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CUTANEOUS RIDGES IN ODONTOCETES

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Abstract

Cutaneous ridges are present at the surface of the skin in many odontocetes, and although often quite faint, may be observed with the naked eye. We have taken surface impressions and measured the ridges of individuals of seven odontocete species, and observed cutaneous ridges on three additional species. In the delphinids and the one *Physeter* neonate studied, spatial periods of the ridges varied from 0.4 mm–1.7 mm and trough-to-peak heights from less than 10 μm to about 60 μm. Two *Delphinapterus* (monodontids) had ridges significantly larger than the *Physeter* and most delphinids, with spatial periods of 1.9–2.4 mm and heights 80–120 μm. We found the ridges distributed over much of the surface of the body, but relatively faint or absent on most of the head, the control surfaces, and the ventral region in some species. In all of the animals we observed, the ridges ran in an approximately circumferential direction around the body trunk rostral to the dorsal fin or mid-body area, but varied somewhat in direction in the caudal region and in other isolated areas. While the function of the cutaneous ridges has not been established, we speculate that they may play some role in tactile sensing, in the hydrodynamic characteristics of an animal, or both.

Key words: odontocete skin, cutaneous ridges, surface ridges, dermal ridges, tactile sensing, hydrodynamics.

Odontocetes which we have observed, possess shallow, regular corrugations of the surface of the skin over much of their bodies. We refer to these structures as cutaneous ridges. They are usually faint and cannot be seen from a distance, but are nearly always visible when one closely inspects the skin of a living animal at an oblique angle. Despite this fact, cutaneous ridges in cetaceans have not, to our knowledge, been described in any detail in the literature in relation to their size, orientation, and their variation between species. While Giacometti (1967) noted that the external surface of the epidermis of a fin whale, a mysticete, was "carved by continuous small furrows," and some workers (Haun *et al.* 1983, Geraci *et al.* 1986) have mentioned the existence of ridges or furrows at the skin surface in dolphins, in many other references the skin of dolphins and small whales has been described as "smooth" (Schevill 1970, Leatherwood and Reaves 1983, Sokolov 1982).

We have made a preliminary, comparative study of the surface characteristics of cutaneous ridges on a number of odontocete species. The ridges were observed on live, adult *Cephalorhynchus commersoni* (Commerson's dolphin), *Delphinapterus leucas* (beluga whale), *Globicephala macrorhynchus* (pilot whale), *Orcinus orca* (killer whale), *Pseudorca crassidens* (false killer whale), and *Tursiops truncatus* and *T. truncatus gilli* (Atlantic and Pacific bottlenose dolphins, respectively), and impressions were made of the skin surface so that they could be measured. Observations and impressions were also made post-mortem on a *Physeter macrocephalus* (sperm whale) neonate. In addition, ridges were observed by inspection on live adult *Grampus griseus* (Risso's dolphin) and *Lagenorhynchus obliquidens* (Pacific whitesided dolphin) and post-mortem on adult *Phocoenoides dalli* (Dall's porpoise).

Materials and Methods

Observations and impressions on live whales and dolphins were made at Naval Ocean Systems Center in San Diego, California, and Kaneohe, Hawaii and Sea World marine park in San Diego. Impressions were made with a quick-setting epoxy mixture (5 Minute Epoxy, Devcon Corp.), from an area 20–50 cm behind the blowhole and 2–5 cm to one side of the midline of each animal (Fig. 1). To take an impression, the skin surface was first dried and cleaned by light wiping with a towel, and then a microscope slide coated with epoxy was applied to the skin, with long axis parallel to that of the animal. When the epoxy mixture had set sufficiently, the slide was peeled from the skin.

This method appeared to give accurate impressions of the skin's surface with little or no discomfort to the animal. The epoxy sets even when submerged, although the rate of the reaction may be reduced by cool water temperatures, and its strength helps prevent deformation on removal. Decrease in linear dimensions during setting is about 2% or less (Rodney Pendleton, product engineer, Devcon, Inc., Danvers, MA, personal communication). The microscope slide was used to stabilize the impression, and to provide a flat surface for the measurement procedure; however, it effectively prevented cross-sectioning of the impression, which might make possible more accurate measurements of ridge height than the methods used in this study. Early impressions made without the slides tended to warp, and the material proved difficult to section as well.

Failures in the impression procedure were due principally to insufficient setting of the epoxy or excessive motion by the animal, which might partly or completely obliterate the ridges on an impression. For these reasons, the components of the epoxy were mixed several minutes before application to minimize the time of contact with the animal (usually three to six minutes).

The impressions were examined under a stereoptic microscope, and the spatial period and trough-to-peak height of the ridges were measured using an optical stage (Line Tool Co. model A LH) equipped with calibrated micrometer heads. The slide bearing the impression was held by two brackets attached to the

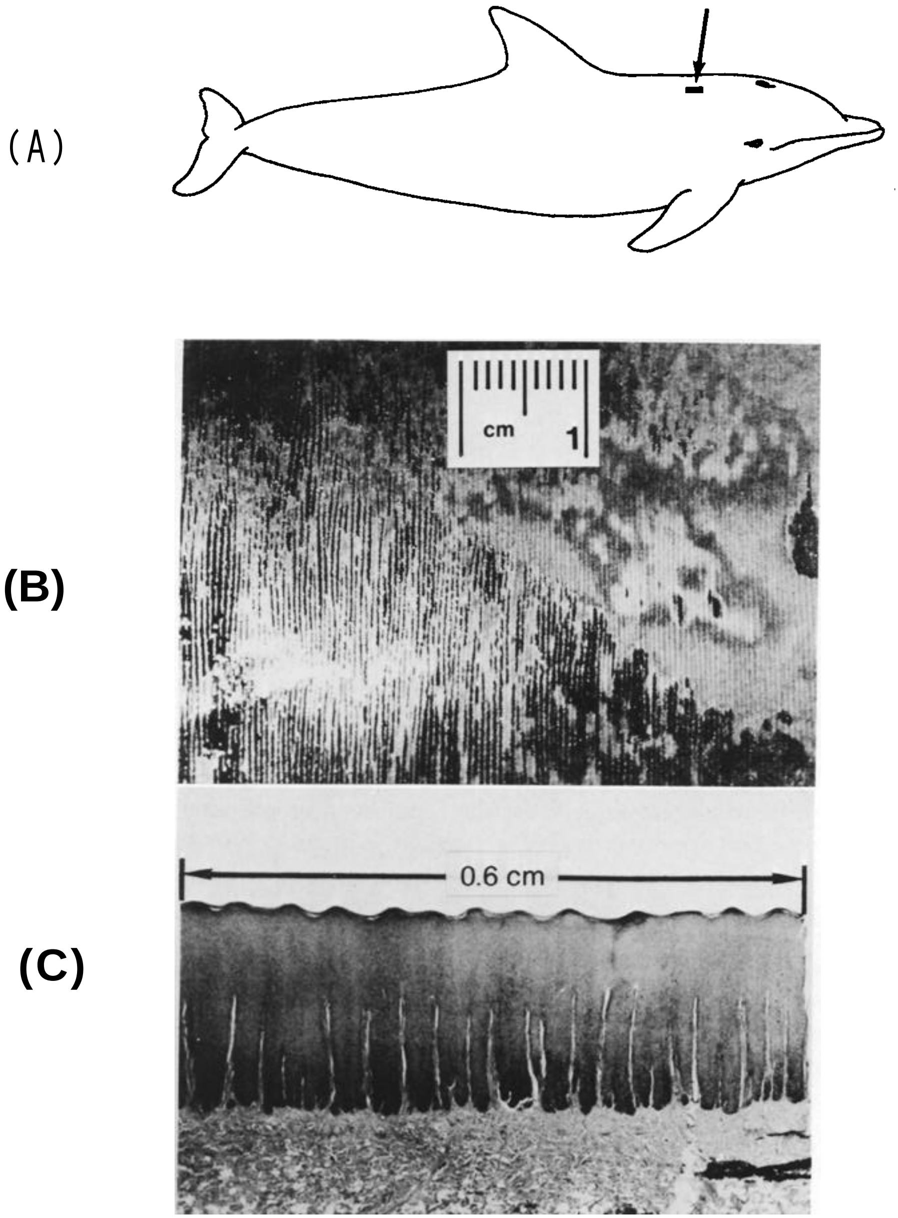

Figure 1. Surface cutaneous ridges on the dorsal thorax of the Atlantic bottlenose dolphin *Tursiops truncatus.* The diagram at top (A) shows the approximate location of the ridges in the photographs. The photograph at center (B) is a surface view of the ridges, which are highlighted by compression of the skin and by reflected sunlight. The upper and lower margins of the white box containing the scale are parallel to the long axis of the animal's body. At bottom is a photomicrograph (C) of a sagittal histological section of the skin in which the ridges are preserved. The dark line of the 0.6 cm scale, with arrows at each end, is parallel to the long axis of the body.

platform of the stage, which was placed under the microscope so that the ridges were clearly visible. A microelectronic probe with a microscopically fine point was positioned perpendicular to and a short distance above the surface of the impression. Lateral measurements were made by moving the slide horizontally with the calibrated micrometer head, using the probe tip for alignment. Measurements of elevation were made by moving the platform of the stage vertically until the tip of the probe just contacted the surface of the impression. Measurements could not be made reproducibly to the 0.1 mil resolution of the micrometer head, so readings of elevation were taken to the nearest one-quarter mil (about 6.4 μm).

The mean spatial period of the ridges was determined by measuring the horizontal distance occupied by five ridges, at six different locations within an area of a few cm^2 on the surface of each impression. In cases where the direction of the ridges deviated noticeably from the perpendicular to the measuring axis, the angle of deviation was measured and the raw spatial periods were multiplied by its cosine to correct their values. Rather than widths occupied by five ridges, the widths of individual ridges were measured on impressions from *P. macrocephalus* due to irregularities in the pattern of the ridges.

To determine mean ridge heights, sets of elevation measurements were made also at six different locations within the same area on each impression. In each set, the elevations of a central crest or trough and two adjacent extrema were read. The mean elevation of the two outlying extrema was used in each case to compute mean ridge height, in order to cancel variation in elevation due to any small slope between the mean surface of the impression at that location, and the horizontal plane of the optical stage.

The number of animals available and the difficulties associated with taking impressions strictly limited the number of impressions which could be made. For most species, a successful impression was obtained from no more than one live individual. However, useable impressions were taken from two *D. leucas,* two *G. macrorhynchus,* and three *T. truncatus,* and visual inspections of the ridges were performed on several other animals of each species if more than one were available. The post-mortem impressions and observations on the *Physeter macrocephalus* neonate, which had been stranded alive but died a week later, were taken from an area on the left dorsal thorax midway between the vertex and the dorsal fin. Impressions unsuitable for measurement with the stage were also taken from a second adult *O. orca* post-mortem, from an area on the thorax above the pectoral flipper.

Impressions were unsuccessful or impractical on available live adult *Grampus griseus* and *Lagenorhynchus obliquidens,* and on two frozen adult specimens of *Phocoenoides dalli* recovered dead from strandings, although visual inspections of the animals and rough measurements (made by hand with a ruler) or estimates of the ridge sizes were made.

Results

Cutaneous ridges were present on all animals which we examined. Their size and distribution appears to be fairly consistent among members of the same species, regardless of sex. Generally, the ridges were distributed over most of the animals' bodies, but appeared to be absent on or near the tail flukes, the dorsal fin (for those species which have one), the pectoral fins, and the head anterior to the blowhole. In *P. crassidens* (W. Friedl, Naval Ocean Systems Center, Kaneohe, HI, personal communication) and *O. orca,* however, faint ridges were observed in some animals on the tail flukes and pectoral flippers, running parallel to their long axes. Ridges tended to be relatively faint on the ventral area, and apparently absent in this region in *O. orca* and *T. truncatus gilli* that we observed. Between the blowhole and the dorsal fin on delphinid species, and along the entire body of *D. leucas,* ridges ran in a circumferential direction, nearly perpendicular to the long axis of the body. On *T. truncatus* and *O. orca* the angle relative to the body axis was slightly oblique in the region behind the dorsal fin, with the direction of the ridges dorsal-rostral to ventral-caudal. On the *P. macrocephalus* ridges were not present immediately behind the blowhole, but appeared behind the head, running circumferentially around most of the body trunk but turning parallel to the long axis of the body on the ventral region. In addition to these trends, the orientation of the ridges on many animals was observed to vary somewhat near the pectoral flippers and dorsal fin. For example, they often ran circumferentially around the base of the dorsal fin.

Over local areas of the skin on the order of a few cm^2, the ridges appeared to the naked eye to be quite regular in their prominence and periodicity, in both the delphinids (Fig. 1) and on *D. leucas.* However, over larger areas, their dimensions could be seen to vary noticeably with stretching or compression of the skin when an animal assumed different postures. They appeared to be particularly variable at the location behind the blowhole from which impressions were taken on living animals, probably because the skin in this area is especially compliant to accomodate body movement. Trainers at Sea World who have ridden the killer whales have noted that their ridges seem to become more pronounced with increasing swimming speed (D. Butcher, Sea World (formerly), San Diego, CA, personal communication), suggesting that hydrodynamic drag influences their characteristics. In addition to the gross distributions of the ridges already noted, their characteristics may also vary subtly with position over the surface of the animals. The longitudinal "stripes" which may sometimes be seen on individuals of *T. truncatus* appear to be due to variations in ridge shape or height along the circumferential directions; these variations are in register from ridge to ridge and give the appearance of longitudinal features.

Occasional deviations from the pattern of strictly parallel individual ridges occurred in all the species from which impressions were taken. One ridge might split and diverge into two, or a single ridge might form between two adjacent ones. Such deviations were frequent in the impressions taken from *P. macrocephalus,* whose ridges seemed less regular than those of the other species. They typically diverge or converge every few cm or less along their lengths.

When examined microscopically in impressions, individual ridges appear to be regular and roughly sinusoidal in shape. The ridges of *G. griseus* (as observed with the naked eye by W. Friedl, Naval Ocean Systems Center, Kaneohe, HI, personal communication) and *D. leucas* are slightly asymmetric in that their

Table 1. Measured ridge heights and spatial periods.

Species/individual	Impression location	Ridge spatial period, mm	Ridge height, µm
Delphinids			
Cephalorhynchus commersoni	20 cm behind blowhole	0.78	7
Tursiops truncatus #1	25 cm behind blowhole	0.65	16
Tursiops truncatus #2	25 cm behind blowhole	0.56	14
Tursiops truncatus #3	30 cm behind blowhole	0.71	41
Tursiops truncatus gilli	30 cm behind blowhole	0.54	7
Pseudorca crassidens	30 cm behind blowhole	0.55	12
Globicephala macrorhynchus #1	45 cm behind blowhole	0.48	8
Globicephala macrorhynchus #2	45 cm behind blowhole	0.41	[a]
Orcinus orca	50 cm behind blowhole	1.16	12
Monodontids			
Delphinapterus leucas #1	40 cm behind blowhole	2.35	89
Delphinapterus leucas #2	35 cm behind blowhole	1.99	114
Physeterids			
Physeter macrocephalus	Midway between vertex and dorsal fin	0.52	58

[a] Poor impression quality precluded this measurement.

crests are somewhat broader and flatter than the troughs. A set of values for spatial periods and ridge heights from individuals of seven different species are given in Table 1. Each represents the average of the six sets of values obtained from measurements of impressions as described above.

Ridges observed by inspection of other adult individuals of *T. truncatus gilli* and *T. truncatus* were consistent in scale with those of the individuals from which impressions were made. Ridges observed on two additional adult *P. crassidens* are also consistent with those on the single impression from this species, with spatial periods between one-third and one-half mm, as determined by hand measurements (W. Friedl, Naval Ocean Systems Center, Kaneohe, HI, personal communication). The impression taken post-mortem from the second *O. orca* exhibits ridges somewhat wider and more prominent than those of the *O. orca* listed in Table 1. Spatial periods of 1.5–1.7 mm were measured by hand.

The ridges of *Grampus griseus* were estimated to have spatial periods of about 1 mm from hand measurements (W. Friedl, Naval Ocean Systems Center, Kaneohe, HI, personal communication), while those of *L. obliquidens* were estimated to have spatial periods comparable to those of human fingerprints, on the order of one-half mm or a little larger (T. Goff, Sea World, San Diego, CA, personal communication). Faint ridges of about the same width were observed on the frozen specimens of *P. dalli*.

Although the mean ridge heights measured on the impressions are given in Table 1, they cannot be taken as strictly indicative of the prominence of the ridges in any individual. Not only are ridge heights near the limits of resolution of the measurement scheme in a number of the impressions, but they are dependent upon location and particularly upon extension or compression of the skin due to postural variations, as noted above. To examine the extent of variability of ridge dimensions, two additional impressions were taken from an adult male *T. truncatus* about 10 cm behind the blowhole. One was made with the animal's head flexed ventrally and one with the head extended dorsally. With the skin stretched by ventral flexion, the mean spatial period of the ridges was measured at 0.71 mm and the mean ridge height was 11 μm. With the skin compressed by dorsal extension of the head, the mean period was 0.55 mm and the mean height was 92 μm.

Discussion

We have examined surface cutaneous ridges in eight delphinid species (including one subspecies), one monodontid species, and one physeterid species, and we have made and measured impressions of the skin surface from individuals of all but three of these. We suggest that such ridges may be ubiquitous in the odontocetes. They are generally quite shallow at the surface (less than ten to slightly over 100 μm high) and range in width from 0.4–1.7 mm in the delphinids, 1.9–2.4 mm in the monodontid *Delphinapterus leucas,* and between 0.5 and 0.6 mm in the one (neonatal) physeterid *Physeter macrocephalus.* There is not a strict correlation between the size of the individuals of the species we have examined, and the dimensions of their ridges.

One reason that odontocete cutaneous ridges may not have been described in more detail in the past is that they are not always visible in histological sections of cetacean skin. Because of their faintness, they are difficult to see in cross-section, and in addition, they may tend to relax or disappear from the surface of dead skin, particularly on a specimen which has been excised from a carcass, as has been observed by one of us (S.R.). Figure 1 shows the cutaneous ridges of the Atlantic bottlenose dolphin *Tursiops truncatus,* both in a surface view and in a histological section in which the structures are preserved. For this section, care was taken to assure that the epidermal surface did not stretch relative to the underlying dermis.

The association of the surface ridges with the underlying dermal ridges and papillae is at present unclear. Earlier workers (Sokolov 1955, Sokolov and Kuznetsov, 1968) report that dermal ridges run parallel to the long axis of the body in *Phocoena phocoena, Delphinus delphis,* and *T. truncatus,* while Purves (1963) shows dermal ridges running mainly at an oblique angle in *D. delphis* and parallel to the body axis in *P. Phocoena.* Stromberg (1989) also reports that dermal ridges run roughly parallel to the long axis of the body in *T. truncatus,* which is generally perpendicular to the direction of the surface ridges we have observed. However, based upon the conception of three-dimensional dermal structure developed by Stromberg (1989), the appearance of the dermal papillae in the cross-section in Figure 1 suggests that the dermal ridges at that location are more nearly parallel to than perpendicular to the surface ridges, which run circumferentially there. Stromberg also reports that the spacing of the dermal ridges is considerably smaller at about 0.1 mm than the surface ridges measured by us in that species. His work, however, was on the skin of a neonate, whereas we examined adult *T. truncatus*. Sokolov and Kuznetsov (1968) report about 60 dermal ridges per 10 mm of skin surface for adult *T. truncatus,* a density around three times that of the surface ridges we report here. It seems clear to us that a careful histological study is needed to clarify the relationship between the subsurface dermal ridges and the cutaneous ridges on the skin surface.

The function of cetacean cutaneous ridges remains to be elucidated. Although the subsurface dermal ridges have been emphasized in the past (Sokolov 1955, Sokolov and Kuznetsov 1968, Purves 1963, Stromberg 1989), we speculate that the cutaneous ridges on the skin surface may play a role in the animals' tactile sense, their hydrodynamic characteristics, or both. They may serve to couple stresses due to the flow field surrounding an animal to mechanical sense organs in the skin in some way which is favorable to transduction, perhaps by setting up minute vibrations which may be detected by receptors sensitive to such motion. It has been suggested that the fingerprint ridges on the palmar skin of humans, which the odontocete cutaneous ridges resemble, might play a similar role (Quilliam 1978). Moreover, in a histological study of the skin of *Tursiops truncatus* (Haun *et al.* 1983), structures which are presumed to be mechanoreceptors were found in the interdigitations of the epidermis with the dermal ridges.

The hydrodynamic consequences of the ridges are unclear. Some investigators have suggested that small cetaceans decrease their hydrodynamic drag by somehow inhibiting or delaying the transition to turbulent flow over their bodies (Kozlov and Shakalo 1973, Kramer 1960, Gray 1936). Qualitatively, however, the ridges might be expected to behave as a "roughness" which tends to induce transition from laminar to turbulent flow (Schlichting 1979, White 1974), since they are approximately perpendicular to the direction of flow over most regions of the surface. If this is the case they could increase the net hydrodynamic drag on the animals, although such an effect might prove to be insignificant due to the faintness of the structures at the surface. A reliable conclusion regarding hydrodynamic consequences of the ridges awaits a study of stability of flows over a compliant boundary with very shallow, regular undulations; no such study has, to our knowledge, been reported to date.

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Literature Cited

Geraci, J. R., D. J. St. Aubin and B. D. Hicks. 1986. The epidermis of odontocetes: A view from within. Pages 3–21 *in* M. Bryden and R. Harrison, eds. Research on dolphins. Clarendon Press, Oxford.

GIACOMETTI, L. 1967. The skin of the whale *Balaenoptera physalus.* Anatomical Record 159:69–76.

GRAY, J. 1936. Studies in animal locomotion, VI. The propulsive powers of the dolphin. Journal of Experimental Biology 13:192–199.

HAUN, J. E., E. W. HENDRICKS, F. R. BORKAT, R. W. KATAOKA, D. A. CARDER AND N. K. CHUN. 1983. Dolphin Hydrodynamics Annual Report FY 82. Technical Report 935, Naval Ocean Systems Center, San Diego, CA 92152-5000, USA.

KOZLOV, L. F., AND V. M. SHAKALO. 1973. Certain results of the determination of pulsation of velocities in the boundary layers of dolphins. Kiev Bionika 7:50–52.

KRAMER, M. O. 1960. The dolphins' secret. The New Scientist 7:1118–1120.

LEATHERWOOD, S., AND R. R. REAVES. 1983. The Sierra Club handbook of whales and dolphins. Sierra Club Books, San Francisco.

PURVES, P. E. 1963. Locomotion in whales. Nature 197:334–337.

QUILLIAM, T. A. 1978. The structure of finger print skin. Pages 1–18 *in* G. Gordon, ed. Active touch, the mechanism of recognition of objects by manipulation. Pergamon Press, Oxford.

SCHEVILL, W. E. 1970. Page 158 *in* P. Gray, ed. Encyclopedia of biological sciences (Second Edition). Van Nostrand Reinhold, New York.

SCHLICHTING, H. 1979. Boundary layer theory. McGraw-Hill, New York.

SOKOLOV, V. E. 1955. Structure of the integument of certain cetaceans. Byulleten Moskovskogo—Otdel Biologischeskii 60:45–60.

SOKOLOV, V. E. 1982. Mammal skin. University of California Press, Berkeley.

SOKOLOV, V. E., AND G. V. KUZNETSOV. 1968. Direction of dermal ridges in dolphins in relation to the streamlining of their body. Byulleten Moskovskogo—Otdel Biologii 3:123–126.

STROMBERG, M. W. 1989. Dermal–epidermal relations in the skin of the bottlenose dolphin (*Tursiops truncatus*). Anatomia, Histologia, Embryologia 18:1–13.

WHITE, F. M. 1974. Viscous fluid flow. McGraw-Hill, New York.

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