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## Olfaction and brain size in the bowhead whale (*Balaena mysticetus*)

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### ABSTRACT

Although there are several isolated references to the olfactory anatomy of mysticetes, it is usually thought that olfaction is rudimentary in this group. We investigated the olfactory anatomy of bowhead whales and found that these whales have a cribriform plate and small, but histologically complex olfactory bulb. The olfactory bulb makes up approximately 0.13% of brain weight, unlike odontocetes where this structure is absent. We also determined that 51% of olfactory receptor genes were intact, unlike odontocetes, where this number is less than 25%. This suggests that bowheads have a sense of smell, and we speculate that they may use this to find aggregations of krill on which they feed.

Key words: bowhead whale, *Balaena mysticetus*, olfaction, anatomy, olfactory receptor genes, brain, evolution.

There is a widespread perception that whales, dolphins, and porpoises have a minimal sense of olfaction or lack it altogether (Dehnhardt 2002, Pihlström 2008). Absence of the sense of smell is unusual among mammals, since most mammals are macrosmatic. Aquatic life is often thought to be at the root of the absence of a sense of smell, because airborne odorants appear irrelevant to an air-breathing mammal that lives and feeds below the water's surface. This is in contrast to the pinnipeds, in

which both anatomical and behavioral evidence points to the presence of olfaction ability (reviewed by Watkins and Wartzok 1985) associated with behaviors out of the water. Detailed studies on the olfactory anatomy of pinnipeds are lacking.

The process of olfaction begins in the olfactory epithelium of the nasal cavity, where odorant molecules bind to olfactory receptor (OR) proteins in the cell membranes of specialized neurons. Olfactory epithelium is specialized and differs from epithelium in other parts of the nasal cavity (respiratory epithelium). From the epithelium, nerve fibers of cranial nerve I (the olfactory nerve) enter into the cranial cavity by passing through a large number of tiny perforations in the ethmoid bone. This part of the ethmoid looks like a sieve and is called the cribriform plate. The entire cribriform plate, including these perforations, is lined by the dura mater, as are the parts of the brain in the cranial cavity. The nerves passing through the cribriform plate arrive in a part of the brain called the olfactory bulb, where initial processing of olfactory stimuli takes place. From here, nerves pass caudally through left and right olfactory tracts to enter the brainstem, where all sensory information from cranial nerves is collected.

In investigated toothed whales, the nervous structures that mediate olfaction are absent: there is no cranial nerve I, no olfactory bulb, and no olfactory tract (Oelschläger and Oelschläger 2008). In addition, more than half of the OR genes of odontocetes have mutated into nonfunctional pseudogenes (Kishida *et al.* 2007, McGowen *et al.* 2008).

There are scattered observations that suggest for some baleen whales that some of these nervous structures may remain (Watkins and Wartzok 1985, Oelschläger and Oelschläger 2008), and there is anecdotal evidence that bowheads react to airborne odorants (Cave 1988). Haldiman and Tarpley (1993) show a photograph (their figure 4.9C) indicating olfactory epithelium. Mammalian olfactory epithelium differs from respiratory epithelium (Moran *et al.* 1982), and is indicative of olfactory abilities. Unfortunately, Haldiman and Tarpley's text (1993, p. 92) is somewhat inconsistent with their figure, and makes no inferences about olfaction. The olfactory bulb is known in some fetal mysticetes (Oelschläger and Buhl 1985, Glezer 2002). However, this does not imply that it is significant after birth, since nervous tissue of the olfactory system is known to regress postnatally in mammals, including humans (Farbman 1991) and odontocete cetaceans (Oelschläger and Kemp 1998). Furthermore, organs related to olfaction also degenerate over life. For instance, foramina of the cribriform occlude during aging (Kalmey *et al.* 1998).

During an anatomical survey of juvenile and adult bowhead whales (*Balaena mysticetus*), we encountered significant olfactory bulbs. This led us to engage in a study of olfactory ability in bowheads using three independent lines of evidence. First, we studied the relative size of the olfactory bulb in the context of total brain size. The size of most parts of the mammalian brain correlates with neocortex size to a remarkable extent: neocortex size explains 80% or more of the variation of most non-olfactory parts of the brain (Finlay and Darlington 1995). The remainder of size variation in parts of the brain is still significant and correlates with function. Unlike most parts of the brain, the olfactory bulb does not scale tightly with the neocortex size, and neocortex size explains less than 40% of variation in the size of the olfactory bulb (Finlay and Darlington 1995). This suggests a strong link between olfactory bulb size and function. Illustrative of this is the mammalian order Primates, where macrosomatic and microsomatic members have vastly different relative sizes of their olfactory bulbs (Stephan *et al.* 1981). Concomitant with olfactory bulb size, cribriform plate size, and numbers of perforations also vary with olfactory abilities

(Pihlström 2008). As such, relative size of the olfactory bulb is indicative of olfactory abilities. Olfactory bulb size needs to be evaluated in the context of total brain size. In the recent past, brain size in cetaceans has commonly been estimated on the basis of endocranial volume (Gingerich 1998, Marino 1998, Marino *et al.* 2000). Marino *et al.* (2000) estimated brain size of some cetaceans by deducting 20% of the endocranial volume, to account for the endocranial rete mirabile, a plexus of blood vessels that fills part of the cranial cavity in cetaceans, but not in other mammals. For bowhead whales, there are no measurements of brain size and endocranial volume that provide a direct assessment of the size of the rete. Our direct measurements allow us to assess olfactory bulb size as a proportion of brain size directly.

Second, we studied the anatomy of the olfactory system of the bowhead whale. We dissected the olfactory bulb, the most rostral part of the bowhead brain (telencephalon), which serves as a relay between the sensory neurons that carry the sense of smell and higher parts of the brain. In mammals the olfactory bulb is a multilayered structure (Mori 1987, Cajal 1995) that processes olfactory stimuli. Different parts of the olfactory bulb are dedicated to specific olfactory stimuli, and there is a close match between anatomical and functional units (Mori *et al.* 2006). Haldiman and Tarpley (1993) described bowhead anatomy and discuss presence of olfactory peduncles and cribriform plate, but not the olfactory bulb. Oelschläger and Oelschläger (2008) state that the olfactory system of mysticetes is small but functional.

Third, we analyzed the OR gene family to determine the relative proportions of OR pseudogenes in the genome. There are multiple types of ORs, and these match aquatic and terrestrial habitats to some extent: ORs in terrestrial tetrapods detect volatile compounds, whereas those in marine fishes detect water-soluble molecules (Freitag *et al.* 1998, Nei *et al.* 2008). As a result, when tetrapods evolved from aquatic vertebrates, large-scale degenerations of OR genes occurred (Niimura and Nei 2005). Furthermore, OR genes degenerated when viviparous elapid snakes became secondarily aquatic (Kishida and Hikida 2010), while novel subfamilies of OR genes evolved, presumably adapted for underwater chemoreception.

A higher proportion of OR pseudogenes in mammals indicates the absence of stabilizing selection that keeps OR genes functional. It has been shown that the OR receptor gene family contains a large percentage of pseudogenes in odontocetes (more than 75%), consistent with anatomical evidence for absence of a sense of smell (Kishida *et al.* 2007, McGowen *et al.* 2008). OR genes of only a single mysticete have been studied in this way: in the minke whale (*Balaenoptera acutorostrata*), 58% of OR genes have mutated to become pseudogenes (Kishida *et al.* 2007), consistent with the interpretation that the olfactory abilities of this mysticete are greater than those of odontocetes, but less than those of land mammals.

## METHODS

We studied samples from bowhead whales caught during the fall season of the biannual Inupiat subsistence hunt along the north coast of Alaska. With the captains' approvals, we removed the brain by chiseling and sawing through the skull roof and into the foramen magnum, and removed the brain using surgical tools. Bowhead whale specimens are catalogued as 07B14, 08B11, 09B9, and 09B11 in the system of the Department of Wildlife Management, North Slope Borough, and all specimens were collected under NOAA/NMFS permit 814-1899. For these specimens we determined brain weight or volume (by displacing water), while still fresh. We

multiplied brain weight (in kilograms) with the factor 1.036 in order to estimate brain volume (in liters). In three specimens, we determined endodural (endoretial) volume by filling the endodural space with known aliquots of pea gravel before removal of any part of the endocranial rete. We then removed the dural retia and determined endocranial volume again. This resulted in three measurements of volume, in increasing order: brain volume (actual volume of nervous tissue), endodural volume (volume of the space for the brain inside the membranes), and endocranial volume (volume of the bony cavity for the brain plus its membranes and associated vasculature).

The olfactory bulb and its adjacent nasal cavity are encased centrally in the enormous bowhead skull. A narrow canal projects forward from the cranial cavity, and the olfactory bulbs are located at the end of it. To gain access, we used a chainsaw to cut a suitcase-shaped block out of the center of the skull. This block consists mostly of massive bone dorsal, ventral, and lateral to the olfactory tract. We poured buffered formalin in the canal, in order to stabilize the bulb before the slow process of removing the bone that encases it. Then, we used a reciprocating electrical saw, hammer and chisel, and surgical tools to expose the olfactory bulbs and remove them from their envelope of dura mater.

Olfactory bulbs of two whales were acquired several hours after death (09B11, 09B14). These bulbs were removed from the olfactory chamber of the brain and preserved in 10% buffered formalin. Prior dissection damaged parts of one of these olfactory bulbs and it could not be weighed. The weights reported below might be a slight underestimate of the bulb, as brain specimens fixed in buffered formalin tend to lose up to 10% of their weight (Bauchot 1967), and we did not correct the reported value for this. The bulbs were processed using standard histological techniques. They were processed in an ethanol dehydration series, embedded in paraffin, cut on a microtome at 6 microns, and stained with thionin.

To study the OR genes, genomic DNA was extracted from bowhead whale muscle tissue. Protocols and procedures for DNA extraction, OR gene amplification, TA-cloning, sequencing and pseudogene classification followed Kishida *et al.* (2007) and Kishida and Hikida (2010), and the same primers were used. Sample processing and laboratory analysis of bowhead samples is still continuing, and we expect to recover additional OR genes, that may help us understand which OR genes are functional.

## RESULTS

### *Brain Size*

Table 1 provides data on the brain size of bowhead whales. We found that the bowhead brain only occupies between 35 and 41% of the volume of the bony endocranial cavity, while most of the rest of the cavity is filled with the dural rete mirabile. The dural rete is mostly distributed on the lateral and rostral sides of the brain, and not on its dorsal and ventral surfaces.

### *Gross Olfactory Anatomy*

Our dissection showed that the olfactory bulbs in the bowhead whale are at the end of a 6-cm-long bony canal that extends anterior from the cranial cavity toward the nasal passages. This canal houses the olfactory tracts and tunnels through a massive

Table 1. Anatomical basic and age estimates on bowhead whales examined in this study.

Specimen	Body length (m)	Approximate age (yr) <sup>a</sup>	Brain weight (g)	Brain volume (mL)	Endodural volume (mL)	Endocranial volume (mL)	Inferred body mass (kg)
07B14	8.1	3		2,935			9,168
08B11	8.9	8	2,950	3,056	4,300	8,400	14,222
09B9 <sup>b</sup>	8.7	>10	2,980	3,087	3,200	8,900	12,555
09B11	7.2	1	2,600	2,694	3,400	6,500	9,526

<sup>a</sup>Ages based on estimates in Lubetkin *et al.* 2008.

<sup>b</sup>This whale is smaller than other bowheads of the same age (see George 2009).

section of bone (Fig. 1). The left and right olfactory bulbs are separated by a bony septum, and are enveloped in separate dural sleeves. Ventrally, laterally, and rostrally the dura and bone are perforated (cribriform plate of the ethmoid bone) and lead into a recess of the nasal passage, the nasal chamber. Together these nerves represent cranial nerve I, the olfactory nerve. The olfactory bulb is roughly oval in dorsal view and flattened dorsoventrally. Its dorsal surface is concave and its ventral surface (where cranial nerve I emerges) convex. The ventricle of the olfactory bulb is widely open dorsomedially, and would be better described as a recess.

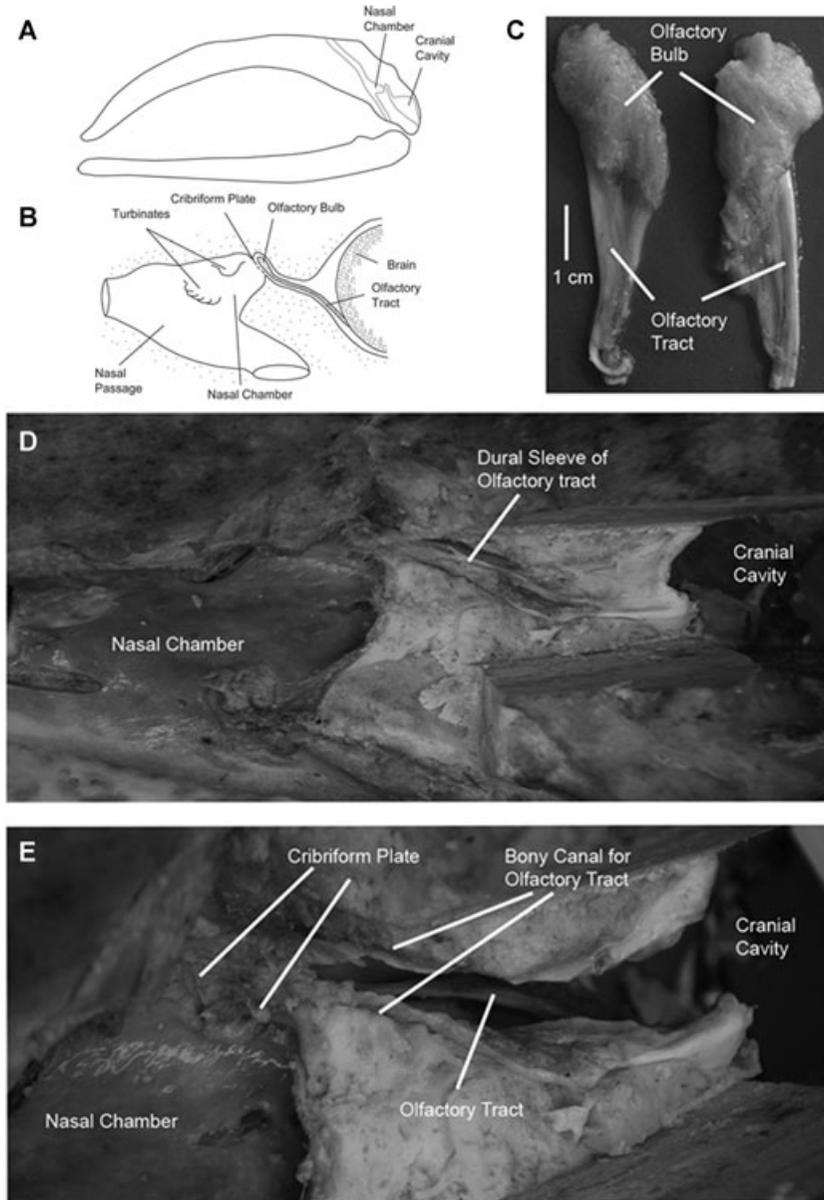
#### *Relative Size of the Olfactory Bulb*

Olfactory bulbs were removed from dissected specimens. In bowhead whale 09B14, the fresh left olfactory bulb was 35 mm long and 16 mm wide. After preservation in neutral buffered formalin, the left and right olfactory bulb together weighed 3.7 g. Using the average brain weight of the bowheads in Table 1 (2,843 g), this indicates that the bowhead olfactory bulb is approximately 0.13% of the size of the brain.

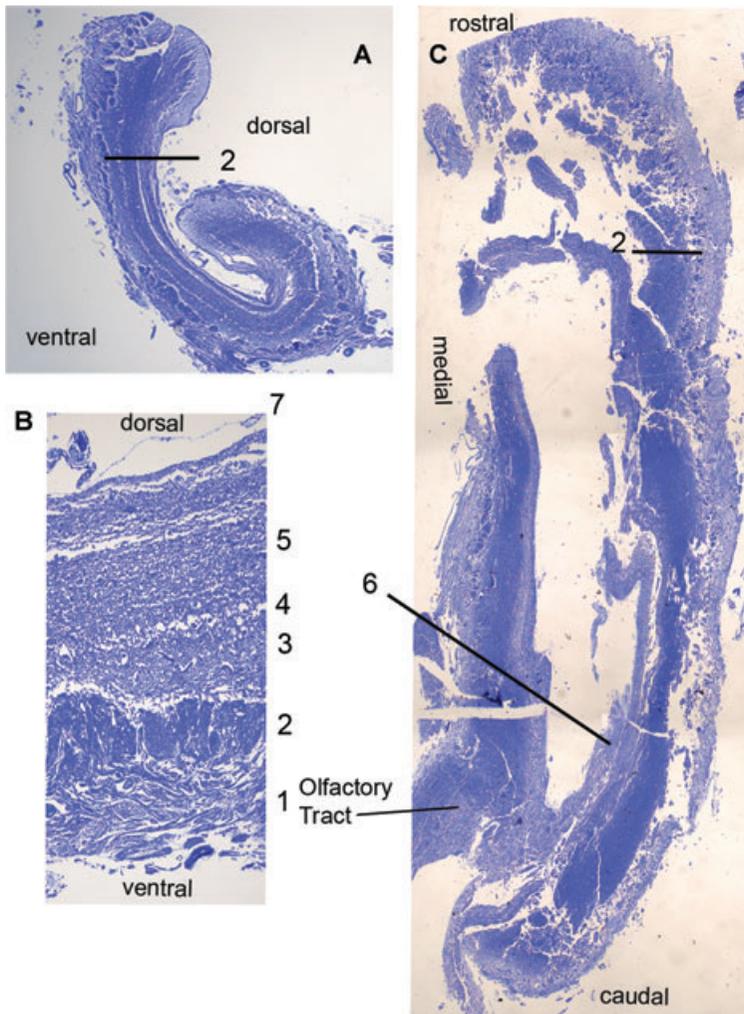
#### *Olfactory Bulb Histology*

We performed histology on the extracted olfactory bulbs. Seven tissue layers we traditionally recognized in the mammalian olfactory bulb (Cajal 1995, MacLeod 1971), and six of these are important in processing olfactory stimuli. Shepherd and Greer (1990) named these, from external to internal: 1, olfactory nerve layer, 2, glomerular layer; 3, external plexiform layer; 4, mitral cell layer; 5, internal plexiform layer; 6, granule cell layer. The seventh layer of Cajal (1995) is the ependymal layer. Bowhead tissue samples were immersion-fixed in formalin several hours after death of the whale, making sensitive stains for neurons difficult to attain, and we therefore used more general histological stains that do not show neural detail. In spite of this, it is clear that the bowhead olfactory bulb has all layers (Fig. 2) with a total thickness that varies between 1 and 2 mm.

Figure 2A, B show a coronal view of a bowhead olfactory bulb, displaying layers 1–5 clearly. The remaining layers are better shown in the horizontal section of the olfactory bulb (Fig. 2C), which also shows the olfactory tract. The olfactory nerve layer (1) displays the fasciculated fibrillar texture described by Cajal (1995), and contains small blood vessels. The glomerular layer (2) is composed of densely packed olfactory glomeruli, and its cells show clear connections to the olfactory nerve layer.



*Figure 1.* Diagram of the location of nasal passage and cranial cavity in the bowhead whale (A), and detail of the nasal chamber and cribriform plate (B) also showing bony canal for olfactory tract, brain (dense stippling) and encasing bone (light stippling). Ventral view of the right and left extracted olfactory bulbs of bowhead whale 09B14 (C). Subsequent dissection stages (D and E) of parasagittal section through the central part of the head of bowhead whale 09B11, showing cranial cavity and nasal chamber, and olfactory tracts.



*Figure 2.* Histological sections through olfactory bulb of bowhead whale. Coronal section of right olfactory bulb of whale 09B11 (A, section 280b, magnification 4 $\times$ ) and detail of this section (B, 10). Horizontal section of olfactory bulb of bowhead 09B14 (C, section 145, 4 $\times$ ). Numbering follows traditional numbering system of olfactory bulb as discussed in text: 1 = olfactory nerve layer, 2 = glomerular layer, 3 = external plexiform layer, 4 = mitral cell layer, 5 = internal plexiform layer, 6 = granule cell layer, 7 = ependymal layer.

In most areas there is a single layer of glomeruli, but in some areas glomeruli are closely spaced and packed in two partly overlapping layers. The external plexiform layer (3) is thick and consists of spongy tissue in our slides. The mitral cell layer (4) is thin and shows large empty spaces with shrunken cells inside. These are arranged in a single layer. The internal plexiform layer (5) is thicker than the external plexiform layer, and also has a spongy texture. The granule cell layer (6) is only recognizable as longitudinal spaces that course parallel to the layers. The ependymal layer (7) is detached in Figure 2, representing a single cell layer that lines the ventricle.

*Olfactory Receptor Gene Repertoire*

We amplified bowhead OR genes and analyzed more than 500 colonies of bacteria expressing these genes. From these, we isolated 43 bowhead OR sequences, and 49% (21) of these can be classified as pseudogenes. Mammalian ORs have been classified into two classes, Class I and Class II, by Glusman *et al.* (2000) on the basis of sequence similarities. All identified bowhead OR sequences in this study pertain to Class II. There is no evidence that a new OR subfamily occurs in cetaceans. This is unlike sea snakes, where a new OR subfamily diverged specifically related to underwater stimuli (Kishida and Hikida 2010), as snakes became marine.

## DISCUSSION

In their surveys of marine mammal brain size data, Glezer (2002) and Marino (2009) did not include the bowhead whale because no data were available. Marino *et al.* (2000) estimated brain size of some cetaceans (not bowheads) by assuming that the brain fills 80% of the endocranial cavity. Our data (Table 1) provides brain size data and shows that Marino's method would overestimate brain size in bowheads by a factor of two. Moreover, the brain is also significantly smaller than the volume of the endoretial cavity, as there is significant space between brain and innermost dura (Table 1).

Bowhead body mass was estimated for several whales using direct weights and estimation methods (George 2009). The body mass data were fit to a length/girth model developed by Rice and Wolman (1971) for gray whales. The resulting model was used to estimate body weight for whales in Table 1. Mean body weight is 13,389 kg, and mean brain weight was 3.0 kg for the two mature individuals (08B11 and 09B9). This allows us to calculate Encephalization Quotients (EQ) for bowhead whales. Jerison (1973) calculated EQs using 0.67 as a scaling coefficient for brain size and the bowhead EQ based on this value is 0.415. EQ values are important and are thought of as correlates of brainpower in taxa where no direct measurement of intelligence is possible, although Marino (2004, 2009) discussed the difficulty of comparing EQ values of mysticetes with those of land mammals.

The importance of our finding that the olfactory bulb makes up 0.13% of brain size in bowheads is best evaluated in the context of an order of mammals for which olfactory abilities and relative olfactory bulb size have been well-studied. Stephan *et al.* (1981) did a comprehensive study of relative sizes of different parts of the brain in primates. There are a number of Old and New World monkeys in which the olfactory bulb makes up approximately 0.1% of brain weight, such as macaques (0.09%), baboons (0.14%), spider monkeys (0.10%), and sakis (0.10%). The relative size of the olfactory bulb in apes (0.06%) and humans (0.008%) is much smaller than in bowheads. Olfaction plays an important role in social behavior and food gathering in Old and New World monkeys (Dominy *et al.* 2001), and less so in apes and humans, although olfaction is by no means absent in any studied primate.

The histological complexity of the olfactory bulb, as determined on the basis of the simple stain that we applied, matches that of other mammals in having six layers involved in transmission of olfactory stimuli (Shepherd and Greer 1990), and is consistent with the interpretation that bowheads have a sense of smell. Interesting differences between bowheads and land mammals are present. For instance, whereas in bowheads the internal layer is thicker than the external plexiform layer, this is

usually the reverse in land mammals (Shepherd and Greer 1990). We cannot evaluate the importance of this difference.

Our data on the OR gene repertoires show that large-scale degeneration of OR genes has occurred in the bowhead genome (49% pseudogenes). However, the proportion of pseudogenes in bowhead whales is much lower than in odontocetes, where it is more than 75% (Kishida *et al.* 2007, McGowen *et al.* 2008). Kishida *et al.* (2007) found that minke whale pseudogene proportions of OR genes are 58%, somewhat higher than what we determined for bowhead whales. This suggests that baleen whale genomes remained under stabilizing selection to maintain OR repertoires after the evolutionary divergence between mysticetes and odontocetes. The difference between bowhead and minke whale percentages may be significant, but this has to be re-evaluated after larger numbers of OR genes are studied. If a larger study upholds these differences, it would imply that stabilizing selection was greater in bowheads than in minke whales.

Again, a comparison with primates can be used to put these data into perspective. Primate OR genes have been investigated by Rouquier *et al.* (2000) and Gilad *et al.* (2004, 2007). These authors found that proportion of OR pseudogenes is more than 50% in humans, around 30%–50% in nonhuman apes, 19%–35% in Old World monkeys, and very small proportions in New World monkeys with the exception of 31% in howler monkeys. It is not possible to compare percentages of pseudogenes in primates and cetaceans directly, since OR gene degeneration occurred earlier in the primate phylogenetic tree and since primates have ancestors with different OR gene/pseudogene proportions than cetaceans. This would have affected the starting point and time period that stabilizing selection worked. In addition, the huge primate-specific OR7E gene subfamily is particularly prone to pseudogenization (Glusman *et al.* 2001, Newman and Trask 2003). However, the primate data suggest a strong correlation between olfactory abilities and OR gene/pseudogene proportions. These results then indicate that baleen whales have a better developed sense of smell than toothed whales.

Our study did not identify Class I ORs. Previously, it was considered that Class I ORs detect water-soluble odorants and Class II ORs detect volatile odorants (Freitag *et al.* 1998). However, recent studies have shown that this view is an oversimplification (Niimura and Nei 2006, Nei *et al.* 2008), and that the correlation between ORs and their ligands are more complicated (Kishida and Hikida 2010). None of the OR receptor genes found in the bowhead belong to novel subfamilies that would be suggestive of underwater chemoreception. This suggests that bowheads have not developed underwater chemoreception based on OR proteins. This may not be surprising, since, in mammals, waterborne chemical stimulants are usually registered by taste buds in the tongue, and are not mediated by proteins from the OR gene family. Our ongoing study focuses on expanding OR gene identification, on recognition of OR gene expression in olfactory epithelium, and on the assessment of gustatory abilities in bowhead whales.

### Conclusion

Taken together, the evidence from olfactory bulb and OR genes make it eminently clear that bowhead whales have a sense of smell. Furthermore, the relative size of the olfactory bulb and OR pseudogene proportions in bowheads suggest that their sense of smell is better developed than in microsmatic mammals such as humans.

Bowhead whales also have a better developed sense of smell than odontocetes, most of which have lost olfactory bulbs altogether (Oelschläger and Oelschläger 2008) and in which many OR genes have mutated into pseudogenes (Kishida *et al.* 2007, McGowen *et al.* 2008). Although it is clear that bowhead whales have a sense of smell, this sensory system is less well developed than that of their closest land relatives, the artiodactyls, consistent with the small number of OR pseudogenes in members of that order (McGowen *et al.* 2008).

Bowhead whales are obligate aquatic mammals that feed underwater, leaving open the question how airborne smells matter in their lives. Possible explanations may involve detection of conspecifics through their exhaled breaths. Smell plays an important role in reproductive functions in the cetacean sister group, members of the artiodactyls, mediated in part by the olfactory and in part by the accessory olfactory systems (*e.g.*, Gelez and Fabre-Nys 2004). Bowheads are polyandrous and males come from far to seek estrous females. Although multiple sense organs probably play a role in mate detection, olfaction could play a role.

Another hypothesis, more plausible in our view, is that bowheads use olfaction to detect clouds of the plankton they feed on. Krill gives off a peculiar odor, partly caused by dimethylsulfide and pyradines (Nevitt 1999). It may be significant that krill-feeding procellariiform birds are attracted to dimethylsulfide (Nevitt *et al.* 1995, Nevitt 1999, Nevitt and Haberman 2003). Unlike most other birds, procellariiforms have well-developed olfactory organs (Hieronymus 2008). Harbor seals have also been shown to have high olfactory sensitivity for dimethylsulfide (Kowalewsky *et al.* 2006). It is possible that krill-odors assist bowhead whales in finding prey. Euphausiid krill form the major part of the diet of western arctic bowhead whales and clouds of krill are known to have a quite patchy distribution both temporally and spatially (Lowry *et al.* 2004). Patches are broadly associated with oceanic fronts such as temperature and salinity discontinuities. However, to feed effectively on krill, bowheads must find areas where prey occurs in high densities (Ashjian *et al.*, in press). Olfaction could aid bowheads in finding these dense aggregations of prey that are scattered across huge areas across their range.

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