SENSORY HAIRS IN THE BOWHEAD WHALE (*CETACEA, MAMMALIA*)

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Sensory hairs in the bowhead whale (*Cetacea, Mammalia*)

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**INTRODUCTION**

The presence of hair is a defining characteristic of mammals. However, there are some orders that are nearly devoid of hair. Among marine mammals, hair occurs in abundance in pinnipeds, but is greatly reduced in sirenians (Reep et al., 2001, 2002, 2011) and cetaceans (Kellogg, 1928; Ling, 1977). Hair in sirenians is found both on the face and body, with the whiskers on the face being 30 times as dense as hairs on the rest of the body (Marshall et al., 1998a, 1998b). These hairs serve a specialized mechanoreceptive role (Reep et al., 2001, 2002, 2011; Dehnhardt and Mauck, 2008; Sarko et al., 2011) that is complementary to their visual abilities, and hairs are actually used in food manipulation (Marshall et al., 1998a, 1998b, 2003). For secondarily aquatic mammals, often living in turbid environments with poor visibility, vibrissae provide an important supplement to vision for sensing the environment.
Vibrissae are a distinct type of hair in mammals and are characterized by a series of morphological specializations, including a blood sinus that surrounds the entire root sheath (Burgess and Perl, 1973). Vibrissae are largest in marine mammals (Dykes, 1975). Vibrissae are thicker and stiffer than pelagic hairs and prominently display a follicle-sinus complex (F-SC) consisting of a dermal papilla wrapped in a dense connective tissue capsule, surrounded by a prominent circumferential blood sinus complex, and dense innervation. A vibrissal hair is associated with static displacement detection (Burgess and Perl, 1973), and it transmits external stimuli down the shaft to transmit vibrotactile information from the surrounding environment to these receptors at the base of the F-SC (Burgess and Perl, 1973; Gottschaldt et al., 1973; Dykes, 1975; Halata, 1975). In addition to a specific histology, Marshall et al. (2006) used four additional criteria to determine if vibrissae from a bearded seal comprised an active-touch receptor systems: (1) relatively high overall number of F-SCs, (2) a specific geometry of individual hairs in a mechanoreceptive region, (3) relatively high number of myelinated axon per F-SC, and (4) a particular distribution of mechanoreceptive areas.

The mechanoreceptive function of hairs has been studied extensively in subterranean mammals, including the nearly hairless naked mole-rat (*Heterocephalus glabas*), which utilizes approximately 40 tactile face and body hairs to assist in mechanosensory-guided orientation (Crish et al., 2003). Park et al. (2003) studied the anatomy of vibrissae, guard hairs, and body hair in several rodents, using a series of antibody stain to distinguish innervation differences. Unlike most mammals, naked mole-rats have rows of sensory
hairs separated by expanses of naked skin on the lateral side of their trunk and abdomen, similar to the hair arrays of bowhead whales near their blowhole. Crish et al. (2003) demonstrated the importance of these hairs in naked mole-rat mechanoreponses. Rice et al. (1986, 1993, 1997) studied facial vibrissae in rats in detail, identifying specific functions for distinct nerve bundles. Medium to large sized myelinated axons run to the F-SC, allowing for tactile sensitivity.

In species where the distribution of hair is uneven over the body, hairs are highest in density in locations that increase the chances of stimulus detection, such as around the eyes, chin, neck, and wrists (Sarko et al., 2011). Facial hair is more common in mysticetes than in odontocetes, although the number of hairs and spatial distribution differs greatly between different species (Yablokov and Klevezal, 1964). Slijper (1962) reports 50-60 hairs on the face of rorquals (Balaenopteridae), implanted in three rows on the face. The same author also reports the bowhead whale (*Balaena mysticetus*) as the most hairy cetacean with about 250 ‘bristles’ on the tips of the lower and upper jaw and around the blowhole (Figure 1A). The chin of the bowhead whale is the most forward projecting part of its body and, if they serve a mechanoreceptive function, this could largely account for the density of hairs found there, compared to the rest of the whale’s body (Japha, 1910). In addition, bowheads have a single bilateral, rostrally concave row of approximately 10 hairs just caudal to the blowhole (Tomilin, 1957; Haldiman et al., 1981; Henry et al., 1983) (Figures 2A and 2B), the only species to be described that possesses hair in this position in addition to the hairs on the chin and rostrum.
Bowheads have a double blowhole, located on an elevation called a crown (Eschricht and Reinhardt, 1866), positioned one fourth its body length caudal to its rostral tip. The bilateral rows of hairs are located just caudal to the crown (Figure 2A). Bowhead eyes are located low on the sides of their head, just above the temporomandibular joint (Tomilin, 1957) (Figure 1A). Due to the eyes’ lateral placement, Slijper (1962) postulated that much of a whale’s surrounding environment is beyond its field of vision, including the area directly before, beneath, and above the animal.

Although Kükenthal (1893) believed that mysticete hair was vestigial, that is not the general consensus among scientists since. Nakai and Shida (1948) postulated that baleen whales use vibrissae as water current receptors, aiding in navigating the open sea, and somehow in the location of food. Upon viewing whales feeding, Yablokov and Klevezal (1964) felt that vibrissae were serving as “closest range receptors” that are sensitive to direct contact from objects and less likely to be used in orientation. Bowhead whales are skim feeders, meaning that they swim at the water’s surface and passively allow their prey to filter through their baleen in a somewhat continuous manner. However, rorquals are lunge feeders and eat in discrete lunges, taking in a large amount of water and prey at one time, then filtering large increments at a time (Croll et al., 2002). Due to the large amount of time that bowheads spend at the interface between the water and the air, it is possible that the hair caudal to the blowhole is relaying spatial information about the environmental interface, and the chin and rostral hairs could be sensing movement from
prey. Herman and Tavolga (1980) suggested a correlation between the persistence of vibrissae into adulthood and the slimness and length of the snout in the different families of mysticetes, reflecting a difference in feeding behavior. However, they stopped short of speculating the mechanism for this association.

Haldiman et al. (1986) discussed the hairs in the bowhead and identified them as vibrissae due to an increased hair follicle diameter and the presence of nerves and blood sinuses within the wall of the follicle. Japha (1910) described blue whale (*Balaenoptera musculus*, a balaenopterid) hairs as vibrissal due to their stiffness and presence of a sinus complex. Haldiman and Tarpley (1993) speculate that the hairs are tactile, due to the presence of innervated sensory follicles, as described by Nakai and Shida (1948) in sei whales (*Balaenoptera borealis*). These observations are consistent with statements by Slijper (1962), Ling (1977), and Sokolov (1982) about the functions in other mysticetes.

Bowhead whale integument is similar to skin in other mammals, although the layers are much thicker than other cetaceans (Nakai and Shida, 1958; Haldiman and Tarpley, 1993). The external skin is generally black in pigmentation, but it displays areas of white skin on the eyelids, flipper insertions, genitoanal area, and the chin and occasionally the rostrum (Haldiman and Tarpley, 1993). Some of these white areas are associated with a hair, which may emerge from the center of the white spots (Haldiman et al., 1981). The skin is comprised of two layers, the pigmented epidermal layer and a deeper dermal layer. The epidermis is the outermost layer and measures from 1-25 millimeters thick (Tomilin,
1957; Albert, 1980; Durham, 1980; Fetter and Everett, 1981; Haldiman et al., 1981, 1985; Haldiman and Tarpley, 1993). Haldiman et al. (1981, 1985) report a thickness between 9-25 millimeters on the chin and 15-24 millimeters on the rest of the head, although we found much thinner epidermis, with ranges of 8.35-10.91 millimeters on the chin, 6.72-7.68 mm on the rostrum, and 9.62-10.2 mm around the blowhole. The white dermis contains blood vessels, connective tissue and blubber. It is in the dermis where the hair follicles originate. The outermost part of the dermis and the innermost part of the epidermis interdigitate with one another, with up to 90% of the epidermis depth being interwoven with the dermis (Haldiman and Tarpley, 1993).

We speculate that due to their extremely thick epidermis, the bowhead whale has co-opted the advantage of growing hair into a mechanoreceptive organ to assist in sensing its environment, in spite of its thick skin, mimicking the successful system established by Crocodilia, where ossifications in the skull limit proprioception, and specialized organs superficial to the keratinized and armored skin relay vibratory and spatial information to the animal (Soares, 2002).

Odontocetes are naked except for a few hairs implanted on the face of fetuses of most species (Japha, 1910; Ling, 1977), such as the phocoenid Phocoena phocoena, the delphinids Delphinus delphis, and Sotalia guianensis (Dehnhardt and Mauck, 2008), the kogiid Kogia breviceps, the platanistid Platanista gangetica (Fraser and Norman, 1948) and Inia geoffrensis (Dehnhardt and Mauck, 2008). In these species (Tomilin, 1957;
Stěrba et al., 2000), there is a row of fewer than ten hairs on either side of the rostrum (Thewissen and Heyning, 2007), and these hairs are lost postpartum (Nakai and Shida, 1948; Sokolov, 1982). Fraser and Norman (1948) reported that the Ganges dolphin *Platanista gangetica*, retains facial vibrissae throughout life. In the dolphin *Sotalia*, hair follicles also remain into adulthood and possess a sinus system (Mauck et al., 2000), and these are thought to be electroreceptors due to high temperature output and innervation (Mauck et al., 2000; Wilkens and Hofmann, 2008; Czech-Damal et al., 2012). It is worth noting that *Monodon monoceros* and *Delphinapterus leucas* never develop fetal hairs (Slijper, 1962; Herman and Tavolga, 1980; Sokolov, 1982). Odontocetes, as opposed to mysticetes, echolocate, and it is likely that they do not primarily depend on skin receptors for spatial information.

We hypothesize that blowhole hairs, as well as chin and rostrum hairs, are vibrissae, and that they have different characteristic features, adjusted for their location on the whale’s body. The vibrissae on the blowhole should be physically different from the hairs on the chin and rostrum, which we hypothesize will be statistically similar to each other.

In spite of a consistent view that whale hairs are important in environmental detection for a century (Japha, 1910), the functional mechanism of vibrissae in bowhead whales is still unclear. It is possible that the hairs could serve a role as water flow detectors. It is necessary for whales to surface to breathe, the blowhole hairs could be functioning to relay the approach of the water’s surface, especially when the species is Arctic and the water is covered in ice. The hairs on the chin and rostrum do not breach the water level,
and they could be serving a mechanoreceptive role similar to each other, but different from the blowhole hairs. The importance of mechanoreception has been shown in seals and muskrats, as this sense can supplement or substitute for poor eyesight (Dehnhardt et al., 1998; Dehnhardt and Mauck, 2008).

Purves (1967) speculated that mysticetes may possess the ability to smell the wind in search of plankton. This hypothesis assumes new importance in light of the recent finding that the sense of olfaction of bowheads is better developed than in most other cetaceans (Thewissen et al., 2011). It is suggested that bowheads may detect clouds of krill by the specific airborne odor of dimethyl sulfide that krill releases when it feeds on phytoplankton (Dacey and Wakeham, 1986). These odors could be transported by the wind across the ocean surface and give a bowhead whale downwind cues to a potential food source (Hagelin et al., 2012). However, olfaction is not a directional sense, and the whale would need to know wind direction in order to locate the food source, which is difficult for a mammal that is mostly submerged. It is here that the vibrissae could play an important role: we hypothesize that they function as weather vanes, relaying the wind direction to the whale.

In this paper, we aim to make evident that bowhead hairs are vibrissae using histology to demonstrate a follicle-sinus complex and its various parts. Using morphometrics on the hair, hair follicle, and epidermal recess, we also aim to demonstrate that the blowhole vibrissae are different from the hairs on the chin and rostrum, due to functional
differences among these areas. In addition, we describe the yet undeveloped follicle sinus complex of a fetal bowhead whale.

**MATERIALS AND METHODS**

Bowhead hair and skin samples were obtained from six adult bowhead whales harvested by native subsistence hunters in Barrow, Alaska in 2011, 2012 and 2013 under the supervision of the Department of Wildlife Management, North Slope Borough, and with permission from the captains and the Alaska Eskimo Whaling Commission under federal permit NOAA-NMFS 814-1899-01. Bowhead whale ages can only be inferred on the basis of observations on the captured animal, thus we report body lengths of whales as a course correlate of relative age (Lubetkin et al., 2008). The six specimens include: 2012B7 (female of 8.99 meters), 2012B9 (unknown gender of 8.79 meters), 2012B18 (female of 9.4 meters), 2012B16 (male of 10.31 meters), 2013B1 (female of 16.46 meters), and 2013B8 (female of 6.78 meters). In the field, slabs of epidermal and dermal layers with hairs and follicles were excised from the tip of the lower and upper jaw and the region of the blowhole. These were preserved in 10% paraformaldehyde solution. In the laboratory, samples were divided and analyzed in several ways.
For histological study, samples were twice rinsed in 1% phosphate buffered saline, and extraneous fat and skin were trimmed away from the follicle. Follicles were dehydrated and embedded in paraffin, cut at 10 micrometers thickness on a microtome, in a plane perpendicular to the skin’s surface, then mounted on plus slides. Slides were deparaffinized and stained with hematoxylin and eosin.

Hair diameters were measured under a Zeiss SteREO Discovery.V8 microscope using an AxioCam MRc camera and AxioVision 4.8.1 11-2009 software (Figure 3A). Hairs are implanted in and emerge from an epidermal recess; the interior wall of the hair’s connective tissue capsule merges with the epidermis at the apical end, which forms a circular opening, from which the shaft of the hair emerges. This structure is described as a funnel shape by Nakai and Shida (1948) (Figure 1B). The epidermis is much thinner at the bottom of the funnel than at the top, allowing the hair some degree of movement at the epidermal surface. The diameter of each hair was measured at the point where it emerged from the epidermis. The diameters of the recesses were also measured in the same manner (Figure 3B). The total length of the hairs, from their epidermal base to the tip, was measured using calipers, although it is possible that some hairs were damaged during capture. The dermal length of the hair follicle was also measured in this manner.
Data were analyzed using Systat 11, using a one way ANOVA with covariate for the hair thickness, epidermal recess, and hair length data sets. A one way ANOVA was used for the follicle data set. A Tukey post-hoc analysis was utilized for all tests.

RESULTS

Histology

The dermis is deep to the epidermis and consists of dense white connective tissue, blood vessels, and adipose tissue. It is from this layer that hair follicles arise (Haldiman and Tarpley, 1993). We did not observe any muscle tissue near the hair follicle, indicative of passive vibrissae, which display connective, vascular, and neural tissue only.

A brief description of hair and hair follicles in bowhead whales was presented without illustrations by Haldiman and Tarpley (1993), who referred for several details to earlier, ‘grey’ literature (Haldiman et al., 1986). These authors concluded, correctly in our view, that hairs in bowhead whales are vibrissae. The main intention of our work is to document differences in hairs from the three regions of the body (chin, rostrum, and blowhole), but we also briefly justify the interpretation of hairs as vibrissae by describing
and illustrating their salient features (Figures 4A-D). Hair follicles from all three regions of the face displayed the structural characteristics associated with vibrissae, including a circumferential blood-filled sinus surrounding the hair shaft and a highly innervated connective tissue capsule surrounding the complex. The exterior of the F-SC is defined by dense connective tissue enclosing the hair shaft and F-SC constituents (Figure 4A). This capsule is embedded in the adipose-rich dermal layer of the skin through connective tissue. The capsule surrounds the dermal papillae of the hair shaft basally, and it terminates on the interior side of the epidermis apically. The inner wall of the ring sinus merges with invaginated epidermal tissue apically, and it is from this opening that the hair emerges on the body surface (Figure 4B). A blood-filled ring sinus occurs between this interior wall of the complex and the dense fibrous tissue capsule. Closer to the epidermis are connective tissue appendages that traverse the ring sinus. The presence of trabeculae indicates the existence of the lower cavernous sinus portion, basal to the ring sinus and lateral to the dermal papillae (Figure 4A). The connective tissue capsule is highly innervated, and neural filaments can be seen traversing the capsule in Figures 4A and 4C, with focus on the deep vibrissal nerve on the basolateral side of the capsule in 4C. The neurofilaments terminate on the interior wall of the ring sinus. A transverse view, near the basal end of the follicle, is shown in Figure 4D. At the level of the ring sinus, all interior walls were torn away from the capsule and the spanning appendages are not visible due to destruction during fixation.
The hair shaft of the approximately four month old fetal bowhead is seen surrounded by a connective tissue covering that fuses with the epidermal layer of skin (Figure 4E), although at this stage there is no ring sinus surrounding the hair shaft, and the high degree of innervation seen in adults is not yet observed. A condensation of tissue is seen around the hair shaft, perhaps indicative of the F-SC yet to develop.

**Morphometrics**

The hairs are straight, do not have appreciable variation in thickness along one hair shaft, do not curl, and display no pigmentation. Each hair emerges from a small round epidermal recess, and otherwise the skin is smooth, lacking depressions (Figure 1B).

There was a significant difference among the thickness of hairs in different regions of the whale. The hairs surrounding the blowhole are significantly thicker at their base than the hairs on the rostrum (p<0.001) and the chin (p<0.001), and the chin and the rostrum hairs are statistically indistinguishable (p=0.986) (Figure 5A). There is no difference among the size of the epidermal recesses in the different regions (Figure 5B).

The dermal portion of the hair follicle is longer in the region of the blowhole and chin than in the region of the rostrum (Figure 6A). The blowhole follicles are not significantly different than the chin follicles (p=0.083), but they are significantly longer than the rostrum hairs (p<0.001), and the rostrum and chin hairs are different lengths (p=0.004)
(Figure 5A). In bowheads studied by Haldiman and Tarpley (1993) the total hair follicle length was approximately 5-6 centimeters, whereas out samples ranged from 21 millimeters to 42 millimeters. There is no difference among the three regions in the measurement of length of the exposed part of the hair shaft, external to the epidermis (Figure 6B). Japha (1910) proposed that whale hairs grow slowly and continuously, and that they break off easily.

**DISCUSSION**

While cetaceans had ancestors that were generalized land mammals with bodies covered by hair (Chen et al., 2013), all modern cetaceans are hairless or nearly so. Among modern cetaceans, bowhead whales have more hair than any other species, having large patches of hair on tip of the rostrum and mandible, and bilateral arch of approximately 10 hairs posterior to the blowhole. A number of authors have claimed that these hairs are vibrissae in bowheads (Tomilin, 1957; Henry et al., 1983; Haldiman et al., 1986; Haldiman and Tarpley, 1993), although that claim has not been substantiated. The purpose of this paper was to determine whether bowhead hair displays the characteristics of vibrissae, and whether there are regional differences between the hairs. Such differences could be used as guides as to the function of bowhead hairs in different regions.
Reep et al. (2001) identified three histological characteristics of vibrissae, and our work indicates that these characteristics are found in bowhead hair. Bowheads possess a prominent and dense connective tissue capsule (Figures 4A and 4B) with a circumferential venous sinus system surrounding the hair shaft (Figure 4A), and is replete with an abundance of sensory nerve endings (Figures 4A and 4C). Thus, our findings support the inference Haldiman et al. (1986) and Haldiman and Tarpley (1993) that bowheads have vibrissae, consistent with similar suggestions in other mysticetes (Japha, 1910; Lillie, 1910; Nakai and Shida, 1948; Slijper, 1962; Yablokov and Klevezal, 1964; Ling, 1977; Sokolov, 1982). In contrast to postnatal specimens, our fetal bowhead lacks the venous system and dense innervation. In addition to a specific histology, Marshall et al. (2006) used four additional gross criteria to determine if vibrissae comprised an active-touch receptor system, and in accordance with these criteria, the whiskers of the bowhead whale are considered vibrissae. Bowheads are the hairiest of mysticetes, possessing hundreds of hairs in a very particular regional distribution over its body. Those hairs also group into specific geometries within their specific region, including a dense patch on the chin and a V-shaped linear section of hairs posterior to the blowhole (Figures 2A and 2B). The F-SCs of all three regions showed substantial innervation to each hair, also indicative of mechanoreceptive vibrissae.

Our measurements show that, in most characteristics, hairs are variable and that there are no consistent differences in hairs between the regions. This is true for epidermal recess
diameter, follicle length, and external hair length (Figures 5A, 6A, 6B). The exception to this pattern, however, is in hair thickness: the hairs posterior to the blowhole are thicker than those in the other areas (Figure 5A). It is possible that the regional thickness variation is an adaptation for specific functions of these hair patches, but it is also possible that there are regional differences in hair thickness across the face in cetacean ancestors. The closest relatives of modern cetaceans are artiodactyls (Thewissen et al. 2001). While many artiodactyls have vibrissae on the rostrum and tip of the mandible (Pocock, 1914), it is not obvious to which area the hairs posterior to the blowhole in whales are homologous. Actually, this may not matter, comparisons of regional differences in hair thickness across the face have been carried out by Yanli et al. (1987) for carnivores, perissodactyls, rodents, and primates, and these authors found no regional trends.

On the other hand, variability in hair shaft diameter is known to occur in mammals with hair patches that have specialized functions. Manatees use their vibrissae in tactile sensing, and food gathering and oripulation (Reep et al., 2001, 2002, 2011). Reep et al. (2001) studied hair diameters in various regions of the manatee face, and they found a distinct characteristic range in hair diameter for each of the facial regions. The hairs that correspond to mystacial and mental hairs are used more often for grasping during the feeding process, and the bristle-like hairs (BLH) of the oral disk are used for tactile exploration.
Also showing regional variation in hair shaft diameters are bearded seals (*Erignathus barbatus*), which demonstrate increased diameter of mystacial vibrissae in a rostral to caudal direction on the snout (Marshall et al., 2006). Vibrissae are well studied in phocid seals, which use them to sense waves in the water (Dehnhardt et al., 1998) and discriminate prey (King, 1983). In eared seals (Otariidae), walruses (Odobenidae), and some phocid seals, the diameter of the vibrissae varies along the hair shaft, with thick and thin areas creating a sinusoidal profile (Watkins and Wartzok, 1985; Hyvärinen, 1989; Dehnhardt and Kaminski, 1995). The morphometrics of the beaded whisker differ among species (Ginter et al., 2012). Although the exact mechanics of this shape have not been determined, Ginter et al. (2010) speculate that the crests and troughs of the hair shaft function to increase sensitivity of reception, and to reduce drag and signal interference.

Due to cold aquatic temperatures, pinnipeds possess an upper cavernous sinus in their F-SC to retain heat and maintain dexterity of the area (Mauck et al., 2000; Dehnhardt and Mauck, 2008), but, in spite of an Arctic habitat, we do not detect an upper cavernous sinus in bowheads. There is extensive innervation to the hair follicle, including a large nerve, the deep vibrissal nerve, traversing the capsule and ending on the lower cavernous sinus (Figure 4C). There is a lack of musculature surrounding the hair follicles, suggesting that hairs are not mobile, unlike the active whisking vibrissae of land mammals (Williams and Kramer, 2010), protracting vibrissae of pinnipeds (Yablokov and Klevezal, 1964) and highly mobile sirenians (Reep et al., 2001). This demonstrates a passive receptive system which reliant on the water medium to move the hair shaft.
Although the blowhole hairs are overall thicker than the other two regions, and the blowhole recesses would be considered larger if 2012B7 were not included, when the ratios of the three regions are compared, there is little difference in hair thickness relative to recess diameter across the three regions. Perhaps the larger hairs require a larger recess, or a larger recess allows a thicker hair to grow. At this time, we have no data to support the idea that these two measurements are not related, but the relationship between these two variables can be examined (Figure 7).

We hypothesize that the hair shaft thickness patterns in bowheads reflect functional specializations. It is possible that these hair patches function similarly to a lateral line system of aquatic vertebrates, or the whiskers on the body of fossorial rodents (Crish et al., 2003; Park et al., 2003) as a general detector of the environment. In that case, hairs near the blowhole could be used for functions related to breathing, to detect the proximity of the water surface when emerging, or to detect ice overhead. Thewissen et al. (2011) found that bowheads have a good sense of smell, and it is possible that these hairs serve as weather vanes, since olfaction, by itself, is not a directional sense. In contract, vibrissae near rostrum and mandible may detect water flow related to feeding, the presence of dispersed food items before the mouth opens, or the presence of inedible items, such as ice.


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FIGURES

Figure 1. A) Bowhead whale fetus (2007B16F) with regions indicated: a) blowhole, b) rostrum, c) chin. B) Patch of adult bowhead skin with hairs, emerging from epidermal recesses. Scale bar applies to image A.
Figure 2. A) Living bowhead whale swimming away from camera. Left and right blowholes are located on an elevated area of the head, and hairs are implanted in a left and right arch posterior to this. It is likely that not all hairs are visible in this figure. Photo by Craig George. B) Slits on left of photo represent the left and right blowhole of bowhead whale (NSB-DWM 2013B1), with anterior to the left. Arrows indicate hairs emerging from epidermal recesses. Due to the lighting of specimen, recesses are most visible near the midline, and hairs are most visible laterally. Skin tears are the artifacts of preservation.
Figure 3. Measurements taken with microscope of A) hair thickness at point of emersion from recess (2012B7, chin region, sample 20, location c) and B) diameter of funnel-shaped epidermal recesses (2012B7, sample 21, locations c, d, e, and f).
Figure 4. Histological sections of bowhead vibrissae. A) A very dense and thick connective tissue capsule is seen on the lateral sides of the follicle. The blood-rich ring sinus is apparent between the capsule and the interior wall of the follicle. The follicle capsule is highly innervated, with axons traversing lateromedially across the capsule near the basal portion of the F-SC (2011B8, rostrum region, slide 33). B) Side-by-side F-SCs with view of epidermis invaginating to form interior wall of F-SC (2011B8, sample 2, slide 10). C) The deep vibrissal nerve and branching
neural tissue can be seen traversing the capsule in a lateromedial fashion near the level of the dermal papillae (2012B18, rostrum region, sample 70, slide 19). D) Transverse section of F-SC at level of ring sinus (2013B1, chin region, slide 10). Hair shaft is absent, but its approximate location has been indicated. Interior wall was torn during preparation and was torn at all levels of the ring sinus. E) Bowhead fetus (2000B3F, chin region, slide 26), approximately 4 months into gestation. Invagination of epidermis and condensation of tissue in the dermal level are observed. No ring sinus is apparent.

**app**=ring sinus appendage, **cap**=highly innervated follicle capsule, **dp**=dermal papillae, **epi**=epidermis, **DVN**=deep vibrissal nerve, **hs**=hair shaft, **inn**=innervation, **iw**=interior wall of F-SC, **lcs**=lower cavernous sinus, **ors**=outer ring sinus, **rs**=ring sinus, **trb**=trabeculae of cavernous sinus. Scale bar is 200 µm.
Figure 5. A) Thickness of bowhead hairs. The hairs surrounding the blowhole are significantly thicker than the hairs on the rostrum (p<.001) and the chin (p<001), except in 2012B16, where the blowhole hair is not significantly larger than the chin hair (p=.125), but both are significantly larger than the rostrum hair (p<.001). B) Diameter of bowhead epidermal recesses. There is no difference among the three regions of the whale. Sample size is shown above each plot.
Figure 6. A) Dermal follicle length. The blowhole follicles are not significantly different from the chin follicles (p=0.083), but they are significantly longer than the follicles of the rostrum hairs (p<0.001), and the rostrum and chin hairs are different lengths (p=.004). Measurements may be somewhat affected by fixation in paraformaldehyde. B) External hair length. There is no difference between the three regions in the measurement of length of the exposed part of the hair shaft. Sample size is shown above each plot.
Figure 7. Ratio of average hair thickness to average recess diameter for all specimen with both values recorded. With the exception of 2012B7, the ratios are tightly grouped across anatomical regions.