Aquatic Mammals 2020, *46*(4), 367-381, DOI 10.1578/AM.46.4.2020.367

Comparative Histological Examination of the Integument of Odontocete Flukes

Jennifer L. Garten and Frank E. Fish

Department of Biology, West Chester University, West Chester, PA 19383, USA
E-mail: ffish@wcupa.edu

Abstract

Cetacean skin is noted for being exceptionally thick and being structurally different from the skin of terrestrial mammals in that it lacks hair, sebaceous glands, and sudoriferous glands. The caudal flukes of cetaceans are the primary propulsive structures, which are subjected to hydrodynamic flows and forces that differ from those experienced by the body. Based on the hydrodynamic function of the flukes, their integument is hypothesized to be histologically distinct from that of the body. The microanatomy of cetacean integument was examined to determine whether structural differences between the flukes and dorsal body skin are present. Integument samples were collected from the dorsal body and five fluke locations for five odontocete species (*Delphinus delphis*, *Stenella coeruleoalba*, *Tursiops truncatus*, *Kogia breviceps*, and *Phocoena phocoena*) and prepared for light microscopy. Statistically significant differences were observed in epidermal thickness and dermal papilla height between the dorsal skin and skin of the fluke; and there were differences between epidermal thickness and dermal papilla height of the leading edge when compared to other locations on the fluke. Dermal papillae deeply penetrated many locations of the fluke, suggestive of functions associated with resisting shear forces, cell proliferation, thermoregulation, and tactile sensitivity.

Key Words: skin, whale, stratum corneum, dermal papillae, shear stress

Introduction

Skin is an important protective barrier that functions in maintaining homeostasis, enhancing locomotion, providing camouflage, repelling microorganisms (Baum et al., 2001, 2003; Reeb et al., 2007), providing tactile sensitivity, and protecting from ultraviolet radiation (Darmstadt & Dinulos, 2000). Comprising the external surface of an animal, the skin is the one organ system that is in intimate contact with the external environment and is, thus, subjected to a variety of physical pressures. The characteristics of the skin relate to the environment that the animal inhabits (Greenwood et al., 1974; Ling, 1974; Sokolov, 1982). In association with the secondary return to an aquatic environment by some lineages of terrestrial mammals, changes in the skin occurred that allowed it to function in water (Harrison & Thurley, 1974; Ling, 1974; Fish, 1993; Reeb et al., 2007).

Akin to other mammals, cetacean (whales, dolphins, and porpoises) skin is composed of epidermal, dermal, and hypodermal layers (Harrison & Thurley, 1974; Sokolov, 1982; Reeb et al., 2007; Berta et al., 2015). However, cetacean skin is highly modified in association with its functioning in an environment different from its land-based ancestors (Ling, 1974). Although many differences between the epidermis of cetaceans and terrestrial mammals exist, two major differences are the absence of hair and the absence of associated sebaceous and sudoriferous glands in the former (Giacometti, 1967; Greenwood et al., 1974; Ling, 1974; Sokolov, 1982; Berta et al., 2015). Contrastingly, cetaceans possess lipokeratinocytes in the epidermis, a cell type not normally found in the epidermis of terrestrial mammals (Menon et al., 1986). Additionally, cetacean epidermis undergoes parakeratosis in which keratinization occurs in the presence of nuclei, whereas the epidermis of terrestrial mammals is generally hyperkeratotic and undergoes keratinization in the absence of nuclei (Spearman, 1972; Harrison & Thurley, 1974; Haldiman et al., 1985). Another difference between the skin of terrestrial and aquatic mammals is its relative thickness. Cetacean skin is considerably thicker than the skin of many terrestrial mammals, even mammals of similar size (Harrison & Thurley, 1974; Ling, 1974; Sokolov, 1982; Reeb et al., 2007). The epidermis of the suborder Odontoceti (toothed whales) is 10 to 20 times thicker than that of terrestrial mammals (Berta et al., 2015), and the hypodermis (i.e., blubber layer) can account for 80 to 90% of

integument thickness in some odontocetes (Struntz et al., 2004).

Although many mammals possess five layers of epidermal strata, cetaceans possess only three (Parry, 1949; Ling 1974; Sokolov, 1982; Reeb et al., 2007; Ginter et al., 2011). The five epidermal strata in mammals, from outermost to innermost, are as follows: (1) stratum corneum, (2) stratum lucidum, (3) stratum granulosum, (4) stratum spinosum, and (5) stratum basale. Cetaceans lack the stratum lucidum and stratum granulosum (Parry, 1949; Sokolov, 1982; Reeb et al., 2007). Harrison & Thurley (1974) and Geraci et al. (1979) described four epidermal strata for cetaceans: (1) stratum externum, (2) stratum intermedium, (3) stratum spinosum, and (4) stratum basale (germinativum). This study considered the epidermis to consist of the stratum corneum, stratum spinosum, and stratum basale (Sokolov, 1982) as these three layers are conventionally used and accepted.

Previous research focused on whether or not cetaceans have specialized skin structures that assist in decreasing drag during swimming (Kramer, 1960a, 1960b; Webb, 1975; Fish & Hui, 1991; Romanenko, 1995; Fish & Rohr, 1999; Fish, 2006). Drag reduction in dolphins is primarily associated with streamlining of the body and appendages, with no contribution from compliant damping, dermal ridges, secretions, skin folds, or boundary-layer heating (see reviews by Fish & Hui, 1991, and Fish & Rohr, 1999). In examining morphological specializations of the skin for features associated with hydrodynamic functions, the focus has been on the skin of the general body surface. The skin of the appendages of cetaceans (i.e., dorsal fin, flippers, and flukes) has received less scrutiny (Ling, 1974; Jones & Pfeiffer, 1994). The appendages have a thinner hypodermis (blubber layer) and operate under different hydrodynamic conditions than the body (Felts, 1966; Webb, 1975; Rohr et al., 1998; Fish & Rohr, 1999; Weber et al., 2009). The flukes, in particular, are the primary propulsive structures for swimming in cetaceans (Fish, 1998a, 1998b). The lunate tail of cetaceans moves dorsoventrally to produce thrust, acting as an oscillating hydrofoil (Gingerich et al., 1994; Pabst, 1996; Fish 1998a, 1998b; Williams et al., 2000; Fish et al., 2014). The hydrodynamics of the flukes differ from those of the body because they are subjected to a higher rate of flow for any given swimming speed. The high water flow, in concert with the kinematics of the flukes, results in them experiencing high longitudinal shear forces and greater perpendicular pressure differences (Fish & Rohr, 1999).

As the skin of the flukes experiences different hydrodynamic effects from the general body surface, we undertook a histological examination of the integument of cetacean flukes to explore potential structural differences relative to the integument of the body. Epidermal thickness of the body has been described for several odontocete species (Parry, 1949; Ling, 1974; Sokolov, 1982; Hicks et al., 1985; Jones & Pfeiffer, 1994), but less attention has been paid to the flukes. Based on the propulsive function of the flukes and the hydrodynamic stresses imposed on them, the integument of the flukes is hypothesized to be histologically distinct from that of the body.

Methods

Skin samples were collected from dead, stranded animals in condition Code 2 (i.e., carcass in good condition, fresh; Geraci & Lounsbury, 2005) and acquired from stranding centers—New Jersey Marine Mammal Stranding Center, Virginia Aquarium, and University of North Carolina Wilmington. Seven individuals of five species of odontocetes were examined, which included *Delphinus delphis* (common dolphin), *Kogia breviceps* (pygmy sperm whale), *Phocoena phocoena* (harbor porpoise), *Stenella coeruleoalba* (striped dolphin), and *Tursiops truncatus* (bottlenose dolphin) (Table 1). Two cm^2 samples from either the left or the right fluke were removed, depending on the condition of each side, from the following locations: fluke tip, fluke blade at 50% of span (mid-span dorsal and ventral), leading edge, and trailing edge on the same fluke (Figure 1). A 2 cm^2 section of integument was removed from the dorsal surface of the body, halfway between the blowhole and the anterior insertion of the dorsal fin. These sections encompass the epidermis and the papillary layer of the dermis at a minimum, and the positions take into account variation between species and size of individual specimens.

Samples were immersed in 10% formalin for 7 d, followed by 1 d in distilled water, and then stored in 70% ethanol (EtOH) until prepared for light microscopy. Tissue samples were obtained from five species (Table 1).

Slide Preparation

Tissue samples were processed for light microscopy at the New Bolton Center's Large Animal Pathology Laboratory, University of Pennsylvania Veterinary School (Kennett Square, PA, USA). All samples were dehydrated via a series of increasing EtOH concentrations (70, 95, and 100%), cleared with xylene, and embedded in paraffin wax at 60°C (Poly Scientific Research and Development, Bay Shore, NY, USA) under vacuum in an automatic tissue processor (Sakura

Table 1. List of specimens investigated in this study

Species	Common name	Family	Number of specimens	Sex	Body length (m)
Delphinus delphis	Short-beaked common dolphin	Delphinidae	1	M*	2.13*
Stenella coeruleoalba	Striped dolphin	Delphinidae	1	UK	UK
Tursiops truncatus	Bottlenose dolphin	Delphinidae	2	F/F*	2.27/1.04*
Kogia breviceps	Pygmy sperm whale	Kogiidae	1	F^	2.37^
Phocoena phocoena	Harbor porpoise	Phocoenidae	2	UK	UK

*Swingle et al., 2016; ^Swingle et al., 2015; and UK = unknown

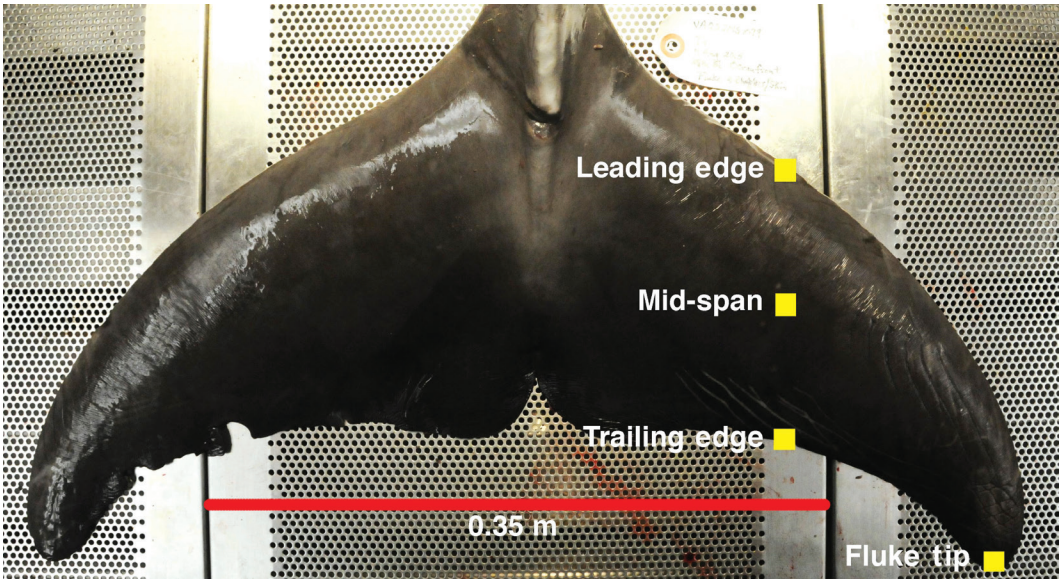

Figure 1. Fluke sampling points on the dorsal surface of a specimen of *Tursiops truncatus*

Tissue TEK VIP; Cardinal Health, Dublin, OH, USA). Samples were then sectioned at 4 µm on a manual rotary microtome and mounted on glass slides. The integument samples were stained with hematoxylin and eosin (*NBC.PATH.112*, Version 2.1, 2014). Hematoxylin and eosin are standard stains that color the cell nuclei and extracellular matrix, respectively. For this study, the stains were used to define cells in the layers of epidermis. For sectioned slides, the paraffin was removed by immersion in three changes of xylene, rehydrated via a series of decreasing EtOH concentrations (100, 95, and 70%), and then rinsed with distilled water. The sectioned slides were placed in Gill's II Hematoxylin (Poly Scientific Research and Development) stain for about 2 min, rinsed with distilled water, placed in Scott's Tap Water Substitute (a bluing reagent; Poly Scientific Research and Development) for about 30 s, rinsed again with distilled water, and stained with an eosin/phloxine solution (Poly Scientific Research and Development) for about 45 s. The slides were again dehydrated via a series of increasing EtOH concentrations (70, 95, and 100%), cleared in three changes of xylene, and had a coverslip applied wet with a mounting medium (CoverSafe; American Master Tech, Lodi, CA, USA).

Microscopic Measurements

The average thickness (µm) of the entire epidermis, the stratum corneum, the stratum spinosum, the stratum basale, the height of dermal papillae, and the lipokeratinocyte height and area (µm^2) for

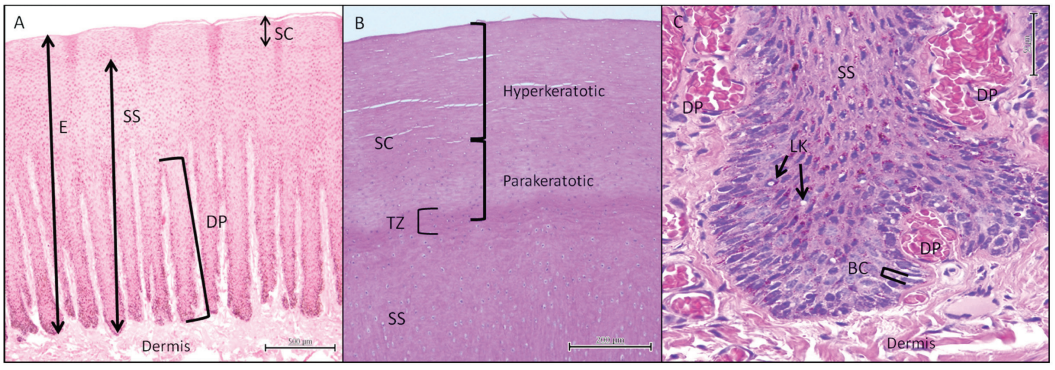

Figure 2. Hematoxylin and eosin (H&E) stained photomicrograph of (A) the dorsal skin of *Delphinus delphis* depicting the measuring scheme for the epidermis (E), stratum spinosum (SS), dermal papilla (DP), and stratum corneum (SC); scale bar = 500 µm, 4x objective lens; (B) the leading edge of the fluke of *T. truncatus* depicting the distinction between a hyperkeratotic and parakeratotic SC and detailing a transitional zone (TZ) between the SS and SC; scale bar = 200 µm, 10x objective lens; and (C) the trailing edge of the fluke of *Kogia breviceps* depicting an example of a basal cell (BC) and lipokeratinocytes (LK); scale bar = 50 µm, 40x objective lens.

the fluke and dorsal body locations were calculated (Figure 2A-C) from 20 replicate measurements per sample. Measurements were made using Olympus DP21 software with an Olympus CX41 light microscope.

The total epidermal thickness includes the stratum corneum, where present, stratum spinosum, and stratum basale. The stratum spinosum was measured from the top of the stratum basale, along the dermis, to the base of the stratum corneum (Figure 2A). In situations in which the stratum corneum was absent, the stratum spinosum was measured to the outer surface of the epidermis. The basal layer is a single layer of columnar cells interspersed with melanocytes that lies along the sides of the dermal papillae and the base of the stratum spinosum and dermis (Geraci et al., 1979; Haldiman & Tarpley, 1993). The thickness of this layer was measured from the top of the papillary layer of the dermis to the base of the stratum spinosum (Figure 2C).

The height of the dermal papillae refers to the basal elevation, the dermal ridge, and the dermal papilla (Stromberg, 1989). Only papillae that were continuous were measured for height, with this being taken from the bottom center of the basal elevation/dermal ridge to the center tip (Figure 2A). The lipokeratinocyte height refers to the maximum diameter of a lipokeratinocyte. The lipokeratinocyte area refers to the area of individual lipokeratinocyte cells averaged together and was measured using the area tool in the Olympus DP21 software. The relative dermal papilla height was calculated as the ratio between the dermal papilla height and epidermal thickness, expressed as a percentage.

Statistical Analysis

For each species, the integument of the sampled regions of the fluke was compared to the integument of the dorsal body to determine whether a statistical significant difference in integumentary characteristics between them was evident. *SPSS*, Version 21 (IBM) was used to statistically analyze average skin measurements from the body and the five locations on the fluke. Significant differences between species and sampling locations were assessed using a two-way analysis of variance (ANOVA) with a Tukey post-hoc comparison to assess variations in integumentary characteristics between these groups. Results were considered statistically significant at $p < 0.05$. Variation about the mean was expressed as ±1 standard error of the mean (SE). Due to the limited number of individuals obtained for this study, it was not possible to perform a two-way ANOVA for each individual species; therefore, a two-way ANOVA for all species combined and a two-way ANOVA for all locations combined were performed.

The integumentary characteristics of the dorsal region of the body were employed as controls, and the various locations on the fluke were compared to this control. The integumentary characteristics under investigation from the fluke locations were also compared to the other locations on the fluke. Measurements from Sokolov (1982) were used for the epidermal thickness (1,000 µm), stratum corneum thickness (36.66 µm), and dermal papilla height (523 µm) of the dorsal body for *S. coeruleoalba* as no dorsal body integument sample from this individual was obtained.

Results

Histological Analysis

Delphinus delphis—A parakeratotic stratum corneum was present in all locations on the body and fluke, although for the leading edge of the fluke, the stratum corneum appeared to be both hyperkeratotic superficially and parakeratotic more deeply (Figure 3A-F). The dorsal mid-span (Figure 3E) did not appear to possess lipokeratinocytes in the epidermis, whereas the other locations on the fluke possessed them. Dermal papillae of the dorsal skin, fluke tip, and leading edge penetrated the epidermis by greater than 50% (Table 2; Figure 3A, B & F), while in the other locations sampled they did not.

Kogia breviceps—For both the fluke tip and ventral mid-span, a true stratum corneum was absent, although a few layers of cells with reduced nuclei were present at the surface of the epidermis (Figure 4A & D). There was no true stratum corneum on the leading edge as the nuclei remained round even in the most superficial layers of the epidermis. A hyperkeratotic stratum corneum was present in the dorsal skin, whereas a parakeratotic stratum corneum was present on the trailing edge (Figure 4C) and dorsal mid-span of the fluke (Figure 4E). Dermal papillae penetrated the epidermis to greater than 50% for all sampled locations (Table 2), with papillae of the leading edge extending nearly to the surface of the epidermis (91%; Figure 4B). The dermal papillae of the

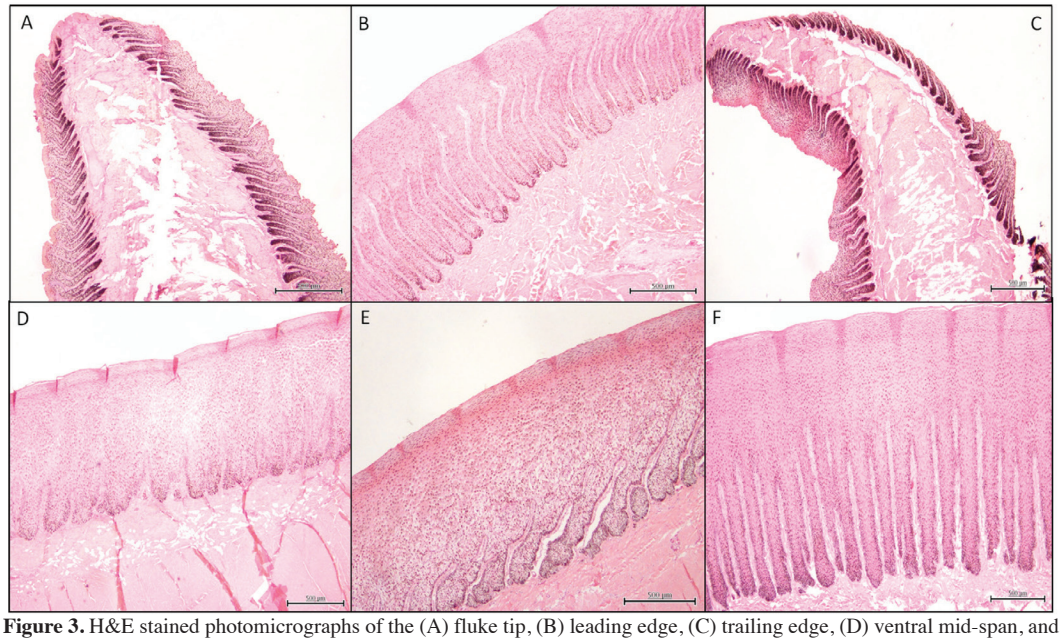

Figure 3. H&E stained photomicrographs of the (A) fluke tip, (B) leading edge, (C) trailing edge, (D) ventral mid-span, and (E) dorsal mid-span of the fluke, and (F) dorsal skin of *D. delphis*. Scale bar: 500 µm, 4x objective.

Table 2. Relative dermal papilla height in each species. Sampling locations with values greater than 50% are indicated in bold text. These values suggest the locations are good thermal windows.

	Location					
Species	Dorsal skin (%)	Fluke tip (%)	Leading edge (%)	Trailing edge (%)	Dorsal mid-span (%)	Ventral mid-span (%)
D. delphis	**53**	**56**	**61**	45	37	32
S. coeruleoalba	**52**	**84**	**59**	50	**56**	**99**
T. truncatus	44	**70**	37	49	42	39
K. breviceps	86	79	91	72	75	76
P. phocoena	30	48	38	40	37	35

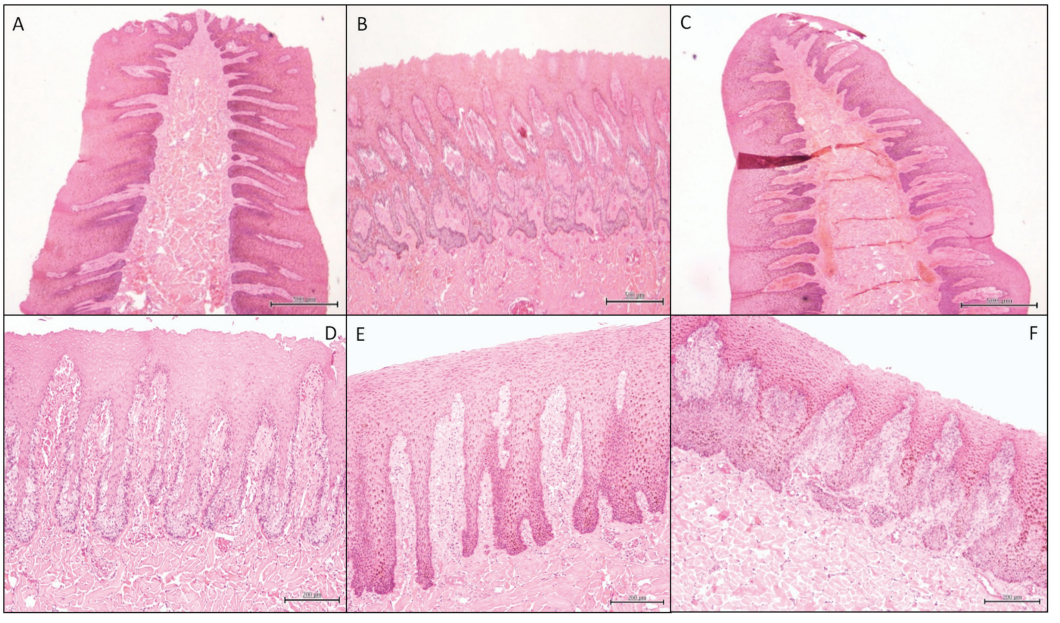

Figure 4. H&E stained photomicrographs of the (A) fluke tip, (B) leading edge, (C) trailing edge, (D) ventral mid-span, and (E) dorsal mid-span of the fluke, and (F) dorsal skin of *K. breviceps*. Scale bar: 500 µm, 4x objective (A-C); scale bar: 200 µm, 10x objective (D-F).

dorsal skin were triangularly shaped with irregular edges—that is, wide near the base and tapering to a narrow tip (Figure 4F). Lipokeratinocytes were present in the skin of the ventral mid-span of the fluke and were scarce at the trailing edge (Figure 4C & D).

Phocoena phocoena—A distinct stratum corneum was present at all sampled locations (Figure 5A-F). Lipokeratinocytes were abundant in the stratum spinosum of all locations and were also present in the stratum corneum of the trailing edge (Figure 5C) and dorsal skin (Figure 5F). A transitional zone appeared to be present between the stratum corneum and stratum spinosum in the dorsal body skin and the ventral mid-span skin (Figure 5D). The dermal papillae, on average, penetrated to less than 50% the depth of the epidermis for all locations (Table 2). The epidermis of the leading edge, ventral mid-span, dorsal mid-span, and dorsal skin was relatively thick in relation to the other species under investigation, with these locations averaging over 2 mm in thickness (Figure 8A).

Stenella coeruleoalba—The stratum corneum of the ventral and dorsal mid-span was absent, potentially due to sloughing or abrasion during stranding (Figure 6D & E). The stratum corneum of all other locations was parakeratotic. No lipokeratinocytes were present in the fluke tip, though they were present in small numbers in all other locations. The surface of the epidermis of the fluke tip was wavy (Figure 6A), likely due to the postmortem drying and deformation of the tissue. Dermal papillae of the fluke tip were taller in relation to the convex portion of the wavy epidermis and were shorter in relation to the concave portion of the wavy epidermis (Figure 6A). Dermal papillae penetrated at least half the depth of the epidermis in all locations sampled (Table 2; Figure 6A-E).

Tursiops truncatus—The stratum corneum was both hyperkeratotic superficially and parakeratotic deep in the fluke's leading edge (Figure 2B), fluke tip, trailing edge, and ventral mid-span (Figure 7A-E). Lipokeratinocytes were almost entirely absent from all locations except the dorsal skin (Figure 7F). A transitional zone was present (Figure 2B) between the stratum spinosum and stratum corneum of the leading edge, dorsal mid-span, and dorsal skin (Figure 7B, E & F).

Comparative Structure of the Integument

Epidermal Thickness—Based on results for the two-way ANOVA, epidermal thickness varied between location ($p = 0.001$, $df = 5$, $F = 10.4362$) and species ($p < 0.001$, $df = 4$, $F = 21.662$) (Figure 8A). When considering all species together in a Tukey post-hoc analysis, the epidermis of the dorsal skin was significantly thicker than that of the fluke tip and trailing edge ($p = 0.001$); the

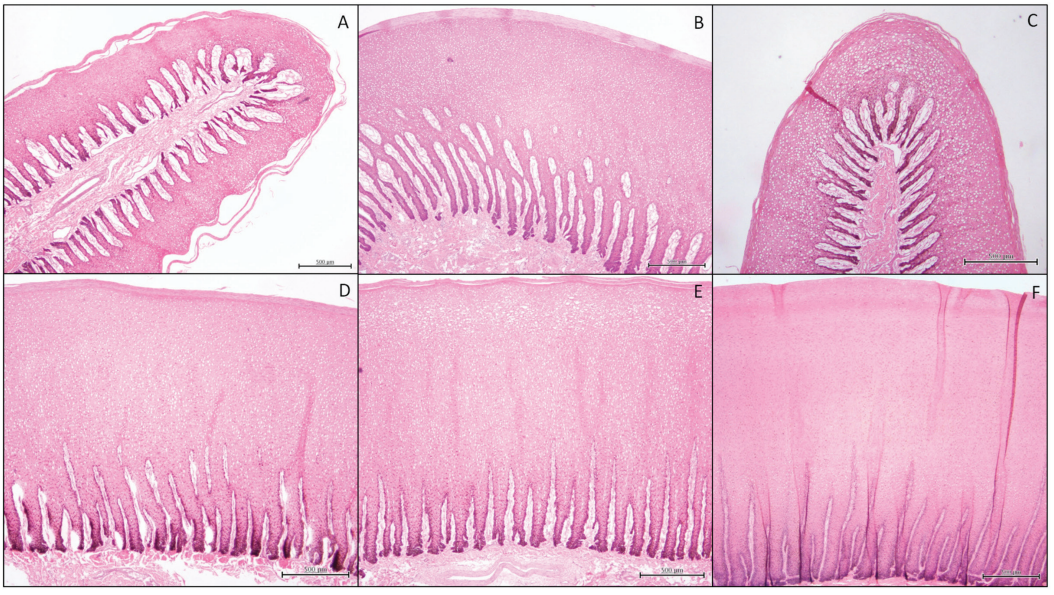

Figure 5. H&E stained photomicrographs of the (A) fluke tip, (B) leading edge, (C) trailing edge, (D) ventral mid-span, and (E) dorsal mid-span of the fluke, and (F) dorsal skin of *Phocoena phocoena*. Scale bar: 500 µm, 4x objective.

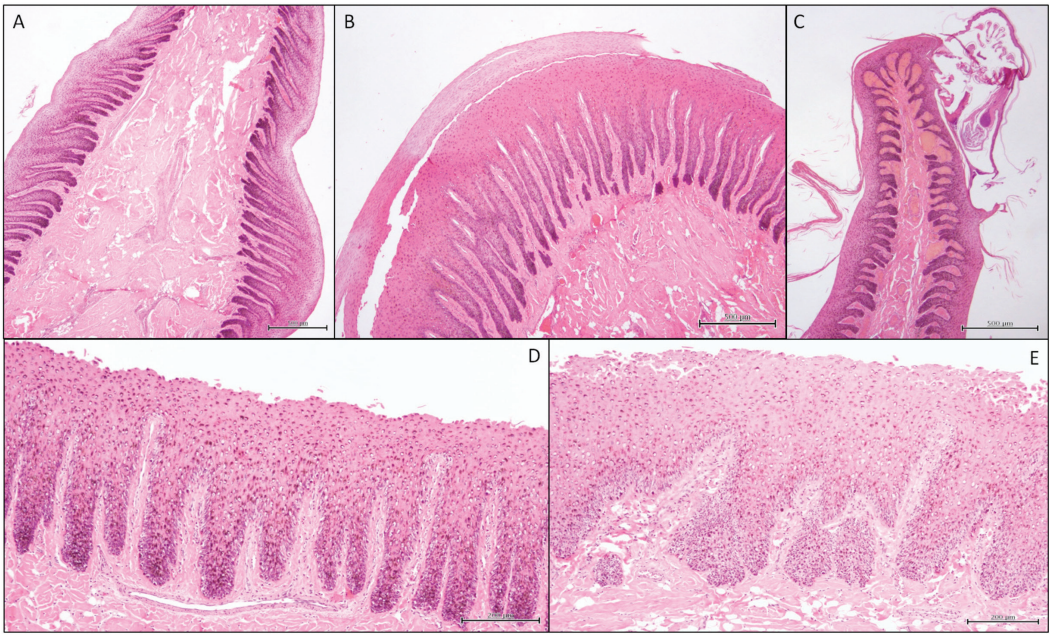

Figure 6. H&E stained photomicrographs of the (A) fluke tip, (B) leading edge, (C) trailing edge, (D) ventral mid-span, and (E) dorsal mid-span of the fluke of *Stenella coeruleoalba*. Scale bar: 500 µm, 4x objective (A-C); scale bar: 200 µm, 10x objective (D-E).

epidermis of the fluke tip was significantly thinner than that of the leading edge, dorsal mid-span, and ventral mid-span ($p < 0.05$); and the epidermis of the trailing edge was significantly thinner than that of the leading edge, dorsal mid-span, and ventral mid-span ($p < 0.05$). When combining all six sampling locations, the epidermis of *P. phocoena* was significantly thicker than that of all other species (p

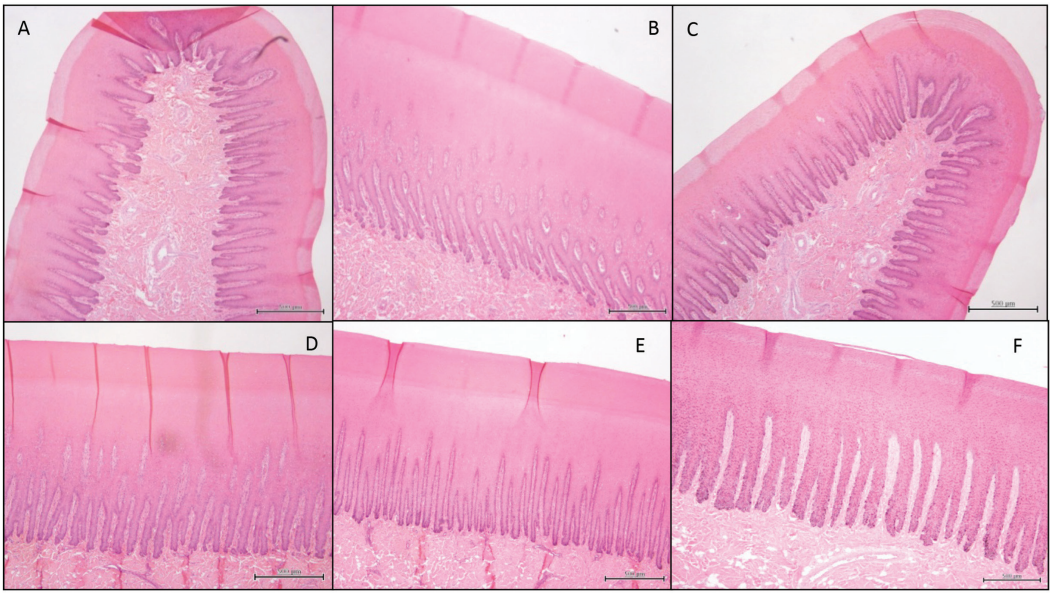

Figure 7. H&E stained photomicrographs of the (A) fluke tip, (B) leading edge, (C) trailing edge, (D) ventral mid-span, (E) dorsal mid-span of the fluke, and (F) dorsal skin of *T. truncatus*. Scale bar: 500 µm, 4x objective.

< 0.05); and the epidermal thickness of *T. truncatus* was significantly thicker than that of *K. breviceps* and *S. coeruleoalba* ($p < 0.05$).

Stratum Corneum—Based on results of the two-way ANOVA, the thickness of the stratum corneum was independent of location ($p = 0.239$, $df = 5$, $F = 1.603$) but was dependent on species ($p < 0.01$, $df = 4$, $F = 9.290$) (Figure 8B). When considering all six sampling locations for the Tukey post-hoc analysis, the stratum corneum of *T. truncatus* was significantly thicker than that of all other species ($p < 0.05$).

Stratum Spinosum—Based on results for the two-way ANOVA, the thickness of the stratum spinosum was dependent on location ($p < 0.005$, $df = 5$, $F = 7.970$) and species ($p < 0.001$, $df = 4$, $F = 20.011$). When considering all species combined for the Tukey post-hoc analysis, the stratum spinosum of the dorsal skin was significantly thicker than that of the fluke tip and trailing edge ($p < 0.01$); the stratum spinosum of the leading edge was significantly thicker than that of the fluke tip and trailing edge ($p = 0.001$); and the stratum spinosum of the ventral mid-span was significantly thicker than that of the fluke tip and trailing edge ($p < 0.05$). When combining all six sampling locations, the stratum spinosum of *P. phocoena* was significantly thicker than that of all other species ($p \leq 0.01$); and the stratum spinosum of *T. truncatus* was significantly thicker than that of *S. coeruleoalba* and *K. breviceps* ($p < 0.05$; Figure 8C).

Stratum Basale—Based on results for the two-way ANOVA, the thickness of the stratum basale was not significantly dependent upon species or location. There was no significant difference in stratum basale thickness when considering all six sampling locations for each species when conducting a Tukey post-hoc analysis.

Dermal Papilla Height—Based on results for the two-way ANOVA, dermal papilla height was significantly dependent on location ($p < 0.005$, $df = 5$, $F = 8.678$) but independent of species ($p = 0.235$, $df = 4$, $F = 1.634$). When considering all species together in a Tukey post-hoc analysis, the dermal papilla height of the dorsal skin was greater than that of the dermal papilla height of the fluke tip ($p < 0.05$) and trailing edge ($p < 0.01$). The dermal papilla height of the leading edge was greater than that of the fluke tip and trailing edge ($p < 0.005$; Figure 8D) and greater than that of the dorsal mid-span and ventral mid-span ($p < 0.05$).

Lipokeratinocyte Height—Based on results for the two-way ANOVA, lipokeratinocyte height was dependent on species ($p < 0.005$, $df = 4$, $F = 8.293$) and independent of location ($p = 0.897$, $df = 5$, $F = 0.310$). When combining all locations in a Tukey post-hoc analysis, lipokeratinocyte height was significantly greater for *P. phocoena* than for *K. breviceps* and *T. truncatus* ($p < 0.01$).

Lipokeratinocyte Area—Lipokeratinocyte cell area was dependent on species ($p < 0.005$, $df = 4$, $F = 8.051$) and independent of sampling location ($p = 0.828$, $df = 5$, $F = 0.417$). When combining all

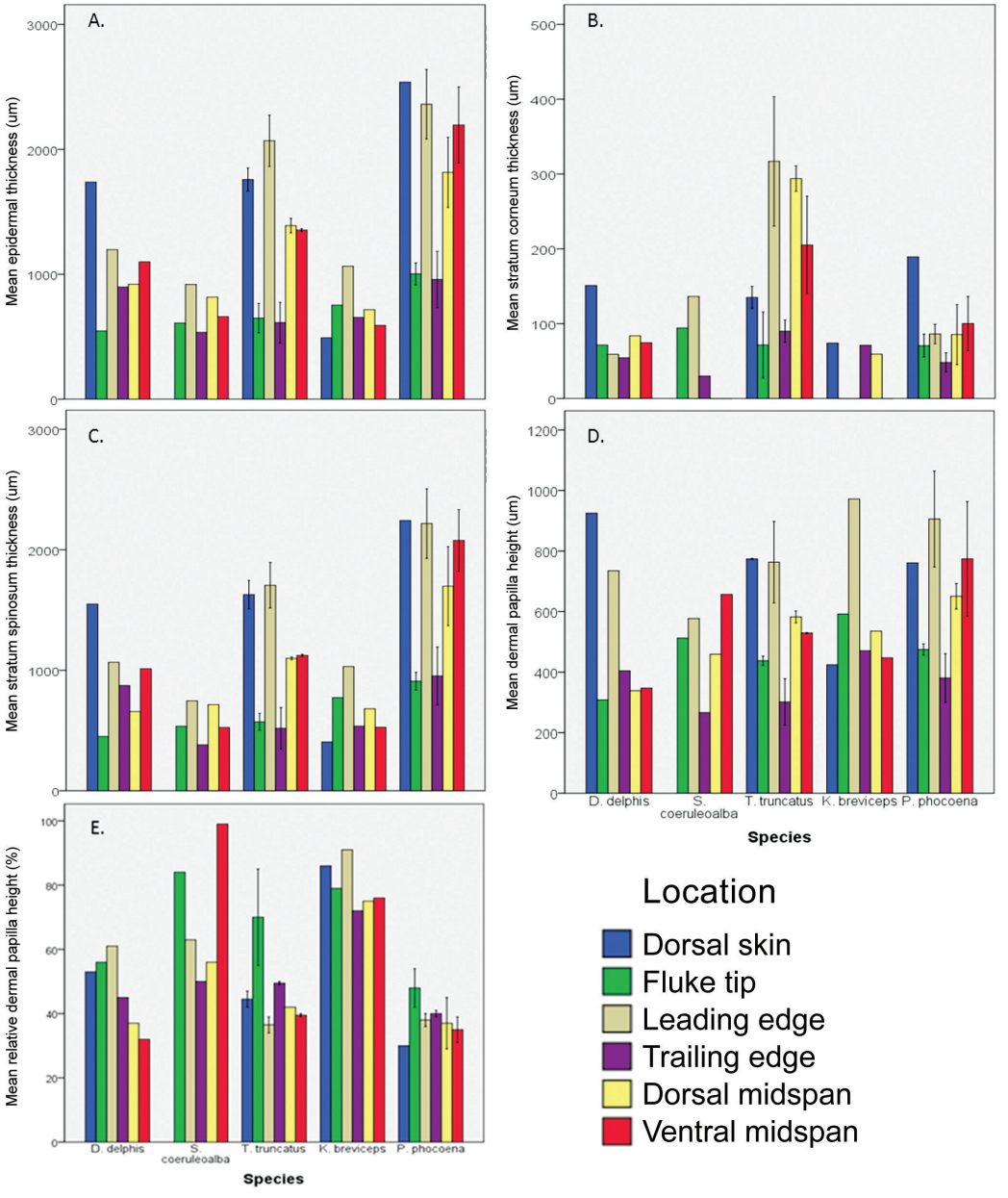

Figure 8. Mean integument characteristics measured for each species. Error bars represent ±1 SE. Legend details the sampling locations.

locations, lipokeratinocyte area was significantly greater for *P. phocoena* than for *K. breviceps* and *T. truncatus* ($p < 0.01$).

Relative Dermal Papilla Height—Based on results for the two-way ANOVA, the relative dermal papilla height was dependent on location ($p < 0.05$, $df = 5$, $F = 3.799$) and species ($p < 0.001$, $df = 4$, $F = 33.776$) (Figure 8E). Based on the Tukey post-hoc analysis, the relative dermal papilla height for all species combined was significantly greater in the fluke tip when compared to the dorsal mid-span and trailing edge ($p < 0.05$). This signifies that the dermal papillae extended further superficially in the fluke tip than in other locations. The relative dermal papilla height was greater for *K. breviceps* than for *D. delphis*,

P. phocoena, and *T. truncatus* ($p < 0.001$). The relative dermal papilla height was greater for *S. coeruleoalba* than for *P. phocoena, D. delphis*, and *T. truncatus* ($p < 0.05$). The dorsal skin of several species exhibited dermal papillae that penetrated the epidermis by greater than 50% (Table 2); and the fluke tip of all species exhibited dermal papillae that penetrated the epidermis by greater than 50% (Table 2).

Discussion

The integument of cetaceans was noted to be extremely thick (Harrison & Thurley, 1972; Ling, 1974; Sokolov, 1982; Jones & Pfeiffer, 1994). There was considerable variation in thickness among different species and regions of the body (Harrison & Thurley, 1974; Sokolov, 1982; Jones & Pfeiffer, 1994). Our study presented data that agreed with these previous findings but additionally presented new data on the composition of the integument of the fluke for a variety of cetacean species.

Differences in composition between fluke integument and dorsal body integument were observed. Overall, except for *K. breviceps*, the epidermis at the different fluke locations was thinner than the epidermis of the dorsal body. These results corresponded to the results of an examination of the epidermis of the flippers of cetaceans (Jones & Pfeiffer, 1994). In the study by Jones & Pfeiffer (1994), the skin of the ventral aspect of the flippers of the mysticete *Megaptera novaeangliae* (humpback whale), and the odontocetes *S. coeruleoalba* and *T. truncatus* was found to be thinner than the skin from the mid-dorsal body wall.

Comparisons of the various areas of the fluke that were sampled showed, for all species examined, that the epidermis of the leading edge was thicker than that of any other location on the fluke, and the leading edge and dorsal skin were generally thicker than the other sampled locations. The thick dorsal skin might be associated with the high rate of epidermal cell production on the body (Palmer & Weddell, 1964; Brown et al., 1983).

Differences in integument composition were also observed between the various species. In some locations and for some species, the stratum corneum was absent, which might have been due to variation between species or location, damage incurred to tissue samples during collection and processing, or natural sloughing of the stratum corneum. Giacometti (1967) found that the stratum corneum was absent from the fin whale (*Balaenoptera physalus*), except in specific locations (e.g., external genitalia and eyelids). Rommel & Lowenstine (2001) considered that the absence of a keratinized stratum corneum was due to continuous desquamation resulting from water friction. Due to the small sample sizes for each species in this study, it was difficult to discern which cause resulted in the absence of this layer.

Differences in the thickness of the integument were not associated with swimming performance. *D. delphis* and *S. coeruleoalba* are considered to be fast swimming species (Weber et al., 2009); *T. truncatus* and *P. phocoena* are medium-speed swimmers; and the deep-diving *K. breviceps* is considered to be a slow swimmer (Davies et al., 1998; Fish & Rohr, 1999; Weber et al., 2009). Both *P. phocoena* and *T. truncatus* possessed a thicker epidermis on the leading edge of the fluke than did faster and slower swimmers (Figure 8A). The thicker epidermis in these medium-speed species was largely attributable to a thick stratum spinosum, although *T. truncatus* also had the thickest stratum corneum of the species examined (Figure 8A-C).

The leading edge of the fluke had a greater epidermal thickness, stratum corneum thickness, stratum spinosum thickness, and dermal papilla height than the trailing edge for all species. In particular, the fluke tip and trailing edge generally had the thinnest epidermis on the fluke. Pavlov (2003) noted that the epidermal thickness of the leading edge was greater than that of the trailing edge of the dorsal fin. Similarly, the tip of the rostrum of *D. delphis* had a thicker epidermis than the rest of the body (Sokolov, 1982).

Webb (1975) and Fish & Rohr (1999) noted that shear stresses were greatest at the leading edge of the fluke, which was associated with a thicker epidermis and stratum corneum. The leading edge meets fast oncoming flow in terms of the vector quantity of the velocity that includes components relating to the animal's swimming speed and the vertical oscillations of the flukes. In addition, the flow over the flukes will be unsteady as the flukes change inclination through the stroke cycle. The stagnation point is in that position in the flow field in which the flow is momentarily stagnant (velocity = 0) (Barnard & Philpott, 1995). During the upstroke, the flukes are angled upwards with the stagnation point for flow located just below the leading edge of the fluke; whereas the stagnation point lies slightly above the leading edge during the downstroke. The shift in position of the stagnation point between upstroke and downstroke produces elevated shear forces due to changes in velocity around the curvature of the leading edge. Furthermore, the vertical oscillations of the flukes result in large accelerations and decelerations of flow. The rounded profile of the leading edge fosters a highly accelerated flow (Fish, 1998b). From the stagnation point on the leading edge, the water flow rapidly changes direction

and increases in velocity to a maximum at this maximum thickness (i.e., leading edge) of the fluke. This change in velocity leads to a steep pressure gradient over the anterior surface of the fluke (Webb, 1975). The boundary layer at the leading edge would be thin, exposing the integument to a high free-stream flow with high shear stress (Rohr et al., 1998). A thick integument at the leading edge would be capable of resisting frictional forces in a similar manner to that of calluses (Kardong, 2015). The accumulation of keratinocytes would resist the increased shear stress on the surface of the integument resulting from accelerated flow around the leading edge.

The generally thin epidermis of the fluke tip and trailing edge may be the result of the tapering of flukes at these locations. Tapering permits increased flexibility that can enhance thrust generation and propulsive efficiency (Fish, 1998b). The tips are bent downward during the upstroke and upward during the downstroke. As the tips lag behind the body of the flukes, this prevents total loss of thrust at the end of each half stroke (Bose et al., 1990). Meanwhile, flexibility at the trailing edge can potentially increase efficiency by up to 20% (Katz & Weihs, 1978). As opposed to the leading edge of the flukes, the flow over the tips and trailing edge would be lower due to flow separation, along with the production of eddies and vortices (Webb, 1975; Zhen et al., 2008), fostering reduced shear stress. The low levels of shear stress may be associated with decreased thickness of the epidermis for each species in the fluke tip and trailing edge.

In cetaceans, as in other mammals, the epidermis is connected to the dermis by thick downward extensions called rete pegs or ridges (Reeb et al., 2007). The deep ridges at the base of the epidermis form slender, flap-like projections that interdigitate with the upward projecting dermal papillae (Spearman, 1972; Reeb et al., 2007). This structural organization helps to anchor the epidermis to the dermis and reduces slippage between the layers when subjected to shear forces (Darmstadt & Dinulos, 2000). In the present study, dermal papillae of the leading edge of all species, except *S. coeruleoalba*, were in general found to be longer than at all other fluke locations. This structure was indicative of a morphology capable of resisting the high shear forces encountered at the leading edge of the flukes.

The epidermis bounding the surface of the dermal papillae is the site of rapid proliferation of epidermal cells (Palmer & Weddell, 1964). The long dermal papillae, by extending into the epidermis, increase the extent of the epidermal germinative layer (stratum basale; Harrison & Thurley, 1974). Sokolov et al. (1969) calculated the ratio of the area of the germinative layer to epidermal surface area of the general body skin of *T. truncatus* to be 13.4:1. Brown et al. (1983) obtained a similar value of 13.1:1. These ratios are nearly nine times greater than those for humans (Brown et al., 1983). The characteristically thick epidermis of cetaceans has a high capacity for cell production, relatively long turnover time, and rapid sloughing rate (Brown et al., 1983; Hicks et al., 1985; Lockyer & Morris, 1990). The rate of mitotic divisions per unit length of skin in *T. truncatus* is 250 to 290 times higher than that for humans (Brown et al., 1983), and the epidermal cells of the bottlenose dolphin are produced 11.3 times faster and have a lifespan 1.7 times longer (Hicks et al., 1985) than those of humans. A high rate of skin sloughing is considered to be a hydrodynamic benefit for cetaceans because it may decrease drag by preventing fouling due to colonization of microorganisms and macrosymbionts (e.g., barnacles; Hicks et al., 1985; St. Aubin et al., 1990; Fish & Hui, 1991).

The skin of dolphins is highly sensitive in the realm of that of human lips and fingertips (Kolchin & Belkovich, 1973; Ridgway & Carder, 1993). Dermal papillae serve a tactile function (Cauna, 1954), contributing to the level of sensitivity. Free and encapsulated (e.g., Meissner corpuscles) nerve endings have been identified within dermal papillae that enhance tactile sensitivity (Cauna & Ross, 1960; Halata & Munger, 1983; Kelly et al., 2005). The highly innervated dermal papillae have their tips closer to the surface of the epidermis. Due to the great penetration in the integument of the dermal papillae, mechanoreceptors, such as the Meissner corpuscles, provide a high detection ability for sensory function for cetaceans (Cauna, 1954; Cauna & Ross, 1960; Palmer & Weddell, 1964; Khomenko & Khadzhinskiy, 1974; Guyton & Hall, 1996). In addition to tactile sensitivity, mechanoreceptors in the dermis of cetaceans may allow for the detection of low-frequency vibrations (Dehnhart, 1990). The abundance of dermal papillae and sensory nerve endings close to the surface of the skin (Table 2) may allow for the ability of cetaceans to sense water movement surrounding the flukes.

Dermal papillae are well supplied with blood vessels (Yen & Braverman, 1976; Braverman & Yen, 1977), including arteriovenous anastomoses (Palmer & Weddell, 1964). In humans, capillaries in the dermal papillae have been shown to provide a nutritive component to the skin, as well as provide a means of temperature control (Braverman, 2000). During diving, marine mammals initiate a dive response (Kooyman, 1989; Williams et al., 1999). The high penetration of the epidermis by dermal papillae in cetaceans may lead to effective

thermoregulatory control during diving, allowing the flukes to act as thermal windows.

Thermal windows are poorly insulated peripheral areas that allow the transfer of excess heat by means of conduction and convection during periods of high activity or in a warm environment (Noren et al., 1999; Williams et al., 1999). Williams et al. (1999) show that the majority of the fluke acts as a thermal window, although, in relation to total surface area, peripheral thermal windows comprise only 30% of the total surface area of *T. truncatus*, limiting overall heat loss from the body (Noren et al., 1999). Possessing papillae, the tips of which lie close to the surface, would enhance heat exchange capabilities even over a limited surface area. In the current study, a high level of penetration (> 50%) of the epidermis by dermal papillae was found generally throughout the flukes with the exception of the *P. phocoena* (Table 2). The lower level of penetration (30 to 48%) by the dermal papillae for *P. phocoena* compared to the other species could be related to its small size and cold-water distribution in high northern latitudes to conserve heat (Bjørge & Tolley, 2018).

For *D. delphis* and *T. truncatus*, the mean dermal papilla height for the dorsal skin was greater than that of all fluke locations (Figure 8D). In deep-diving cetaceans, such as the sperm whale (*Physeter macrocephalus*), the dermal papillae tended to penetrate further into the stratum corneum than in shallow diving cetaceans (Sokolov, 1982). Ling (1974) and Sokolov (1982) noted that the height of the dermal papillae and epidermal pegs of deep-diving cetaceans are greater (i.e., extending further into the stratum corneum) than those of cetaceans living and foraging in shallow water. The relative increased height of the dermal papillae in deep divers helps to strengthen the epidermal-dermal junction and enable it to accommodate changes in the shape of the skin resulting from compression during a dive (Ridgway et al., 1969; Greenwood et al., 1974; Moore et al., 2011). Stromberg (1989), however, considered any functional explanation for the size difference associated with foraging depth to be unsubstantiated. *K. breviceps*, examined in this study, was closely related to *P. macrocephalus*, a deep diver. Although the mean relative dermal papilla heights for the leading edge, trailing edge, and fluke tip of *K. breviceps* were greater than those of any of the other cetaceans examined in this study, the dermal papillae of the dorsal skin were shorter than those of *D. delphis*, *P. phocoena*, and *T. truncatus*. It was interesting to note that the morphology of the dermal papillae of *K. breviceps* was distinctly different from that of the other cetaceans examined. This triangular shape displayed branching and variable thickness, which was not evident in the straight and narrow morphology generally observed for cetaceans. It was also interesting to note that *K. breviceps* is the only species sampled that possessed dermal papillae that penetrated the depth of the epidermis by greater than 50% for all locations. The form and size of the dermal papillae of *K. breviceps* would yield a relatively greater surface area, which would potentially resist slippage between the epidermis and dermis, provide greater tactile sensitivity, aid in epidermal cell proliferation, and increase vascularization for thermoregulation.

Analysis of the epidermis of the flukes of five species of cetacean revealed a relatively thick epidermis along the leading edge, with thinner epidermis at the fluke tip and trailing edge. Because the leading edge is the location on the fluke that is exposed to the greatest water pressure, a thicker epidermis and taller dermal papillae may be adaptations for withstanding the increased shear force to which this region is subjected. Increased sloughing may occur on the leading edge to compensate for wear induced by friction with the water. Tall dermal papillae in the leading edge result in a large surface area and complex interdigitation of the stratum basale, and, thus, high cell proliferation capabilities.

Acknowledgments

We wish to express our appreciation to Danielle Adams, William Gough, Kelsey Tennett, and Dr. Anne Boettger at West Chester University for specimen preparation and to Kathleen Dudzinski and the reviewers for their helpful comments on the manuscript. We are grateful for the specimens collected by the New Jersey Marine Mammal Stranding Center, the Virginia Aquarium, and University of North Carolina Wilmington. Tissue samples were processed for light microscopy by Karie Durynski at the New Bolton Center Histology Lab of the University of Pennsylvania Veterinary School. Specimens were collected under a letter to FEF from the National Marine Fisheries Service. This work was supported by a grant from the Multidisciplinary University Research Initiative of the Office of Naval Research (N000141410533, 2014) to FEF.

Literature Cited

Barnard, R. H., & Philpott, D. R. (1995). *Aircraft flight*. Longman.

Baum, C., Meyer, W., Roessner, D., Siebers, D., & Fleischer, L. G. (2001). A zymogel enhances the self-cleaning abilities of the skin of the pilot whale (*Globicephala melas*). *Comparative, Biochemistry and Physiology A*, *130*, 835-847. https://doi.org/10.1016/S1095-6433(01)00445-7

Baum, C., Simon, F., Meyer, W., Fleischer, L. G., Siebers, D., Kacza, J., & Seeger, J. (2003). Surface properties of the skin of the pilot whale *Globicephala melas*. *Biofouling*, *19*, 181-186. https://doi.org/10.1080/0892701031000061769

Berta, A., Sumich, J. L., & Kovacs, K. M. (2015). *Marine mammals: Evolutionary biology* (3rd ed.). Academic Press. https://doi.org/10.1016/B978-0-12-397002-2.01001-2

Bjørge, A., & Tolley, K. A. (2018). Harbor porpoise. In B. Würsig, J. G. M. Thewissen, & K. M. Kovacs (Eds.), *Encyclopedia of marine mammals* (pp. 448-451). Academic Press. https://doi.org/10.1016/B978-0-12-804327-1.00144-8

Bose, N., Lien, J., & Ahia, J. (1990). Measurements of the bodies and flukes of several cetacean species. *Proceedings of the Royal Society of London B: Biological Sciences*, *242*, 163-173. https://doi.org/10.1098/rspb.1990.0120

Braverman, I. M. (2000). The cutaneous microcirculation. *Journal of Investigative Dermatology Symposium Proceedings*, *5*, 3-9. https://doi.org/10.1046/j.1087-0024.2000.00010.x

Braverman, I. M., & Yen, A. (1977). Ultrastructure of the human dermal microcirculation: II. The capillary loops of the dermal papillae. *Journal of Investigative Dermatology*, *68*, 44-52. https://doi.org/10.1111/1523-1747.ep12485165

Brown, W. R., Geraci, J. R., Hicks, B. D., St. Aubin, D. J., & Schroeder, J. R. (1983). Epidermal cell proliferation in the bottlenose dolphin (*Tursiops truncatus*). *Canadian Journal of Zoology*, *61*, 1587-1590. https://doi.org/10.1139/z83-213

Cauna, N. (1954). Nature and functions of the papillary ridges of the digital skin. *Anatomical Record*, *119*, 449-468. https://doi.org/10.1002/ar.1091190405

Cauna, N., & Ross, L. L. (1960). The fine structures of Meissner's touch corpuscles of human fingers. *Journal of Biophysical and Biochemical Cytology*, *8*, 467-482. https://doi.org/10.1083/jcb.8.2.467

Darmstadt, G. L., & Dinulos, J. G. (2000). Neonatal skin care. *Pediatric Clinic of North America*, *47*, 757-782. https://doi.org/10.1016/S0031-3955(05)70239-X

Davies, R. W., Fargion, G. S., May, N., Leming, T., Baumgartner, M., Evans, W. E., Hansen, L. J., & Mullin, K. (1998). Physical habitat of cetaceans along the continental slope in the north-central and western Gulf of Mexico. *Marine Mammal Science*, *14*, 490-507. https://doi.org/10.1111/j.1748-7692.1998.tb00738.x

Dehnhart, G. (1990). Preliminary results from psychophysical studies on the tactile sensitivity in marine mammals. In J. A. Thomas & R. A. Kastelein (Eds.), *Sensory abilities of cetaceans* (NATO ASI Series [Series A: Life Sciences], Vol. 196, pp. 435-446). Springer. https://doi.org/10.1007/978-1-4899-0858-2_30

Felts, W. J. L. (1966). Some functional and structural characteristics of cetacean flippers and flukes. In K. S. Norris (Ed.), *Whales, dolphins, and porpoises* (pp. 255-276). University of California Press.

Fish, F. E. (1993). Influence of hydrodynamic design and propulsive mode on mammalian swimming energetics. *Australian Journal of Zoology*, *42*, 79-101. https://doi.org/10.1071/ZO9940079

Fish, F. E. (1998a). Comparative kinematics and hydrodynamics of odontocete cetaceans: Morphological and ecological correlations with swimming performance. *Journal of Experimental Biology*, *201*, 2867-2877. https://jeb.biologists.org/content/201/20/2867.short

Fish, F. E. (1998b). Biomechanical perspective on the origin of cetacean flukes. In J. G. M. Thewissen (Ed.), *The emergence of whales: Evolutionary patterns in the origin of cetacean* (pp. 303-324). Plenum Press. https://doi.org/10.1007/978-1-4899-0159-0_10

Fish, F. E. (2006). The myth and reality of Gray's paradox: Implication of dolphin drag reduction for technology. *Bioinspiration and Biomimetics*, *1*, R17-R25. https://doi.org/10.1088/1748-3182/1/2/R01

Fish, F. E., & Hui, C. L. (1991). Dolphin swimming—A review. *Mammal Review*, *21*, 181-195. https://doi.org/10.1111/j.1365-2907.1991.tb00292.x

Fish, F. E., & Rohr, J. J. (1999). *Review of dolphin hydrodynamics and swimming performance* (Technical Report 1801). U.S. Navy SPAWAR Systems Center. https://doi.org/10.21236/ADA369158

Fish, F. E., Howle, L. E., & Murray, M. M. (2008). Hydrodynamic flow control in marine mammals. *Integrative and Comparative Biology*, *48*, 788-800. https://doi.org/10.1093/icb/icn029

Fish, F. E., Legac, P., Williams, T. M., & Wei, T. (2014). Measurement of hydrodynamic force generation by swimming dolphins using bubble DPIV. *Journal of Experimental Biology*, *217*, 252-260. https://doi.org/10.1242/jeb.087924

Geraci, J. R., & Lounsbury, V. J. (2005). *Marine mammals ashore: A field guide for stranding* (2nd ed.). National Aquarium in Baltimore.

Geraci, J. R., Hicks, B. D., & St. Aubin, D. J. (1979). Dolphin pox: A skin disease of cetaceans. *Canadian Journal of Comparative Medicine*, *43*, 399-404.

Giacometti, L. (1967). The skin of the whale (*Balaenoptera physalus*). *Anatomical Record*, *159*, 69-76. https://doi.org/10.1002/ar.1091590110

Gingerich, P. D., Raza, S. M., Arif, M., Anwar, M., & Zhou, X. (1994). New whale from the Eocene of Pakistan and the origin of cetacean swimming. *Nature*, *368*, 844-847. https://doi.org/10.1038/368844a0

Ginter, C. C., Boettger, S. A., & Fish, F. E. (2011). Morphology and microanatomy of harbor porpoise (*Phocoena phocoena*) dorsal fin tubercles. *Journal of Morphology*, *272*, 27-33. https://doi.org/10.1002/jmor.10891

Greenwood, A. G., Harrison, R. J., & Whitting, H. W. (1974). Functional and pathological aspects of the skin of marine mammals. In R. J. Harrison (Ed.), *Functional anatomy of marine mammals* (Vol. 2, pp. 73-110). Academic Press.

Guyton, A. C., & Hall, J. E. (1996). *Textbook of medical physiology*. Saunders.

Halata, Z., & Munger, B. L. (1983). The sensory innervation of primate facial skin. II. Vermilion border and mucosa

of lip. *Brain Research Reviews*, *5*, 81-107. https://doi.org/10.1016/0165-0173(83)90022-X

Haldiman, J. T., & Tarpley, R. J. (1993). Anatomy and physiology. In J. J. Burns, J. J. Montague, & C. J. Cowles (Eds), *The bowhead whale* (pp. 71-154). Allen Press.

Haldiman, J. T., Henk, W. G., Henry, R. W., Albert, T. F., Abdelbaki, Y. Z., & Duffield, D. W. (1985). Epidermal and papillary dermal characteristics of the bowhead whale (*Balaena mysticetus*). *Anatomical Record*, *211*, 391-402. https://doi.org/10.1002/ar.1092110404

Harrison, R. J., & Thurley, K. W. (1974). Structure of the epidermis in *Tursiops*, *Delphinus*, *Orcinus*, and *Phocoena*. In R. J. Harrison (Ed.), *Functional anatomy of marine mammals* (Vol. 2, pp. 45-71). Academic Press.

Hicks, B. D., St. Aubin, D. J., Geraci, J. R., & Brown, W. R. (1985). Epidermal growth in the bottlenose dolphin, *Tursiops truncatus*. *Journal of Investigative Dermatology*, *85*, 60-63. https://doi.org/10.1111/1523-1747.ep12275348

Jones, F. M., & Pfeiffer, C. J. (1994). Morphometric comparison of the epidermis in several cetacean species. *Aquatic Mammals*, *20*(1), 29-34.

Kardong, K. V. (2015). *Vertebrates: Comparative anatomy, function, evolution*. McGraw-Hill.

Katz, J., & Weihs, D. (1978). Hydrodynamic propulsion by large amplitude oscillation of an airfoil with chordwise flexibility. *Journal of Fluid Mechanics*, *88*, 485-497. https://doi.org/10.1017/S0022112078002220

Kelly, E. J., Terenghi, G., Hazari, A., & Wiberg, M. (2005). Nerve fibre and sensory end organ density in the epidermis and papillary dermis of the human hand. *British Journal of Plastic Surgery*, *58*, 774-779. https://doi.org/10.1016/j.bjps.2004.12.017

Khomenko, B. G., & Khadzhinskiy, V. G. (1974). Morphological and functional principles underlying cutaneous reception in dolphins. *Bionika*, *8*, 106-113.

Kolchin, S., & Belkovich, V. (1973). Tactile sensitivity in *Delphinus delphis*. *Zoologocheskii Zhurnal*, *52*, 620-622.

Kooyman, G. L. (1989). *Diverse divers*. Springer-Verlag. https://doi.org/10.1007/978-3-642-83602-2

Kramer, M. O. (1960a). Boundary layer stabilization by distributed damping. *Journal of the American Society of Naval Engineers*, *72*, 25-33. https://doi.org/10.1111/j.1559-3584.1960.tb02356.x

Kramer, M. O. (1960b). The dolphins' secret. *New Scientist*, *7*, 1118-1120.

Ling, J. K. (1974). The integument of marine mammals. In R. J. Harrison (Ed.), *Functional anatomy of marine mammals* (Vol. 2, pp. 1-44). Academic Press.

Lockyer, C. H., & Morris, R. J. (1990). Some observations on wound healing and persistence of scars in *Tursiops truncatus*. *Reports of the International Whaling Commission*, *12*, 113-118.

Menon, G. K., Grayson, S., Brown, B. E., & Elias, P. M. (1986). Lipokeratinocytes of the epidermis of a cetacean (*Phocena phocena*). *Cell and Tissue Research*, *244*, 385-394. https://doi.org/10.1007/BF00219214

Moore, M. J., Hammar, T., Arruda, J., Cramer, S., Dennison, S., Montie, E., & Fahlman, A. (2011). Hyperbaric computed tomographic measurement of lung compression in seals and dolphins. *Journal of Experimental Biology*, *214*, 2390-2397. https://doi.org/10.1242/jeb.055020

Noren, D. P., Williams, T. M., Berry, P., & Butler, E. (1999). Thermoregulation during swimming and diving in bottlenose dolphins, *Tursiops truncatus*. *Journal of Comparative Physiology B*, *169*, 93-99. https://doi.org/10.1007/s003600050198

Pabst, D. A. (1996). Springs in swimming animals. *American Zoologist*, *36*, 723-735. https://doi.org/10.1093/icb/36.6.723

Palmer, E., & Weddell, G. (1964). The relationship between structure, innervation and function of the skin of the bottle nose dolphin (*Tursiops truncatus*). *Proceedings of the Zoological Society of London*, *143*, 553-568. https://doi.org/10.1111/j.1469-7998.1964.tb03881.x

Parry, D. A. (1949). The structure of whale blubber, and a discussion of its thermal properties. *Quarterly Journal of Microscopical Science*, *3*, 13-25. https://doi.org/10.1086/266134

Pavlov, V. V. (2003). Wing design and morphology of the harbor porpoise dorsal fin. *Journal of Morphology*, *258*, 284-295. https://doi.org/10.1002/jmor.10135

Reeb, D., Best, P. B., & Kidson, S. H. (2007). Structure of the integument of southern right whales, *Eubalaena australis*. *Anatomical Record*, *290*, 596-613. https://doi.org/10.1002/ar.20535

Ridgway, S. H., & Carder, D. A. (1993). Features of dolphin skin with potential hydrodynamic importance. *IEEE Engineering in Medicine and Biology*, *12*, 83-88. https://doi.org/10.1109/51.232347

Ridgway, S. H., Scronce, B. L., & Kanwisher, J. (1969). Respiration and deep diving in the bottlenose porpoise. *Science*, *166*, 1651-1654. https://doi.org/10.1126/science.166.3913.1651

Rohr, J., Latz, M. I., Fallon, S., Nauen, J. C., & Hendricks, E. (1998). Experimental approaches towards interpreting dolphin-stimulated bioluminescence. *Journal of Experimental Biology*, *201*, 1447-1460.

Romanenko, E. V. (1995). Swimming of dolphins: Experiments and modeling. *Experimental Biology*, *49*, 21-33.

Rommel, S. A., & Lowenstine, L. J. (2001). Gross and microscopic anatomy. In L. A. Dierauf & F. M. D. Gulland (Eds.), *Marine mammal medicine* (pp. 129-164). CRC Press. https://doi.org/10.1201/9781420041637.sec2

Sokolov, V. E. (1982). *Mammal skin*. University of California Press.

Sokolov, V., Bulina, I., & Rodionov, V. (1969). Interaction of dolphin epidermis with flow boundary layer. *Nature*, *222*, 267-268. https://doi.org/10.1038/222267a0

Spearman, R. I. C. (1972). The epidermal stratum corneum of the whale. *Journal of Anatomy*, *113*, 373-381.

St. Aubin, D. J., Smith, T. G., & Geraci, J. R. (1990). Seasonal epidermal molt in beluga whales, *Delphinapterus leucas*. *Canadian Journal of Zoology*, *68*, 359-367. https://doi.org/10.1139/z90-051

Stromberg, M. W. (1989). Dermal-epidermal relationships in the skin of the bottlenose dolphin (*Tursiops truncatus*). *Anatomia, Histologia, Embryologia*, *81*, 1-13. https://doi.org/10.1111/j.1439-0264.1989.tb00575.x

Struntz, D. J., McLellan, W. A., Dillaman, R. M., Blum, J. E., Kucklick, J. R., & Pabst, D. A. (2004). Blubber development in bottlenose dolphins (*Tursiops truncatus*). *Journal of Morphology*, *259*, 7-20. https://doi.org/10.1002/jmor.10154

Webb, P. W. (1975). Hydrodynamics and energetics of fish propulsion. *Bulletin of the Fisheries Research Board of Canada*, *190*, 1-156. http://pascal-francis.inist.fr/vibad/index.php?action=getRecordDetail&idt=PASCAL7536509928

Weber, P. W., Howle, L. E., Murray, M. M., & Fish, F. E. (2009). Lift and drag performance of odontocete cetacean flippers. *Journal of Experimental Biology*, *212*, 2149-2158. https://doi.org/10.1242/jeb.029868

Williams, T. M., Noren, D., Berry, P., Estes, J. A., Allison, C., & Kirtland, J. (1999). The diving physiology of bottlenose dolphins (*Tursiops truncatus*). III. Thermoregulation at depth. *Journal of Experimental Biology*, *202*, 2763-2769.

Williams, T. M., Davis, R. W., Fuiman, L. A., Francis, J., Le Boeuf, B. J., Horning, M., Calambokidis, J., & Croll, D. A. (2000). Sink or swim: Strategies for cost-efficient diving by marine mammals. *Science*, *288*, 133-136. https://doi.org/10.1126/science.288.5463.133

Yen, A., & Braverman, I. M. (1976). Ultrastructure of the human dermal microcirculation: The horizontal plexus of the papillary dermis. *Journal of Investigative Dermatology*, *66*, 131-142. https://doi.org/10.1111/1523-1747.ep12481678

Zhen, L., Hyun, B. S., Kim, M. R., & Jin, J. Y. (2008). Experimental and numerical study for hydrodynamic characteristics of an oscillating hydrofoil. *Journal of Hydrodynamics Series B*, *20*, 280-287. https://doi.org/10.1016/S1001-6058(08)60058-X