© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/

# The Structure of the Flukes in Relation to Laminar Flow in Cetaceans

By P. E. Purves[1]

*Eingang des Ms. 5. 12. 1967*

## Introduction

In drawing attention to the strong dorsal curvature of the flukes of cetaceans during the downstroke of the tail, Felts (1966) stated "We have found nothing in fluke anatomy proper which explains this difference in linearity during the powerful fluke beat, but we believe the answer will be found in differential output by dorsal and ventral tail musculature, with variation in movement compensated for by the difference in dorsal and ventral areas of the body and by corrective flipper movements".

However, in a discussion of "Gray's Paradox", Purves (1963) pointed out that the weight of the epaxial locomotor muscle-mass is approximately double that of the hypaxial mass and that in maintaining power on the upstroke alone, the effective length of the animal, for the purpose of calculating Reynold's Number, was reduced below the level at which turbulence was likely to occur. In these circumstances, if flexure of the flukes were due to muscular action, the former would be expected to curve more strongly in a ventral direction, rather than dorsally during the power stroke.

It is the purpose of this paper to demonstrate that the upward curvature of the flukes is not due to differential muscular action but to the anatomy of the flukes themselves, and that their differential flexure is of supreme importance in the maintenance of laminar flow over the body.

The anatomy of the flukes in cetaceans was examined in very great detail by Roux (1883) and little can be added to his description at the macroscopic level, but a very brief recapitulation is required here. The main body, or central core of the fluke is constituted from a great number of closely packed, anteroposteriorly directed laminae of white-fibrous tissue fig. 1 (B) in which each individual lamina consists of a reticulum of collagen fibres vertically and diagonally orientated, see fig. 1 (C). Overlying these laminae of the dorsal and ventral aspects of the flukes are several layers of radiating collagen fibres fig. 1 (A), and the whole assembly is covered by the black, external epithelium.

The flukes of a living, or recently dead cetacean will bend much more readily in a dorsal direction by manual pressure than in the ventral direction, the difference in flexibility varying between the species. An extreme example of this differential flexibility is to be found in the Long-snouted Dolphin *Stenella longirostris* and the flukes of this species were used in the present investigation. The specimen had been presented deep-frozen by Marineland of the Pacific and was used for casting and anatomical studies. After the black epithelium had been removed, the appearance of the dorsal and ventral surfaces seemed identical, and gross sectioning of one of the flukes in several directions revealed no anatomical reason for the differential flexibility.

However, when the layers of radiating collagen fibres had been removed from the dorsal and ventral surface of the other fluke, the core was found to bend with

[1] See D. van Heel, Z. Säugetierkunde, 33 (1968), H. 6, S. 383.

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/



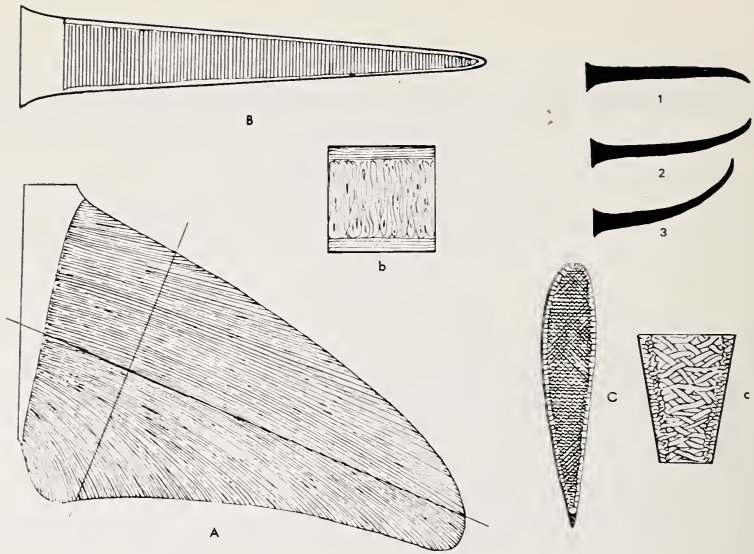



*Fig. 1.* Diagram showing distribution of collagen fibres in the flukes of a cetacean
A = Shows the surface appearance of radiating collagen fibres on the dorsal and ventral aspects of the flukes after the black epithelium has been removed. B, b = A schematic diagram of a section of the fluke along the indicated macroaxis showing anteroposteriorly directed laminae of white fibrous tissue covered dorsally and ventrally by layers of radiating collagen fibres. C, c = Schematic diagram of a section of the fluke through the indicated transverse axis showing vertically and diagonally orientated collagen fibres.
Diagram (after Felts) showing the from of the flukes during (1) the upstroke (2) the glide and (3) the downstroke

equal facility in both dorsal and ventral directions. Clearly then, the reason for the differential flexibility resided in the radiating collagen fibres on the surfaces of the flukes and not in the structure of the core.

Teased and sectioned fibres were examined by phase-contrast and electron microscopy, the photomicrographs being shown in fig. 2 (A—D) and the electronmicrographs in fig. 3 and 4. The original material had been preserved in formalin for about a year. It was dehydrated and embedded in epoxy resin and the sections were stained with uranyl acetate and lead citrate. It will be seen that the collagen fibres of the ventral aspect of the flukes have a strongly pleated appearance whilst those on the dorsal aspect are nearly straight. Indeed in *Stenella longirostris* the dorsal fibres seem actually to be "prestressed" since initially perfectly parallel cross sections of the fresh fluke assume a wedge-shape a short time after sectioning. Examination of foetal material shows that this difference in structure is embryonic in origin and that even the developing fibroblasts of the ventral surface have an undulating distortion.

It can readily be seen that the radiating fibres of the ventral surface are capable of expansion, with the pleats opening out like the bellows of a concertina but of reasserting and assuming their original shape when tension is released. This clearly could not happen whith the initially straight fibres of the upper surface, since collagen fibres are known to be virtually inextensible, under normal conditions. These fibres could, of course shorten by being thrown into minute, sinusoidal wrinkles. It is well known that when any flat plate bends, the surface on the convex side of the curvature must expand, whilst that on the concave side must shrink by a corresponding amount. When the fluke is perfectly horizontal, the collagen fibres on the ventral surface are pleated

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/



whilst those on the dorsal surface are staight. Under these conditions appreciable bending can only take place in a dorsal direction, and it is noteworthy that when this happens, the external epithelium of the upper surface exhibits minute wrinkles which lie at right angles to the axes of the radiating collagen fibres. Examination of the orientation of the fibres with respect to the total shape of the fluke shows where dorsal flexure can be expected i. e. along the macroaxis of the fluke towards the distal extremity and along the thin, trailing edge, especially in its proximal region. In the ventral direction, the fluke will be much more rigid, since the initially straight fibres of the dorsal surface would have to stretch beyond breaking point to produce any appreciable bending.

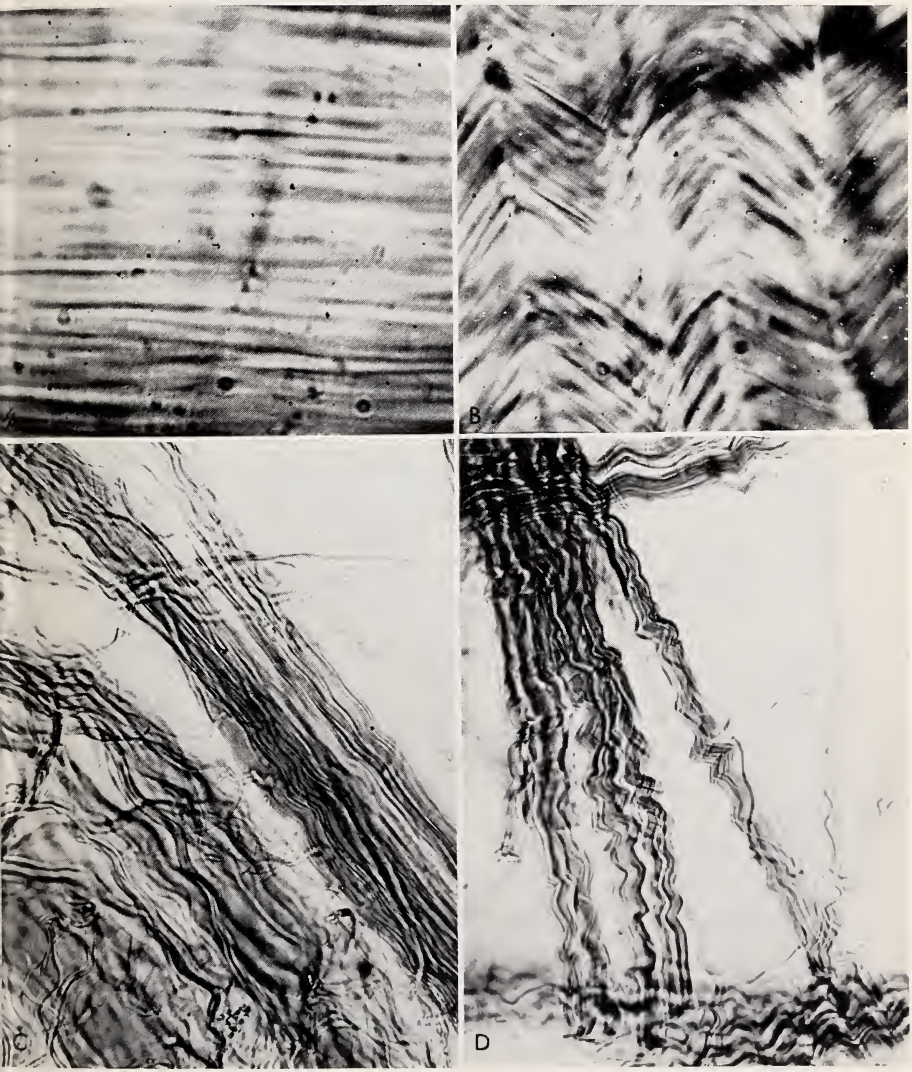
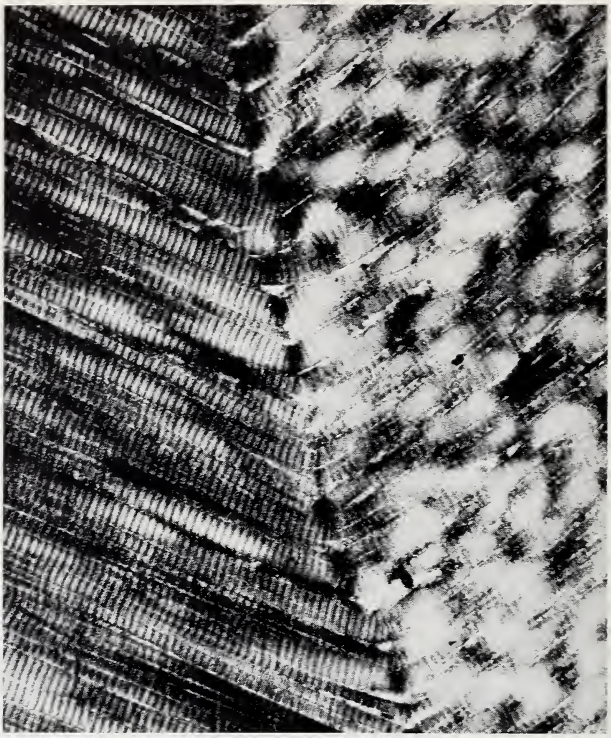



*Fig.* 2. Phase contrast photomicrographs mag x 300 showing (A) straight layers of collagen fibres on dorsal aspect of flukes (B) pleated layers of collagen fibres on ventral surface (C) teased fibres from dorsal aspect (D) teased fibres from ventral aspect

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/





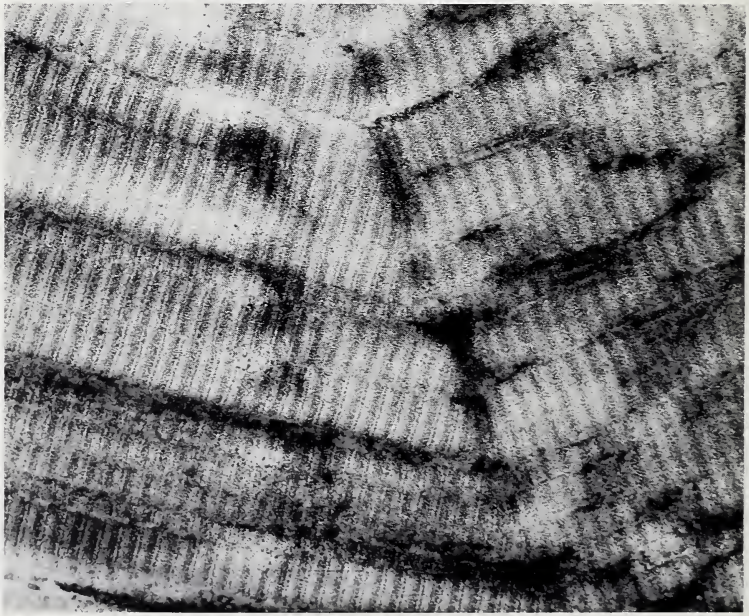


*Fig. 3.* Electron-micrograph mag x 18,000 of collagen fibrils on ventral aspect of flukes — *Fig. 4.* Electron-micrograph mag x 50,000 indicating distortion of collagen molecules on ventral aspect of flukes

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/



Since the orientation of the radiating fibres varies slightly between the species, dependent upon the overall shape of the flukes, there are slight differences in the distribution of dorsal flexibility.

It should be pointed out that *Stenella longirostris* is a conspicuos example of a cetacean showing differential distortion of the radial collagen fibres — but that all the cetaceans examined demonstrate it to a greater or lesser degree.

A study of the insertions of the tendons of the epaxial and hypaxial muscles of locomotion shows that a large angle of incidence can develop on the upstroke but that this is prevented to some extent during the downstroke. For a demonstration of the reason for this phenomenon it is convenient to describe the epaxial muscles first fig. 5 A. In the caudal segment, the epaxial muscles consist only of two major portions which are prolongations of the spinalis dorsalis (MSD) and the longissimus dorsalis (MDL). In this region, the muscles are heavily developed, but quite discrete, since they must permit of the relative movement which is concomitant of the sinuous, vertical movement of the tail. The spinalis dorsalis has very powerful attachments to the upper half of all the neural spines (NS) and to the dense fibrous tissue which forms the dorsal

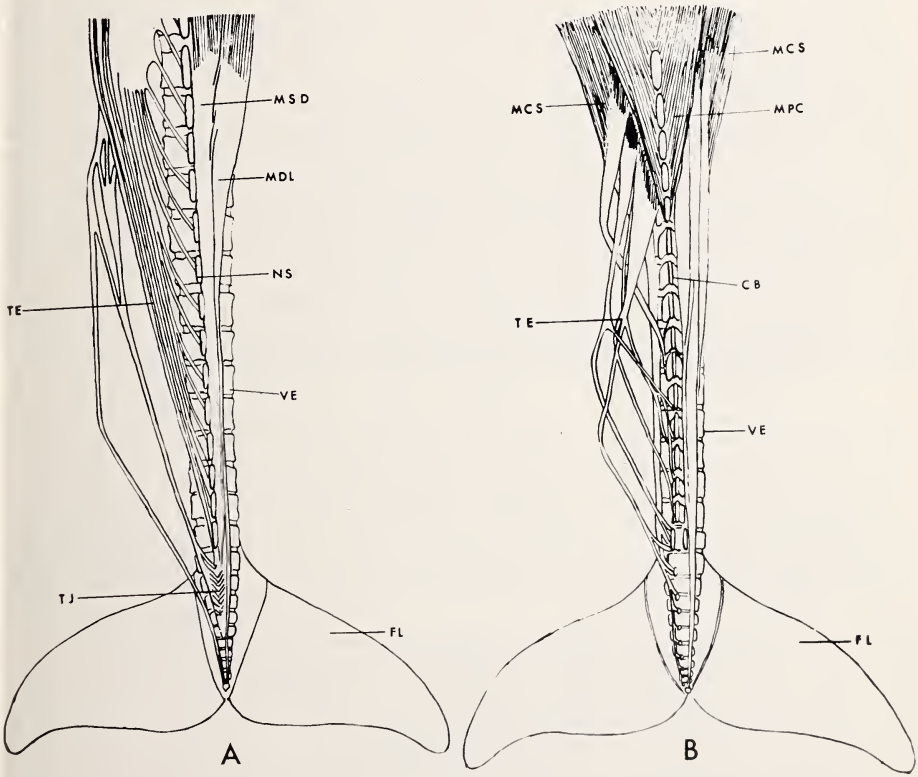



*Fig. 5 A.* Diagram of the distal end of the epaxial muscles of locomotion in the tail of a Common Porpoise *Phocoena phocoena.* The tendon sheaths have been removed from the muscles of the left side and the individual tendons partially separated to show their insertions on the neural spines — *B.* Diagram of the distal end of the hypaxial muscles of locomotion in the tail of a Common Porpoise *Phocaena phocaena.* The tendon sheaths have been removed from the muscles of the right side and the individual tendons partially separated to show their insertions on the chevron bones

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/



border of the tail. It is important to note that the posterior attachment to the vertebrae ceases at the commencement of the tail flukes (FL) at a point (TJ) where the neural spines are inconspicuous or absent. A single, slender tendon of the longissimus extends to the very end of the tail.

Contraction of the epaxial caudal muscles would therefore act mainly in lifting the tail and the anterior part of the flukes allowing the posterior part of the flukes to lag under water pressure.

Turning now to the hypaxial caudal muscle (fig. 5 B) which consists only of the sacrococcygeus (MCS) it will be seen that its numerous tendons (TE) are inserted into the lateral surfaces of all the chevron bones (CB) which extend to the very end of the tail. Although the sacrococcygeus is a relatively weak muscle compared with the combined spinalis and longissimus dorsi, its contraction would cause uniform flexion of the entire caudal peduncle with no sharp angle at the anterior insertion of the flukes. The pubococcygeus (MPC) takes no part in flexion of the tail and indeed has been referred to as part of the levator ani.

## Discussion

The combination of differential angle of incidence of the flukes with reciprocal flexure is such that during rapid acceleration from slow speed, the water is driven posterodorsally on the upstroke but that there is no drive on the downstroke, the water being "spilled" dorsally by the upward curvature of the flukes, and the small angle of incidence. This arrangement ensures that the direction of water-flow relative to the body does not alternate with changes in the direction of the tail-beat, a factor of great importance in the prevention of large turbulences and in the initiation of laminar flow.

In a more comprehensive paper to be published later, it will be demonstrated that the total body contours and the mode of locomotion serve to keep the water flowing in a constant direction relative to the surface of the body. See Fig. 6.

In support of the general theory of locomotion in cetaceans propounded above — a few observations made on living specimens in clear water are noteworthy. In addition to the gross distribution of pigment on the external skin, as depicted in various text

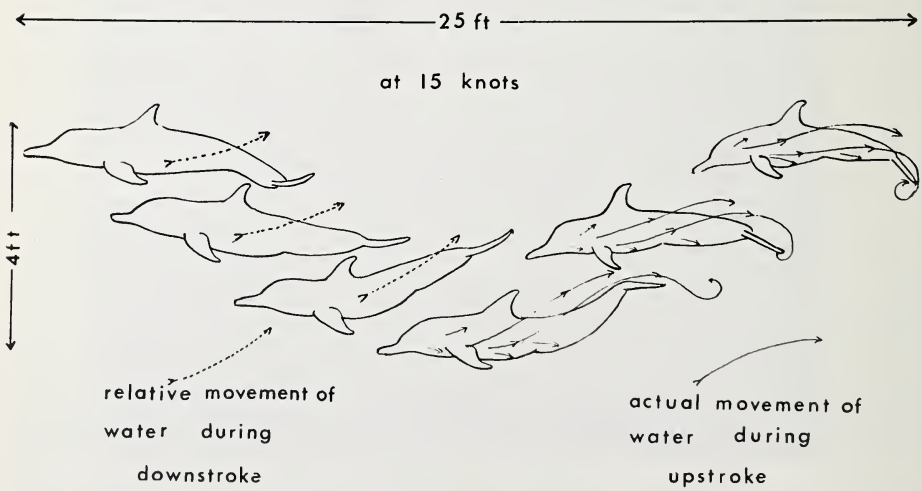



*Fig. 6.* Diagram showing undulating movement of the body of a cetacean during one complete cycle of the tail and the movement of water relative to the flanks

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/



books there are fine "brush-marks" leading posterodorsally along the entire flank from head to tail. These are particularly conspicuous in the Californian variety of the Bottle-nosed dolphin *Tursiops truncatus* and in the Pacific striped-dolphin *Lagenorhynchus obliquidens*. These "brush-marks" follow the orientation of the dermal ridges beneath the external epithelium, PURVES (1963), and they also indicate the direction of the water flow relative to the body (Fig. 6).

It is also notable than when dolphins "stand on their tails" as they have been trained to do in most "dolphinaria" there is a tendency for the body to oscillate in a vertical direction with the dorsal component of movement occurring during extension of the tail. Since, however, the animals are also able to move backwards during this process, a small amount of thrust during flexion must be involved.

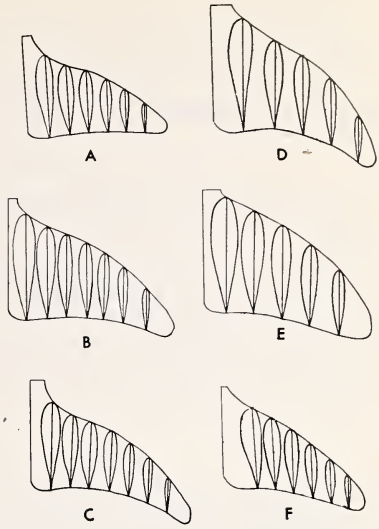



*Fig. 7.* Diagram showing hydrofoil cross section of the flukes in various species of cetacean. The vertical lines represent the positions of sections of a cast of the flukes, and the curved lines on the right and left side of each vertical line represent the contour of the dorsal and ventral surfaces respectively. A = *Stenella roseiventris* (Gray, 1866), B = *Stenella graffmani* (Lönnberg, 1934), C = *Stenella longirostris* (Gray, 1828), D = *Sousa plumbea* (G. Cuvier, 1829), E = *Lagenorhynchus cruciger* (Quoy and Gaimard, 1824), F = *Neomeris phocaenoides* (G. Cuvier, 1829)

As stated, the strong dorsal flexure of the flukes referred to above, occurs mainly during rapid acceleration from a slow speed, when strong muscular effort is required for flexion of the tail. During sustained, high-speed swimming, both the amplitude of the tail-beat and dorsal flexure of the flukes are very small, extension and flexion of the tail take place extremely rapidly and it is difficult to detect with the unaided eye that the downstroke is the slower one. This can, however, be seen from examination of cinematograph frames, PURVES (1963). In terrestrial mammals, flexion of the tail is gravity assisted and the hypaxial musculature is therefore greatly reduced. Although due to the relatively large amount of bone and reduced blubber content, the caudal region has a higher specific gravity than other parts of the body, the effect, in water of the downward pull of gravity is to a large extent counteracted by buoyancy so that if muscular effort is to be avoided during flexion of the tail, at high speed, some other mechanism must be invoked to assist in returning the tail to its position before the power stroke.

It is postulated that this assistance is provided by the hydrofoil cross section of the flukes. Fig. 7 (A—F) shows a series of diagrams of the flukes of various species of cetacean with profiles of the cross sections at regular intervals. The profiles are asymmetrical in outline with the side of greatest curvature representing the ventral surface. The arrangement is the reverse of the aerofoil in which "lift" is provided by reduced pressure on the upper surface of the wing. Provided the angle of incidence is kept small, the reduced pressure on the ventral surface draws the flukes rapidly downwards after the forward velocity has been provided by the upstroke. Since the density of water is approximately 1,000 times greater than that of air, the downward pull on the hydrofoil would be an equivalent amount greater than the "lift" on an aerofoil of the same size for any given velocity and angle of incidence. The ventral movement will also be assisted by the extreme dorsal "fairing" on the caudal peduncle.

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/



Experiments are now proceeding at the Delft Hydraulics Laboratory to determine quantitatively, the differential drive on the flukes at various angles of incidence and various velocities so that this can be correlated with the known difference between epaxial and hypaxial muscle weights.

## Summary

Direct observations of living dolphins, the study of the locomotor muscles and insertion of tendons indicate that the only upstroke of the tail is a power stroke — the downstroke being passive.

Examination of the fine structure of the horizontal collagen fibres in the flukes of cetaceans shows that differential distortion of the fibrils is correlated with the upward curvature of the flukes when muscular effort is required for flexion of the tail during rapid acceleration from slow speed. At high speed, flexion of the tail is assisted by the hydrofoil section of the flukes, and dorsal streamlining of the caudal peduncle. Both of these phenomena help to reduce the turbulence that would otherwise be generated by alternate movements of the tail.

## Zusammenfassung

Beobachtungen an lebenden Delphinen sowie das Studium der Bewegungsmuskulatur und des Sehnenansatzes ergaben, daß der Aufwärtsschlag der Schwanzflosse eine aktive, der Abwärtsschlag eine passive Bewegung darstellen.

Die Untersuchung der Feinstruktur der horizontal verlaufenden Collagenfibrillen in der Schwanzflosse der Cetacea zeigt, daß eine Beziehung zwischen der Verdrehung dieser Fibrillen und dem Aufbiegen der Schwanzflosse besteht, und zwar dann, wenn bei schneller Beschleunigung aus langsamer Bewegung heraus eine starke Muskelbeanspruchung zur Durchbiegung des Schwanzes erforderlich wird. Bei hoher Geschwindigkeit wird die Bewegung des Schwanzes unterstützt durch das strömungstechnisch günstige Profil der Schwanzflosse sowie durch die dorsale Stromlinienführung des Rumpfhecks (n. Cassell's: Blumenstiel).

Beide Phänomene helfen mit, die Turbulenz zu verringern, die sonst durch die beidseitige Bewegung des Schwanzes entstehen würde.

## Acknowledgements

Acknowledgements are due to Mr. J. V. Brown for phase-contrast photomicrography and to Miss D. Parry for the electron-micrographs. I also wish to thank the Director, Mr. E. F. den Herder, of the Dolphinarium, Harderwijk, Netherlands, and the Curator, Dr. W. H. Dudok van Heel for the opportunity to study live cetaceans at close-quarters.

## Bibliography

Felts, W. J. L. (1966): Some Functional and Structural Characteristics of Cetacean Flippers and Flukes: in Whales, Dolphins and Porpoises. Edit. Norris, K. S., Univ. Calif. Press, 255—276.

Purves, P. E. (1963): Locomotion in Whales. Nature **197**, 334—337.

Roux, W. (1883): Beiträge zur Morphologie der functionellen Anpassung. I. Structure eines hoch differenzierten bindegewebigen Organs (der Schwanzflosse des Delphins). Arch Anat. Entw., **4**, 76—162.

*Address of the author:* Dr. P. E. Purves, British Museum (Natural History), Cromwell Road, London S. W. 7, Great Britain

# ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: Mammalian Biology (früher Zeitschrift für Säugetierkunde)

Jahr/Year: 1967

Band/Volume: 34

Autor(en)/Author(s): Purves P. E.

Artikel/Article: The Structure of the Flukes in Relation to Laminar Flow in Cetaceans 1-8