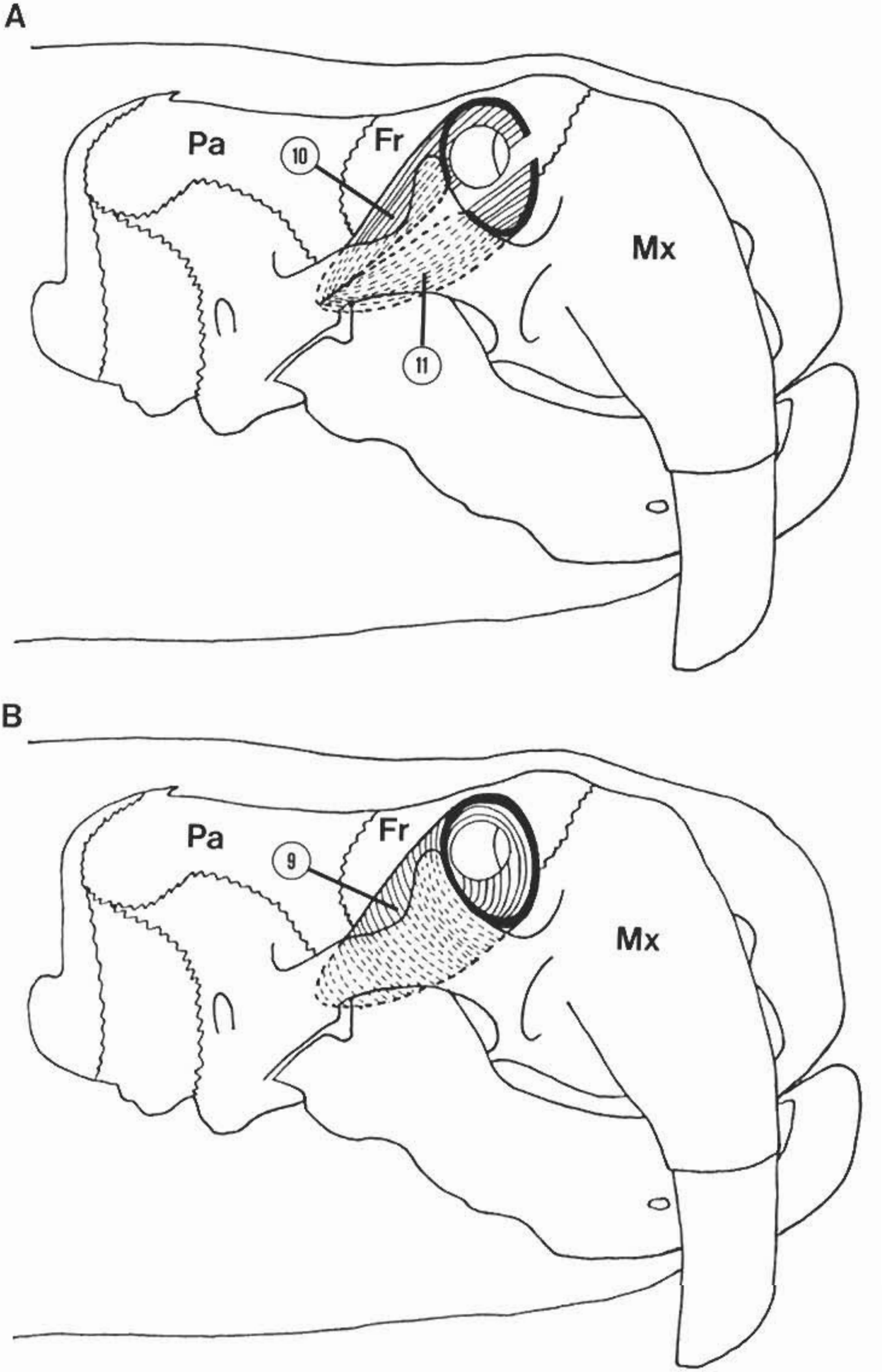


Figure 9. Side view of a walrus skull, showing (A) The muscles (10) *M. levator palpebrae superioris* and (11) *M. depressor palpebrae inferioris* that open the eyelids and, by thickening, protrude the eyeball, and (B) The muscle (9) *M. orbitalis* that aids in the protrusion of the eyeball. Bones: Mx = Maxilla, Fr = Frontal, Pa = Parietal (Drawings: Ron Kastelein).

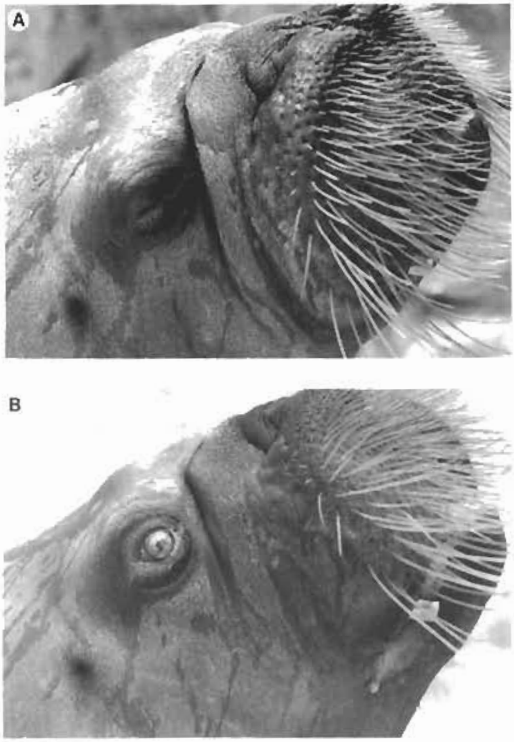


Figure 10. Side view of the head of a 16-year-old female Pacific walrus. (A) Eye closed by contraction of the *M. orbicularis oculi*, and (B) Upper eyelid opened by contraction of the *M. superciliaris* and the *M. levator palpebrae superioris*, and the lower eyelid by the *M. malaris* (a slip of the *M. sphincter colli*) and the *M. depressor palpebrae inferioris* (Photos: Henk Merjenburgh).

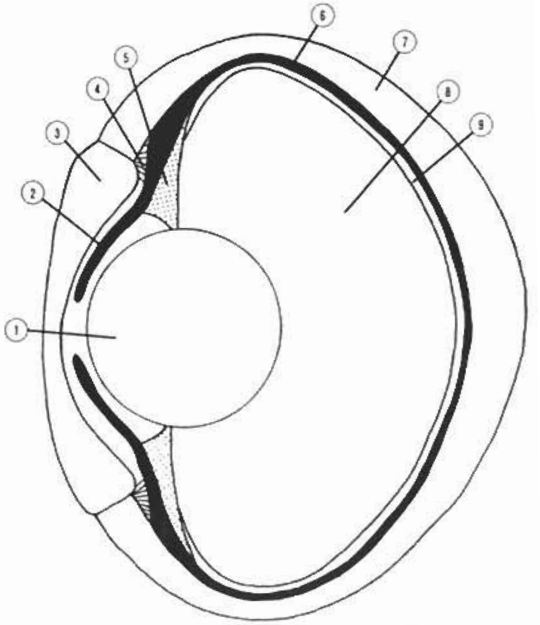


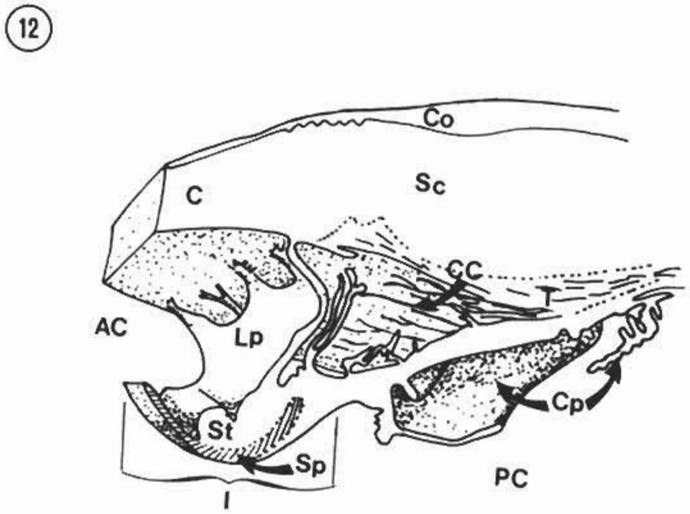
Figure 11. A drawing of a vertical cross-section of the eye of an adult walrus. (1) Lens, (2) Iris, (3) Cornea, (4) Ciliary cleft, (5) Ciliary process, (6) Chorioidea, (7) Sclera, (8) *Corpus vitreum*, (9) Retina (adapted from Pütter, 1903).

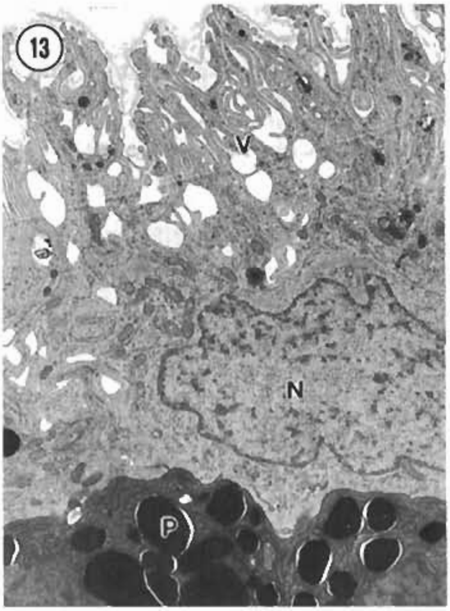
Some information suggests good vision in walruses, although other senses may have been of more importance. Some observations in zoological parks indicate that walruses use their eyes (Bartlett, 1940; Atz, 1961). The walruses at the Harderwijk Marine Mammal Park often spend much time

Table 1. The eye dimensions (mm) of 4 adult walruses.

Walrus	#448[1]	A1758[2]		A1759[2]		Pütter (1903)[3]
Subspecies	Atlantic	Pacific		Pacific		Atlantic
Sex	Male	Male		Male		—
Age (year)	11	15–20		25+		Adult
Eye		left	right	left	right	
Eye length dorso-ventral direction	30	30	29	30	30	29.5
Eye length sagittal (axial length)	25	29	27	28	27	24.5
Diameter optic nerve	2.5	—	—	—	—	—
Scleral thickness near optic nerve	2.1	2.5	2.4	2.3	2.3	—
Scleral thickness near equator	—	1.9	1.4	1.4	1.5	1
Scleral thickness near iris	0.88	1.3	1.3	1.1	1.3	2
Cornea thickness in centre of eye	0.40	1.3	1.2	1.6	1.4	0.85
Cornea thickness at chamber angle	0.90	1.8	1.6	1.9	1.85	3
Cornea diameter	—	—	—	—	—	18.6
Tapetum lucidum thickness	—	0.17	0.17	0.14	0.11	—
Axial diameter of lens	9	—	—	—	—	9
Dorso ventral diameter of lens	10	10	10	—	—	—

[1] Peters' fixative, 1 hour after death. [2] 10% formalin, several hours after death. [3] Müller fixative, time after death not reported.





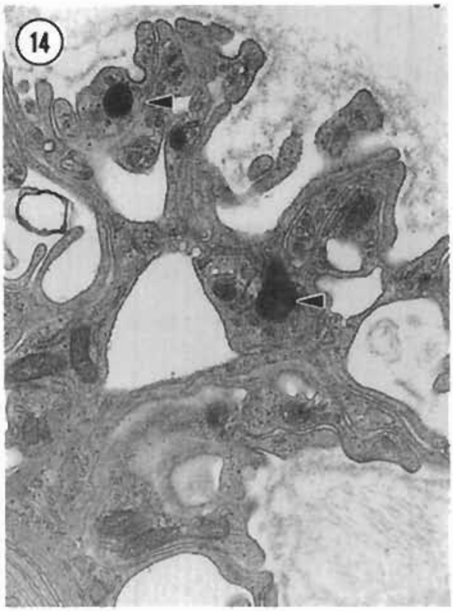


Figure 12. Artists impression of the anterior—and posterior eye chamber after a whole mount preparation. AC=anterior eye chamber, C=cornea, CC=ciliary cleft, Co=conjunctiva, Cp=ciliary processes, I=iris, Lp=ligamentum pectinatum, PC=posterior eye chamber, Sc=sclera, Sp=sphincter, St=stroma, T=trabeculum (6 ×).

Figure 13. Epithelial cells of ciliary body. P=pigment of pigmented epithelial cell. V=villi of unpigmented cells. N=nucleus (3.780 × , EM=electron micrograph).

Figure 14. Villi of unpigmented epithelial cells. Arrowheads indicate secretive vesicles (11.260 × , EM, Drawing and photos: Ruud Zweypfenning).

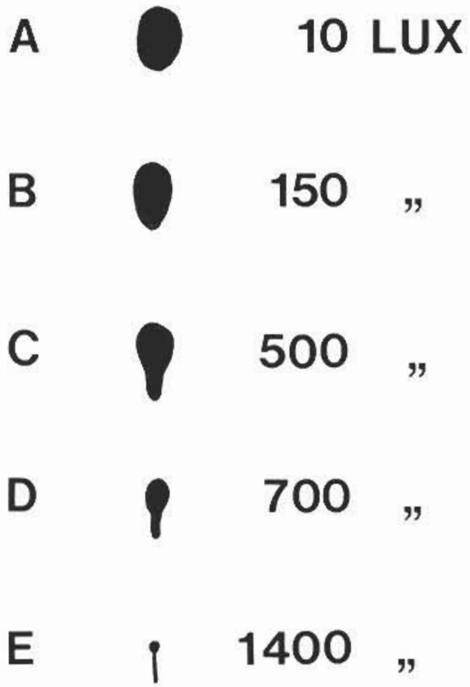


Figure 15. A–E. The pupil of a Pacific walrus under several light levels (Drawing: Ron Kastelein).

watching the trainers (which are between 1 and 4 m away) with 1 eye through 5 cm diameter holes in the doors of their quarters. These walruses get many of their cues to perform particular behaviours by visual signals from the trainers. These cues may vary from small hand movements to entire body gestures. Most signals are (by tradition, but not necessarily by limitation) given when the trainer is within 4 m of the animals' eyes (Kastelein pers. obs.). Whether the walruses can distinguish subtle hand gestures at greater distances has not yet been investigated. However, they can recognize individual people. Hermes (1884) describes a trained Atlantic walrus which seemed to recognize its trainer from a distance by the way he walked. At the Harderwijk park, the walruses can identify a familiar person in a crowd at a distance of at least 4 m. Dittrich (1990) notes that walruses at Hannover Zoo were able to catch gulls that were feeding on fish remains in the indoor enclosure under a variety of circumstances. Lamont (1861) and Koldewey (1874) describe interactions between hunters and walruses in which the use of in air vision by walruses seems necessary.

Anatomical evidence

Without providing quantitative data, Von Baer (1837) and Murie (1871) note that walrus eyes are relatively small compared to those of other pinnipeds. Crile and Quiring (1940) report an eye

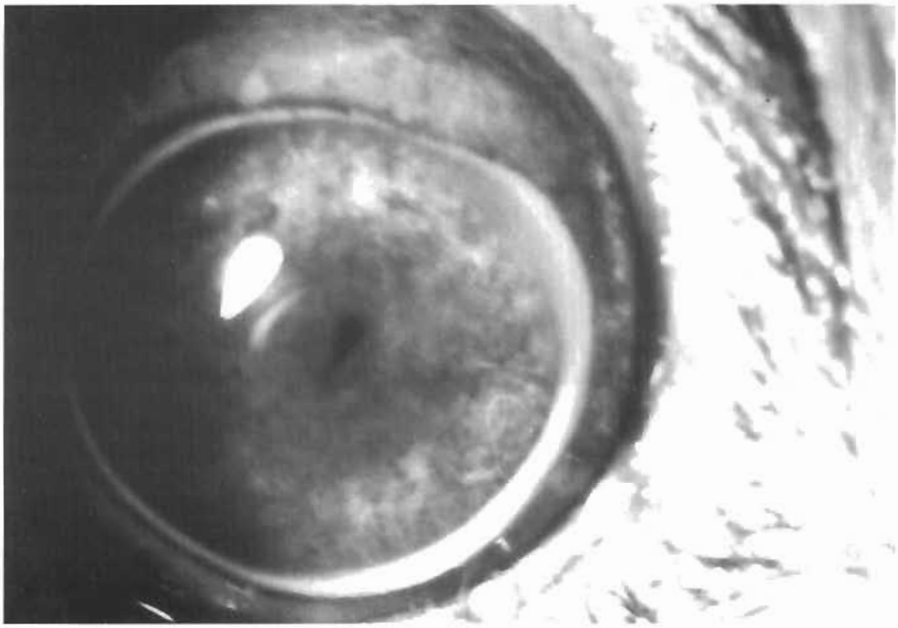
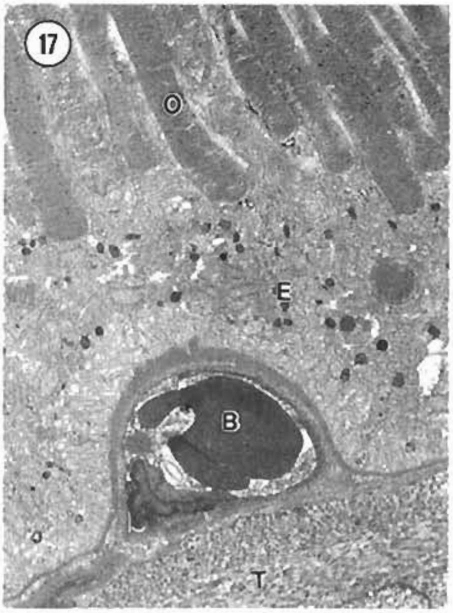
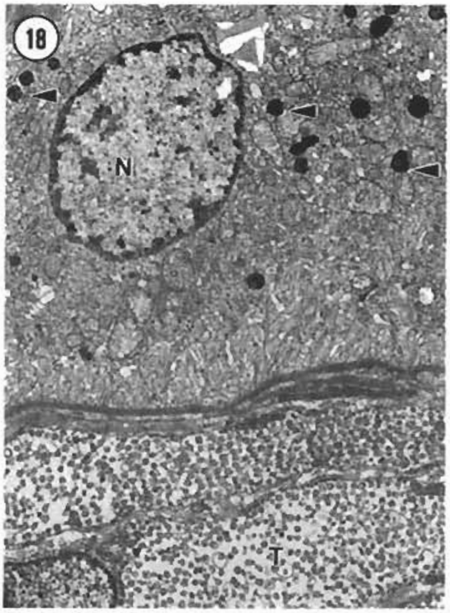


Figure 16. The pupil of an 8-year-old male Pacific walrus during exposure to around 700 lux (Photo: Ron Kastelein).





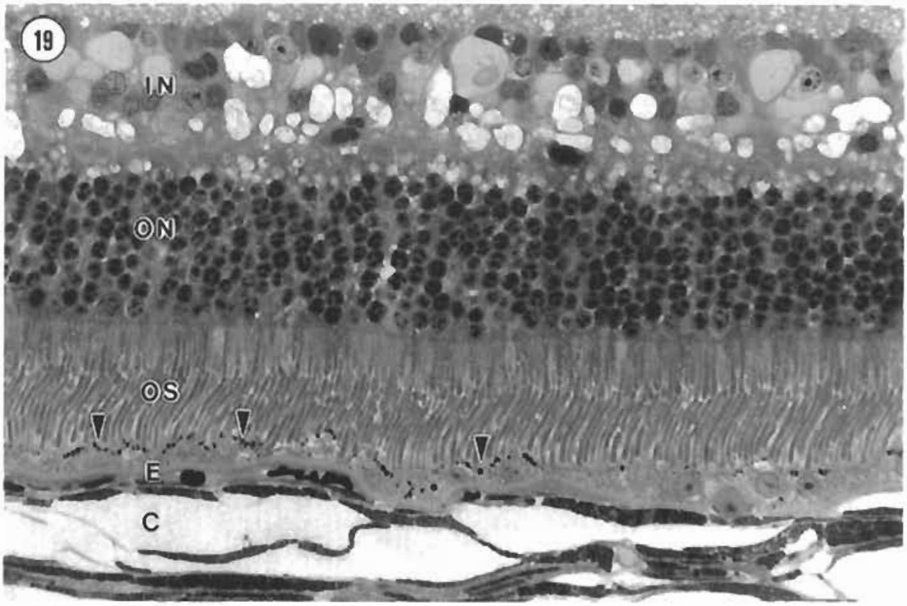
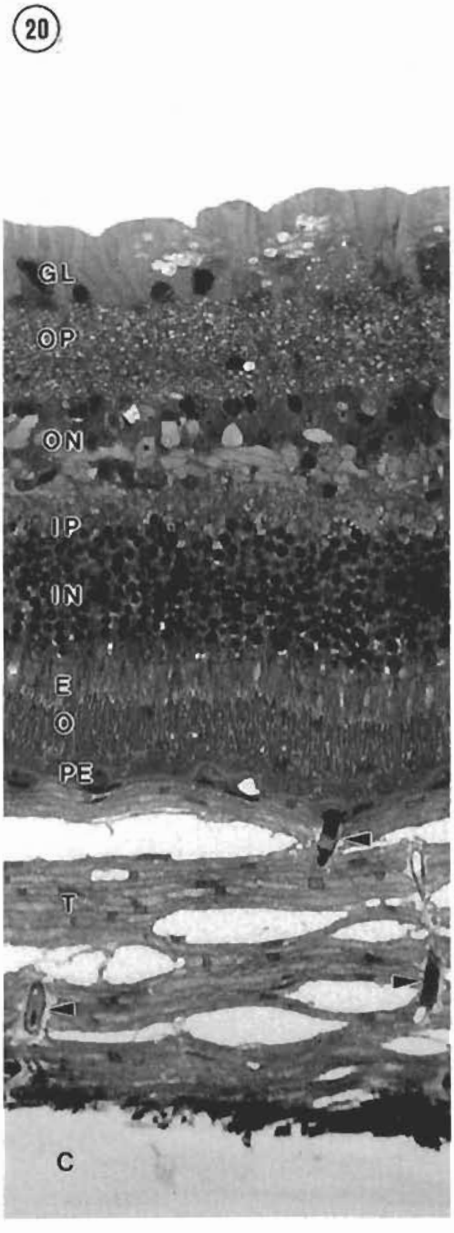
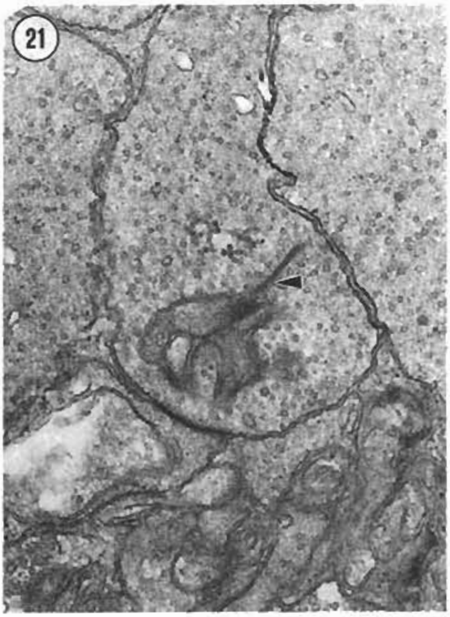


Figure 17. Retina and tapetum lucidum. The choroid is separated from the retinal pigment epithelium (E) by the tapetum lucidum (T). Small blood vessels (B) embedded in the epithelium take care of the nutrition of the pigment epithelium. O=outer segments, N=nucleus (6.700 ×, EM).

Figure 18. The retinal pigment epithelium situated at the tapetum lucidum contains very small pigment granules (arrowheads), only visible with the electron microscope. The endothelial cells of the tapetum (T) contain numerous double refracting crystals. (10.000 ×, EM).

Figure 19. Retina outside the tapetum lucidum. In the retinal pigment epithelium (E) pigment granules (arrowheads) are clearly visible at low magnifications. IN=inner nuclear layer, ON=outer nuclear layer, OS=outer segments, C=blood vessels of the choroid (550 ×, LM=light micrograph, Photos: Ruud Zweypfenning).





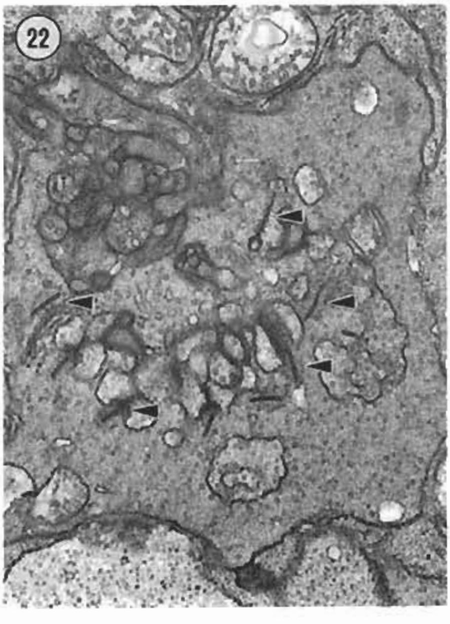


Figure 20. Overview of the retina at the *tapetum lucidum*. C=blood vessels of choroid, E=elipsoids of cones and rods, Gl=ganglion cell layer, IN=inner nuclear layer, IP=inner plexiform layer, O=outer segments of cones and rods, ON=outer nuclear layer, OP=outer plexiform layer, PE=retinal pigment epithelium, T=*tapetum lucidum* (260 × , LM).

Figure 21. Rod pedicle showing only one synaptic ribbon (arrowhead) (27.300 ×).

Figure 22. Cone pedicle showing numerous synaptic ribbons (arrowheads) (16.700 × , EM, Photos: Ruud Zweypfenning).

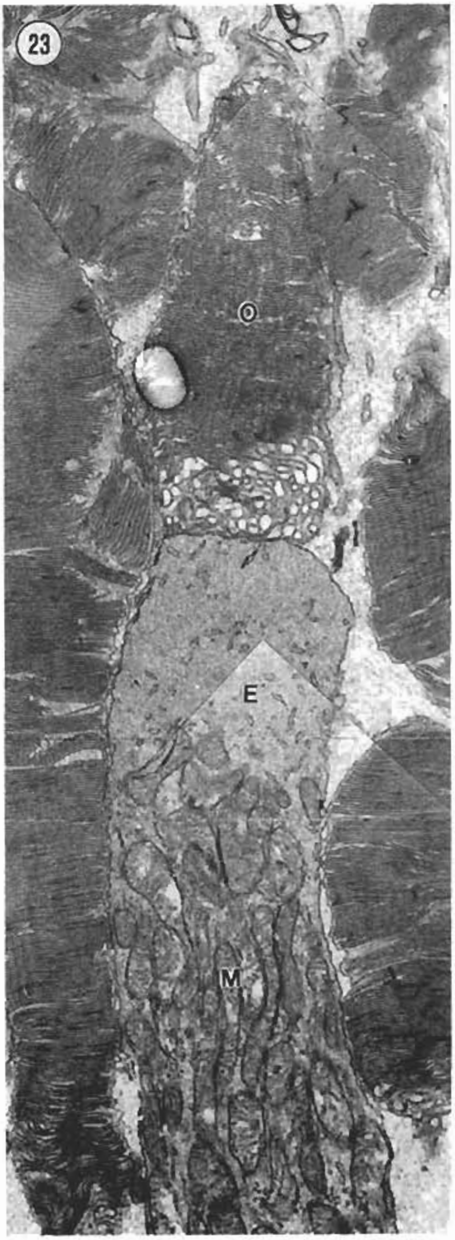


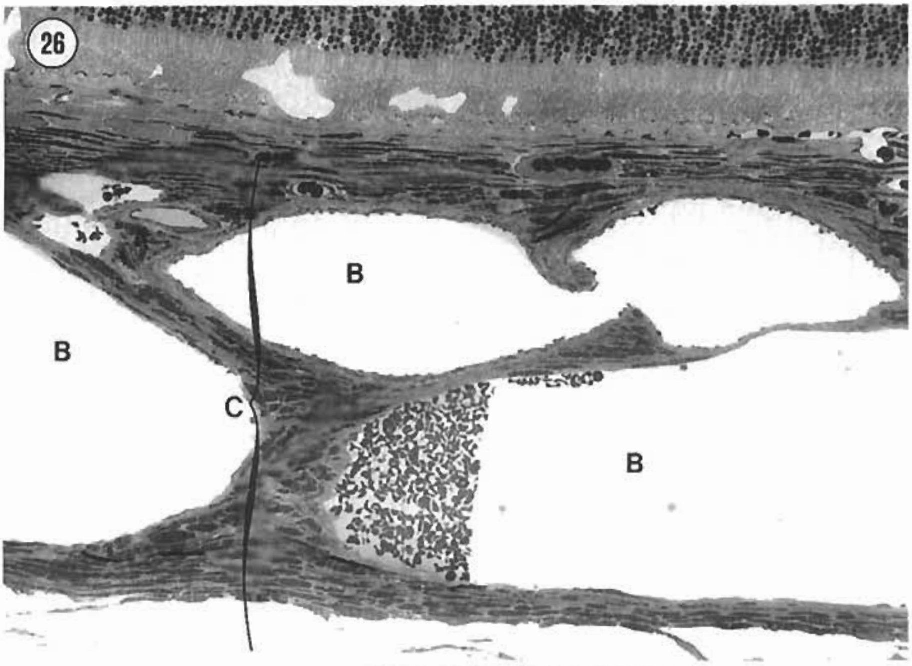
Figure 23. Outer segment (O) and elipsoid (E) of a cone receptor cell. M = mitochondria (14.400 ×, EM).

Figure 24. Outer segment (O) and elipsoid (E) of a rod receptor cell. (27.340 ×, EM).

Figure 25. Small blood vessels (B) running from the choroid to the retinal pigment epithelium in the tapetum lucidum (600 ×, LM, Photos: Ruud Zweypfenning).

weight of 6.6 g for a 56 kg 3-month-old female walrus and an eye weight of 13.3 g for a 667 kg male walrus.

In a descriptive study, Pütter (1903) compares the anatomical features of the eyes of an adult walrus with those of 4 other pinnipeds (Elephant



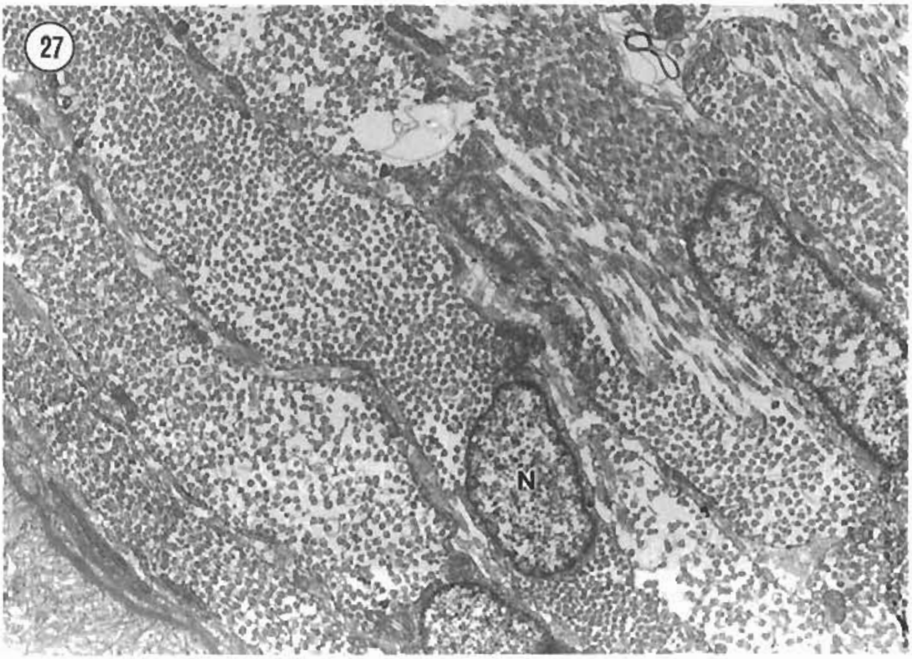


Figure 26. Low power light micrograph showing the very thick blood vessels (B) in the choroid (C) (85 × , LM).

Figure 27. Endothelial cells of the *tapetum lucidum* showing double refractive crystals. N = nucleus (6.700 × , EM, Photos: Ruud Zweypfenning).

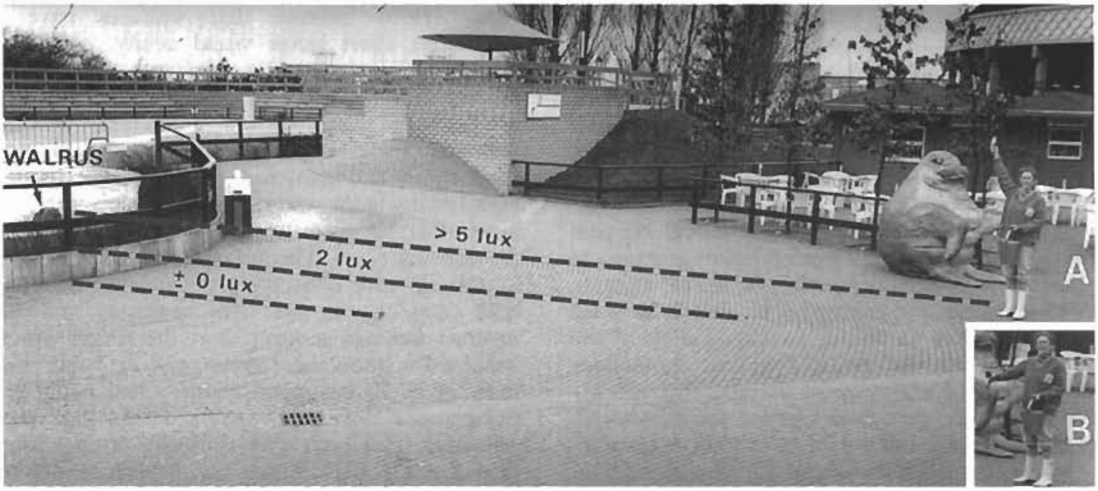


Figure 28. The distances at which an 18-year-old female Pacific walrus was able to distinguish between 2 different presentations of fish (A & B) at different light levels.

seal *Mirounga sp.*, Harbour seal *Phoca vitulina*, Bearded seal *Erignathus barbatus*, and South American sea lion *Otaria*). A summary of his findings: the walrus has the smallest eyes in relation to body length of all 5 species; the eyeball volume of an adult walrus (muscles removed) is 12 cm^3. The eyeball of the walrus deviates from a perfect sphere. The sclera is very thick. The cornea is extremely thick at its parameter and the pupil in a dead walrus is bean-shaped. The chorioidea is relatively thin, while the *tapetum lucidum* is of intermediate thickness (60 μ). Of the 5 species, the walrus has the thinnest *ligamentum pectinatum*, and the thickest blood vessel layer in the iris. The walrus has a fairly well-developed *M. tensor chorioideae*. The ciliary extensions have an unusual shape in the walrus; the distal end is not thickened and folded, but of equal thickness to the proximal end, and smooth. According to Pütter the adult walrus has the thickest retina; an outer nuclear layer of 110 μ composed of 18–20 sublayers with 722 000 nuclei of a diameter of 4 μ per mm^2 and an inner nuclear layer of 44 μ composed of 4–5 sublayers, with 82 000 nuclei of a diameter of 6 μ per mm^2. The walrus has the thickest reticular layer (30 μ) and the smallest retina surface (1790 mm^2), the lowest number of optical nerve fibres (maximum 111 000), a low number of rods (256 million) and the lowest number of nerve fibres per surface unit of retina (62/mm^2). Thus the walrus has the highest number of rods per optical nerve fibre (2300) of the above-mentioned pinnipeds.

Mass (1992) studied the ganglion cells in the walrus retina. She found that ganglion cells of the walrus vary in size from 10 to 37 μm (mean 21 μm). The mean total size of the retina from 3 adult walruses is 653 mm^2 and the total number of ganglion cells 102 000. High densities of ganglion cells were distributed as a horizontal streak, which makes the eye better adapted to panoramic vision. There is a spot of maximal cell density (1184 cells/mm^2) in the temporal part of the streak, 6–7 mm from the optic disc. Outside this spot in the streak, the ganglion cell density is less than 500 cells/mm^2. Outside the streak the ganglion cell density is less than 250 cells/mm^2. The radius of the retinal hemisphere is 12.5 mm. So the mean peak ganglion cell density is 56 cells/deg^2, 30–35° from the optic disk. This means an intercellular distance of 0.13° and the retinal resolution of 3.7 cycle/deg. The number of ganglion cells reported by Mass (1992) corresponds very well with the number of optical nerve fibres independently reported by Pütter (1903). However, the surface area of the retina described by Mass (1992) differs greatly from the 1790 mm^2 reported by Pütter (1903). Mass reports the radius of the retinal hemisphere as 12.5 mm, which would mean a surface area of about 0.5×1962 mm^2 = 981 mm^2. This is more than the 653 mm^2 she reported. On the other hand, Pütter (1903) reports a diameter of about 14 mm, and his graph shows that the retina runs until the iris. Considering the eye as a ball, the total surface area would be about 2461 mm^2. We show that the retina (containing rods and cones) stretches up to the beginning of the iris (Fig. 11). This would mean that about 34% of the circle is not covered with retina cells (836 mm^2). Thus the retina surface area would be about 2461–836 = 1624 mm^2. This figure is closer to the surface area reported by Pütter than that reported by Mass.

The pinniped eye is well-adapted for high visual acuity under water because of the almost circular lens, the increased light sensitivity due to a thick retina, and the well-developed *tapetum lucidum*. The number of cell layers in the general pinniped tapetum is considerably greater than in mammals, such as felids, which are considered to be well-adapted to night vision (Walls, 1963; Hobson, 1966). In nocturnal animals, the retinal pigment consists of few and very small pigment granules, to absorb as little light as possible. In diurnal animals, these are large and numerous to absorb as much light as possible. In diurnal animals, the blood vessels lie under the retinal pigment epithelium, among the pigment cells. In walruses they are embedded among the retinal pigment epithelium cells to make the tapetum mirror as smooth as possible.

In air, the combination of the cornea and the bulbous lens probably makes the eye strongly myoptic. However, in most pinnipeds this seems to be at least partly compensated by a reduction in the size of the pupils by the pupil reflex. When the light level increases (the usual situation when going from the water into the air), the pupil of many pinnipeds becomes a narrow slit or pinhole (Schusterman, 1972; Jamieson and Fisher, 1972; Lavigne and Ronald, 1972 & 1975; Nachtigall, 1986). The present study suggests that the same principle applies to the walrus eye. It is not clear whether the walrus can change the curvature of its lenses. The lenses observed in the present study were hard, but this could be a fixation artifact. Maybe, in addition to changing the pupil shape, the walrus can create a clear image on its retina in air by shortening the axial length of its eyeball or the curvature of the inside of the cornea by changing the pressure in its eye with the circulatory system (after death, the pressure in eyeballs quickly diminishes, which causes a decrease in the diameter of the eyes), and/or by contractions of some strong extrinsic eye muscles. These suggestions are highly speculative, but by changing the shape of the eyeball by pushing on it with a finger, many near-sighted humans can improve their vision.

The rough visual acuity test showed a very distinct maximum distance at which the walrus was able to give correct responses over a very large light level range (6000–5 Lux). The acuity (as measured with this rough technique) only decreased when the light level decreased below around 5 Lux. This rough test cannot be compared to other tests, but it showed that the visual resolving power of the walrus is less than in humans. It also indicated that the eyes of this walrus are relatively light sensitive.

Concluding remarks about visual acuity

The anecdotal information, results from the present study and the information from Pütter (1903) and Mass (1992) indicate that walruses have a reasonable short range visual acuity, and their vision seems more sensitive to moving objects in the horizontal plane. Because the retina of the walrus eye is smaller than that of most pinnipeds, and has relatively few rods per unit of surface area (and some cones) and many rods per optical nerve fibre, visual acuity in the walrus is probably lower than in most other pinnipeds (most of which usually catch fast-moving prey). The bulbous lens and the large number of rods converging towards the ganglion cells (making the eye light sensitive) and the *tapetum lucidum*, indicate that the walrus eye is suitable for underwater vision, and probably used in foraging. To investigate walrus visual acuity in a comparative way, psychophysical tests like those on other pinnipeds (Schusterman *et al.*, 1965; Schusterman, 1972; Busch and Dücker, 1987) are required. No anatomical differences were observed between the eyes of Pacific and Atlantic walruses. However, only a few samples were examined.

Colour vision

Some anecdotal information suggests that walruses can see colours. Inuit and Canadian Indians believe that a walrus will not attack a boat with a red bottom (Perry, 1967). Walrus hunters from the Thule area in Greenland believe that walruses can see hunters dressed in brightly coloured clothes sooner than when they wear less conspicuously coloured clothes (Born, pers. obs.). On Svalbard, Atlantic walruses became frightened when humans approached in bright yellow oil gear. No flight reactions were seen during similar (crawling) approaches with other coloured (i.e. red) clothes (Gjertz, pers. obs.). At Bremerhaven Zoo, 3 young walruses each learned to take food from only 1 of 3 food bowls which had the same shape but different colours (Ruempler, 1976); however, the bowls were not tested for brightness differences. The possibility that walruses use brightness cues to distinguish between objects cannot be excluded; Lamont (1861) reports that the boats used for hunting walruses are always painted white outside to simulate ice.

Our results show that at least 2 anatomically different light receptors exist in the retina of the walrus. This indicates that the walrus can probably see colours. Two types of light receptor cells (1 of which might have cone properties) are also found in the retina of the Harp seal (*Pagophilus groenlandicus*) (Nagy and Ronald, 1975) and the Harbour seal (*Phoca vitulina*) (Wartzok, 1979). Which colours walruses can distinguish is still to be tested in experiments like those done on other pinnipeds (Warzok and McCormick, 1978; Busch and Dücker, 1987; Bernholz and Matthews, 1975;

Lavigne and Ronald, 1972; Griebel and Schmid, 1992).

Visual field and stereoscopic vision

Several authors describe walrus eyes as small, but prominent, and sometimes as protruding from their sockets. The position of the eyes near the top of the head and their great mobility probably give the animals a good range of vision (Von Baer, 1837; Murie, 1871; Elliot, 1875; Vaigachev, 1958; Pedersen, 1962; Perry, 1967). The present study shows that this is in part due to the absence of the supra-orbital processes, and the presence of large extrinsic eye muscles. Purely based on his anatomical investigations on the extrinsic eye muscles, Pütter (1903) also concluded that the walrus can move its eyes more than other pinnipeds. His conclusion is confirmed by the present study. Egede (1741) suggested that the great mobility of the eyes has something to do with the size of the neck: "the neck of the walrus is so extremely thick, that he cannot easily look around it; therefore he turns his eyes in his head, when he wants to see something". Several observations indicate that walruses have binocular vision, the basic requirement for stereoscopic vision. The mobility of the eyes, and the capability to protrude them, increase the monocular visual field.

The wide visual field created by rolling the eyes can be used when walruses are hauled out on land; they often lie on top of each other, up-side down, and sometimes sink their tusks nearly to the base into the gravel (Bel'kovich and Yablokov, 1961; Kastelein, pers. obs.). In these conditions the walruses are often very immobile, and it would cost a lot of energy, and disturb many animals, to turn the entire body or neck to investigate the surroundings. The walrus is able to see much of what is happening around it by simply rolling its eyes.

If simply the rolling of eyes does not suffice in certain circumstances, the walrus can extend its range of vision by flexing its neck. Lamont (1861) describes head movements of walruses; "they can turn their necks with great facility and quickness, and can strike either upwards, downwards or sideways, with equal dexterity". When alarmed and excited, walruses sometimes stretch their necks to look around them (Sokolowsky, 1908), and sometimes even raise themselves out of the water, and swing their heads from side to side (Pedersen, 1962; Perry, 1967).

Fay (1985) states that walrus eyes are placed laterally, and provide limited binocular vision. However, when attentive or excited, walruses protrude their eyeballs (Loughrey, 1959) which enlarges the visual field. When the eyes are then rolled forward or dorsally, binocular vision is possible. When approaching an object closely, walruses usually try to touch it with their mystical vibrissae. This is necessary because they cannot see objects that are within 30 cm in front of their mouth due to the size of the mystacial pads (Kastelein, pers. obs.). At the Harderwijk Marine Mammal Park, Pacific walrus OrZH002 always attempts to look a person straight in the eyes when he is within 2 m in front of the animal. Examining one eye of this animal is impossible, since she always turns her head to see the observer using binocular vision. Binocular vision does not automatically mean stereoscopic vision. In order to have stereoscopic vision, the information received by each eye has to be integrated by the brain. The information of each eye can be distributed over the brain hemispheres by partial crossing of the optic nerves, by decussations within the brain or by a combination of these two possibilities. Whether the optic nerves cross completely or partially in the walrus has not been investigated. The walrus probably has both monocular and stereoscopic vision.

Protection of the eyes

A. Eye lid

Most seals have superciliary vibrissae which probably serve as levers pushing against mechanoreceptors housed in a follicle. Sokolowsky (1908) reports that the walrus has a small fold above each eye with a short, but fairly thick, sinus hair. Fay (in Miller, 1975*b*) observed 1 to 3 superciliary vibrissae per eye which were up to 10 mm long. These were found especially in foetuses and young calves, and disappeared later in life, perhaps by breakage. We observed that there is great individual variation in the presence and size of the superciliary vibrissae. However, they are scarcer, and if present, much shorter than in phocids and otariids, indicating a less important, or other, function of these vibrissae in walruses.

The eyes have to be protected when walruses are lying or moving on top of each other, or when they are fighting (Bel'kovich and Yablokov, 1961; Miller, 1976). Bel'kovich and Yablokov (1961) saw a walrus with a large bruise around the eye. Eyes are also sensitive to small particles. Gray (1939) reports that the best defence against enraged walruses is sea sand, which is thrown into their eyes, and causes temporary blindness. Schmidt (1885) noted that the walrus eyes have heavy eyelids, which are surrounded by deep ring-shaped folds of skin. The present study shows that the eyelids can be closed tightly by the strong *M. orbicularis oculi*, and thus may serve as a protective barrier against U.V. light, cooling, objects or chemicals.

In addition to the external eyelids, the eye is protected by a broad, thin *membrana nicticans* (Owen, 1853). Allen (1880) describes an Atlantic walrus embryo which was 4 cm long and had its eyes closed. The palpebral fissure (opening between the eyelids), was directed obliquely upward and forward. Pütter (1903) and the present study show that the *membrana nicticans* of adult walruses has a similar shape. It may act to wipe particles off the cornea while the eyelids remain open. However, this has never been observed at the Harderwijk park, so that the membrane may act mainly to close the eye off from the environment fully, when the eyelids are tightly closed. The *membrana nicticans* was clearly visible in an adult male Atlantic walrus which was anaesthetized with etorphine HCl. It ran obliquely from rostal-dorsal to ventral-caudal between the eyelids, and moved in the dorso-caudal direction when the eyelids were touched with a finger. The eyelids themselves closed slowly (Kastelein, pers. obs.). Possibly this is an eyelid closure reflex.

B. Eye glands

Owen (1853) and Pütter (1903) describe a small Harderian gland, but no *ductus nasolacrimalis* in walruses. These findings are confirmed by the present study. After a walrus has been hauled out for a few days, its eyes swim in mucus (Arsen'ev, 1927). The mucus prevents the cornea from drying out, and protects the eye from particles (under water or in air), chemicals (under water) and infections.

C. Blood vessels in the conjunctiva and choroid

Von Baer (1837) and Murie (1868 & 1871) noticed bloodshot eyes on dead walruses that they examined, and thought at first that the redness of the conjunctival membrane was due to pathological conditions. Von Baer (1835) noted bloodshot eyes in a young walrus and thought this phenomenon was due to a cold caught during transport. However, bloodshot eyes were later documented by observers in the field (Lamont, 1861). Allan (1880) also noticed red eyes in the Atlantic walrus and speculated that this phenomenon did not occur in the Pacific walrus, because Elliot (1875) describes their sclerotic coats as yellow or brown with some white, and the iris as light brown with dark rays and spots. Hills (1990) observed red eyes in most wild Pacific walruses. This contradiction with Elliot's work probably indicates that the redness is temporary, due to environmental conditions, or due to the behaviour of the animals. Red eyes are not only related to stress during or immediately after diving, because Pedersen (1962) and Kastelein (pers. obs.) noted bloodshot eyes after Atlantic walruses in the wild had been asleep for a long time. The colour of the sclera of Pacific walruses at the Harderwijk park varies between red and white (Kastelein, pers. obs.). The factors which influence it are unknown. Maybe the redness is a reaction to sunlight, temperature, and/or physical damage.

The blood vessels in the conjunctiva could have 1 or several of the following functions: (1) Repair of damage to the sclera, (2) Prevention of eye infections, and (3) Prevention of cooling of the eyeball when the walrus is under water. Water conducts heat 25 times better than air, and according to Perry (1967), Tomilin and Kibal'chich (1975) and Fay *et al.* (1984), walruses can stay under water for as long as 10 min. Born and Knutsen (1990) report an average dive time of 5.5 min, a maximum dive time of 38 min and, during foraging, a walrus can spend around 50 minutes out of 1 hour underwater. In addition, walruses expose their eyes to very low temperatures (maybe as low as − 50°C) when they surface during winter. The other Arctic seals, ringed seals (*Phoca hispida*) and bearded seals, that spend the winter at high latitudes, keep breathing holes open in the dense ice cover. These holes are covered by a layer of snow. Hence, during breathing the animals do not become directly exposed to the severe low air temperatures. Walruses do not keep open such breathing holes, and during winter they expose their head and eyes to low temperatures.

The choroid of the walrus seems too thick to function only in retaining homeostasis in the retina cells. It probably also plays an important role in thermoregulation. Possibly these thermoregulatory adaptations in walrus eyes are necessary because the eyes of this species protrude much, making them lose more heat to the water through conduction.

D. Tissues around the eyes

The walrus' orbital perimeter is enclosed for two-thirds of its circumference by bony structures. In other pinnipeds, the dorsal side of the orbital perimeter consists of a small supra orbital process. Possibly as a way to compensate for the lack of a protective bony structure in the dorsal direction, the walrus can retract its eyes deep into the orbital cavity (Fig. 1). This protects the eyes from physical threats (such as tusks). When touching the eyelids of a 15-year-old male Atlantic walrus which was anaesthetized with etorphine HCl with a finger, the eye (which was not protruded) was quickly retracted 2 cm into the orbital cavity, then covered with the *membrana nicticans*, and finally slowly closed off from the environment by the eyelids (Kastelein pers. obs.). The fat-rich connective tissue, extrinsic eye muscles, and the Harderian gland seem to function as a protective cushion between the eyeball and the cranial bones when pressure increases during diving. The tissues surrounding the eye in the orbital cavity may also protect the eyes from hypothermia. Blood-vessels supply the eye with warm blood from the core of the body, while the fat-rich connective tissue functions as an insulator. The fact that the walrus eye is so small might be due to thermoregulatory stress, since the eyes are protruded more during usage than in other pinnipeds. Pütter (1903) points out that the energy of muscles is only partly transformed to mechanical performance, while a significant portion is transformed into heat. He suggests therefore that the well-developed extrinsic eye muscles in the walrus may play some role in the thermoregulation of the eyes.

Importance of vision in walrus ecology

A. Social interactions

In social interactions between walruses, vision seems to play an important role. The size of the male walrus and his tusks are important physical parameters in social interactions. Adult males with a large size difference do not fight; a ritualized visual display with the tusks and the vibrissae suffices. Adult male walruses can be recognized visually not only by the size of their body and tusks, but also by the development of knobs on the skin of their neck (Krylov *et al.*, 1964; Krylov, 1967). In female threat interactions, the tusks are also important (Miller, 1975*a*, 1976 & 1982; Krusinkaja and Lisicyna, 1983). To estimate the distance to the tusks of other walruses (Fig. 29A), but also during agonistic encounters in which walruses stab each other with their tusks (Fig. 29B), stereoscopic vision could be beneficial. The mystacial whiskers and movements of the lips and eyes are used to indicate a variety of emotions (Miller, 1975*b*; Kastelein *et al.*, 1991*a*). These short distance social optical signals require good short range visual acuity in air. Lamont's description (1861) suggests that walruses can recognize other individuals from their heads only, and that this information influences their behaviour. Lamont (1861) and Fay *et al.* (1984) report simultaneous surfacing of walruses after diving. This probably requires visual and/or acoustical contact between the animals under water. Colour vision in walruses could have a social function since walruses vary in colour depending on age and sex (Fay, 1982).

Vision probably also plays an important role in mother-pup interactions. Young calves only follow moving objects (Kibal'chich and Lisitsina, 1979). On land it is important for the mother and pup to estimate the distance between each other and between them and other mature walruses, so that the pup does not get crushed. In case of danger, the mother always shelters her young with her body (Bel'kovich and Yablokov, 1961). To estimate distance, stereoscopic vision could be used (Fig. 29C). The walrus mother may rely on vision to protect her pup against predators, as seen in Lamont's (1861) description of a harpooning: the walrus cow seemed to watch the direction of a harpoon and interposed her own body between the hunter and her calf.

Walruses show a strong tendency to support wounded individuals in the water, and to push them to the surface. They even lift up the head of the animal in distress which tends to sink into the water due to the weight of the tusks, so that the animal can breathe (Tomilin and Kibal'chich, 1975). This rescue behaviour may require the use of underwater vision. Nikulin (1941) describes a walrus which saw a dead walrus on an ice floe, swam to it and, in an attempt to help it, pulled it into the water with its tusks.

B. Navigation and selection of haulout areas

Walruses probably use vision for navigation. In northeastern Greenland, walruses were observed when returning from feeding excursions which usually lasted several days. In many cases the walruses were swimming fast for several km in a straight line toward their terrestrial haul out site (Born, pers. obs.). These animals probably used visual cues such as land contours and/or sun position for navigation. Before hauling out, walruses approach land cautiously and swim near the shore for a few hours, while watching the land by rising a little from the water (Krylov *et al.*, 1964). Tomilin and Kibal'chich (1975) noticed that when walruses saw movements of a man or a dog on the shore, they dove at once. Pedersen (1962), however, describes walruses coming close to his camp to watch activities on the beach, such as the movements of the dogs, and Popov (1958) reports of walruses that swam close to shore to look with curiosity at a campfire. Collins (1940) describes walruses patrolling the edge of the ice where hunters had hauled out for safety after they had attacked walruses. Walruses select particular sizes of ice floes to haul out on (Fay, 1974), and seem to prefer large ice floes of multi-year ice which have no cracks or water holes (Bel'kovich and Yablokov, 1961). They also choose the correct side of the floe to haul out on, so that it does not tip over (Tomilin and Kibal'chich, 1975). All these observations require visual inspection of their environment. When hauling out, adult walruses try to find a place in the middle of the herd (Krusinkaja and Lisicyna, 1983). This would require the use of vision.

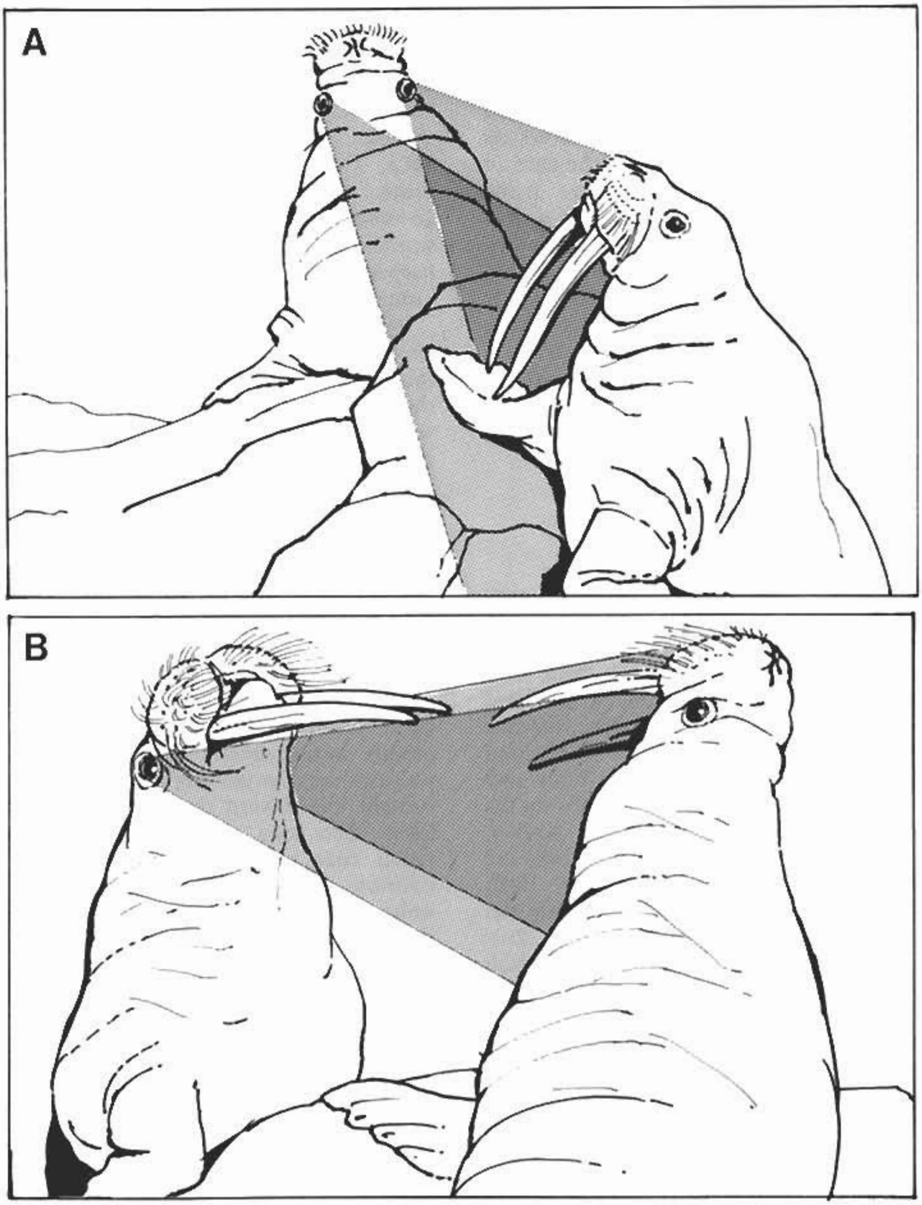


Figure 29A, B.

C. Detection of predators

In a group of sleeping walruses, often some are awake. On the approach of danger, these animals will rouse those next to them, making the whole herd alert (Brown, 1868). When excited, both young and adult walruses stretch their necks to look around (Kane in Allan, 1880; Sokolowsky, 1908; Bel'kovich and Yablokov, 1961), and usually inhale through their nose, apparently to catch a smell (Born, pers. obs., and Kastelein, pers. obs.). If a herd of walruses on land is approached upwind to within about 20 m, the animals farthest from the water, usually old bulls, are the first to perceive the intruder. They rise up, in alert or threatening postures, with their eyeballs protruding and nostrils distended. They swing their heads from side to side, apparently to obtain a better view and/or scent of the approaching object. After a retreat into the water, they raise the upper half of their bodies out of the water, again apparently to obtain a better

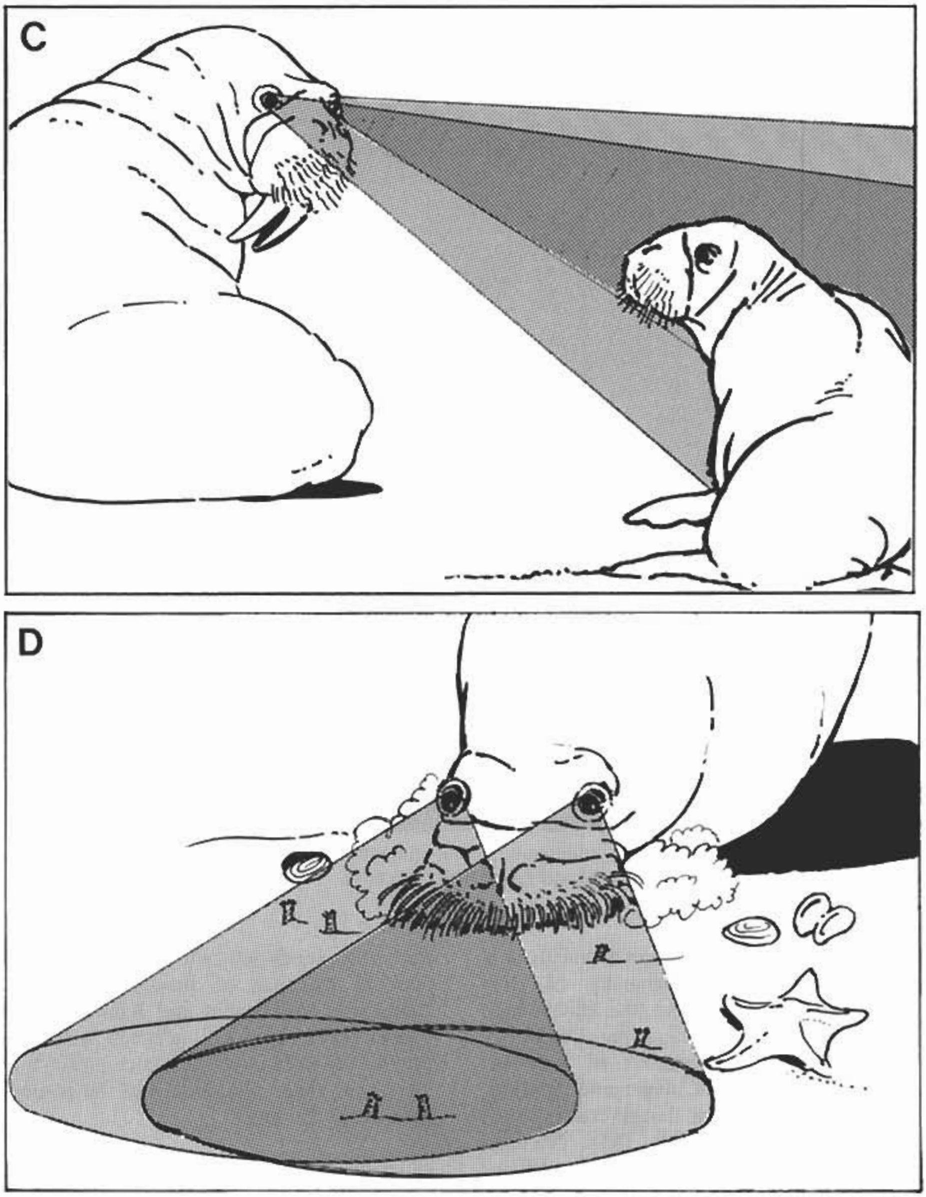


Figure 29C, D.

Figure 29. The estimated visual field of each walrus eye in 4 situations: (A) Looking rearward on land, (B) While threatening or fighting on land, (C) Looking forward on land, and (D) Digging for food in the ocean floor. Note the overlap of the cones, which is the suggested area of stereoscopic vision, and thus the area in which the walrus can estimate distances accurately (Drawings: Rijkent Vleeshouwer).

view and/or scent of the object which made them leave (Loughrey, 1959). Walruses can also be attracted optically; Pavlikov (1966) describes walruses that left the shore to approach and (possibly visually) examine a ship.

According to the Inuit people, the walrus keeps its eyes closed while breathing loudly for 3 minutes after a deep dive and opens them for a final look around before diving again. The eskimos take advantage of this when hunting walruses from the

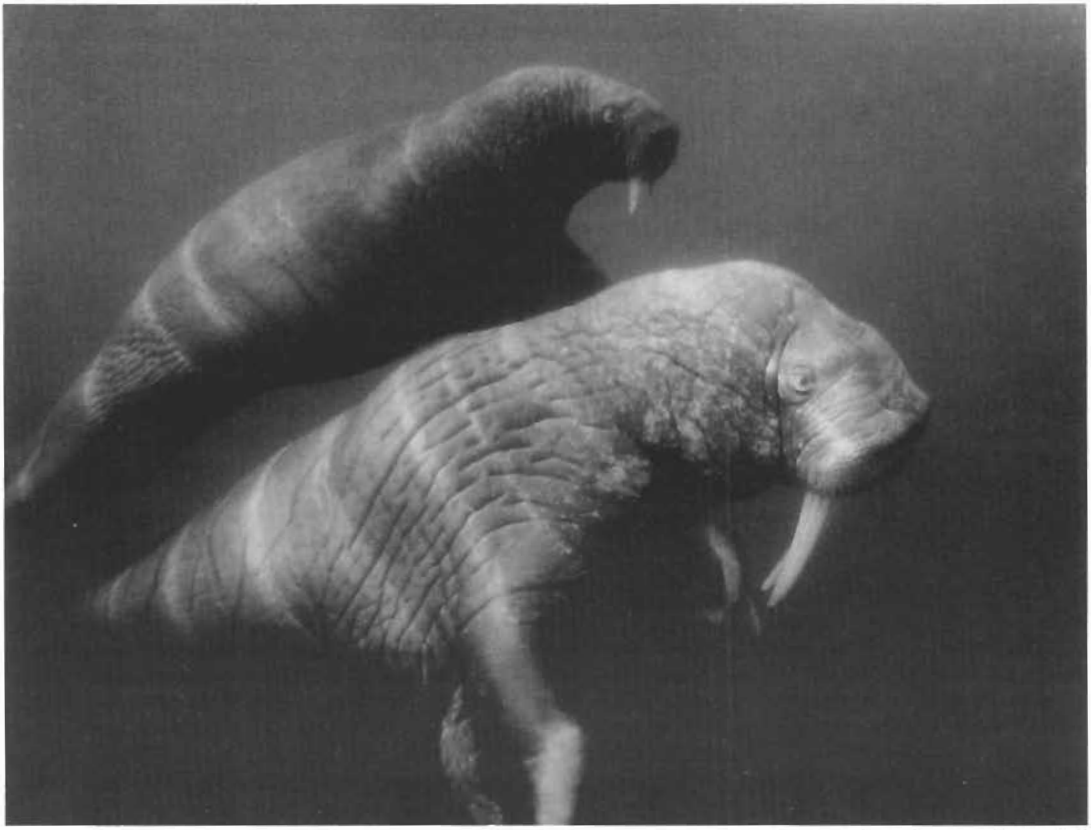


Figure 30. Two Pacific walruses swimming underwater. Note the eyes which are rolled so that they can be used for forward vision (Photo: Bill Curtsinger (c) National Geographic Society).

ice, remaining motionless only when the walrus is surfacing and when it is preparing to dive (Loughrey, 1959). Apart from man, the killer whale (*Orcinus orca*) and polar bear (*Ursus maritimus*) are the two most important predators of walruses (Collins, 1940; Gjertz, 1990; Calvert and Stirling, 1990). The polar bear can be dangerous to both calves and adult animals (Popov, 1958; Nikulin, 1941). The horizontal streak of high density ganglion cells in the retina of the eye may aid in scanning the horizon. This could be used to spot approaching polar bears. Whether colour vision in the walrus is used to detect its predators is not clear. The killer whale has no colours, but large black and white contrasting surface areas, while the polar bear is yellowish.

A stampede reaction of walruses hauled out on land has been observed in response to the sound of low flying aircraft, especially if the herd was approached downwind. In contrast, a stampede reaction evoked by a sight warning stimulus only, was never observed by Loughrey (1959). His observations, and those of Müller (1911), suggest that walruses depend more on hearing and smell to provide warning of predators than on vision. According to Tomilin and Kibal'chich (1975) and Gjertz (pers. comm.) walruses are very afraid of any movements overhead, such as birds flying over. However, these reactions may be responses to the sounds of the birds.

D. Foraging

The molluscs that the walrus usually feeds on are buried in several centimeters of mud and gravel, but the mollusc siphons protrude above the surface. In feeding, the walrus dives to the bottom and probably assumes an inverted vertical position or 'headstand'. The walrus probably ploughs with its nose through the bottom using a forward thrusting motion of the head (Loughrey, 1959; Fay, 1982). The absence of supraorbital processes allows the walrus a visual field in the dorsal direction, which could be useful when ploughing through the substrate in this position (Figs. 4 & 29D). The absence of supraorbital processes is a primitive feature in pinnipeds. Large processes only evolved in Otariidae, whose eyes are always pointed forwards (Barnes, 1989). The horizontal high density streak of ganglion cells may aid in scanning the ocean floor just in front of a ploughing walrus.

Kastelein and Mosterd (1989) describe how, in a 4 m deep pool with clear water, walruses excavated molluscs from a sand substrate with their eyes open. When exploring concrete pool floors with their vibrissae, walruses also keep their eyes open (Fay, 1982, Fig. 102; Kastelein and Wiepkema, 1989), and they have been observed swimming with their eyes open in the wild (Fig. 30; Ray, 1979). Walruses find their food at a maximal depth of 100 m (Fay, 1982). In the daytime, there should be enough light at this depth for an animal with a well-developed *tapetum lucidum* and a thick retina in which many rods converge to few ganglion cells, to see clam beds or individual siphons. Born and Knutsen (1990) describe walruses feeding in daylight. The animals progressed slowly, breathing at 5–6 min intervals and moving in an unidirectional manner which does seem to require underwater orientation. How long the turbidity (which influences vision), which is created during excavations of clams, lasts and how far it extends, depends on the sediment and water current.

In spite of this possible use of vision in foraging, walruses do often forage at night when ambient light levels are low (Fay, 1982; Born and Knutsen, 1990). Whether the well-developed *tapetum lucidum* and a thick retina make the walrus eye sensitive enough to be useful during nocturnal foraging is unknown. Whether colour vision has a function in prey selection is not clear as well. Straight furrows 47 m in length made in the ocean floor by walruses (Nelson and Johnson, 1987) indicate that at least in some cases (maybe only at night or in deep or murky water) walruses do not rely upon vision, but simply plough in a fairly straight line and eat any prey that they come across. Even when a walrus detects a clam visually, he probably excavates it by water jetting (Kastelein and Mosterd, 1989; Kastelein *et al.*, 1991*a*). This action makes the surrounding water murky, and so decreases the usefulness of vision for detecting and identifying further objects in the nearby surroundings. In addition, when a walrus gets nearer than 30 cm to an object, it can no longer use its eyes in the forward direction to see it. In these conditions the walrus probably identifies and manipulates a potential prey object with its sensitive vibrissae (Fay, 1982; Kastelein and van Gaalen, 1988; Kastelein *et al.*, 1990).

Walruses occasionally hunt seals (Collins, 1940; Breshin, 1958; Perry, 1967; Lowry and Fay, 1984; Fay *et al.*, 1990; Timoshenko and Popov, 1990), may eat odontocetes (Gray, 1939) and occasionally catch birds (Fay, *et al.*, 1990). In such situations, walruses probably use their eyes for the detection and during pursuit of their prey.

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