# Functional Morphology of the Nasal Complex in the Harbor Porpoise (*Phocoena phocoena* L.)

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## ABSTRACT

Toothed whales (Odontoceti, Cetacea) are the only aquatic mammals known to echolocate, and probably all of them are able to produce click sounds and to synthesize their echoes into a three-dimensional "acoustic image" of their environment. In contrast to other mammals, toothed whales generate their vocalizations (i.e., echolocation clicks) by a pneumatically-driven process in their nasal complex. This study is dedicated to a better understanding of sound generation and emission in toothed whales based on morphological documentation and bioacoustic interpretation. We present an extensive description of the nasal morphology including the nasal muscles in the harbor porpoise (*Phocoena phocoena*) using macroscopical dissections, computer-assisted tomography, magnetic resonance imaging, and histological sections. In general, the morphological data presented here substantiate and extend the unified "phonic lips" hypothesis of sound generation in toothed whales suggested by Cranford et al. (J Morphol 1996;228:223–285). There are, however, some morphological peculiarities in the porpoise nasal complex which might help explain the typical polycyclic structure of the clicks emitted. We hypothesize that the tough connective tissue capsule (porpoise capsule) surrounding the sound generating apparatus is a structural prerequisite for the production of these high-frequency clicks. The topography of the deep rostral nasal air sacs (anterior nasofrontal and premaxillary sacs), narrowing the potential acoustic pathway from the phonic lips to the melon (a large fat body in front of the nasal passage), and the surrounding musculature should be crucial factors in the formation of focused narrowbanded sound beams in the harbor porpoise. Anat Rec, 292:902–920, 2009. © 2009 Wiley-Liss, Inc.

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In 350 BC Aristotle stated that the air passage of a whale is situated in the forehead but in a dolphin it "goes through its back". Although being correct with the first part of his remark, this author obviously mistook the position of the dolphin's blowhole by identifying the bulbous epicranial forehead of the dolphin as the neurocranium and brain. Today it is known that the forehead (nasal complex) of toothed whales is highly modified compared with other mammals and produces sounds serving echolocation and/or communication (Norris, 1968; Cranford et al., 1996; Cranford, 2000; Cranford and Amundin, 2004).

In historical terms, the harbor porpoise (*Phocoena phocoena*) is one of the few toothed whale (odontocete) species which have been studied in some detail but, for the most part, this was a long time ago. It was not until 1826 that Karl-Ernst von Baer described and identified the epicranial complex as the true nose of the porpoise and suggested that the blowhole (Spritzloch) does not serve to squirt water. Some years later Francis Sibson (1848) considered that the function of the air sacs was to float the blowhole above the water surface during sleep and during the act of copulation. Around the turn of the last century, several anatomists presented a number of different and sometimes conflicting ideas about the function of the porpoise nose: Willy Kükenthal (1893) stated that the nasal air sacs might help to lock the nasal passage against the penetration of water, since he found no musculature to close it. Bernhard Rawitz (1900) wrote that the only explanation for the peculiar anatomy of the porpoise nose is hydrodynamics. Georg Boenninghaus (1903) noticed that the nasal plugs and the epicranial musculature lock the respiratory tract but this author did not suggest a function for the nasal diverticula, whereas Kurt Gruhl (1911) stated that the facial muscles can slide over the surfaces of the air sacs.

The development of modern hypotheses regarding the function of the odontocete nose began in the 1950's when the sonar system of dolphins was discovered (Kellogg et al., 1953; Kellogg, 1958; Norris et al., 1961). In 1969, Kenneth S. Norris (Norris, 1969) reported a sputtering of air and fluid over the lateral edge of the nasal plug in the open airways of trained dolphins during click production. Cranford et al. (Cranford et al., 1997; Cranford, 2000; Cranford et al., 2001; Cranford and Amundin, 2004), using high-speed video endoscopy, confirmed these observations and noticed a synchronization of vibrations at the monkey lips (valve-like structures in the soft nasal tract dorsal to the nasal plugs; cf. Cranford et al., 1996) with the emission of sonar signals. These and other observations (Norris et al., 1961; Evans and Maderson, 1973; Norris and Harvey, 1974; Dormer, 1979; Ridgway et al., 1980; Mackay and Liaw, 1981; Amundin and Andersen, 1983; Amundin, 1991; Cranford et al., 1996; Aroyan et al., 2000; Au et al., 2006; Cranford et al., 2008a) provide strong evidence for nasal sound production in odontocetes. The exact mechanism is unclear but probably involves a complex of tissues and structures including the monkey lips and a set of fat bodies and other associated structures (Pouchet and Beauregard, 1885; Norris and Harvey, 1972; Cranford et al., 1996; Cranford, 1999). Cranford et al. (1996) characterize the dorsal bursae, a pair of small elliptical fat bodies, located in the monkey lip (monkey lips/dorsal bursae—MLDB) complex on each side of the head as the
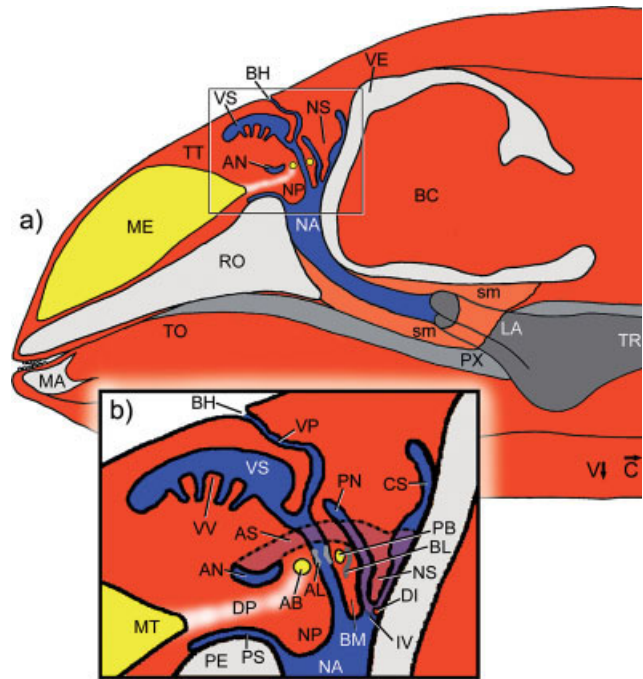


Fig. 1. Schematic sagittal reconstruction of an adult harbor porpoise (*Phocoena phocoena*) head showing the nasal structures and the position of the larynx (LA). (**a**) overview. (**b**) detail of boxed area in (a). Blue, air spaces of the upper respiratory tract; gray, digestive system; light gray, cartilage, and bone of the skull; yellow, fat bodies. AB, rostral bursa cantantis; AL, rostral phonic lip; AN, anterior nasofrontal sac; AS, angle of nasofrontal sac; BC, brain cavity; BH, blowhole; BL, blowhole ligament; BM, blowhole ligament septum; C, caudal; CS, caudal sac; DI, diagonal membrane; DP, low density pathway; IV, inferior vestibulum; MA, mandible; ME, melon; MT, melon terminus; NA, nasal passage; NP, nasal plug; NS, nasofrontal septum; PB, caudal bursa cantantis; PE, premaxillary eminence; PN, posterior nasofrontal sac; PS, premaxillary sac; PX, pharynx; RO, rostrum; sm, sphincter muscle of larynx; TO, tongue; TR, trachea; TT, connective tissue theca; V, ventral; VE, vertex of skull; VP, vestibulum of nasal passage; VS, vestibular sac; VV, folded ventral wall of vestibular sac.

site of sound production (Fig. 1). Accordingly, these authors proposed the terms "bursae cantantes" for the dorsal bursae and "phonic lips" for the monkey lips (Cranford et al., 1996; Cranford, 2000; Cranford and Amundin, 2004) and these new terms are used in this study. The proposed mechanism is a pneumatically-driven "clapping" process at the phonic lips (Ridgway et al., 1980; Amundin and Andersen, 1983; Marten et al., 1988; Cranford, 2000) which creates an initial sound vibration in fat tissue within the bursae cantantes (Cranford et al., 1996; Cranford and Amundin, 2004). From here vibrations are guided into the water via the melon, a large body of "acoustic fat" (Litchfield and Greenberg, 1974; Litchfield et al., 1975; Au et al., 2006) comprising most of the bulbous forehead region in dolphins (delphinids) and porpoises (phocoenids; Fig. 1). The nasal air sacs and specific features of the skull and associated connective tissue may help to focus and to guide the sound to the front (Fleischer, 1975, 1976, 1982; Oelschläger, 1990; Cranford et al., 1996; Aroyan et al., 2000; Rauschmann et al., 2006).

Toothed whales seem to be peculiar in that they have no facial expression (Caldwell and Caldwell, 1972; Manger, 2006) although their facial musculature is well developed and highly complicated. In these animals it is concentrated around the blowhole as part of the nasal complex (Lawrence and Schevill, 1956; Mead, 1975) which represents a unique modification of the mammalian upper respiratory tract (Huber, 1934). In contrast to baleen whales (mysticetes), all odontocetes show at least some degree of asymmetry in the skull roof and the overlying epicranial complex (Ness, 1967; Schenkkan, 1973; Cranford et al., 1996). For detailed reviews and latest results on odontocete forehead anatomy and function the reader is referred to Lawrence and Schevill (1956), Schenkkan (1973), Mead (1975), Heyning (1989), Rodionov and Markov (1992), Cranford et al. (1996, 2008a,b), Cranford (2000), Cranford and Amundin (2004), Huggenberger (2004), Prahl (2007), and Cranford et al. (2008a,b).

When compared with the small number of dolphin species, which have been investigated more extensively, the sound repertoire of harbor porpoises seems to be somewhat restricted (Au, 1993; Wartzok and Ketten, 1999) and their sonar signals differ from those of most delphinid species in several respects. Whereas echolocation clicks of dolphins are broad-band signals with three to seven pressure cycles in the time domain and peak frequencies of up to 80 kHz, harbor porpoises emit narrow-band clicks with peak frequencies of 130–140 kHz and 8–20 pressure cycles (polycyclic signals; Au et al., 1999; Kastelein et al., 1999; Cranford, 1999, 2000; Villadsgaard et al., 2007). Apart from the intense high-frequency component in the signals of harbor porpoises, a low-frequency component of lower intensity can be found. Amundin (1991) demonstrated that this low-frequency component is an air-borne effect and probably a by-product of the pneumatically-driven process generating the tissue-borne high-frequency sounds (Cranford et al., 1996). Whistle-like sounds of porpoises were reported only a few times (Verboom and Kastelein, 1995).

In comparison with most dolphin species studied so far, the sonar system in the harbor porpoise should have a higher physical resolution due to the higher frequencies emitted and a high signal-to-noise ratio due to their narrow bandwidth. Both of these sonar characteristics may be adaptations to the detection of small prey in coastal habitats (Goodson et al., 2004). Differences between the acoustic properties of echolocation sounds in harbor porpoises and delphinids point to group-related adaptations in the click production and/or emission mechanisms. In turn, these differences in mechanism should be linked to morphological specializations of the sound generator and/or emitter. The forehead anatomy of harbor porpoises was described in some detail by Curry (1992). In general, the author (Curry, 1992) states that sound production occurs at the same level as in dolphins, i.e., above the nasal plugs at the "elliptical bodies" (bursae cantantes). Curry (1992) suggests that differences between dolphins and porpoises as to sound production can be attributed to differences in the size of the nasal sacs, the control of air flow through the nasal passages, and in the mode of sound transmission. In the present article on the nasal complex of the harbor porpoise, new bioacoustic interpretations of detailed three-dimensional morphological data (using conventional histological and macroscopic methods and modern imaging techniques) are presented and compared with the extant information on delphinids.

## MATERIAL AND METHODS

The nasal complex of the harbor porpoise (*Phocoena phocoena* L.) was investigated in 17 specimens by means of macroscopic dissection, routine histology, cryo-sectioning, X-ray computer-assisted tomography (CT), and magnetic resonance imaging (MRI). The harbor porpoise is a coastal toothed whale species, which, in the adult stage, has about the same dimensions as the human (body length 160 cm, body mass 60 kg; Bjørge and Tolley, 2002). The 12 porpoises donated by German Oceanographic Museum (Stralsund, Germany) and Research and Technology Centre Westcoast, (Büsum, Germany; Table 1) were stranded dead animals or accidental bycatch and frozen after being collected by the "German stranding network". During routine necropsies, samples appearing to be fresh macroscopically and without visible pathological alterations were taken (for more information of animal collection and necropsies cf. Benke et al., 1998; Siebert et al., 2006) and either stored at $-20°C$ or fixed in formaldehyde solution (36% formaldehyde 1:10 in tap water). These samples were examined afterwards by (macroscopic) cryotomy, CT and/or MRI (cf. Table 1).

For the scanning procedure the frozen specimens were thawed to room temperature and packed in plastic bags. The fixed specimens were transferred into plastic bags without changing the fixation fluid. CT scans were performed in the transverse plane, MRI slices in all three major planes. The horizontal plane was established in parallel to two diameters through the skull, i.e., one (a) from the tip of the rostrum to the ventralmost border of the foramen magnum, and another (b) between the basal surfaces of the two tympanic bones (or between the eyes in cases where the ear bones had been removed earlier). The midsagittal plane was established as perpendicular to the horizontal plane at (a) and transverse planes standing at right angles to the latter. The lines and planes were set using prescans before the final scans were conducted. Measurements of anatomical structures given in the text refer to adult porpoises examined (Table 1). During macroscopic dissections, surface areas of the vestibular and premaxillary sacs were photographed with a digital camera in dorsal view for measurements.

The upper respiratory tract of one harbor porpoise specimen (ID-No. 905, Table 1) was filled with a commercial contrast agent ($BaSO_4$ solution) before CT scanning. The CT data of this specimen were used to reconstruct a 3D model of the skull, the nasal fat bodies and air sacs using the Amira Graphics Software package (Indeed-Visual Concepts, Germany).

During the dissections, tissue samples of the nasal complex were taken from three harbor porpoises (Table 1). Larger samples (e.g., four blocks of tissue from the phonic lips area of $\sim7$ cm$^3$) were cryo-sectioned at 50 µm thickness. Smaller samples were embedded in paraffin and cut at 14–20 µm. Sections were stained with AZAN (azocarmine and aniline blue), Resorcin-Fuchsin, and/or methylene blue (Romeis, 1989). In addition, the transverse microslide series of a 16.7 cm harbor porpoise

**TABLE 1. List of material examined (species cf. Rice, 1998)**

| Species | Institution[a] | ID number | Age | Body length (cm) | Sex | Fixation | Method applied |
|---|---|---|---|---|---|---|---|
| *Delphinus delphis* | NMNH | – | Adult | – | – | Frozen | DS |
| *Delphinus delphis* (?) | SAI | – | Fetal | (10.8 CBL) | – | Ethanol | CS |
| *Globicephala melas* | SMF | – | Fetal | – | – | Formaldehyde | CS |
| *Grampus griseus* | NMNH | WJW 012 | Adult | – | – | Frozen | DS |
| *Lagenorhynchus albirostris* | DMM | – | Adult | – | – | Formaldehyde | CS |
| *Phocoena phocoena* | DMM | – | Adult | – | f | Frozen | CT, MRI, CS |
| *Phocoena phocoena* | FTZ | 898 | Neonate | 78 | m | Formaldehyde | MRI |
| *Phocoena phocoena* | FTZ | 903 | Fetal | 62 | f | Frozen | MRI, HS |
| *Phocoena phocoena* | FTZ | 905 | Adult | 161.5 | f | Frozen | CT (nasal sacs filled by BaSO$_4$ in liquid) |
| *Phocoena phocoena* | FTZ | 1281 | Subadult | 106 | m | Frozen | CT, MRI, DS |
| *Phocoena phocoena* | FTZ | 1321 | Adult | 131 | m | Formaldehyde | DS |
| *Phocoena phocoena* | FTZ | 1366 | Adult | 110 | f | Formaldehyde | MRI, HS |
| *Phocoena phocoena* | FTZ | 1367 | Adult | 102 | m | Formaldehyde | DS |
| *Phocoena phocoena* | FTZ | 1369 | Adult | 116.5 | f | Formaldehyde | CT, MRI, DS |
| *Phocoena phocoena* | FTZ | 1370 | Adult | 136.5 | m | Formaldehyde | DS, HS |
| *Phocoena phocoena* | FTZ | – | Adult | – | f | Frozen | DS |
| *Phocoena phocoena* | FTZ | – | Adult | – | f | Frozen | DS |
| *Phocoena phocoena* | SAI | – | Adult | – | m | Frozen | CS (sagittal) |
| *Phocoena phocoena* | SAI | – | Adult | – | m | Frozen | CS (transverse) |
| *Phocoena phocoena* | SAI | MK 48 | Fetal | 16.7 | – | ? | HS (transverse) |
| *Phocoena phocoena* | SMF | – | Neonate | 72 | – | Ethanol | CT, MRI |
| *Phocoena phocoena* | ZMUC | CN 138 | Fetal | 42 | – | Ethanol | CT, MRI |
| *Tursiops truncatus* | SMF | – | Fetal | – | – | Formaldehyde | CS |
| *Tursiops truncatus* | NMNH | 01-TTR 031 | Adult | – | – | Frozen | DS |
| *Tursiops truncatus* | NMNH | MMSC 98-081 | Adult | – | – | Frozen | DS |
| *Tursiops truncatus* | NMNH | NJ 00-110 | Adult | 315 | m | Frozen | DS |
| *Tursiops truncatus* | NMNH | REL 017 | Adult | – | – | Frozen | DS |
| *Tursiops truncatus* | SAI | SAI 7928 | Subadult | – | – | Formaldehyde | CT, MRI |

CBL, condylobasal length; CS, (macroscopy) cryo-sectioning; CT, computer-assisted tomography; DS, macroscopical dissection; HS, histological sections; MRI, magnetic resonance imaging.
[a]Abbreviations of donating institutions where the material is archived: DMM, Deutsches Meeresmuseum (Stralsund, Germany); FTZ Forschungs- und Technologiezentrum Westküste (Büsum, Germany); NMNH, National Museum of Natural History (Washington DC); SAI, Dr. Senckenbergische Anatomie (Department of Anatomy III, Johann Wolfgang Goethe-University, Frankfurt a.M., Germany); SMF, Research Institute and Natural History Museum Senckenberg (Frankfurt a.M., Germany); ZMUC, Zoological Museum of the University of Copenhagen (Denmark).

fetus (10 μm, AZAN; part of the extensive collection of prenatal cetaceans of Prof. Dr. Milan Klima located in the Department of Anatomy III at the Johann Wolfgang Goethe-University Frankfurt am Main, Germany) was included in the analysis. For comparison, the heads of two common dolphins (*Delphinus delphis*), one Risso's dolphin (*Grampus griseus*), one long-finned pilot whale (*Globicephala melas*), one white-beaked dolphin (*Lagenorhynchus albirostris*), and six bottlenose dolphins (*Tursiops truncatus*) were examined. The delphinid species donated by the National Museum of Natural History (Smithsonian Institution, Washington, DC; Table 1) were dissected carefully as part of routine necropsies after the animals (stranded dead and stored frozen) were thawed. For the other specimens examined for this study no further information is available (Table 1).

Because the organization of the nasal complex in toothed whales is unique among mammals, there have been only minor attempts to establish a valid terminology for these structures since there are so few homologous counterparts in other (terrestrial) mammals (Lawrence and Schevill, 1956). If not cited otherwise, the nomenclature for these nasal structures characteristic of cetaceans follows Mead (1975) and Cranford et al. (1996).

## RESULTS

The nasal (epicranial) complex of the harbor porpoise is situated in a facial depression of the skull (facial skull). The bony nostrils are located in the middle of this depression and in the center of the skull, respectively, immediately in front of the brain case. The single external nasal opening (blowhole) is situated dorsal and rostral to the vertex of the skull (Fig. 1: BH). While being closed the blowhole resembles a transverse semicircular slit with its convexity pointing caudally. Only the rostral lip of the blowhole can be moved significantly as shown by careful movements of these structures by hand. Below the blowhole, the nasal passage runs vertically, i.e., nearly perpendicular to the beak-fluke axis. The dorsal part of the upper respiratory (nasal) tract consists of a flattened and unpaired transverse vestibulum (Figs. 1 and 2: VP) which slightly bulges caudally. The vestibulum is ~1.5 cm long (dorsoventral extension). The surfaces of its rostral and caudal walls are in
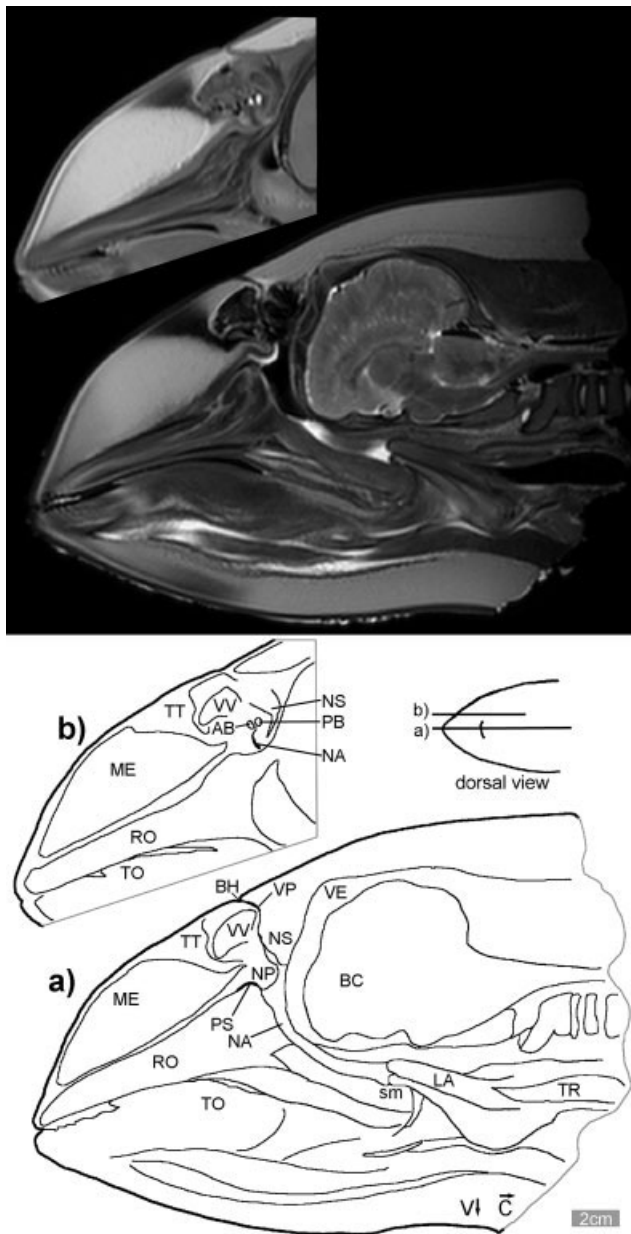
Fig. 2. Sagittal MRI scans of an adult harbor porpoise (*Phocoena phocoena*) head. (**a**) Midsagittal T1-weighted scan of an entire head. (**b**) right parasagittal T2-weighted scan of the nasal complex at the level of the bursae cantantes. This comparison reveals that the contrast in the MR images of this thawed specimen (no. 1281; Table 1) is generally dominated by differences in the relaxation time constant T1. However, the T2 relaxation time constant reveals more contrast within the dense connective tissue of the theca (TT) and the vestibular sac (VV). For abbreviations see Fig. 1.

intimate contact with each other in the postmortem specimens examined in this study. Below the vestibulum, the nasal passage is divided into two nasal passages by the sagittal soft nasal septum. Ventral to the border between the vestibulum and the paired nasal passages, the phonic lips (monkey lips) are situated (Fig. 1: AL). These lips are represented by two low horizontal

band-like prominences in the rostral and in the caudal wall of each nasal passage which oppose each other and thus stand perpendicular to the air stream: according to our macroscopical dissections, delicate horizontal folds on the surface of the rostral phonic lip fit in corresponding grooves on the caudal lip. Apart from the blowhole region, this mortise and tenon complex seems to be another sealing mechanism of the nasal passage (not shown). Furthermore, parallel to the air stream, a group of ∼10–15 minute dorsoventral wrinkles on the lips are oriented perpendicular to the "closing" (mortise and tenon) folds and grooves (not shown in Figures). Small ellipsoid fat bodies, the bursae cantantes (dorsal bursae), are located at this level adjacent to the rostral and the caudal wall of each nasal passage below the epithelial lining (Figs. 1–3, 4a, and 5–8). The bursae are situated ∼1.0–1.2 cm lateral to the nasal midline (nasal septum) and thus flank the lateral half of each nasal passage (Fig. 4a). The long axes of the ellipsoids stand more or less transversely. Each pair of bursae (left and right) is embedded in the connective tissue of the phonic lips and thus part of the so-called monkey lips/dorsal bursae complex. The bursae cantantes exhibit slight asymmetry in porpoises (Fig. 5): on the right hand side both bursae are 1.0–1.2 cm wide (mediolateral extension) and ∼0.4 cm in height and in thickness (dorsoventral and rostrocaudal extension). The left bursae are 0.8–1.0 cm wide and slightly smaller in height and in thickness. In addition, each rostral bursa is not as wide as its caudal counterpart (∼0.1 cm shorter) but instead a little thicker in the dorsoventral and rostrocaudal dimension.

Below the phonic lips, the nasal passages run nearly vertically to enter the bony nares. Here, both passages are occluded by the nasal plugs, paired bodies of connective tissue interspersed with muscle fiber bundles. Each of these plugs bulges from the rostral wall of the nasal passage into the lumen of the latter (Figs. 1 and 2); by this, the ventrocaudal edge of each plug contacts the caudal border of the bony naris. In porpoises, small nodules consisting mainly of connective tissue are located medially on the ventrocaudal edges of the plugs (not shown in Figures; whereas in delphinids the nodules stand laterally on the ventrocaudal margins of the plugs).

The epithelial lining of the vestibulum is black or dark brown, similar to the epidermis of these animals. At the level of the phonic lips, the color of the epithelium changes and continues to become brighter in the paired nasal passages. On the phonic lips it is up to twice as thick as that of the soft nasal passage (Fig. 3). In the bony nasal passage, the mucous membrane appears red; in its rostral (ventral) wall, the epithelium seems to contain glands, which are characterized by pinhole-like openings. In our fetus of 16.7 cm TL (Table 1), the glands are obvious but they have not been analyzed yet histologically.

## Nasal Diverticula

In the harbor porpoise, three pairs of air sacs (nasal diverticula) communicate with the nasal passages. On each side of the head, these sacs can be taken as extensions of the accessory nasal passage. The three pairs of diverticula lie in separate horizontal levels of the epicranial complex (Fig. 4c: I–III): dorsoventrally the vestibu-
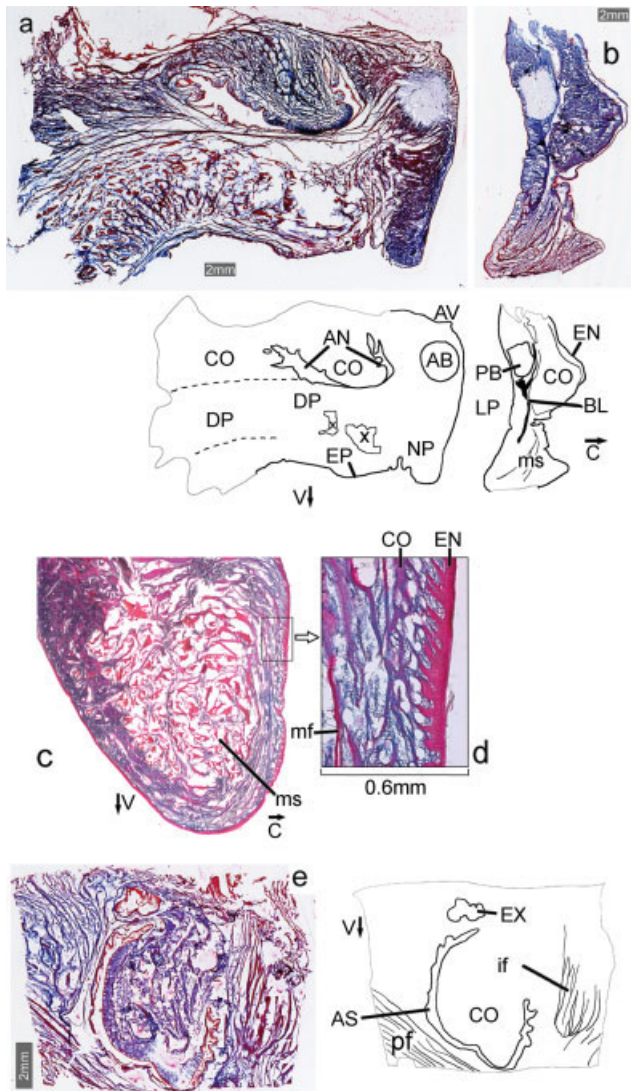
Fig. 3. Histological sections of an adult harbor porpoise (*Phocoena phocoena*) nasal complex stained with AZAN. Cut edges are drawn in light gray in the schematic drawing. (**a**) Parasagittal section through the nasal plug (NP), rostral dorsal bursa (AB), and anterior nasofrontal sac (AN). (**b**) Parasagittal section through the blowhole ligament septum with the ligament (BL) and the caudal bursa cantantis (PB). Note that (a) and (b) are different histological sections but arranged in their natural orientation and separated by an artificially wide left nasal passage (LP). (**c**) Parasagittal section through the blowhole ligament septum medial to (a) and (b) showing its intrinsic muscle (ms, red reticulated material). (**d**) Close-up of (c) showing the subepithelial papillae (blue) projecting into the epithelium (EN; red). (**e**) Transverse section (frontal view) through the angle of the left nasofrontal sac (AS). Note its U-shaped cross section and the small dorsal extension of the air sac (EX). AV, aperture of vestibular sac (ventral wall); C, caudal; CO, connective tissue of porpoise capsule; DP, low density pathway; EP, dorsal epithelium of premaxillary sac; if, intrinsic muscle fibers of nasofrontal sac; mf, muscle fiber bundle; pf, *M. maxillonasolabialis profundus*; V, ventral; x, artifact.

lar sacs are followed by the nasofrontal sacs and the premaxillary sacs. These diverticula communicate with their soft nasal passage by slit-like apertures.

As the dorsalmost diverticulum, each vestibular sac (Figs. 1, 6: VS) is situated rostrolateral to its nasal pas-

sage and thus further rostral to the blowhole than in the delphinid species examined in this study. The slit-like entrances from the nasal passages into these sacs are orientated horizontally and located in the rostrolateral walls of the nasal passages dorsal to the phonic lips and to the nasal septum, respectively. The inner surface of each vestibular sac is thin and lined by smooth black epithelium; its dorsal wall is smooth and flexible whereas the ventral wall of the sac is rigid and composed of dense connective tissue with plicae of up to 1.5 cm height (Fig. 2). These plicae and furrows, respectively, converge in the direction of the slit-like entrance into the nasal passage (Fig. 7). In all the specimens examined, a prominent central furrow was visible (coined "ausführender Spalt" by Gruhl, 1911; or "hendidura central" by Gallardo, 1913; not labeled in Figures) which divides the vestibular sac into a rostral and a caudal portion. In the vestibular sac, only this central furrow is in direct contact with the slit-like opening into the nasal passage, whereas the other plicae merge in the central groove in the direction of the midsagittal plane. The left/right asymmetry of the vestibular sacs was obvious in all the harbor porpoise specimens investigated (Figs. 5–7): Here, the right sac is always more expanded than the left. However, this lateralization varies in harbor porpoises from a nearly symmetrical situation to slight asymmetry (compared to other odontocetes). Maximal asymmetry in the vestibular sacs was found in porpoise no. 1369 (Fig. 7, see Table 1) where the surface area of the right sac was approximately twice that of the left sac. On an average, the surface area of the left vestibular sac is equivalent to about 70% of the right one. (Note that the surface measurements were taken from photos in dorsal view and do not include the epithelial surface in the furrows.) Concluding from the specimens examined here, the degree of asymmetry in the vestibular sacs does not seem to be age-dependent.

The nasofrontal sacs are situated ventral and caudal to the vestibular sacs. On each side, the nasofrontal sac comprises a rostral part (anterior nasofrontal sac; Figs. 1 and 5: AN) situated rostral to the nasal passage and a caudal part behind the nasal passage (Figs. 1 and 5: CS, PN). A slit-like aperture in the ventrocaudal wall of the soft nasal passage on both sides communicates with this air sac system. Each aperture leads first into a small chamber, the inferior vestibulum (Fig. 1: IV), which connects the caudalmost part of the nasofrontal sac with the nasal passage (Fig. 5: green arrow). A thick septum of connective tissue projects from the dorsal wall into the caudal portion of the nasofrontal sac ("nasofrontal septum"; Figs. 1 and 8: NS). This septum was called "hintere Klappe" by Gruhl (1911) or the "posterior septum of the blowhole ligament" by Curry (1992). The cavity rostral to the septum is the posterior nasofrontal sac (PN), whereas the caudal part is termed caudal sac (Fig. 1: CS). The caudal epithelium of the latter sac on each side attaches to the cranium in a smooth depression between the vertex of skull and the caudal border of the bony nostrils. The epithelium covering the ventral margin of the nasofrontal septum (on a horizontal level with the inferior vestibulum) is nonpigmented and intensively linked to the subepithelial layer via papillae of connective tissue (Fig. 3d).
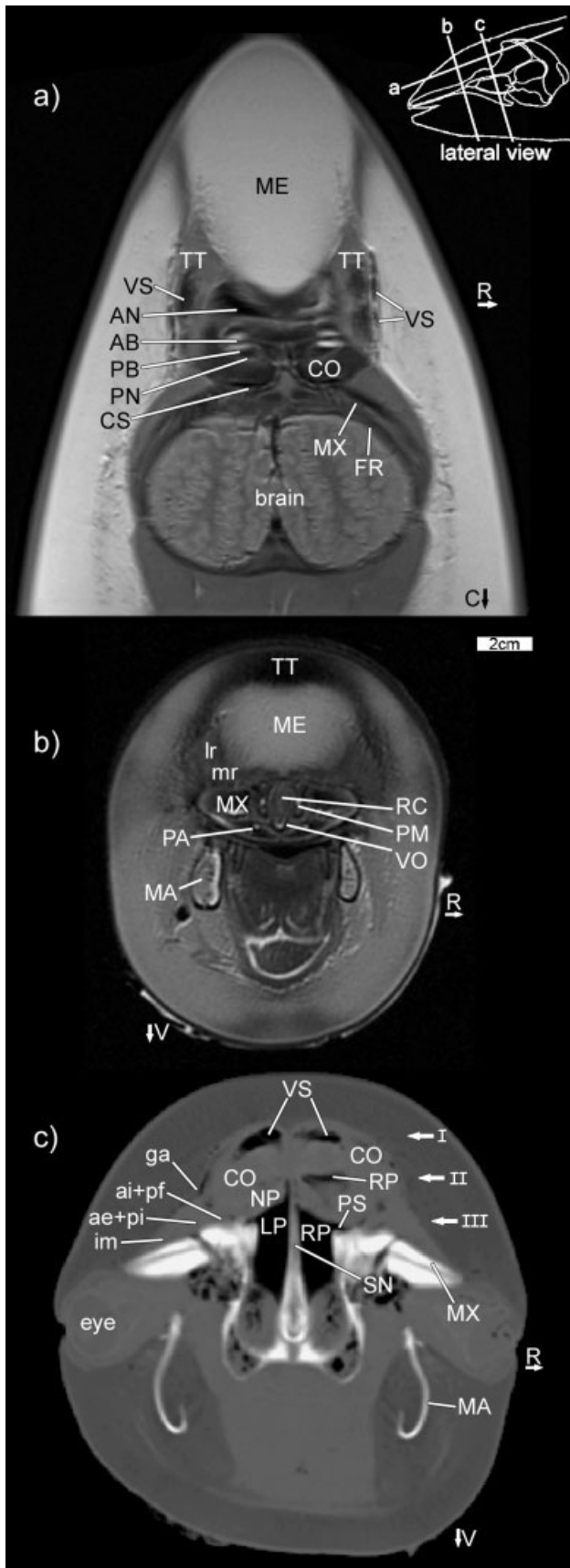
A thin but tough fold, the so-called diagonal membrane (Figs. 1 and 8: DI), protrudes from the caudal surface of the inferior vestibulum and the caudal sac. This fold, only 1–2-mm wide and directed rostrally, stretches across the laterocaudal edge of the nasal passage and the inferior vestibulum to the medioventral border of the nasal bone in the caudal sac.

On each side, the transition between the caudal parts of the nasofrontal sac (CS and PN) continues into its rostral part (AN) at the so-called angle (Figs. 1, 5, and 8: AS). The angle is situated lateral to the nasal passage, and from here the rostral sac runs in a medial direction and ends just rostral to the accessory nasal tract near the midsagittal plane (Figs. 5 and 8: AN). Consequently, the whole nasofrontal air sac system encircles the nasal passages on both sides in the horizontal plane (Figs. 5 and 8). The angle is U-shaped in transverse section (Fig. 3e: AS). At its caudal end, just before the caudal sac, each nasofrontal sac bears a small dorsal extension (Fig. 3e: EX). The anterior nasofrontal sac resembles a dorsoventrally flattened tube or gutter (Fig. 5) which is slightly U-shaped in the sagittal plane (Figs. 1, 3a, and 8: AN). The inner surface of the sac is lined by nonpigmented thin epithelium which is again linked to the underlying connective tissue via papillae of loose connective tissue.

The ventralmost pair of nasal air sacs, the premaxillary sacs, rest on the caudal half of each premaxillary eminence rostral to the bony nares (Figs. 1, 5, and 9: PS, PE). Each of these air sacs is 1.0–1.5 cm long so that, in relation to skull size, the surface area of the premaxillary sac in the harbor porpoise approximates only 1/5 that in the delphinids examined. The dorsal epithelium of this sac is linked to the tissue of the nasal plug via papillae of connective tissue as found in parts of the nasofrontal sac (Fig. 3). The entrance of each premaxillary sac extends in a laterocaudal direction, circles around the bony naris (Fig. 4c: PS; Fig. 7: not labeled) and communicates with the slit-like aperture in the inferior vestibulum. The diagonal membrane forms a thin valve through the inferior vestibulum connecting this laterocaudal extension of the premaxillary sac with the corresponding caudal sac (not shown in Figures).

Fig. 4. The nasal complex of the harbor porpoise (*Phocoena phocoena*). (**a**) Horizontal T2-weighted MRI scan showing the bursae cantantes (AB and PB, paired light patches). (**b**) Transverse T1-weighted MRI scan of the rostral region rostral to the antorbital notch showing the rostral musculature. (**c**) Transverse CT scan at the level of the bony nares showing the "porpoise capsules" (left and right CO). I–III mark the three levels of nasal air sacs (see text). The positions of muscular layers (ga, im, ae, pi, ai, pf) were determined with other techniques used. AB, rostral bursa cantantis; ae, *M. maxillonasolabialis anteroexternus*; ai, *M. maxillonasolabialis anterointernus*; AN, anterior nasofrontal sac; C, caudal; CS, caudal sac; FR, frontal bone; ga, Galea aponeurotica; im, *M. maxillonasolabialis intermedius*; LP, left nasal passage; lr, lateral rostral muscle; MA, mandible; ME, melon; mr, medial rostral muscle; MX, maxilla; NP, nasal plug; PA, palatine; PB, caudal bursa cantantis; pf, *M. maxillonasolabialis profundus*; pi, *M. maxillonasolabialis posterointernus*; PM, premaxilla; PN, posterior nasofrontal sac; PS, premaxillary sac; R, right; RC, rostral cartilage; RP, right nasal passage; SN, nasal septum; TT, connective tissue theca; V, ventral; VO, vomer; VS, vestibular sac.
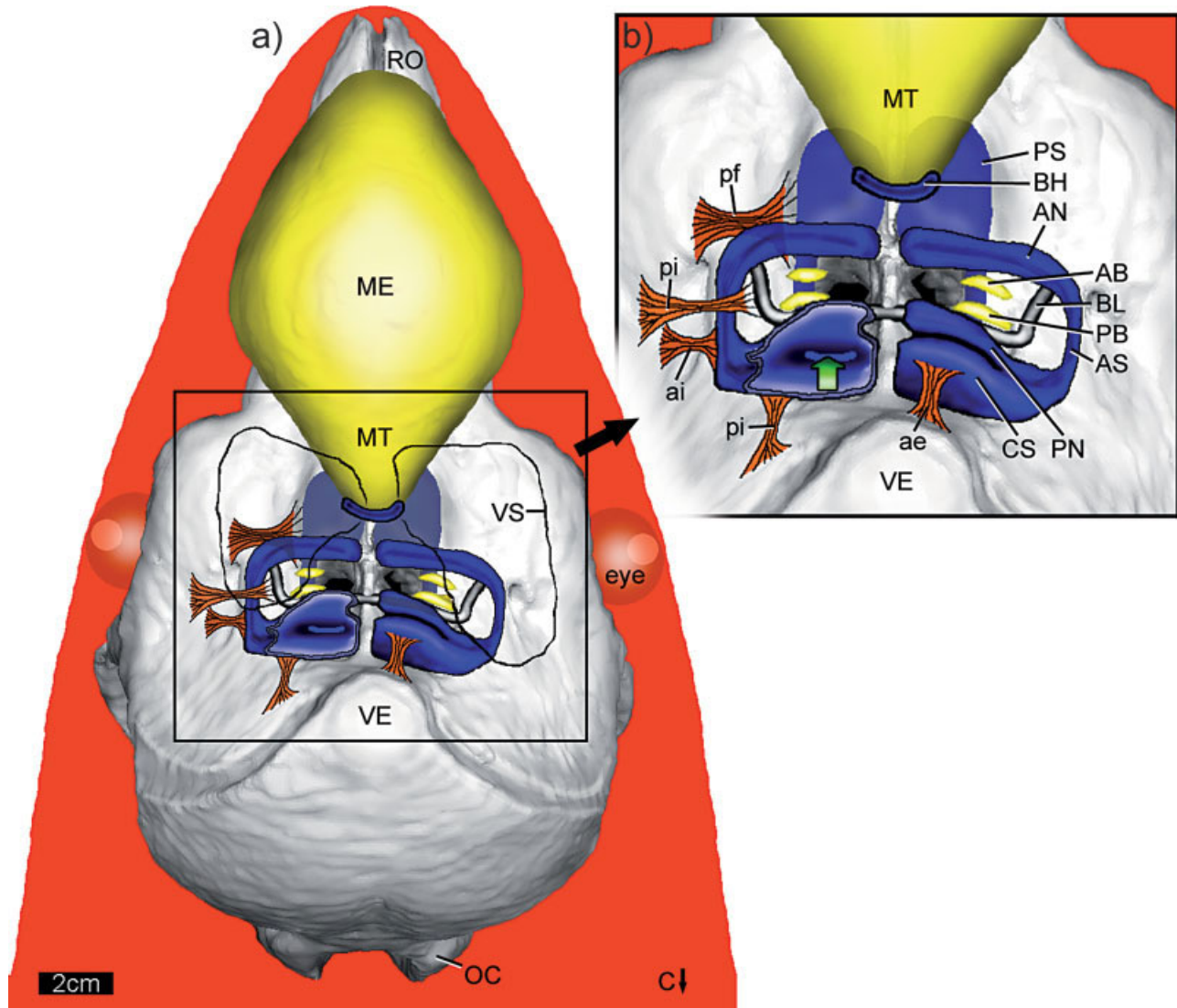
Fig. 5. Three-dimensional reconstruction of the harbor porpoise (*Phocoena phocoena*) nasal complex in dorsal view showing the structures ventral to the vestibular sacs (VS; black contours) and indicating the topographic relations of the skull, melon (ME), bursae cantantes, the nasofrontal sac system and premaxillary sac (PS). (**a**) overview. (**b**) detail of boxed area in (a). The left caudal and posterior nasofrontal sacs are opened dorsally to show their entrance into the inferior vestibulum [green arrow in (b)]. Laterocaudal extensions of the premaxillary sacs (not labeled) are situated lateral to the bony nares and are seen below the rostral and caudal bursae cantantes (AB, PB; color code see Fig. 1). Soft nasal passages omitted. The facial musculature, which is organized in sheets, is shown here by strings since in their full size they would hide each other in dorsal view. ae, *M. maxillonasolabialis anteroexternus*; ai, *M. maxillonasolabialis anterointernus*; AN, anterior nasofrontal sac; AS, angle of nasofrontal sac; BH, position of blowhole; BL, blowhole ligament; C, caudal; CS, caudal sac; MT, melon terminus; OC, occipital condyle; pf, *M. maxillonasolabialis profundus*; pi, *M. maxillonasolabialis posterointernus*; PN, posterior nasofrontal sac; RO, rostrum; VE, vertex of skull. The openings of the nasal passages are given in black.

## Melon and Associated Connective Tissue

Each pair of bursae cantantes is located in the center of dense connective tissue referred to as the porpoise capsule (Fig. 4c: CO). Both capsules (left and right) are continuous in the midsagittal plane (Fig. 4c). They are enclosed by air spaces of the upper respiratory tract: the vestibular sacs dorsally and rostrolaterally, the premaxillary sacs ventrally and the caudal sacs caudally, whereas the angles of the nasofrontal sacs are embedded in the capsules laterally, the anterior nasofrontal sacs rostrally and the nasal passages being in a central position (Fig. 4a,c). The capsules are permeated by muscle fiber bundles laterally and dorsocaudally (see below).

A large bulbous fat body, the melon, is situated rostral to the porpoise capsules (Figs. 1, 2, 4, 5, and 9: ME). The melon is symmetrical, ovoid in shape and flattened dorsoventrally. In the harbor porpoise, this fat body is supported ventrally by the maxillary and premaxillary bones, covering the short rostrum for nearly its total length (Fig. 6). Therefore, in its location, the melon is responsible for the typical "beakless face" of porpoises and
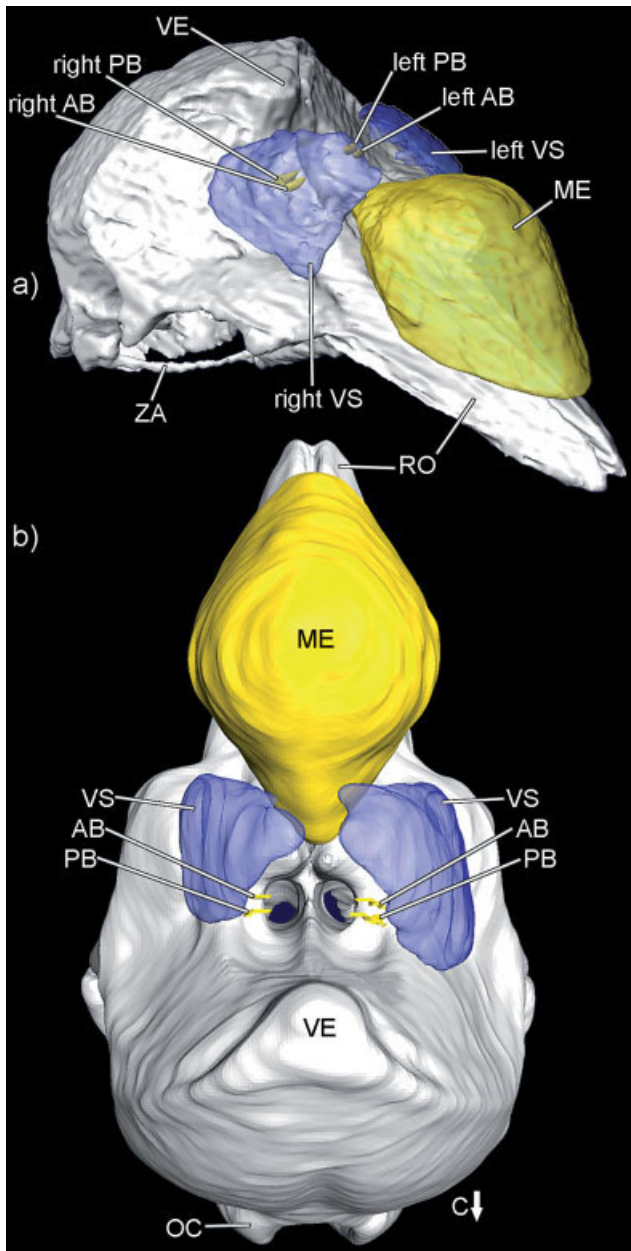
Fig. 6. Three-dimensional reconstruction of the harbor porpoise (*Phocoena phocoena*) nasal complex showing the topographic relations of the skull (light gray), melon (ME, yellow), and bursae cantantes (yellow) in right anterodorsolateral view (**a**) and in dorsal view (**b**). Note the position and angles of the vestibular sacs (VS, blue). AB, rostral bursa cantantis; C, caudal; OC, occipital condyle; PB, caudal bursa cantantis; RO, rostrum; VE, vertex of skull; ZA, zygomatic arch.
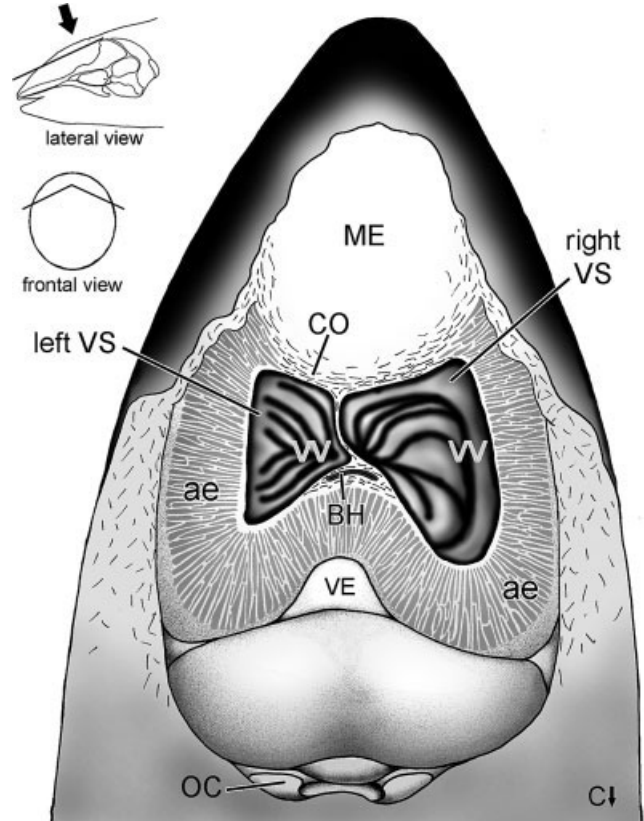


Fig. 7. Schematic reconstruction of the vestibular sacs (VS) and anteroexternus muscle (ae) in the harbor porpoise (*Phocoena phocoena*) in dorsal view based on macroscopical dissection of animal no. 1396 (Table 1) which showed the highest degree of asymmetry in the vestibular sacs of all specimens examined (see text). The surface of the convex forehead has been cut obliquely from both sides (for orientation of the cuts see small inserts) and the upper walls of the vestibular sacs were omitted. Note that the lips of the blowhole (BH) were removed. C, caudal; CO, connective tissue of porpoise capsule; ME, melon; OC, occipital condyle; VE, vertex of skull; VV, folded ventral wall of vestibular sac.

the convex forehead contour of many toothed whales. Whereas its core is nearly free of dense connective tissue, the fiber content increases towards the periphery of the melon (Figs. 2 and 4a). Ventrolaterally, these collagen fibers are interwoven with fiber bundles of the rostral facial muscles (Fig. 4b; see below).

Caudally the melon is covered by a sheet of dense collagen (connective tissue theca; Figs. 2 and 4a: TT) which merges in the porpoise capsules (Fig. 4a,b). On both sides, the ventrolateral part of the theca is continuous with the nasal plug muscles which are rich in connective tissue (see below). Lateral and caudal to the theca, the subcutaneous connective tissue has similar properties as in the thick blubber which covers the head except the area above the melon and the theca, respectively (Figs. 2 and 4a,b). The caudal end (terminus) of the melon (Figs. 1 and 8: MT) enters the theca and the capsules in the midline. Here, a low-density pathway (Figs. 1 and 3: DP) exists on both sides ventral to the anterior nasofrontal sac; it runs from the area of the rostral dorsal bursa to the terminus of the melon. Whereas in delphinids the bifurcate terminus of the melon is in direct contact with the rostral bursae, this "pathway" in the harbor porpoise consists mostly of loose but coarse connective tissue interspersed with fiber bundles from the nasal plug muscle (Fig. 3; see below). According to our macroscopical dissections, the pathway appears to consist of fatty collagenous connective tissue. Histological sections (Fig.
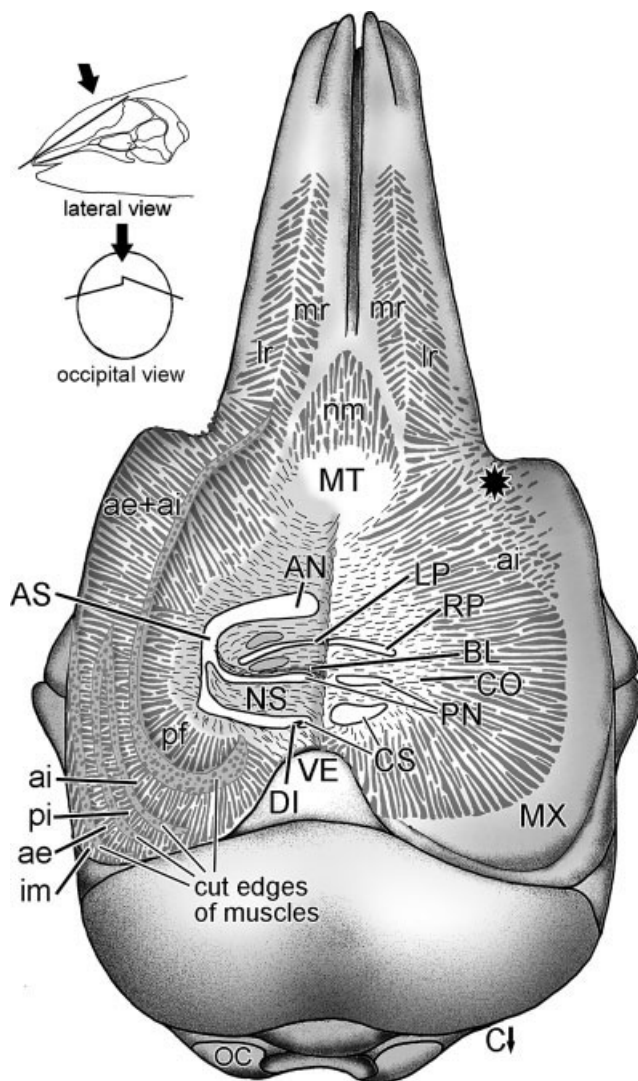
Fig. 8. Schematic horizontal reconstruction of the nasal muscula-ture of the harbor porpoise (*Phocoena phocoena*) in two different oblique sectional planes (cf. inserts). The nasal diverticula of the sub-horizontal planes are shown divided by the midline: On the right side the plane passes above the bursae cantantes and the anterointernus (ai) and lateral rostral muscles (lr) are complete. At the antorbital notch fibers of the anteroexternus concentrate in a strong muscle fiber bun-dle together with the anterointernus muscle (asterisk; see text). On the left hand side, the sectional plane of which corresponds to that on the right but cuts further ventrally, the nasal sacs (white) are cut at the level of the bursae cantantes [small gray ellipsoids rostral and cau-dal to the left nasal passage (LP)]. Note that on the left the muscle layers of im, ae, pi, and ai are removed near their origins (cut edges), but the profundus muscle (pf) is complete as is the anterointernus muscle (ai) on the right side. Rostrally, the base of the nasal plug mus-cle (nm) and the oblique cut of the melon terminus (MT) are shown. The vestibular sacs and the Galea aponeurotica are omitted. ae, *M. maxillonasolabialis anteroexternus*; AN, anterior nasofrontal sac; AS, angle of nasofrontal sac; BL, blowhole ligament; C, caudal; CO, con-nective tissue of porpoise capsule; CS, caudal sac; DI, diagonal mem-brane; im, *M. maxillonasolabialis intermedius*; mr, medial rostral mus-cle; MX, maxilla; NS, nasofrontal septum; OC, occipital condyle; pi, *M. maxillonasolabialis posterointernus*; PN, posterior nasofrontal sac; RP, right nasal passage; VE, vertex of skull.

3) reveal the differences between the porpoise capsule dorsal to the anterior nasofrontal sac and the connective tissue ventral to the sac where the low-density pathway is located. Within the pathway, the interspace between the collagenous fibers seem to be increased and the fibers are orientated more or less in parallel to its axis (Fig. 3a). On the other hand, the fibers of the pathway are rather thick in comparison with, e.g., those in the blowhole ligament septum (Fig. 3b).

The ribbon-shaped blowhole ligament (Figs. 1, 3b, 5, and 8: BL) on both sides originates from the maxilla in an area laterocaudal to the premaxillary eminence (Fig. 5). From here it runs through the porpoise capsule later-ally and continues through the lip between the posterior nasofrontal sac and the nasal passage along the caudal margin of the caudal bursae cantantes. Therefore, this lip is referred to as "blowhole ligament septum" (Figs. 1, 3b, and 8: BM; referred to as "tissue peninsula" by Cran-ford et al. 1996). Both halves of the blowhole ligament, which consists of dense (collagenous) connective tissue, unite in the midsagittal plane. In the harbor porpoise, the blowhole ligament shows the same topographical relationships with respect to the caudal bursae can-tantes as in dolphins (Figs. 1, 3, 5, and 8). It is bordered caudally by dense connective tissue as part of the por-poise capsule (Fig. 3b). Ventral to the ligament, the blowhole ligament septum consists of loose connective tissue and houses an intrinsic muscle (Fig. 3c: ms; see below). The ventral edge of the blowhole ligament sep-tum forms the rostral border of the aperture leading from the nasal passage into the inferior vestibulum (Fig. 1: IV). The nasal plug (protruding rostrocaudally) fits into this aperture of the inferior vestibulum (Figs. 1 and 2) and closes it tightly even in dead specimens (in Fig. 1 the upper respiratory tract is somewhat inflated for bet-ter demonstration of its components). Thus, if the nasal plug is shifted in a caudal direction by hand during the dissections, the lower part of the blowhole ligament sep-tum becomes part of a sealing mechanism at the upper margin of the bony naris for both the nasal passage and the inferior vestibulum.

## Nasal Musculature

The structure of the epicranial musculature in the harbor porpoise shows a pattern similar to that in the Delphinidae. Several thin muscle layers lie on top of each other to form a cone around the soft nasal passages (Fig. 4), resembling an onionskin-like organization (Figs. 7 and 8). Because of this complicated three-dimensional configuration of the layered blowhole (facial) muscula-ture and its intricate topographical and functional corre-lations with the air sac system, not every single detail can be shown in the figures (cf. Figs. 4, 5, and 7–9). In the harbor porpoise, the musculature originates from the facial skull provided by the caudal extensions of the maxillary bones. Five bilaterally fan-shaped muscle layers originate concentrically from the maxilla and run more or less dorsomedially in the direction of the soft nasal passages. Seen from above, the contours of the muscle sheets on each side describe semicircles around the nasal passages, starting out from the vertex (VE) and extending more or less in parallel to the facial bor-ders of the skull roof (lateral and caudal margins of the maxillary bones) to the antorbital region and rostrum
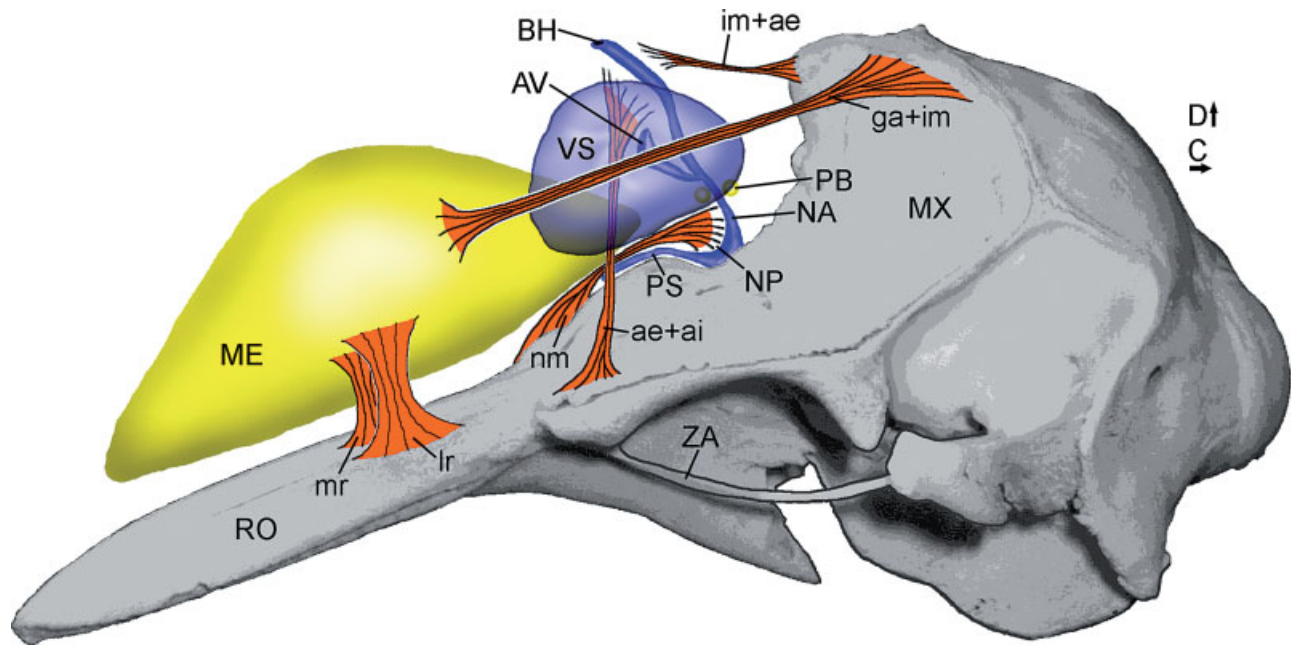
Fig. 9. Three-dimensional-reconstruction of the harbor porpoise (*Phocoena phocoena*) nasal complex in left side view showing the topographic relations of the skull (gray), melon (ME), left bursae cantantes (PB, caudal bursa cantantis; rostral bursa not labeled), vestibular sac (VS), and the nasal tract. The muscles are represented by strings since in their full size they would hide each other in lateral view. The nasofrontal sacs are omitted (color code see Fig. 1). ae, *M. maxillonasolabialis anteroexternus*; ai, *M. maxillonasolabialis anterointernus*; AV, aperture of vestibular sac; BH, blowhole; C, caudal; D, dorsal; ga, *M. maxillonasolabialis posteroexternus*; im, *M. maxillonasolabialis intermedius*; lr, lateral rostral muscle; mr, medial rostral muscle; MX, maxilla; NA, nasal passage; nm, nasal plug muscle; NP, nasal plug; PS, premaxillary sac; RO, rostrum; ZA, zygomatic arch.

(Figs. 7 and 8). Rostral extensions of the muscles are associated with the melon (see below).

On top of the five layers in the cone-shaped block of facial musculature, a sheet of loose connective tissue is attached to the hypodermal fat deposits (Fig. 4: ga) and blends caudally in the hypodermal connective tissue sheath. The fiber bundles of the sheet, which originate on both sides from the mediocaudal borders of the facial skull, run to the connective tissue theca lateral to the melon (Fig. 9: ga). von Baer (1826) termed this layer "Galea aponeurotica" and Curry (1992) "superficial facial tendon". When passing over the caudal and ventral parts of the vestibular sacs (not shown in Figures) the tendon is up to 4 cm wide and ~0.8 cm thick. Here a thin sheet of muscle fibers is embedded in the tendon. A few muscle fiber bundles diverge ventrally and attach to the supraorbital process of the maxillary bone (caudal to the eye), and a thin fascia of this muscle bundle inserts at the rostrum. Following the terminology of Lawrence and Schevill (1956), this thin muscle layer is homologous to the *Musculus maxillonasolabialis posteroexternus* in delphinids (Curry, 1992; Fig. 9: ga).

In general, the different components (parts) of the facial musculature are named after topographic criteria. The uppermost sheet of the muscular cone, *M. maxillonasolabialis intermedius* (Figs. 4 and 8: im) is situated medial to the posteroexternus muscle and the Galea aponeurotica, respectively, and originates from the posterolateral part of the facial skull. The fibers are orientated in a rostral direction and insert in the connective tissue theca. There is a tendinous area of this muscle superficial

to the caudal part of the vestibular sac. Careful manipulatory simulation of muscle action revealed that, together with the small posteroexternus layer, this muscle may pressurize the central part of the nasal complex by pulling the connective tissue theca in the caudal direction. This process compresses the air diverticula, in general, with the vestibular sacs presumably being influenced most effectively by the contraction of these two muscle sheets (Fig. 9: ga+im). Furthermore, the dorsomedial part of the intermedius muscle can retract the posterolateral part of the caudal blowhole lip (Fig. 9: im).

Medioventral to the posteroexternus and intermedius, the anteroexternus component of the *M. maxillonasolabialis* (Figs. 4, 7, and 8: ae) originates in a typical concentric pattern near the facial border. The muscle fiber bundles of the thicker rostral part run more or less perpendicular to the axial course of the intermedius component (Fig. 9) and insert on the lateral border of the vestibular sac, some rostralmost fiber bundles blending in the connective tissue anteroventral to the blowhole (Fig. 9: ae). The thin caudal portion of this muscle is attached via a flat aponeurosis to the connective tissue caudal to the nasal passage and the caudal sac (Figs. 5 and 9). Some laterocaudal fibers blend in the connective tissue lateral and rostral to the nasal passage and in the wall of the latter at the aperture of the vestibular sac (not shown in Figures). A division of this anteroexternus muscle into a rostral and a caudal portion, as described by Lawrence and Schevill (1956) in dolphins, was not found in the harbor porpoise. In delphinids, the anteroexternus serves as the dilatator of the unpaired upper

nasal passage (vestibulum). In the harbor porpoise, the caudal portion of the anteroexternus may pull back the caudal wall of the nasal passage only slightly whereas its rostral portion (Fig. 9: ae) may draw the rostral blowhole lip to the front. The lateral part of this muscle seems to control the volume of the vestibular sac and its opening into the nasal passage; this was tested by careful manipulatory simulation of muscle action (not shown in Figures).

The *M. maxillonasolabialis posterointernus* (Fig. 8: pi) originates from the facial skull medial to the intermedius and anteroexternus portions and between the supraorbital process of skull and the vertex. This muscle is not clearly defined at its rostral end where it disappears between the anteroexternus and anterointernus portions (see below). The rostral part of the posterointernus and deep fibers of the anteroexternus portion insert to an aponeurosis which, in turn, attaches ventrally to the junction of the vestibular sac with the nasal passage and thus may control air flow into this sac (not shown in Figures). Caudally, the posterointernus muscle was found to insert in a region of the porpoise capsule above and adjacent to the posterior nasofrontal and caudal sacs (Fig. 5: pi). Manipulatory simulation of muscle action demonstrated that this part of the posterointernus may modulate the tension of the nasal passage at the phonic lips via the blowhole ligament (Fig. 5: pi). It should also dilate the inferior soft nasal passage by pulling its wall caudally and laterally. The contraction of the caudal portion of the posterointernus (manipulatory simulation) may also control the tension of the dorsolateral walls of the posterior nasofrontal and caudal sacs (Fig. 5: pi) as well as the nasofrontal septum (Fig. 1: NS). A distinct intrinsic muscle ventral to the blowhole ligament (Fig. 3b,c: ms) is continuous with the posterointernus portion and should be able to control the tension within the blowhole ligament septum.

The *M. maxillonasolabialis anterointernus* (Fig. 8: ai) originates medial to the posterointernus portion. Its rostral part merges with the overlying anteroexternus muscle. Both rostral components of this muscular complex (ae+ai) originate from the maxilla at the transition from the rostrum to the nasal skull in the dense connective tissue rostral to the antorbital notch (Fig. 8: asterisk). They embrace the posterointernus portion (pi) and stretch to the porpoise capsule rostral to the nasal passage (Figs. 8 and 9: ae+ai) and between the rostral portion of the vestibular sac and the anterior nasofrontal sac (not shown). Thus, the rostral part of the anterointernus muscle may exert pull on the connective tissue dorsal to the anterior nasofrontal sac and the rostral bursa cantantis as was shown by manipulatory simulation of muscle action. The lateral part of this muscle attaches to the connective tissue dorsal to the angle and the inferior vestibulum and may control air movement and pressure in the angle and the nasofrontal sac (Fig. 5: ai). Moreover, the anterointernus muscle attaches to the blowhole ligament and to the nasofrontal septum (Figs. 1, 5, and 8). The caudal portion of the anterointernus muscle is connected to the dorsal part of the caudal sac.

The deepest layer of the muscular cone around the soft nasal passage, the *M. maxillonasolabialis profundus* (Fig. 8: pf), originates from the maxilla beneath and medial to the anterointernus muscle and does not reach the base of the vertex (as is true for the anterointernus). It attaches to the caudal sac only laterally (Fig. 8). The profundus muscle can be divided into a rostral and a caudal portion by means of their fiber orientation (Fig. 8: pf). The rostral portion is bound to the connective tissue theca ventrolateral to the melon terminus and its fiber bundles are orientated in a dorsomediocaudal direction. The fiber bundles of the caudal part run rostromedially, in parallel to those of the anterointernus muscle (Fig. 8). The profundus muscle attaches to the connective tissue lateral and ventral to the angle, to the posterior nasofrontal sac, and the caudal sac (not shown). Moreover, as shown by manipulatory simulation, this muscle may also alter the volume of the laterocaudal extension of the premaxillary sac since its fiber bundles insert into connective tissue dorsal to the extension (Fig. 5: pf).

The rostrum is associated with two slender bilateral muscles as extensions of the anteroexternus, anterointernus, and profundus muscle portions (layers). The more extended lateral rostral muscle (Fig. 9: lr) originates mainly from the maxilla and its fibers have a dorsolaterocaudal orientation, blending on each side in the connective tissue lateroventral to the melon. This muscle is continuous with the strong muscle sheet formed by the rostral parts of the anteroexternus and anterointernus portions (Fig. 8). The narrower part, the medial rostral muscle (Fig. 9: mr), originates from the dorsal surfaces of the maxilla and premaxilla and is in contact with the connective tissue ventral to the melon. The medial rostral muscle is continuous with the rostral part of the profundus muscle (Fig. 8).

Between the caudal parts of the left and right medial rostral muscles the nasal plug muscles (Figs. 8 and 9: nm) originate from the premaxillary bones rostral to the premaxillary sacs. The muscle fiber bundles (not labeled) have a dorsocaudal orientation, run in parallel to the dorsal walls of the premaxillary sacs (Fig. 3: EP), and enter the connective tissue of the nasal plugs and up to the rostral bursae cantantes dorsocaudally (Fig. 3). The nasal plug muscle is compact and strong but rich in connective tissue fibers (not labeled). Manual simulation showed that the action of this prominent muscle widens the air passage at the level of the entrance into the bony naris by moving the nasal plug in the rostral direction (Fig. 1).

The vestibular sac is surrounded by an intrinsic muscle. Its fiber orientation largely parallels that of the anteroexternus portion. The nasofrontal sac is also surrounded by an intrinsic muscle embedded in connective tissue but the texture of its fibers does not parallel that of other muscle layers (Fig. 3e: if).

In the harbor porpoise, the well-developed facial nerve (not shown in Figures) was found to have a similar diameter and course as in delphinids. The nerve runs from the otic region along the slender zygomatic arch to the antorbital notch where it turns dorsally. Beyond this point, it branches diffusely in the dorsal and caudal directions and enters the different layers of the maxillonasolabialis muscle. A small rostral portion of this nerve is in contact with the rostral muscles. The trigeminal nerve invades the facial complex with branches coming from the various infraorbital foramina but the course and distribution of this nerve was not traced further.

## DISCUSSION

As in other mammals, the primary and main function of the nasal tract in toothed whales (Odontoceti) is respiration. Olfaction in the usual way is unlikely in toothed whales because the olfactory bulb disappears at the beginning of the fetal period (Oelschläger and Buhl, 1985; Buhl and Oelschläger, 1988; Oelschläger and Kemp, 1998). The second major functional aspect of the nasal apparatus is sound generation and transmission for echolocation and communication (Cranford et al., 1996; Cranford, 2000; Cranford and Amundin, 2004). In this respect, the mammalian bauplan was profoundly modified and some structures in the nose are even unique to odontocetes (Klima, 1999; Rauschmann et al., 2006).

### Opening and Closing of the Nasal Tract

The biomechanics of nasal respiration and phonation are difficult to separate from each other because they share the nasal passages and the facial (maxillonasolabialis) muscles. For respiration, two antagonistic muscle strands may open the dorsal part of the nasal tract including the single blowhole and vestibulum. In front, the strong complex of the anteroexternus and anterointernus muscles pull the rostral wall of the vestibulum and the rostral lip of the blowhole rostroventrally (Fig. 9: ae+ai). At the rear, the dorsomedialmost fiber bundles of the intermedius (im) and anteroexternus (ae) portions (Figs. 8 and 9) pull the caudal wall of the vestibulum and the caudal lip of the blowhole in the caudal direction. Thus, the simultaneous action of these two antagonistic muscle groups should open the blowhole and the vestibulum, respectively. The lower (paired) section of the soft nasal tract is opened by the nasal plug muscles, which pull the nasal plugs rostrally (Fig. 9: nm; Lawrence and Schevill, 1956; Mead, 1975).

Correspondingly, the relaxation of the nasal plug muscles should cause the nasal plugs to slide back over the premaxillary eminences/premaxillary sacs into their intranarial position. As outlined by Lawrence and Schevill (1956) for dolphins, it is also plausible for harbor porpoises that the nasal portions of the anterointernus muscles indirectly force the nasal plugs into the bony nares and, at the same time, dilate the lower nasal passages. In addition, the posteroexternus and intermedius muscles may pull the melon terminus and surrounding connective tissue caudally (Fig. 9: ga+im). This action should close the paired section of the nasal tract tightly. However, it seems unlikely that laterocaudal portions of the anteroexternus and posterointernus muscles contribute to the closing of the nasal passages at the level of the vestibulum (Mead, 1975) since their fibers are not orientated to pull the rostral lip of the blowhole caudally (Figs. 5 and 8). But in principle, the opening and closing mechanisms proposed above for the harbor porpoise are similar to those outlined for dolphins (Mead, 1975) and the vestibulum and the nasal plugs seem to represent parts of tight closing mechanisms (Mead, 1975). Apart from that, the most superficial muscular layer (posteroexternus portion) and the Galea aponeurotica (Fig. 4c: ga) which is continuous with the subdermal sheath of connective tissue on the trunk seem to form a functional unit involved in harbor porpoise locomotion (Curry, 1992; Pabst, 1996).

## Sound Generation

The nasal structures potentially involved in sound generation exhibit the same topographical relationships in our harbor porpoises as in delphinids (cf. Cranford et al., 1996). Thus the "unified hypothesis" for odontocete sound generation as suggested by Cranford et al. (1996) is substantiated by this detailed study on harbor porpoises. In short, their "phonic lips hypothesis" (Cranford et al., 1996) implies that piston-like movements of the larynx build up positive air pressure in the area of the bony nares (Houser et al., 2004). Because of that pressure, air quanta are driven through the lower nasal passage and into the vestibular sacs. Between the bony nares and the vestibular sacs, however, each air stream passes a pair of phonic lips and causes them to separate and then to slap together in a series of events (by Bernoulli or other fluid dynamic forces; Cranford and Amundin, 2004; Dubrovskiy and Giro, 2004; Dubrovskiy et al., 2004). Here, the upper part of each blowhole ligament septum (Figs. 1 and 3) including the caudal phonic lip acts like a hammer that slaps against the opposing rostral epithelium of the nasal passage with the rostral phonic lip and the rostral bursa cantantis. The frequency and amplitude of these events are, among other factors, controlled by the tension of the blowhole ligament and the maxillonasolabialis muscles, respectively (see below). Each clapping event causes the respective rostral phonic lip to vibrate, creating an initial sound wave that is guided via the low density pathway (potential acoustic pathway) from the rostral bursa to the melon and from there into the surrounding water (Cranford et al., 1996; Cranford and Amundin, 2004; Au et al., 2006). The expanded air in the vestibular sacs should be recycled into the soft nasal passages (as shown by Norris et al., 1971; cited after Norris, 1980) via the contraction of the three superficial layers of the maxillonasolabialis muscles including the intrinsic muscles which altogether control the volume of these sacs (Figs. 4c, 7, and 9: ga, im, ae, ae+ai): From here, the recycled air should be shifted into the bony nasal passages and the throat by the retraction of the larynx into its initial position (Huggenberger et al., 2008).

Despite the principal correspondence in the organization of their nasal structures, there are some significant differences between porpoises and other toothed whales. The spherical porpoise capsules, consisting of homogeneous coarse connective tissue (collagen), with the right one being only slightly larger than the left (Fig. 4: CO), have not been found in dolphins (Cranford et al., 1996). Therefore, our results corroborate the assumption of these authors (Cranford et al., 1996) that the symmetry of the capsules and the embedded bursae cantantes (Figs. 1 and 4c) may represent a prerequisite for the formation of the characteristic narrow-banded harbor porpoise clicks. Furthermore, we hypothesize that the density and stiffness of the surrounding connective tissue (with the exception of the potential acoustic pathway, see below) should mean a limited potential for vibration in the bursae cantantes and thus favor the generation of narrow-banded high-frequency clicks. In addition, the mechanical properties of the sound generator might be controlled by the coordinated comprehensive and differential contraction of the various portions of the facial musculature via the tension throughout the porpoise

capsule. Also, on a smaller scale, the capacity of the (caudal) phonic lips to vibrate may be controlled by actions of the posterointernus muscle via the tension of the blowhole ligament (Fig. 5: pi). On a larger scale, the intranarial air pressure can be controlled by piston-like movements of the larynx (Cranford et al., 1996; Huggenberger et al., 2008) and/or the compression of the soft nasal passages by actions of the posteroexternus and intermedius muscles (Fig. 9: ga+im). These two parameters (tension of the phonic lips and intranarial air pressure) should enable porpoises to control the click repetition rate (Cranford et al., 1996; Dubrovskiy and Giro, 2004).

Bursal cartilages were not found in our harbor porpoise specimens, neither macroscopically nor histologically (Fig. 3b), but were found in all the other toothed whale species examined (Table 1). This result is in line with recent findings indicating that these cartilages appear in neonate and juvenile harbor porpoises but not in adults (Prahl, 2007). In most nonphyseterid toothed whales, the bursal cartilages are located exactly caudal to both caudal bursae cantantes and near the blowhole ligament, and Cranford et al. (1996) hypothesized that the cartilages may be remnants of the tectum nasi in the odontocete embryo (Klima, 1999). The same authors (Cranford et al., 1996) stated that these cartilages possibly serve as stiffening devices for the caudal bursae cantantes. The absence of these cartilages in the harbor porpoises examined here, however, does not contradict this idea (Cranford et al., 1996) since, in these animals, the bursae are embedded in dense connective tissue and may not need additional stiffening devices. The absence of bursal cartilages and other anatomical differences between our specimens and the descriptions in the literature (e.g., the structure of the deep layers of the nasal muscles (see below; Curry, 1992) may thus be explained as potential morphological peculiarities of different ontogenetic stages. Although it is not likely that these characteristics imply significant deviations regarding sonar function, it cannot be excluded that they indicate individual characteristics of single animals with respect to phonation.

The echolocation pulses of Commerson's dolphin (*Cephalorhynchus commersonii*), a delphinid species which inhabits coastal waters of the Southern hemisphere (Rice, 1998), are also known to be polycyclic and similar to those of the harbor porpoise (Kamminga and Wiersma, 1982; Cranford, 2000). If our hypothesis is correct that the dense and stiff porpoise capsule is one of the prerequisites for the production of such narrow-band high-frequency signals, Commerson's dolphins should have a similar device for increasing the stiffness within the sound generation apparatus. Unfortunately, only little is known on the anatomy of this dolphin but there are some structural similarities in the harbor porpoise and Commerson's dolphin that, in some way, set both apart from most delphinids. In these two species, the anterior nasofrontal sacs are similar in shape (Amundin and Cranford, 1990) and the caudal terminus of the melon is located in the midsagittal plane (Heyning, 1989) as was found in our harbor porpoises investigated. Furthermore, the dorsal aspect of the cranium shows the same slight degree of asymmetry in harbor porpoises and Commerson's dolphin (Schenkkan, 1973; Huggenberger, 2004). Nevertheless, so far there is no report of a

structure in Commerson's dolphin (or in Hector's dolphin, *C. hectori*; Mead, 1975) which may have similar properties as the porpoise capsule and future anatomical studies should focus on such structures in these species.

Goodson and Datta (1995) and Goodson et al. (2004) presented a model describing that the frequency spectrum and the envelope of a harbor porpoise click (increase in amplitude during the first five cycles, then a decrease) as well as the strong high-frequency component result from reverberations of an initial pulse between the deep basal folds of the two vestibular sacs and the sound channel (potential acoustic pathway). These furrows are a peculiarity of phocoenids and the vestibular sacs are located further rostral to the blowhole than in delphinids (Mead, 1975; Curry, 1992). Therefore, the absence of such tough collagenous folds in the floor of the vestibular sacs and the position of these sacs in the two *Cephalorhynchus* species (Schenkkan, 1973; Mead, 1975; Heyning, 1989; Amundin and Cranford, 1990) indicate that these plicae and their position are probably not involved in the generation of the polycyclic click sounds in harbor porpoises. Moreover, the model proposed in Goodson et al. (2004) is based on the assumptions that (i) sound is processed in the dense connective tissue (as part of the porpoise capsule) surrounding the vestibular sac folds, (ii) the …"vestibular air sacs wrapped around the acoustic channel can be considered a very short megaphone"… in the forward direction, and (iii) that there are usually five folds in each sac (Goodson and Datta, 1995). If sound is processed in the dense connective tissue of the vestibular sac folds (Goodson and Datta, 1995; Goodson et al., 2004), it should enter the potential acoustic pathway (low density pathway) and the melon to be guided into the water. However, this seems to contradict the hypothesis on the function of this potential acoustic pathway (including the melon) as a "sound guide" (Cranford et al., 1996) because there seems to be a high impedance mismatch between the dense connective tissue ventral to the vestibular sacs and the low density pathway. Furthermore, our results contradict the model of Goodson and co-workers (Goodson and Datta, 1995; Goodson et al., 2004) in that the vestibular sacs narrow the proposed sound path in the rostral direction and do not widen it like a "megaphone" (Figs. 2 and 6) and that there are at least six folds or more in each sac (Fig. 7; the "best-fit model" of Goodson et al. (2004) proposed five folds).

Evidence from high-speed video endoscopy suggests that whistle sounds are produced in the nasal passages of dolphins (Cranford, 2000; Cranford et al., 2001). These signals are likely generated at the nasal plugs (Mead, 1975; Ridgway et al., 2001) which are good candidates for this function since, at this level, each of the nasal passages could act as a variable pipe with a slit-like opening between the phonic lips. Even though whistles are not part of the normal sound repertoire of porpoises, a general potential to produce sounds other than pulses could explain the peculiar whistle-like vocalizations of harbor porpoises recorded by Verboom and Kastelein (1995).

## Sound Emission

As in dolphins, the nasal air sacs of the harbor porpoise surround the potential sound-generating system at

the phonic lips (Figs. 1 and 4–9). Only in the rostral direction, where the melon enters the porpoise capsule (Figs. 1, 2, and 9), the array of covering air sacs is incomplete (Figs. 1 and 3). As a consequence, Norris (1964) took up the idea of Forrest G. Wood and Paul Asa-Dorian that the melon of dolphins transmits sound from the center of the nasal complex into the surrounding water and that parts of the nasal diverticula and/or the skull serve as acoustic reflectors to guide the sound to the melon (Evans and Maderson, 1973; Au et al., 2006; Cranford et al., 2008a). In the harbor porpoise, the structure and topography of the premaxillary, posterior nasofrontal, and the caudal air sacs suggest functional properties as potential sound reflectors in the direction of the melon (Figs. 1–5). Besides, these sacs may help insulate the neurocranium and, above all, the ears from sound traveling caudally (Fleischer, 1975; Oelschläger, 1990). The air volume and pressure in the premaxillary, posterior nasofrontal, and caudal sacs may be controlled by the posterointernus muscle (see above; Fig. 5: pi), which could also modulate the tension of the blowhole ligament and its septum. Accordingly, this muscle layer should regulate air flow through the nasal passages and into the posterior nasofrontal sac and caudal sac by adjusting the tension in the blowhole ligament septum (Fig. 1). Concluding from the morphology and close topographical relationships of the blowhole ligament septum, nasofrontal septum, and the diagonal membrane, these structures seem to represent a mechanical device allowing the functional separation of these sacs (posterior nasofrontal and caudal sacs) from their nasal passage. By this mechanism, air quanta in the nasal passages and in the nasofrontal sacs may be pressurized independently. The deepest layers of the maxillonasolabialis muscle (Figs. 4c, 5, and 8: ai and pf) seem to regulate air flow into the caudal and premaxillary sacs independent of the blowhole ligament septum by opening and closing the laterocaudal extensions of the premaxillary sacs which communicate with the inferior vestibuli and, thus, with the caudal sacs (Fig. 5). In this context, the fold of the diagonal membrane may help to seal this premaxillary sac/caudal sac transition from the nasal passages. In contrast to the premaxillary sacs and the nasofrontal sac system, the vestibular sacs with the conspicuous folding of their floor (Fig. 7) do not look like typical sound reflectors since they lack smooth surfaces. Instead these two sacs could avoid the loss of sound energy in the dorsal and lateral directions (Fig. 6).

In the harbor porpoise, the anterior nasofrontal sacs are situated directly in front of the proposed click sound generators at the rostral bursae cantantes and slightly larger than in most dolphins in relation to head size (Schenkkan, 1973). The glandular appearance of the epithelium of these sacs, as suggested by Mead (1975), cannot be confirmed in our specimens (Fig. 3). Ventral to the anterior nasofrontal sacs loose but coarse collagen fiber bundles (low density pathway) run more or less in parallel along the presumed sound channel (Fig. 3a) suggesting an acoustic coupling of the rostral bursae and the melon. Because of their close topographical relations to the potential acoustic pathways (extending from both rostral bursae to the melon terminus, cf. Fig. 3a) it is likely that the anterior nasofrontal sacs are involved in the modulation of sound beam directionality. The activity of the nasal plug muscles, which radiate into the

connective tissue of the nasal plugs, may be another parameter for changing the geometry of the potential acoustic pathway(s) (Harper et al., 2008). So far, however, it is not clear how these factors actually influence the sound field. The premaxillary sacs are located ventral to the low density pathways on the premaxillary eminences which are typical for harbor porpoise skulls (Heyning, 1989). These bulbous protuberances in front of the bony nostrils raise the premaxillary sacs above rostrum level and bring them closer to the potential acoustic pathway. Concluding from their shape, position and smooth dorsal and ventral walls, these sacs should influence the transmission of the sound beam as likely candidates for sound reflectors.

With their geometry and close proximity, the premaxillary and anterior nasofrontal sacs narrow the potential acoustic pathway dorsoventrally and thus may channel the sound beam before it enters the melon. In this context, these air spaces seem to be key parameters for sound field formation and frequency filtering in the harbor porpoise. At the same time, the premaxillary sacs can be regarded as contact surfaces on which the nasal plugs can slide rostrally (analogy to synovial bursae) to open the nasal passages (see above).

Au et al. (2006) stated that the melon and the connective tissue theca of harbor porpoises channel sound to form a directional echolocation beam. Accordingly, a change in the shape of the melon should influence the shape of a sound beam before it enters the water (Mead, 1975; Norris, 1975; Au, 1993; Aroyan et al., 2000; Harper et al., 2008). The more or less bilaterally symmetrical rostral muscles of the nasal complex (Fig. 8: lr and mr) presumably modulate the melon's shape by pulling its lateroventral parts in a ventral direction (Mead 1975; Fig. 9), thus flattening the melon with respect to the rostrum. Furthermore, the intermedius muscle (im) may pull the dorsal part of the melon caudally (Fig. 9) and rostral parts of the anterointernus muscle (ai) may pull the melon terminus ventrally, thus changing its height (Harper et al., 2008). However, it would be a matter of speculation to decide how much such a change in shape can contribute to a potential modulation of the sonar beam.

## Comparative and Evolutionary Aspects of the Odontocete Nasal Musculature

The general arrangement of nasal muscles in the harbor porpoise resembles the situation found in delphinids indicating similar functional implications as to vocalization. However, there are some peculiarities in the porpoise. Curry's description (Curry, 1992) of nasal muscles in the harbor porpoise does not distinguish a separate profundus muscle. She followed the description of Mead (1975) of delphinids who recognized a fusion of Lawrence and Schevill's (1956) anterointernus and profundus portions (Fig. 7 in Curry, 1992). In the harbor porpoise specimens examined here, the anterointernus and profundus muscles resemble the situation in dolphins as described by Lawrence and Schevill (1956) but these authors could not discriminate a rostral and caudal division of the profundus muscle. In contrast, they described an outer and a deeper layer of the profundus. According to their figures of bottlenose dolphins (*Tursiops truncatus*; Figs. 16 and 17 in Lawrence and Schevill 1956),

these layers could be homologous to the rostral and caudal portions of this muscle in the harbor porpoise. Differences in the descriptions of the medialmost muscle layers (ai and pf) in the literature may, at least in part, be due to different quality in the fixation of the material examined or to the fixation methods applied since separate profundus and anterointernus portions were found in very fresh or well-fixed specimens only.

Curry (1992) reported that the vestibular sac is surrounded by an intrinsic muscle that has no distinct fiber orientation but may be continuous with the anteroexternus and anterointernus portions. Probably the same intrinsic muscle was found in the harbor porpoises examined here, but its fiber orientation paralleled that of the anteroexternus portion. A diagonal membrane muscle as described for dolphins by Lawrence and Schevill (1956) and Mead (1975) could not be identified in the harbor porpoise.

The musculature of the epicranial complex in toothed whales is derived from the paired *Musculus maxillonasolabialis* in mammals (Huber, 1934). In nonphyseterid toothed whales, it can be subdivided topographically and functionally into two major parts: the rostral musculature associated with the melon and the caudal musculature controlling the nasal passages and their diverticula (Fig. 8). However, careful anatomical dissections reveal that the rostral muscles are continuous with caudal muscle layers arranged around the nasal passages. Accordingly, each maxillonasolabialis muscle can also be divided into two parts (Fig. 8): (i) the medial one consisting of the medial rostral muscle (mr) rostrally and the profundus component (pf) caudally and (ii) the lateral one comprising the lateral rostral muscle (lr) rostrally and the anterointernus (ai), posterointernus (pi), anteroexternus (ae), and intermedius (im) components caudally. A similar arrangement, i.e., the division of the odontocete maxillonasolabialis muscle into a medial and a lateral part, was reported by Mead (1975) for delphinids. However, this author (Mead, 1975) did not define a profundus muscle (see above) and found the anterointernus to be continuous with the medial rostral component in dolphins. Nevertheless, as suggested by Mead (1975), the relative position of the medial components speaks for their identity as derivatives of the nasal portion and the topography of the lateral components seems to be homologous to the labial portion of the mammalian maxillonasolabialis muscle. This interpretation is in contrast to Huber (1934) who considered the caudal odontocete nasal musculature to be a homolog of the pars nasalis and the rostral muscles a homolog of the pars lateralis of other mammals. At the moment, the phylogenetic relationships between the nasal muscles in toothed whales and in terrestrial mammals cannot be assessed here. Rodionov and Markov (1992) presented an extensive study on the bottlenose dolphin based on a Russian investigation of mammalian facial muscles which, however, was not available for this study.

Sensory innervation of the facial structures in toothed whales is supplied by the maxillary division of the trigeminal nerve (Rauschmann, 1992; Pabst et al., 1999; Rommel et al., 2002; Rauschmann et al., 2006); however, the nasal diverticula and the melon do not appear to be heavily innervated (Mead, 1975). Motor innervation of the nasal musculature is provided by the facial nerve (Mead, 1975; Rauschmann, 1992; Pabst et al., 1999; Rommel et al., 2002; Rauschmann et al., 2006). In toothed whales, the highly differentiated nasal musculature should have the capacity of discrete but complicated intrinsic movement patterns needed for the modulation of the nasal complex as a whole and in detail. The potential functional implications of this complex, to some degree, are related to its three-dimensional organization and, in principle, the complexity of this system is reminiscent of the situation in primates. In the latter, the facial musculature is thin but widely distributed in numerous subdivisions underneath and attached to the facial skin, able to change its topographical features in many characteristic ways resulting in highly complex two-dimensional dynamic patterns (expressions) used for interindividual visual communication. In comparison, dolphins live in a dense medium in permanent locomotion and sometimes move at high speed (Fish, 2000). Here, the terrestrial (e.g., primate) principle of facial expression as the transmitter of social information would be inadequate, presumably because of water resistance (disturbances in expression, loss of hydrodynamics) and at night or during diving and in murky waters where vision is poor. Accordingly, dolphins are no longer capable of such visual facial expressions (Caldwell and Caldwell, 1972; Manger, 2006). Instead the facial musculature of odontocetes has been concentrated around the upper respiratory tract which was transformed into the epicranial (nasal) complex by the addition of phylogenetically new structures as, e.g., the melon, bursae cantantes, phonic lips, blowhole ligament, and the accessory nasal air sacs. Most of the facial musculature is concentrated in a flattened cone around the nasal air spaces. This cone is subdivided on both sides into different muscle layers, the texture of which is more or less the same throughout the consecutive layers. Looking closer, it seems likely that single layers of the nasal muscles or parts of these layers are innervated by individual branches or fiber bundles of the facial nerve and that these axons belong to specific neuron populations of the facial motor nucleus in the brain stem as is true for various components of the facial muscles in other mammals (Papez, 1927; Breathnach, 1960; Voogd et al., 1998; Sherwood, 2005; Furutani and Sugita, 2008). This hypothesis has to be tested in the future by careful comparative investigations including ungulates and cetaceans. Such a detailed functional organization within the facial musculature and its innervation should allow highly complicated changes in the shape of nasal components and their associated air spaces (as well as their intrinsic air pressure) so that toothed whales would possess fine control of sound production, as evidenced, e. g., by their proficiency at vocal mimicry (Reiss and McCowan, 1993; Tyack, 1999; Foote et al., 2005; Herman, 2006). This is all the more plausible because the organization and functional implications of the epicranial complex seem to be valid for all the toothed whales investigated so far (Cranford et al., 1996). Quantitative analysis revealed that dolphins have three to nine times more axons in their facial nerve than the human (harbor porpoise: 4.5 times more; Jacobs and Jensen, 1964; Blinkov and Glezer, 1968; Jansen and Jansen, 1969; Morgane and Jacobs, 1972; Pilleri and Gihr, 1970; Oelschläger and Oelschläger, 2002; Oelschläger et al., 2008). Thus, dolphins and porpoises should be able to make "facial expressions" of considerable subtlety

not for visual but for auditory communication (Oelschläger 2008). Structural facial variation and asymmetry may even increase this remarkable capability with respect to acoustic individuality in these animals.

## ACKNOWLEDGMENTS

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