Microstructure and Innervation of the Mystacial Vibrissal Follicle-Sinus Complex in Bearded Seals, *Erignathus barbatus* (Pinnipedia: Phocidae)

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ABSTRACT

Vibrissal follicle-sinus complexes (F-SCs) are sensory receptors of the mammalian integument system. They are best developed within Pinnipedia. The objective of this study was to investigate the F-SCs of bearded seals (*Erignathus barbatus*) for benthic foraging adaptations. Bearded seals possessed approximately 244 mystacial F-SCs. In this species, F-SCs consisted of an outer dermal capsule (DC) surrounding a blood sinus system [upper cavernous sinus (UCS), ring sinus (RS), and lower cavernous sinus (LCS)] and concentric rings of epidermal tissue. The UCS comprised up to 62% of the F-SC length and may function as thermal protection for mechanoreceptors. A large asymmetrical ringwulst was located in the RS. A deep vibrissal nerve penetrated the DC at its base and terminated on mechanoreceptors in the epidermal tissues of the LCS and RS. The mean number of myelinated axons per F-SC was 1,314 (range, 811–1,650) and was among the highest number of axons per F-SC reported to date. An estimated mean number of 320,616 myelinated axons innervate the entire mystacial vibrissal array. Merkel-Neurite complexes (MNCs) and small simple laminated corpuscles were found in the region of the LCS. Myelinated axons also terminated on MNCs and lanceolate endings apical to the ringwulst. The number of F-SCs, their geometry in the mystacial region, the number of myelinated axons per F-SC, and the distribution of mechanoreceptors support the premise that pinniped vibrissae are sensitive active-touch receptor systems, and that structural differences in bearded seals, relative to other phocids, may be adaptations for benthic foraging.

Key words: whiskers; tactile sensory systems; foraging; pinnipeds; aquatic mammals

Vibrissae (whiskers) or vibrissal follicle-sinus complexes (F-SCs) are specialized sensory structures of the mammalian integument system. These structures relay vibrotactile information from the environment to the central nervous system (Burgess and Perl, 1973; Gottschaldt et al., 1973; Dykes, 1975; Halata, 1975). Most mammals possess vibrissae; however, their location, numbers, and arrangement are variable, as is their function. In general, many mammals use mobile vibrissal F-SCs for active-touch discrimination of tactile cues (e.g., rodents, felids, manatees, and many pinnipeds), whereas in some taxa vibrissal movement is relatively passive, and the hair shaft of F-SCs is reduced in size (e.g., canids and ursids). Marine mammals have taken vibrissal function in new directions. The hairless follicular pits of odontocetes are thought to possess a rich and patent blood supply (Slijper, 1962; Mauck et al., 2000) and may serve to detect pressure changes during dives (Yablokov and Klevezal, 1964). Walruses and sirenians not only detect tactile cues with

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vibrissae, but they are able to use them to manipulate food and inanimate objects (Fay, 1982; Marshall et al., 1998a, 1998b, 2003). In fact, Florida manatees (*Trichechus manatus latirostris*) possess a tactile resolving power similar to the trunk of Asian elephants (*Elephas maximas*) (Bachteler and Dehnhardt, 1999). However, the F-SCs of pinnipeds are the most elaborated among mammals (King, 1983). California sea lions (*Zalophus californianus*) and harbor seals (*Phoca vitulina*) can discriminate objects using their vibrissae as effectively as monkeys can when using their hands during active-touch experiments (Dehnhardt and Kaminski, 1995; Dehnhardt and Dücker, 1996). Recent evidence demonstrates that the F-SCs of harbor seals also function to detect water movement and hydrodynamic trails (Dehnhardt et al., 1998a, 2001). Such abilities could explain cases of blind seals successfully foraging for fish, despite their lack of vision. It is hypothesized that the pinniped mystacial sensory system is an aquatic adaptation that allows this taxa to navigate and forage in conditions where vision is limited (Hyvärinen, 1989; Dehnhardt, 1994). However, it is clear that there is a lot of diversity in the structure and function of vibrissal F-SC among pinnipeds.

Most of our knowledge of vibrissal F-SCs is derived from terrestrial taxa (e.g., Davidson and Hardy, 1952; Melaragno and Montagna, 1953; Andres, 1966; Burgess and Perl, 1973; Gottschaldt et al., 1973; Halata, 1975; Rice et al., 1986, 1993, 1997; Ebara et al., 2002). Although the general vibrissal F-SC form is similar among mammals, species-specific differences are evident in both structure and innervation. This is particularly true between aquatic and terrestrial taxa. However, only a few F-SCs of pinniped species have been investigated at the light and electron microscopy level [southern elephant seal, *Mirounga leonina*, Ross seal, *Ommatophoca rossii* (Ling, 1968, 1972), California sea lion (Stephens et al., 1973), ringed seal, *Pusa hispida* (Hyvärinen and Katajisto, 1984; Hyvärinen, 1989)]. Although pinniped vibrissae are similar to terrestrial taxa in many ways, distinct differences in the structure of pinniped F-SCs are immediately evident, even at a cursorial level.

First, the blood sinus complex of pinnipeds is tripartite; a ring sinus (RS) is juxtaposed between a lower cavernosal sinus (LCS; as in terrestrial species) and a novel upper cavernosal sinus (UCS) (Ling, 1968, 1972; Stephens et al., 1973; Hyvärinen and Katajisto, 1984; Hyvärinen, 1989). In ringed seals, this UCS comprises 60% of the total follicular length (Hyvärinen, 1995). One functional hypothesis for this elongated additional UCS is to maintain mechanoreceptors within F-SCs at body temperature (Dehnhardt et al., 1998b, 1999; Mauck et al., 2000).

Second, the deep vibrissal nerve (DVN) of pinnipeds penetrates the follicle near its base, rather than at the lateral side of the dermal capsule (DC). The nerves ramify immediately after penetrating the DC, distribute themselves evenly around the perimeter, and course apically along the mesenchymal sheath (MS) and trabeculae of the LCS, toward the RS, where they terminate on several types of mechanoreceptors in, near, and just apical to the ringwulst (RW).

Third, the number of myelinated axons per F-SCs of terrestrial taxa is much less than that of aquatic mammals (Hyvärinen, 1995; Dehnhardt et al., 1999). Terrestrial mammals such as rodents, rabbits, cats, and monkeys receive only $\sim$ 200 myelinated axons per F-SC or less (Halata, 1975; Halata and Munger, 1980; Rice et al., 1986, 1997). Myelinated axon counts in aquatic mammals tend to be higher; to date, data are available for Florida manatees (225 axons per U2 bristle) (Reep et al., 2001), certain cetaceans (250–300 axons per vibrissa) (reviewed by Ling, 1977), beavers (*Castor sp*.; 120 axons per vibrissa) (Hyvärinen and Katajisto, 1984), and the Australian water rat (*Hydromys crysogaster*; 500 axons per vibrissa) (Dehnhardt et al., 1999). Although few data are available for pinnipeds, the vibrissal F-SCs of ringed seals are innervated by 1,000–1,500 myelinated axons each. This number is by far the highest innervation investment per F-SC documented to date for any mammal (Hyvärinen, 1995). In addition, F-SCs of ringed seals exhibit an abundance of mechanoreceptors, upon which axons of the deep vibrissal nerve terminate. The number of Merkel-Neurite complexes (MNCs) within a single F-SC of a ringed seal is approximately 10,000 to 20,000; the number of lanceolate endings ranges from 1,000 to 4,000 (Hyvärinen, 1995). In contrast, MNCs and lanceolate mechanoreceptors of terrestrial mammals range from 500 to 2,000 and 20 to 100, respectively, per F-SC (Hyvärinen, 1995). Such data suggest that pinnipeds rely heavily on tactile senses and possess higher vibrissal discrimination abilities than terrestrial taxa. However, among pinnipeds, such quantitative neural data are available only for ringed seals.

Several species-specific differences of F-SCs structure, function, and geometric arrangement on the face are apparent within Pinnipedia. This is particularly true between benthic and nonbenthic foraging species. For example, the mystacial vibrissae of walruses and bearded seals (*Erignathus barbatus*), two benthic foraging pinnipeds, are more numerous than nonbenthic foraging species, and these vibrissae are oriented on the anterior end of a flat, broad muzzle, rather than on the lateral portions of the muzzle (Ling, 1977; Fay, 1982).

Bearded seals are the largest of the arctic phocids. They are solitary, pagophilic seals that inhabit remote regions, where the ice is in constant motion, and therefore their biology is not well known (Burns, 1981; Kovacs, 2002). Their numerous and broadly distributed mystacial vibrissae, for which they are named, are presumably an adaptation for discriminating benthic prey (King, 1983). This assumption seems reasonable given their dietary overlap with walruses, which are known to possess high discriminatory abilities using their vibrissae (Fay, 1982; Kastelein and van Gaalen, 1988; Kastelein et al., 1990). Presumably walrus's and bearded seal's use of vibrissae would be very different from that of ringed seals. However, no data are available to substantiate or refute this hypothesis. We believe that the mystacial vibrissal F-SC array of benthic foraging seals, like bearded seals, are considerably different than those of nonbenthic foraging seals. We hypothesize that the vibrissal F-SC of benthic foraging seals possess an even greater neural investment in terms of the number of myelinated axons per F-SC and to the entire mystacial vibrissal F-SC array due to their benthic foraging niche and potentially strong selection pressures for increased tactile discrimination and other foraging-related behaviors. Therefore, this study investigated the mystacial vibrissal array of bearded seals by characterizing the number and distribution of F-SCs, the F-SC microstructure, innervation pattern, and by quantifying the number of myelinated axons per F-SC and to the entire mystacial array. The type and distribution of mech-

anoreceptors were also characterized at the light microscopy level.

MATERIALS AND METHODS

Specimen Collection

Whole heads (n = 16) and mystacial vibrissal pads (n = 5) of bearded seals were collected from legal hunts in Barrow and Little Diomede Island, Alaska (AK), and in the Svalbard Archipelago, Norway. All material was collected fresh (< 12 hr postmortem) and either frozen or immersed in 10% phosphate-buffered formaldehyde.

Morphometrics, Microstructure, and Innervation

Muzzle height, width, and greatest mystacial vibrissal span were measured from whole heads. The number and location of each mystacial vibrissal were mapped in situ either from whole heads or entire mystacial pads and muzzles that were dissected from heads as a single structure. Lengths and diameters of individual vibrissae were measured with digital vernier calipers.

Mystacial F-SCs were frozen-sectioned in the longitudinal plane and in cross-section using a Lipshaw 80A sliding stage microtome, fitted with a circulating water freezing stage (Physitemp Instruments, Clifton, NJ) at 20–40 μm, on a Micron cryostat at 7–10 μm, or they were infiltrated and embedded in paraffin and sectioned at 7–10 μm on a Leica 2200 RM rotary microtome. A total of 109 F-SCs were histologically processed; 44 longitudinal and 65 cross-sections. Both longitudinal sections and cross-sections were used for microstructural morphometrics, and these sections were chosen based on the orientation of the cut and location of the section (longitudinal: near midline of the axis; cross-sections: midway through the LCS). Sections were stained with hematoxylin and eosin, a modified Masson's trichrome stain, a modified Bodian silver stain, or toluidine blue (Armed Forces Institute of Pathology, 1968, 1994; Reep et al., 2001, 2002). Traditional histocytochemical stains were used because it was not possible to collect samples from remote locations in a manner that would have allowed immunolabeling techniques (e.g., Rice et al., 1997; Ebara et al., 2002). All micrographs were adjusted for brightness and contrast using Adobe Photoshop 7.0.

The following morphometric data were collected from histologically processed longitudinal sections: maximum F-SC length, maximum total sinus length (UCS + RS + LCS), maximum RS width, maximum DC thickness, and maximum hair shaft (HS) diameter at the level of the RS. The following morphometrics were collected from histologically processed cross-sections: maximum diameter of section (including DC), maximum longitudinal axis diameter of HS, maximum perpendicular axis diameter of HS, DC thickness, MS thickness, and collagenous trabeculae (CT) thickness.

F-SC innervation patterns, myelinated axon counts, and mapping of mechanoreceptors were investigated using longitudinal sections and cross-sections stained with a modified Bodian silver stain, toluidine blue, or hematoxylin and eosin. Myelinated axons were identified in cross-sections by their myelinated sheaths and were quantified midway along the length of the LCS. Axons were counted at this location because axon numbers decrease as the DVN ascends toward the RS (Rice et al., 1986). When silver staining was inconsistent throughout a section, axon counts were made on half of the 360° cross-section and subsequently multiplied by two. This is possible due to the uniform distribution of axons around the capsule at this level of section in all species reported (Andres, 1966; Stephens et al., 1973; Ling, 1977; Rice et al., 1986; Dehnhardt et al., 1999; Reep et al., 2001).

RESULTS

Mystacial Vibrissal Pattern, Number, and Gross Morphometrics

Relative to other phocids, bearded seals possess a broad and somewhat anteriorly flattened snout, on which two large arrays of mystacial vibrissae are embedded. In this study, the mean number of mystacial vibrissae was 121.8 ± 5.2 (n = 21) per side, or approximately 244 mystacial vibrissae per seal. The mean number of vibrissal rows was 10.9 ± 1.46 and ranged from 9 to 13. The mean number of columns was 18.1 ± 1.29 and ranged from 17 to 21 (Fig. 1). The HS of mystacial vibrissae was shorter on the rostrodorsal-most portion of the muzzle and became progressively longer at the caudoventral edge of the mystacial pad. The mean HS length of rostral (columns 1–3), middle (columns 8–10), and caudal F-SCs (columns 15–18) were 8.2 ± 3.92, 30.3 ± 9.69, and 81.8 ± 31.5 mm, respectively (n = 11). One specimen possessed a caudal mystacial vibrissa that measured 215 mm in length. The mean minimal HS diameters of rostral, middle, and caudal F-SCs were 2.0 ± 0.05, 5.0 ± 0.09, and 8.0 ± 0.15 mm. The mean maximum in situ vibrissal span (greatest width of mystacial vibrissae) measured from whole heads was 265 ± 0.31 mm.

All mystacial F-SCs extended from the epidermis to the deepest layers of the hypodermis and communicated with the underlying facial musculature. Individual bearded seal F-SCs are large (Fig. 2) and caudal F-SC could be as long as 22 mm (Table 1). Striated muscle fibers originating from the underlying facial musculature were attached to F-SC bases; no arrector pillar muscles were observed. Collagenous connective tissue filled the spaces between all F-SCs of the mystacial pad. Presumably this allows all the vibrissae to be rotated from a resting position (lateral to the face and vibrissae pointing caudally) to an active position in which the caudal vibrissae of the mystacial pad are approximately perpendicular to the long axis of the body, and the rest of the vibrissae creates an increasingly rostral oriented arc from the sides of the face to the nares (Fig. 1D).

F-SC Microstructure

The F-SC was tripartite and composed of several concentric layers of tissue (Fig. 3). It was comprised of an LCS basally, an UCS apically, and an RS located between the two. Collagenous trabeculae of loose connective tissue traversed both the UCS and the LCS, but not the RS. These sinuses were filled with red blood cells (rbc). F-SC morphometric data are summarized in Tables 1 and 2. The mean length of the UCS and LCS was 9.8 ± 1.59 and 5.3 ± 1.59 mm, respectively. The mean length and width of the RS was 2.3 ± 0.53 and 0.7 ± 0.14 mm, respectively. The UCS comprised a mean 56% ± 4.15% of the total F-SC length but was as high as 62.3% in caudal F-SCs (Table 1). The LCS and RS comprised 30.6% ± 3.82% and 13.4% ± 2.45% of the total F-SC length, respectively. The RS was

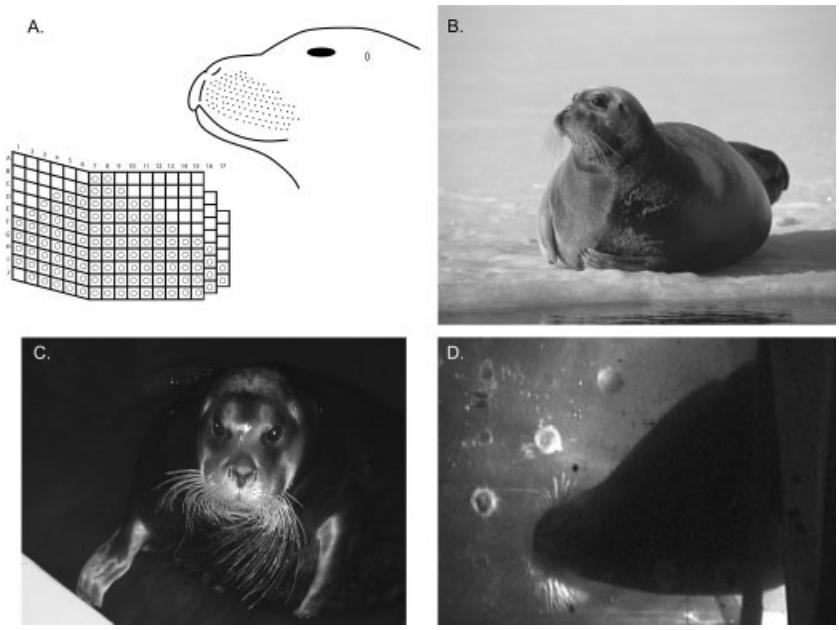

Fig. 1. Bearded seal mystacial vibrissae. **A:** Map of individual F-SCs in the mystacial region and the location of the entire array on the left side of the muzzle in bearded seals. **B** and **C:** Mystacial vibrissal F-SCs in living bearded seals (Svalbard and Polaria, Tromsø, Norway). Note the numerous whiskers and length of caudal HSs. **D:** Silhouette from beneath a bearded seal with mystacial F-SCs in the active mode.

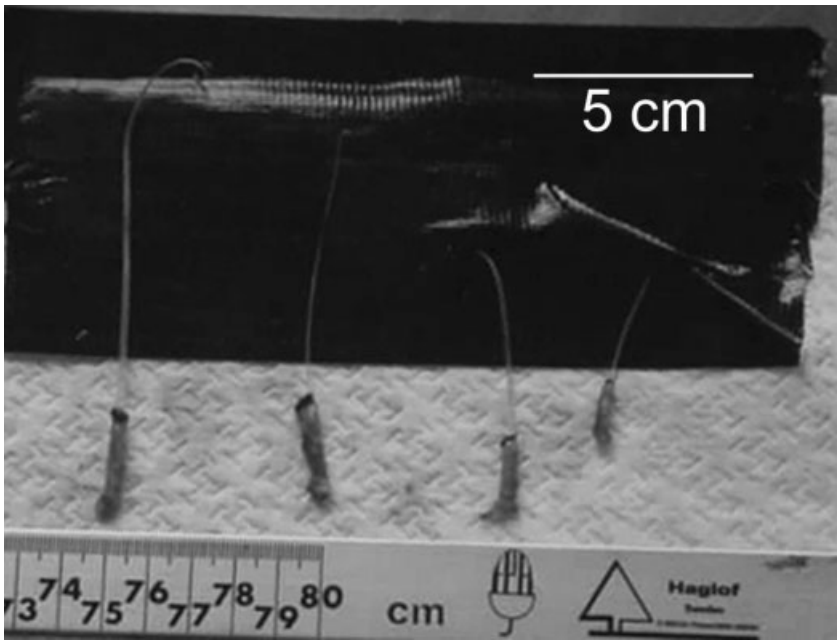

Fig. 2. Examples of individual F-SCs dissected with the HSs intact.

bounded by the inner conical body (ICB) apically, which separated it from the UCS (Figs. 3A and 7A). The dominant feature of this sinus was the large asymmetrical ringwulst (RW), or ringbulge, that protruded into the ring sinus (Figs. 3A and 4A). The tripartite sinus complex was encased by a thick DC that corresponded to the reticular layer of the dermis. It had a mean thickness of 0.4 ± 0.09 mm; at the RS level, $n = 15$). The MS was located deep to the CT along the entire length of the F-SC. A thin glassy membrane (GM), deep to the mesenchymal (MS), separated it from the outer root sheath (ORS). The GM corresponded to the basal lamina deep to the epidermis. Insin-

TABLE 1. Longitudinal F-SC morphometrics

	Mean	S.D.	Minimum	Maximum
Mean Max F-SC Length (mm)	19.1	1.78	15	22
Mean Max. UCS Length (mm)	9.8	1.59	7.0	12
Mean Max. RS Length (mm)	2.3	0.50	1.4	3.0
Total Sinus Length (mm)	17.6	2.14	14	21
Mean Max. LCS Length (mm)	5.3	0.79	4.8	6.3
% UCS Length to Total F-SC Length	56.0	4.15	47.1	62.3
Mean Max. RS Width (mm)	0.7	0.14	0.5	1.0
Mean Max. F-SC Width (cm)	0.4	0.01	0.05	0.03
Mean Max. HS Width (mm)	0.7	0.17	0.4	1.0
Mean Max. DC Thickness (mm)	0.39	0.086	0.3	0.5

N = 15

uating tongues of the GM were found along the entire length of the LSC, RS, and the ICB, but were particularly prominent and deep at the junction between the LSC and the RS. Deep to the ORS was the inner root sheath (IRS), which extended from the hair matrix (hm) to the surface of the skin.

The HS of bearded seals was oval in cross-section (Fig. 3B). The maximal and minimal mean diameters of the HS, near the level of the ring sinus, were 1.1 ± 0.14 (n = 30) and 0.7 ± 0.14 mm (n = 15), respectively (Table 2). The mean ratio of the maximal to minimal diameter of the HS was 1.8 ± 0.25 (n = 15). The HS included epithelial cells that comprised a medulla, cortex, and cuticle. The cortex was composed of keratinized cells, and the cuticle was comprised of a single layer of thin flattened dead keratinized cells (Fig. 3B). The HS was keratinized through the majority of its length. The base of the HS was comprised of the hm and the hair papilla (hp; Fig. 4B and C). The ORS and IRS surrounded both the hm and hp. The hp was connected with the DC by numerous small collagenous fibers (Fig. 4B and C).

Dominant features of the UCS were 2–4 sebaceous glands (Gl) located ~ 4 mm deep to the apical surface the F-SC (Fig. 5). Each gland was bilobed and emptied directly onto the hair shaft. No sweat glands were observed.

F-SC Innervation

The mystacial F-SC of bearded seals appears to be innervated only by the deep vibrissal nerve (DVN; a branch of the infraorbital nerve), whereas in terrestrial taxa, the F-SC is innervated by the DVN basally and the superficial vibrissal nerve (SVN) apically. No fibers of the SVN were observed in any section. In bearded seals, the DVN penetrates the DC at its base, not on the lateral side of the F-SC as in terrestrial taxa (Figs. 4C and 6A). Once inside the LCS, the DVN ramifies into numerous branches that encircle the F-SC and course apically along the junction of the MS and the CT (Fig. 5). The mean number of nerve branches encircling the HS midway through the LCS was 42.4 ± 18 (n = 5). The mean number of myelinated axons at the level of the LCS was 1,314 ± 269.8 and ranged from 811 to 1,650 (n = 5). To determine if innervation was greater in larger F-SCs, the perimeter of the MS and the area of the LCS were measured in the same five cross-sections in which axon counts were conducted. A linear regression analysis found no correlation of number of myelinated axons with MS perimeter ($P = 0.674$) or LCS area ($P = 0.556$).

Branches of the DVN could be seen leaving the nerve bundles to terminate on mechanoreceptors throughout the region of the LCS and in the RS near the ICB (Figs. 6 and 7). Within the LCS, these branches penetrate the MS and GM to terminate on what appear to be the Merkel-Neurite complexes (MNCs; Fig. 7D and E). An occasional small simple laminated corpuscle was observed in the MS of the LCS region, but rarely. When present, these corpuscles possessed only 1–2 laminations. Numerous myelinated axons branched off the DVN within the LCS to terminate in the MS near the GM, presumably as free nerve endings (Fig. 7D). Within the ring sinus and near the ICB, branches of the DVN can be seen terminating on both lanceolate receptors within the MS and numerous MNCs within the ORS (Fig. 7A–C). The shape of the lanceolate receptors was straight, no hooked or bent lanceolate receptors were ever observed. Merkel-Neurite complexes were clear palisades of alternating Merkel touch cells and neurite endings and were the dominant receptors of the RS and the entire F-SC (Fig. 7). No MNCs were observed at a location homologous with a rete ridge collar in the UCS as found terrestrial taxa (Rice et al., 1986). Validation of these receptor types awaits via further investigations of bearded seal F-SCs using electron microscopy.

DISCUSSION

Bearded Seal Mystacial F-SCs

The number of mystacial F-SCs of bearded seals is the highest of any phocid and second only to walruses among all pinnipeds (Mohr, 1950; Yablokov and Klevezal, 1964; Ling, 1968, 1972, 1977; Stephens et al., 1973; Fay, 1982; Hyvärinen and Katajisto, 1984; Hyvärinen, 1989). The number of rows containing F-SCs in bearded seals is comparable to walruses (13–18 rows) (Fay, 1982). The HS of bearded seals was also flat, similar to walruses, without the beaded appearance that is observed in some phocids (e.g., ringed seals) (Hyvärinen and Katajisto, 1984). The ratio of the maximal to the minimal hair shaft diameter of bearded seals is greater than that of walruses (1:8 vs. 1:3 for walruses) (Fay, 1982). However, the maximal values of the base of mystacial F-SCs in walruses (2.2–2.9 mm) (Fay, 1982) were greater than bearded seals (maximum value = 0.9 mm). The maximum length of the HS in this study was 215 mm and was likely an underestimate since the majority of samples were from juveniles. However, this is much greater than the maximal HS length measured in walruses (~ 45 mm) by Fay (1982). The differ-

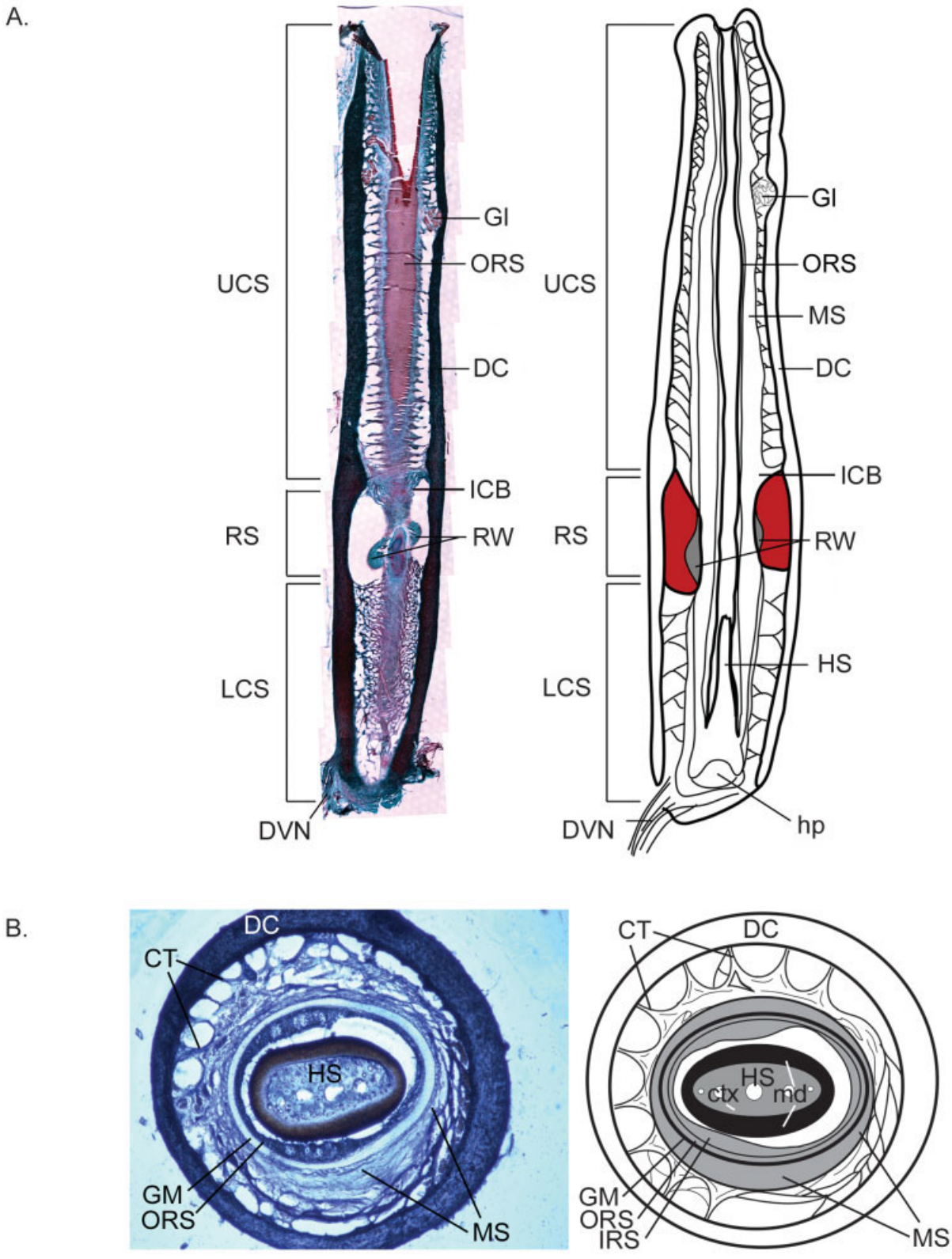

Fig. 3. Microstructure of bearded seal F-SCs. **A:** Longitudinal section and schematic depicting the major regions and tissue layers of the F-SC. **B:** Cross-section and schematic depicting the major regions and tissues layers of the F-SC. Note the cortex and cuticle of the HS.

TABLE 2. Cross-sectional F-SC morphometrics

	Mean	S.D.	Minimum	Maximum
Max. Diameter (mm)	2.9	0.33	2.4	3.7
Mean Longitudinal Axis of HS (mm)	1.1	0.14	1.0	1.5
Mean Perpendicular Axis of HS (mm)	0.7	0.14	0.4	0.9
Mean DC Thickness (mm)	0.3	0.10	0.1	0.4
Ratio HS Diameter	0.6	0.01	0.42	0.8
Mean MS Thickness (mm)	0.2	0.08	0.1	0.3
Mean CT Thickness (mm)	0.4	0.11	0.3	0.6

N = 15

ences in HS morphology alone suggest differences in function between these two benthic foraging pinnipeds

The variation in the number of bearded seal F-SCs, columns, and rows in this study is due to several factors. The first is that specimens were obtained from legal hunts and in some specimens a small portion of the mystacial vibrissal array may have been damaged. The second is that the region of skin between the nares and the upper lip was often abraded and cornified. F-SCs were found in this region in specimens where the skin was not abraded and cornified. Therefore, the mean number of F-SCs reported is likely an underestimate. Such abrasion and cornification also occur in walruses (Fay, 1982). The abrasion pattern on the muzzle of walruses is most severe on the anterior and dorsal portion, and the skin is highly cornified. This suggests that the greatest force is along the upper edge of the snout (Fay, 1982). The different abrasion pattern of the muzzle in some bearded seals suggests that the muzzle is not being used to move sediment, but rather to scan the surface of the sediment. The wide vibrissal span of bearded seals and the orientation of the entire mystacial vibrissal array support this hypothesis.

The absolute length of bearded seal F-SCs was longer than any other mammal reported, although walrus F-SCs are likely longer. F-SC lengths are available for the Australian water rat (6.3 mm), domestic guinea pig (3.6 mm), laboratory rat (4.0 mm), domestic cat (5.5 mm) (Dehnhardt et al., 1999), large cats, including lynx (*Lynx lynx*; 5.6 mm), and leopard (*Panthera pardus*; 6.5 mm) (Dehnhardt et al., 1999), as well as two small aquatic mammals, the coypu (*Myocastor coypus*; 6.9 mm) and the river otter (*Lutra lutra*; 7.1 mm) (Dehnhardt et al., 1999). Among marine mammals, the F-SC lengths of mysticetes (baleen whales) are reported to range from 5 to 30 mm (Ling, 1977), Florida manatees perioral bristles range from 3.51 to 18.2 mm (Reep et al., 2001), Ross seals up to 18 mm (Ling, 1972), and ringed seals up to 20 mm (Hyvärinen, 1989). F-SC follicle length appears to scale to body size among terrestrial taxa, but among aquatic mammals, functional requirements might supercede such scaling effects (Dehnhardt et al., 1999).

Bearded Seal F-SC Microstructure

Other than differences in the length of the UCS, the vibrissal F-SC microstructure of bearded seals was generally similar to that of other pinnipeds, for which data are available (Ling, 1968, 1972; Stephens et al., 1973; Hyvärinen and Katajisto, 1984; Hyvärinen, 1989). The mean length of the UCS of bearded seals is similar to ringed seals (60% of the total F-SC length) (Hyvärinen and Katajisto, 1984; Hyvärinen, 1989, 1995) and the UCS length of caudal F-SCs (62%) exceeded that of ringed seals. One functional hypothesis for the elongated UCS is thermal protection of the underlying mechanoreceptors within the RS and LCS tissues. The lack of innervation of the UCS by a SVN supports this hypothesis. The UCS of southern elephant seals is reported to be 40% of the total follicular length (Ling, 1968). Further comparisons with other pinnipeds cannot be made due to the lack of microstructural data. However, true functional differences of sensory capability within Pinnipedia likely lie in differences in patterns of innervation, innervation investment (numbers of axons/F-SC and total number of axons to mystacial F-SC array), and in the diversity, number, and distribution of mechanoreceptors.

No sweat glands were observed in any of the 109 F-SCs examined. This may be due to the method of sample processing since not much of the surrounding tissue was processed except for the apical end, where the hair shaft left the surface of the skin. However, sweat glands in phocids are reported to occur within the UCS, basal to the sebaceous glands, which is an unusual condition in mammals and proposed to have taxonomic significance (Ling, 1965, 1972). Sebaceous glands were observed within the DC in most sections. If present within the UCS, merocrine sweat glands should have been observed. We conclude that sweat glands are not located in the F-SC of bearded seals and are likely restricted to the hairy skin adjacent to the F-SCs.

Bearded Seal F-SC Innervation

The mean number of myelinated axons was greater in bearded seals than in ringed seals (Hyvärinen, 1995), and for any other mammal reported to date (e.g., Lee and Woolsey, 1975; Ling, 1977; Halata and Munger, 1980; Hyvärinen and Katajisto, 1984; Rice et al., 1986; Marotte et al., 1992; Halata, 1993; Rice et al., 1997; Dehnhardt et al., 1999; Reep et al., 2001). However, the range of myelinated axons/F-SCs in bearded seals overlaps that of ringed seals, and it is unclear whether the greater mean number of axons/F-SC in bearded seals represents a significant functional difference between the two. Psychophysical experiments that compare the haptic sense of bearded seals and ringed seals would help in identifying the functional significance in innervation and behavioral differences between these two species. Therefore, the data presented here do not support our initial hypothesis that benthic foraging pinnipeds possess a greater number of myelinated axons per F-SC. However, our data do support Dehnhardt et al.'s (1999) hypothesis that an aquatic or amphibious lifestyle results in a greater innervation of

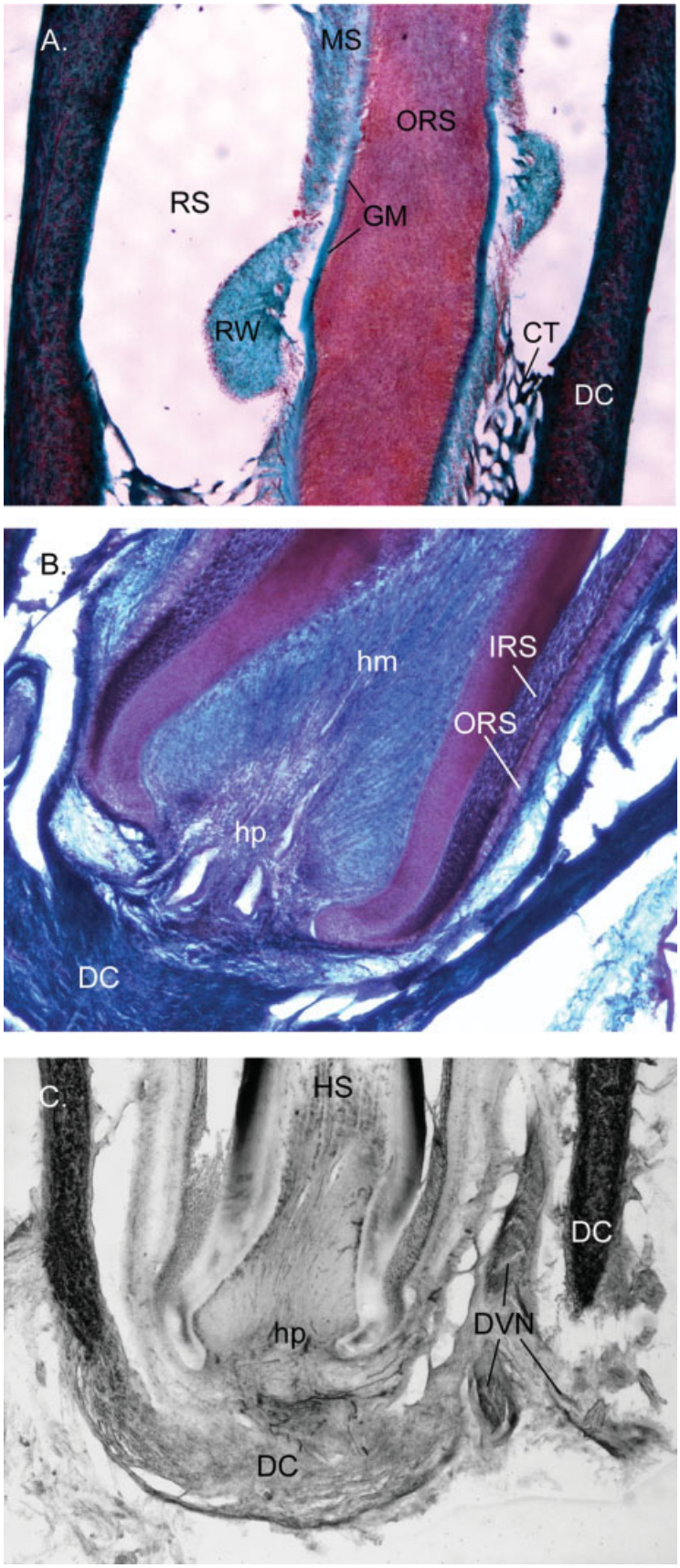

Fig. 4. Specialized structures within the F-SC. **A:** Micrograph depicting the RW within the RS (Masson's trichrome). **B:** Base of the F-SC depicting the hm and hp in relation to the DC, ORS, and the IRS. Note the extent of keratinized hair (Masson's trichrome). **C:** Base of the F-SC showing the penetration of the DC by the DVN (modified Bodian silver stain).

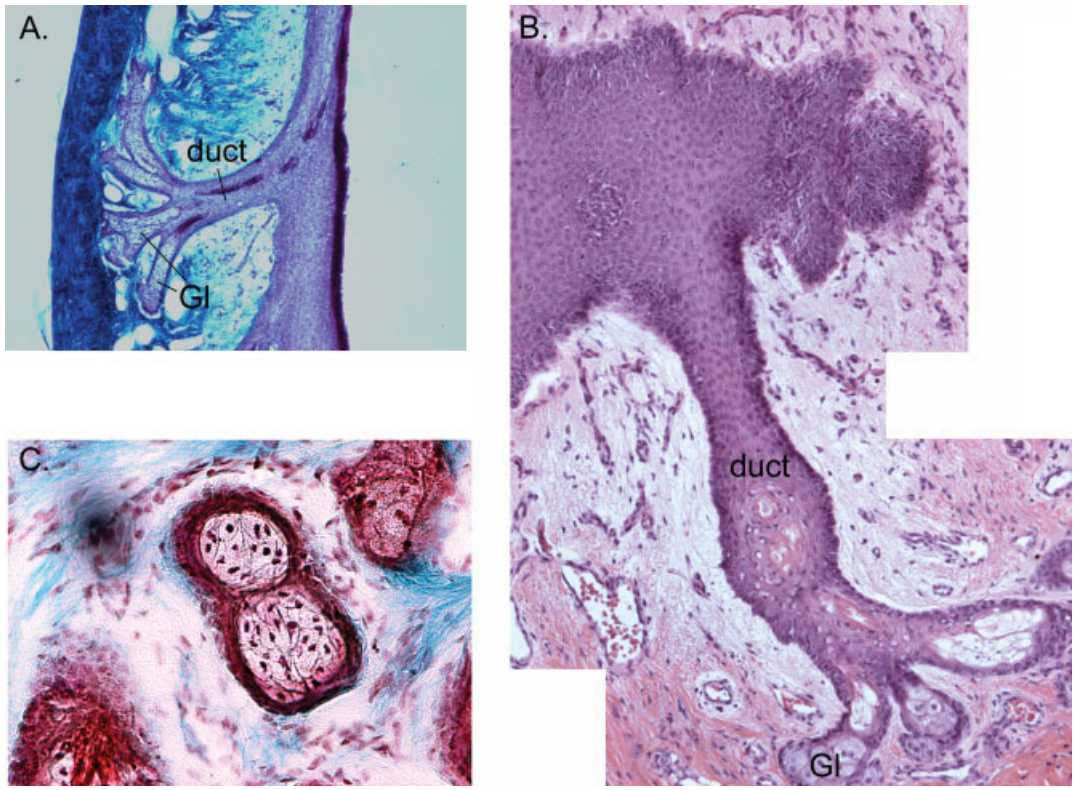

Fig. 5. Sebaceous glands of the upper cavernosal sinus. **A:** Low-power micrograph of an entire sebaceous gland including the tubular component that connects the gland to the HS space (Masson's trichrome). **B:** Composite of several micrographs depicting the main duct of a group of sebaceous glands emptying into the HS space (hematoxylin and eosin). **C:** Micrograph depicting the cellular composition of the sebaceous glands (Masson's trichrome).

vibrissal systems through increased myelinated axons per F-SC.

There are two factors to consider regarding the functional significance of mystacial F-SC innervation, the inherent neural properties of each F-SC and the geometry (and number) of F-SCs in the mystacial region. The inherent neural properties of each F-SC include the number of myelinated axons per F-SC, the branching of myelinated axons, the number and density of mechanoreceptors, the diversity and distribution of mechanoreceptors, and the correspondence of the number of myelinated axons to the number of mechanoreceptors. All of these properties are likely related to the sensitivity and function of each individual F-SC. Unfortunately, our poor understanding of the physiology of F-SCs and mechanoreceptors, as well as the lack of comparative neural F-SC data, hampers our understanding of the importance of these properties. However, it is likely the second factor, the geometry and number of mystacial F-SCs, is most important to discriminatory ability and function of the mystacial F-SC array. This is particularly true for benthic versus non-benthic foraging pinnipeds. Predominately benthic foraging pinnipeds, such as bearded seals and walruses, possess a broad and anteriorly flattened snout (bearded seals less so than walruses). Mystacial F-SCs in these species are more numerous and are arranged across the muzzle facing forward instead of laterally as in relatively non-benthic foraging pinnipeds. In contrast, the laterally oriented mystacial F-SCs of harbor seals are probably optimal for hydrodynamic trail following. The geometric distribution of mystacial F-SCs among pinnipeds likely helps to shape its function.

In addition, the increase in the number of F-SCs in benthic foraging pinnipeds has important consequences for tactile discriminatory abilities. For example, although bearded seals and ringed seals have similar number of myelinated axons per F-SC, the numerous mystacial F-SCs in bearded seals translate to a mean of 320,616 myelinated axons innervating the entire mystacial vibrissal array (range, 197,884–402,600 axons). This is 1.94 times greater than ringed seals (Hyvärinen, 1995) and overshadows any slight increase in axons/F-SC that bearded seals may exhibit compared to ringed seals. Even at the high end of the range of the number of axons per vibrissal F-SC for ringed seals (1,500) and a reported 132 mystacial F-SCs (Ling, 1972), the number of myelinated axons innervating the entire mystacial vibrissal array of ringed seals is 198,000, just overlapping the minimal value for bearded seals. Among phocids, ringed seals possess the second highest number of vibrissal F-SC, next to bearded seals. Unfortunately, data regarding vibrissal F-SC innervation (and microstructure) for other pinniped species are limited. Such data exist for only one other pinniped species, the harp seal *Phoca groenlandica*, which has 40–290 myelinated axons innervating each F-SC. Harp seals possess 90–98 mystacial vibrissae (Ling, 1972) and therefore

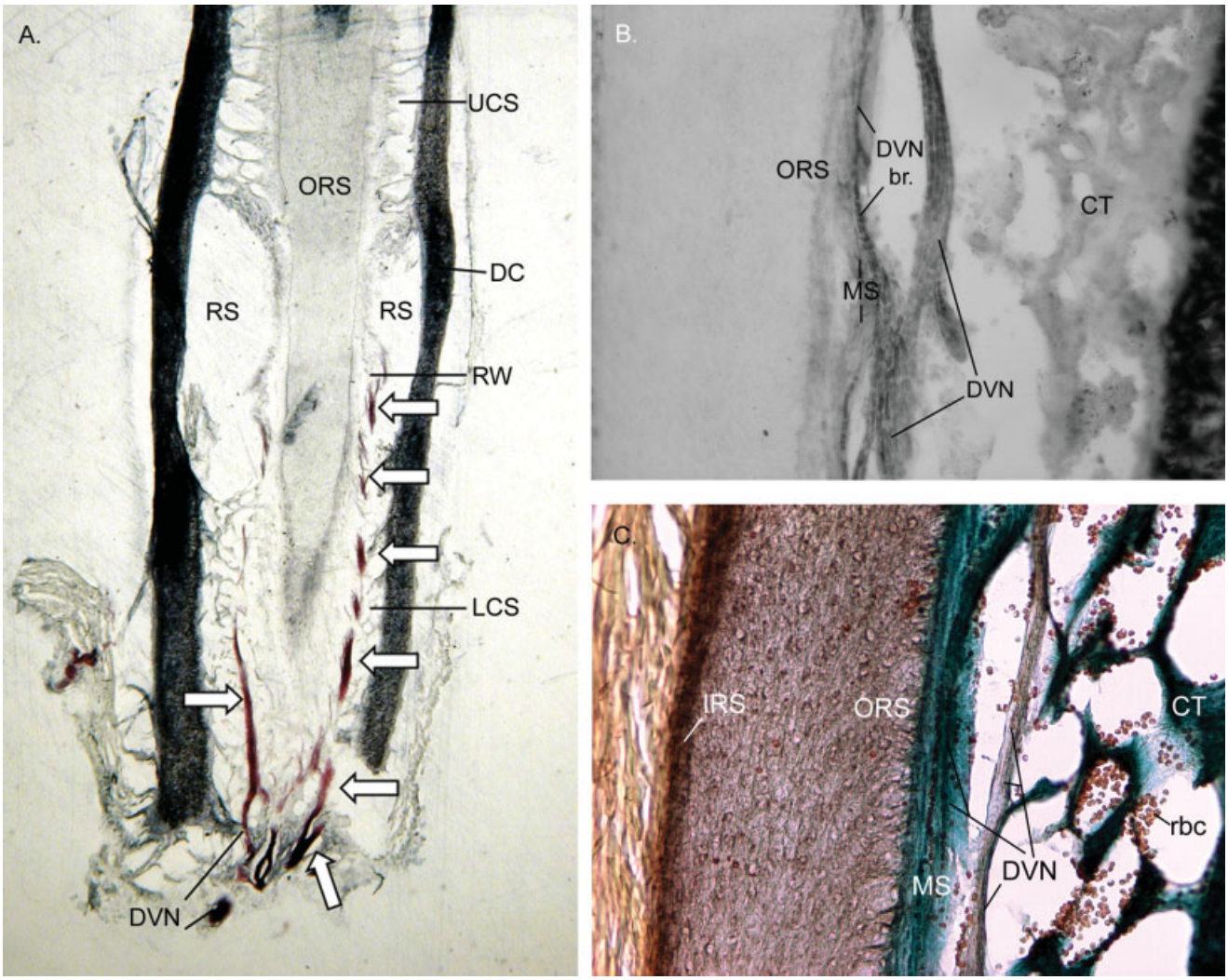

Fig. 6. Course of the deep vibrissal nerve. **A:** Bodian silver stain depicting the entire course of the DVN from the penetration of the base of the DC to the innervation of the RW and associated regions. **B** and **C:** Branches of the DVN within the LCS region (modified Bodian and Masson's trichrome).

would have a maximum number of 28,420 myelinated axons innervating the entire mystacial vibrissal array. All other phocids have far fewer vibrissal F-SCs and therefore far less innervation investment to the mystacial array, assuming that the number of myelinated axons/F-SCs are the same. It is probable that the mystacial array of walruses, due to their high number of F-SCs relative to other pinnipeds, will possess the greatest investment of innervation to the mystacial vibrissal array of any mammal. For example, if the mean number of myelinated axons innervating a single walrus F-SC were 1,000 (likely an underestimate), then the minimal number of myelinated axons innervating the mystacial vibrissal array would be at least 600,000. The increased innervation to the entire mystacial F-SC in bearded seals and likely walruses supports our hypothesis that benthic foraging pinnipeds require increased tactile discriminatory capabilities, which is accomplished by a high number of myelinated axons per F-SC (relative to terrestrial taxa) and an increase in the number of F-SCs.

The total number of bearded seal mystacial F-SCs is similar to the number of perioral bristles in Florida manatees (Reep et al., 1998). However, all hairs on manatees are vibrissal F-SCs and the facial region possesses approximately 2,000 F-SCs (Reep et al., 1998). In spite of the large number of manatee F-SCs, the mean number of myelinated axons innervating just the mystacial vibrissal array of bearded seals is 2.9 times greater than in the entire facial region of Florida manatees (Reep et al., 2001). Although most terrestrial species possess few F-SCs and in general each F-SC is innervated by fewer myelinated axons, the Australian water rat is an exception. This semiaquatic murid rodent hunts in freshwater lakes and rivers, and in marine beach areas for fish, crustaceans, and mollusks (McNally, 1960) using its mystacial vibrissae exclusively for detecting prey (Dehnhardt et al., 1999). Australian water rats possess 170 mystacial F-SCs, each innervated by a mean number of 537 myelinated axons (Dehnhardt et al., 1999). Therefore, the estimated mean number of myelinated axons to the entire mystacial array

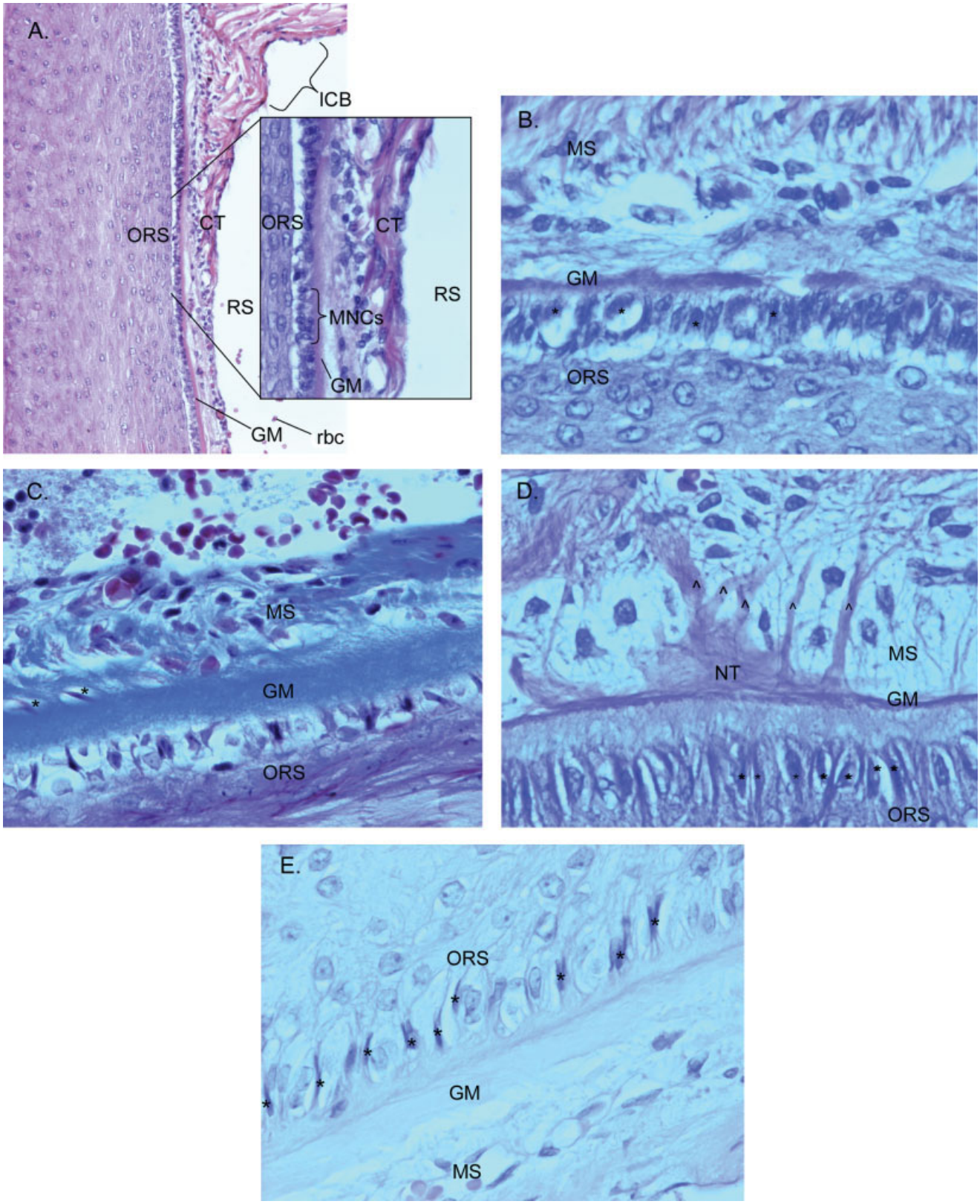

Fig. 7. Mechanoreceptors of the F-SC (all figures are stained with H&E). **A:** Distribution of MNCs in the RS near the ICB. The inset is a close-up view of the MNCs between the GM and the ORS. **B:** Close-up of MNCs in the RS near the ICB. Asterisks indicate Merkel touch cells and adjacent neurites. **C:** Lanceolate and MNCs of the RS. Note the adjacent location of the lanceolate receptors (indicated by asterisks) in the MS relative to the MNCs in the ORS, with only the GM separating the two. **D:** Nerve tuft and presumable MNCs of the LCS region. Note individual fiber bundles (indicated by carets) accumulating near the GM as a large nerve tuft (NT); asterisks indicate mechanoreceptors in the ORS. **E:** Presumptive MNCs of the LCS region. Asterisks depict mechanoreceptors within the ORS. Note the adjacent neurites.

would be 91,290, or 3.2 times greater than for harp seals. Life history data for Australian water rats describe their aquatic foraging behavior as benthic. Even among aquatic mammals there is a lot of variation in form, number, and distribution of F-SCs and the amount of innervation to these sensory structures.

The three types of mechanoreceptors receptors observed in the F-SCs of bearded seals correspond to the type I (free nerve ending and MNCs) and type II [lanceolate and simple encapsulated (paciniform) corpuscles] receptors described in detail by Halata (1975). The Merkel cell structure within F-SCs is similar to that of glabrous skin (Halata, 1975) and their function is among the best known of mechanoreceptors. They are type I slowly adapting mechanoreceptors (Iggo, 1963, 1966; Munger et al., 1971) that detect compression stimuli (Andres, 1966; Johansson et al., 1982a, 1982b; Johansson and Vallbo, 1983). A remarkable finding in this study is the observation of receptors resembling MNCs in the region of the LCS in addition to the ICB region of the RS. This is surprising since MNCs have only been documented in the RS near the ICB, and in many terrestrial species in the rete ridge collar area at the apex of the F-SC (Andres, 1966; Stephens et al., 1973; Hyvärinen and Katajisto, 1984; Rice et al., 1986; Hyvärinen, 1989, 1995). However, myelinated nerves can be seen penetrating the GM to terminate on receptors in the region of the LCS of bearded seals. MNCs were not found at the most apical region (rete collar) of the F-SC. Electron microscopy investigations of these receptors are needed to validate that these structures are indeed MNCs. It is possible that MNCs of the RS and the LCS region in bearded seals act as a deeper dual system, as do the MNCs of the rete ridge collar and the RS described by Rice et al. (1986). A deeper location of mechanoreceptors supports the hypothesis that the UCS serves to insulate these receptors.

Small and simple laminated corpuscles were observed within the MS of the LCS. These receptors were similar to paciniform corpuscles (sensu Halata, 1975), which are rapidly adapting nerve fibers that detect velocity (Schmidt, 1971). Paciniform corpuscles are similar to the type III Vater-Pacini corpuscles (sensu Halata, 1975), which are larger, possess more lamellae, and function to detect acceleration instead (Schmidt, 1971). Numerous branches of the DVN were observed within the MS near the GM and are presumably free nerve endings. The function of such structures is not currently known, but they likely serve to detect stretching and compression of the MS due to bending of the HS. The HS of bearded seals is keratinized along almost the entire length and therefore could translate bending moments from the individual's periphery to the deep portions of the LCS region.

Lanceolate mechanoreceptors are a specialized type of dendritic bulboid nerve ending (type II) (Halata, 1975). Some studies indicate that lanceolate endings are rapidly adapting stretch receptors (Tuckett, 1978; Tuckett et al., 1978). Rice et al. (1986) hypothesized that the lanceolate ending, in conjunction with the MS, RS, and RW, "constitute an integrated accessory structure that interacts with the lanceolate endings in order to encode dynamic properties of vibrissal deflection such as acceleration and deceleration." Although mechanoreceptors were not counted, qualitatively lanceolate receptors in bearded seals were fewer than described for California sea lions or ringed seals (Stephens et al., 1973; Hyvärinen and Katajisto, 1984; Hyvärinen, 1989). The functional significance in the fewer number of lanceolate receptors in bearded seals could mean that detection of acceleration and deceleration of the HS is not as important as angular deflections that Merkel-Neurite complexes could detect.

Overall, the number of mystacial F-SCs, the high number of myelinated axons innervating each F-SC, and the type and distribution of the mechanoreceptors in the mystacial vibrissae of bearded seals support the premise that pinniped mystacial vibrissae are sensitive active-touch receptor systems. We hypothesize that the high number of mystacial F-SCs, their geometry, the high number of myelinated axons per F-SC, and the derived distribution of MNCs in bearded seal mystacial vibrissae are adaptations for a benthic foraging niche. Further investigations involving electron microscopy and immunofluorescent labeling will provide further insight into the structure, distribution, and function of the F-SC mechanoreceptors of bearded seals.

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