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Morphology and Microanatomy of Harbor Porpoise (Phocoena phocoena) Dorsal Fin Tubercles

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Title: Morphology and Microanatomy of Harbor Porpoise (*Phocoena phocoena*) Dorsal Fin Tubercles

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Short title: Harbor Porpoise Dorsal Fin Tubercles

ABSTRACT

The unique pattern of small tubercles on the leading edge of the dorsal fins of harbor porpoises (*Phocoena phocoena*) has been widely noted in the literature, though their structure or function has never been conclusively identified. We examined external morphology and microanatomy of the tubercles for further understanding of the nature of the tubercles. Measurements were taken of height and peak-to-peak distance of the tubercles (*n* = 12-19/fin) using scaled photographs. Mean tubercle height was standardized as a percentage of the dorsal fin height and ranged from 0.63% to 0.87%. Mean peak-to-peak distance ranged from 4.2 ± 2.0 mm to 5.6 ± 2.0 mm. The microstructure analysis of the dorsal fin leading edge, trailing edge and tubercles revealed an epidermal thickness of 0.7-2.7 mm with the thickest epidermis at the tubercular apex. The epidermis contained three distinct strata (=layers), including stratum corneum, spinosum and basale. The stratum corneum was significantly thickened in tubercles ($P < 0.001$), over four times thicker than in the leading or trailing edge of the fin. The stratum spinosum, composed of lipokeratinocytes, was significantly thinner ($P < 0.001$) in the trailing edge than in the other two sites. There was no significant difference in the stratum basale among the three sites. **Volume fraction of lipokeratinocytes was significantly higher ($P = 0.002$) at the sides of the leading edge and the apex of the tubercles, while volume fraction of lamellar oil bodies was significantly lower at the apex of the tubercles**. Though the function of the tubercles is unknown, their position, hardened structure and increased epidermal stratum corneum suggest that they may have hydrodynamic importance.

KEYWORDS: harbor porpoise, *Phocoena phocoena*, tubercle, epidermal strata, dermal composition

INTRODUCTION

Species of the taxonomic family Phocoenidae possess small tubercles on the leading edge of the dorsal fin (Evans et al., 2001; Fish et al., 2008), with the exception of Dall's porpoise (*Phocoenoides dalli*; Willis et al., 2004). This phenomenon has been best recorded for the harbor porpoise (*Phocoena phocoena*), though the tubercles have never been studied in detail (Read, 1999a; Fish et al., 2008).

Efficient movement through water is known to be one of the greatest challenges faced by marine organisms, particularly cetaceans. Since cetaceans must also navigate at the water surface to breathe, they incur wave and spray drag components in addition to the frictional and pressure drag components experienced by a fully submerged object (Hoerner, 1965; Fish et al., 1991). The relatively large body sizes of cetaceans, compared to many other marine animals, also results in greater drag and have required these animals to develop novel adaptations to increase their swimming efficiency. One adaptation that has only recently been investigated is the use of tubercles, or bumpy projections, to regulate water movement around the body. Large tubercles on the leading edge of humpback whale (*Megaptera novaeangliae*) flippers have previously been shown to modify water flow and provide hydrodynamic advantage (Miklosovic et al., 2004).

The epidermis of *P. phocoena* has been described previously (Parry, 1949; Sokolov, 1960; Harrison and Thurley, 1974; Ling, 1974; Sokolov, 1982; Menon et al., 1986; Knospe, 1998), although the numbers of different strata have been debated. Parry (1949) noted a superficial stratum corneum and deep stratum germinativum (or basale) in his analysis of *P. phocoena* epidermis. However, Ling (1974), Sokolov (1960, 1982) and Pfeiffer and Jones (1993) documented three out of the five typical mammalian epidermal layers in cetaceans: the stratum germinativum (basale), stratum spinosum and stratum corneum, while Harrison and Thurley

(1974) described four epidermal layers: stratum basale, stratum spinosum, stratum intermedium and stratum externum. Dermal papillae extending into the epidermis from dermal ridges have also been documented (Parry, 1949; Pavlov, 2006). These studies have never included descriptions of the tubercle projections. To our knowledge, the edges of the dorsal fin have not been specifically characterized and there is no quantitative data on the epidermal and dermal composition of the tubercles. Determining the composition of these structures is the first step in revealing their origin and influence, if any, on the hydrodynamics of the porpoise. In this study, we examine external morphological characteristics and microanatomy of the tubercles, as well as the leading and trailing edges of the dorsal fin.

MATERIAL AND METHODS

Dorsal Fin Samples

Dorsal fins from five adult harbor porpoises (*Phocoena phocoena*), three males and two females, were analyzed. All samples were obtained, under a letter from NMFS Northeast Regional Office held by FEF, from beached animals that were recovered by the Marine Mammal Stranding Center (Brigantine, NJ) from 2004 to 2006 and necropsied at the University of Pennsylvania Veterinary School, New Bolton Center.

External Morphology

For analysis of the external morphology, scaled photographs of each fin were made using a Sony Cyber-shot DSC-W5 camera. Measurements were made of the height of each tubercle to the nearest 0.1 mm and the peak-to-peak distances between tubercles to the nearest 0.1 mm (Fig. 1A) using ImageJ software (NIH: available at http://rsbweb.nih.gov/ij/). **Photographs of the whole dorsal fins were used in ImageJ to measure the total dorsal fin height to the nearest**

0.1 mm, following the Committee on Marine Mammals (1961) and Read and Tolley (1997). Tubercle height was standardized as a percent of the total dorsal fin height. Overall length, weight and sex were obtained from the Level A data sheets for the porpoises (NOAA) and measurements made during necropsies.

Microanatomy Samples

Three *P. phocoena* dorsal fins were used for microanalysis. Each fin was sampled at five locations: one smooth leading edge section, two leading edge tubercles and two trailing edge sections (Fig. 1B). Trailing edge sections were taken at approximately the same height as the leading edge sample and one tubercle sample. **All samples penetrated 5 mm into the tissue to enable us to sample differences in the epidermal and dermal structure. The epidermis in the family Delphinidae has been documented between 0.6-3.5 mm (Harrison and Thurley, 1974).**

Sample Fixation and Embedding

Each sample was fixed for 2 h in primary fixative (3% glutaraldehyde in 0.2 ~~M~~ M sodium cacodylate buffer), washed in cacodylate buffers of decreasing salt concentrations and followed by decalcificat in 5% sodium salt EDTA (Ethylenediamine Tetraacetic acid) in sodium cacodylate buffer. Post-fixation in 1% osmium tetroxide in 0.2 ~~M~~ M cacodylate buffer to establish presence of lipids in the lamellar bodies of the stratum spinosum was followed by dehydration in increasing ethanol concentrations up to 100% followed by xylene.

Samples were embedded in paraffin and sectioned to 5 µm by the University of Pennsylvania Veterinary School New Bolton Center's Large Animal Pathology Laboratory. The

slides were rehydrated and stained with hematoxylin and eosin. Following dehydration all slides were mounted with Permount (Fisher Scientific).

Microanatomy

Epidermal strata were defined and described previously by Ling (1974), Sokolov (1960, 1982) and Pfeiffer and Jones (1993) and their definitions for three epidermal layers, stratum corneum, stratum spinosum and stratum basale (or germinativum), were retained. The thickness (mm) of each of the three observed epidermal strata was measured using an Olympus BX40 microscope (Hiltech Instruments, Edgemont, PA) and recorded as apical and lateral measurements (top of the section and both sides, respectively; Fig. 1C). The stratum spinosum was measured from the end of the stratum corneum to the top of a dermal papilla and from the end of the stratum corneum to the bottom of a dermal papilla and all measurements were averaged. The thickness of the stratum basale was measured at both the top and bottom of a dermal papilla and measurements were averaged. The height of the dermal papillae (mm) was measured for 10 apical and 10 lateral papillae for each sample to analyze the mechanical connection of the epidermis and underlying dermis.

Stereology

Lamellar oil bodies were only obvious in the stratum spinosum of the dorsal fin. Volume fractions (the relative proportion of the different cell types) of lipokeratinocytes and their lamellar oil bodies (terminology following Menon et al., 1986) were determined using stereology. A 0.1 mm^2 grid was used with a camera lucida and overlaid over a 10X magnified area of each sample. Measurements were again divided into apical and lateral measurements, i.e.,

the top of the section (0.5 mm on each side of the apex) and the right and left sides (compiled as lateral). Photographs of sections were taken using a Zeiss Axioplan 2 microscope and AxioVision 4.6 software.

Statistical Analyses

All macro and microanatomy measurements were compared using a One-Way ANOVA in SigmaStat (Systat Software, Inc., San Jose, CA). Correlations were evaluated using JMP (version 8; SAS Institute, Inc., Cary, NC). Prior to statistical analyses, assessments of the assumptions of normality (Kolmogorov-Smirnov Test) and homoscedacity (Spearman-Rank Correlation) were conducted. An arcsine transformation was conducted to normalize the external morphology data prior to statistical analysis. Means were expressed as ± one standard deviation. Results were determined to be statistically significant at $P < 0.05$.

RESULTS

External Morphology

The number of tubercles per dorsal fin ranged from 12 to 19. The tubercles were located along the leading edge of the dorsal fin, although they were present primarily at the fin tip. **The area along the leading edge in which tubercles were found was not a fixed distance but a proportion of the overall fin size**. Mean tubercle height as a percentage of dorsal fin height ranged from 0.63% to 0.87% but there were no significant differences between individuals (P = 0.956; Fig. 2A). Mean peak-to-peak distance between tubercles ranged from 4.2±2.0 mm to 5.6±2.0 mm and porpoises did not significantly differ from each other (P = 0.204; Fig. 2B). The porpoise with the lowest mean tubercle height showed the greatest mean peak-to-peak distance

(Fig. 2A,B) but there was no significant correlation between tubercle heights and peak-to-peak distances ($P = 0.858$). The number of tubercles along the fin did not appear to affect either height or peak-to-peak distance.

Microanatomy

Three of the five typical mammalian epidermal strata were observed during microanalysis: a stratum corneum (Fig. 3A,B), stratum spinosum (Fig. 3C) and stratum basale (Fig. 3D). Mean values for the measured thickness of the total epidermis were 2.3±0.1 mm, 2.6±0.3 mm and 1.0±0.1 mm for the leading edge, tubercle and trailing edge samples, respectively (Fig. 4A). The apex of the tubercle samples showed the greatest mean stratum corneum thickness at 1.1±0.0 mm (Fig. 3A, 4B) while the thickness of the stratum corneum was similar in lateral parts of the tubercles, and both the apical and lateral parts of the leading and trailing edges of the dorsal fin. It was observed that the stratum spinosum was composed of previously described lipokeratinocytes containing lamellar oil bodies (Fig. 3C inset). The thickness of the stratum spinosum was significantly decreased at a mean of 0.6±0.1 mm between the apical and lateral portions of the trailing edge of the dorsal fin ($P < 0.001$). The stratum basale did not differ in thickness between the leading edge, tubercle and trailing edge at either the apical or lateral portion ($P = 1.000$).

Dermal papillae (extensions of the dermis into the epidermis) were significantly larger ($P < 0.001$) at the apex of the leading edge and tubercle with 1.2±0.1 mm and 1.1±0.1 mm, respectively, compared to the **apical dermal papillae** of the trailing edge and the **lateral dermal papillae** of leading, trailing edge and tubercle (Fig. 5).

Stereology

The distribution of lipokeratinocytes and lamellar oil bodies in the stratum spinosum was quantified using stereology. Volume fractions of lipokeratinocytes were significantly higher in the lateral portions of the leading edge and apical portion of the tubercle (P = 0.002) at 58.89±4.00% and 62.83±0.85%, respectively, than in any other portion of the fin (Fig. 6). The volume fractions of lamellar oil bodies were significantly lower in the apical portion of the tubercle ($P < 0.001$) at 37.17±0.37%.

DISCUSSION

Cetaceans have a thick epidermis that ranges from 1.0-3.5 mm among species (Pfeiffer and Jones, 1993). Mean epidermal thickness in this study falls within this range for all sites investigated along the dorsal fin of *P. phocoena*. Pavlov (2003) found that epidermal thickness of *P. phocoena* dorsal fins generally decreases from leading edge to trailing edge. **However, the present study documents an increase in epidermal thickness along the leading edge of the dorsal fin at the sites of the tubercles.** Sokolov (1982) analyzed *P. phocoena* and reported a significant difference in thickness of the stratum corneum on the posterior and anterior edges of the dorsal fin, 28 µm and 830 µm, respectively. Sokolov (1982) also noted the presence of 10 to 11 corneous protuberances on the anterior edge of the dorsal fin and gave maximum measurements of 3 mm long, 2 mm wide and 0.9 mm high. **The results of the present study recorded the largest tubercle height of 1.1 mm, which is very close to the maximum height reported by Sokolov (1982), though the average tubercle height in the present study was much lower.** Sokolov (1982) also concluded that the tubercles were part of the epidermal stratum corneum and histologically similar to it. Liu (1985) and Liu and Harrison (1986)

described the ultrastructure of the skin of the finless porpoise (*Neophocaena phocaenoides*), including the tubercles. The numerous encapsulated nerve endings and myelinated nerve fibers led Liu (1985) to conclude that the tubercles could serve as sensory structures.

Harbor porpoises are somewhat sexually dimorphic, with females being longer and heavier than males (Read and Tolley, 1997). However, the two longest porpoises in the present study were males and the shortest porpoise analyzed was a female. Though classified as adults, the animals in the present study were likely immature based on measurements of overall length, mass and dorsal fin height, which were all lower than averages given for mature animals (Read and Tolley, 1997). There is an ontogenetic component to the development of the tubercles, as they are not present in fetal (CCG, pers. obs.) or very young porpoises (Read, 1999b). It is unknown at what age the tubercles appear and what correlation that may have to the function of the tubercles.

Based on their location along the leading edge of the dorsal fin, the tubercles could serve a hydrodynamic function (Fish et al., 2008). It is possible that the tubercles act as a passive flow-regulating mechanism that minimizes surface disturbance at the air-water interface. This type of adaptation would be useful for predator avoidance, given that the porpoise resurfaces to breathe frequently between shallow, short duration dives (Otani et al., 2000). There is a great energetic cost of increased drag for an animal swimming at the surface (Fish, 1996; Williams, 2001) and tubercles could offset this cost by reducing wave and spray drag forces. Both wave and spray drag result in energetic losses at the water surface due to the vertical displacement of water against gravity (Hoerner, 1965; Fish et al., 1991). Wave drag is due to the acceleration of water upward by an object moving at the water surface, while spray drag is due to water piling up against the front of a surface-breaking object and being shot into the air (Fish et al., 1991). The

most effective shape for reducing spray drag is a pointed leading edge, rounded trailing edge and long forebody region (Fish et al., 1991). The cross-sectional profiles of typical cetacean dorsal fins have elongate fusiform shapes with rounded leading edges (Lang, 1966; Fish and Rohr, 1999). The shape and placement of the tubercles on the dorsal fin of *P. phocoena* create a more pointed leading edge at the top of the dorsal fin. In optimizing the hull of an autonomous underwater vehicle (AUV) for hydrodynamic performance near the air-water interface, Alvarez et al. (2009) found that a shape with both ends pointed and a thick middle significantly reduced wave resistance. The dorsal fin of *P. phocoena* may approximate this shape with the tubercles creating one pointed end and the thin trailing edge of the fin creating the other pointed end. The resulting decrease in wave and spray drag forces **could** explain how the porpoise is able to use a "slow roll" (Amundin, 1974; Law and Blake, 1994) technique at the surface, making them virtually silent when swimming at the air-water interface and thereby difficult to observe in the wild.

Epidermal lipids in cetaceans have been described for *P. phocoena*, bottlenose dolphins (*Tursiops truncatus*), long-finned pilot whales (*Globicephala melaena*), fin whales (*Balaenoptera physalus*) and humpback whales (*Megaptera novaeangliae*; Menon et al., 1986; Pfeiffer and Jones, 1993). Lamellar oil bodies observed in the stratum spinosum were also noted by Sokolov (1982) as lipid granules, along with pigment granules, for *P. phocoena* skin. The apical portion of the tubercles showed the greatest volume fractions of lipokeratinocytes and lowest volume fractions of lamellar oil bodies. Menon et al. (1986) suggested that these two types of cells may both function in osmoregulation by preventing water from being lost into the hypertonic environment or replacing water that is lost. Lamellar body secretions may also be important for cornified cell cohesion (Menon et al., 1986). The low volume fraction of lamellar

oil bodies may be the factor that allows the stratum corneum to form the tubercles, by not adhering cornified cells as tightly to each other. The intercellular lipids may also function in hydrodynamic efficiency (Menon et al., 1986). A high volume fraction of these cells in the apical portion of the tubercles might increase the streamlining of these structures. Pfeiffer and Jones (1993) argued that evidence has not supported the many proposed functions of the unique epidermal lipids observed in cetaceans, and instead suggested that cetacean epidermal lipids may exist to fulfill the metabolic requirement of the epidermis. The high volume fraction of lipokeratinocytes observed in the apical portion of the tubercles may be due to the unusually thickened epidermis that is maintained in that area of the dorsal fin.

The only species of family Phocoenidae that does not possess tubercles along the leading edge of the dorsal fin is Dall's porpoise (*Phocoenoides dalli*), although tubercles are sometimes seen in hybrids with *P. phocoena* (Willis et al., 2004). *P. dalli* is the fastest of the Phocoenidae and will sometimes produce a cone shaped "rooster tail" of spray when surfacing (Morejohn, 1979). Rooster-tailing is unique to *P. dalli* and only occurs at swim speeds of 3.4 m/s and greater (Law and Blake, 1994). At swim speeds of 1.6 to 2.1 m/s, *P. dalli* uses the slow roll surfacing technique seen in *P. phocoena* (Law and Blake, 1994). Law and Blake (1994) observed *P. dalli* reaching speeds of 6.0 m/s and Leatherwood and Reeves (1986) suggested *P. dalli* may be able to attain speeds up to 15.3 m/s for a short time. Like *P. phocoena*, *P. dalli* is preyed upon by killer whales (*Orcinus orca*) and white sharks (*Carcharodon carcharias*; Morejohn, 1979; Read, 1999b) but has been observed to increase speed around killer whales (Jefferson, 1987). It may be that *P. dalli* avoids predators by swimming at high speed, whereas, *P. phocoena* uses stealth by limiting surface disturbance by use of dorsal fin tubercles.

The small tubercles along the leading edge of the dorsal fin are unique to five of the

six species within the family Phocoenidae. We have analyzed the external form of the tubercles and the composition of the underlying epidermis and dermis to determine differences between the tubercles and the leading and trailing edges of the dorsal fin. Our analysis of the size, shape and composition of the tubercles is the first step towards elucidating a possible hydrodynamic function of the tubercles.

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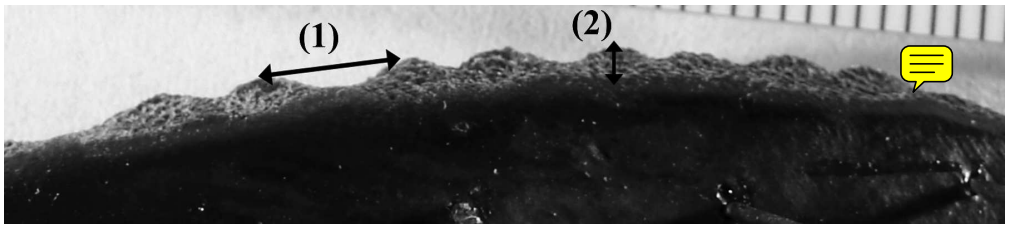

Figure 1. Photographs showing sites of measurements. (A) Macroanatomical measurements documented as (1) mean peak-to-peak distance between tubercles (mm) and (2) mean tubercle height (mm as a percent of dorsal fin height) for all tubercles found on the dorsal fin of five porpoises.
152x33mm (600 x 600 DPI)

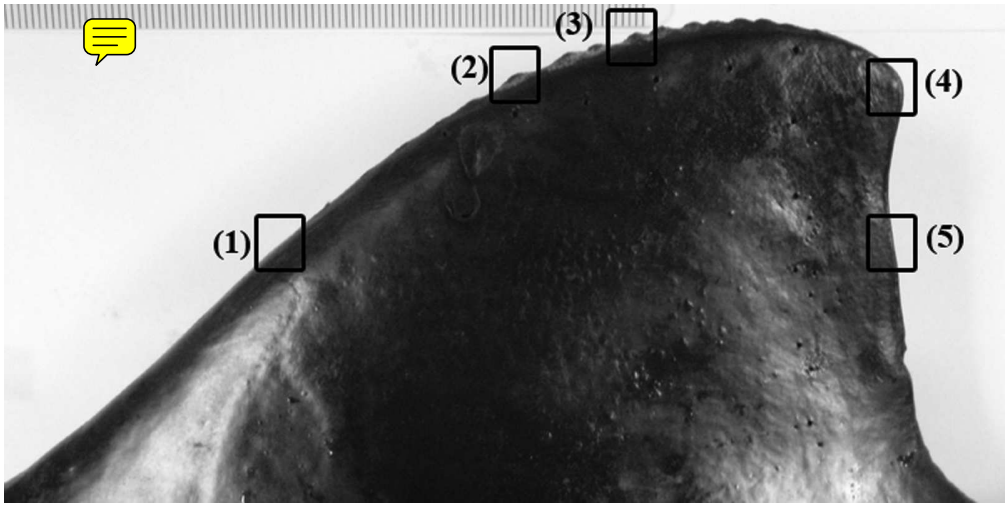

Figure 1. Photographs showing sites of measurements. (B) Locations of microanatomical sample sites on the dorsal fins of three porpoises: (1) leading edge, (2) first tubercle, (3) fourth tubercle, (4) trailing edge at the height of the first tubercle and (5) trailing edge at the same height as the sample of the leading edge.
203x101mm (600 x 600 DPI)

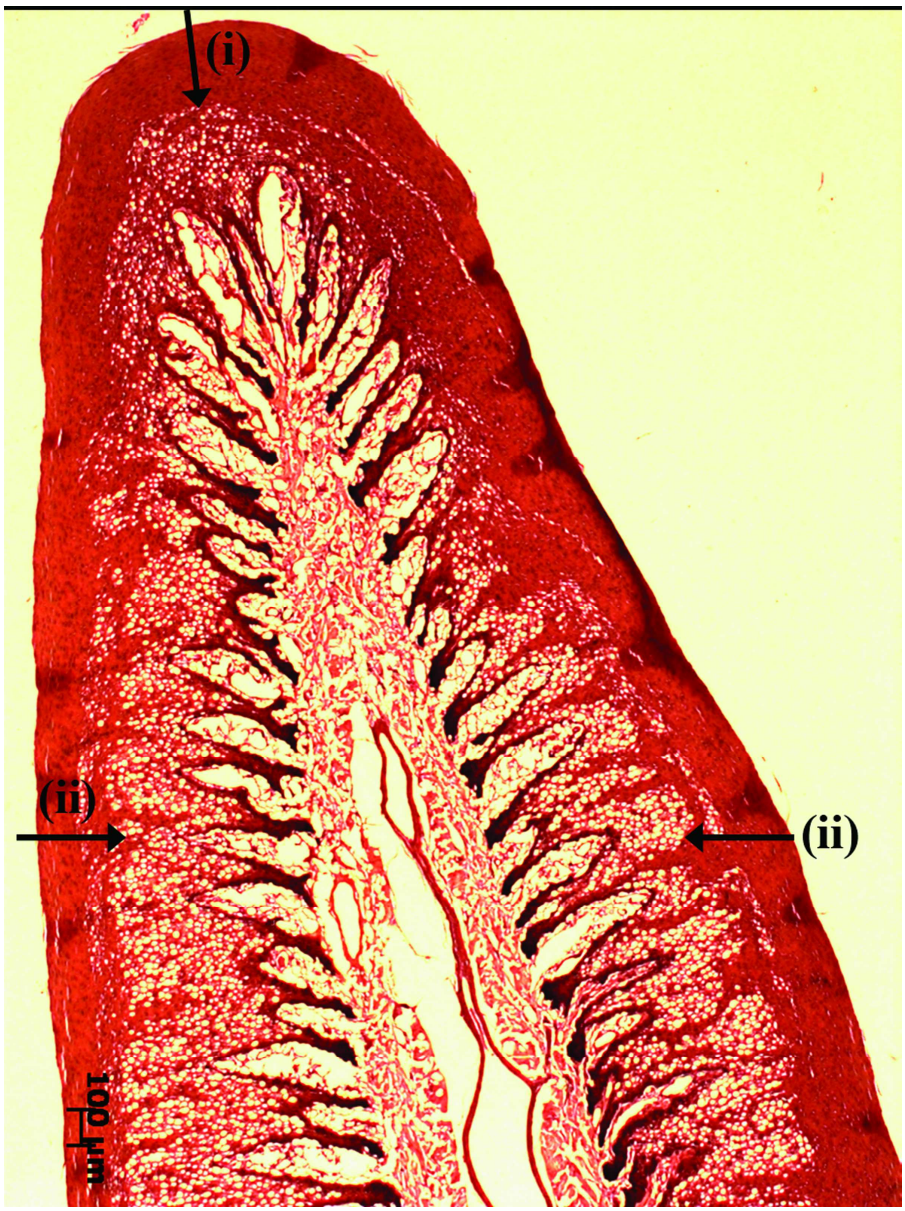

Figure 1. Photographs showing sites of measurements. (C) Location of measurements for (i) apical and (ii) both lateral portions of each section of the dorsal fin.
101x135mm (600 x 600 DPI)

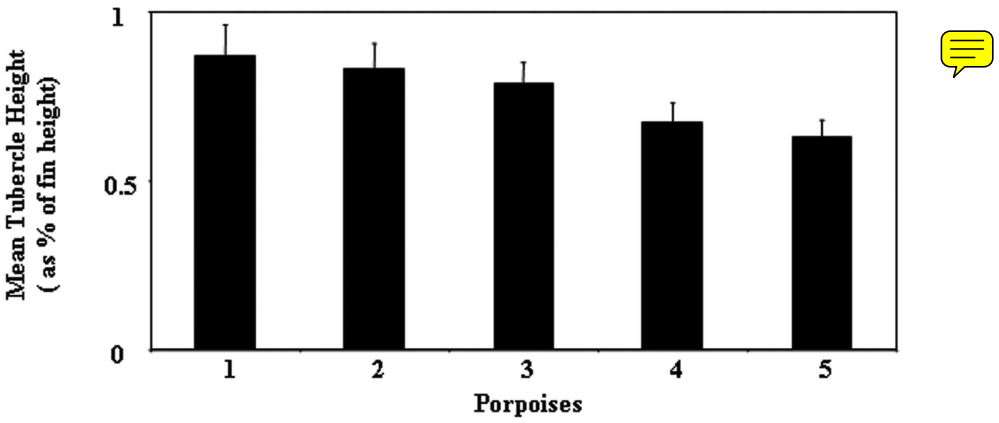

Figure 2. Results of macroanatomical measurements. (A) Mean heights of tubercles along five *P. phocoena* dorsal fins. Porpoises 1 and 2 had significantly greater mean tubercle heights ($P < 0.001$) than the other individuals.
163x84mm (600 x 600 DPI)

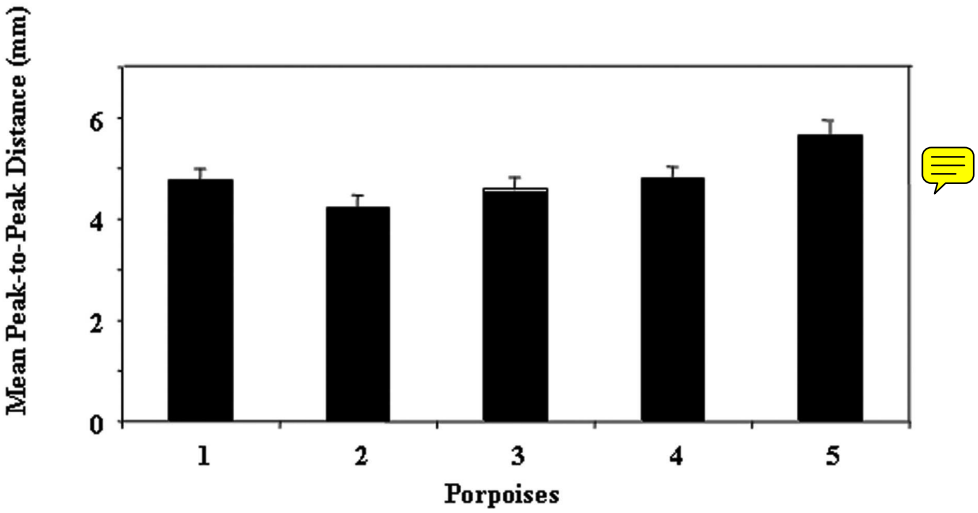

Figure 2. Results of macroanatomical measurements. (B) Mean peak-to-peak distances between tubercles along five *P. phocoena* dorsal fins. The five individuals were not significantly different from one another (P = 0.204).
163x91mm (600 x 600 DPI)

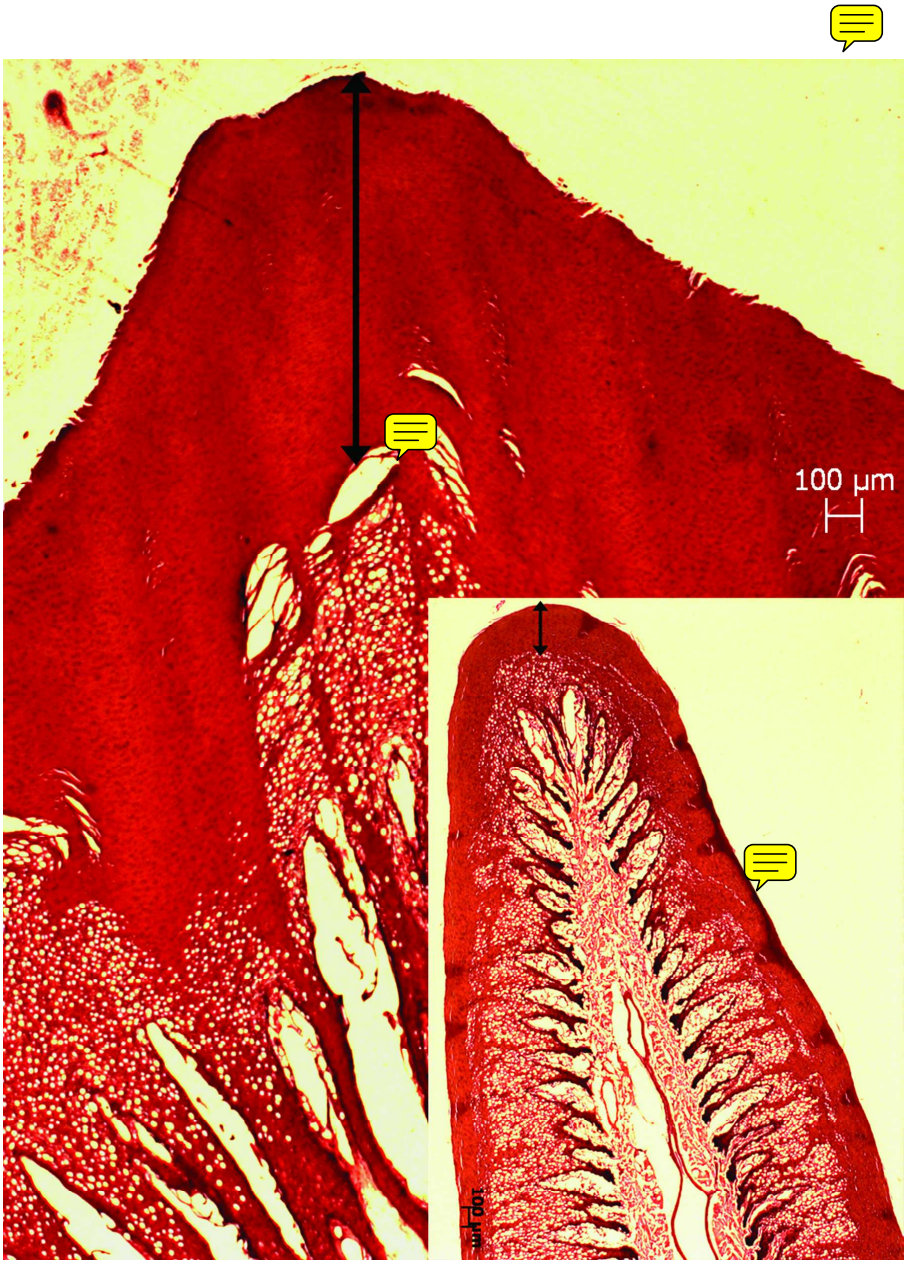

Figure 3. Photographs of histological sections of *P. phocoena* dorsal fins showing the epidermal strata. (A) Histological section of a tubercle with an insert of a trailing edge section for comparison. Arrows indicate the width of the stratum corneum.
152x202mm (600 x 600 DPI)

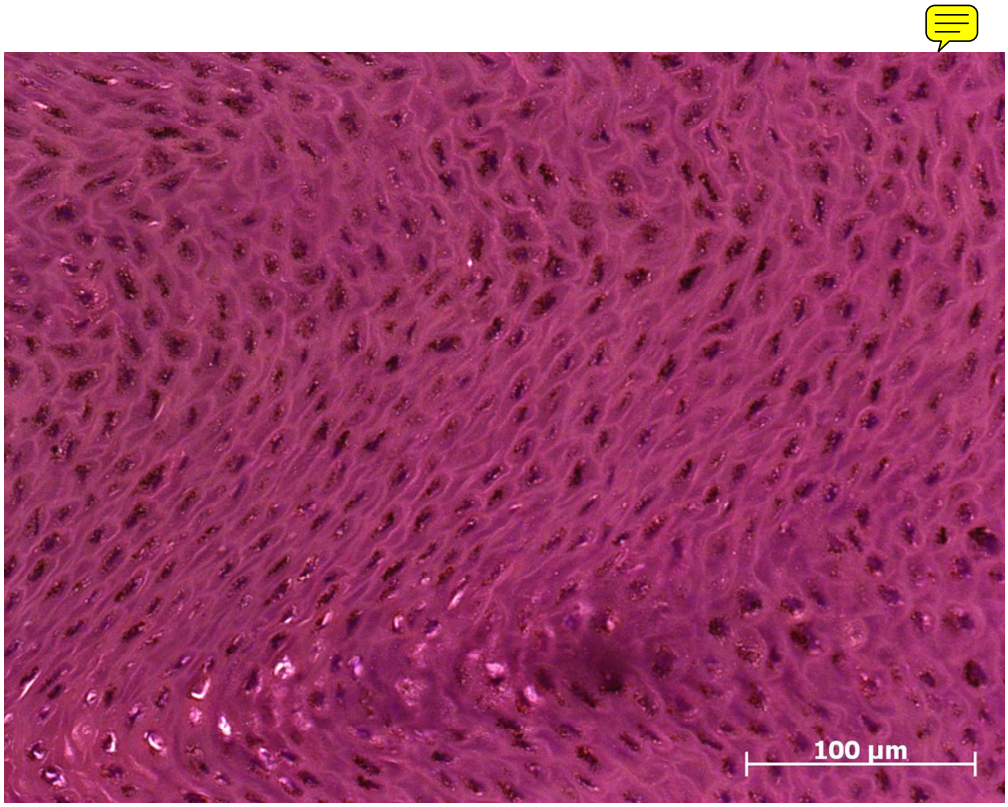

Figure 3. Photographs of histological sections of *P. phocoena* dorsal fins showing the epidermal strata. (B) Stratum corneum of the epidermis, characterized by flattened cells and nuclei without significant lamellar oil bodies.
152x114mm (600 x 600 DPI)

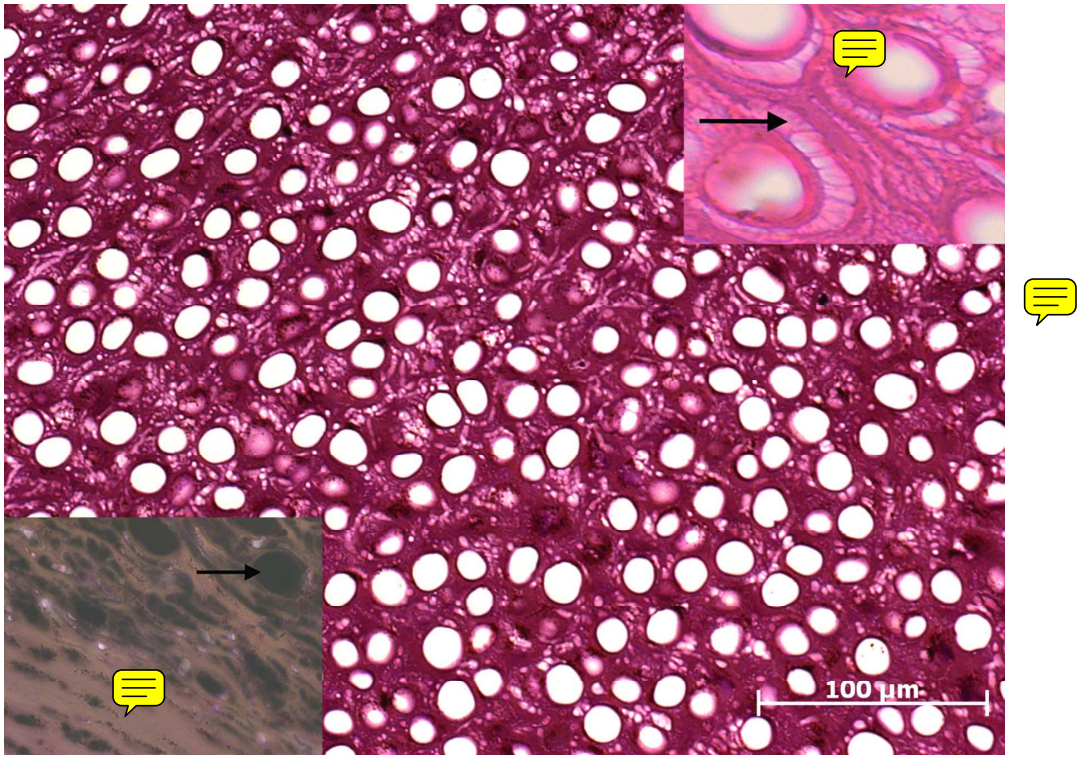

Figure 3. Photographs of histological sections of *P. phocoena* dorsal fins showing the epidermal strata. (C) Stratum spinosum of the epidermis, characterized by the presence of spiny cell appearance (arrow in top inset) and the presence of significant lamellar oil bodies (arrow in bottom inset).
152x114mm (600 x 600 DPI)

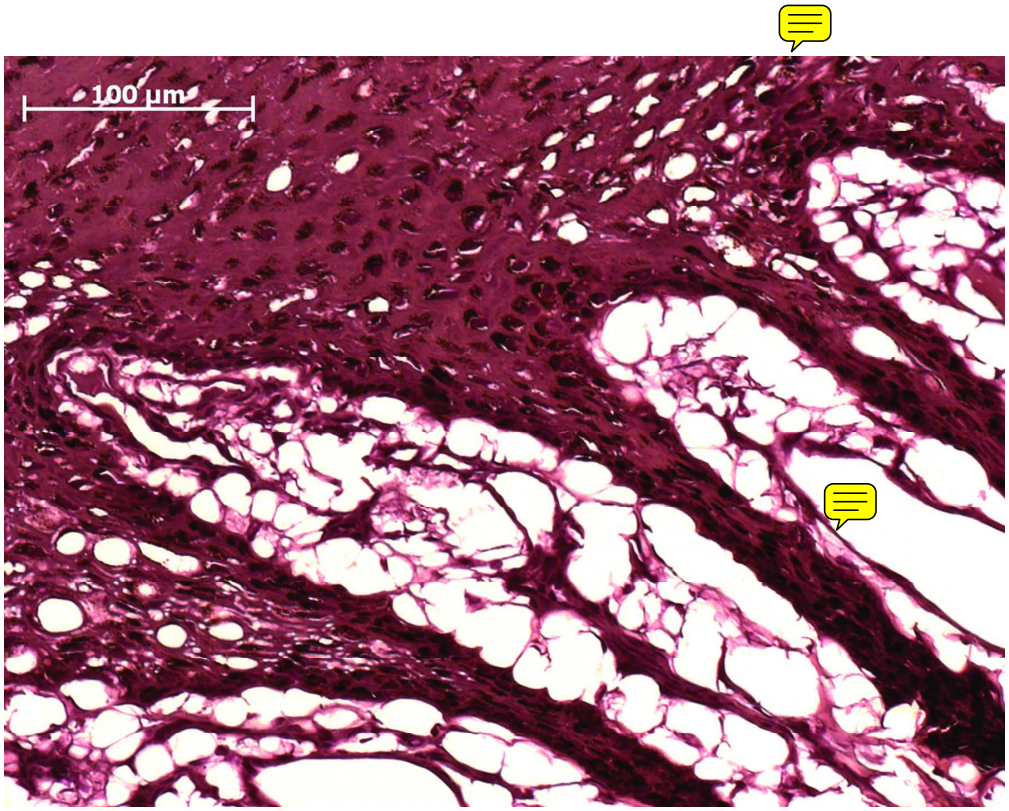

Figure 3. Photographs of histological sections of *P. phocoena* dorsal fins showing the epidermal strata. (D) The stratum basale (germinativum) of the epidermis is the mitotic epidermal cell layer characterized by the presence of rounded and live nuclei. This layer is seen lining the dermal papillae.
152x114mm (600 x 600 DPI)

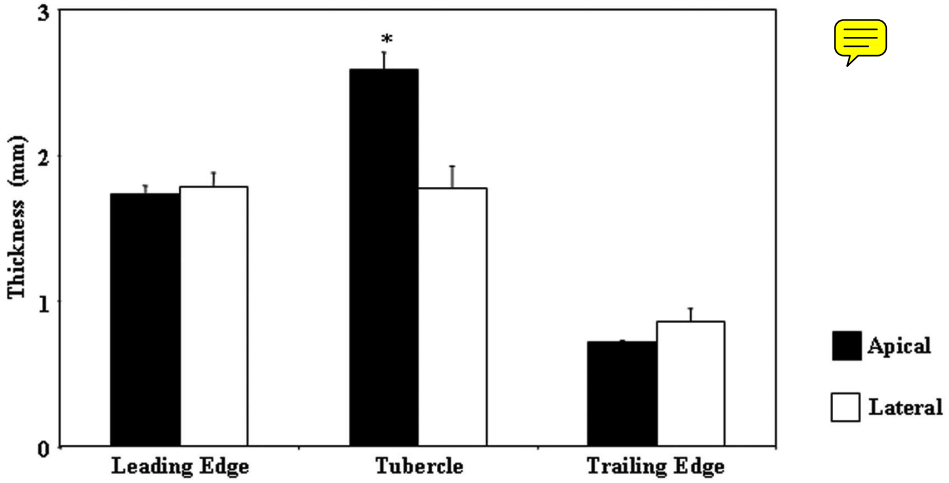

Figure 4. Results of microanatomical measurements. (A) Mean thickness (mm; mean+SD) of the complete epidermis. Measurements are divided into apical (black) and the lateral (white) portions of the section. Asterisks indicate significant differences.
152x83mm (600 x 600 DPI)

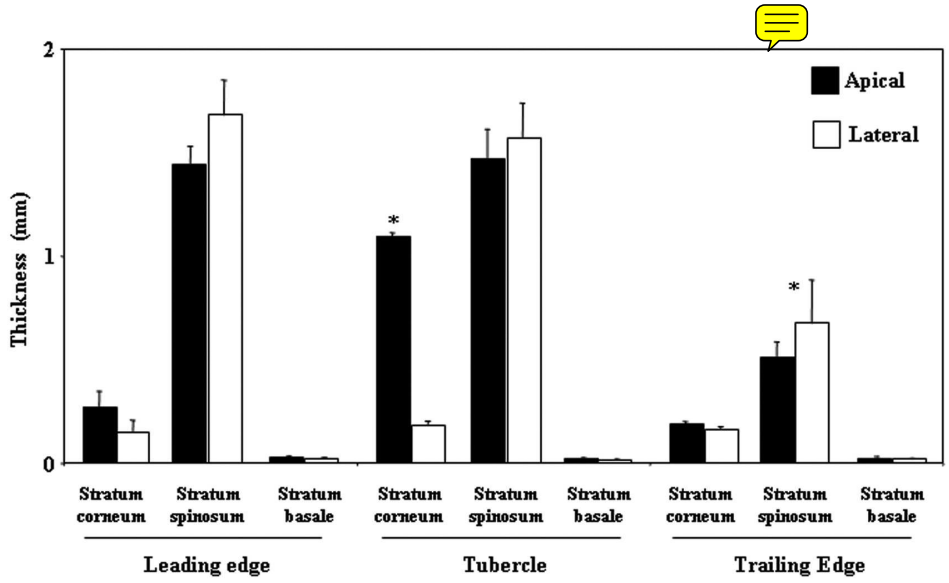

Figure 4. Results of microanatomical measurements. (B) Mean thickness (mm; mean+SD) of all epidermal strata at the leading edge, tubercles and trailing edge. Measurements are divided into apical (black) and the lateral (white) portions of the section. Asterisks indicate significant differences.
152x88mm (600 x 600 DPI)

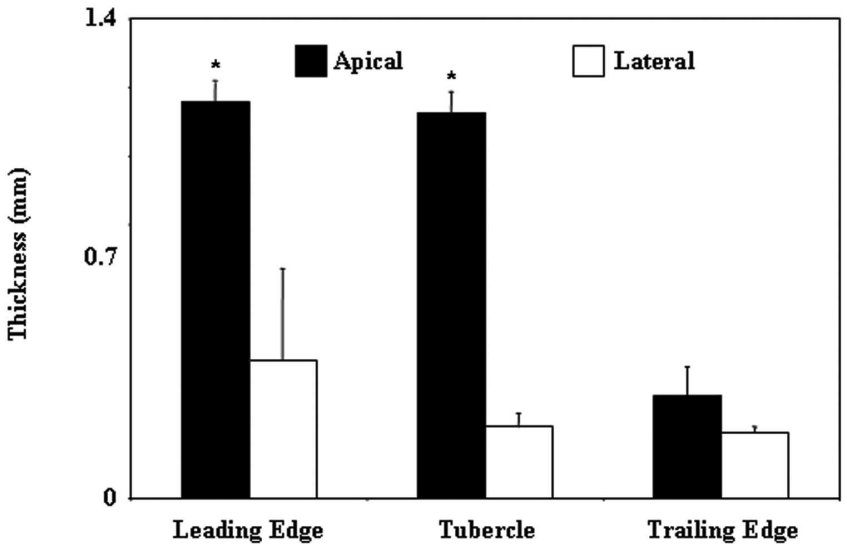

Figure 5. Mean height of dermal papillae (mm; mean+SD) generated for ten apical (black) and lateral (white) papillae per section. Asterisks indicate significant differences.
152x106mm (600 x 600 DPI)

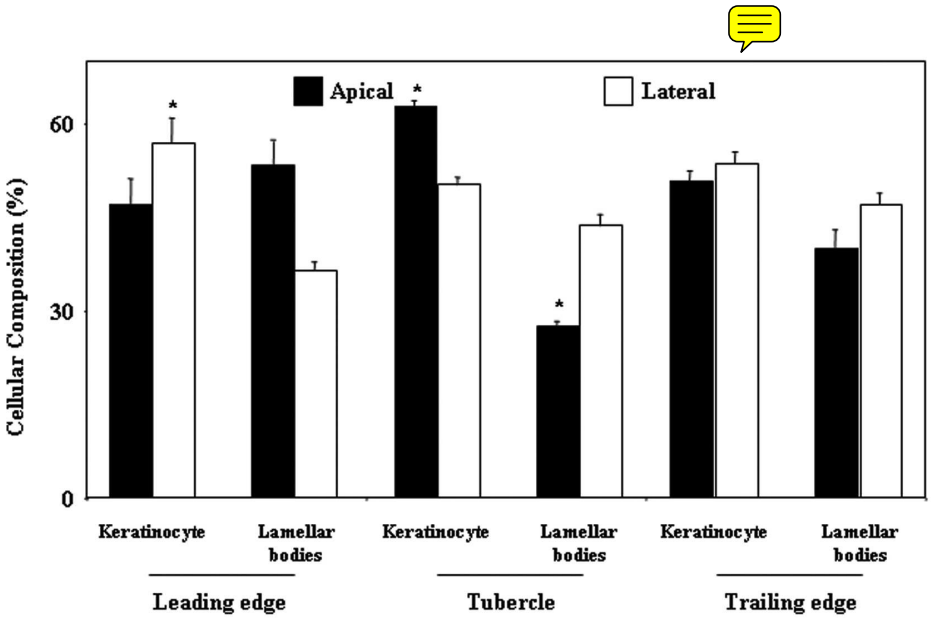

Figure 6. The cellular composition of the stratum spinosum was determined by separating all sample sites (leading edge, tubercle and trailing edge) into keratinocytes and lamellar oil bodies (%+SD) for the apical (black) and lateral (white) portions of the sections. Asterisks indicate significant differences.
152x96mm (600 x 600 DPI)