Original Paper

Brain, Behavior and Evolution

Brain Behav Evol 2002;59:141–154

Received: January 10, 2002
Returned for revision: February 25, 2002
Accepted after revision: March 20, 2002

Tactile Hairs on the Postcranial Body in Florida Manatees: A Mammalian Lateral Line?

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Key Words
Sirenia · Manatee · Vibrissae · Hair · Lateral line · Mammal

Abstract

Previous reports have suggested that the sparsely distributed hairs found on the entire postcranial body of sirenians are all sinus type tactile hairs. This would represent a unique arrangement because no other mammal has been reported to possess tactile hairs except on restricted regions of the body, primarily the face. In order to investigate this issue further, hair counts were made systematically in three Florida manatees *(Trichechus manatus latirostris)*, and hair follicle microanatomy was studied in 110 specimens gathered from 9 animals. We found that the postcranial body possesses approximately 1500 hairs per side, and hair density decreases from dorsal to ventral. External hair length ranged from 2–9 mm, and most hairs were separated from their nearest neighbor by 20–40 mm, resulting in an independent domain of movement for each hair. All hairs exhibited the anatomical characteristics of follicle-sinus complexes typical of tactile hairs, including a dense connective tissue capsule containing an elongated circumferential blood sinus and innervation by 20–50 axons which ascend the mesenchymal sheath. We conclude that this represents a unique distributed underwater tactile system capable of conveying detailed and significant external information concerning approaching animals, water currents and possibly the presence of large stationary features of the environment. Such a system would be analogous to the lateral line in fish, and would be particularly useful in the turbid habitat frequented by Florida manatees.

Introduction

Mammalian hair exhibits many elaborate and interesting variations including increased density related to thermoregulation, specialization as quills, spines and vibrissae, and in some cases reductions associated with aquatic, fossorial or armored existence. All mammals possess hair of some kind during at least a portion of their ontogeny. Of particular interest in the present context are vibrissae, or tactile hairs, and their distribution in aquatic mammals. Vibrissae are known to provide detailed textural information about surfaces and objects in the immediate environment [Dykes, 1975; Brecht et al., 1997]. Vibrissal

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follicles are referred to as follicle-sinus complexes (F-SCs) or sinus hairs because of their specialized structural features [Rice et al., 1986]. Terrestrial mammals possess vibrissae on restricted regions of the body, most notably the face [Eisenberg, 1981].

Among aquatic mammals there is great variation in hair distribution. Baleen whales possess vibrissae on the head, but in most odontocetes hair is present only as prenatal sinus hairs that atrophy prior to birth, leading to a completely hairless condition postnatally [Ling, 1977]. An important exception is freshwater river dolphins (Platanistidae), that exhibit reduced visual systems and well developed bristle-like vibrissae along the upper and lower jaws. These vibrissae are reportedly used to detect fish and crustacean prey along river bottoms [Norman and Fraser, 1948, cited in Ling, 1977; Layne and Caldwell, 1964]. Among pinnipeds, in addition to dense pelage hair covering the body, elaborate vibrissae are found on the face [Ling, 1977; Mauck et al., 2000] and these are used in tactile exploration and a wide variety of social displays [Peterson and Bartholomew, 1967; Miller, 1975; Kastelein and Van Gaalen, 1988; Dehnhardt, 1994; Dehnhardt and Kaminski, 1995; Dehnhardt and Ducker, 1996]. Recently it has been shown that harbor seals can use their facial vibrissae to detect water movements associated with prey [Dehnhardt et al., 1998; 2001]. All sirenians possess sparse hair on the body. The facial bristles and hairs are used not only for tactile exploration and discrimination [Marshall et al., 1998; Bachteler and Dehnhardt, 1999] but also for oripulatory grasping of plants during feeding [Marshall et al., 1998; 2000]. Recently, we reported that all the hairs and bristles in the facial region of the Florida manatee are modified vibrissae associated with F-SCs having substantial innervation [Reep et al., 2001]. Dosch [1915] reported that all hairs on the bodies of sirenians were sinus hairs. This conclusion has been supported in dugongs by the findings of Bryden et al. [1978] and Kamiya and Yamasaki [1981], and in Antillean manatees *(T. manatus manatus)* by Sokolov [1986]. The presence of vibrissae on the entire body would provide sirenians with a distributed tactile system potentially capable of detecting and localizing water displacements associated with significant environmental stimuli, analogous to the lateral line system in fish.

In no sirenian has there been a systematic study of hair on the postcranial body. Variations in hair length and diameter, follicle structure, and follicle innervation patterns are parameters thought to be important determinants of the response properties of single F-SCs to hair displacement [Woolsey et al., 1981; Rice et al., 1986]. Therefore, we proposed to map the distribution of hair on the postcranial body and to systematically investigate the microanatomical structure of the follicles of these hairs, including their innervation.

Materials and Methods

Hair counts were made on three fresh postmortem Florida manatees *(Trichechus manatus latirostris)*: MSE 9807, a 321 kg female, length 250 cm, that died as a result of watercraft impact; MEC 9903, a 300 kg male, length 257 cm, that apparently died of natural causes; and MEC 9952, a 123 kg female, length 171 cm that died from human-related causes. The first two of these carcasses were in the subadult range of body length, corresponding to 1.5–4 years of age, and the third carcass was a small calf of 1–6 months age, according to criteria developed by the USGS Sirenia Project (unpublished data). Hair counts were made at the Florida Department of Environmental Protection Marine Mammal Pathobiology Laboratory in St. Petersburg, Fla., USA. The right side of the postcranial body was divided into 24 regions (fig. 1), including 20 on the main body, 2 on the tail and 2 on the pectoral flipper, and the boundaries of these regions were marked with a grease pencil. The dorsal-most boundary corresponded to the dorsal midline, and the ventral-most boundary corresponded to the ventral midline. The longitudinal boundary line separating regions 1–5 from 7–11 was equidistant between the dorsal and ventral boundaries. The dorsal and ventral sectors so defined were further subdivided into a and b regions. A series of six dorsoventral boundary lines was demarcated. The most cranial of these was placed a few cm caudal to the eye, where a prominent skin crease denotes the boundary between the neck and caudal body. Similarly, the caudal margin was located at the base of the fluke along a prominent crease. Four additional dorsoventral boundary lines were spaced equally between these cranial and caudal margins.

Hair follicles were counted independently in each region by two observers and the area of each region was computed in order to derive estimates of hair density on a regional basis. Follicles without external hairs were visible as papillae, and were also included in these counts. In specimen MEC 9952 we were unable to obtain counts from regions 7b and 8b due to surface damage. Also, counts were not made on the tail in this specimen. Hair lengths and interhair distance were also measured on a regional basis in specimens MSE 9807 and MEC 9903, using random sampling within each region. Hairs and bristles on the head were counted in multiple specimens and these data were reported previously [Reep et al., 1998].

A total of 110 follicles were analyzed histologically in this study. They were collected from 9 fresh (w/in 24 h) postmortem manatee carcasses (table 1), in conjunction with the statewide manatee carcass salvage program managed by the Marine Mammal Pathobiology Laboratory in St. Petersburg, Fla., USA (Permit PRT-684532). By the criteria mentioned above, 7 of these carcasses were from the subadult-adult age classes, whereas 2 were small calves. In cases MSE 9807, MEC 9903 and MEC 9952, collections were made from regions defined by the grid procedure described above. For follicles taken from the other carcasses we estimated their regional location by visual inspection, and consequently these are designated more generally. For example, region 10/11 indicates a follicle located in the ventral portion of the body immediately cranial to the fluke.

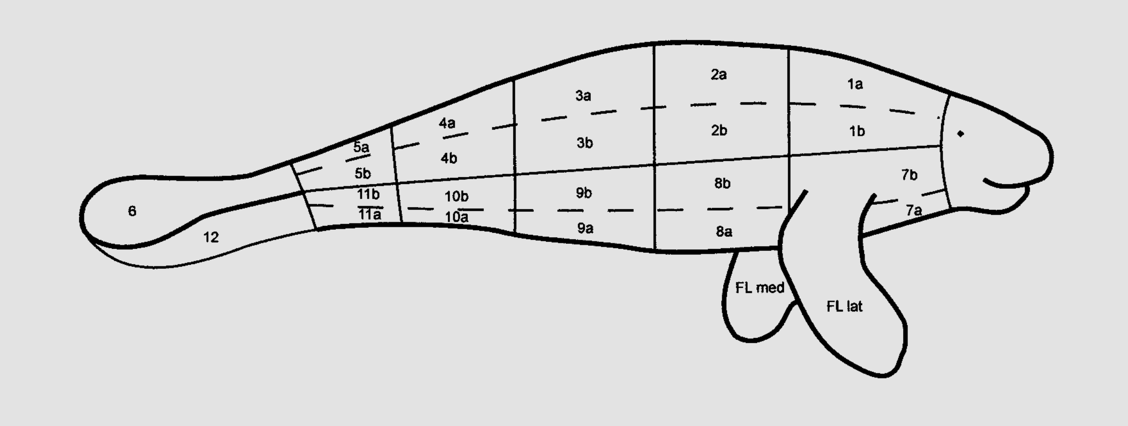


Fig. 1. Scheme by which the bodies of three postmortem manatees were subdivided in order to make regional counts of hairs. Regions 1-5a abut the dorsal midline; regions 7-11a abut the ventral midline.

Table 1. Source of 110 follicle samples taken from nine specimens

Animal specimen number	Sex	Weight kg	Length cm	Age class	Dorsal anterior (reg. 1)	Ventral anterior (reg. 7)	Dorsal mid (reg. 2–3)	Ventral mid (reg. 8–9)	Dorsal posterior (reg. 4–5)	Ventral posterior (reg. 10–11)	Dorsal fluke (reg. 6)	Ventral fluke (reg. 12)	Lateral flipper	Medial flipper
MNW 9425	M	458	301	adult	1	1	0	0	0	0	0	0	0	0
SWFTM 9515	M	31	119	small calf	2	0	0	0	0	0	0	0	0	0
SWFTM 9534	M	370	267	adult	2	0	2	0	0	0	2	0	2	4
SWFTM 9607	M	387	278	adult	6	2	0	4	2	2	0	3	0	0
MSE 9807	F	321	250	subadult	1	2	1	1	1	1	1	1	2	0
MEC 9903	M	300	257	subadult	2	3	7	8	7	7	1	1	2	2
MEC 9952	F	121	171	small calf	0	0	0	2	5	2	0	0	0	2
HS 8701	F	457	352	adult	0	0	0	1	2	6	0	0	0	0
MNW 0020	F	346	347	adult	0	0	0	1	1	2	0	0	0	0

Follicle specimens were collected and processed using procedures described previously [Reep et al., 2001]. Longitudinal sections were used for measurements of follicle morphology and to identify deep vibrissal nerve bundles and their trajectories. In 31 longitudinal sections oriented as closely as possible to the central longitudinal axis of the hair shaft, we measured maximum follicle length, maximum total sinus length, maximum sinus width, maximum follicle capsule thickness, and hair shaft diameter at the midpoint of the length of the follicle. These measurements were made on an AIS/C imaging workstation (Imaging Research, Inc.) interfaced with a Zeiss Axiophot 2 microscope and Dage 72 video camera. The left and right sides of each section were measured, and we retained only the maximum values. Twenty-six cross-sections were used for counting the number of axons innervating a follicle, using methods described previously [Reep et al., 2001].

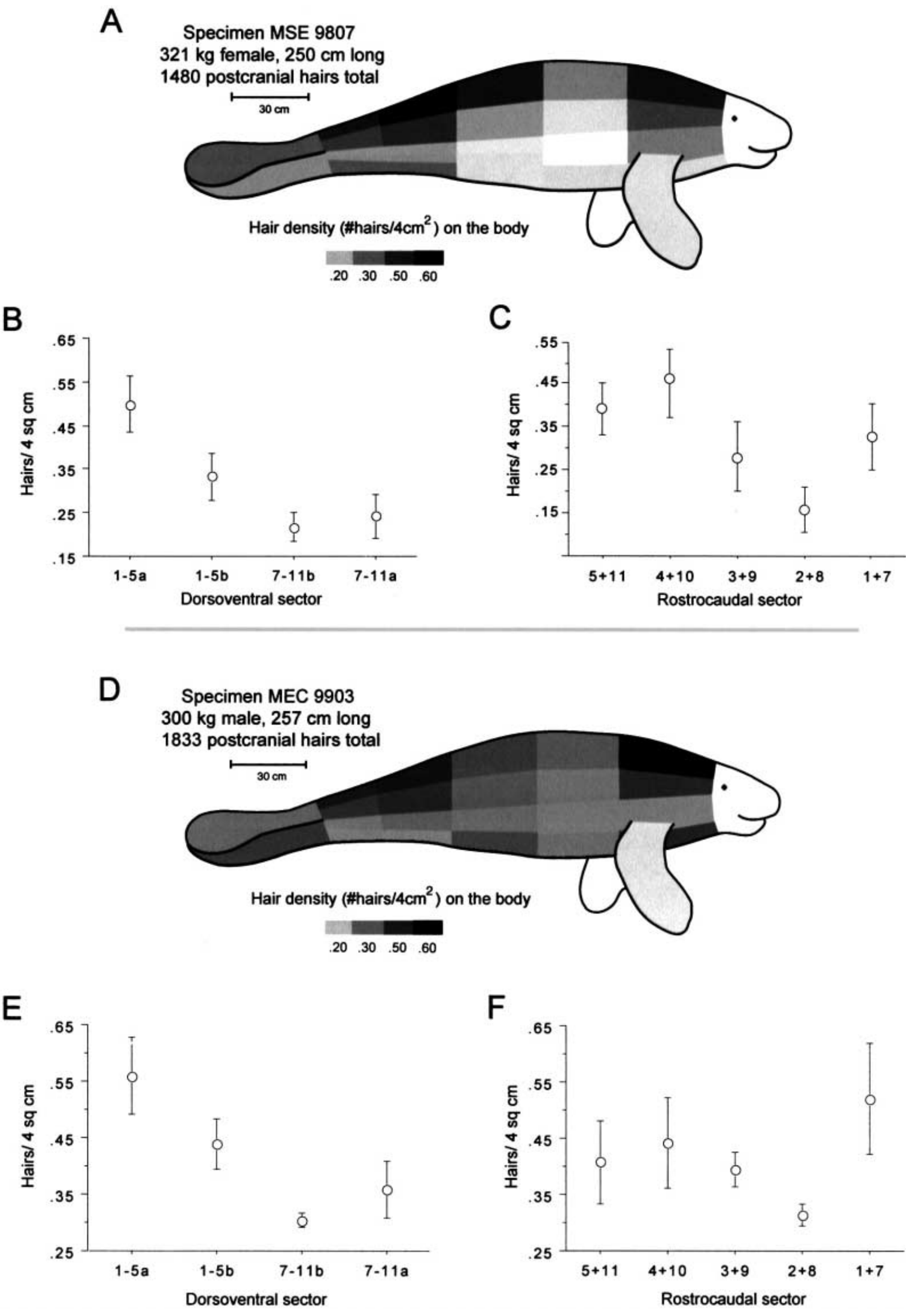
Statistical tests were performed using Statview software (SAS Institute, Inc.). Analysis of variance resulting in significant main effects were followed by post-hoc tests using Fisher's protected least significant difference test.

Results

Hair Distribution

The total number of hairs on the right side of the postcranial body for the two subadult specimens was 1480 for specimen MSE 9807 and 1833 for specimen MEC 9903. Hair was distributed as shown in figure 2A and D.

There was a dorsoventral gradient in hair density in both subadult specimens, as shown in figures 2B and E. Case MSE 9807 exhibited a steady decrease in density from dorsal to ventral, and analysis of variance revealed a significant trend by region ($F_{3,16} = 5.98$, $p < 0.01$). Subsequent post-hoc tests indicated significant differences at $p < 0.04$ between region 1–5a and the other regions. Regions 1–5b, 7–11b and 7–11a did not differ significantly from each other. Case MEC 9903 exhibited a similar


A
Specimen MSE 9807
321 kg female, 250 cm long
1480 postcranial hairs total
30 cm
Hair density (#hairs/4cm²) on the body
.20 .30 .50 .60
B
Hairs/ 4 sq cm
.65
.55
.45
.35
.25
.15
1-5a
1-5b
7-11b
7-11a
Dorsoventral sector
C
Hairs/ 4 sq cm
.55
.45
.35
.25
.15
5+11
4+10
3+9
2+8
1+7
Rostrocaudal sector
D
Specimen MEC 9903
300 kg male, 257 cm long
1833 postcranial hairs total
30 cm
Hair density (#hairs/4cm²) on the body
.20 .30 .50 .60
E
Hairs/ 4 sq cm
.65
.55
.45
.35
.25
1-5a
1-5b
7-11b
7-11a
Dorsoventral sector
F
Hairs/ 4 sq cm
.65
.55
.45
.35
.25
5+11
4+10
3+9
2+8
1+7
Rostrocaudal sector

dorsoventral trend (F3, 16 = 5.31, $p < 0.01$). Post-hoc tests indicated that region 1–5a differed significantly ($p < 0.01$) from regions 7–11a and 7–11b. The range of mean hair density within the four dorsoventral sectors was similar in both specimens, between 0.2–0.6 hairs/4 cm^2.

In both subadult specimens the expanded mid-region of the body (regions 2,3,8 and 9) appears to exhibit somewhat lower hair density than the regions more rostral and caudal (fig. 2A and D). Although this visual impression was not supported by analysis of variance in either case, the distribution of hair in the small calf specimen MEC 9952 is suggestive in this regard (fig. 3). The half-girth measurements shown in figure 3 indicate how the middle portion of the body is unexpanded in MEC 9952 compared with subadult cases MSE 9807 and MEC 9903. Total hair number for the regions counted in MEC 9952 was 900, compared to 1103 for the comparable regions in specimen MSE 9807 and 1283 in MEC 9903. Compared to the subadult cases, this calf exhibited much greater hair density in all regions, and hair density in the relatively unexpanded mid-body region did not appear to be different than in the other regions. This was confirmed by the finding that ANOVA and post-hoc tests revealed no significant density differences among rostrocaudal or dorsoventral regions. The greater density of hair in the calf MEC 9952 is undoubtedly associated with its small body size, because mammals are generally born with a fixed number of follicles and thus hair density decreases with growth [Szabo, 1958; Scheffer, 1964].

In the above analyses, hair density was assessed as a single value for each region sampled, by computing the number of hairs per unit area per region. However, we also wished to determine the extent of variation in density within regions. This was done by sampling interhair distances in each region of the subadult specimens MSE 9807 and MEC 9903 (fig. 4). In case MSE 9807 interhair distances ranged from 2–55 mm, with most values between 20–40 mm. Except for region 5 (SE = 0.68), standard errors were all in the range of 1.2–1.9 mm. In MEC 9903 the range in interhair distance was similar at 15–42 mm, with most values between 20–35 mm. Standard errors ranged from 2.7–6.5 mm. These data suggest that interhair spacing is relatively uniform both within and between individuals of similar size.

Fig. 2. Pattern of hair distribution in subadult specimens MSE 9807 and MEC 9903. A, D Hair density by region. B, E Dorsoventral trends in hair density. The sectors are represented on the x-axis in dorsal to ventral order, matching the body map in figure 1. C, F Rostrocaudal trends in hair density. Sectors are represented on the x-axis in caudal to rostral order, matching the body map in figure 1.

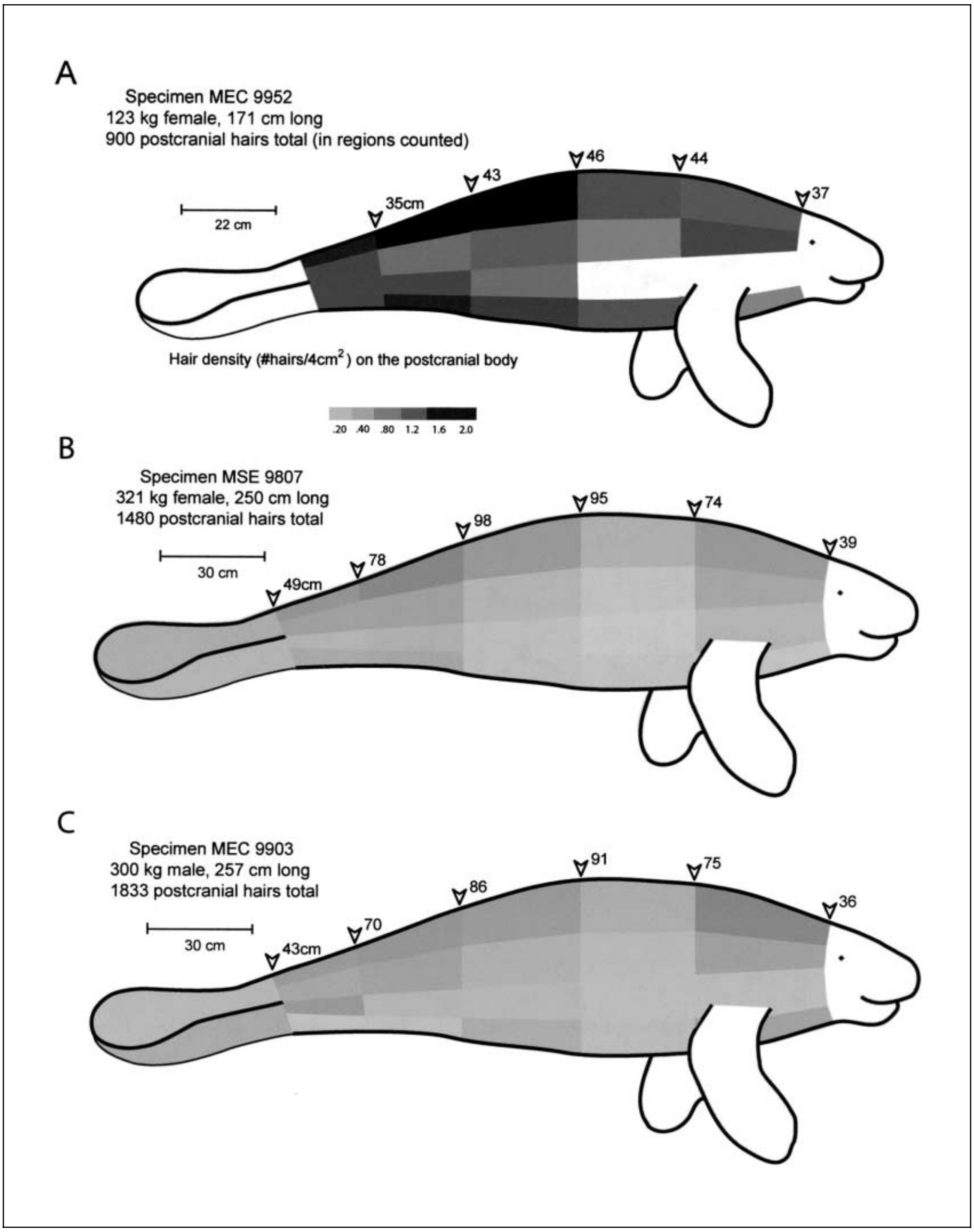
Hair length was assessed by region in specimen MEC 9903. External hair length ranged from 2–9 mm, with the shortest hairs found on the pectoral flipper and dorsal surface of the tail (fig. 5). Ventral body regions 7–11 contained more variation in hair length than the dorsal areas 1–5, due to greater numbers of shorter hairs. Specimen MSE 9807 showed similar trends, but measurements were made on only 7 regions. Measured hair diameters ranged from 62–158 μm (table 2), resulting in mean hair length/diameter ratios of 47–98.

Follicle Microanatomy

All follicles examined microscopically exhibited characteristics of follicle-sinus complexes (F-SCs), including an elongated circumferential blood sinus, dense connective tissue capsule and substantial innervation (figs. 6, 7). In no case was there a true ring sinus, defined as a distinctly enlarged non-trabeculated region located between upper and lower trabeculated cavernous sinuses. Rather, most specimens exhibited a dorsal enlargement in the sinus but still retained connective tissue trabeculae that spanned the width of the sinus (fig. 6B, E, F). In some cases the sinus appeared to be uniform in width throughout its length and no dorsal enlargement was apparent (fig. 6A, C, D). This variation did not appear to depend upon overall length of the F-SC, as dorsal enlargement was observed in both short and long F-SCs.

There was substantial variation in F-SC size within a given region, and no striking differences in follicle geometry across regions, as shown in table 2. Measured F-SCs varied in length from 3.5–9.9 mm, with most in the range of 4–7 mm and substantial overlap in these values across regions. The length of the sinus complex often comprised as much as 70–80% of the overall length of the F-SC. Sinus width and capsule thickness also exhibited variation but did not show obvious region-specific differences.

At the basal aspect of the follicle 1–3 nerves penetrate the capsule then branch and ascend in 6–15 smaller evenly spaced bundles along the mesenchymal sheath (fig. 7). Myelinated axon counts were obtained from 26 cross sectioned specimens (fig. 8) and ranged from 21–47 per follicle.



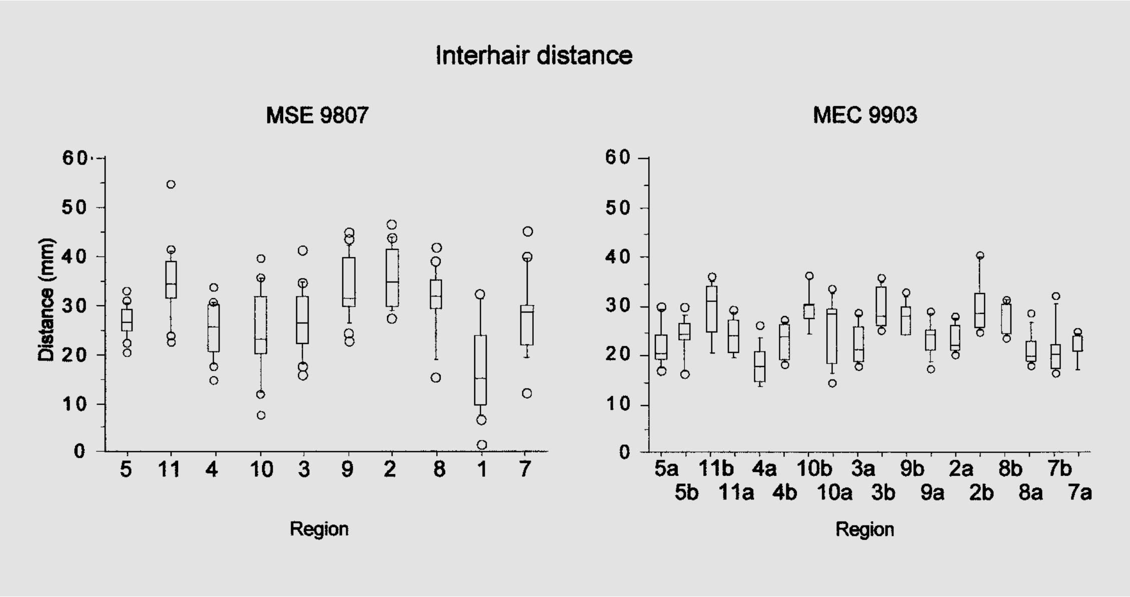
3

Fig. 3. Pattern of hair distribution in the small calf MEC 9952. A Hair density by region. Note that the density scale is different than that used in figure 2. B, C Hair density in MSE 9807 and MEC 9903, re-plotted using the same scale as in A, to facilitate comparison among the three specimens In all panels, numbers represent half-girth measurements in cm.

Fig. 4. Interhair distances in the subadult specimens MSE 9807 and MEC 9903. Data are plotted by region with caudal to the left, rostral to the right, in correspondence with the body maps illustrated in figures 1–3. Horizontal lines associated with each box plot indicate the 10th, 25th, 50th, 75th and 90th percentile values; outliers are plotted as circles.

Fig. 5. Hair length in specimen MEC 9903. A Pictoral representation of mean hair length by region. B Ranges for hair length are plotted for each region, in the same order in which they appear on the body map in A. FLm = medial flipper; FLl = lateral flipper.

4


Interhair distance
MSE 9807
MEC 9903
Distance (mm)
60
50
40
30
20
10
0
5 11 4 10 3 9 2 8 1 7
5a 11b 4a 10b 3a 9b 2a 8b 7b
5b 11a 4b 10a 3b 9a 2b 8a 7a
Region
Region

5

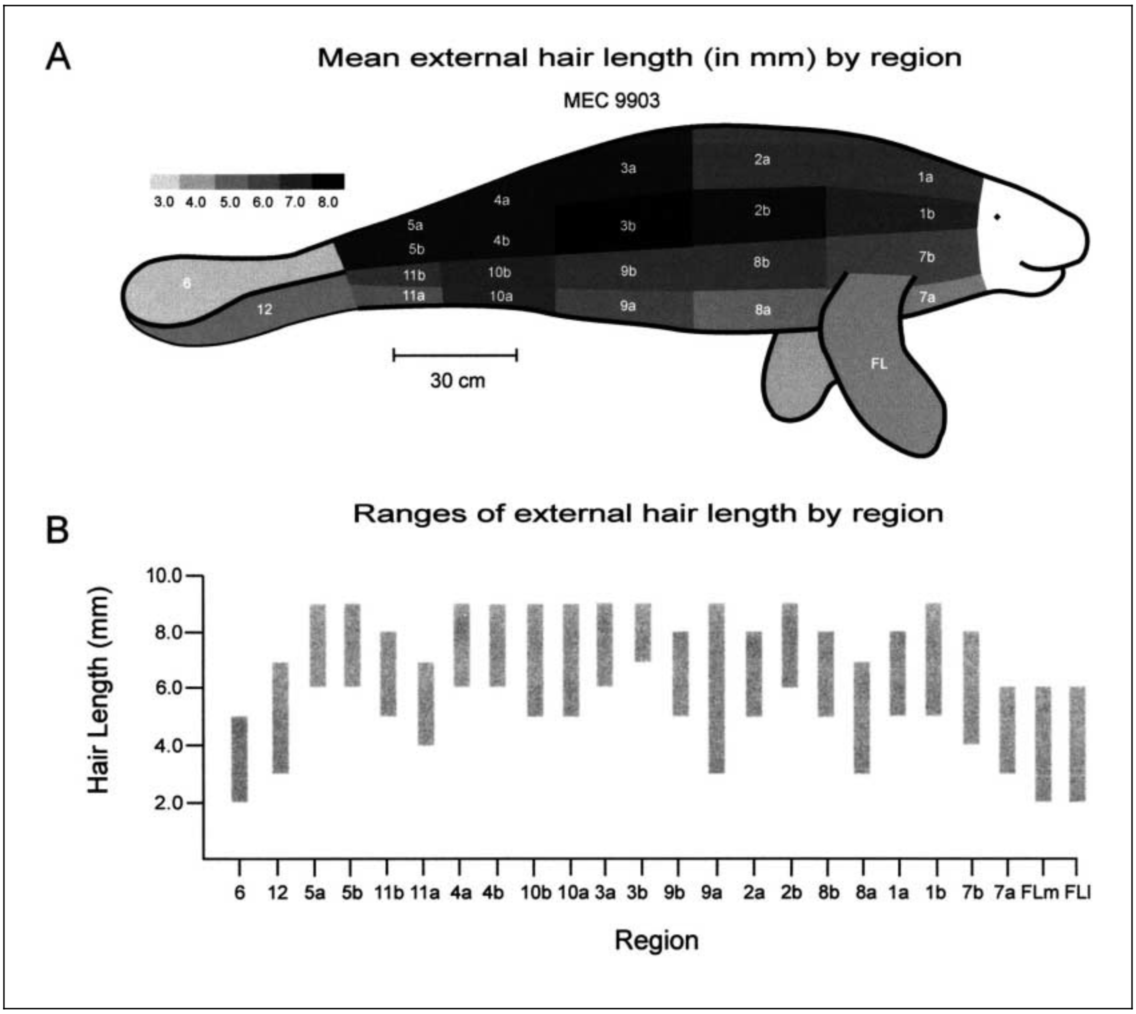

A
Mean external hair length (in mm) by region
MEC 9903
3.0 4.0 5.0 6.0 7.0 8.0
6
12
5a
5b
11b
11a
4a
4b
10b
10a
3a
3b
9b
9a
2a
2b
8b
8a
1a
1b
7b
7a
FL
30 cm
B
Ranges of external hair length by region
Hair Length (mm)
10.0
8.0
6.0
4.0
2.0
6 12 5a 5b 11b 11a 4a 4b 10b 10a 3a 3b 9b 9a 2a 2b 8b 8a 1a 1b 7b 7a FLm FLl
Region

Table 2. Microanatomical attributes of body hairs. Each column represents data from a designated region of the body

	1	2/3	4/5	7	8/9	10/11	Dorsal fluke, 6	Ventral fluke, 12	Lateral flipper	Medial flipper
Follicle length, mm	4.62–7.37	5.78–9.93	7.85–9.51	3.55–5.64	5.28–8.39	4.33–9.38	4.70–5.38	3.70–7.03	4.23–6.46	4.22–5.43
Max total sinus length, mm	2.37–6.25	5.30–6.84	6.45–9.00	2.15–2.80	4.66–6.16	3.35–7.51	2.14–5.28	3.02–5.17	3.14–5.08	2.61–3.32
Max sinus width, µm	231–469	186–346	277–487	269–449	315–546	292–424	138–331	200–338	321–338	315–393
Max capsule thickness, µm	127–313	123–246	231–353	121–246	161–331	128–258	191–212	107–224	118–229	173–309
Axons per follicle	38	32–47	21–33	33–41	23–37	23–40	26	21	22	21–25
Hair length, mm	5–11	5–9	6–10	3–8	3–9	4–10	2–8	3–8	2–7	2–6
Hair diameter, µm	62–100	85–115	78–100	69–100	70–97	108–158	77	85–92	62–130	64–100
Hair length/dia ratio, mean	98	75	90	65	72	53	65	63	47	49
Samples for geometry	3	4	3	3	4	4	3	2	3	2
Samples for nerve counts	1	2	7	2	4	5	1	1	1	2

Discussion

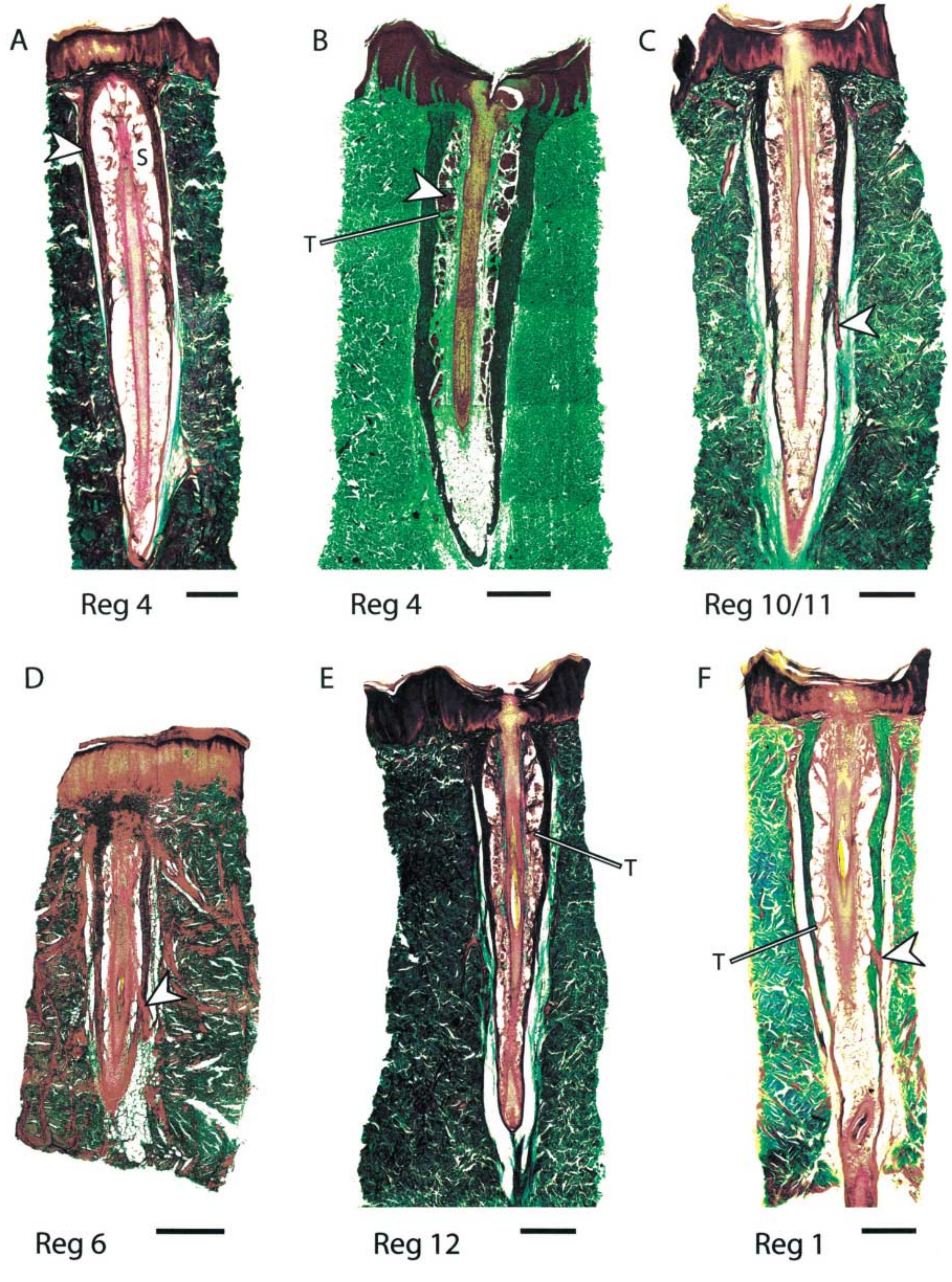
The most significant finding of the present report is that all the postcranial hair follicles examined have the structural features of tactile hairs. Together with our earlier findings on facial hairs and bristles [Reep et al., 1998], this makes the Florida manatee and other sirenians unique among mammals because all of their hair follicles have the structural form of follicle-sinus complexes, and these are distributed over the entire body. These traits appear to be present in sirenians generally, based on the relatively few data that exist [Dosch, 1915; Bryden et al., 1978; Kamiya and Yamasaki, 1981; Sokolov, 1986]. Because of the known tactile role played by F-SCs that have been investigated experimentally in other taxa, the present anatomical findings have direct and testable functional implications.

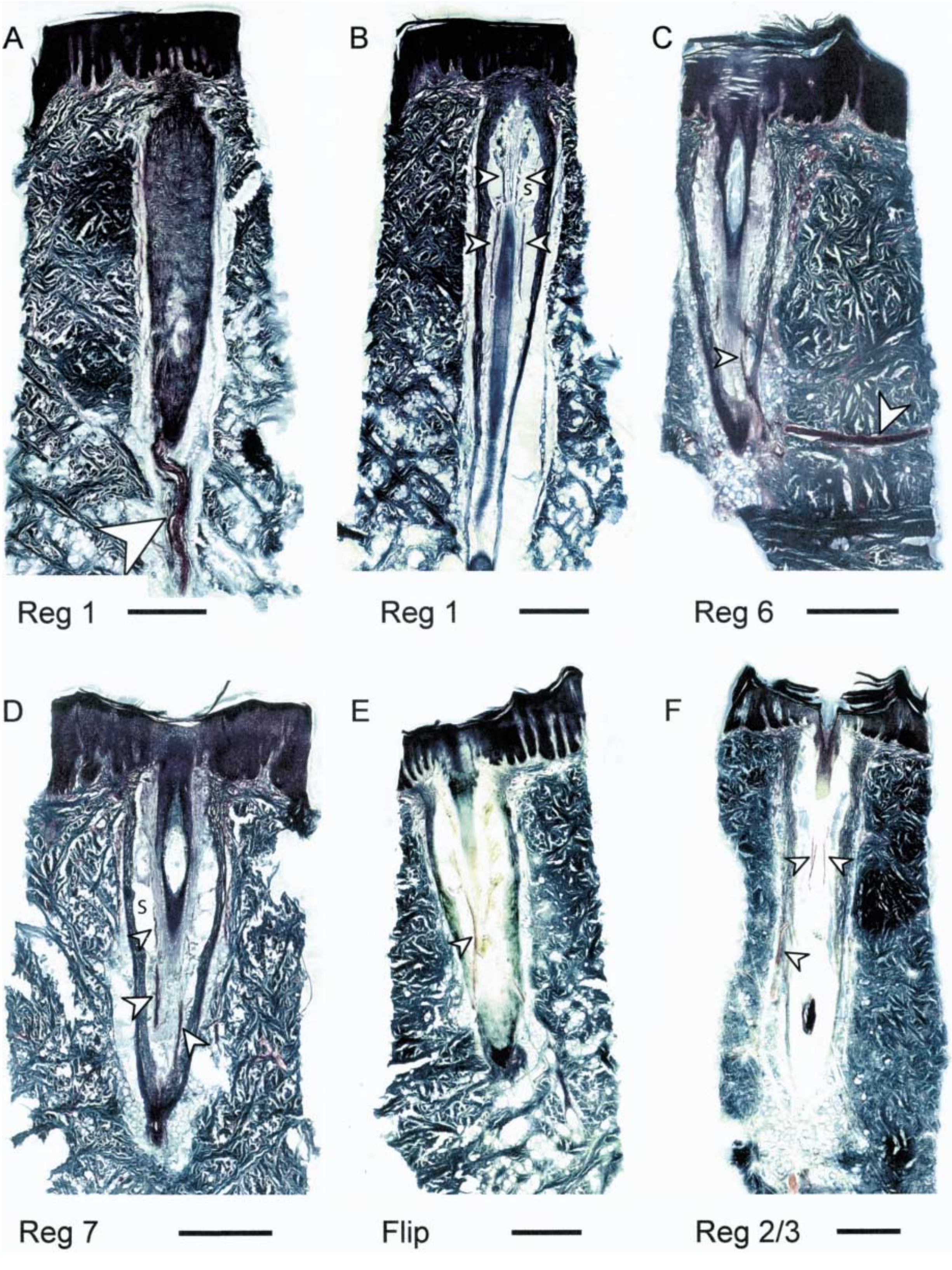
A Mammalian Lateral Line?

Manatees are large-bodied, obligatorily aquatic mammals, are relatively slow-moving, usually reside in turbid water habitats, have greatly reduced visual systems [Marshall and Reep, 1995] and poor visual acuity [Colbert et al., 2001], do not appear to utilize echolocation [Gerstein et al., 1999], and possess no thick pelage. We hypothesize that these behavioral and anatomical characteristics would make it adaptive to utilize tactile hairs distributed over the body as a three-dimensional somatosensory array capable of encoding the intensity and direction of water displacements and low-frequency vibrations impinging on the body surface. This information would be useful for the detection and localization of significant environmental stimuli, such as approaching conspecifics and other animals, water currents and tidal flows. Indeed, in his pioneering study of Florida manatees, Hartman [1979] suggested that the body hairs were used to sense currents in the water and that this capability might be the basis for detecting approaching conspecifics, and the means by which a group of animals resting with eyes closed rises in unison to breathe. Reynolds [1979] made a similar conjecture and even used the term 'lateral line' as an analogy to describe the presumed function of the postcranial hairs. Hyvarinen [1995] hypothesized a lateral line type function of the body hairs in Sirenia and seals. Gerstein et al. [1999] proposed that this system of hairs might also detect low frequency acoustic energy in the form of near-field particle displacements, and noted that improvement in detection at low frequencies occurs within the range of frequencies (0.1–0.2 kHz) that correspond to lateral line detection in fish.

This conception of the function of manatee body hairs is quite similar to Dijkgraaf's [1963] original view of the function of the lateral line system as mediating the sense of touch at a distance in fish and amphibians, and to the demonstrated ability of the lateral line system to mediate behavioral orientation to water currents [Montgomery et

Fig. 6. Follicle microanatomy as seen in trichrome stained sections. A Follicle from region 4, specimen 41. Note elongated sinus (S) and capsule (arrowhead). B Dorsally expanded sinus (arrowhead) containing blood in a follicle from region 4, specimen 13. Trabeculae denoted by T. C Follicle from region 10/11, specimen 32. Arrowhead denotes nerve traversing capsule. D Follicle from region 6, specimen 39. Arrowhead denotes nerve traversing capsule. E Follicle from region 12, specimen 40. Note dorsally expanded sinus. Trabeculae denoted by T. F Follicle from region 1, specimen 45. Arrowheads denote nerves traversing capsule. Sinus is expanded dorsally; T = trabeculae. Scale bars = 1 mm.


A
S
Reg 4
B
T
Reg 4
C
Reg 10/11
D
Reg 6
E
T
Reg 12
F
T
Reg 1



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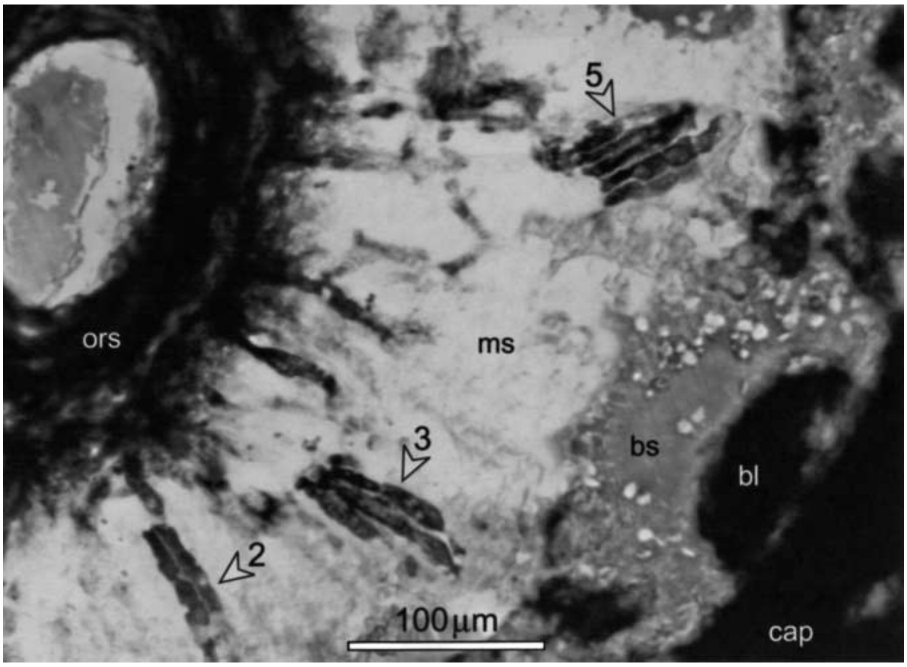

Fig. 8. Nerve bundles in a cross section of a follicle from region 4b, specimen 141. Arrows point to bundles containing the specified number of axons. Abbreviations: bl = blood, bs = blood sinus, cap = follicle capsule, ms = mesenchymal sheath, ors = outer root sheath.

al., 1997]. Pressure waves, including compression waves (sound), travel 4.5 times faster in water than air (depending on temperature, depth and salinity), and undergo less rapid energy dispersal than in air [Urick, 1983; Kalmijn, 1989]. Therefore, they are potentially useful stimuli in the denser aquatic environment. Manatee postcranial F-SCs may also be used to detect and localize fixed objects in the underwater environment, including limestone formations and boundaries such as river banks. Stationary underwater objects create distortions in the flow fields generated by animals moving through water, and unequivocal information about object size and distance can be obtained by the lateral line system of fish through analysis of the velocity distribution of the flow field over the entire body [Hassan, 1989]. If the distributed system of postcranial F-SCs in the Florida manatee is used in a similar way, the large body size of manatees might facilitate this capability by providing a larger detector array. The exact way in which the distribution of body hairs and size of the animal could influence spatial resolution remains to be determined, and undoubtedly also depends upon unknown attributes of the responses of single F-SCs and the central nervous system to near-field water displacement stimuli. Vibrissae F-SCs in cats and seals are not particularly specialized for directional sensitivity [Dykes, 1975]. However, even in the absence of directional selectivity, a three-dimensional array of F-SCs such as that on the postcranial body of manatees could convey information pertaining to the location and intensity of a stimulus through place coding and temporal differences in the firing of individual F-SCs.

Fig. 7. Follicle innervation as seen in longitudinal Bodian stained sections from case MSE 9807. Arrowheads indicate nerves. A Follicle from region 1, specimen 80. In this section off the central axis of the follicle, note the large nerve entering from below. B A more central section from the same follicle as in panel A. Note the two nerves ascending along the mesenchymal sheath, and the dorsally expanded sinus (S). C Follicle from region 6 (dorsal tail), specimen 89. A large nerve approaches the follicle from the right side, and a smaller branch traverses the capsule then ascends along the sinus margin. D Follicle of region 7, specimen 90. Two prominent nerve bundles ascend along the sinus border. Note also the dorsal expansion of the sinus (S). E Follicle from the lateral side of the pectoral flipper, specimen 76. A nerve is located along the sinus margin. F Follicle from region 2/3, specimen 72. One nerve penetrates the capsule; two others ascend along the sinus margin. Scale bars = 1 mm.

To a first approximation, we can consider the postcranial F-SCs (excluding those on the tail and pectoral flippers) as a uniform distributed array of identical modular tactile sensors. In reality, variation in parameters such as F-SC spacing (density), hair length and innervation density might contribute to regional specificity of func-

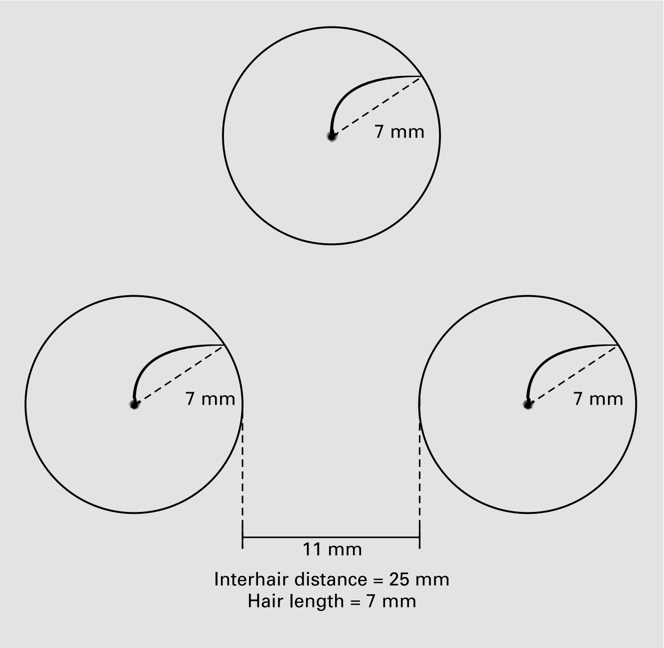

Fig. 9. Relationship between hair spacing and length. For the typical parameters shown, each hair functions independently within its 360° range of rotation.

tion. This could be tested behaviorally by modifying the same/different behavioral response paradigm developed for investigating the auditory capabilities of Florida manatees [Gerstein et al., 1999]. Thus, controlled underwater stimuli could be presented to restricted portions of the body and discriminative performance compared across body regions.

Comparison with Facial F-SCs

The postcranial F-SCs differ from those on the face [Reep et al., 2001] in several respects. Perhaps most notable with regard to their presumed sensory function, the postcranial F-SCs lack a ring sinus and have substantially less innervation than those on the face (~20–40 vs. ~40–200 axons per follicle). Follicle length and sinus length exhibit comparable ranges in both regions, but the capsule is much thinner in postcranial F-SCs. The F-SCs of the supradisk region of the face are most similar in structure to those of the postcranial body. The ring sinus of supradisk F-SCs is located dorsally like the dorsal enlargement seen in most postcranial F-SCs. Compared to other facial F-SCs, the supradisk F-SCs have thinner capsules, fewer axons per follicle, and much greater external hair length/diameter ratios [Reep et al., 1998; 2001].

The hair length/diameter ratio represents the stiffness of the hair, and this influences the compliance of the hair in response to mechanical stimuli such as water displacements. The length/diameter ratios of 47–98 reported here can be compared to those from the facial region. The hairs on the supradisk region fall into this range, having a length/diameter ratio of approximately 80. Those of the oral disk, that are used in tactile exploration, have ratios of approximately 30. The stout bristles of the face that are used in oripulation of plants have much lower ratios, ranging from 3–8 when everted [Reep et al., 1998].

Hair Distribution and Length

What determines the spacing of hair (and thus, F-SCs) on the body? If we assume that the role of postcranial hairs is sensory detection, it is possible that spacing is a tradeoff between sensitivity/acuity and neural and metabolic resource allocation. For 3000 postcranial F-SCs, each supplied by 30 axons, this represents 90,000 axons projecting centrally, together with the central nervous tissue necessary to process and distribute this information. This compares with the approximately 103,000 axons supplying F-SCs of the face [Reep et al., 2001]. Hair spacing might also be constrained by optimization criteria because it appears that each postcranial F-SC functions independently. Using the data from specimen MEC 9903 on interhair distance and hair length (figs. 4, 5), we can deduce the following. For a body region with typical interhair distances of 25 mm and typical hair lengths of 7 mm, each hair would have a 360° field of movement that would not overlap with that of any other hair (fig. 9). Furthermore, at this interhair distance, overlap would not occur until hair length exceeded 12.5 mm, and such lengths were not observed. Even for observed low interhair distances of 18 mm, hair length would have to be greater than 9 mm for overlap to occur, and no lengths were observed in this range. In any case, overlap is unlikely to occur in less than the most turbulent situations, because the tips of adjacent hairs are almost never pointed toward each other. As a manatee swims, all the postcranial hairs (excluding those on the tail and pectoral flippers) tend to be displaced in the same general direction, and display their nearly maximal horizontal lengths as they lie against the body (personal observation). Under these conditions hair length would have to equal interhair spacing for a hair to interact with its nearest neighbor. Because in the present study there was no overlap between the ranges of interhair distance (15–42 mm) and hair length (2–9 mm), this apparently never happens. For a stationary manatee in the field of a typical propagating underwater displacement like that created by a moving conspecific, the postcranial hairs are rarely displaced enough to become horizontal, and adjacent hairs are displaced in the same general direction, again making it unlikely that interaction would occur between nearest neighbors. Only when there is a large amplitude displacement followed by subsequent rebound movements does one observe asynchronous and thus anisotropic movement of adjacent hairs.

Hair length could be a significant factor influencing the response of a F-SC to water displacement. Longer hairs would be more compliant in response to such stimuli. Depending upon the relationship between this external movement and movement of the portion of the hair inside the F-SC, this could influence the degree of contact between the internal hair shaft and the sinus wall containing sensory receptors, thereby amplifying the neural response to a stimulus of a given amplitude. However, hair length is probably influenced in a haphazard way by environmental factors. Manatees damage hair as they rub against objects, hairs accumulate algae, and some follicles are missing external hairs altogether. There might be enough redundancy built into the array that disturbances such as these have a minor detrimental influence on function.

Postcranial F-SCs in Other Taxa

No non-sirenian mammalian species has been reported to possess F-SCs over the entire body. However, there are several suggestive reports in this regard, and ample opportunities for further investigation. Many squirrel species are reported to have vibrissae on their feet and the outside of the legs as well as on the head [Milton, 1984]. Naked mole-rats possess sparsely distributed, evenly spaced vibrissae-like body hairs on their otherwise furless bodies, and these are densely innervated though lacking blood sinuses [Park et al., 2000]. Furthermore, this system is used in behavioral orientation responses [Crish et al., 2000]. Sale [1970] reported that hyraxes possess vibrissae on the entire body, but this was based only upon external features, unconfirmed by histological observations. He also commented on the potential utility of this system for tactile exploration within rock crevices and tunnels under low light conditions. Sokolov [1982] also reported that three species of hyraxes have vibrissae on the trunk skin as well as the face. However, no data were given except for follicle length and one brief statement concerning the presence of a blood sinus.

We conclude that the system of postcranial hairs and F-SCs in the Florida manatee represents a novel development, akin to other mammalian mechanosensory innovations such as the bill of the platypus [Pettigrew et al., 1998] and the nasal appendages of the star-nosed mole [Catania, 2000].

Acknowledgements

We thank Tom O'Shea and Woodie Hartman for inspiration in pursuing the 'lateral line' hypothesis. We greatly appreciate the technical contributions of Ms. Betty Hall and Jennifer Sivinski. Thanks to Gabe Trinity for composing the figures. Tom Pitchford, Butch Rommel, Donna Szemer and Scott Wright at the Marine Mammal Pathobiology Laboratory helped us to procure the specimens for this study. Conversations with Daniel Bachteler, Guido Dehnhardt, Ed Gerstein, Jack Johnson, Lee Weller and Wally Welker were very helpful. Daryl Domning provided several useful comments on the manuscript. Supported by the University of Florida College of Veterinary Medicine and The Maxwell Fund. College of Veterinary Medicine Journal Series No. 611.

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