DO INNERVATION PATTERNS OF MYSTACIAL VIBRISSAE IN HARBOR SEALS, *PHOCA VITULINA*, EXPLAIN SPECIALIZATION IN TRAIL FOLLOWING BEHAVIOR?

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ABSTRACT

Do Innervation Patterns of Mystacial Vibrissae in Harbor Seals, P*hoca vitulina*, Explain Specialization in Trail Following Behavior?

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The microstructure of vibrissae, or whiskers, of terrestrial mammals has been well-studied, but the study of marine mammal vibrissae is relatively overlooked. The lack of comparative data regarding the vibrissae, or follicle-sinus complex (F-SC) of marine mammals has hampered the ability to answer questions about the function and evolution of these sensory structures. Harbor seals, *Phoca vitulina*, are a well-studied pinniped species with readily available data regarding their feeding ecology and prey tracking behavior using vibrissae. This latter behavior termed "hydrodynamic trail following" behavior is well documented. To best understand the functional use of harbor seal vibrissae, however, the microstructure and innervation patterns need to be understood to compare harbor seals to phocids for which neurological data is already available. To close this gap in the phocid dataset, the largest F-SCs from five individuals were processed histologically. Axon counts were obtained to study innervation investment, while morphometric data was collected to study the microstructure of F-SCs. Harbor seal vibrissae had similar axon counts/F-SC and microstructure to other phocid species. Axon counts were converted to densities in the lateral columns of vibrissae, to correct for size, and compared to harp seals. The lateral vibrissae of harbor seals had more axons per mm^2 than harp seals, which accounts for the harbor seals specialization for trail following.

Whether this difference in is typical for phocids needs to be better understood by comparing innervation investment to other pinnipeds, such as otariids, and phocid species that diverge from the phocid pattern, like bearded seals (*Erignathus barbatus*).

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NOMENCLATURE

F-SC	Follicle Sinus Complex
LCS	Lower Cavernous Sinus
RS	Ring Sinus
UCS	Upper Cavernous Sinus
RW	Ringwulst
ICB	Inner-conical Body
DVN	Deep Vibrissal Nerve
DC	Dermal Capsule
CT	Cutaneous Trabeculae
MS	Mesenchymal Sheath
HS	Hair Shaft

CHAPTER I

INTRODUCTION

Background

Marine mammals are among a group of species with the most recent and advanced adaptations for the aquatic environment. Marine mammals started returning to the sea as early as the Eocene era; and some families can still be seen adapting to the aquatic environment such as otters of family Mustelidae, a closely related group belonging to order Carnivora. Extinct lines of phocids did not start returning to the aquatic environment until the late Oligocene. Pinnipeds stem from Arctoidean mammals, and extinct stem phocids make an appearance beginning 15 ma, although the exact lineage is unclear from the fossil record (Marshall and Pyenson, in press). Among the many challenges overcome by early pinnipeds for adapting from a terrestrial to an aquatic environment are pressure, temperature and viscosity since water is twenty-five times more viscous than air. These factors alter not only the physical morphology of animals inhabiting water in comparison to their terrestrial relatives, but the sensory systems behind the function of their morphological features.

Vibrissae, or whiskers, make an excellent example of an innovation to allow formerly terrestrial animals to detect prey within the aquatic environment. Terrestrial mammal vibrissae have been studied in many rodents, particularly rats, *Rattus norvegicus* (Rice and Munger 1986). The structure and functional use of vibrissae by rats during investigation of potential prey items and unknown objects in their environment have been well studied (e.g., Williams and Kramer 2010; Hartmann *et al.* 2003). Water rat vibrissae (*Hydromas chrysogaster*), a semi-aquatic mammal, have also been studied by Dehnhardt *et. al* (1999) to understand the difference in

function and structure from their fully terrestrial counterparts. Not only has the physical appearance of aquatic vibrissae altered from terrestrial ancestors of marine mammals, but the function of vibrissae in the aquatic environment has expanded greatly.

Vibrissae offer an additional sense to confront the problems encountered by aquatic mammals and increase awareness of the animals to their environment. It has been observed that one of the most derived vibrissae of marine mammals belong to phocids, or the group marine mammals commonly referred to as true seals. Their vibrissae are the largest known, and have been shown to be ten times more sensitive to their surrounding environment than whiskers of closely related terrestrial counter-parts (Hyvärinen *et al.* 2009, Rice *et al*. 1986). Phocid vibrissae have a specialized, beaded morphology along the entire hair shaft that reduces drag by improving water flow over the hair shaft in the viscous marine environment (Ginter *et al*. 2010; Williams and Kramer 2010). Reducing the vortices created by the overall drag of the water flow over the whisker allows for a more accurate perception of the seal's environment based on direct sensory reactions to changes in pressure over the whisker hair shaft (Hanke *et al.* 2010). Pinniped whiskers contain Merckel cell mechanoreceptors that serve the function to receive pressure based stimulation from the environment in the Inner-Conical Body (ICB). Phocid whiskers also directly differ from terrestrial whiskers by the structure of their follicle-sinus complex (F-SCs), or the portion of their vibrissae that lies beneath the surface muzzle tissue and serves as the center for communication with the brain. There are three sinuses in pinniped vibrissae rather than the two sinuses found in vibrissae of their terrestrial counterparts. Pinniped mammals have a ring sinus (RS) separating the upper (UCS) and lower (LCS) cavernous sinuses of the F-SC that is completely filled with blood (Hyvärinen *et al.* 2009). The LCS and RS are highly innervated in marine mammals by a single nerve, the deep vibrissal nerve (DVN), from the bottom of the F-SC

and course through the LCS branching off along the way. This differs from terrestrial F-SCs in which the DVN enters the F-SC at the side of the whisker near the RS and a superficial vibrissal nerve from the dorsal side of the F-SC. In pinnipeds, the branched nerves travel up the F-SC to the RS and terminate near the RW and ICB of the RS. In addition to the RS function for innervation, the RS serves as thermoregulation providing continuous blood flow important for heat distribution in the body (Marshall *et al.* 2006; Hyvärinen *et al.* 2009). The UCS has been speculated to serve an insulation function keeping the muzzle warm allowing the mechanoreceptor function to remain successful even in very low temperatures. The UCS also protects the follicle from bending under the pressure of water flow allowing for better sensory function (Erdsack *et al.* 2014; Hyvärinen *et al.* 2009). Terrestrial mammals have additional innervation in the apical regions of the F-SC but their marine counterparts tend to focus their innervation on the F-SCs in their muzzle. The vibrissae of seals are distributed on the facial region, although their largest vibrissae are in the muzzle. These three adaptations: three sinus complexes instead of two, lacking innervation in the apical regions of the F-SCs, and innervation from the whisker's base rather than the side provide an increased sensitivity to phocids' awareness of their surrounding environment.

Phocids have the ability to track prey using various methods since many of their sensory organs have been adapted to the aquatic environment. The purpose of having an additional sense in the aquatic environment can be related to the lateral line present in fish species. Phocids have adapted changes for their vision through their eyes, reduced hearing and ears, adequate smell on land and in air but relatively poor in water, and increased touch sensory using their vibrissae. Tracking prey is a necessary activity for successful growth and reproduction in seals making these sensory adaptations to the aquatic environment essential (Wieskotten *et al.* 2010).

Vibrissae allow seals to find prey when the possibility of finding prey are inhibited by conditions that do not allow them to hunt using vision, a reliable foraging strategy when conditions are favorable. Low water quality requires extra sensitivity to the environment to compensate for decreased function of their other sensory organs (Hyvärinen 1989). Mammals have motor control over their vibrissae, and mobile vibrissae increase successfulness of seals to distinguish size of objects in front of their muzzle (Hyvärinen 1995). Pinnipeds prefer using their vibrissae for close interaction when they are investigating a potential prey object (McGovern *et al.* 2015, Grant *et al.* 2014). Their excellence at distinguishing size of an object using only their vibrissae is comparable to that of a chimp using its hands and fingers to investigate and object (Dehnhardt and Kaminski 1995).

The best known species regarding vibrissal function in living pinnipeds are harbor seals (*Phoca vitulina*). Harbor seals are easily held in captivity and cooperative for training with researchers regarding answering questions regarding their life history. Harbor seals have been studied extensively regarding the use of their vibrissae during feeding behaviors in captivity (Grant *et al.* 2014). Marshall *et al.* (2014) showed that harbor seals use a variety of techniques to feed on different prey types, including suction, biting, and hydraulic jetting. They utilize the full range of their vibrissae for all the foraging strategies they employ for all types of feeding. Before the seal has the opportunity to feed, however, they must find their prey. Harbor seals tend to do this using their vibrissae to follow the trails of fleeing fish. Harbor seals excelled during experiments studying their capabilities to follow narrow trails, succeeding at least 70% of the time for quite some time following the fleeing object (Wieskotten *et al.* 2010). Therefore in close ranges they are likely following the vortices of fish left behind as their prey attempts to escape,

and then using their vibrissae to actively sense the prey's movement as they investigate the prey item.

Research Objectives

Although data regarding the neurobiology of pinniped vibrissae exists for several species, no such data exists for harbor seals despite the fact that our understanding of phocid whisker functional behavior is best known for this species. Therefore this work will fill the gap so that a truly integrated understanding (microanatomy, neurobiology, behavioral performance) of whisker function in this species can be reached. Harbor seals are an ideal model system for this kind of research.

To fill this crucial data gap, this study will investigate the microstructure and innervation of harbor seal vibrissae using histological methods. Although vibrissae are present in other regions on the head of a seal (supraorbital and rhinal), the largest vibrissae are the mystacial vibrissae in the muzzle, and the vibrissae referred to here-on-out will be mystacial vibrissae. First, the number of F-SCs in our harbor seal specimens will be mapped and quantified. Second, axons will be quantified to determine the number of axons per F-SC. This mean value will be multiplied by the total number of vibrissae to approximate the total innervation of the muzzle, which will serve as a platform for comparison of harbor seals to other phocid species. Due to harbor seals' excellence at trail-following behavior, I predict that the total innervation of the muzzle to be higher for harbor seals than other phocid species. I will be testing two hypotheses in this project as follows: 1) I expect the innervation per F-SC for harbor seals to be in similar range to other pinniped species and 2) the number of F-SCs per muzzle for harbor seals to be higher than other pinniped species resulting in a higher overall innervation of the muzzle. Results supporting these hypotheses would support that the innervation per F-SC is a conserved trait

among phocid and perhaps all pinnipeds, but the number and distribution of F-SCs across the muzzle determines differences in sensitivity and function of seals' vibrissae between species, as found in other species. In addition to mapping the number of F-SC of harbor seal muzzles and quantifying the number of axons per F-SC and in total to the mystacial whisker pads, the microstructure F-SC morphometrics will be characterized following Marshall *et al*. (2006). This morphometric data will also serve as a platform for comparison across phocid species to determine if a difference in structure is present between harbor seals and other phocids for which morphometric data are available. I predict there to be no difference between harbor seals and other phocid seals in overall microstructure of the vibrissae.

CHAPTER II

METHODS

Five harbor seal masks were obtained from the Marine Mammal Center in Sausalito, California. These were salvaged from stranding networks, therefore no IACUUC compliance was necessary for this study. The necropsy sheets were not obtained from the stranding networks, so no information regarding age, sex, or cause of death for any of the samples are provided for any of the individuals.

For the five masks, or muzzles of individual seals, the F-SCs on both sides were mapped to show each whisker's placement on the seal's muzzle and to count the individual mystacial whiskers present (Fig. 1). The six largest F-SCs were dissected and the following measurements were collected: hair shaft length, major and minor hair shaft axes at the skin, and the length of the follicle from the base to the skin surface. F-SCs were histologically processed for axon counts (cross sections) and morphometrics (longitudinal cross sections). Sections were cut on a Leica 80A microtome with a freezing stage attachment (PhysioTemp) at 30 micrometers for cross sections and 25 micrometers for longitudinal cross sections. Sections were stained with modified Bodian silver stain for the innervation pattern and a modified Masson's trichrome stain for generalized structures.

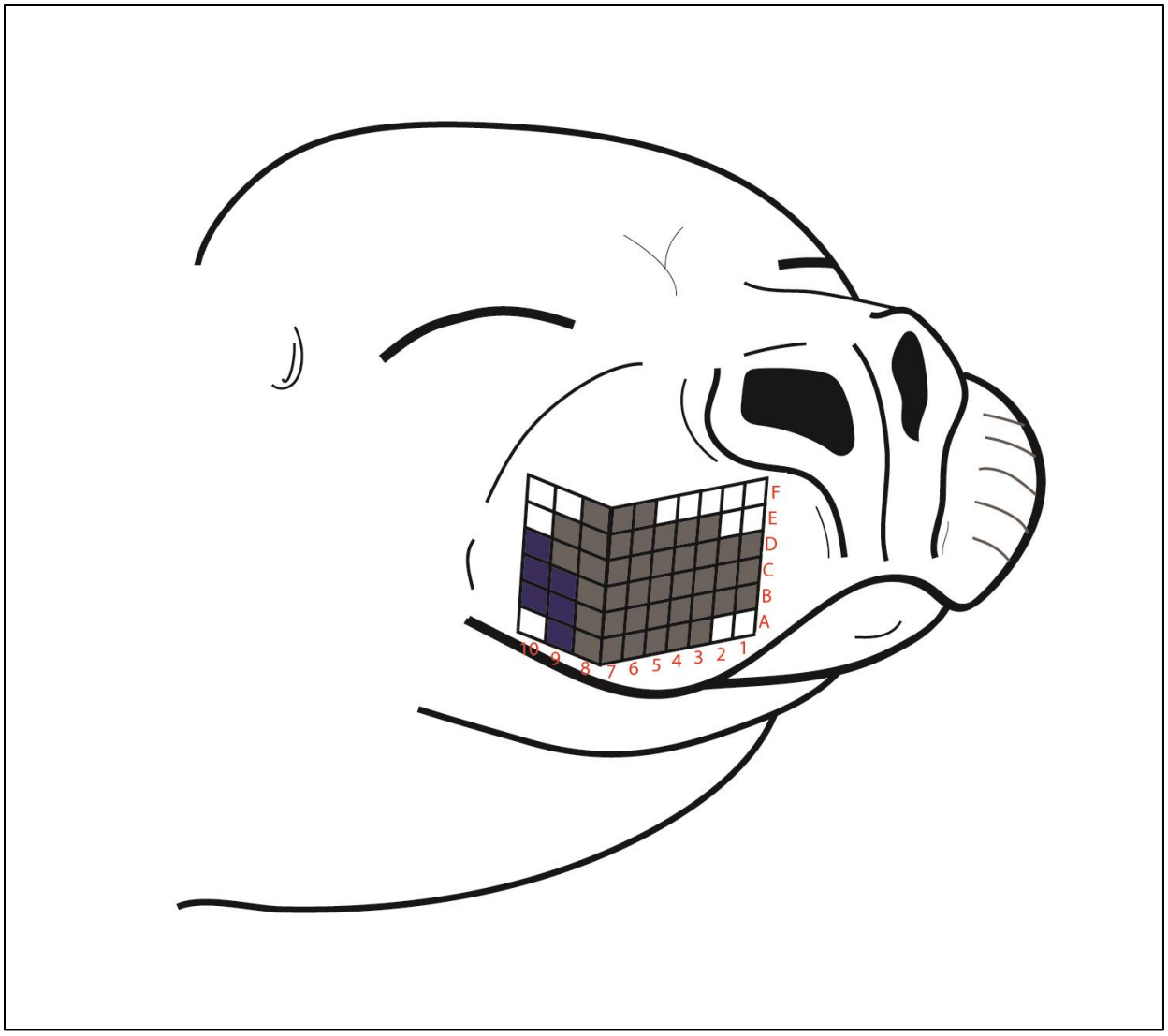

Fig. 1. Mesh representation of a harbor seal mask. The gray boxes represent individual F-SCs on a harbor seals right muzzle. Lateral whiskers removed are marked with navy boxes. Columns and rows of F-SCs are labeled in red.

Axon counts were conducted on non-stained mounts following Mattson and Marshall 2016. Up to five sections from the mid-LCS were used since the DVN branches as it courses through the LCS in several thick nerve fibers following its penetration of the F-SC base (Fig. 2) (Hyvärinen 1989). Axon counts were determined using light microscopy (Nikon Eclipse E400) at 4x objective and 40x objective and digital micrographs were taken using SPOT Advanced Version 5.2. Images were analyzed using Adobe Photoshop cs2 Version 9.0 for axon counts (Fig.

3). Some sections were counted by multiple readers to compare consistency between readers. The counts by different readers were analyzed with a One-Way ANOVA (α=0.05) and no significant difference between two readers was found. The same cross-sectional images were used for morphometric measurements following Marshall *et al.* (2006). In total, 44 whiskers were processed and axon counts were obtained from 114 cross sections. Full morphometric data was done on 10 cross sections.

As past studies of similar nature (Marshall *et al*. 2006; Marshall *et al*. 2014) used a modified Bodian's silver stain to obtain axon counts, sixteen sections were selected to compare wet and stained section. These sections were stained and pictured using the same software as the wet sections. The counts obtained from the stained sections were compared against the wet axon counts to determine if there was a difference in reliability between the two processes. Since no difference was determined, further staining was not carried out and the reported axon counts are from unstained sections.

After histological processing the following morphometrics were collected: dermal capsule thickness, mesenchymal sheath thickness, cutaneous sheath thickness, hair shaft major axis, hair shaft minor axis, hair shaft circumference, cross section diameter (maximum and minimum), length of the line of action across the major and minor axis of the hair shaft for the whole cross section, and the circumference of the cross section. Diameters and thickness measurements were represented with lines, while the CT and HS areas were calculated with ellipse model (Fig. 4). The area of the HS ellipse was subtracted from the ellipse around the CT, reporting the surface area of the where axons are found. The corresponding axon counts for the morphometric data were divided by the CT surface area to report the density of axons per F-SC surface area (mm^2).

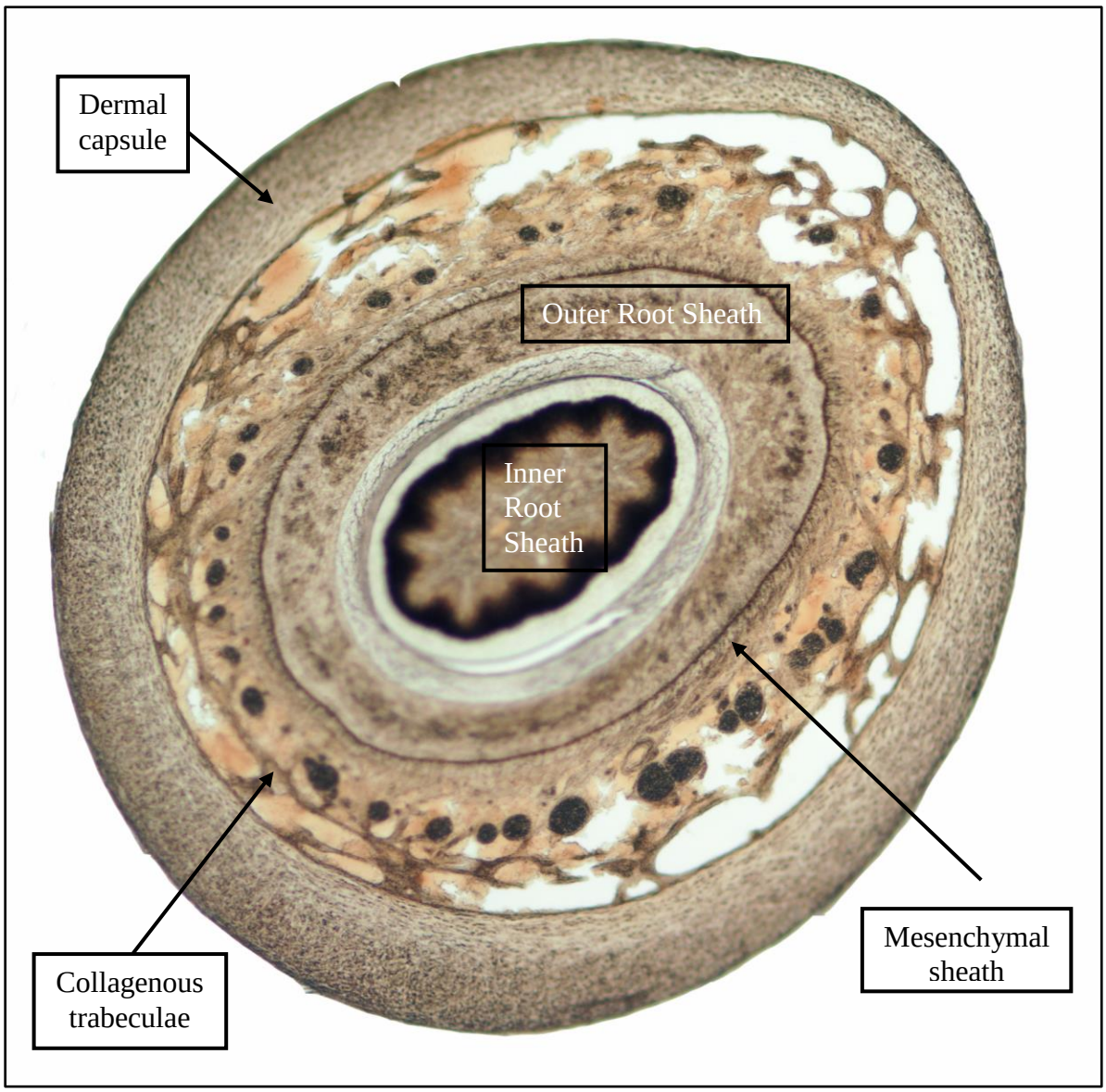

Fig. 2. Cross section of a whisker with hair shaft inner and outer root sheaths, dermal capsule, collagenous trabeculae, and mesenchymal sheath labeled.

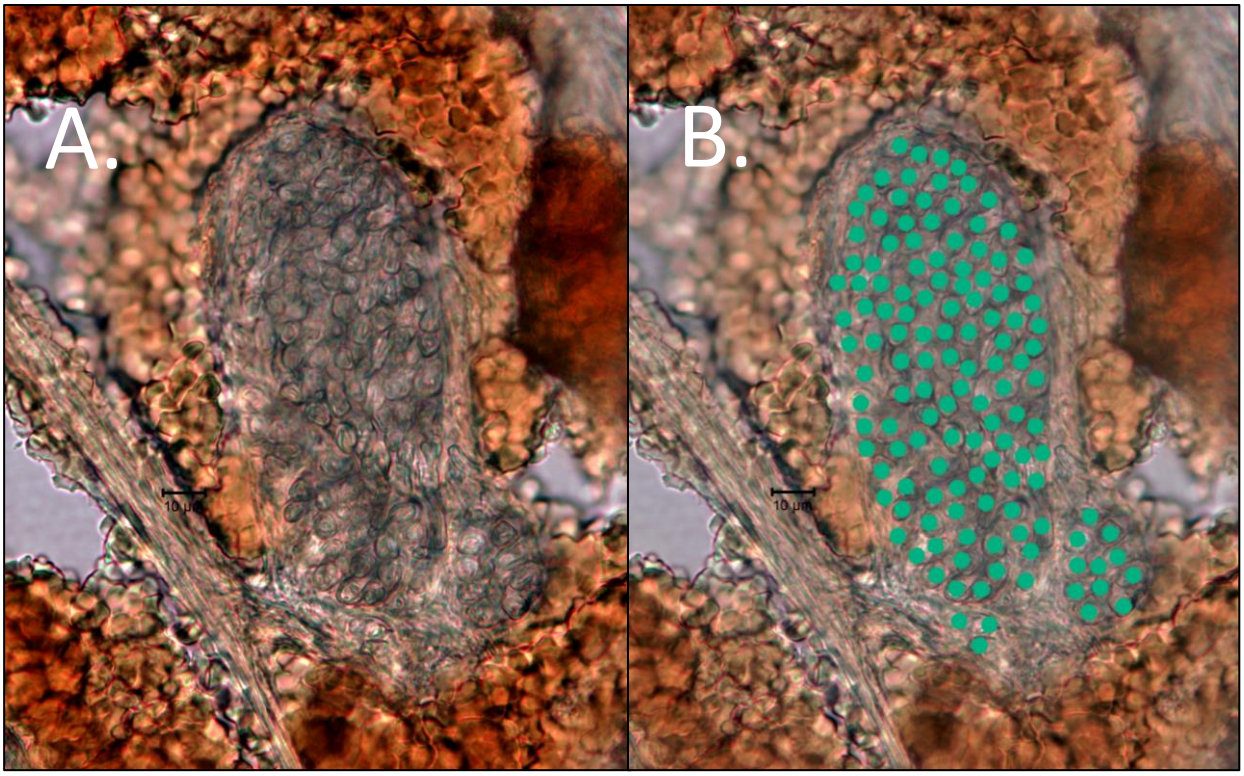

Fig. 3. A. Unstained axon bundle with no counts **B.** Unstained axon bundle counted with markers

Longitudinal morphometric measurements were also taken for ten longitudinal sections from five individuals. The length of the LCS, RS, and UCS were taken. These values were added to give the total sinus length (LCS + RS + UCS). The mean total sinus length was compared to the dissection measurements taken of F-SC length. The length of the total sinus was used to determine what percent each sinus took up within the F-SC. The width of the RS and DC were also taken (Fig. 5). Each measurement was taken three times and reported as mean values.

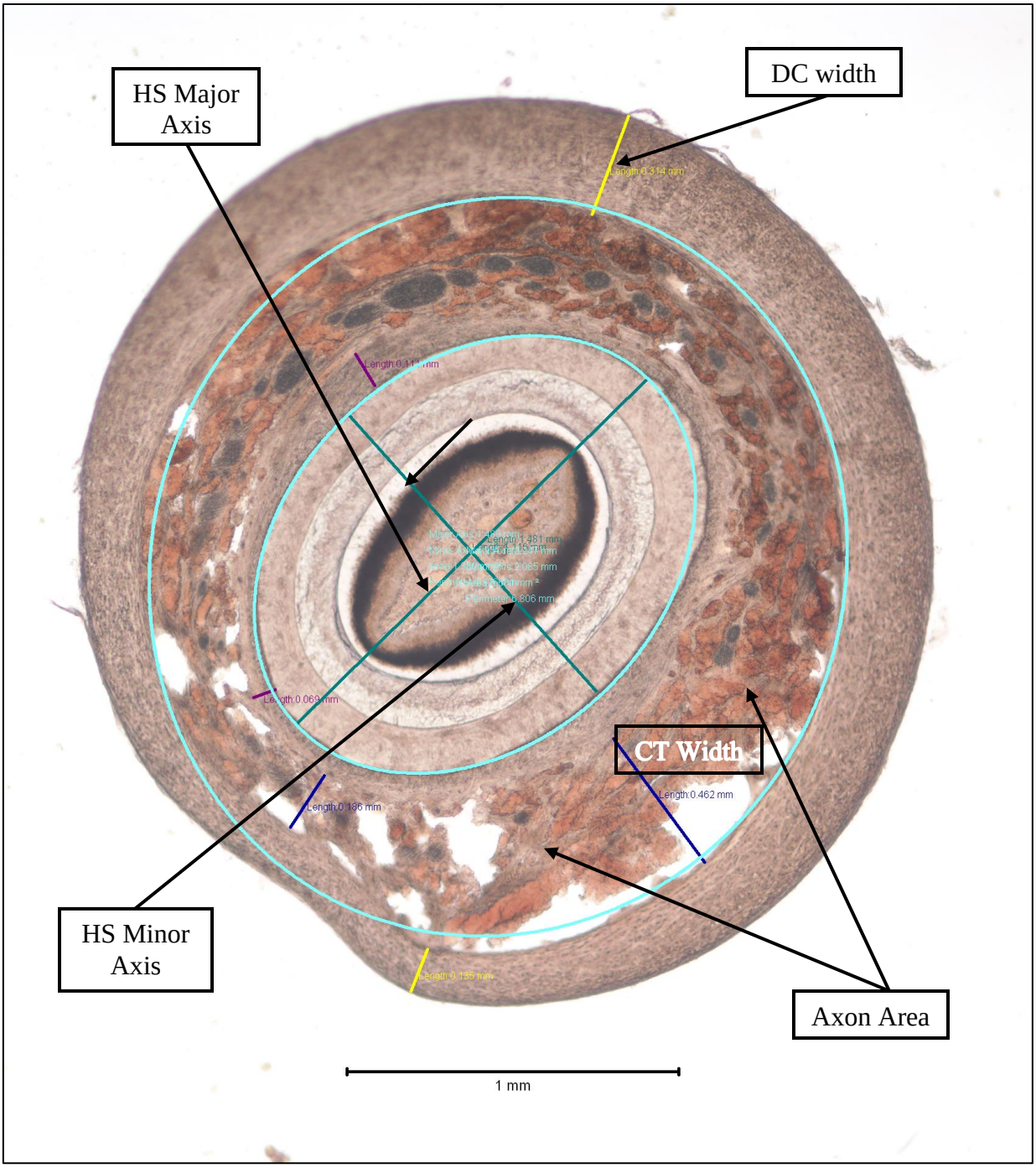

Fig. 4 (above). Example of morphometric measurements labeled on an unstained cross section.

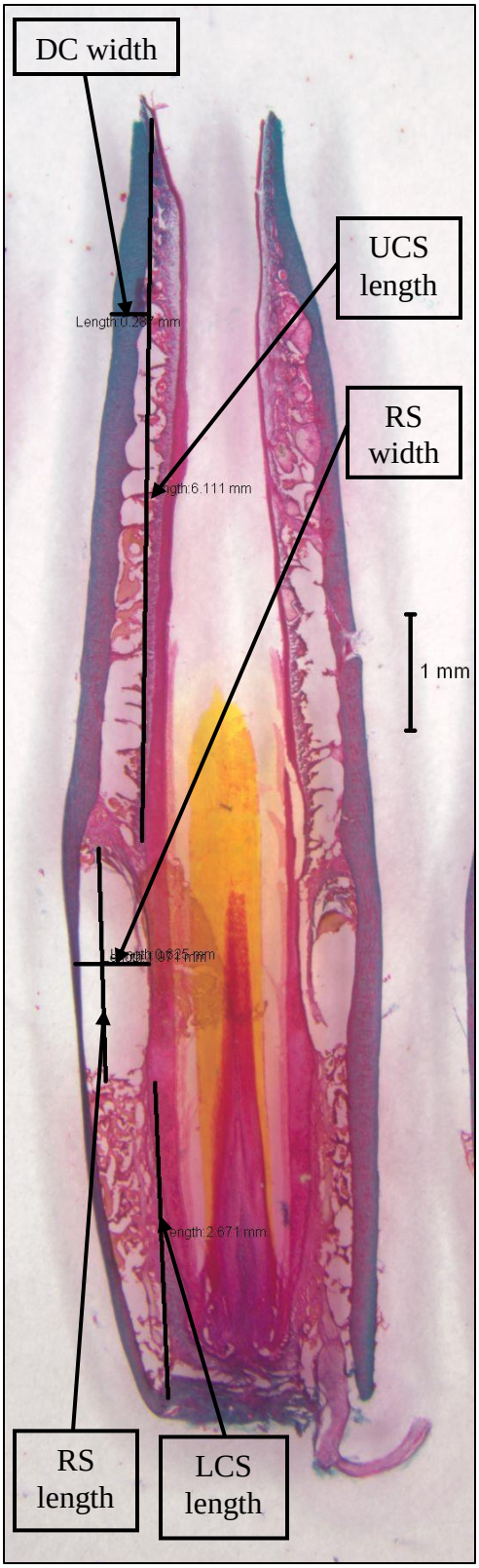

Figure 5. Morphometric measurements taken for longitudinal sections labeled on a stained section with Masson's trichrome stain.

CHAPTER III

RESULTS

The mystacial vibrissae of harbor seals demonstrated a typical phocid pattern of the largest F-SCs located ventro-laterally and decreased in F-SC width and length and HS width and length dorso-medially across the muzzle. All mystacial vibrissae displayed the beaded morphology previously reported (Hanke et al. 2010). The mean value of F-SCs per muzzle was 88 ± 6.3 F-SCs with a mean length of 1.4 ± 0.11 cm (Fig. 1). The mean length of lateral vibrissal hair shafts was 6.5 ± 1.2 cm from the surface of the follicle to the tip. Since the hair shaft was elliptical, the major axis of the hairshaft measured 0.01 ± 0.002 cm and the minor axis of the hair shaft measured 0.006 ± 0.001 cm (Fig. 4).

Harbor seals have three sinuses of unequal lengths (Fig. 6). The UCS length was the longest sinus and took up 53 ± 4% of the F-SC, while the shorter LCS accounted for 32 ± 4% and the RS accounts for 15 ± 3%. (Table 1).

No superficial vibrissal nerves or axons of any kind were observed in the UCS. The DVN penetrated the base of the F-SC and coursed apically through the LCS. Portions of the DVN branched off in the upper LCS while other portions of the DVN continued to branch and provided major terminating branches in the RS and ICB. The mean axon count from the mid-LCS was 1627 ± 201.8 and ranged from 1200-2337 axons per F-SC. The total innervation of the mystacial vibrissae was estimated to be 143,176 ± 26,737 axons.

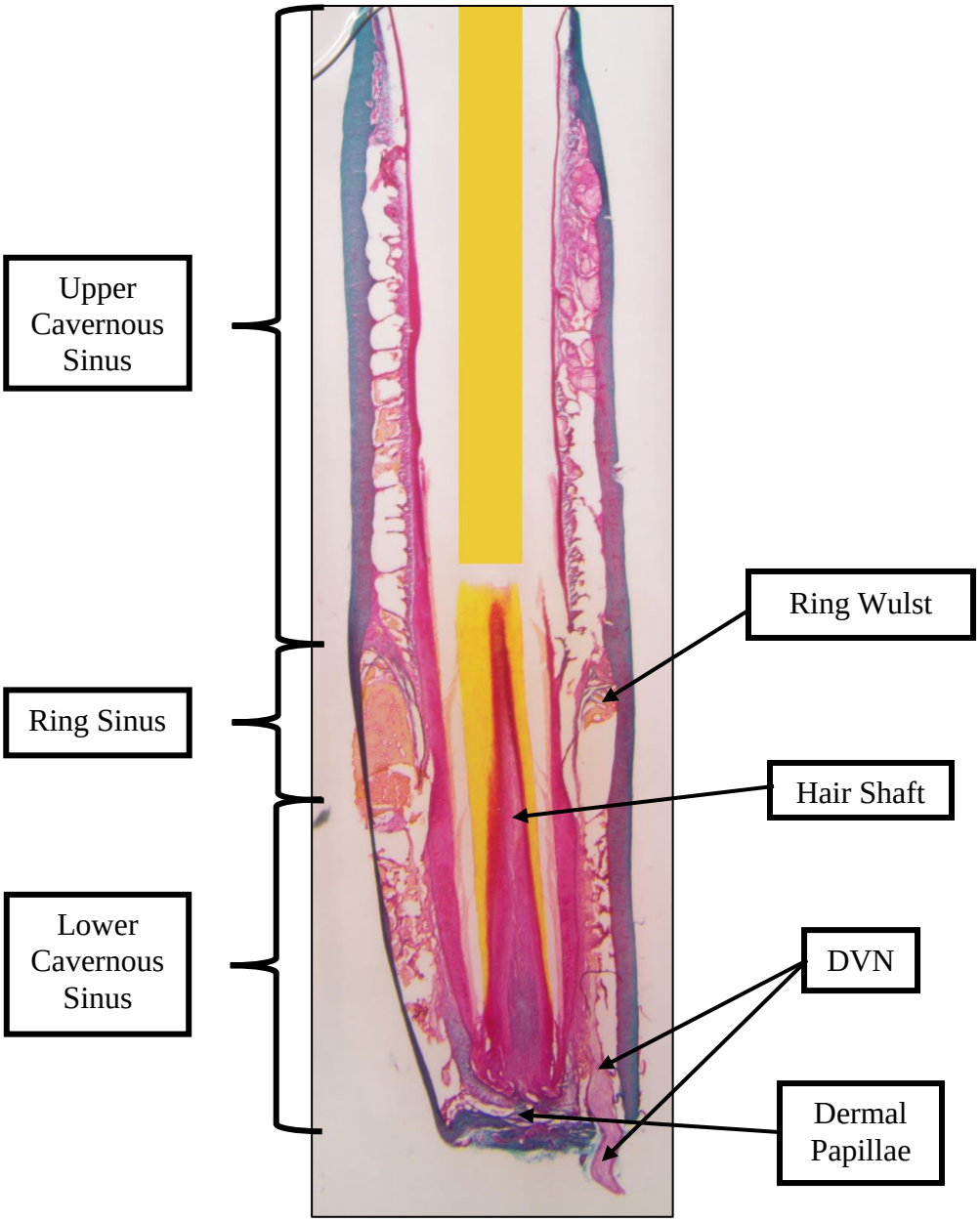

Fig. 6. Longitudinal section of an F-SC. The tripartite system is labeled as LCS, RS, and UCS. The DVN path is traced with three arrows. The hair shaft is represented by a yellow bar since it fractured during staining.

Table 1. Morphometric measurements of longitudinal sections

Measurement	Mean Value (mm)
LCS Length	3.8 ± 0.8
RS Length	1.8 ± 0.2
UCS Length	6.3 ± 0.8
Total Length of Combined Sinuses	11.9 ± 1.4
Maximum RS Width	0.6 ± 0.1
Maximum DC Width	0.3 ± 0.04
% LCS of F-SC	32 ± 4%
% RS of F-SC	15 ± 3%
% UCS of F-SC	53 ± 4%

Table 2. Mean morphometric measurements of cross sections

Measurement	Mean value (mm)
DC thickness (large)	0.35 ± 0.05
DC thickness (small)	0.15 ± 0.03
CT thickness (large)	0.45 ± 0.03
CT thickness (small)	0.20 ± 0.06
MS thickness (large)	0.17 ± 0.04
MS thickness (small)	0.05 ± 0.01
HS area	1.00 ± 0.16
HS length (major)	1.30 ± 0.13
HS length (minor)	0.96 ± 0.07
CT area	3.37 ± 0.71

The morphometric measurements of cross sections are summarized in Table 2. The mean surface area of the CT was 3.09 ± 0.7 mm². The mean number of axons per mm surface area CT was similar across the three most lateral columns of vibrissae, columns 8, 9 and 10 and are summarized in Table 3 (Fig 1). Although the axon count per F-SC increased among the three columns, the density remained similar since the surface area increased in the more lateral whiskers.

Table 3. Axon densities across columns of lateral vibrissae in harbor seals

Column of Vibrissae	Axons/F-SC for particular column	Axons/mm² for particular column
Column 8	1536 ± 166	437 ± 77
Column 9	1607 ± 87	437 ± 124
Column 10 (most lateral)	1851 ± 172	427 ± 21

CHAPTER IV

DISCUSSION AND CONCLUSION

The microstructure of harbor seal vibrissae followed the now established phocid pattern. As in other pinniped species, harbor seals possess three blood sinuses in their F-SCs (Dehnhardt 1999, Marshall *et al.* 2006). Further following the observations of Marshall (2006) and Dehnhardt (1999), the UCS accounted for approximately 50% of the total F-SC length and lacked innervation from a superficial vibrissal nerve, supporting the proposed function of the UCS as thermal protection for the mechanoreceptors within the RS and the LCS. The number of axons for the largest ventrolateral vibrissae and total estimate of the mystacial field were similar to that reported for other phocid species (Table 4). As reported by Mattson and Marshall (2016), this likely overestimates innervation to the muzzle by approximately 10% since only the largest F-SCs were measured. A corrected mean value for innervation of the whole muzzle would be approximately 128,858 axons per muzzle instead of 143,176 axons. Regardless, the total innervation still falls within the phocid pattern of mystacial vibrissal innervation.

Harbor seal muzzles had a similar number of F-SCs across their muzzle compared to many phocid species with the notable exception of bearded seals, *Erignathus barbatus* (Table 4). Bearded seals have a flatter anterior muzzle surface and are benthic foragers, compared to the more pointed muzzle surface and hydrodynamic trail following behavior of harbor seals and other phocids (Marshall *et al.* 2006; Wieskotten *et al.* 2010). Benthic versus hydrodynamic trail following is not explained by innervation investment (number of axons per F-SC), which is similar among all phocids, including bearded seals. Instead, benthic foraging appears to require a greater number of F-SCs on the muzzle, rather than an increase in the number of axons per F-SC.

This suggests phocids innervation is maximized by size of the F-SC so seals accomplish increased tactile sensitivity through other mechanisms.

Table 4. Comparison of innervation investment across phocid species and pinniped species

Species	Mean Axons/F-SC	Mean F-SCs/Mask	Mean Axons/Mask
Harbor Seal	1627 ± 201	88 ± 6.3	143,176
Harp Seal (Mattson and Marshall 2016)	1413 ± 327	96 ± 3.7	135,648
Elephant Seal (McGovern *et al.* 2015)	1585 ± 281	100 ± 2.6	158,340
Ringed Seal (Hyvärinen 1989)	1350	110 ± 1.7	160,000
Bearded Seal (Marshall *et al.* 2006)	1314 ± 270	244 ± 52	320,636
Sea Otter (Mustelidae) (Marshall *et al.* 2014)	1339 ± 408.3	120.5	161,313

Although the number of axons per F-SC is a useful measure for comparing innervation investment across species, it does not account for body size. To account for body size the density of axons in the LCS is a better measure. A comparison of the density of axons per F-SC with harp seals (Mattson and Marshall 2016; the only other phocids for which density data are available) suggests that the lateral-most vibrissae of harbor seals are specialized for trail following behavior. The density of axons in the columns 8, 9 and 10, although relatively similar among columns, have higher density of axons in harbor seals than similar vibrissae in harp seals (Table 3) (Mattson & Marshall 2016). Harp seal vibrissae from column 8 had 297.7 axons per mm^2 compared to the 437 axons per mm^2 in harbor seal column 8 vibrissae. Since the value for

harp seals does not fall within the variance for harbor seal vibrissae this suggests a difference in innervation investment between the two species. The data suggest an underlying neural investment difference that may explain why harbor seals excel at hydrodynamic trail following over other pinnipeds. However, other factors likely contribute such as increased vibrissal hair stiffness, the beaded morphology of the hair shaft, and the diversity and distribution of mechanoreceptors within the F-SCs.

Current psychophysical performance data suggests a dichotomy in mystacial whisker sensory function. Although harbor seals (a phocids) excel at trail-following, they do not perform as well as california sea lions (an otariid) at investigating prey objects by active touch (i.e. haptics). Conversely, california sea lions do not perform as well at hydrodynamic trail following as harbor seals (Grant *et al.* 2013; Wieskotten *et al.* 2010; Dehnhardt 1994; Miersch et al. 2011). Since harbor seals are considered generalist foragers, it may be that hydrodynamic trail following is typical for phocids, with the exception of specialized benthic foragers like bearded seals. Additional studies that characterize the investment of their innervation pattern by a model otariid species, like California sea lions (*Zalophus californicus*), could further shed light on the role that innervation investment plays in explaining these divergent innervation patterns and vibrissal performance.

To further comprehend the relationship between vibrissal performance and investment could aid in understanding foraging behaviors in species difficult to study in the wild. Harp seals, for which the vibrissal data already exists, are difficult to study since their habitat in the wild is covered with land fast ice. As their habitat is rapidly disappearing, understanding their ecology grows more important. The similarities between harbor seals and harp seals vibrissal pattern regarding total innervation and increased innervation in the lateral whiskers indicates potential

for similarities in foraging behavior. This is supported by the collected vibrissal investment data which indicated a difference between benthic and non-benthic foragers. The behavioral use of vibrissae contributes to understanding predatory roles of phocids in their environments; and developing this understanding across more families of pinnipeds would further the narrative between pinnipeds that employ haptic touch versus trail following.

Understanding how marine mammals interpret their environment also carries potential for the field of biomimetics. As we understand the differences in structure and function, it can improve detection structures proposed for naval submarines (Stocking *et al.* 2010). Sensory technology can prove useful for defense and undersea travel technology with the growth of demand for interpretation of the aquatic environment.

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