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The anatomy of the walrus head (*Odobenus rosmarus*). Part 4: The ears and their function in aerial and underwater hearing

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Summary

Walrus ears have special features which are not found in the ears of most terrestrial carnivores. These are: the lack of pinnae, the long, tubular outer ear of which the lateral side is covered with fat and skin, the ability to open and close the external meatal orifice by auricular muscles, the lining of the cartilaginous and bony parts of the outer ear canal by vascularized tissue, the copious amount of earwax, the large middle ear cavity, the lining of the middle ear cavity by vascularized tissue, the elastic fibres, collagen tissue and cartilaginous rods in the wall of the Eustachian tube, and the dense bones surrounding the base of the outer ear and the entire middle and inner ears.

When the ambient pressure increases during diving, the pressure increases in the entire body including the organs and the blood vessels. The pressure in non-collapsible spaces with strong casings can be regulated in two ways: (1) by being in contact with collapsible spaces or (2) by being lined with vascularized mucosa which can contain a varying amount of blood. In the walrus, pressure equilibration between the outer and middle ear likely occurs in both ways. The middle ear cavity is in contact with the respiratory tract via the Eustachian tube and the bony part of the outer ear canal is in contact with the cartilaginous part of the outer ear canal. The middle ear cavity and the outer ear canal are lined with vascularized mucosa.

In air, sound waves probably reach the walrus' tympanic membrane in the same way as they do in terrestrial mammals. Under water, due to large impedance differences between water and the cranial bones, sounds may be reflected off the bones which surround the middle ear. The impedance difference between water and the soft tissues is less, so sound travels most easily through these tissues (cartilage, skin, fat and muscles) to the outer ear canal. The cartilaginous tubular outer ear with its vascular lining is probably the main pathway by which sound is conducted to the tympanic membrane under water. The vascularized mucosa lining the middle ear may alter the resonance of the middle ear cavity, and when inflated during diving, rigidify the ossicle chain and improve the conduction of high frequency sounds.

Introduction

Walruses (*Odobenus rosmarus*) are vocal pinnipeds. A variety of walrus vocalizations have been described (Schevill *et al.*, 1966; Ray & Watkins, 1975; Miller & Boness, 1983; Miller, 1985; Stirling *et al.*, 1987; Verboom & Kastelein, 1995; Kastelein *et al.*, 1995), but their function in walrus ecology is not yet fully understood.

The level of man-made noise in the distribution areas of walruses is steadily increasing. To determine the impact of such noise on walruses, it is necessary to determine whether they can hear it. Two studies have been done on the aerial hearing sensitivity of walruses. The first was done on wild walruses with a broadband ambient noise level of 45 ± 3 dB(A) re 20 μPa (Kastelein *et al.*, 1993*b*). The second study was done with a trained walrus in an environment with a background noise level of 52 ± 4 dB(A) re 20 μPa (Kastelein *et al.*, 1996). The data suggest that the thresholds derived in both studies were masked thresholds.

How walruses can hear both in air and under water is not fully understood. The morphology and anatomy of the hearing organs of walruses have been studied previously. Laet (1633) and Elliot (1875) describe the outer ears as simple openings in the skin. Schmidt (1885) notes that the outer ear ends as a small closable opening surrounded by a circular fold. Murie (1870 and 1871) describes a cartilaginous tube and three auricular muscles, which he considered to be large for an animal without pinnae. He thought the auricular muscles moved the distal part of the meatus. Allen (1880) describes the outer ear canal of a 4 cm long Atlantic walrus embryo as a membranous fold on the head. Doran (1878) describes the ossicles. Repenning (1972) describes the middle ear in detail, and Wyss (1987) describes the auditory region, with emphasis on the middle ear and the shape of the ossicles.

The aim of the present study was to describe the anatomy of the walrus' outer and middle ears and discuss their function in aerial and underwater hearing. The study is Part 4 of a larger investigation of the anatomy of the walrus head. Part 1 describes the cranial bones in relation to feeding and hauling out (Kastelein & Gerrits, 1990), Part 2 describes the head muscles and their function in feeding and other behaviour (Kastelein *et al*, 1991) and Part 3 describes the eyes and their function in walrus ecology (Kastelein *et al.*, 1993*a*).

Materials and methods

Study animals

The ears of seven walruses were studied.

W1. To study gross morphology, the head of an approximately 8-year-old female Atlantic walrus (*Odobenus rosmarus rosmarus*, KFHB#19) was used. The head was obtained from Inuit subsistence hunters in the Hudson Bay area, Canada, in June 1988, frozen immediately after death, and kept frozen during shipment. To investigate the location of the outer and middle ears in relation to other head tissues, the frozen head 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. Each slice was washed, photographed from both sides against a 2 cm grid background and stored in fixative (2 phenoxy ethanol, 1% solution).

W2. To study details of the outer and middle ears, the head of an approximately 8-year-old female Atlantic walrus (KFHB#20) was used. The head was obtained from Inuit subsistence hunters in the Hudson Bay area, Canada, in June 1988, frozen immediately after death, and kept frozen during shipment. The frozen head was cut mid-sagitally, and put into fixative (2 phenoxy ethanol, 1% solution). After fixation, tissue layers were removed so that the outer ear canal and the auricular muscles could be photographed and drawn. The *bulla tympanica* were removed with a dentist's drill, to expose the middle ear. Photographs and notes were taken during the tissue removal process.

W3. To investigate the gross anatomy of the outer and middle ears, the ears of a 15-year-old male Pacific walrus (*Odobenus rosmarus divergens*, OrZH001) which lived for 14.5 years at the Harderwijk Marine Mammal Park, were used. These were put into fixative (2 phenoxy ethanol, 1% solution) 30 h after death.

W4. To investigate the gross anatomy of the outer and middle ear, the ears of a 2-year-old male Pacific walrus (OrZH010) which lived for 1.5 years at the Harderwijk Marine Mammal Park were also used. These were put in fixative (10% formalin) 5 h after death.

W5. Photographs were taken from the lateral, dorsal and ventral sides of the skull of a 5-year-old male Pacific walrus (OrZH005), which had lived for 5 years at the Harderwijk Marine Mammal Park.

W6 and W7. For histological investigation, the outer ear canals from 2 male Pacific walruses (A1758, estimated age 15–20 years and A1759, age over 25 years) were used. The walruses died of natural causes near Cape Pierce, Alaska, between August and September 1990. The outer ear tubes were dissected several hours after death and stored in 10% formalin. The quality of the material was less than optimal due to the late preservation of the tissues. The outer ear canals were cut on a Reichert slicing sledge microtome into 40 μm frozen sections. These cross sections were stained by either the Van Giesson technique (Bradbury & Gordon, 1990) for connective tissue, Weigert's resorcin fuchsin method for elastic fibres (with Van Giesson as counter-stain; Bradbury & Gordon, 1990) or the Azan stain for connective tissue (Burck, 1982).

Results

Auditory meatal orifice

Walruses lack pinnae; the external ear opening (*Porus acusticus externus*) is a small hole a few millimetres in diameter. The orifice of the auditory meatus is located a few centimetres below the plane through the nostrils and the eyes (Fig. 1).

Outer ear canal

The following description is based on an 8-year-old female Atlantic walrus (W2) and of an 15-year-old male Pacific walrus (W3); animals of different gender, age and subspecies. Further on, the measurements of W3 are given in square brackets after the measurements of W2. No major differences in anatomy were found between the animals, other than size.

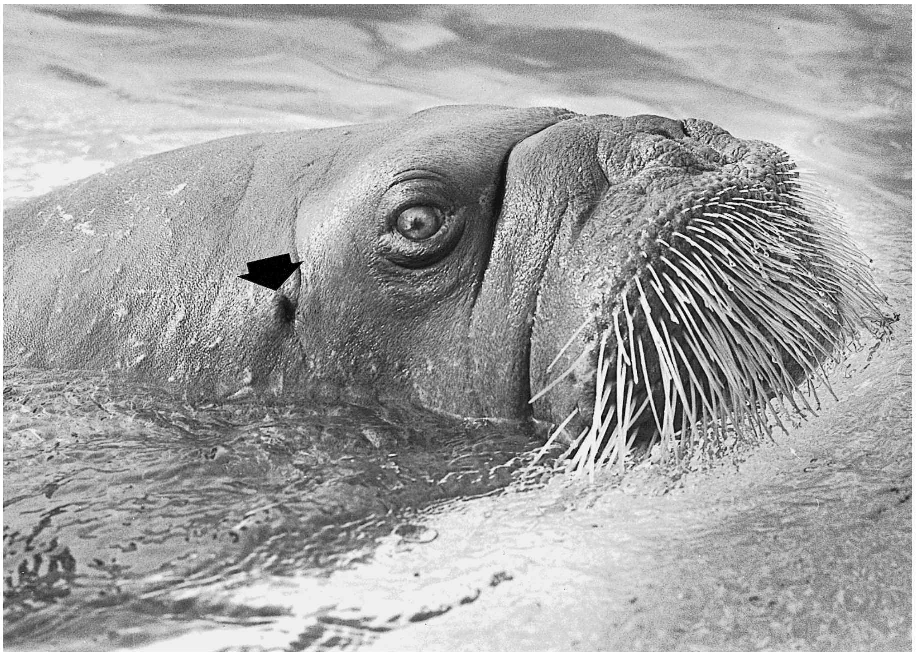


Figure 1. Lateral view of a 15-year-old female Pacific walrus (OrZH002). When the animal swims at the surface, the external meatal orifice (indicated by the arrow), the eyes, the nares and most of the mystacial vibrissae are above the water (Photo: Henk Merjenburgh).

The outer ear tube (*meatus acusticus externus*) consists of a 15 cm long canal with two perpendicular flexures that make it roughly S-shaped (Fig. 2). The proximal 3 cm consists of the funnel-shaped bony auditory canal (*meatus acusticus externus osseus*) formed by the squamosal bone and the *bulla tympanica*. The rest of the outer ear tube is cartilaginous (*meatus acusticus externus cartilagineus*). The cartilaginous tube enters the funnel-shaped bony canal between the squamosal bone and the *bulla* and ends 10 mm [28 mm] in front of the tympanic membrane (Fig. 7A). In a recently deceased (still warm) animal the proximal end of the cartilaginous canal was only loosely connected to the bone. The first flexure occurs where it leaves the bone. From there it runs in the rostro-dorsal direction at an approximately 60 degree angle to the length axis of the skull (Figs. 2 and 3B). The distal part, which is about 2 cm long, curves laterally towards the external orifice (Figs. 2 and 3B). The cartilaginous part of the outer ear tube is covered with a 15–30 mm thick adipose layer and a 17–20 mm thick cutaneous layer (Fig. 3B and C).

The outer ear tube has an outer diameter of 11 mm [14 mm] and is composed of a layer of tough connective tissue surrounding auricular cartilage elements which are incompletely circular in cross section; its lumen can vary from a circle to an oval (Figs. 4 and 5). The non-cartilaginous part of the perimeter of the outer ear tube contains a great deal of connective tissue with small muscle bundles. In the distal 2 cm of the tube, the cartilage is a semi circle (with the non-cartilaginous part on the ventral side). In the dorsal flexure the cartilage is irregular. In the part of the tube that lies against the squamosal bone and the thin part of the *m. temporalis* (Fig. 3B; for walrus head muscles see Kastelein *et al*., 1991) the cartilage is horseshoe-shaped (with the non-cartilaginous part towards the skull). In the ventral flexure and the part that enters the bony part of the outer ear it is almost a complete circle (with the non-cartilaginous side towards the skull; Fig. 4).

The inside of the tubular cartilage is lined with richly vascularized tissue (i.e. the part of the tube ventral to the most dorsal flexure; Fig. 6). Blood vessels are absent in the non-cartilaginous side of the canal, which is closed by connective tissue with many elastic fibres. The rather large lumina of these vessels and their distinct walls with few muscle fibres indicate a venous character. The blood vessels run predominantly parallel to the canal. The vascularized tissue of the outer ear is much denser than the tissue lining the middle ear. Between the proximal end of the tubular cartilage and the tympanic membrane, the vascularized tissue is thinner ($\pm$ 1 mm) [$\pm$ 0.5 mm] than in the distal part of the outer ear canal, and it encloses the lumen

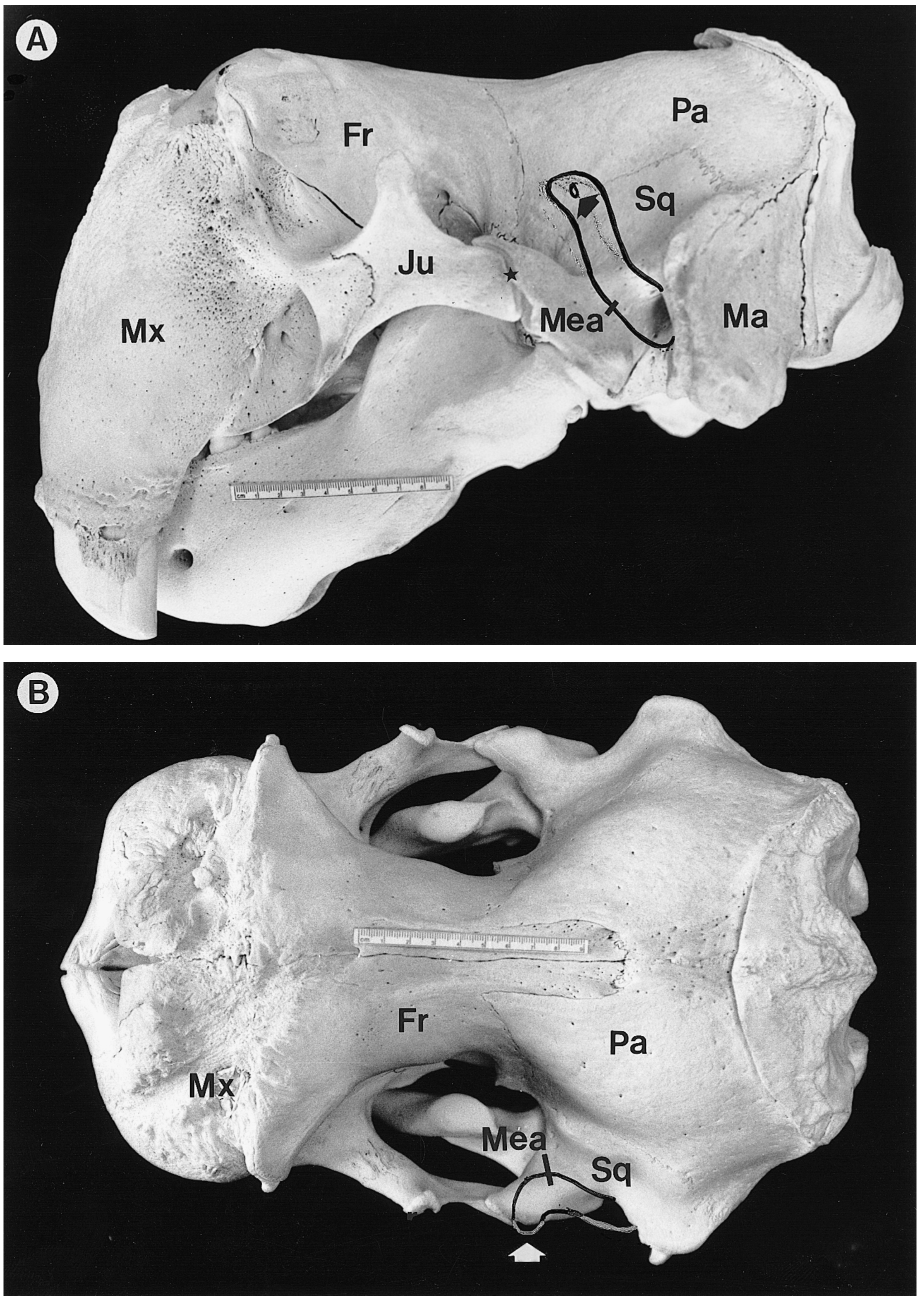


Figure 2. The position of the external auditory meatus in relation to the skull of a 5-year-old male Pacific walrus (no. W5). (A) Lateral view, and (B) dorsal view. The arrows indicate the auditory meatal orifice. Ma=*processus mastoideus*, Mea=*meatus acusticus cartilagenous*, Mx=maxilla, Fr=*os frontale*, Pa=*os parietale*, Sq=temporal bone, *pars squamosa*, Ju=*os jugale*. The * indicates the cleft in the zygomatic arch which, in life, is filled with cartilage (Photos: Ron Kastelein).

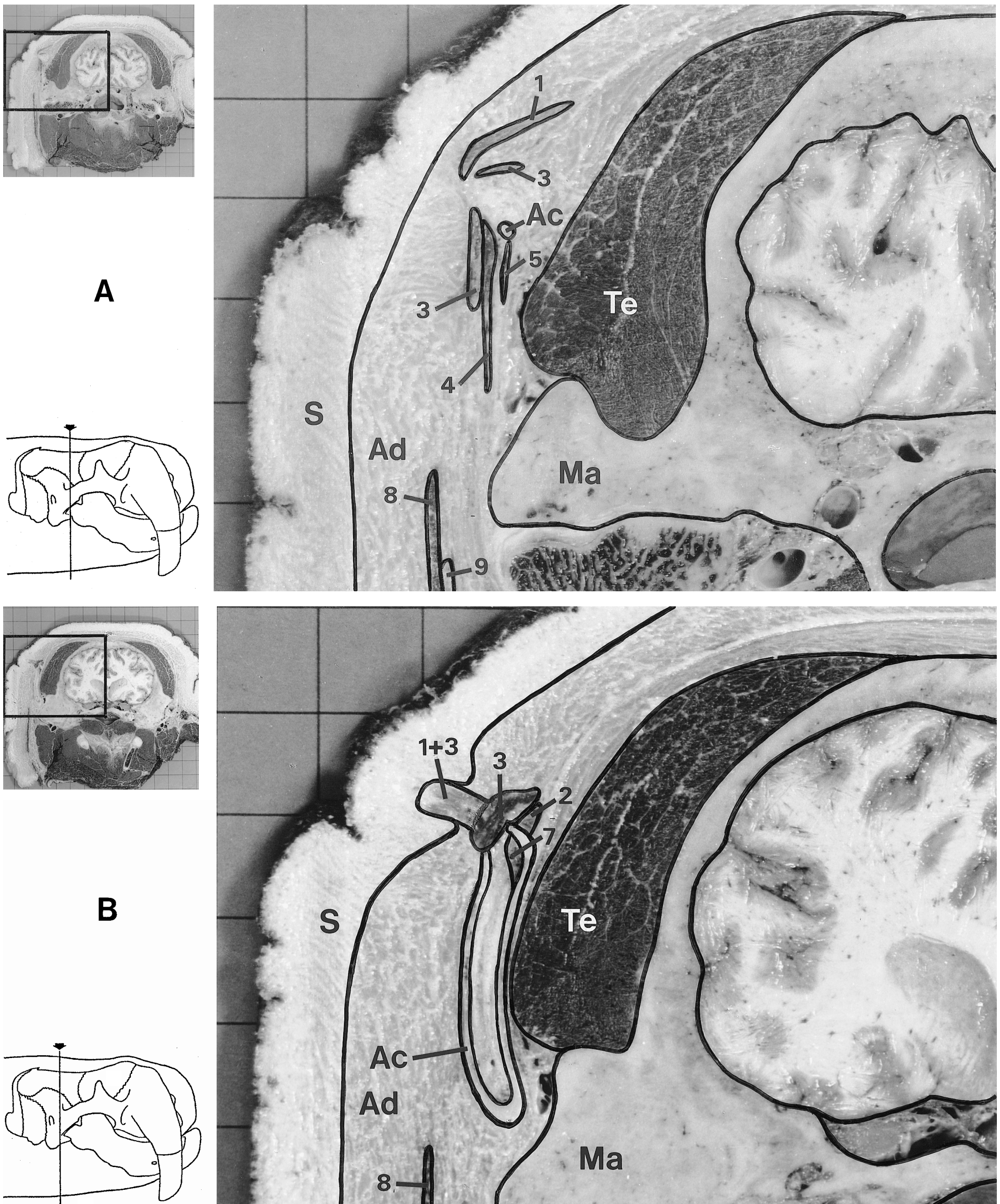
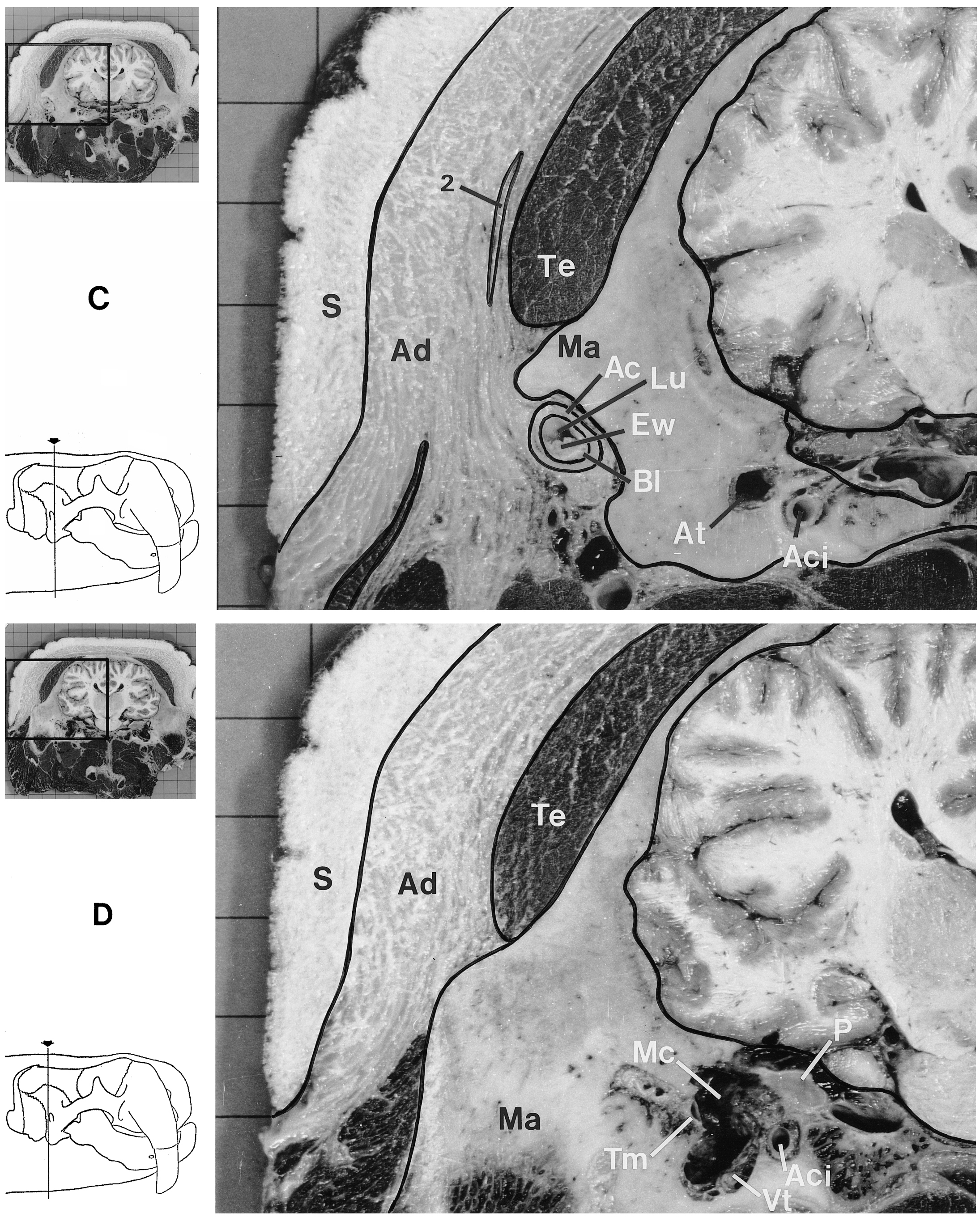


Figure 3. Frontal view of transverse sections through an 8-year-old female Atlantic walrus (no. W2) head showing the position of the auricular muscles (A and B), the outer ear canal (B and C), the *arteria carotis internus* (Aci), the Eustachian tube (*tuba auditiva*) (C), the middle ear (D and E), and part of the semi-circular canals (F) in relation to the skull, cranial muscles and skin. Ac = auricular cartilage, Ad = adipose tissue, At = auditory tube, S = skin, Ew = ear wax, Bl = blood vessels, Co = cochlea, M = malleus, Ma = mastoid process of the temporal bone, P = petrous bone, Te = temporal muscle, Vt = vascularized tissue, Tm = tympanic membrane, Sc = semicircular canal; Mc = middle ear cavity. (1) *m. fronto-auricularis*, (2) *m. temporo-auricularis*, (3) *m. zygomatico-auricularis superficialis*, posterior part, (4) *m. zygomatico-auricularis superficialis*, anterior part, (5) *m. zygomatico-auricularis profundus*, anterior part, (6) *m. zygomatico-auricularis profundus*, posterior part, (8) *Platysma*, (9) *m. sphincter colli profundus*. The arrows indicate the locations of the cross-sections. Background grid: 2 × 2 cm (Frozen material. Photos: Henk Merjenburgh).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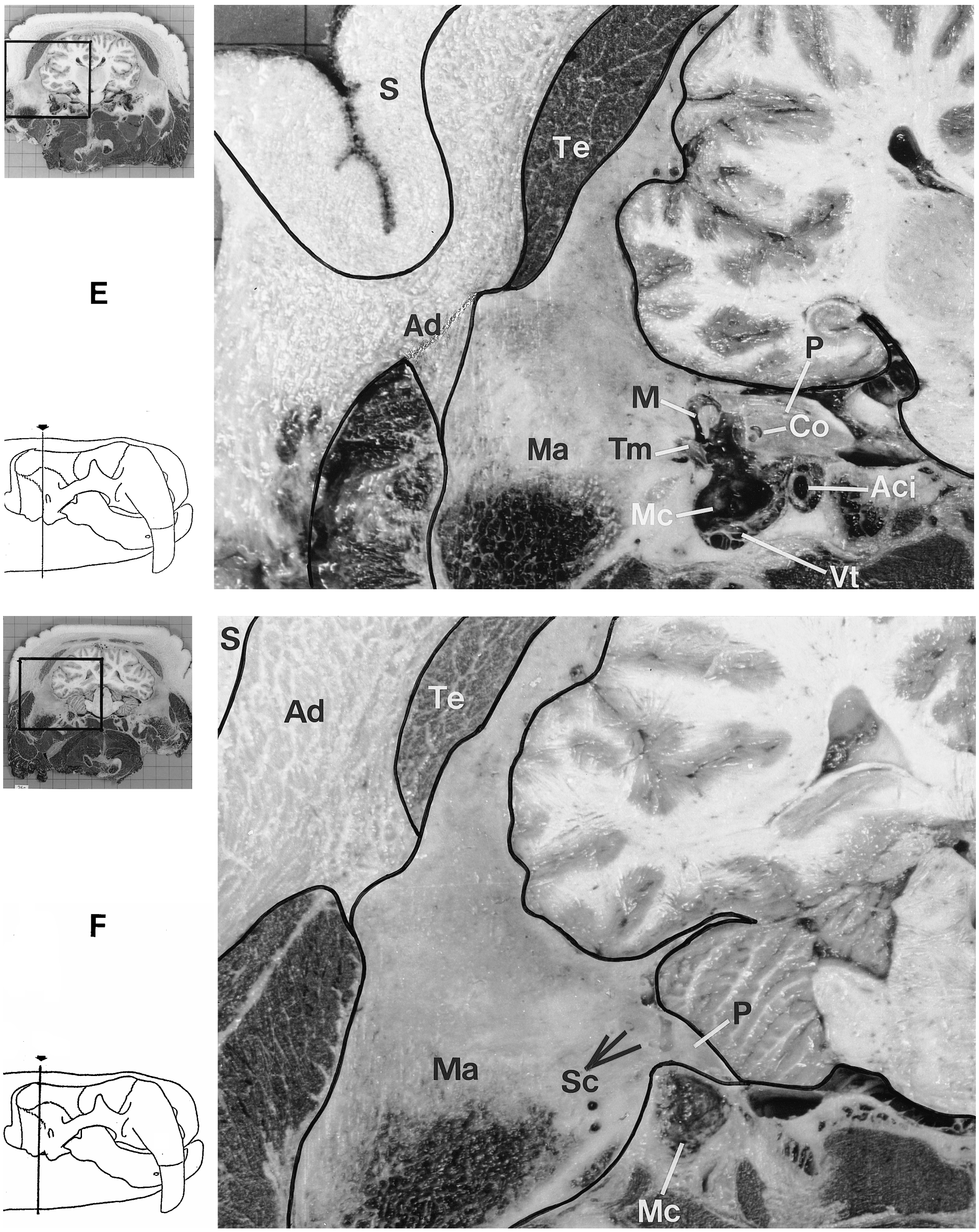
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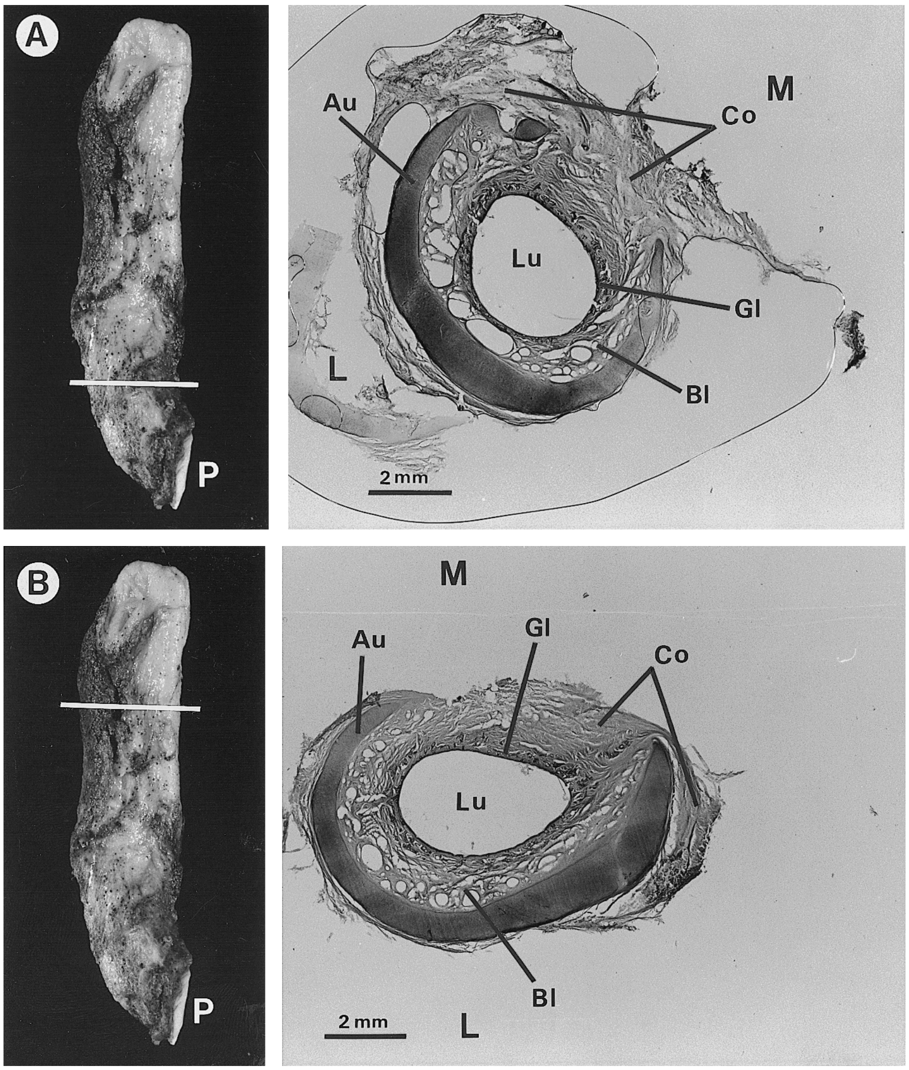


Figure 4. Transverse sections of the left outer ear canal from a 15-year-old male Pacific walrus (no. W3). (A) proximal end, (B) distal end. Au=auricular cartilage, Bl=blood vessels, Gl=glandular tissue, Co=connective tissue. Lu=lumen, L=lateral, M=medial, P=proximal end. The white bars indicate the locations of the cross sections. HE stained (Photos: Merijn de Bakker).

completely (Fig. 7A). The vascularized tissue is attached in a ring to the perimeter of the oval (approx. 7×9 mm) tympanic membrane which itself is attached to bone (Fig. 7B).

The inner-most layer lining the approximately 5 mm diameter lumen of the outer ear canal contains many *glandulae ceruminosae* and sebaceous glands (Fig. 8). In only one of the 15 sections investigated, a Pacinian corpuscle was found just beneath the epithelium (Fig. 9), suggesting that these corpuscles occur in low numbers. Hair follicles occur in the epithelium and the hairs are directed into the lumen. The hairs are only present in the distal end of the outer ear tube (Fig. 10).

The outer ear canal is lined with a 0.5–1 mm layer of earwax (cerumen), except for the proximal 2 cm (the bony part of the outer ear canal), of which 90% is filled with wax (Fig. 7A). A very thin layer of wax covers the tympanic membrane. In live animals earwax often runs out of the auditory orifice and is visible on the skin around and above the orifice, like coagulated wax on a candle.

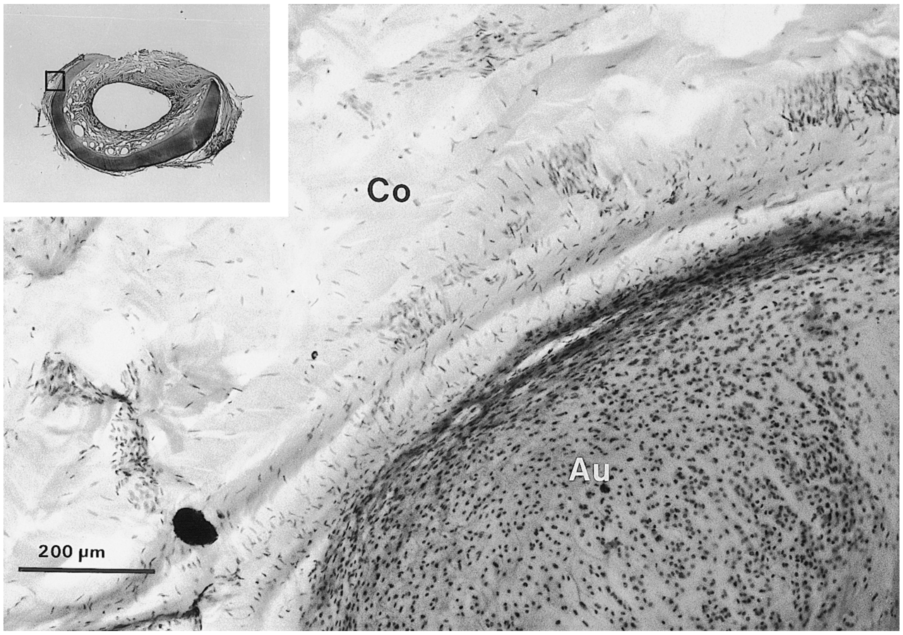


Figure 5. Detail of a transverse section of the outer ear canal of walrus no. W3, showing the auricular cartilage (Au) and the surrounding connective tissue (Co). HE stained (Photo: Merijn de Bakker).

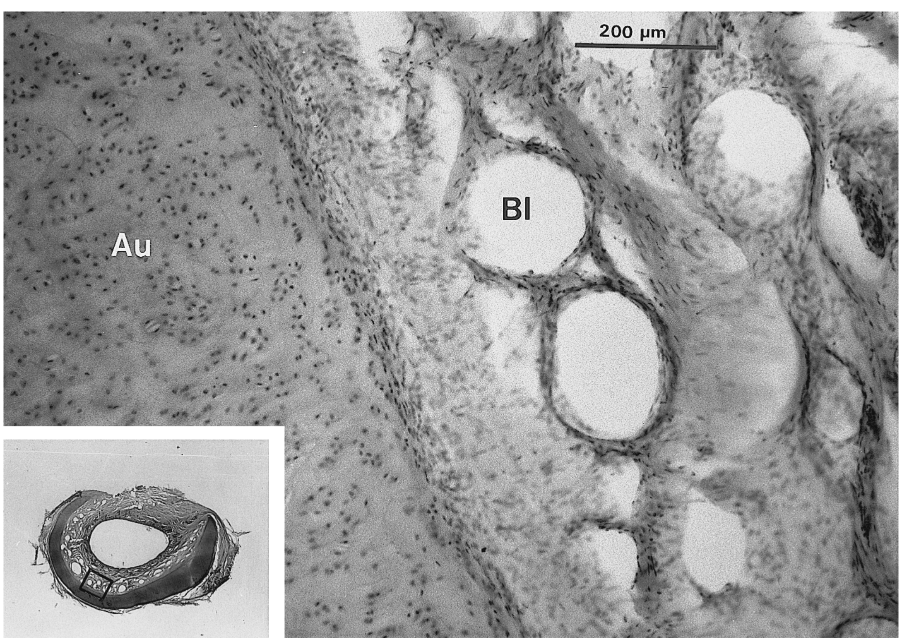
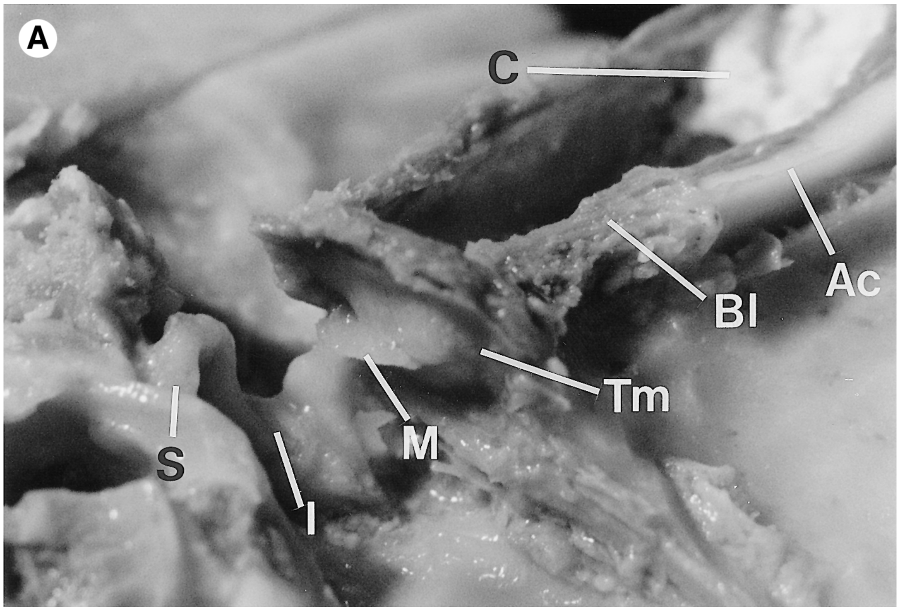


Figure 6. Detail of a transverse section of the outer ear canal of walrus no. W3, showing the blood sinuses (Bl) and the auricular cartilage (Au). HE stained (Photo: Merijn de Bakker).



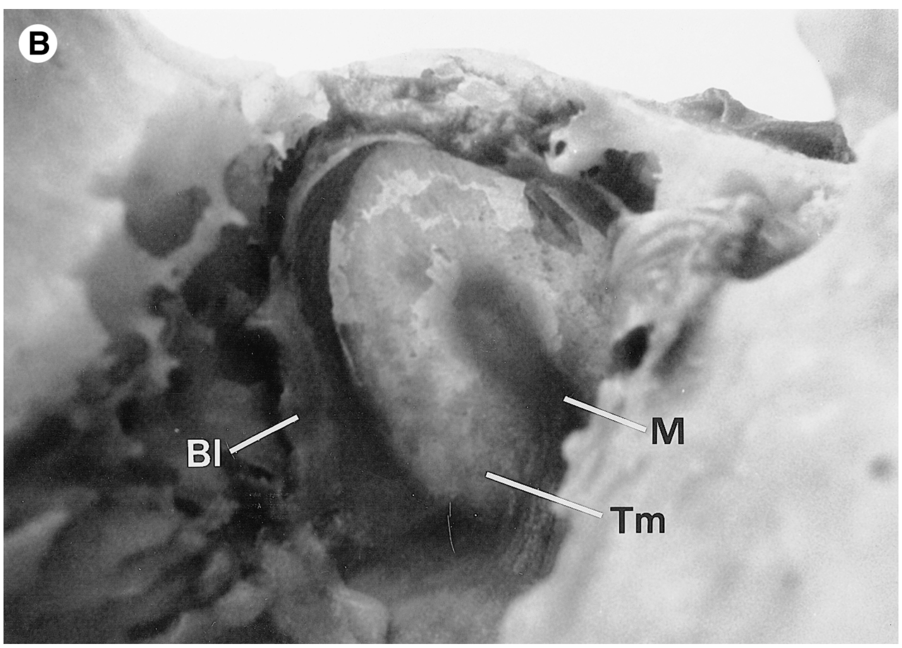


Figure 7. (A) Ventro-medial view of the right middle ear of W2 (view in the direction of the arrow in Figure 13B). The bone of the bony part of the outer ear canal and the ventral side of the cartilagenous part have been removed. The mucosa lining the middle ear and covering the ossicles has also been removed. (B) Lateral view of the right tympanic membrane (outer ear removed) of walrus no. W3 showing that the vascularized tissue which lines the outer ear canal connects in a ring to the perimeter of the ear drum. It also shows the manubrium of the malleus on the tympanic membrane. Bl=vascularized tissue lining the canal, C=cerumen which has been piled up with a probe, Tm=tympanic membrane, M=Malleus, S=Stapes, I=Incus, Ac=cartilagenous part of the outer ear canal (Photos: Ron Kastelein and Henk Merjenburgh).

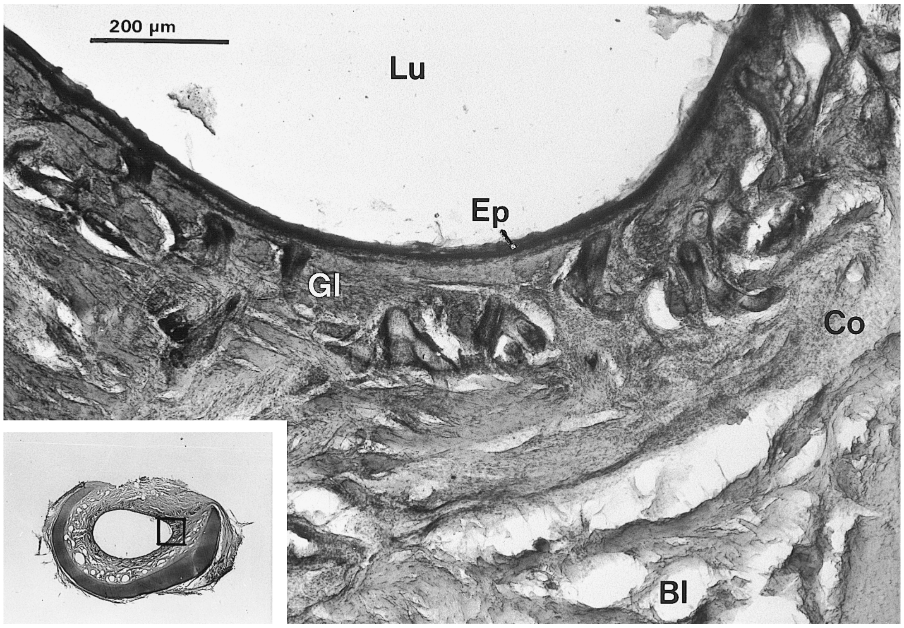


Figure 8. Detail of a transverse section of the outer ear canal of walrus no. W3, showing the glandular tissue (Gl) lining the lumen (Lu) of the tube. Bl=blood vessels, Co=connective tissue, Ep=epithelium. HE stained (Photo: Merijn de Bakker).

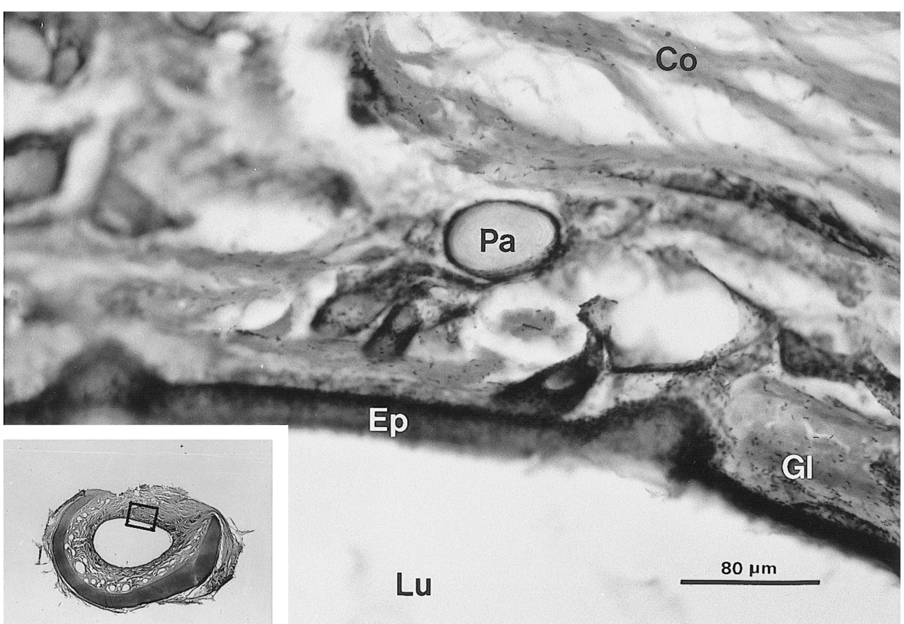


Figure 9. Detail of a transverse section of the outer ear canal of walrus no. W3, showing a Pacinian corpuscle (Pa) between the glandular tissue (Gl) and the connective tissue (Co). Lu=lumen, Ep=epithelium. HE stained (Photo: Merijn de Bakker).

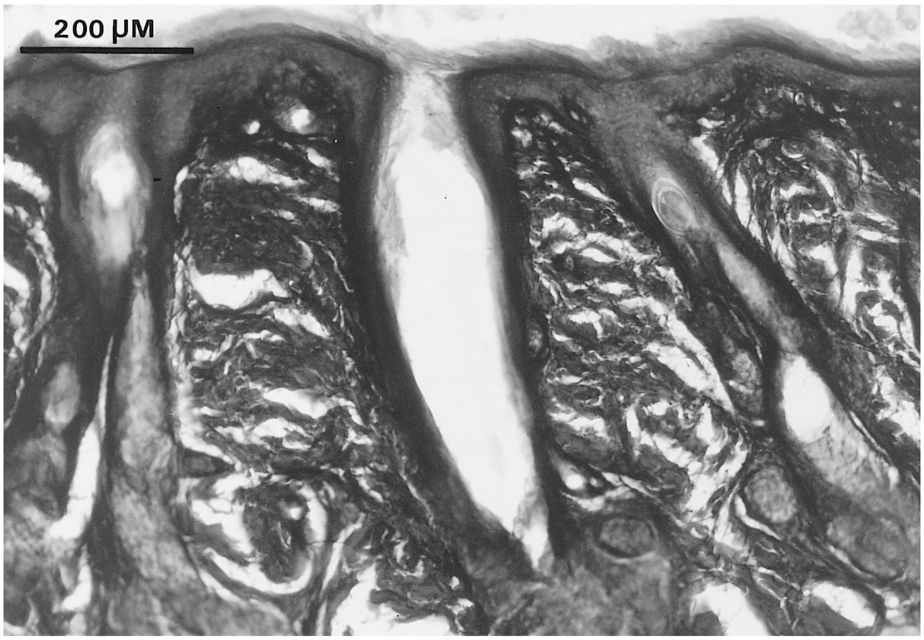


Figure 10. Enlargement of the tissues around the perimeter of the outer ear canal lumen of walrus no. W3 showing hair shafts (Photo: Merijn de Bakker).

Auricular muscles

The distal, outwardly projecting part of the auricular tube is surrounded by a number of auricular muscles. The cartilage and the auricular muscles are probably homologous with similar elements of the ears of terrestrial carnivores. However, the differences in shape and position are so great that the individual pieces of cartilage have not been named. Similarly, the names of the muscles listed below as numbers 2–7 (the same designation as in Figs. 3, 11 and 12) were inspired by topography alone.

(1) *m. fronto-auricularis*

This muscle originates on the fascia of the *m. frontalis* and runs through the subcutaneous fat to insert on the dorso-rostral side of the tube.

(2) *m. temporo-auricularis*

The origin is in the superficial layers of the fascia of the *m. temporalis*. The muscle runs deep to the *m. zygomatico-auricularis superficialis* and its fibres follow the tube in the distal direction.

(3) *m. zygomatico-auricularis superficialis, posterior part*

The posterior and anterior parts of this muscle have a common origin in the superficial fascia over the zygomatic arc on which the *platysma* also inserts, but are discontinuous with the latter. The fibres of the posterior part spiral upwards to insert on the posterior and dorsal aspect of the tube.

(4) *m. zygomatico-auricularis superficialis, anterior part*

The anterior part of the muscle inserts on the anterior surface of the tube, and is almost in contact with fibres from the posterior part.

(5) *m. zygomatico-auricularis profundus, anterior part*

This thin muscle originates on the zygomatic arch and runs directly superficial to the parotid fascia. It inserts at the base of the distal part of the auricular tube.

(6) *m. zygomatico-auricularis profundus, posterior part*

The posterior part of this L-shaped muscle also originates on the zygomatic arch, but is firmly embedded in the parotid fascia. It has a final tendinous insertion slightly deeper than the anterior part of this muscle.

(7) *m. auricularis internus*

This muscle, which is somewhat triangular in cross-section, has its origin on the cartilage forming the basis of the distal tube, deep to the lumen. It runs upwards, rostral to the lumen almost to the skin

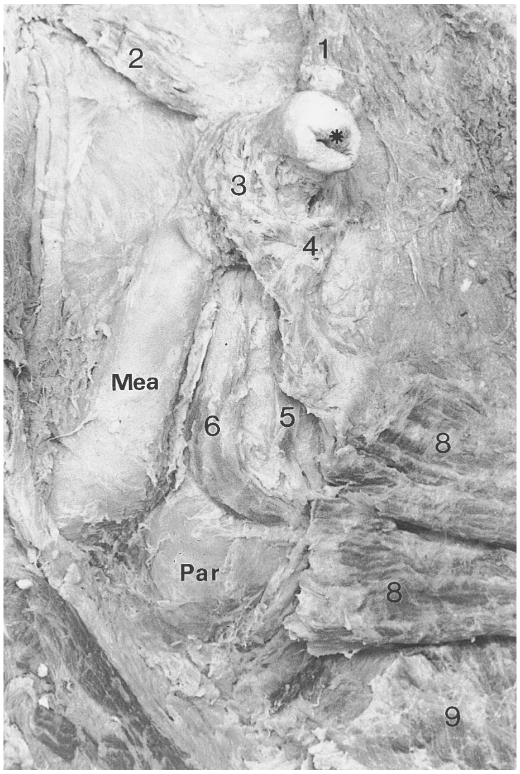


Figure 11. The arrangement of the external auricular muscles of the right auditory canal of an 8-year-old female Atlantic walrus (no. W2). The nose of the animal is to the right. *auricular orifice and lumen. (1) *m. fronto-auricularis*, (2) *m. temporo-auricularis*, (3) *m. zygomatico-auricularis superficialis*, posterior part, (4) *m. zygomatico-auricularis superficialis*, anterior part, (5) *m. zygomatico-auricularis profundus*, anterior part, (6) *m. zygomatico-auricularis profundus*, posterior part, (8) *Platysma*, (9) *m. sphincter colli profundus.* Mea = *Meatus acousticus cartilagenous*, Par = parotid gland (Photo: Nico Gerrits).

covering the orifice of the tube and inserts on the entire free margin of the most dorso-rostral cartilage element.

Role of the auricular muscles

Considering the arrangement of the different insertions, it seems likely that the distal part of the lumen of the tube and the orifice can be opened by contraction of the fronto-auricular muscle, probably supported by the posterior part of the superficial zygomatico-auricularis muscle. This would create a backward rotation of the distal tube. Simultaneous contraction of the *auricularis internus* and both parts of the superficial zygomatico-auricularis muscles will result in a powerful constriction of the distal tube. A larger volume of muscle is dedicated to closing the tube than to opening it.

Middle ear

The walrus' middle ear is in the *bulla tympanica* which is surrounded by several openings in the skull (Figs. 3C, D, E and 13A): on the lateral side the *foramen stylomastoideum* for the *nervus facialis* and the *meatus acousticus externus osseus*; on the rostral side the *foramen ovale* for the *nervus trigeminus* and the *canalis musculotubarius* the opening of the osseus part of the auditory (Eustachian) tube (*tuba auditiva*); on the medial side the *canalis caroticus* and the *foramen lacerum* for the *arteria carotis internus*, and on the caudal side the *foramen jugulare* for the *vena jugularis interna* and Nerves 9, 10 and 11.

The endotympanic (*pars endotympanica*) constitutes about 1/4 of the *bulla tympanica*, forming the *canalis caroticus* for the *arteria carotis internus*. This artery has a thick wall (3 mm in contracted state) and an outer diameter of 8 mm; the lumen has a diameter of 2 mm, but this is probably larger in a living animal (Fig. 13B). The rest of the *bulla* is formed by the ectotympanic. The *bulla tympanica* is fused to the *processus mastoideus* of the temporal bone. On the ventro-caudal side, the *bulla tympanica* is very dense and about 1 mm thick. The tympanic bone between the *n. facialis* and the articulation joint between the incus and stapes is also about 1 mm thick. The thickness of the *bulla tympanica* increases to around 20 mm on the rostral side, where the bone is somewhat softer and penetrated by many small blood vessels (Fig. 13C).

The walrus middle ear cavity is large (about 9 cm^3 in an adult animal), and consists of the tympanic cavity, the epitympanic recess, a side pocket and the tympanic orifice of the auditory tube (Fig. 13B and C; For a view of a latex mould of the walrus middle ear cavity see Fig. 6 in Repenning, 1972). The Eustachian tube is flattened, so that hardly any lumen is left; it is difficult to push a 1 mm diameter probe through it. Low numbers of small arteries are found in the wall of the Eustachian tube (Fig. 14). In the 15-year-old male Pacific walrus (W3), the part of the Eustachian tube that runs through the *bulla* is 26 mm long. There the walls of the tube are thickened and the lumen is reduced (the *isthmus*; Fig. 13B). This thickened part consists of dense collagen tissue with some cartilaginous rods and elastic fibres (Fig. 15). Within the collagen tissue, glands (*glandulae tubariae*) occur, which open into the lumen of the Eustachian tube (Fig. 16). The part of the Eustachian tube between the *bulla* and the opening in the nasopharynx (*ostium pharyngeum tubae auditivae*) is 19 mm long in the 15-year-old male Pacific walrus (W3), and the opening of the auditory tube in the nasopharynx

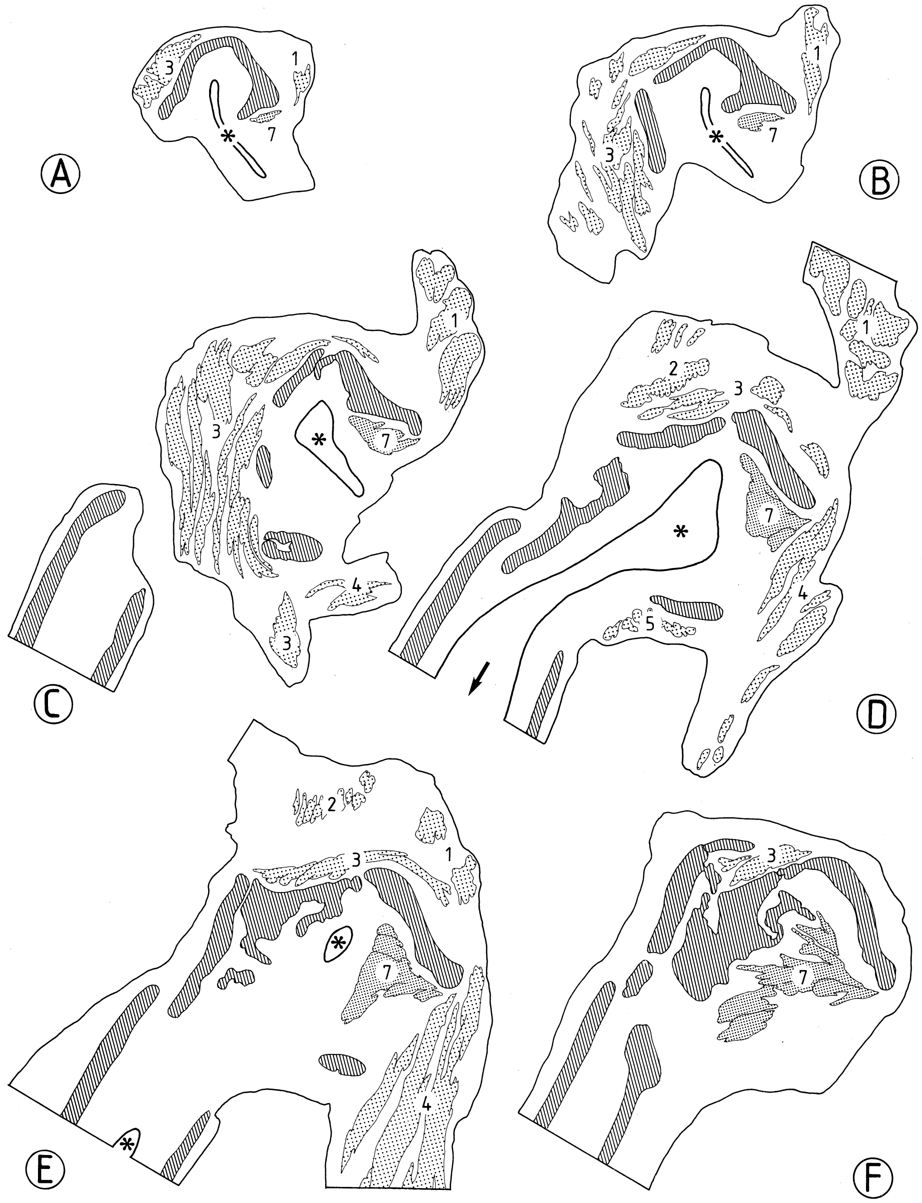


Figure 12. Series of six equally spaced transverse sections through the outer ear canal from lateral (A) to medial (F), showing the distal part of the tubular cartilage elements (C–F, lower left side) and the individual distal cartilage (hatching), and the muscles (stippled) surrounding the distal part of the lumen (*). The orientation of the sections is the same as in Figure 11; the arrow points in the direction of the tympanic membrane. (1) *m. fronto-auricularis*, (2) *m. temporo-auricularis*, (3) *m. zygomatico-auricularis superficialis*, posterior part, (4) *m. zygomatico-auricularis superficialis*, anterior part, (5) *m. zygomatico-auricularis profundus*, anterior part, (6) *m. zygomatico-auricularis profundus*, posterior part, (7) *m. auricularis internus*, (8) *Platysma*, (9) *m. sphincter colli profundus* (Drawings: Nico Gerrits).

lies 3.5 cm immediately dorsal of the distal end of the *hamulus pterygoideus*, and is 8 mm wide and shaped like an arch (Fig. 17).

The tympanic cavity contains the large auditory ossicles (Figs. 3E, 7, 13B, 18 and 19). For other views of walrus ossicles, see Fig. 5 in Repenning (1972) and Wyss (1987). Two muscles are associated with the ossicles. The *m. tensor tympani* has its base in the *fossa tensor tympani* (Fig. 18). The tendon of insertion is attached to the muscular process of the malleus (Fig. 19). The *m. stapedius* has its origin in the *fossa musculi stapedii* and attaches to the muscular process of the stapes (Fig. 19B).

The middle ear cavity is lined with a mucous membrane with loose connective tissue, which in some areas is richly vascularized. On the floor the vascularized tissue is 4 mm [only 1 mm in animal W3, which was raised and housed in a pool] thick, and here the blood vessels are relatively large (Figs. 3C, D, E, 13C, 20 and 21). The tissue is about 1 mm [0.5 mm] thick on the sides of the cavity; here the vessels are smaller. On the roof of the middle ear cavity the mucosa is not vascularized, except in the pocket medial to the beginning of the Eustachian tube (3/4 of this bony pocket is filled with vascularized tissue when this tissue is not engorged with blood), and the dorsal side of the middle ear between the tympanic orifice of the Eustachian tube and the tympanic membrane, where the vascularized tissue is approximately 0.5 mm thick. The vascularized tissue seems to be loosely connected to the floor and walls of the middle ear cavity, and more tightly connected to the roof. This was the case in all investigated walruses (W2, W3 and W4). The mucous membrane lining the middle ear is not vascularized near the tympanic membrane. Towards the epitympanic recess the vascularized tissue is folded and covers a ridge in the bone, the *m. tensor tympani*, the ossicles and the tympanic nerve (*chorda tympani*). After leaving the facial nerve, the tympanic nerve passes through the tympanic cavity medial to the malleus to join the lingual nerve.

Inner ear

The foot of the stapes (Fig. 19C) connects to the oval window (Figs. 7A, 13B and 18). The inner ear is located between the oval window and the tympanic cavity (Figs. 3E and 13B). The petrous bone anterior to the cochlea is large (Fig. 3E and F). For a dissection of the petrosum and cochlea, see Figure 2 in Repenning (1972). The semi-circular canals lie in the petrosum (Fig. 3E).

Discussion and Conclusions

Requirements the walrus ear has to fulfil

The walrus ear has to fulfil a double function and allow hearing in air (Kastelein *et al.*, 1993*b*; 1996) and hearing under water (Stirling *et al.*, 1987). Probably, both functions require different mechanisms to transmit sounds from the environment to the sense organ proper; an impedance switching mechanism has been suggested for phocids (Møhl, 1968*a*, 1975; Terhune, 1989). Functioning of the hearing mechanism is further complicated by the fact that it also has to cope with pressure changes during diving. Walruses dive to a maximum depth of 100 m (Fay, 1982; Fay & Burns, 1988). They have to cope with consequences of underwater eating: excavation and food processing requires large pressure changes in the oral and pharyngeal cavity (Kastelein *et al.*, 1994). The structural features of the hearing system must be considered in the light of these requirements.

Special features of the walrus ear

Walrus outer and middle ears have special features which are not usually found in terrestrial carnivores. These are: the lack of pinnae, the long, tubular outer ear which is completely embedded in blubber and covered by thick skin, the ability to open and close the external orifice by auricular muscles, the lining of the cartilaginous and bony parts of the outer ear canal with vascularized tissue, the copious amount of earwax, the large middle ear cavity, the lining of the middle ear cavity with vascularized tissue, the elastic fibres, collagen tissue and cartilaginous rods in the wall of the Eustachian tube, and the dense bones surrounding the base of the outer ear and the entire middle and inner ears.

Hypothesis of the function of walrus hearing

(A) Hearing in air

Pressure regulation

While above the water, the walrus hearing system probably functions like that of most terrestrial mammals. In the case of a pressure difference between the environment and the middle ear cavity, the animal can swallow or yawn. This will probably open the Eustachian tube, so the air pressures in the outer and middle ears can be equalized (Fig. 22A).

Hearing

The long outer ear canal in walruses ensures that the meatal orifice (*porus acousticus*) is above water during surface swimming (Fig. 1). Walruses often sleep in a vertical position at the water surface with their pharyngeal pouches inflated (Fay, 1960). In this posture the whole head and part of the neck are out of the water, which means that the entire outer ear is above the surface (Francis H. Fay, pers. comm.) and the walrus can hear air-borne sounds. When swimming at the water surface, the meatus is

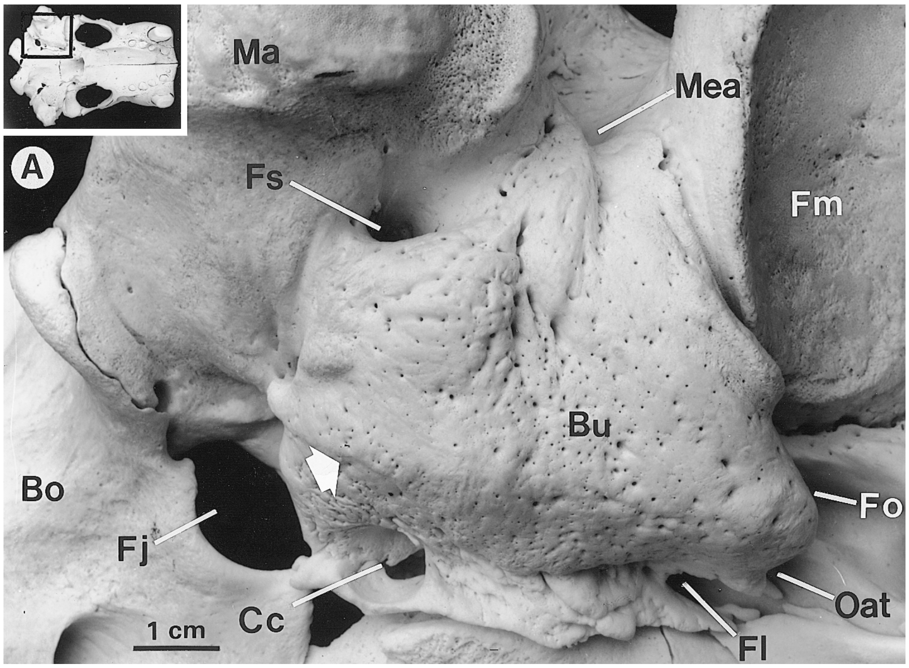


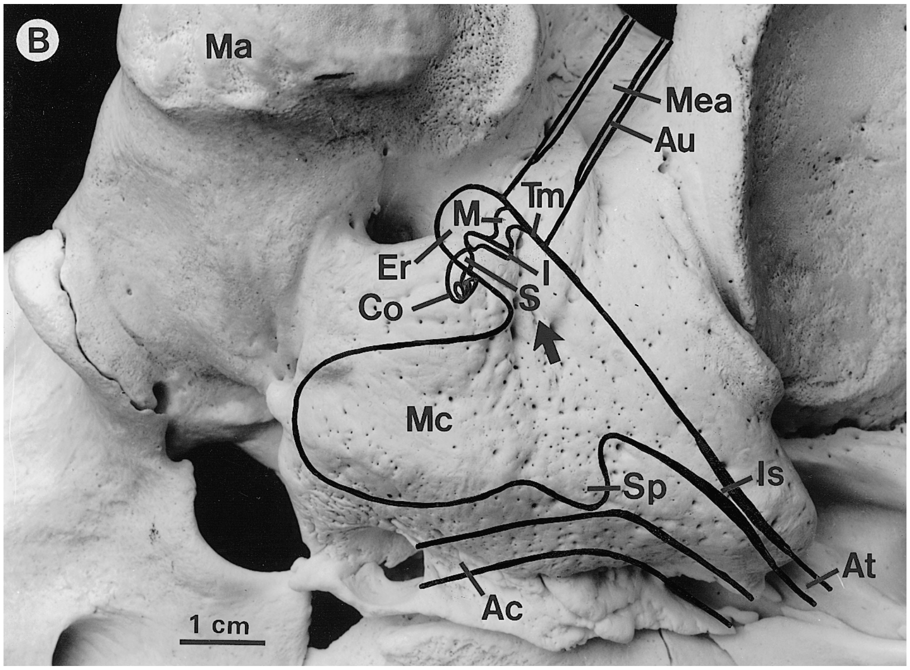
Figure 13. (A) Ventral view of the right *bulla* of of a 5-year-old male Pacific walrus (no. W5). (B) Ventral view of the *bulla*, indicating the location of the middle ear cavity as observed in an 8-year-old female Atlantic walrus (no. W2), (C) Medial view of the *bulla* with the ventral side up for easy comparison with Figures A and B. Ac=*arteria carotis internus*, At=auditory tube, Au=auricular cartilage, Bo=basioccipital bone, Bu=*bulla* (note the large thickness of the *bulla* on the rostral side), Cc=*canalis caroticus*, Co=cochlea, Er=epitympanic recess, Fj=*foramen jugale*, Fl=*foramen lacerum*, Fo=*foramen ovale*, Fm=*fossa mandibularis*, Fs=*foramen stylomastoideum*, I=incus, Is=*isthmus*, M=malleus, Ma=mastoid process of the temporal bone, Mc=middle ear cavity, Mea=*meatus acousticus externus*, Oat=osseus auditory tube, S=stapes, Sp=side pocket, Tm=tympanic membrane, Vt=vascular tissue. The white arrow in (A) indicates the location of the hole shown in Figure 20. The black arrow in (B) indicates the view direction in Figures 7A and 18 (Photo and drawings: Ron Kastelein).

probably kept open, so that sounds can enter the outer ear canal. In air, the rigidity of the tubular cartilage of the outer ear canal probably keeps the canal open. Where the cartilage is absent in the external meatus, its supporting role is taken over by the bony canal composed of the squamosal bone and *bulla tympanica*. The walrus' outer ear canal is long with two perpendicular flexures, but because the orifice is funnel-shaped, the length and flexures are probably of minor influence on hearing sensitivity. The walruses' lack of pinnae probably limits their aerial hearing sensitivity to a small extent and should almost certainly limit their ability to notice whether single sounds come from in front or from behind them unless they move their head (Kietz, 1953).

Walruses are gregarious animals which usually lie against or on top of each other. They are also very vociferous and sometimes produce very loud sounds (Loughrey, 1959; Miller, 1985; Verboom & Kastelein, 1995). They haul out in areas with high levels of background noise caused by waves and breaking ice. However, they only seem to haul out to sleep (Krusinskaja & Lisicyna, 1983). Because of these loud sounds in their environment, one could speculate that walruses may close off (if they are capable of voluntarily doing so) their meatus when hauled out to rest. Experiments with a Harp seal (*Pagophilus groenlandica*) indicate that, in air, sound enters the ear via the meatus. Closing the meatal orifice with a finger reduced the sound levels received at the cochlea, especially for frequencies of around 5 kHz (Møhl & Ronald, 1975).

(B) Hearing under water

Many of the special features of the walrus outer and middle ears probably have both acoustic and pressure-regulating functions. Under water, the walrus ear probably functions in a similar way to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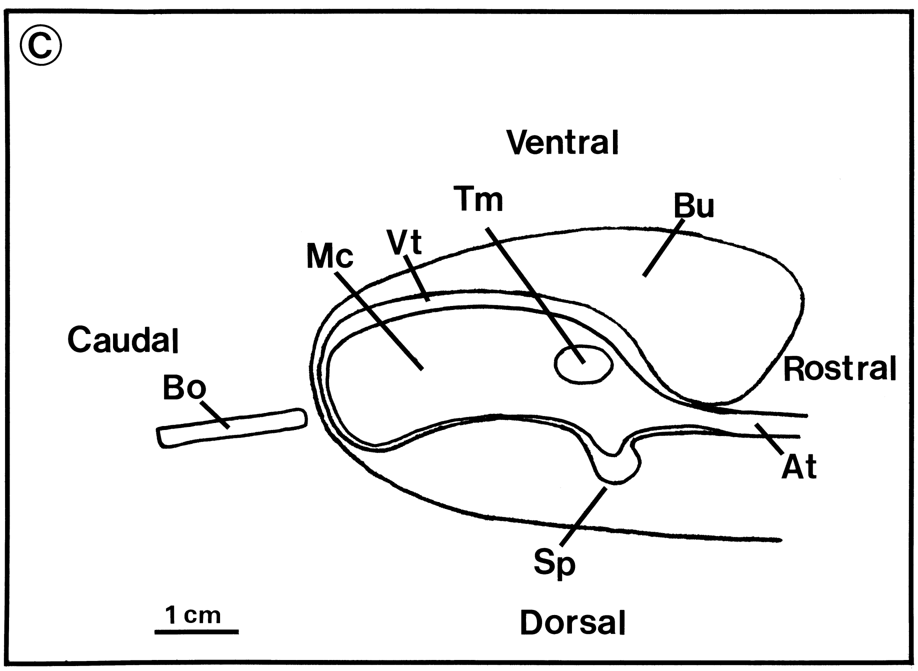
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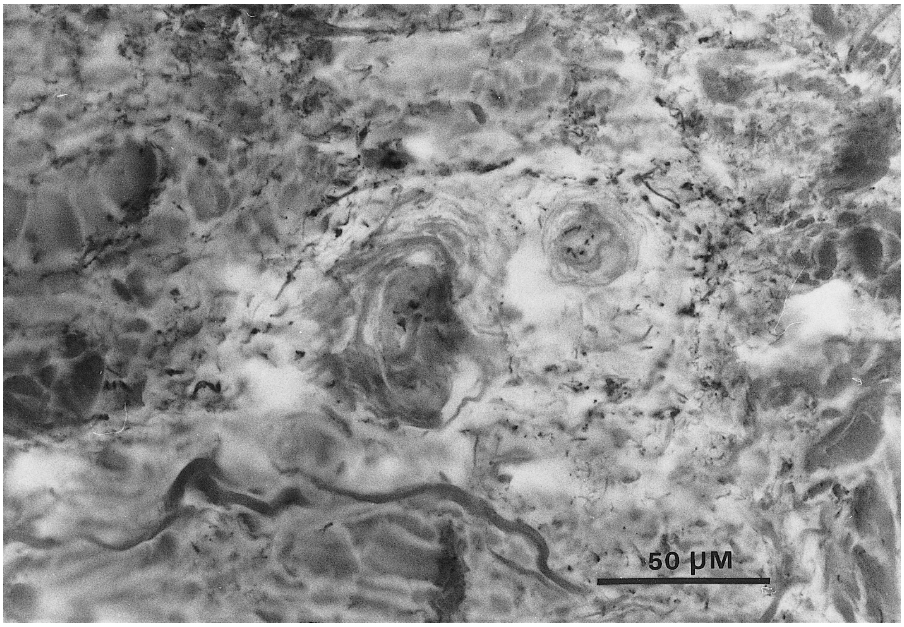


Figure 14. Collapsed arteries surrounded by elastic fibres in the wall of the Eustachian tube (Photo: Merijn de Bakker).

that of other pinnipeds. The following hypothesis on the function of walrus hearing under water is highly speculative because it is based only on anatomical findings. Under water acoustic and pressure regulation experiments on walruses have not yet been conducted.

Pressure regulation

Diving requires mechanisms that serve to equalize the pressure on both sides of the tympanic membrane. If, during descent, the increase in pressure in the outer ear canal is not counteracted by a similar increase in pressure in the middle ear, pain is felt, and, in extreme cases, the tympanic membrane may rupture.

When a walrus submerges, its meatus is closed by the auricular muscles, so that water cannot penetrate the outer ear canal (Fig. 22B). The tube is also narrow, long, waxy and lined with hairs and thus difficult to fill with water (and it would be even more difficult to empty). A few drops of water would reduce aerial hearing sensitivity. It is not clear which stimulus is responsible for activating the auricular muscles. When the skin around the meatal orifice of a walrus is touched, no movements of the underlying auricular muscles can be seen as are in Harbour seals, *Phoca vitulina* (Møhl, 1968*a*). However, this could be because the walrus skin and the underlying blubber layer are very thick (Fig. 3A and B). Kastelein *et al.* (1996) report that the use of open headphones did not result in a reduction in hearing sensitivity in walruses. Even open headphones with a grid did not induce the closure of the meatal orifice although the grid touched the skin very close to the meatal orifice. A reflex triggered by submerging is possible, although voluntary control over the auricular muscles cannot be ruled out. Møhl & Ronald (1975) thought harp seals actively controlled the closure of the meatal orifice.

If closure is instigated just before or immediately after submerging, an air-filled cylinder will be formed which is closed at both ends. As the animal dives, the ambient pressure increases. If during initial descent, the cartilaginous part of the outer ear tube resists deformation due to its own rigidity (which is needed to keep the lumen open for in-air hearing during head movements, which may change the pressure of skin and blubber on the outer ear) and that of the surrounding tissues, the pressure in the lumen might temporarily become less than the ambient pressure. If this occurs, the sinuses in the outer ear tube may engorge with blood, since the cardiovascular system will be at ambient pressure. The filling of the blood sinuses is probably passive, and drainage is facilitated by the elastic fibres in the walls of the blood vessels.

The outer ear is probably not rigid enough to withstand a great increase in ambient pressure without deformation. Light pressure was enough to cause collapse of the outer ear tube of a recently deceased walrus, but because it was very resilient, it resumed its original shape immediately after the pressure was released.

The outer ear deformation hypothesis is supported by the absence of vascularized tissue in the non-cartilaginous side of the outer ear canal. If blood vessels were present there, inflation would counteract the deformation of the auricular cartilage. The bony part of the outer ear tube cannot collapse and here the vascularized tissue encloses the entire canal and is attached to the perimeter of the tympanic membrane. This was also observed in the Harp seal (Ramprashad *et al.*, 1972). Møhl (1967) observed a similar lining in the outer ear of a Grey seal (*Halichoerus grypus*). He suggests that the lining may have a pressure regulating function, but that other possible functions need to be investigated.

The lungs and trachea of seals are severely compressed by increased pressure during diving (Kooyman *et al.*, 1970), so that the air in the respiratory tract is expected to be at ambient pressure. The nasopharynx is linked to the middle ear by the Eustachian tube, which can be opened by swallowing and, in air, by yawning (assuming that this system in pinnipeds acts in the general mammalian way). By opening the Eustachian tube, the pressure of the middle ear may come close to the ambient pressure. The Eustachian tube is closed by the elasticity of its wall. The robust wall of the auditory tube in pinnipeds suggests that it may provide a strong structural base, which enables muscular opening of the tube under increased pressure in the nasopharynx during diving.

Because of the high density of water compared to air, pressure changes occur more rapidly in water than in air when moving vertically. A positive pressure in the middle ear is easier to overcome than a negative pressure. When small negative changes occur in humans in air, they swallow. However, under water human divers have to use the Valsalva manoeuvre (forced exhalation against a closed mouth and nostrils) to overcome negative pressure in the middle ear (Odend'hal & Poulter, 1966). Such negative pressure in the middle ear of the walrus may be prevented from occurring by cavernous tissue (*corpus cavernosum*) in the middle ear. During a dive, as negative pressure develops in the middle ear, the mucosa is probably filled with blood. The filling of the cavernous tissue with blood could be a passive process as was suggested by Tandler (1899) after examining phocid ears. However, if it was a completely passive process, the tissue might be expected to fill with blood when the pinniped was in air, as blood pressure normally exceeds the ambient air pressure. Graham (1967) proposes that it may be a cardiovascular adjustment as a part of the overall diving reflex in pinnipeds which includes bradycardia. The venous drainage may be blocked, and thus the blood pressure may increase, expanding the mucosa. The expanding mucosa compresses the air until the pressure becomes equal to that on the outside of the body. When descending, the pressure on the body and on the circulatory system increases. Under water, the walrus would have to swallow almost continuously while descending or ascending, if it did not have special pressure regulating features in its ears. If a pressure difference occurs between the ear cavities and the vascular system, the cavernous tissues become engorged with blood. The degree of inflation depends on the pressure difference. The uneven distribution of the mucous membrane in the middle ear cavity may be caused by entrances of the vessels which supply the blood to this area.

In support of the pressure equilibration function hypothesis of the cavernous tissue of the walrus middle ear is the fact that this tissue was hardly present in the 15-year-old male which had spent its entire life in a pool which was only 4 m deep. Perhaps not being exposed to high ambient pressure limited his need to develop or maintain this tissue. Less cavernous tissue was found in the middle ear of a walrus pup than in that of phocids or otariids (Repenning, 1972), so the walrus seems less able to reduce the volume of air in the middle ear than other pinnipeds. This is confirmed in the present study: all ears contained a small amount of cavernous tissue, regardless of the method of fixation. Therefore it seems to be a property of the species. Repenning (1972) suggests that the walrus middle ear has a small amount of cavernous tissue, but not enough to substantially reduce the air volume in the middle ear cavity, because walruses do not dive as deep as most other pinnipeds (up to 100 m, Fay, 1982). They feed mainly on bivalve molluscs which usually live up to a depth of 100 m (Fay & Burns, 1988).

Once a walrus has found a foraging area in the form of a bivalve mollusc bed, it stays at a relatively constant depth and pressure until it has to go to the surface to breathe. The Eustachian tube probably opens frequently when walruses forage, because they swallow benthic prey under water. In the walrus, the Eustachian tube seems more rigid than in terrestrial mammals, as its wall contains a great deal of collagen. This probably means that it is more difficult to open the tube. This might be necessary when large pressure fluctuations occur in the pharyngeal area during water jetting (Kastelein *et al.*, 1991) and oral suction (Kastelein & Mosterd, 1989; Kastelein *et al.*, 1991; Kastelein *et al.*, 1994). The strong development of the *m. tensor veli palatini* and the *m. levator veli palatini* which are attached to the well-developed hamuli (Kastelein & Gerrits, 1990; Kastelein *et al.*, 1991) may allow the

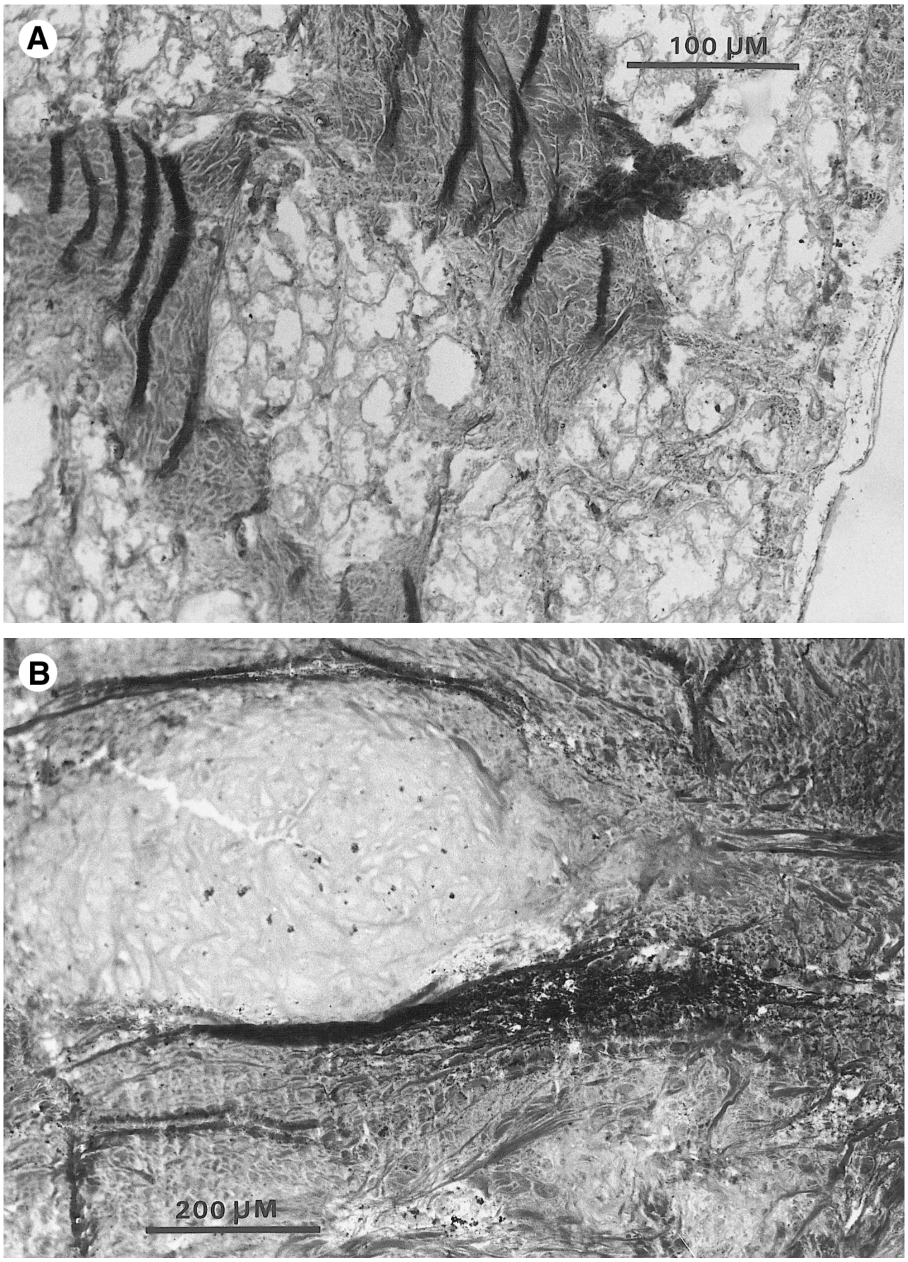
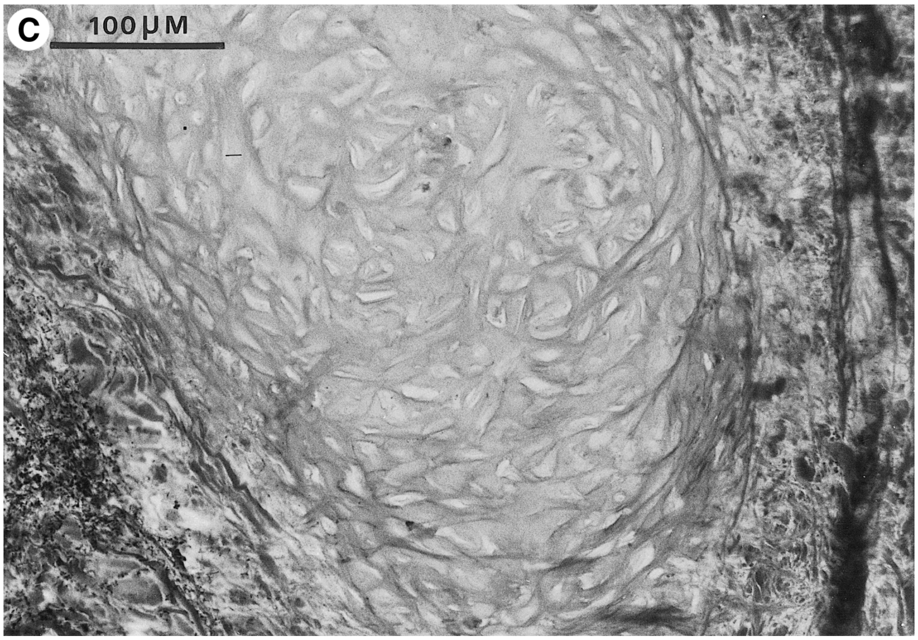


Figure 15. (A) The wall of the Eustachian tube with glands (*Glandula tubaria*) between collagen connective tissue. The black bands are folds in the section. (B) Section through the Eustachian tube with a cartilagenous rod surrounded by collagen connective tissue. (C) Section through the thickest part of the Eustachian tube with a cartilagenous rod surrounded by elastic connective tissue (Photos: Merijn de Bakker).

walrus to separate the oro- and naso-pharynx with the soft palate when producing oral suction.

Odend'hal & Poulter (1966) report that the mucosa lining the middle ear of Steller sea lions (*Eumetopias jubata*) and California sea lions (*Zalophus californianus*) was only attached to the middle ear wall in the area of the epitympanic recess, probably to avoid interference with the ossicles. The



mucosa in the walrus ear is attached to the entire tympanic bone. The mucosa does not contain blood sinuses in the epitympanic recess, and during deep dives the remaining air space is probably restricted to this recess. Thus the tympanic membrane and ossicle chain may remain functional in sound conduction. This could be another species specific feature.

The outer ear tube probably regains its original shape just below the water surface as the animal ascends, as the auricular cartilage of the walrus is very resilient like the cartilage in a human ear. Thus, airborne sound can reach the tympanic membrane when walruses surface. Some of the auricular muscles serve to open the meatal orifice during surfacing. A female walrus at the Harderwijk Park often swims around her pool in a particular circle. At one point in the circle she lifts her head and neck out of the water for about 1.5 seconds to breathe. If her name is called during the short period when her meatal orifice is out of the water, she immediately reacts by swimming towards the caller, indicating that the outer ear can be opened quickly. She does not react to the call when her head is below the surface.

Odend'hal & Poulter (1966), Repenning (1972), Ramprashad (1975) and Ramprashad *et al.* (1972) suggest that the distension of the cavernous tissue in the middle ear mucosa of pinnipeds plays an accessory role in equilibration of the pressure of the middle ear cavity with that of the outer ear canal and the nasopharynx. The pressure changes due to swallowing would occur more gradually. During descent the opening of the Eustachian tube by muscular contraction may be facilitated by reducing the pressure difference between the middle ear cavity and the nasopharynx by the inflation of the cavernous tissue. If the cavernous middle ear mucosa only plays an accessory role in pressure regulation, the relatively small amount of cavernous tissue in the walrus compared to phocids and otariids may be explained by the slow speed of descent and ascent of the walrus, which does not have to chase fast swimming prey like other pinniped species.

The walrus tympanic membrane is large, like that of phocids. The ratio of the surface area of the tympanic membrane to the surface area of the oval window is about 20:1, similar to the ratio in humans, and mid-range for pinnipeds (Repenning, 1972). Repenning suggests that this ratio is related to the diving depths of pinniped species. The deeper a species dives, the smaller the ratio. However, the relatively large tympanic membrane may not be related to pressure regulation, but may also be an acoustic adaptation to hear airborne sounds produced by walruses (Schevill *et al.*, 1966; Miller & Boness, 1983; Miller, 1985; Verboom & Kastelein, 1995; Kastelein *et al.*, 1995).

Hearing

The impedance of water differs from that of air. The impedance of a material is calculated by multiplying its specific gravity by the sound propagation

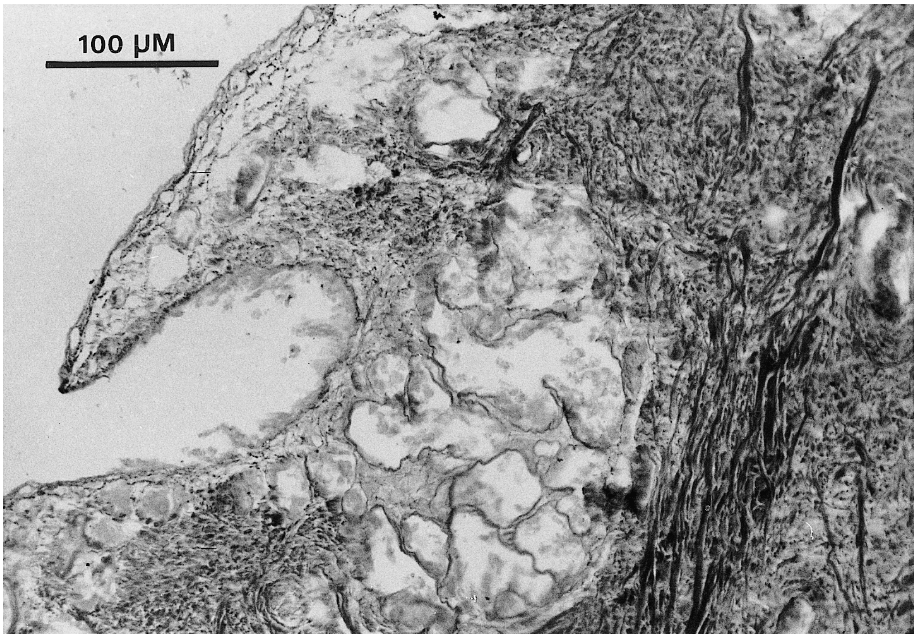


Figure 16. Section of the Eustachian tube with glands which exit in the tube's lumen. The dark fibres are elastic connective tissue (Photo: Merijn de Bakker).

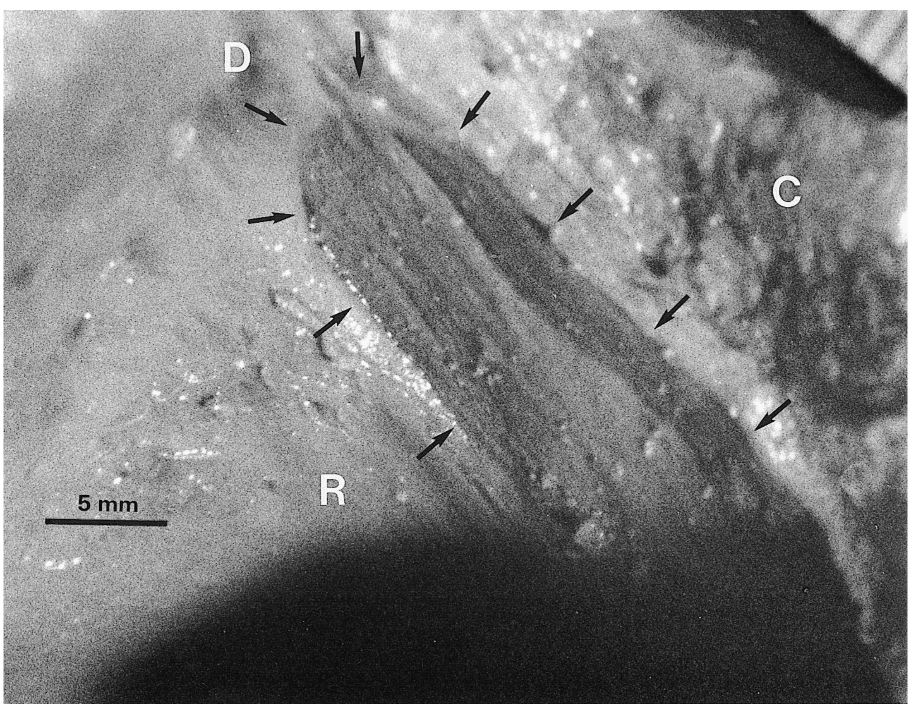


Figure 17. The bow-shaped entrance of the Eustachian tube of the right middle ear of a 15-year-old male Pacific walrus (W3) in the nasopharynx. R = rostral, C = caudal, D = dorsal, which is in the direction of the distal end of the *hamulus pterigoideus*. The arrows point out the perimeter of the entrance (Photo: Ron Kastelein).

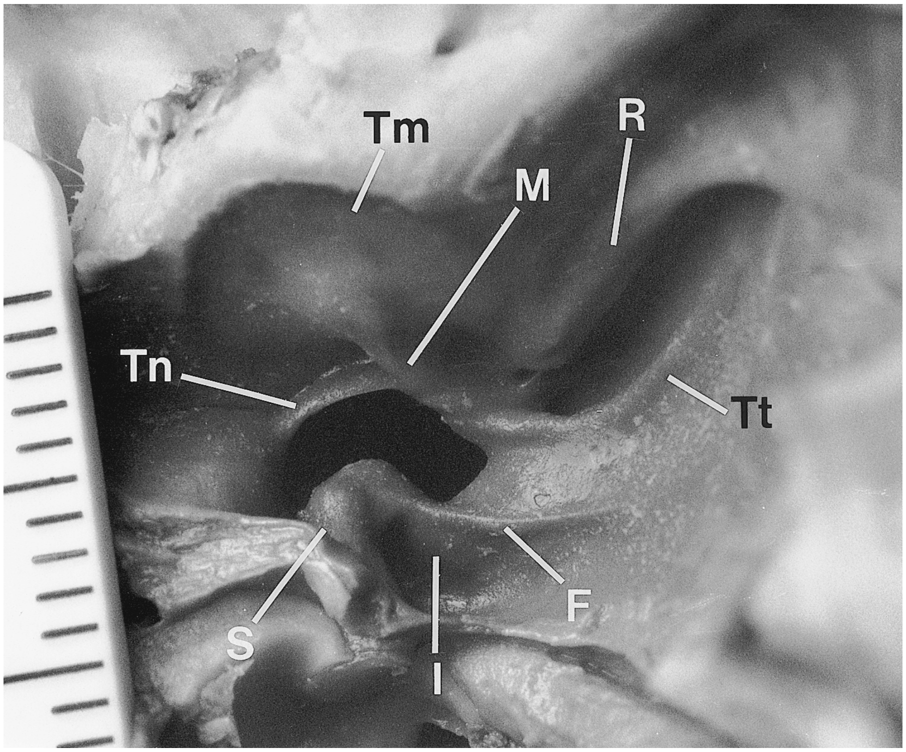


Figure 18. View of the middle ear cavity of the right ear of a 15-year-old male Pacific walrus (W3) towards the tympanic recess (the direction of view is indicated by a black arrow in Figure 13B), showing the tympanic membrane (Tm), the malleus (M), incus (I), stapes (S), tympanic nerve (Tn), *tensor tympani* (Tt), a ridge in the bone (R), and a fold in the mucosa caused by a ventral ridge on the long crus of the incus (F). The ruler has a mm division (Photo: Henk Merjenburgh).

velocity in it. An impedance difference exists between body tissues and sea water. However, large impedance differences exist between different body tissues such as skin, fat, muscles and bone. Underwater sounds probably travel with little attenuation to the walrus middle ear via tissues which have a small impedance difference with water. This would be the softer tissues such as the outer ear canal. The walrus outer ear canal is surrounded by large, hard bones (Kastelein & Gerrits, 1990); caudally the extremely large mastoid process of the temporal bone and rostrally the zygomatic process of the squamosal bone (Fig. 2). The middle ear is laterally shielded by the mastoid process, and ventrally and rostrally by the thick, hard *bulla* (Figs 3 and 4). These bones have dense surfaces, and may act as selective sound reflectors. Sounds, especially those of high frequency, may be refracted away from the denser margins of these bones, and thus ‘piped’ along the bones (Repenning, 1972). Sound reaching the walrus head seems to be focused towards the outer ear canal, which may function as an acoustic antenna and conduct sound to the middle ear (Tonndorf 1966, 1968; Ramprashad, 1975). Evidence that non-bony tissues are used for sound conduction comes from a study on directional hearing of a Harbour seal by Terhune (1974). In this species the directionality of hearing is similar in air and in water, indicating that the auditory pathways originate at or near the meatal orifice, and are thus a similar distance apart, in both air and water. Experiments with a harp seal which was forced under water indicate that in this species the meatus is closed under water. Closing the meatal orifice under water with a finger had no effect on underwater hearing (Møhl & Ronald, 1975). The same experiments also showed that in a Harp seal in shallow water, the area most sensitive to underwater sounds is just below the meatal orifice (Møhl & Ronald, 1975). This is the location of the outer ear canal. Møhl & Ronald (1975) suggested that a model of the pinniped auditory system should employ both sound transparent and sound opaque tissues.

If in walruses the outer ear canal is the main pathway by which underwater sounds are received,

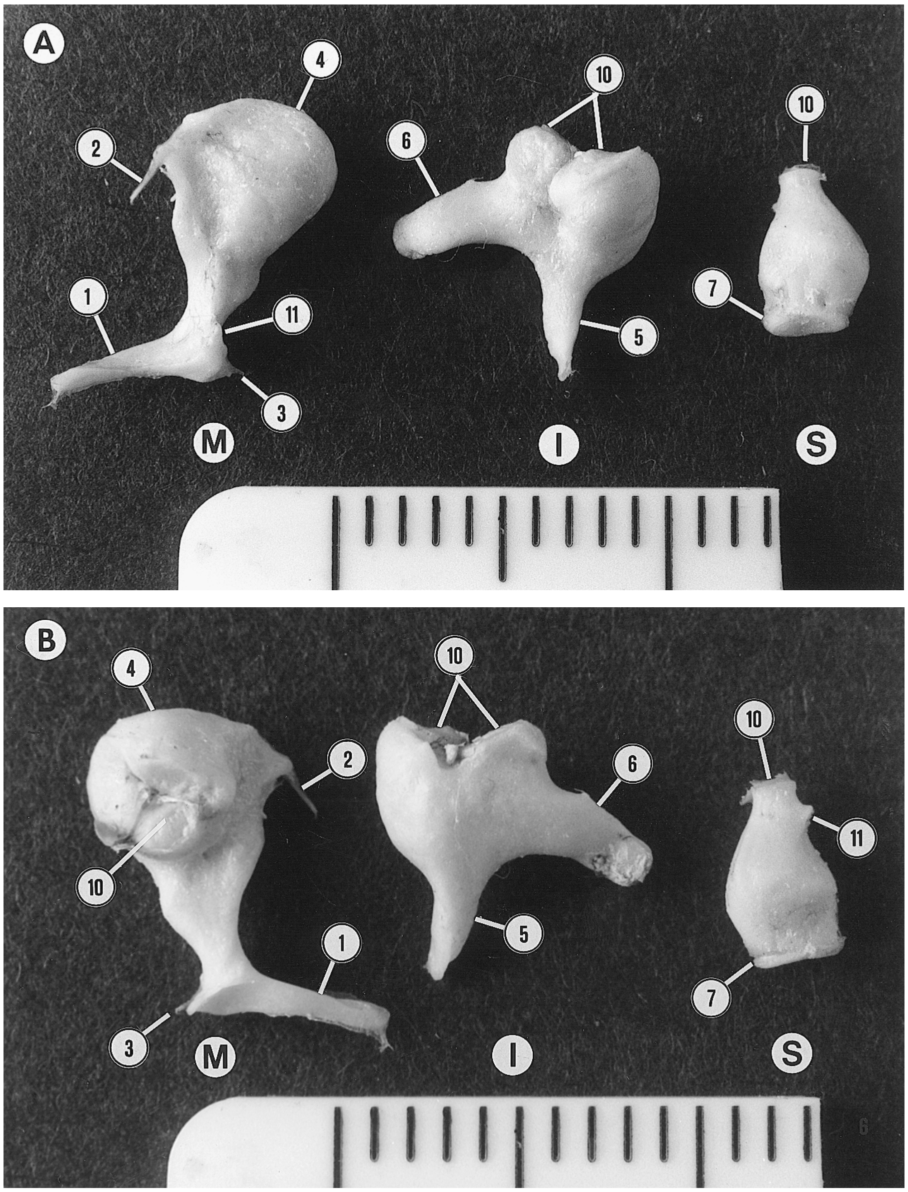
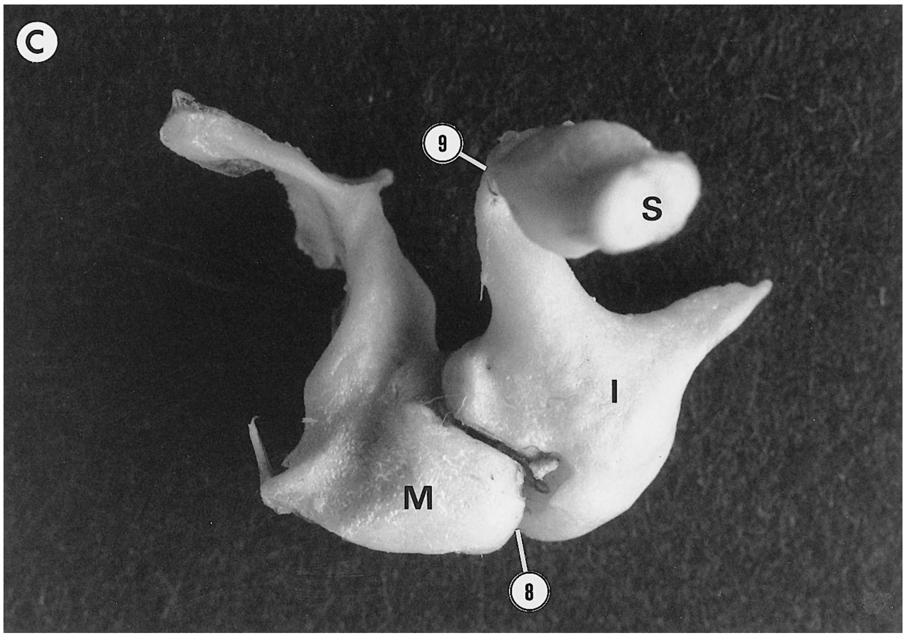


Figure 19. The ear bones of the left ear of a 2-year-old male Pacific walrus. (A) view of individual ossicles from one side, (B) view of the same ossicles from the other side, and (C) view of the ossicles in their natural arrangement. (M) malleus, (I) incus, (S) stapes. (1) manubrium, (2) anterior process, (3) lateral process, (4) head, (5) short crus, (6) long crus, (7) footplate, (8) incudomalleolar articulation, (9) incudostapedia articulation, (10) articulation surface, (11) muscular process. The ruler has a mm division (Photo: Henk Merjenburgh).

then how are they conducted to the inner ear? All tissues of the outer ear tube may be involved in underwater sound conduction towards the middle ear. The longitudinal blood vessels themselves, which extend to the tympanic membrane, may serve as a wave guide for under water sound (Møhl, 1968*b*; Ramprashad, 1975).

The walrus has a large head and a long interaural distance which leads to a long interaural time delay, favouring directional hearing. Directional hearing



under water may be important to walruses, since during the breeding season reproductive males deter other males and attract females in oestrus by means of underwater calls (Miller & Boness, 1983; Stirling *et al*., 1987). If underwater sound reached the inner ear by bone conduction, one would have expected a very loose connection between the left and right middle and inner ears in order to maintain directional hearing. Such a construction is seen in dolphins (McCormick *et al.*, 1970), but this separation is not found in walruses. Walruses might also use directional hearing to decode the acoustic signature of a water volume; a sort of passive sonar for general orientation.

Conduction of vibrations from the walrus' viscerocranium to the neurocranium and ears may be limited by the cartilaginous cushion in the zygomatic arch (Fig. 2A and Kastelein & Gerrits, 1990). Vibrations can be caused by the walrus hitting the substrate to haul out or to keep a breathing hole in the ice open (Fay, 1982). In NE Greenland, walruses have been observed to create breathing holes in 10 cm thick ice by hitting it with their heads from below the surface (Møhl, pers. comm.). The zygomatic cartilage may prevent damage to the ears and distortion of the vestibular system. It may also reduce noise reaching the ears by bone conduction and caused by the tusks scraping along the substrate when a walrus is pushing its nose through the substrate during foraging (see fig. 102 in Fay, 1982, and Fig. 2 in Kastelein & Mosterd, 1989). Such noise, which may continue for a long time, as walruses dig long furrows in the ocean floor (Oliver *et al.*, 1983; Nelson & Johnson, 1987), may otherwise mask more relevant sounds.

Other than to equalize pressure, the vascularized tissue in the walrus' middle ear may also have an acoustic function. Only the non-vascularized part of the mucosa touches the ossicle chain. If the vascularized part of the mucosa touched the ossicle chain, this would result in friction and attenuation. Inflation of the mucosa probably increases the tension on the ossicle chain, and the stiffer the chain, the better it conducts high frequency sounds (Ramprashad *et al.*, 1972). Under water it may be important for walruses to hear the high frequency sounds produced by killer whales (*Orcinus orca*) which predate on walrus pups (Fay, 1982).

Repenning (1972) suggests that in pinnipeds the middle ear cavernous tissue may transmit sounds across the tympanic cavity to the cochlear shell. Terhune (1989) proposes that the cavernous tissues which line the walls of the outer and middle ears always engorge with blood when phocids are submerging, and that this has a mainly acoustic function: 'When the tissues are filled with blood, the acoustical impedance would be high, thus facilitating greater sensitivity underwater and producing a 30 dB loss of sensitivity in air. When the tissues are drained, the acoustical impedance would be lower, thus facilitating greater sensitivity in air'. However, this model does not fit the walrus in which the vascularized tissue of the middle ear does not touch the tympanic membrane.

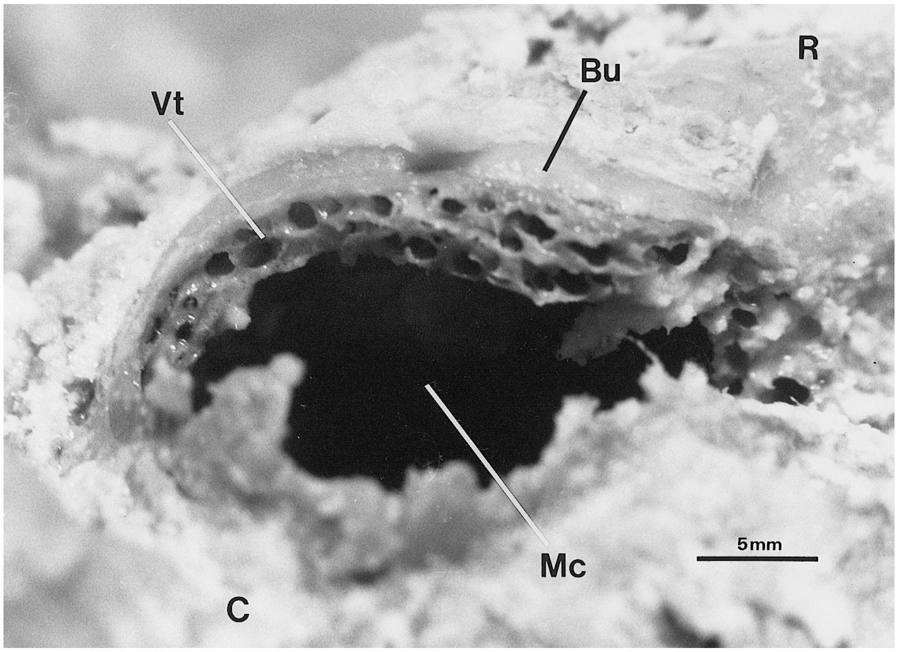


Figure 20. A hole in the ventro-caudal part of the *bulla* (Bu) of an 8-year-old female Atlantic walrus, the location of the thickest vascularized tissue (Vt) lining the middle ear cavity (Mc). R=rostral, C=caudal. For the location of the hole, see the arrow in Figure 13A (Photo: Ron Kastelein).

Møhl (1968*b*) suggests that the vascularized tissue lining the middle ear can change the volume of the middle ear cavity, thus changing the resonance frequency.

Lipatov (1992) conducted experiments on the outer ears of seals and sea lions. He concluded that during diving, the outer ear remains air-filled and functions as 'a distributed-exitation closed tube'. He concluded that air in the outer ear is essential to underwater hearing, and that this air in the cartilaginous tube is the basic path of sound conduction from water to the middle ear. He suggests that underwater hearing involves the excitation of the tympanic membrane and the auditory ossicles. However, some of his methods may have interfered with the mechanism that occurs during diving. The insertion of a glass or metal tube in the outer ear probably interfered with the muscles involved with the closure of the outer ear opening, and in addition probably prevented deformation of the tube under pressure. Some of Lipatov's observations may also have been influenced by the shallow depth at which his underwater experiments were conducted. The outer ear probably only deforms after the external pressure surpasses a certain level, which may not be reached in a shallow experimental tank. Pushing out the air in the external ear with a finger was another method used by Lipatov (1992). This resulted in a reduced underwater hearing sensitivity, but the presence of the finger may have caused the decrease in hearing sensitivity. Filling the outer ear with water also reduced the underwater hearing sensitivity. This is an unnatural situation because pinnipeds have adaptations to prevent water from entering the outer ear canal. Therefore filling the outer ear with water will most likely have reduced the animals' hearing capabilities, because the water reached the tympanic membrane. However, although Lipatov's methods may have altered certain mechanisms of the outer ear, that does not mean that air in the outer ear does not play a role in underwater hearing.

Ear wax (cerumen)

The greater the distance between the meatus and tympanic membrane, the smaller the chance of any water, which accidently passes the zone with auricular muscles, reaching the tympanic membrane. Such a long tube, which is probably poorly ventilated and kept at around core body temperature due to the thick blubber and skin layers, would be an ideal place for the growth of micro organisms and parasites. However, the copious amount of ear wax lining the lumen of the outer ear canal probably inhibits their proliferation. In humans, the cerumen reduces the growth of bacteria and fungi, which are

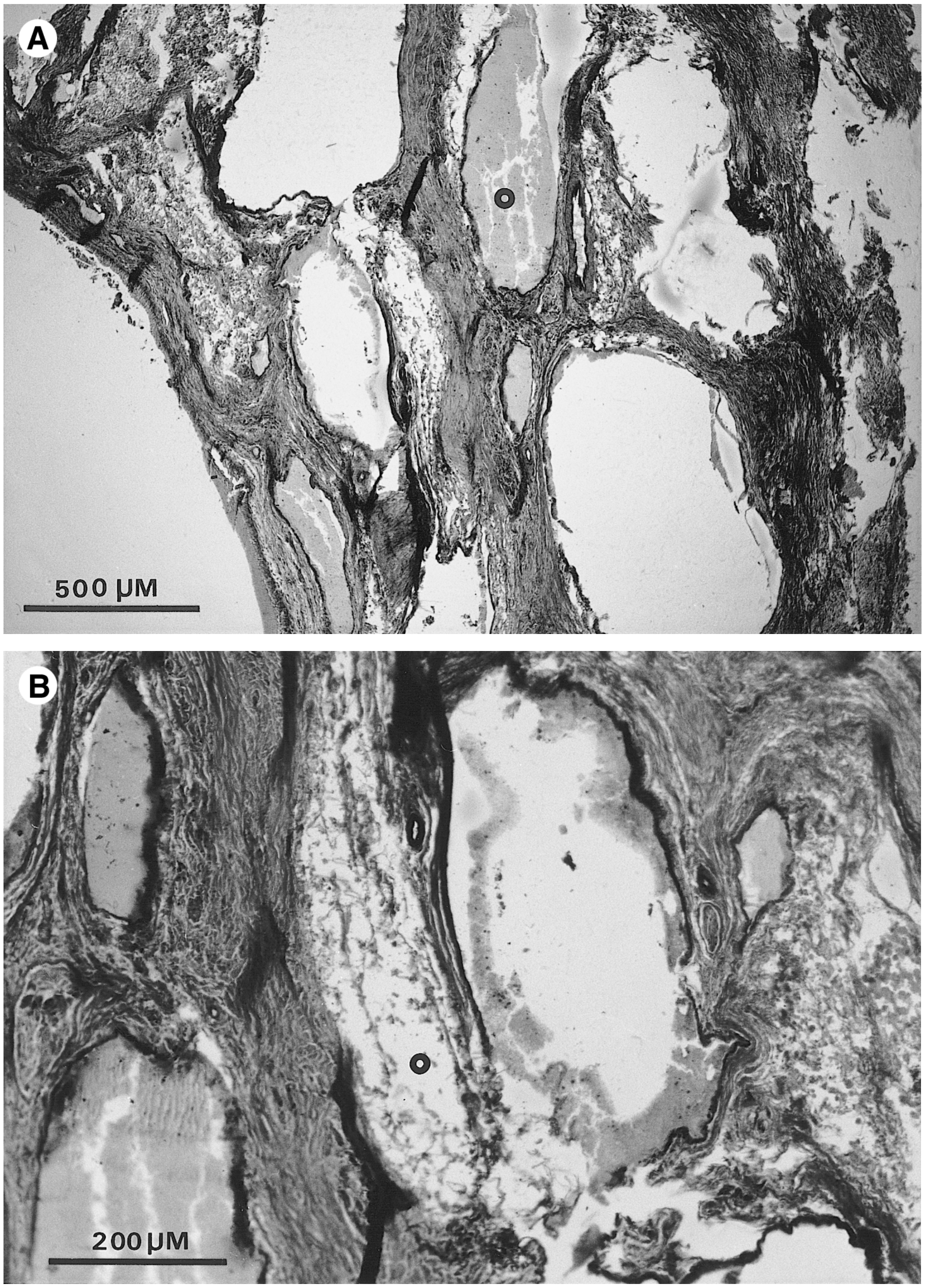


Figure 21. (A) The strongly vascularized lining of the middle ear. Some vessels contain remnants of blood. (B) A larger magnification of Figure A. The wall of the vessels consists of collagen connective tissue (Photos: Merijn de Bakker).

often found in the outer ear. This is mainly because the ear wax contains heavy metals such as copper and has a low pH of between 5 and 5.7 (Bongers *et al*., 1990). In terrestrial mammals the sticky cerumen may also function to prevent insects from reaching the tympanic membrane. The anopluran louse (*Antarctophthirus trichechi*), which resides in skin folds in wild walruses, has also been found in the walrus' outer ear canal (Fay, 1982). Possibly the ear wax in walruses prevents these lice from

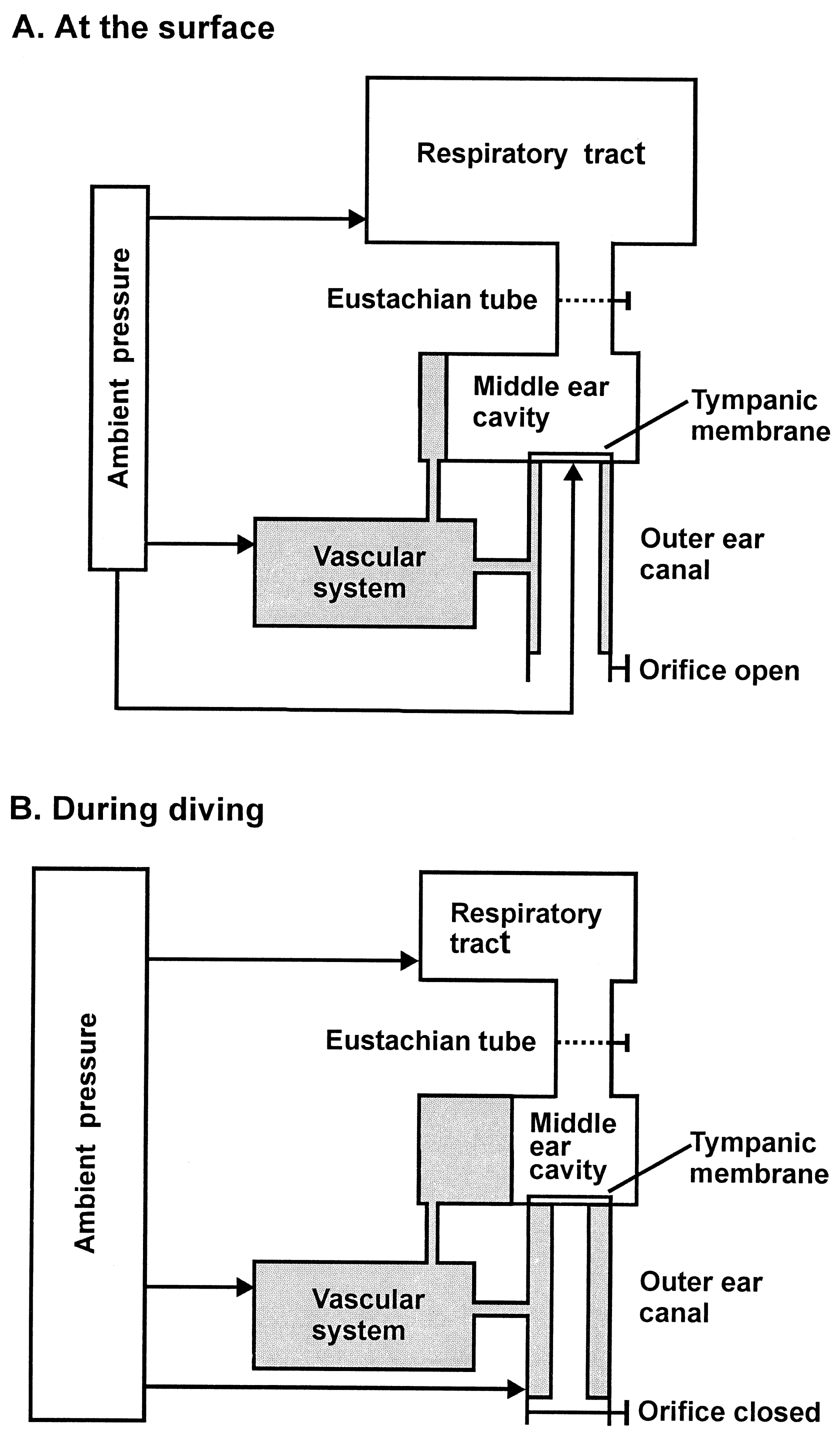


Figure 22. The schematic anatomy of the respiratory tract, vascular system, Eustachian tube and external and middle ears of a walrus when in air (A) and while diving (B) (Drawings: Ron Kastelein and Rob Triesscheijn).

Figure 23. A group of male Atlantic walruses at Sarstangen, Svalbard, resting on the beach. The upside-down and lateral positions may allow drainage of the copious amounts of earwax produced in the walrus ear. If not drained regularly, the earwax may come in contact with the tympanic membrane (Photo: Ron Kastelein).

reaching the tympanic membrane. In walruses ear wax production may be stimulated by small amounts of water which enter the outer ear canal, as is the case in humans.

During diving, some of the ear wax is probably pushed towards the tympanic membrane due to a reduction of the lumen size of the outer ear canal either by engorgement of the blood vessels and/or by deformation of the canal. In addition to gravity, this could be the cause for the large amount of ear wax accumulated in the bony part of the outer ear. If the amount of ear wax in the proximal part of the outer ear canal became so large that it touched the tympanic membrane, it would reduce in-air hearing. This is prevented from happening because walruses lie sideways or upside-down for a large proportion of the time when hauled out (Fig. 23). This posture causes surplus ear wax to drain from the outer ear canal by gravity. Ear wax can often be seen around the external orifices of hauled out walruses, also on the dorsal side.

In addition to functioning in pressure regulation, heat from the blood vessels in the walrus' outer ear canal may keep the cerumen at the right viscosity. In humans, the cerumen is semi fluid at 31°C, the temperature of the outer ear (Bongers *et al.*, 1990). In a walrus, the temperature of the outer ear would be lower due to low ambient temperatures if no vascular system lined the outer ear canal. Possibly the blood vessels in the outer ear keep the cerumen at such a temperature that it remains semi-fluid.

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