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The anatomy of the walrus head (*Odobenus rosmarus*). Part 5: The tongue and its function in walrus ecology

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Summary

The tongues of several walruses were examined in terms of gross morphology, anatomy and histology. Compared to the tongues of other pinnipeds, most of which eat fish, the tongue of the walrus is broad, thick, short and smooth. The tip of the tongue can be rounded or bifid, and tip shape seems to be unrelated to the sub-species, gender or age of the walrus, and to whether it is living or dead.

The tongue almost fills the buccal cavity and consists mainly of muscle. When it is retracted and depressed in the buccal cavity, it creates a very low pressure, by means of which the edible parts of bivalve molluscs are extracted from their shells.

The dermis of the tongue consists of a thick layer of connective tissue with dermal papillae protruding into a clearly cornified epidermis. Lamellated corpuscles are mostly found just below the epidermis; many are found at the tip of the tongue. The ventral half of the epidermal cones at the tip of the tongue are densely innervated. Fourteen circular protrusions, in the median part of the tongue, have more innervation than the surrounding tissue, and lamellated corpuscles are found directly under them. The tip of the tongue has good tactile sense, and is probably used for identifying objects and for checking the position of bivalve molluscs in the mouth. There are seven circumvallate papillae at the caudal end of the tongue. Compared to many terrestrial mammals, the walrus has relatively few, but large taste buds. Caudal of the circumvallate papillae, fusiform papillae are present in a V-shape, pointing in the caudal direction, which are shorter at the rostral end than at the caudal end. The inside of the fusiform papillae consists of serous glands, and the salivary glands under the papillae are also serous.

The tongue of the walrus is adapted to the manipulation of its main prey: bivalve molluscs.

Introduction

The tongues of mammal species are of various sizes, shapes and surface textures, according to their functions. The aim of the present study was to describe the gross morphology, anatomy and histology of the tongue of the walrus and to discuss its function in the ecology of the species. So far, a few studies on the walrus tongue have been published: an anatomical study indicating the location of the vallate papillae (Murie, 1871), a morphological study on the sense organs of the tongue (Sonntag, 1923), and a superficial (Fay, 1982) and a more thorough (Kastelein *et al.*, 1991*b*) description of the tongue muscles.

The present study is part 5 of a larger investigation of the anatomy of the walrus head. Part 1 described the cranial bones in relation to feeding and hauling out (Kastelein & Gerrits, 1990), part 2 described the head muscles and their function in feeding and other behaviour (Kastelein *et al.*, 1991*b*), part 3 described the eyes and their function in walrus ecology (Kastelein *et al.*, 1993), and part 4 described the ears and their adaptations to aerial and underwater hearing (Kastelein *et al.*, 1996).

Materials and methods

Gross morphology

For morphological investigations the tongues of two male Atlantic walruses (*Odobenus rosmarus rosmarus*), more than 8 years old, received from Inuit from the Thule area in Greenland in May 1989, were preserved in 4% formaldehyde in tap water. The tongue of a 15-year-old male Pacific walrus (*Odobenus rosmarus divergens*; OrZH001) was put in fixative 30 h after the animal died. The tongue of an 17-year-old male Atlantic walrus (IGOR93-53) was preserved in 10% formaldehyde in tap water 6 h after death, having been kept on ice.

A tongue tip survey was held among seven facilities that keep walruses. They were asked the following questions about each of their walruses: subspecies, name or I.D. number, sex, age, whether it had a cleft in the tip of the tongue, and whether the animal was dead or alive when the tongue was examined.

An 8-year-old male Pacific walrus (OrZH003) at the Harderwijk Park was trained to stick its tongue out, and photographs were taken from the front and side.

Anatomy
The position of the tongue in the skull and the anatomy of its muscles were investigated in the heads of two approximately 8-year-old female Atlantic walruses of similar sizes (KFHB#19 and KFHB#20). The heads were obtained from Inuit from the Hudson Bay area, Canada, in June 1988, frozen immediately after death. One 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 still 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 with a 2 × 2 cm grid in the background. 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 mid-sagittally along the longitudinal axis and 2 cm lateral of the mid-sagittal plane and the sides were photographed against the 2 × 2 cm grid background.

Histology
The histology of the dermis and epidermis are described. For histological investigation the tongue of a 1.5-year-old male Pacific walrus (OrZH010) was preserved 4 h after death. Earlier attempts to preserve tongues had shown that especially the peripheral nerve tissue did not preserve and stain well when tongues were simply put into a jar with the fixative (4% formaldehyde in tap water). Therefore, several cuts were made through the cornified skin of this tongue so that the fixative could reach the underlying tissue.

The positions at which samples for histological investigation were taken are indicated in Figure 1. An 11 mm × 4 mm sample was taken from the tip of the tongue (sample a in Fig. 1). Sample b included three conical papillae at the tip of the tongue. Sample c was 20 mm × 5 mm and cut from the middle of the dorsum of the tongue. Sample d contained a circumvallate papilla. Sample e from the base of the tongue contained several foliated protrusions or fusiform papillae. In addition, a sample was taken from the side of the tongue. All samples were dehydrated using alcohols and embedded in paraplast. Eight 1 μm thick sections were cut on a Leitz rotary microtome. The sections were stained with either the Van Gieson trichrome method (Bancroft & Stevens, 1990) or the silver impregnation method for nervous tissue (Sevier & Munger, 1965). Prior to the silver staining, the dewaxed sections were soaked overnight in 4% formaldehyde in tap water (pH ± 7) to enhance the staining of the nerve tissue. Some sections of the circumvallate papillae and the protrusions at the base of the tongue were stained with the combined Alcian blue-PAS technique according to Mowry to distinguish between serous and mucous cells (Bancroft & Stevens, 1990).

Results

Gross morphology
The walrus tongue is very broad and thick and can be extended to about 1 cm beyond the upper and lower lips (Fig. 2A, B). The roof of the buccal cavity is strongly arched (Figs 3, 4 and 5A–E), thus accommodating the thick tongue.

In some animals the tip of the tongue is slightly bifid (Figs 1, 2 and 4), while in others it is rounded (Fig. 5A). The results of the tongue tip survey are shown in Table 1. The cleft in the tip of the tongue occurs in both sub-species, both genders and in all investigated ages. The cleft was sometimes observed in tongues of live and dead walruses.

The surface of the tongue of the walrus is smoother than that of most other pinnipeds, and the sides of the tongue are also smooth (Figs 1, 2 and 5A–D).

Anatomy
The tongue fills most of the buccal cavity (Figs 5 and 6), and consists mostly of muscle. The muscles have been described previously in detail by Kastelein *et al.* (1991*b*). Four muscles can be distinguished, 3 extrinsic and 1 intrinsic.

(1) The well-developed *M. genioglossus* (Figs 5B–I and 6A, B). During their predominantly backward course, the muscle fibres at first lie lateral to the *M. geniohyoideus* and more caudally dorsal to the *M. mylohyoideus* (Fig. 5D–J). A bundle of fibres runs posteriorly to insert on the basihyoid and ceratohyoid bones (Fig. 5I). It depresses the tongue, and the posterior fibres draw the tongue forward.

(2) The well-developed *M. hyoglossus* is located in the root of the tongue (Fig. 5E–J). In its forward course, it runs dorsal to the *M. mylohyoideus* and lateral to the *M. geniohyoideus* and the *M. genioglossus*. At the base of the tongue it crosses the medial side of the *M. styloglossus* to insert in the muscular posterior two-thirds of the tongue. It retracts and depresses the tongue.

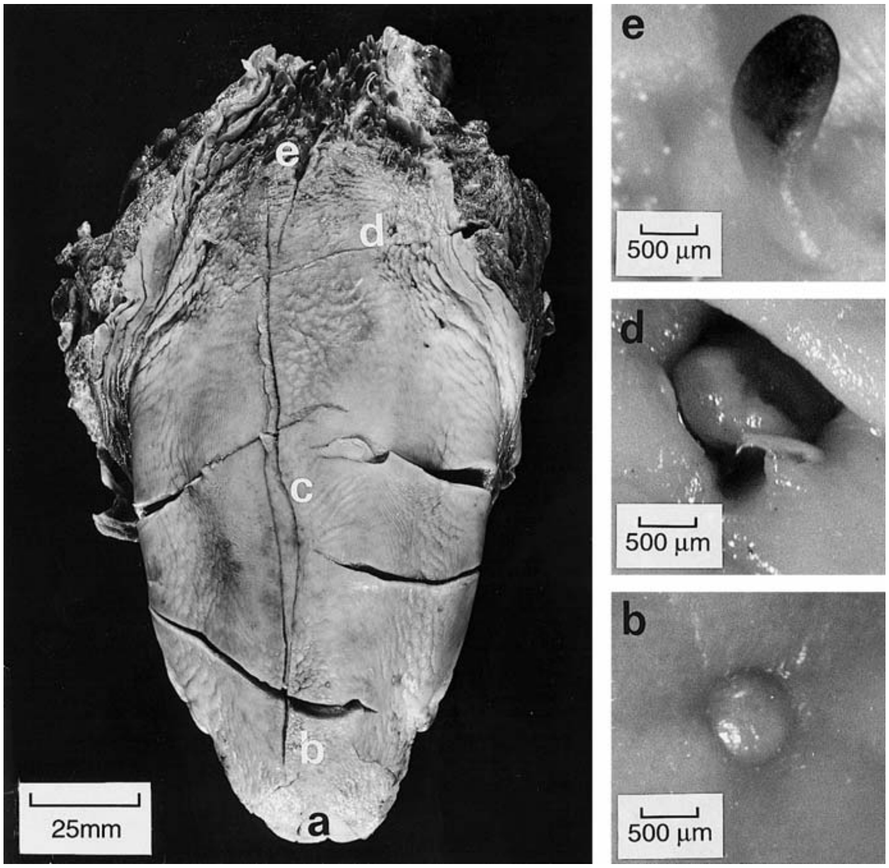


Figure 1. Macro photograph of the slightly bifid tongue of a 1.5-year-old male Pacific walrus. The letters indicate the locations of the samples used for histological investigation: (a) tip of the tongue, (b) conical papillae—shows an enlargement, (c) middle of the tongue, (d) circumvallate papillae (see enlargement), and (e) fusiform papillae (see enlargement) (Photos: Merijn de Bakker).

(3) The well-developed *M. styloglossus* passes from the stylohyoid bone to the tongue, lateral to the *M. genioglossus* and *M. hyoglossus* (Figs 5B–H and 6b). It draws the tongue backwards.

(4) The *M. lingualis proprius* consists of many poorly delineated muscle bundles which are located among the fascicles of insertion of the tongue's extrinsic muscles (Figs 5D–H and 6A, B). These bundles run in diverse directions. By intrinsic movements the muscle bundles shape the tongue, even protruding the tongue by lengthening it.

Histology

The dermis of the tongue consists of a considerably thick (1.0–2.0 mm) layer of connective tissue with dermal papillae protruding into a clearly cornified epidermis (Figs 7A and 9). The horny layer of the epidermis, the *stratum corneum*, is about 50 µm thick (Figs 7A and 9); it is similar in thickness to the cornification of the human body skin. It is thinnest (12.5 µm) at the rostral part of the tongue. The epidermis is thicker and the dermal papillae are longer in the tip of the tongue than in other parts (compare Figs 7 and 9). The sample taken from the side of the tongue was very similar to sample C from the middle of the tongue (Fig. 9), and is therefore not described separately.

Nerve bundles were present in most parts of the dermis, but their appearance suggested that the fixation of the tissue was not optimal. However, small lamellated corpuscles could be recognized in the silver stained sections (Figs 7–9). These corpuscles have a diameter of 34 ± 10 µm ($n=30$) and are mostly just below the epidermis, between dermal papillae or occasionally within these papillae. In a single sample from area a (Fig. 1) 36 lamellated corpuscles were counted, whereas in single sections from most other samples only

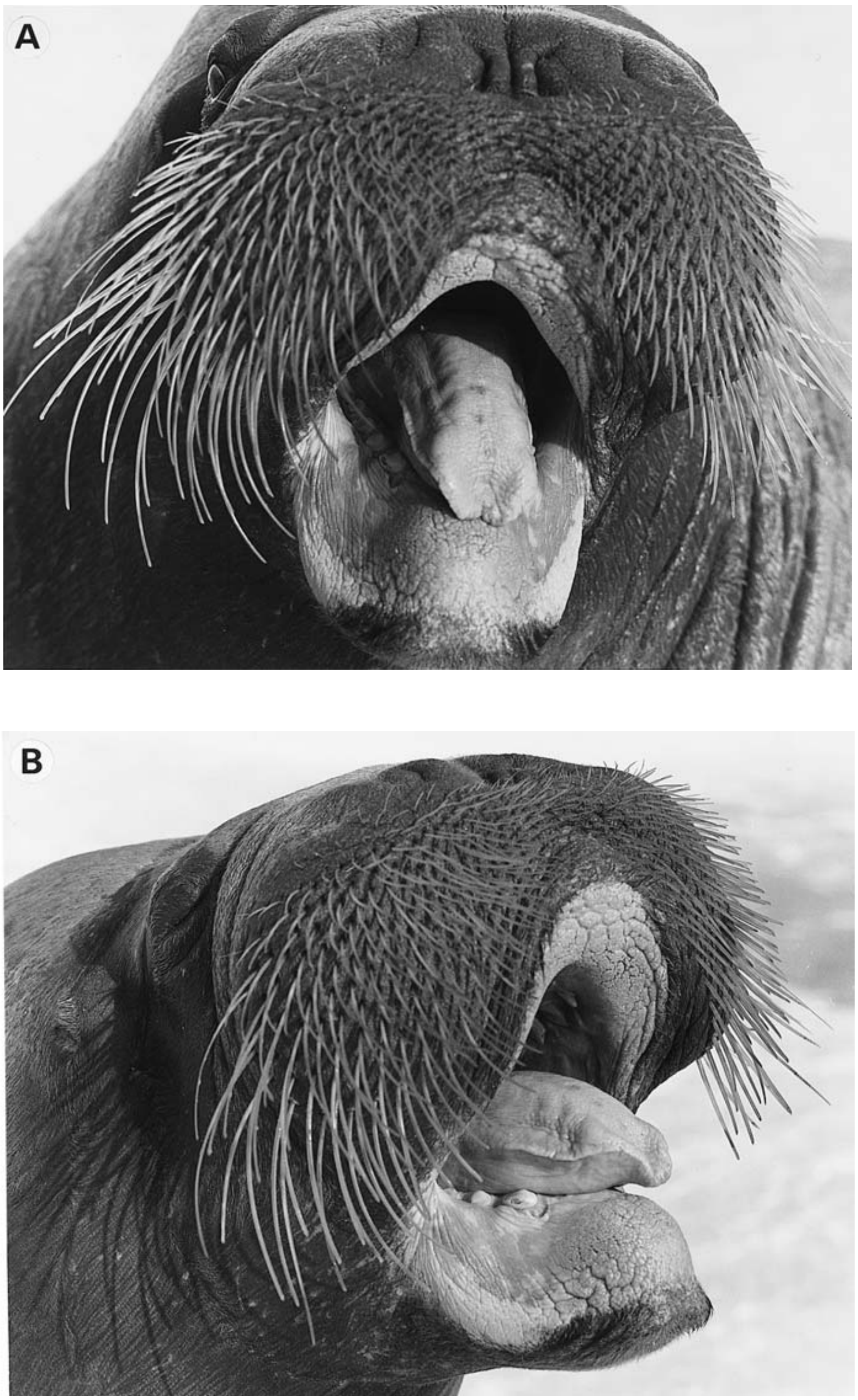


Figure 2. A 7-year-old male Pacific walrus sticking its tongue out; (A) frontal view, (B) lateral view (Photos: Henk Merjenburgh).

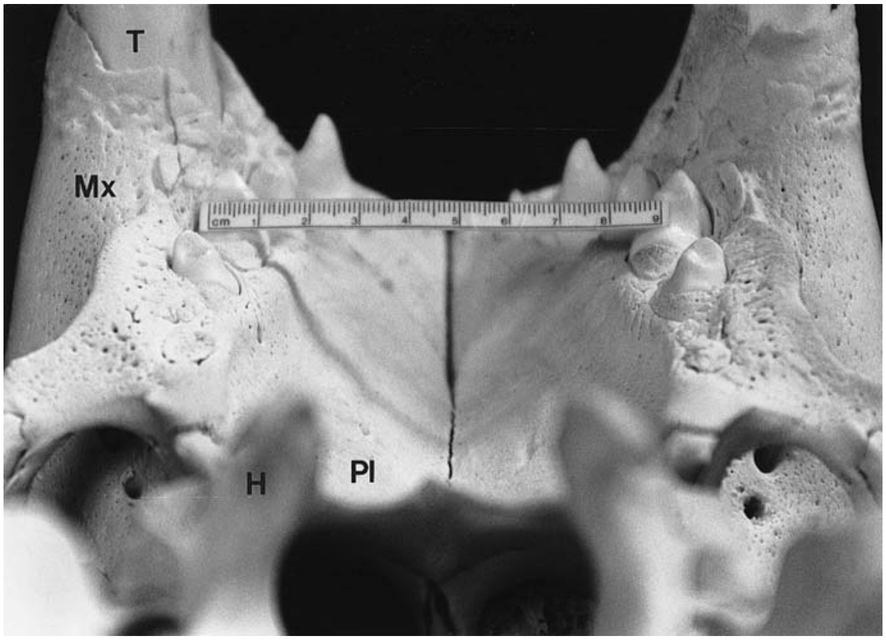


Figure 3. Ventral view of the up-side down skull of a 6-year-old male Pacific walrus which lived in human care (and thus does not have worn teeth), showing the arched shape of the roof of the buccal cavity. T=tusk, H=*Hamulus pterygoideus*, Mx=Maxilla, Pl=Palatine (Photo: Ron Kastelein).

1–3 corpuscles were found. No other types of mechanoreceptors were detected; this is probably partly due to the imperfect fixation and poor silver staining. The ventral half of the epidermal cones at the tip of the tongue, however, were rather densely innervated by free nerve endings (arrows in Fig. 7C).

Fourteen circular protrusions each with a diameter of 1.5 mm were present in the sample from area b (Fig. 1). These protrusions correspond to the conical papillae described by Sonntag (1925). These papillae had a stronger innervation than the surrounding tissue, with nerves ascending in the centre of the papillae (arrows in Fig. 8). Five to 10 lamellated corpuscles per section were found directly under the papillae.

Seven circumvallate papillae (or vallate papillae; Sonntag, 1925) were configured in a V-shape in the sample from area d (Fig. 1). In the seventy 8 µm transverse sections of one of these circumvallate papillae 7 taste buds were found (Fig. 10). No taste buds were found in other parts of the tongue. The total length of the sample examined was 0.56 mm and the diameter of the circumvallate papilla was 1.5 mm. In the outer wall of the circumvallate papilla no taste buds were discovered. The number of taste buds per circumvallate papilla of the walrus is estimated to be around 20 ($1.5/0.56 \times 7 = 18.75$). The taste buds have a diameter of 75 µm and a height of 125 µm (Fig. 10A, B). The salivary glands under the circumvallate papilla, also known as glands of Von Ebner, consist predominantly of serous cells with occasionally a mucous cell (Fig. 10A).

At the base of the tongue, just behind the circumvallate papillae, protrusions (fusiform papillae; Sonntag, 1925) were present in a V-shape pointing in the caudal direction (e in Fig. 1). The length of the protrusions increases from 4 mm at the rostral end to 7 mm at the caudal point; the inside consists of a serous gland. The salivary glands underneath these protrusions are also serous.

Discussion

Gross morphology

Laet (1633), Murie (1871) and Sonntag (1923) describe the tongue of the walrus as short (or wide compared to its length) and thick compared to the tongue of other pinnipeds. Murie (1871) describes the dorsal surface of the tongue of the walrus as smoother than that of other pinnipeds (Eastman & Coalson, 1974). Sonntag (1923) noticed that the borders of the tongue were massive and smooth. Similar observations were made in the present study. The tongue of the walrus may be adapted to

Figure 4. Frontal view of the mouth of a 7-year-old male Pacific walrus sticking his tongue out. Note the slightly bifid tip of the tongue and the thick lips (Photo: Henk Merjenburgh).

its main prey: bivalve molluscs (Fay, 1982). Other pinnipeds may need longer and rougher tongues to manipulate slippery fish so that they go head-first through the oesophagus.

Daubenton (in Murie, 1871) described the tongue of an Atlantic walrus foetus as 'split at the tip like that of a seal'. Murie (1871) found that the tip of the tongue of an Atlantic walrus of less than one year old was rounded and smooth, in contrast to tongues of many other pinnipeds of which the tip is bifid. Sonntag (1923) and King (1923) agree that the walrus tongue is round and entire. Fay (1985) describes the tip of the tongue as rounded or weakly bifid. The present study shows that the tip of the walrus tongue can be rounded or bifid, and that the shape of the tongue tip is probably individually variable.

Anatomy

The tongue can be shaped by the intrinsic tongue muscle (*M. lingualis proprius*) to fit the shape of the mouth cavity's highly vaulted palate (see also illustrations in Kastelein & Gerrits, 1990). The tongue can be forcefully retracted by the large *M. styloglossus* and *M. hyoglossus* and depressed by the large *M. genioglossus* and the infrahyoidal muscles (see illustrations in Kastelein *et al.*, 1991*b*). In this way the tongue works like a piston to create negative pressure in the buccal cavity. Perhaps this is why the tongue is short and thick. The flexible and muscular lips ensure that the full effect of the vacuum is exerted only on objects held in the incisive area at the front of the mouth. To withstand the large pressure changes in the buccal cavity the internal choana is short, requiring only a short soft palate which can be stretched by the strong *M. tensor veli palatini*, and raised by the strong *M. levator veli palatini* (see illustrations in Kastelein *et al.*, 1991*b*).

Fay (1982) describes a walrus which produced a pressure of around − 91.4 kPa (− 0.914 Bar) when sucking a tube connected to a mechanical pressure gauge. At the time of measurement, the animal was sucking air along the mouth piece. Kastelein *et al.* (1994) measured the pressure in the oral cavity of a female Pacific walrus during several in-air and underwater suction tests with a pressure transducer. The lowest pressure recorded in air was − 87.9 kPa (− 0.879 Bar, almost vacuum) when the walrus sucked on the pressure transducer. The lowest pressure recorded under water was − 118.8 kPa (− 1.188 Bar) when the walrus was sucking on a mackerel. The study indicated that the walrus had good control over its tongue muscles and thus over both the pressure and the duration of suction.

Mechanoreception

The shape, size and position in the dermis of the lamellated corpuscles in the tongue in the present study are consistent with descriptions given by Halata (1975) who called them paciniform corpuscles or encapsulated corpuscles with inner core, by Chouchkov (1978) who called them Kraus

Figure 5. (A–J) The rostral side of transverse sections through an 8-year-old female Atlantic walrus head (KFHB#19), showing the position of the tongue in the buccal cavity and the tongue muscles. (1) *M. genioglossus*, (2) *M. hyoglossus*, (3) *M. styloglossus*, (4) *M. lingualis proprius*, (5) *M. mylohyoideus*, (6) *M. geniohyoideus*, (7) *M. ceratohyoideus*, (8) Hyoid bone. Mn = Mandible, Mx = Maxilla, T = Tusk. The arrows in the upper left hand corner indicate the locations of the sections. The rounded tip in (A) is indicated by a white arrow. Background grid: 2 cm × 2 cm (Photos: Henk Merjenburgh).

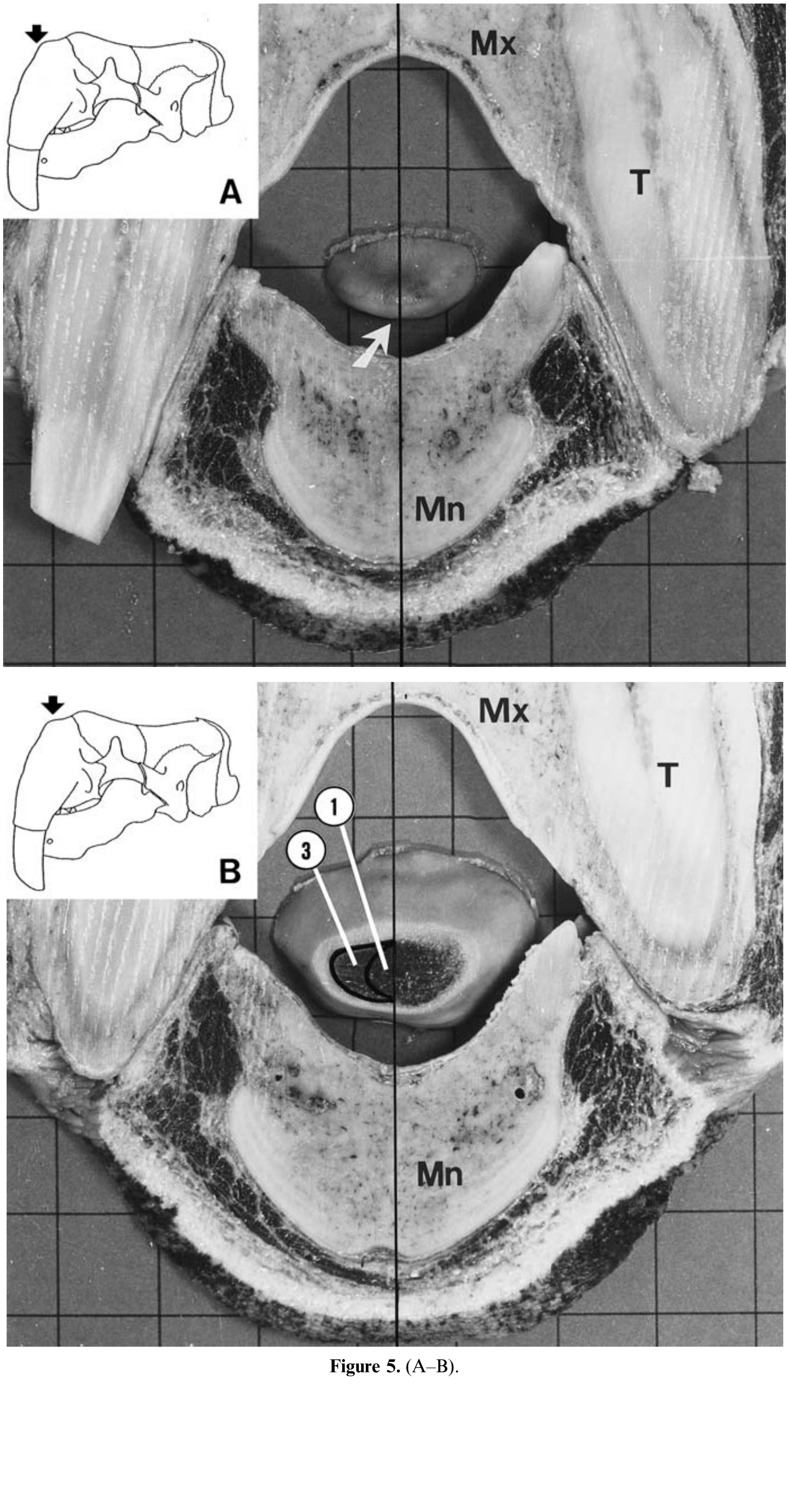


Figure 5. (A–B).

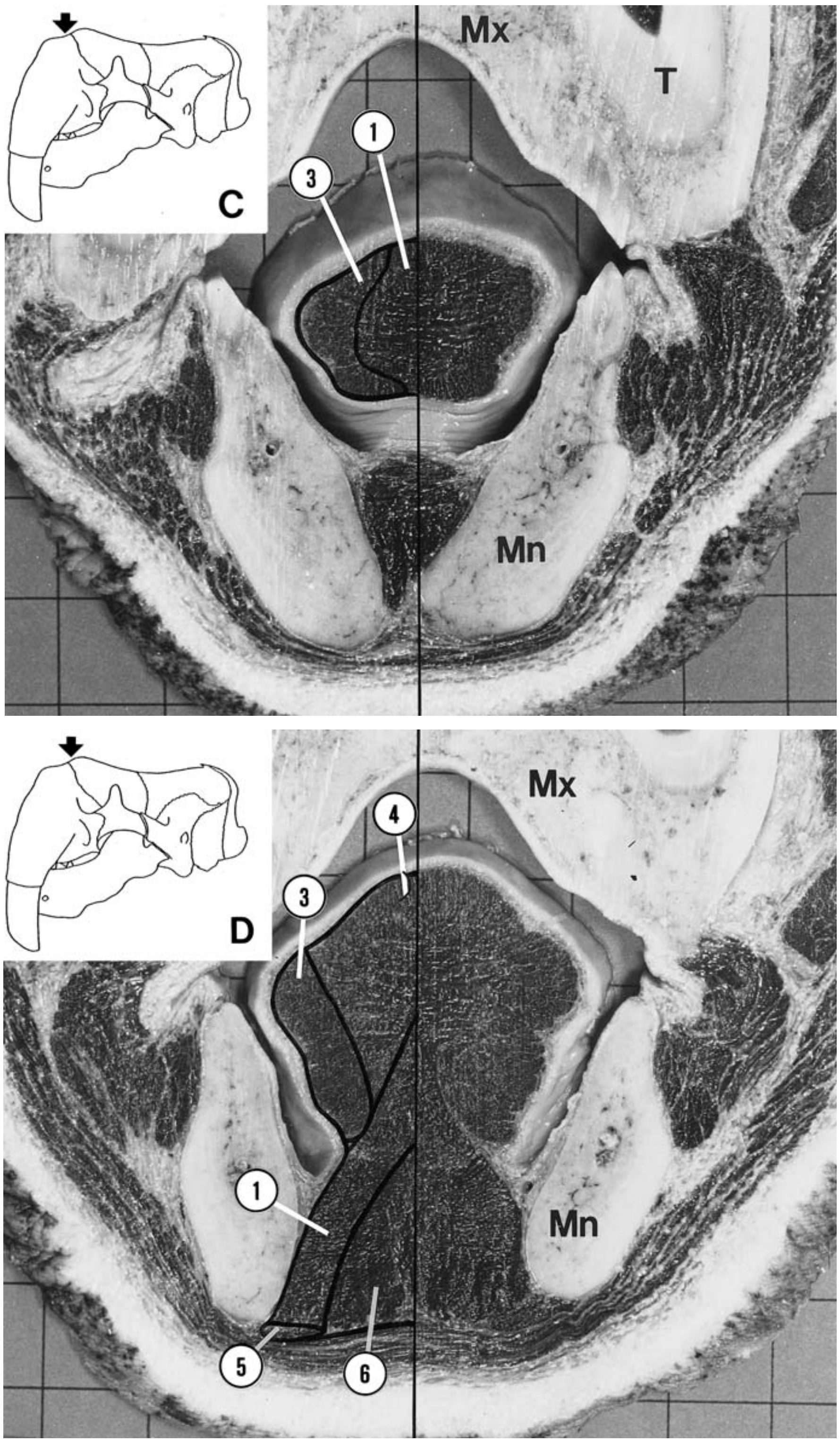


Figure 5. (C–D).

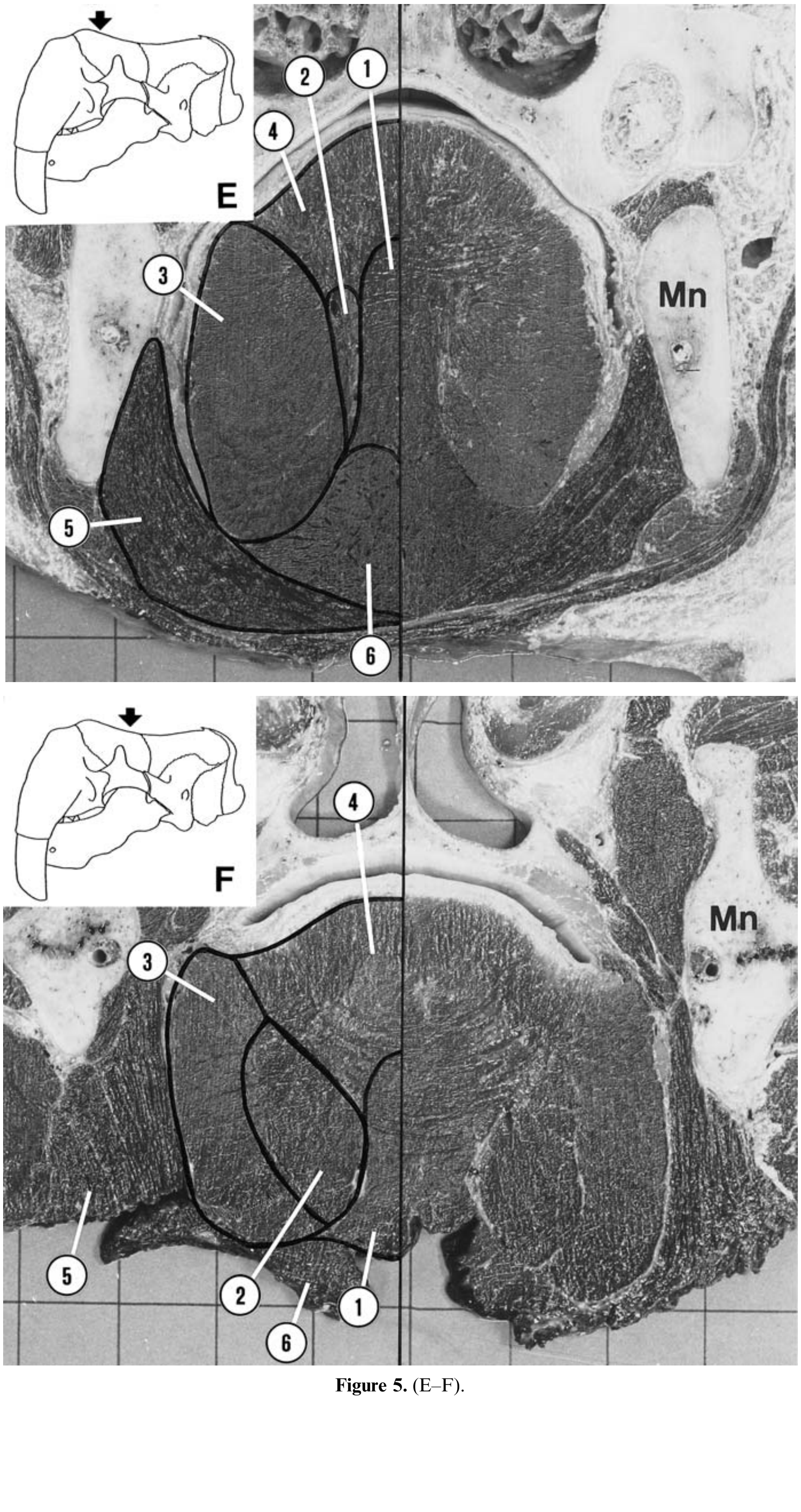
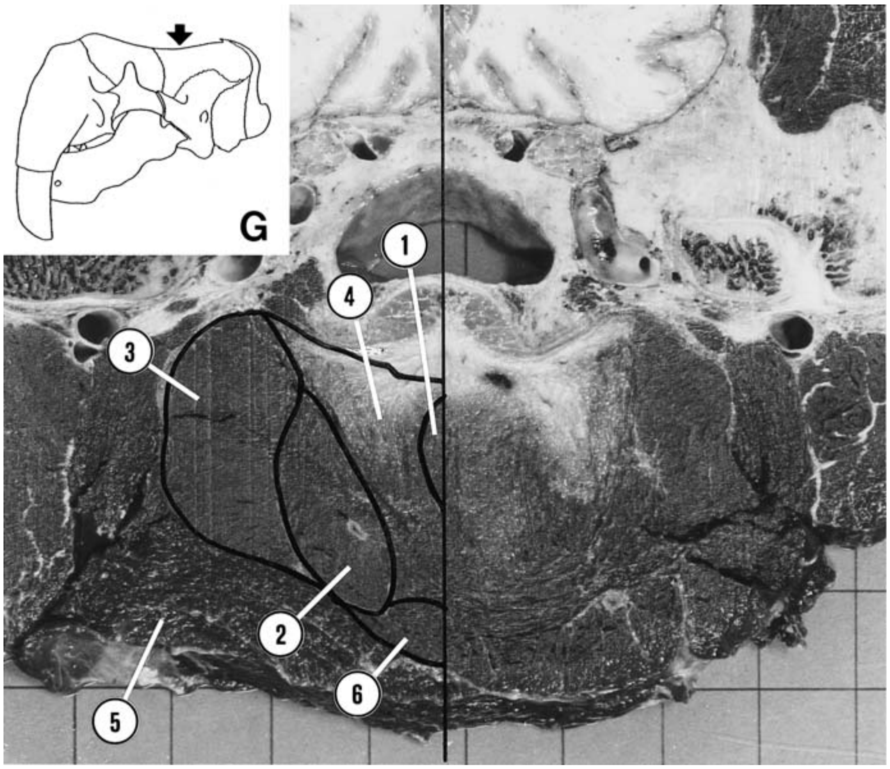


Figure 5. (E–F).



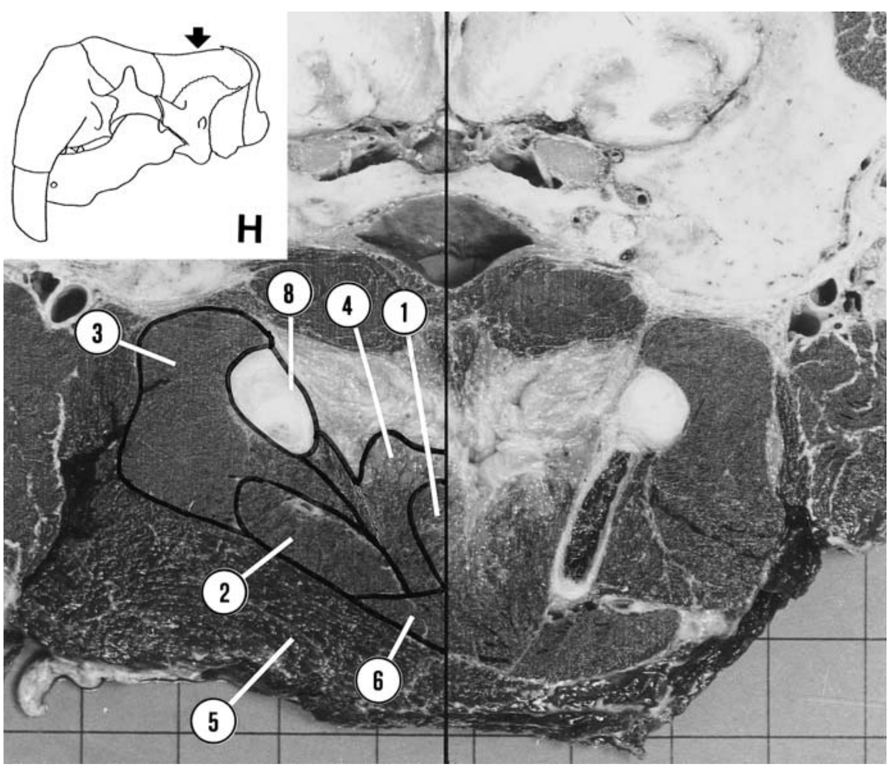


Figure 5. (G–H).

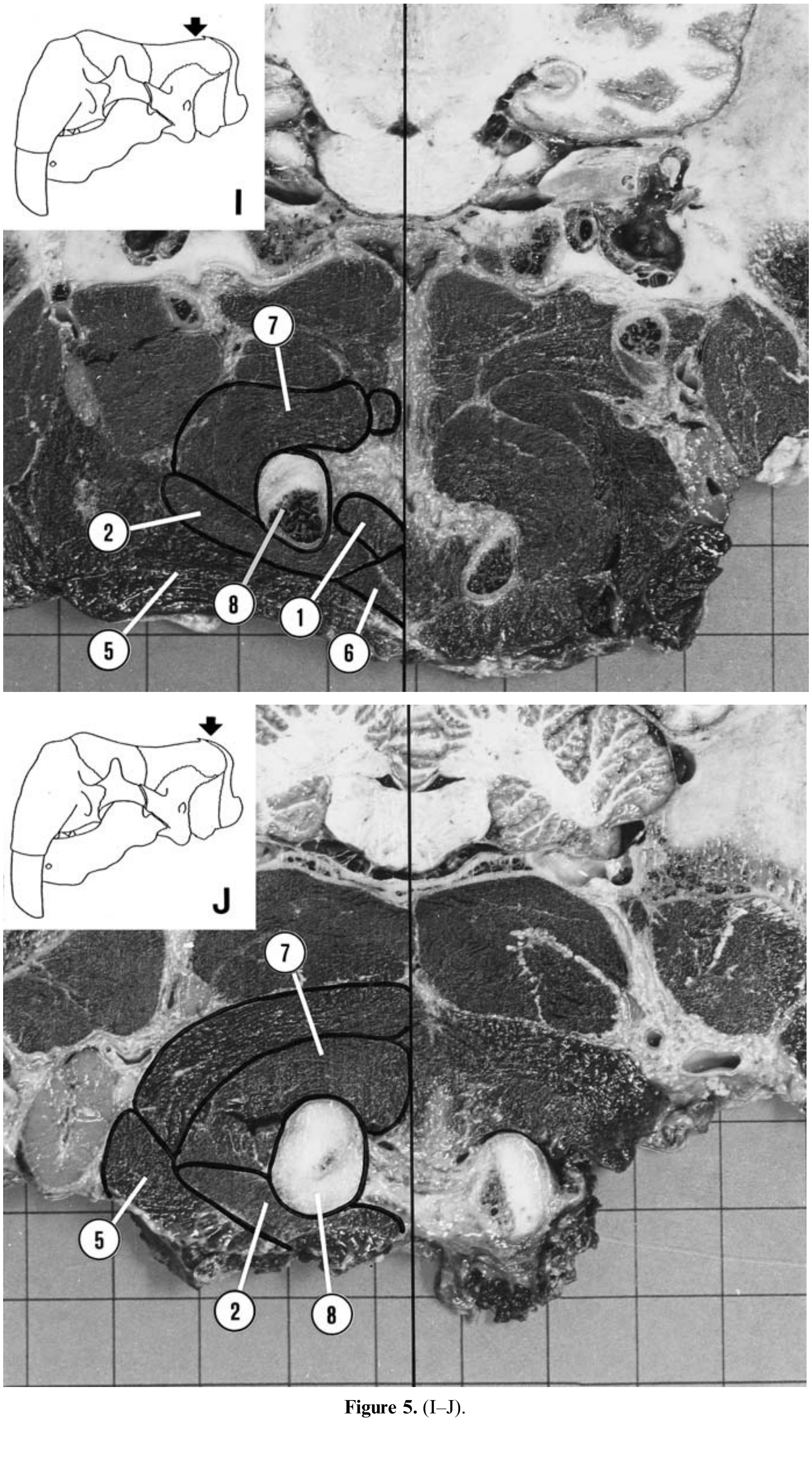


Figure 5. (I–J).

Table 1. The results of a literature survey and a survey among institutes which keep walruses of the presence or absence of a cleft in the tip of the walrus tongue

Sub-species	Code	Sex	Age (years)	Observed when		Cleft	
				alive	dead	yes	no
Pacific	OrZH002	F	15	x		x	
	OrZH001	M	15		x		x
	OrZH004	F	8	x		x	
	OrZH003	M	8	x		x	
	OrZH009	M	2	x		x	
	OrZH010	M	2		x	x	
	OrZH011	M	0.5	x		x	
	Bruiser	M	11	x			x
	Aituk	F	11	x			x
	E.T.	M	8	x			x
	G. Girl	F	9	x			x
	8701	M	3	x			x
	8729	M	12	x			x
	8231	M	8	x		x	
	81162	F	9	x			x
	8779	M	3	x			x
	8780	M	3	x			x
	7801	F	12	x			x
	7806	F	12	x			x
	7501	F	15	x		x	
	7807	M	12	x		x	
	8326	F	7	x		x	
Atlantic	KFHB88#19	F	8		x		x
	EBTA89#1	M	8+		x		x
	EBTA89#2	M	8+		x		x
	CHT	F	13	x		x	
	8730	F	12	x		x	
	8727	F	24	x			x
	8733	F	3	x		x	
	Murie,1871	M	0		x		x
	Daubeton,1765	—	foetus		x	x	
	Sonntag,1923	—	—		x		x
	62 cm tusks	M	>15	x			x
	48 cm tusks	M	15	x			x
	IGOR93-53	M	17		x	x	

simple Endkolben (end-bulbs with a 30–50 μm width) and by Malinovský & Páč (1982) who called them lamellated simple sensory corpuscles. Paciniform corpuscles are fast-adapting receptors, which means that they are suitable for touch. The poor fixation of the material in the present study did not allow the identification of types of mechanoreceptors other than lamellated corpuscles. Better fixation would be needed to make definite conclusions.

The high density of lamellated corpuscles and of free nerve endings innervating the epidermal cones and circular protrusions at the tip of the tongue indicate that the tip possesses a well developed tactile sense. The tip of the tongue was used to identify objects in a psychophysical test on the tactile sensitivity of the mystacial vibrissae of a Pacific walrus, when the objects were too small to be identified with the vibrissae (Kastelein & van Gaalen, 1988; Kastelein *et al.*, 1990; Fig. 11). The animal could hardly reach the objects with its tongue because of the thick mystacial pads and lower lip. Whether transmodal signal recognition took place (from vibrissae to tongue) could therefore not be determined. To determine the mechanical sensitivity of the tip of the tongue, more psychophysical tests are needed.

The mechanoreceptors around the base of the filiform papillae of the walrus tongue possibly register the movement of food over the tongue.

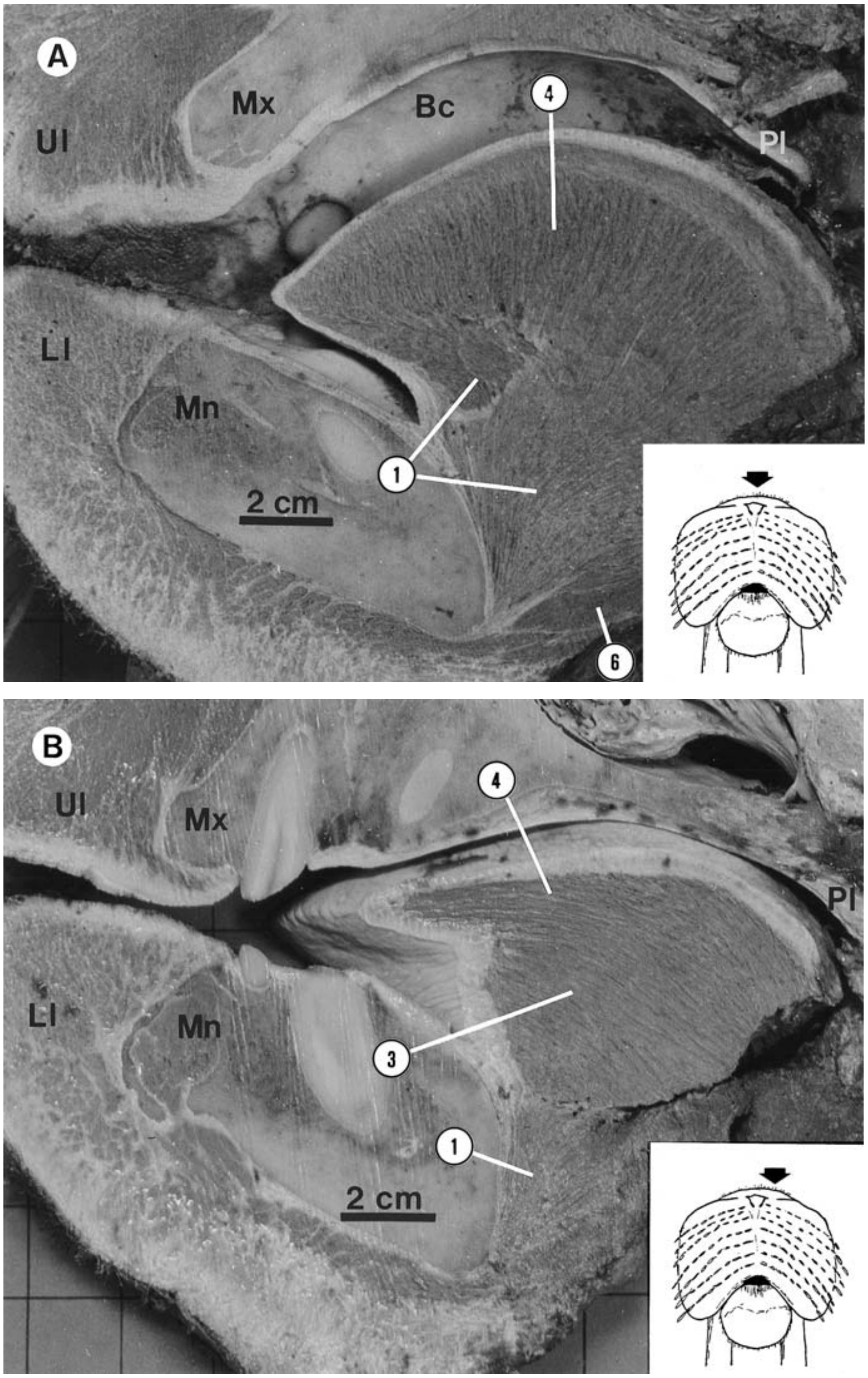


Figure 6. Lateral view of sagittal sections through an 8-year-old female Atlantic walrus head (KFHB#20), showing the position of the tongue in the buccal cavity and the tongue muscles. (A) Mid-sagittal plane; (B) 2 cm lateral of the mid-sagittal plane. (1) *M. genioglossus*, (3) *M. styloglossus*, (4) *M. lingualis proprius*, (6) *M. geniohyoideus*. Bc = Buccal cavity, Mx = Maxilla, Mn = Mandible, Pl = Palatum, Ul = Upper lip, Ll = Lower lip. The arrows in the lower right hand corner indicate the location of the sections. Background grid: 2 cm × 2 cm (Photos: Henk Merjenburgh).

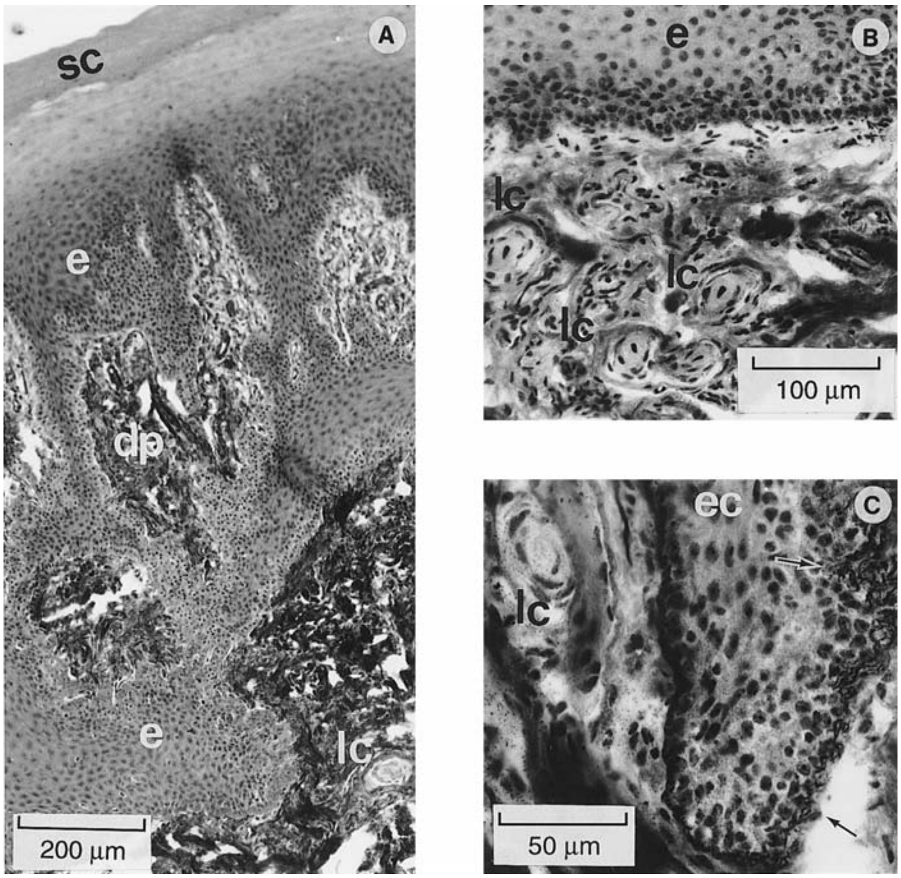


Figure 7. Histology of the tip of the tongue of a 1.5-year-old male Pacific walrus (sample a in Fig. 1). (A) A section through the tip of the tongue showing the relatively thick epidermis. dp=Dermal papilla, e=epidermis, lc=lamellated corpuscle, sc=stratum corneum. Van Gieson trichrome staining. (B) A group of lamellated corpuscles just underneath the epidermis of the tongue tip. e=Epidermis, lc=lamellated corpuscle. Sevier and Munger silver staining. (C) Free nerve endings innervating an epidermical cone next to a lamellated corpuscle. Arrows indicate free nerve endings, ec=Epidermical cone, lc=lamellated corpuscle. Sevier and Munger silver staining (Photos: Merijn de Bakker).

Gustation

Murie (1871) observed rasp-like conical or filiform papillae anteriorly on the dorsum of the tongue and larger fungiform papillae posteriorly. Seven circumvallate papillae in a V-shaped row were located in the posterior region of the walrus tongue in the present study. Murie only found six circumvallate papillae. Sonntag (1923) observed seven circumvallate papillae on a walrus tongue, which were arranged in a V-shape. According to him, these circumvallate papillae are the chief gustatory organs in the walrus, which has no lateral taste organs. Based on the morphological development of the gustatory organs he judged the gustation of the walrus of intermediate between greatest development in Harbour seal (*Phoca vitulina*) and the poorest in California sea lion (*Zalophus californianus*) and Grey seal (*Halichoerus grypus*).

The number of taste buds per circumvallate papilla in the walrus of the present study is extremely low compared to that found in a number of terrestrial mammals (Table 2). However, the taste buds of the walrus are larger than those of other mammals.

The walrus' habit of swallowing food whole does not seem to require a great development of the gustatory sense. Two observations at the Harderwijk Marine Mammal Park suggest that the walrus has very little sensitivity for chemicals that are detectable by most terrestrial mammals: firstly, on several occasions an adult female Pacific walrus (code: OrZH002) ate fish dosed with a large amount

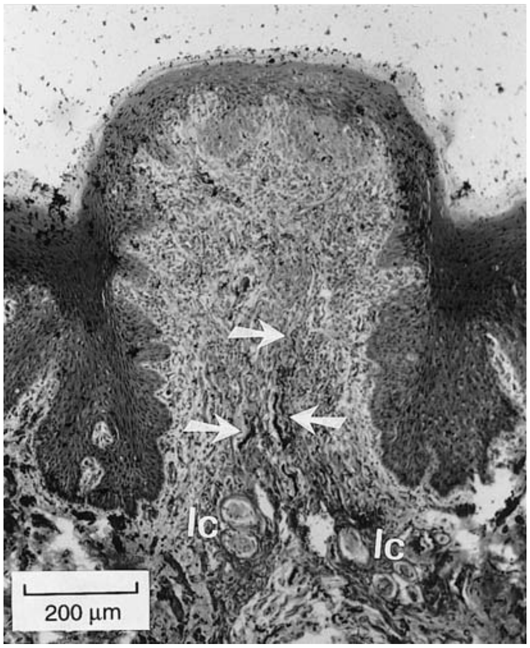


Figure 8. Section of a conical papilla (sample b in Fig. 1) with lamellated corpuscles (lc) and ascending nerves (arrows). Sevier and Munger silver staining (Photo: Merijn de Bakker).

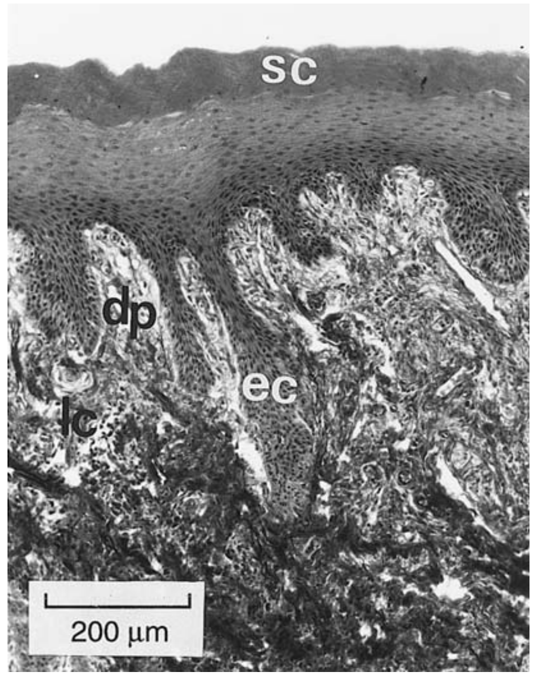


Figure 9. Section of the middle of the tongue (sample c in Fig. 1) with a thinner epidermis, compared to that of the tip of the tongue (Fig. 7A). dp=dermal papilla, ec=epidermical cone, lc=lamellated corpuscle, sc=*stratum corneum*. Van Gieson trichrome staining (Photo: Merijn de Bakker).

of *Radix gentianae*, a bitter herb that disgusts most mammals, and secondly, a male Pacific walrus was frequently given paraffin oil to prevent constipation. The animal drank this oil and cod-liver oil voluntarily from the bottle. However, insensitivity for these chemicals does not necessarily mean that the walrus has little or no sense of taste, as the chemicals do not occur in its natural environment. Walruses may be more sensitive to chemicals that are important to their feeding ecology. At the Harderwijk Park, they are selective and have individual food preferences. However, it is difficult to judge whether their selectivity is based on the taste, smell, texture or shape of the food. Psychophysical tests are needed to determine the gustatory sensitivity of the walrus.

Function of the tongue in walrus ecology

That suction is often used by feeding walruses was noticed by many authors observing walruses kept in human care before it was clear what role oral suction played in walrus ecology. Von Baer (1837) noted that young walruses which were fed soup sucked it from the bucket in which it was offered; Sokolowsky (1908) and Alving (1939) noticed walruses sucking food. Schmidt (1885) noticed that a walrus did not grab food with its lips or jaws, but sucked it with an air current, which created a gulping sound. The animal made a great effort to move the food to the front of its mouth with its snout. He suspected that the suction was strong enough to pull a piece of flesh from a whale carcass. Coates & Atz (1958) observed that a walrus held down a fish with his whiskers while sucking off the flesh. At Hagenbeck Zoo a walrus was able to suck the 2.3 kg metal plug from the pool drain, 110 cm below the water surface (Hagenbeck, 1962). Rysaard (in Pedersen, 1962) noticed that the walruses in Kopenhagen Zoo were able to suck holes in the wooden planks that separated the animals. He suspected that this suction was powerful enough to suck the contents from a shell. Kastelein *et al.* (1991*a*) developed a food dispenser for walruses in zoological parks, which also required oral suction to obtain the food.

The first function of the tongue of the walrus is to aid in suckling. Ray (1960) observed a walrus calf which emptied a 225 ml baby bottle with a rubber nipple in 15 s, and often sucked the plastic container until it was flat. The drinking speed was 15 ml/s. Kastelein *et al.* (1996) describe two walrus pups which were raised on formula sucked from a

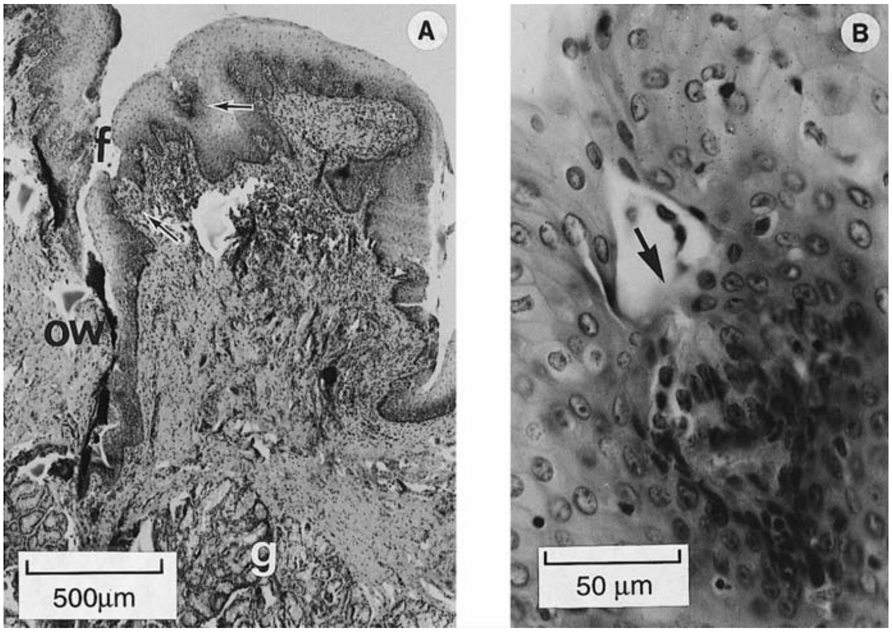


Figure 10. (A) Section of a circumvallate papilla (sample d in Fig. 1) with two taste buds (arrows). f=Circular furrow, g=gland of Von Ebner, ow=outer wall of furrow. Haematoxylin and eosin staining. (B) Magnification of the upper-most taste bud, the arrow points at the taste pore. Haematoxylin and eosin staining (Photos: Merijn de Bakker).

trough (drinking speed 15–22 ml/s). Pigs, terrestrial carnivores and odontocetes have marginal tongue papillae during the suckling period (Kastelein & Dubbeldam, 1990), which are thought to prevent milk from seeping from the buccal cavity during suckling. These marginal papillae are not observed in the walrus. Maybe the papillae are not necessary in the walrus because its gape is short and the lips very pliable due to the various directions of the muscle fibres in them (Kastelein *et al.*, 1991*b*). The pups can create a close fit between their mouth and their mothers' nipples, which allows them to suckle underwater (Kastelein, pers. obs.).

Later in the life of walruses, the tongue plays an important role in foraging. As an explanation for the absence of shells in the stomachs of walruses, Vibe (1950) was the first to suggest that the walrus might suck the contents from shells, and eject the shells. To effectively suck the contents from a bivalve mollusc, the main food of the walrus (Fay, 1982), it is necessary to manipulate the clam in such a way that the siphon is directed towards the oesophagus. This is probably achieved by movements of the vibrissae, the upper lip, the lower lip and the tip of the tongue. If some of the manipulation and the evaluation of the position of the clam in the mouth is done by means of the tip of the tongue, this would explain the large number of mechanoreceptors there. One would expect fast-adapting mechanoreceptors for purposes such as recognition. Once the siphon or foot is directed towards the pharynx, the clam is held tightly between the lower and upper lips. Due to the negative pressure created by the tongue, the siphon and sometimes parts of the body of a clam are sucked out of the shell.

Because the walrus consumes large numbers of clams every day, the feeding actions described have to be performed very quickly and very often. Oliver *et al.* (1983) recorded a speed of 6 clams per minute while Born & Knutsen (1990) found 6400 individual prey in a walrus stomach. Walruses eat up to 6000 individual prey per meal (Fay, 1985). At a rate of 6 clams per minute, this would require 16–17 h of foraging. In the arctic summer walruses forage for 7–10 days after which they haul out and sleep for 2–4 days (Hills, 1992). The skin on the lips has to be very tough to allow so much usage. Schmidtsdorf (1916) observed that the histological composition of the lower, bare, part of the upper lip, which he called 'subphiltrum', resembled that of the foot pads of the dog.

During foraging, some sand and shell parts probably enter the buccal cavity and cause considerable abrasion to the walrus' teeth (Fay, 1982). The thick cornified dermis of the walrus tongue observed

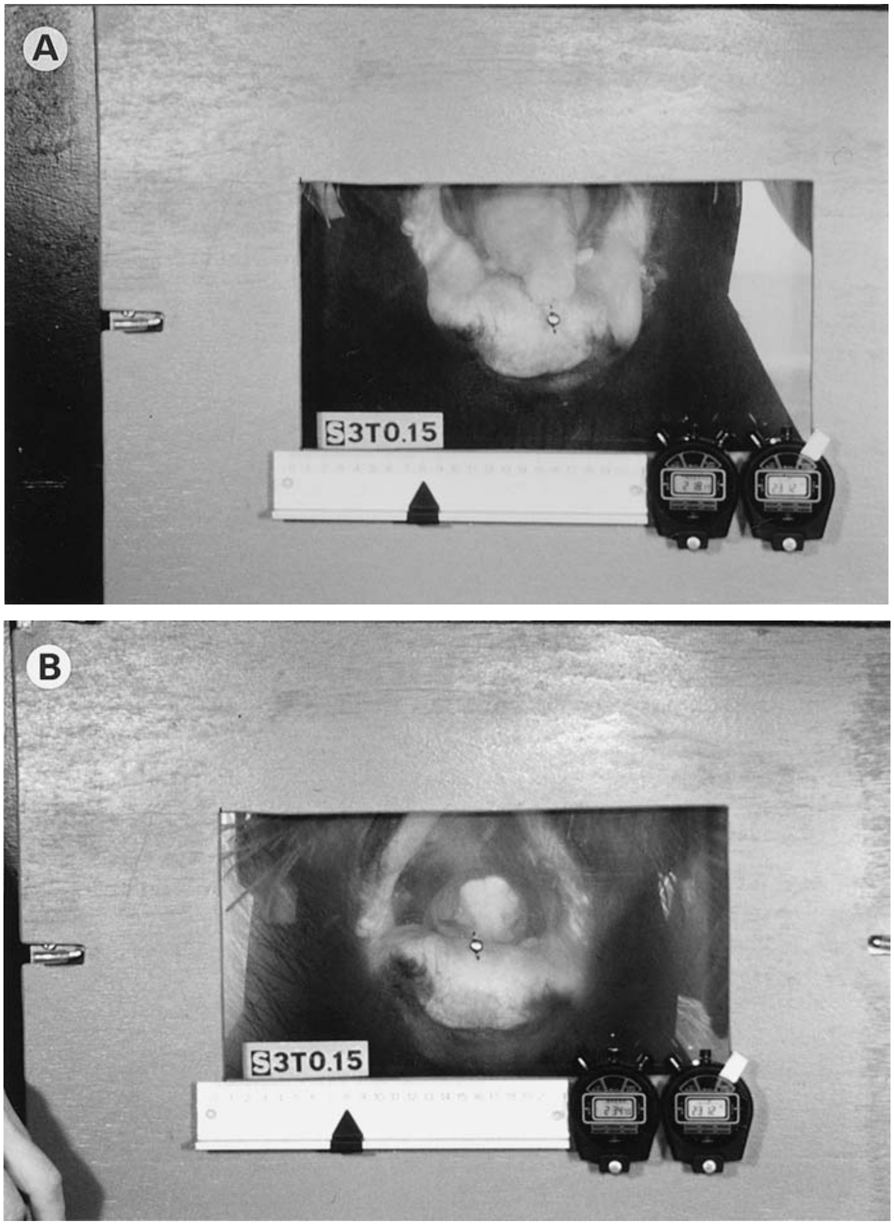


Figure 11. A blindfolded 5-year-old male Pacific walrus trying to touch a 3 mm thick, 0.15 cm^2 triangle which was too small to be identified by the mystacial vibrissae (see Kastelein & van Gaalen, 1988), with the tip of his tongue. Note the slightly bifid tongue tip (Photos: Ron Kastelein).

in the present study may protect the tongue against the grinding action of such particles.

Some walruses occasionally eat seals and birds; they suck away the skin, blubber and intestines (Fay, 1982; Lowry & Fay, 1984; Fay *et al*, 1990).

Conclusion

All the features of the tongue of the walrus described here appear to be adaptations for feeding on bivalve molluscs. The tongue is muscular and

Table 2. Number of taste buds per circumvallate papilla for some mammals (from Bradley, 1971 and the present study)

Mammal	Number of buds	Source
Pig	5380	Tuckerman (1890*d*)
Ox	1460	Tuckerman (1890*d*)
Adult human	254	Arey *et al.* (1935); Bloom & Fawcet (1968)
Grey squirrel	250	Tuckerman (1890*d*)
Woodchuck	200	Tuckerman (1890*d*)
Walrus	20	Present study

Table 3. Maximal dimensions of taste buds in circumvallate papillae (from Bradley, 1971 and the present study)

Animal	Diameter (μm)	Height (μm)	Source
Bat	14	26	Tuckerman (1890*d*)
Mink	24	39	Tuckerman (1890*d*)
Pig	36	92	Tuckerman (1890*d*)
Ox	40	100	Tuckerman (1890*d*)
Horse	70	80	Fish *et al.*(1944)
Walrus	75	125	Present study

thick, and can be used to create low pressure in the mouth. The tip of the tongue is probably adapted to the manipulation and identification of objects in the mouth, and mechanoreception may be more important to the walrus than gustation.

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