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The olfactory regions in the nose of the harbour porpoise *Phocoena phocoena* (Linne, 1758)

Günther Behrmann

Alfred-Wegener-Institut für Polar-und Meeresforschung. Am Handelshafen 12, D 2850 Bremerhaven, West Germany

Zusammenfassung

Die Riechzonen in der Nase des Schweinswals *Phocoena phocoena* (Linne, 1758).

Weil der Riechnerv (*Bulbus olfactorius*) bei den Zahnwalen vollkommen zurückgebildet ist, ging man bisher davon aus, daß auch der Geruchssinn verloren gegangen ist. Nun wurden in den Nasen von Schweins-walen Riechzonen (*Regio olfactoria*) mit funktions-fähigen Riechzellen gefunden, deren Sinnesgeißeln als Chemorezeptoren identifiziert werden konnten. Daraus kann postuliert werden, daß die Schweinswale doch in der Lage sind, bestimmte chemische Verbindungen mit der Nase zu erfassen.

Introduction

'The anatomy of the odontocete brains indicates that they can taste but cannot smell. Apparently, when the blowhole migrated to the top of the head, the neural pathways for smell were sacrificed' (Caldwell & Caldwell, 1972). Today it is generally accepted that toothed whales are unable to smell because of the above mentioned observation.

However in the nose of three harbour porpoises a large number of chemoreceptor cells have been discovered during a histological investigation of the olfactory regions. Why are the olfactory regions and olfactory cells retained, if at the same time the olfactory nerves are sacrificed? What is the function of such cells?

Materials and methods

To study the olfactory regions, three harbour porpoises heads were examined. The three animals were caught as bycatches in the North and Baltic Seas. Short time after death they were deep frozen. In this condition the heads were sectioned into slices of some millimetres in thickness.

These sections were fixed with formalin under vacuum at a lower temperature. After this, the sections of two heads were embedded in paraffin, and the sections of one head was prepared using the plastination method by resins (von Hagens, 1979). Selected parts of the paraffin embedded material were cut into histological sections.

Findings

After death mucous layers disintegrate very quickly, and along with the mucosa the olfactory cells get lost. Therefore, in all harbour porpoise noses examined, the olfactory regions were only partly preserved. They were found in the vestibular sac (*Saccus vestibularis*) and in the frontal sac (*Saccus frontalis*) (Fig. 1). Olfactory cuticles are situated on the folded integument on the floor of the vestibular sac (Fig. 2), as well as in the frontal sac where they cover the

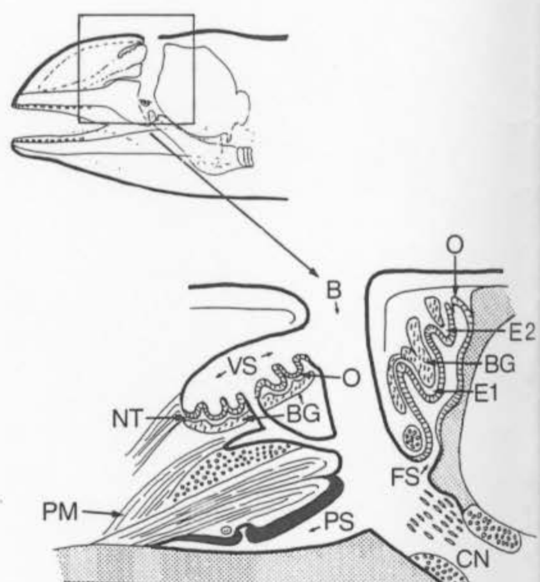

Figure 1. Schematic section through the nose of the harbour porpoise. Blowhole (B), Bowman-glands (BG), ethmoidal (E), frontal sac (FS), nosehole (CN), nasoturbinal (NT), plugmuscle (PM), premaxillary sac (PS), vestibular sac (VS), olfactory cuticles (O).

Figure 2. Longitudinal section through the vestibular sac, magnification 10 ×. The different cuticles of the sac are clearly distinguishable. The integument above is dark like the epidermis. At the bottom of the sac the integument is thin and has a striped olfactory cuticle.

Figure 3. Section through a fold in the bottom of the vestibular sac with a view of the cells of the olfactory region, magnification 25 ×.

ethmoturbinals 1 and 2 (Fig. 6). The third ethmoturbinal is sacrificed. The olfactory regions differ from the respiratory regions by their colour and morphology (Fig. 2). The olfactory regions are yellowish brown and the mucosa is thicker than the dark mucosa of the respiratory cuticles. The brownish colour originates from pigment corpuscles (Melanosome) which are situated in the base of the olfactory cuticle. The yellowish colour is caused by cell fluids. The base of the olfactory cuticle is arranged in a network similar to the retina in the eye (Fig. 3, Fig. 4). Splash nozzles protrude from the cuticle; they are the openings of the Bowman-glands which extend below the whole olfactory regions (Fig. 5). The retina-like cuticle is covered with a layer of olfactory cells which are protected by the thick mucosa (Fig. 6).

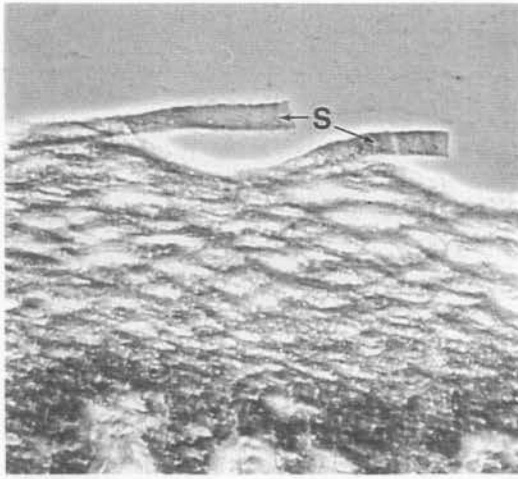

Figure 4. View of the outside of the retina, magnification 100 ×. The mucosa is lost and only the relics of two olfactory cells (S) are preserved.

Figure 5. Section through the Bowman-gland below the frontal sac, magnification 25 ×. The opening (T) leads to the splash nozzles.

The olfactory cells have a longitudinal shape with a length of up to 100 μ and a diameter of nearly 12 μ. The nucleus of a cell is very large and surrounded by Golgi-complexes. Neurites pass through the cell and end up in the sense whip. The sense whips have a length of nearly 25 μ. Their walls have many pores like chemoreceptors of other vertebrates which are adapted to living in water (Fig. 7, Fig 8).

Discussion

The evolutionary migration of the blowhole included a transfer of the olfactory regions (Gruhl, 1911). Nowadays they are located in the integuments of the

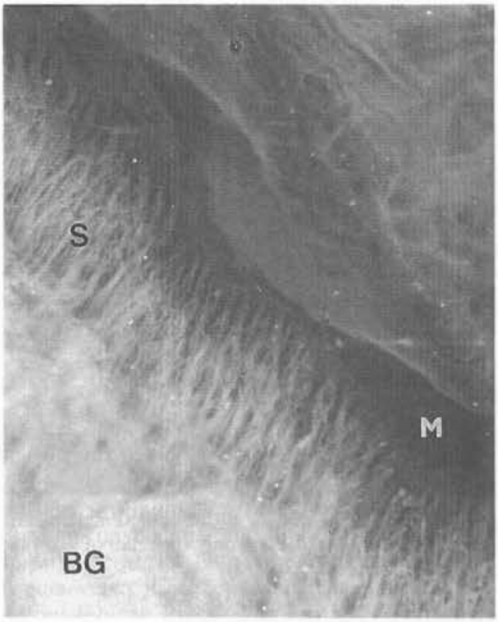

Figure 6. Section through the olfactory region in the frontal sac, magnification 50 ×. The region is covered with a thick mucous layer. The olfactory cells (S) are clearly recognizable in the well preserved mucosa (M). Below the olfactory cuticle is situated the Bowman-gland (BG).

frontal sac and the vestibular sac. The olfactory region in the frontal sac is comparable with the ethmoturbinals, and the olfactory region in the vestibular sac is comparable with the naso-turbinal (*Turbinale nasalis*) of other mammals. The olfactory epithelia, the stock of distinctive chemoreceptory cells and the position of the Bowman-glands below the olfactory regions' support Gruhl's (1911) hypothesis that toothed whales could have an olfactory sense.

Experiments with toothed whales to check their reactions to chemical compounds are described, but we still know very little about dolphin chemoreception (Nachtigall, 1986).

As mucous epithelia decays very quickly after death, olfactory cells are destroyed along with the mucosa, and relics of the cuticles were presumably overlooked. In assuming that the bulbi of the olfactory nerves (*Bulbus olfactorius*) were sacrificed, Kückenthal (1893), Radwitz (1900), Boenninghaus (1911) and Caldwell and Caldwell (1972) stated that toothed whales are unable to smell.

Because the harbour porpoises were quickly deep frozen after their decease, large parts of the olfactory regions were preserved. By the careful fixation at low temperatures under vacuum, the cells appear well preserved. The well preserved cellular organelles and the form of the cells demonstrate that they had a real function.

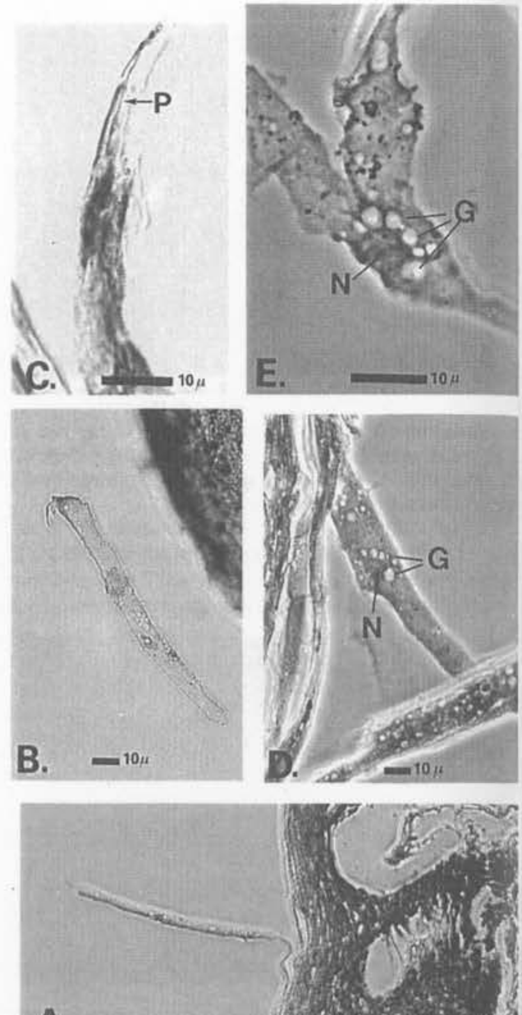

Figure 7. Details of the olfactory cells. A. The olfactory cell originates between the cell layer above the retina. B. A separate olfactory cell with a sense whip. C. Sense whip with pores (P), which are characteristic for chemoreceptors. D. The middle part of the olfactory cell with the cell nucleus (N), surrounded by vesicles (G). E. The nucleus (N) with Vesicles (G).

All olfactory cells which were found were innervated. The existence of sense-hairs with pores, which is a characteristic for chemoreceptors, proved this. It follows that harbour porpoises are able to detect chemical particles.

However, the preservation of olfactory regions during evolution seems paradoxical in case the olfactory nerves have disappeared. On the other hand, the well preserved innervated olfactory cells do indicate that they have a function. Human beings whose

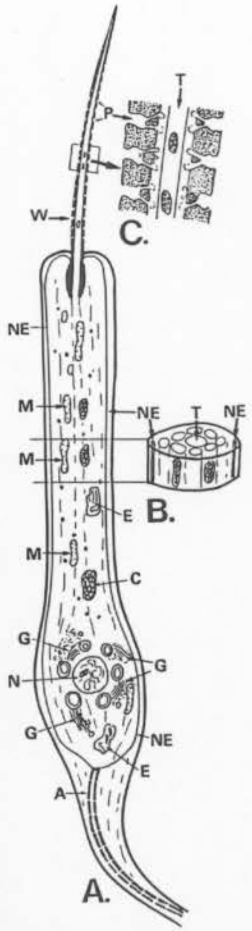

Figure 8. Model of one olfactory cell *A*. with a transverse section through the cell *B*. and a longitudinal section through the whip *C*. Axon (A), cyclocyst (C), endoplasmatical reticulum (E) Golgi complex with vesicles (G), mitochondria (M), nucleus (N), neurite (NE), pore (P), tubulus (T), sense whip (W).

olfactory nerves have been destroyed are able to take up odours from chemical compounds of nitrate, ammonia and sal ammoniac (Schiefer *et al.*, 1986). Those odours are taken up by the nerve-ends of the trigeminal nerve. The branches of the trigeminus (*Rami nasales interni*; *Rami terminalis*) lead to the olfactory region of the brain (Rauber & Kopsch, 1953; Corning, 1942). It may therefore be possible that the harbour porpoise nose has a function similar to a destroyed nose of a human being. This would explain the presence of the well preserved olfactory cells.

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