THE CARTILAGINOUS ROSTRUM AND THE ASSOCIATED ROSTRAL SENSE-ORGAN OF TOOTHED WHALES (ODONTOCETI)

by

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1. Introduction

The cartilaginous rostrum (cartilago rostralis) of toothed whales is a long, oval (in transverse section), rod-shaped cartilage, which extends centrally through the whole upper jaw, and which slightly extends beyond the osseous rostrum (fig. 1). In the literature, this cartilago is also called cartilaginous septum (Boenninghaus, 1903), cartilago nasalis (Kuzmin, 1976), cartilaginous vomer (Clarke, 1979), vomerine cartilago rostrum (Pilleri et al., 1983), and rostrum nasi (Klima et al., 1986). The length of the cartilage is dependent on the length of the osseous rostrum; it can be a few meters long in large whales.

The primary function of the cartilaginous rostrum is to initiate the formation of bone during the embryonic phase in the growth of the head, before the osseous elements appear (Klima & Van Bree, 1985). The cartilage was not known to have another function in post-natal life. Because of its good sound conductivity properties, Pilleri et al. (1983) and Purves & Pilleri (1983) believe that the cartilage may be part of the echo-sounding system.

More recent dissection methods have enabled us to obtain large sections which, because of their transparency, give us a better insight in the structure of the head. In analysing such sections of the harbour porpoise *Phocoena phocoena* (L., 1758), an organ was found in association with the cartilaginous rostrum, which in view of its morphology is believed to be a sense-organ able to record sound waves.

2. Material and methods

For the analysis of the rostrum four heads of stranded harbour porpoises were available. The skulls of two females had a total length of 86 and 110 cm, those of two males measured 140 and 163 cm, respectively. It was thus possible to study the cartilaginous rostrum and the associated rostral organ in very young as well as in full-grown specimens. The skull of the smallest animal was fixated completely, then the cartilaginous rostrum was removed and histological sections were prepared. The heads of the two largest animals were impregnated with paraffin. After this preparation cross-sectons were made at regular intervals. The head of the larger female was deep-frozen, then cut into 4-6 mm thick slices which were dehydrated in frozen state, and finally cleared and embedded into synthetic resin. By this method (von Hagens, 1979) the fluid-filled cavities of the rostral organ remained well-preserved.

The photographs of the histological sections were taken with phase-contrast objectives.

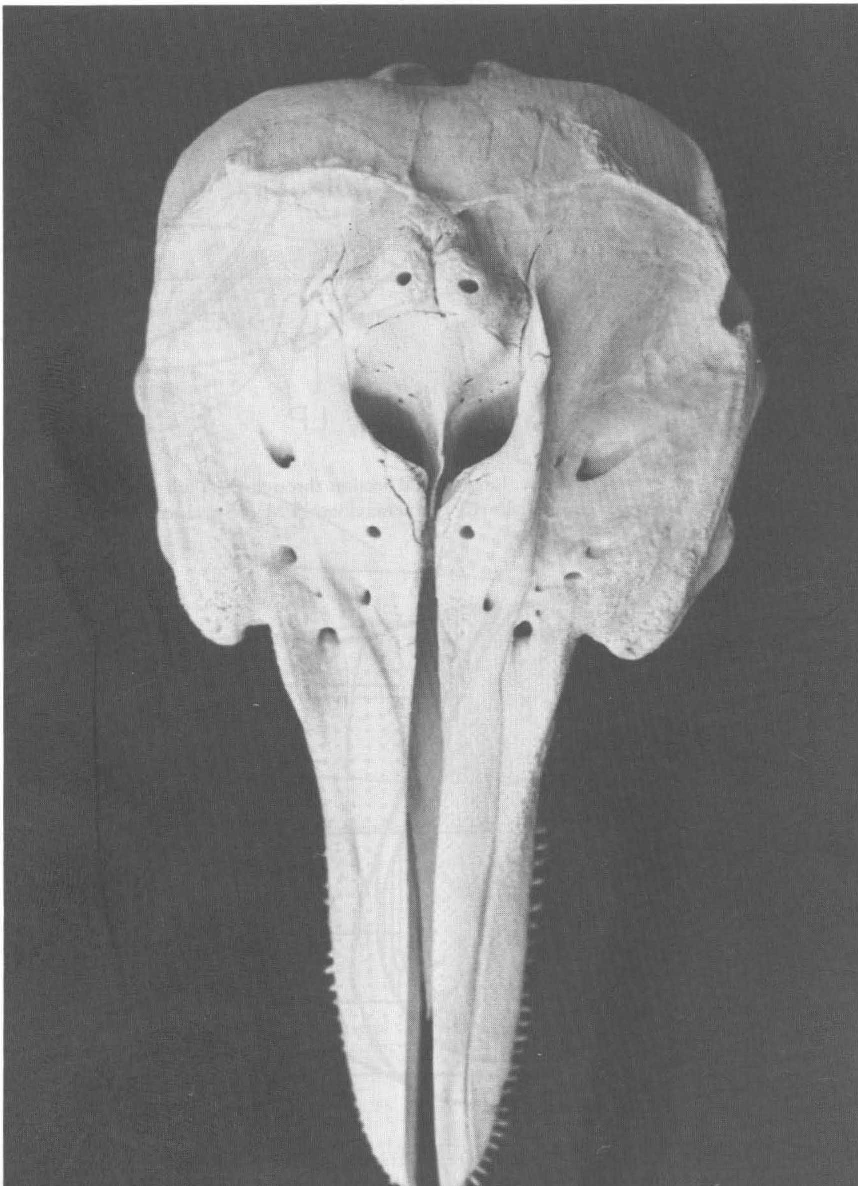

Fig. 1. White-beaked dolphin *Lagenorhynchus albirostris*: skull from above. In the middle of the rostrum the cartilaginous rostrum is embedded in a deep channel.

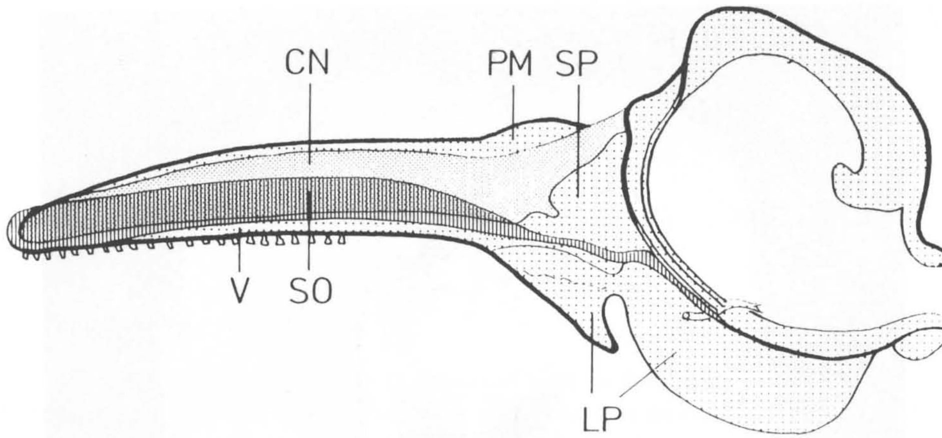

Fig. 2. Harbour porpoise *Phocoena phocoena*: longitudinal section through the skull. Cartilaginous rostrum (CN), lamina perpendicularis ossis ethmoidalis (LP), praemaxillare (PM), rostral sense-organ (SO), septum praesphenoidale (SP), vomer (V).

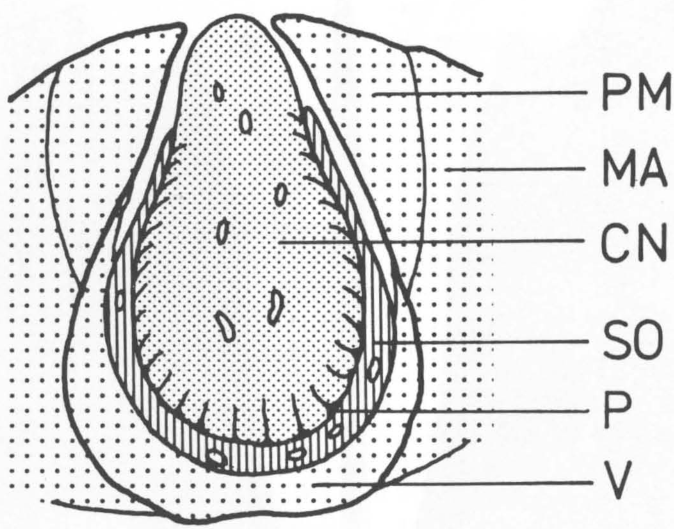

Fig. 3. Harbour porpoise *Phocoena phocoena*: transverse section through the rostrum. Cartilaginous rostrum (CN), upper jaw (MA), perichondrium (P), praemaxillare (PM), rostral sense-organ (SO), vomer (V).

3. Results

The cartilaginous rostrum (fig. 2) starts caudally at the septum praesphenoidale or crista praesphenoidalis (Boenninghaus, 1903). The connection is very strong and totally different from any other bone-cartilage connection in the body. Cartilage and bone are so tightly linked that separating both parts is impossible without damaging

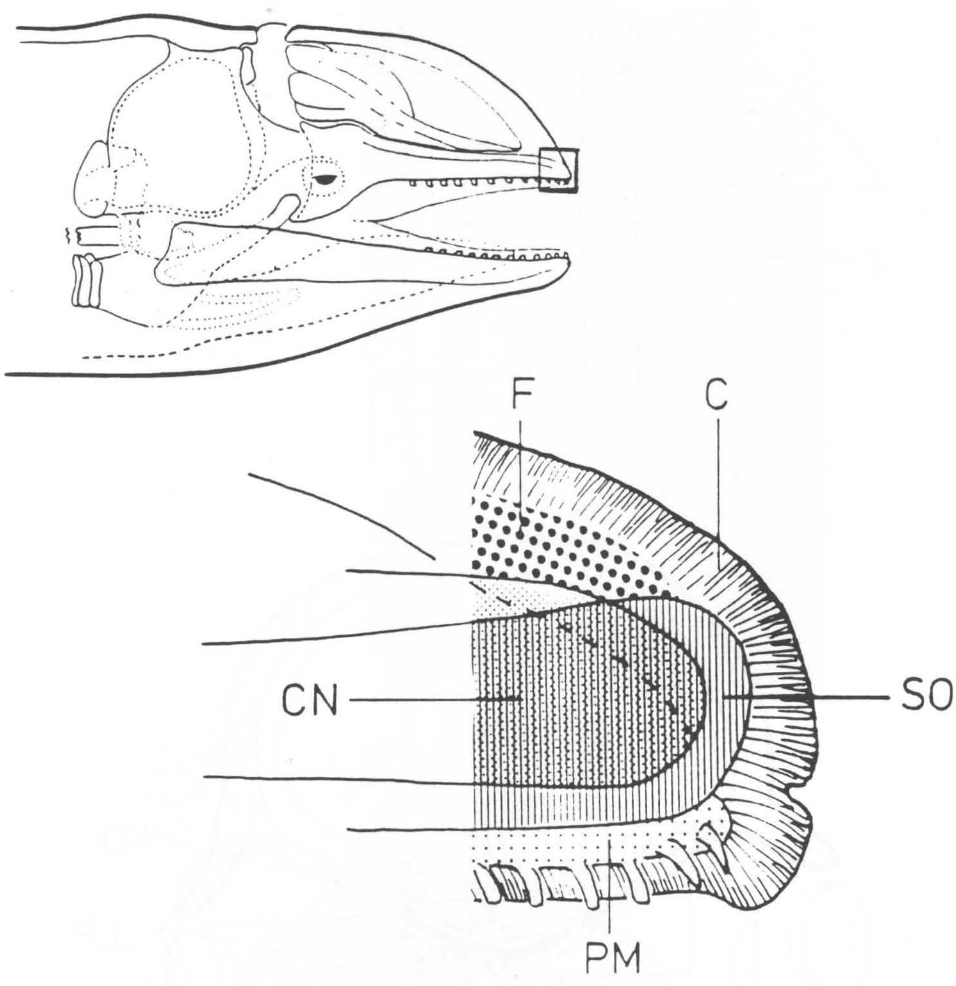

Fig. 4. Harbour porpoise *Phocoena phocoena*: tip of the rostrum. Cutis (C), cartilaginous rostrum (CN), blubber (F), praemaxillare (PM), rostral sense-organ (SO).

them. The cartilaginous rostrum and the rudiments of the cartilaginous nasal septum become fused in an early prenatal phase (Klima & Van Bree, 1985; Klima, 1987), reason why the caudal area of attachment is enlarged. On the contrary, the lamina perpendicularis ossis ethmoidalis only becomes fused with the septum praesphenoidale at an adult stage. Maxillare, praemaxillare and vomer form a deep channel, dorsally open over its entire length, in which the cartilaginous rostrum is embedded. Rostrally to the vomer, the ventral side of the cartilage is not covered by bone either. The cartilaginous rostrum is not connected to the osseous rostrum, nor to the tissue covering it dorsally and ventrally. Also, the cartilage is easily separated from the osseous nasal septum.

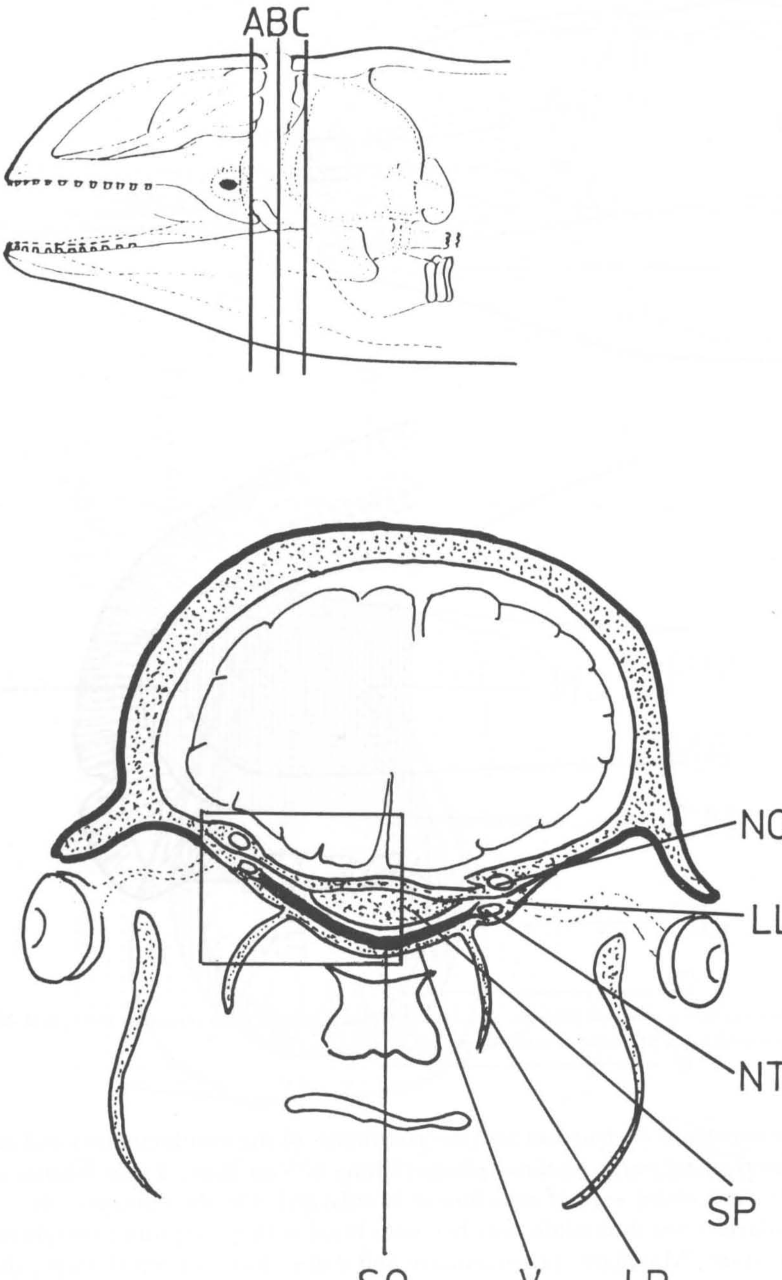

Fig. 5a. Harbour porpoise *Phocoena phocoena*: transverse section at C, magnification 5 × . Between the vomer (V), sphenoid bone (SP), and laminae laterales proc. pterygoidei (LLP), the rostral sense-organ (SO) extends as a nerve fibre to the trigeminus nerve (NT), the alae majores ossis sphenoidalis (LP), and the optical nerve (NO).

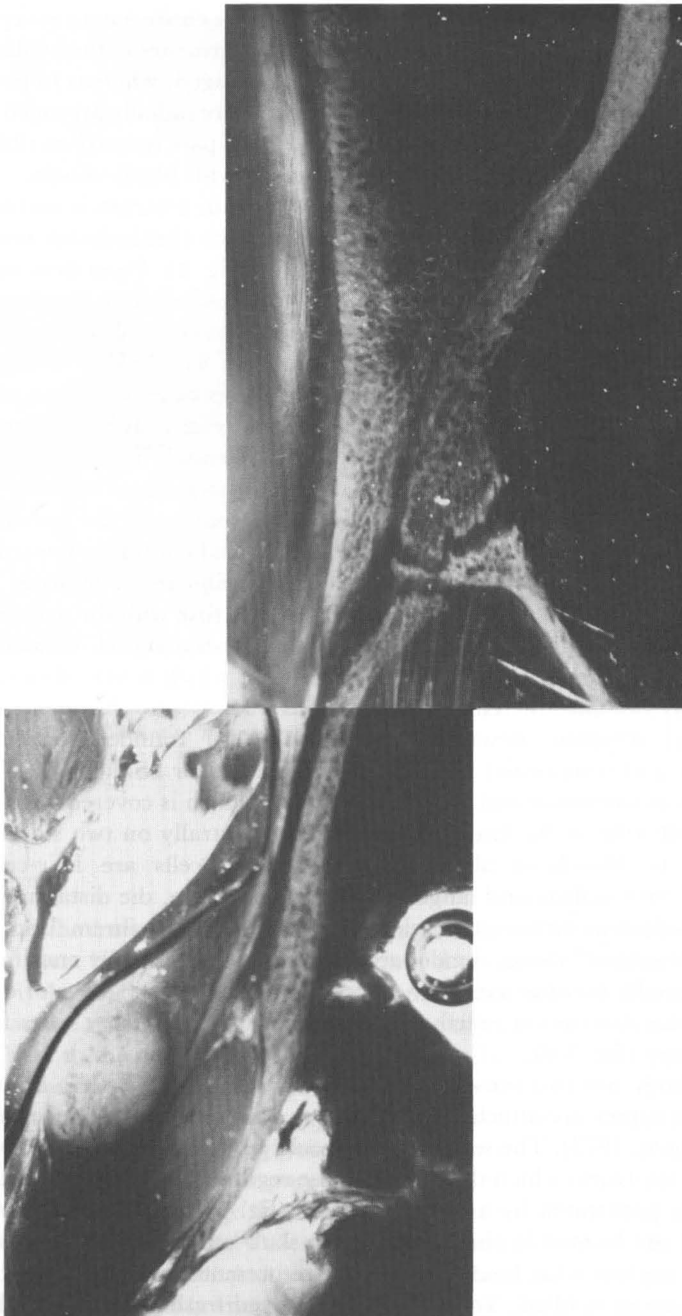

Fig. 5b. Harbour porpoise *Phocoena phocoena*: transverse section at C in fig. 5a, magnification 5×.

In a cross-section the cartilage is oval-shaped over its entire length except at the two ends (fig. 3). In sections one can also see the peculiar structure of the hyaline cartilage. In the central part, cells and fibres are vertically arranged, whereas in the peripheral area a segmented zone is found where cells and fibres are radially arranged. The entire cartilage is covered by a perichondrium. In its central part isolated cartilaginous capsules appear. Caudally the cartilage is interspersed with blood-vessels.

So far it was unknown that most of the cartilaginous rostrum is surrounded by a peculiar structure, which extends upwards beyond the cartilaginous rostrum like a padding under the cuticle of the tip of the rostrum (fig. 4). From here this structure extends caudally, ventrally and laterally along the cartilaginous rostrum and passes between the vomer and the osseous nasal septum to reach the lateral alae of the ossa sphenoidalia (laminae laterales proc. pterygoidei, fig. 5a). In this area the structure divides and becomes increasingly smaller, the caudal ends only existing of connective tissue and nerve fibres (fig. 5b). Laterally of the central alae (alae majores ossis sphenoidalis) and dorsally of the lateral alae of the sphenoid, the tissue of the structure is connected with that of a thick nerve-fascicle which passes here medially through the fissura orbitalis superior. The nerve-fascicle originates at the ganglion Gasseri (Kükenthal, 1889) or ganglion trigeminale, and rostrad continues towards the upper jaw, probably to the nervus maxillaris. With the available material it was not possible to photograph the connection of the nerves of the structure with the nervus maxillaris; to do this it is necessary to make further studies of fresh material. Caudally-ventrally the structure is covered with a flattened epithelium, which is very thin caudally and which rostrally becomes increasingly thicker.

The rostral structure described here consists of rounded vessels extending longitudinally and compressed laterally, filled with a clear fluid (fig. 7, 8). The walls consist of connective tissue and a basal membrane, which is covered with sensory and supporting cells (fig. 8, 9), laterally on one side, ventrally on two sides.

According to Hirsch et al. (1973) the sensory cells are hair-cells carrying stereociliae: ''Stereocilien sind lange schlanke Sinneshaare, die distal in einer stumpfen Spitze auslaufen, während sie sich proximal kurz von ihrem Usprungsort am Zellkörper verjüngen'' (long, slender sensory hairs which distally end in a truncated tip and proximally become narrower where approaching their place of origin on the cell body). This description exactly corresponds with the sensory hairs found in the rostral structure (fig. 7-9).

Each cell body has two sensory hairs of different length. To the basis of the cell bodies, two synapses are attached. The sensory and hair-cells are mechano-receivers (Welsch & Storch, 1973). The sensory hairs would perceive any movements of the fluid in the rostral structure, which therefore is to be regarded as a sense-organ. The entire sense-organ is penetrated by a neural network (fig. 6). It is supplied with blood by vessels which are located in the region of the skull-base next to the nerve-fascicles.

It remains unclear what kind of synapses are present here and with what fluid the rostral sense-organ is filled. To clarify this we need fresh material which, however, could not be obtained because of the prevailing protective legislation.

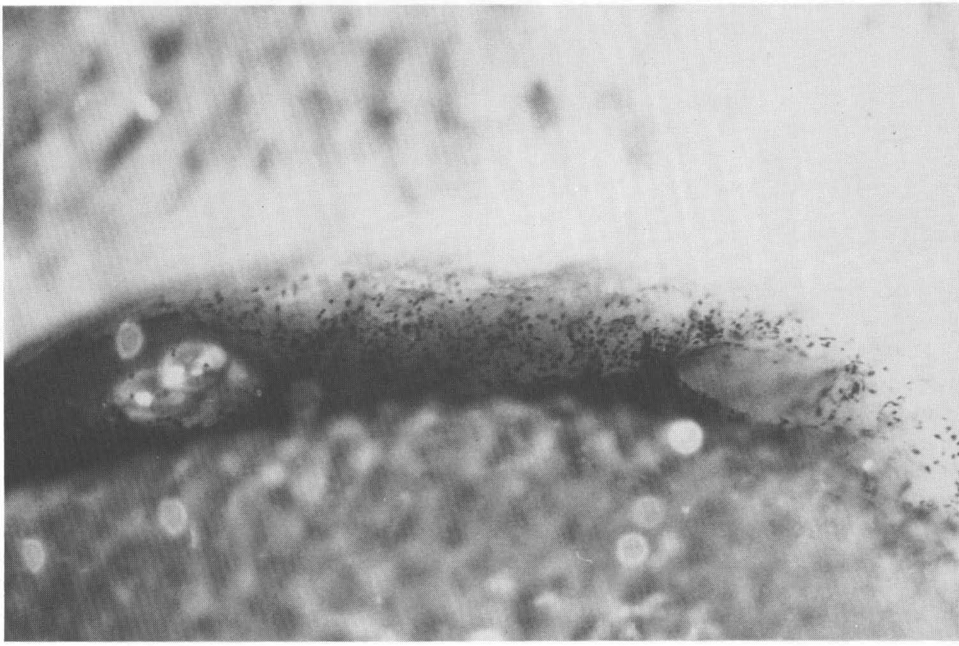

Fig. 6. Harbour porpoise *Phocoena phocoena*: transverse section through the rostral sense-organ at B in fig. 5a, magnification 10 × . The entire sense-organ is penetrated by a neural network: the dark points are neurons.

4. Discussion

The fact that the importance of the cartilaginous rostrum had not been discovered until present, must be due to its location. Removal of the cartilage from the skull is only possible if the head is sawn through, or by maceration. In the first case the skull is destroyed, in the second case the cartilage will be of little use scientifically, and the sense-organ next to the cartilage gets completely lost. In using formalin for fixation, the tissue of the sense-organ shrinks considerably and is no longer detectable. Only fixation in a frozen state allows the preparation of a well-preserved sense-organ.

As all odontocetes have a cartilaginous rostrum, one may conclude that the structure described here for the harbour porpoise is present in all toothed whales. Because of the fact that this large cartilage does not become ossified, it has been assumed that it has a function in post-natal life. Pilleri et al. (1983) and Purves & Pilleri (1983) concluded from the good sound-conductive properties of the cartilage (the sound velocity in the cartilage seems to be in the order of 1.5 m/sec.) that it must have a function in the orientation system. But since there are no nerves in the cartilage which could receive sound waves, it can only play a secondary role in echolocation.

Because of the different densities of the various tissues, sound waves pass through the head with different velocities. The osseous rostrum remains rigid and does not

Fig. 7. Harbour porpoise *Phocoena phocoena*: transverse section through the rostral sense-organ and its wall, magnification 160 × .

change its shape. As for the cartilage and associated sense-organ, however, sound waves may slightly change their shape, which would then be recorded by the ciliae. As the sensory cells of the rostral sense-organ are comparable to those in the organ of equilibrium in mammals, they supposedly react in the same sensitive way. It is therefore assumed that the sensory hairs perceive oscillations of a very low intensity.

To locate food, toothed whales use sonar waves of high frequencies. These have a range of a few meters only, but it is easy to focus them (Purves, 1966). The echo waves reflected from the prey, in particular from cephalopods, may be of a low intensity. Therefore it would be an advantage to have a sound-receiving sense-organ in the rostrum. The tube-shaped channel in the osseous rostrum would be a further advantage, as this may allow the animal to take a direct bearing on the prey: the head can be moved until the echo waves directly hit the sense-organ. The idea that the rostral sense-organ has the function of a directional microphone seems attractive. In this connection the cartilage, which only caudally is firmly connected with the bone, might have two functions. First of all it could act like a spiral spring which contracts and expands in a longitudinal direction. Secondly, the waves passing the tube exert a pressure which must be released. This could happen via the cartilaginous rod by slightly compressing it laterally. The different structures in the cartilage may be connected with this function. This would explain why this cartilage does not ossify, as ossification would reduce its plasticity. The relationship between sense-organ and car-

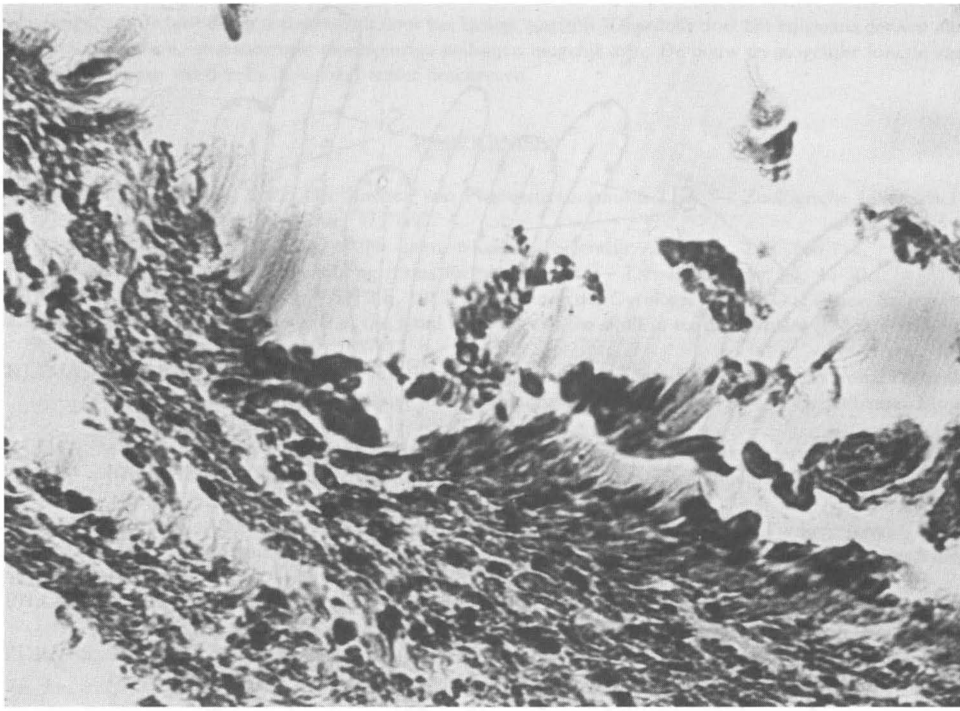

Fig. 8. Harbour porpoise *Phocoena phocoena*: horizontal section through the rostral sense-organ, magnification 250 ×. A number of sensory cells with their stereociliae are sectioned, see fig. 9.

tilage makes us assume that the cartilaginous rostrum is developed at a very early embryonic stage prior to the development of the osseous rostrum (Klima & Van Bree, 1985). Thus the development of the latter would be determined by the cartilage-related sense-organ, which has to function right from birth.

ZUSAMMENFASSUNG

Das knorpelige Rostrum und das damit verbundene rostrale Sinnesorgan von Zahnwalen (Odontoceti)

Mitten im knöchernen Rostrum der Zahnwale zieht sich in Längsrichtung eine tiefe Rinne, in der ein länglicher Knorpelstab, knorpeliges Rostrum genannt, liegt. Pilleri et al. (1983) vermuteten, daß dieser Knorpel, im Zusammenhang mit dem Orientierungssystem, eine Funktion haben könnte.

Nun wurden am knorpeligen Rostrum des Schweinswals *Phocoena phocoena* (L., 1758) Gewebeformen gefunden, die nach ihrer Anlage und Morphologie ein Sinnesorgan sein dürften, mit dem Schwingungen registriert werden können.

Daß das knorpelige Rostrum ventral und lateral ummantelnde Organ besteht aus länglichen, mit Flüssigkeit gefüllten Hohlräumen, deren Wände mit Sinneszellen bedeckt sind, aus denen Sinneshaare (Stereozilien) in die Hohlräume hineinragen. Das ganze Sinnesorgan ist von einem neuralen Netzwerk durchzogen.

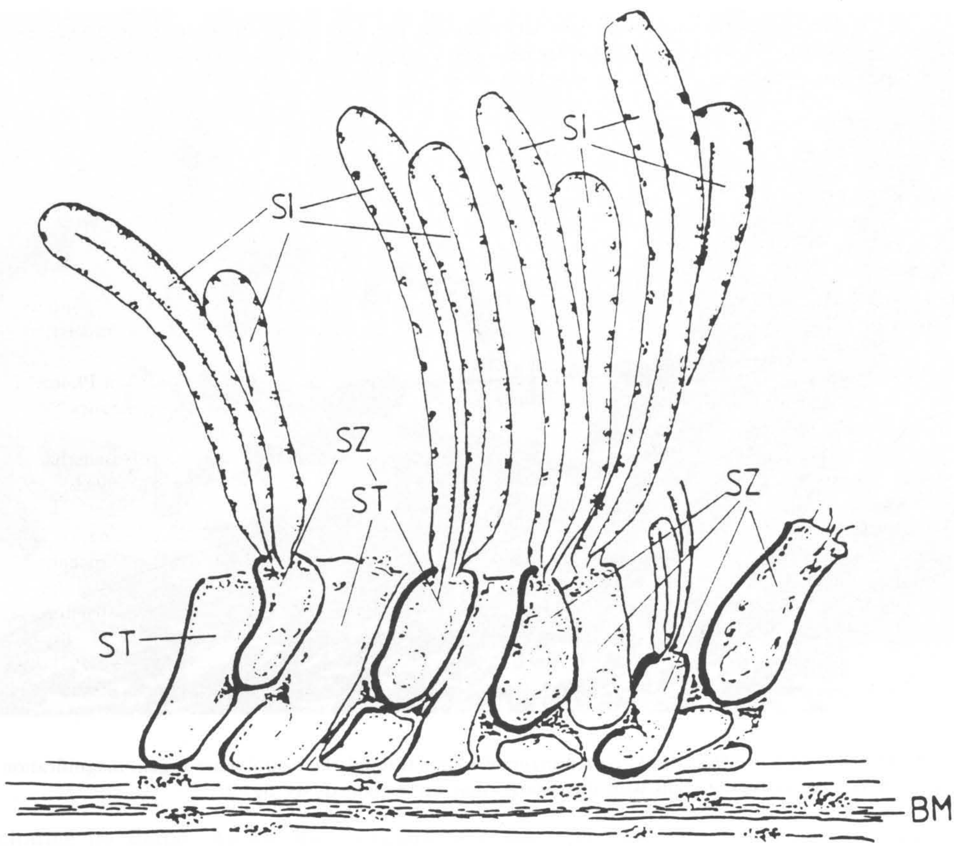

Fig. 9. The rostral sense-organ, magnification 630 ×. Walls with the membrane (BM), sensory hairs (SI), sensory cells (SZ), supporting cells (ST) (termed after Welsch & Storch, 1973).

Weil das Organ in einer sehr langen, gleichförmigen Röhre liegt, die vom knöchernen Rostrum gebildet wird, wäre damit eine sehr gezielte Ortung möglich. Die Morphologie und die mögliche Funktion werden in der vorliegenden Arbeit beschrieben.

SAMENVATTING

Het kraakbenige rostrum en het daarmee verbonden zintuigorgaan bij tandwalvissen (Odontoceti)

Het benige rostrum der tandwalvissen is over zijn gehele lengte doorsneden door een diepe groef waarin zich een kraakbenige staaf bevindt: het kraakbenige rostrum of de cartilago rostralis. Door Pilleri et al. (1983) is dit kraakbeen in verband gebracht met het oriëntatiesysteem van tandwalvissen (echolocatie).

Bij de bruinvis *Phocoena phocoena* (L., 1758) is nu een weefselstructuur gevonden die hecht verbonden is met het kraakbenige rostrum. Te oordelen naar bouw en vorm gaat het hier vermoedelijk om een zintuigorgaan, dat geringe trillingen kan registreren.

Dit orgaan bedekt het kraakbenige rostrum ventraal en lateraal. Het is opgebouwd uit langgerekte, met vloeistof gevulde holten. De wanden van deze holten zijn bedekt met zintuigcellen (stereociliae), die naar binnen gericht zijn. Het gehele zintuigorgaan bevat een dicht netwerk van neuronen. Het orgaan ligt in

een lange, rechte buis die gevormd wordt door het benige rostrum. Daardoor doet het enigszins denken aan een richtmicrofoon, waarmee zeer nauwkeurige peilingen mogelijk zijn. De bouw en mogelijke functie van dit zintuigorgaan worden in dit artikel nader beschreven.

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