

## CHAPTER 10

# Biomechanical Perspective on the Origin of Cetacean Flukes

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### 1. Introduction

The evolution of aquatic forms from terrestrial ancestors has been a reoccurring event in the history of the vertebrates. As these animals adapted to the aquatic environment, the most derived representatives developed structures and mechanisms for high-performance propulsion in water. These organisms converged on propulsive modes that utilized oscillating hydrofoils for rapid and sustained swimming (Howell, 1930; Webb, 1975; Webb and Buffrénil, 1990; Fish, 1993a).

Swimming is the only mode of locomotion for cetaceans, which moved into the water and abandoned the terrestrial environment in the Eocene (Gingerich *et al.*, 1983, 1994; Thewissen *et al.*, 1994). For modern whales, the horizontally oriented tail flukes represent a hydrofoil. Whales use their axial muscles to propel themselves by vertical oscillations of flukes (Parry, 1949a; Slijper, 1961; Strickler, 1980; Bello *et al.*, 1985). These oscillations produce hydrodynamic thrust that opposes the drag experienced by the body as a result of the viscosity and the flow pattern of the medium. The thrust generated is a resultant force from lift created by the hydrofoil (Webb, 1975; Fish, 1993a; Vogel, 1994). An effective hydrofoil produces a large lift (force acting perpendicular to the flow) while minimizing drag (force acting parallel to flow; Weihs, 1989; Vogel, 1994). Although the sirenians also developed tail flukes, it is the cetaceans for which flukes have been most associated with rapid and relatively high-powered swimming (Fish and Hui, 1991). The force generated by the flukes is sufficient to drive a dolphin through the water at speeds exceeding 10m/s or launch a 30-ton whale out of the water.

This chapter will focus on how thrust is generated by the action of the flukes in accordance with the varied morphological designs exhibited by whales. A biomechanical analysis of extant species is required to evaluate mechanisms by which the flukes of cetaceans would have evolved. Such an understanding permits a functional interpretation of the limited fossil remains of primitive cetaceans. Although we understand the evolution

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of terrestrial locomotion because of the available physical evidence such as skeletal remains and footprints, no such record exists for swimming by cetaceans as no fossilized imprints of the flukes have been unearthed and the sea leaves no tracks.

## 2. Morphology Design and Construction of Flukes

### 2.1. Structure

The flukes are lateral extensions of the distal tail. Structurally, the flukes are composed of a cutaneous layer, a subcutaneous blubber layer, a ligamentous layer, and a core of dense fibrous tissue (Felts, 1966). Both the cutaneous and subcutaneous layers are continuations of their respective layers covering the rest of the body.

The bulk of the fluke is composed of the core of fibrous tissue. The core of collagen fibers forms a thick solid attachment on the numerous, short caudal vertebrae and intervertebral disks (Felts, 1966). This attachment unites the caudal vertebrae associated with the flukes into a single resilient element. Within the fluke, the collagen fibers are arranged in horizontal, vertical, and oblique bundles (Felts, 1966; Purves, 1969). Horizontal fibers radiate out through the fluke. The pattern of fiber bundles indicates an orientation appropriate for incumng high tensile stresses.

Similarly, the ligamentous layer is arranged to resist tension of the flukes particularly at the trailing edge and tips. In these regions, the core of fibrous tissue is thin, whereas the ligamentous layer is relatively thick (Felts, 1966). In addition, the ligamentous layer is thickest at the tips and inserts perpendicularly at the trailing edge. This architecture during the stroke cycle would limit bending, which is variable between species. The harbor porpoise (*Phocoena phocoena*) displays almost no bending at either the fluke tips or the trailing edge, whereas the white-sided dolphin (*Lagenorhynchus acutus*) with larger flukes shows 35 and 13% deflections across the chord (i.e., distance from leading to trailing edges) and tip-to-tip span, respectively (Curren et al., 1994). Such differences in flexibility may reflect modification of the fibrous layers, which could affect swimming performance. Flexibility across the chord can increase propulsive efficiency by 20% compared with a rigid propulsor executing similar oscillations (Katz and Weihs, 1978).

The posteriormost caudal vertebrae continue into the flukes and end immediately anterior to the fluke notch (Rommel, 1990). Vertebrae anterior to the flukes are laterally compressed, whereas vertebrae within the flukes are dorsoventrally compressed. The peduncle-fluke junction is characterized by relatively large intervertebral spacings (Rommel, 1990; Long et al., 1997). The intervertebral joint at the base of the flukes mechanically functions as a low-resistance hinge acting as a center of rotation about the sagittal plane (Parry, 1949b; Long et al., 1997). In addition to the low stiffness of the joint, rotation is aided by the "ball" vertebrae (Watson and Fordyce, 1993). Located at the peduncle-fluke junction, the ball vertebrae have convex cranial and caudal surfaces. Fluke rotation is controlled by the epaxial m. extensor caudae lateralis and the hypaxial m. hypaxialis lumborum (Pabst, 1990).

Resistance to fossilization of the soft anatomy of the flukes poses difficulties for reconstruction of the ancestral form. Modern cetaceans, however, possess various skeletal

features associated with the flukes that may be compared with fossils to indicate the course of fluke evolution. This evolution has led to designs that provide high thrust production and efficiency in modern cetaceans.

## 22 Design and Physics of Flukes

Biomechanically, the flukes act like a **pair** of wings (Vogel, 1994). However, unlike the static wings of airplanes and jets, the flukes oscillate to generate a lift-derived thrust. As winglike structures, the flukes can be analyzed as engineered air- and hydrofoils to determine their effectiveness in lift generation. The shape of the flukes influences the energy requirements for swimming.

Fluke planforms have a sweptback tapered design that varies between different species with respect to hydrodynamically relevant parameters (Figs. 1, 2). For the fluke planform, measurements can be made on the span ( $S$ : tip-to-tip distance), root chord ( $RC$ : distance from base of fluke to trailing edge), sweep ( $\Delta$ : angle between a perpendicular to  $RC$  and one-quarter chord position), and planform area ( $A$ ).

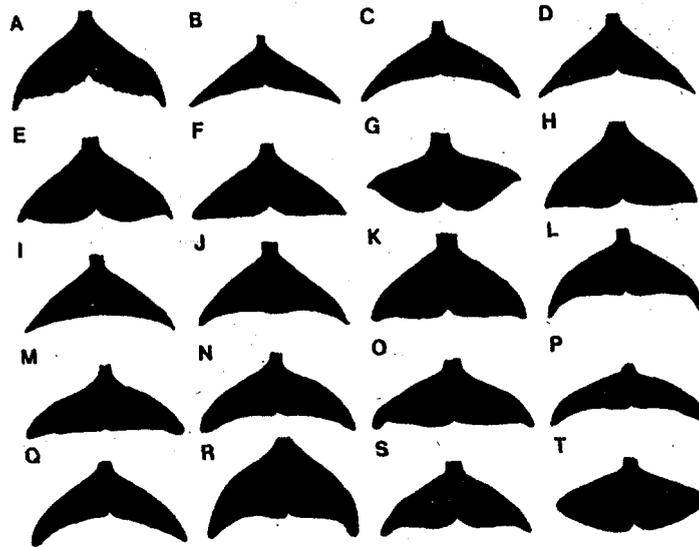


FIGURE 1. Planforms of flukes from representative cetacean species: A, humpback whale (*Megaptera novaeangliae*); B, blue whale (*Balaenoptera musculus*); C, minke whale (*Balaenoptera acutorostrata*); D, right whale (*Eubalaena glacialis*); E, gray whale (*Eschrichtius robustus*); F, sperm whale (*Physeter macrocephalus*); G, narwhal (*Monodon monoceros*); H, beluga (*Delphinapterus leucas*); I, Sowerby's beaked whale (*Mesoplodon bidens*); J, northern bottlenose whale (*Hyperoodon ampullatus*); K, Amazon river dolphin (*Inia geoffrensis*); L, long-finned pilot whale (*Globicephala melaena*); M, bottle-nose dolphin (*Tursiops truncatus*); N, Pacific white-sided dolphin (*Lagenorhynchus obliquidens*); O, killer whale (*Orcinus orca*); P, false killer whale (*Pseudorca crussidens*); Q, Heaviside's dolphin (*Cephalorhynchus heavisidii*); R, northern right whale dolphin (*Lissodelphis borealis*); S, harbor porpoise (*Phocoena phocoena*); T, Dall's porpoise (*Phocoenoides dalli*).

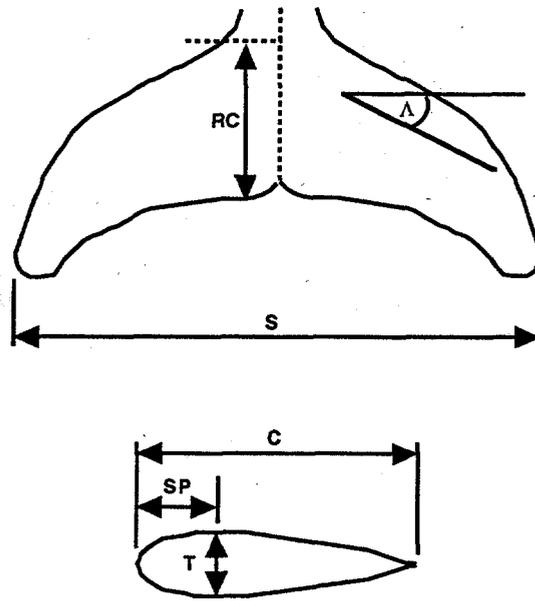


FIGURE 2. Fluke dimensions of planform (above) and cross-sectional profile (below). Explanation of dimensions is given in text.

Data from 34 cetacean species show that  $S$  and  $A$  are directly related to increasing body length (Fig. 3). This trend is expected because the fluke span and area determine the mass of water that is affected for thrust generation. Larger  $A$  would generate more thrust. Because thrust developed by the flukes is necessary to counter the drag incurred by the body as determined by its surface area (Bose et al., 1990),  $S$  and  $A$  are associated with body length ( $BL$ ) where  $S$  is proportional to  $BL$  and  $A$  is proportional to  $BL^2$ . Fluke span displayed a slight positive allometry according to the relationship  $S = 0.11 BL^{1.128}$ , whereas fluke projected area displayed a slight negative allometry according to the relationship  $A = 0.017 BL^{1.946}$ . Large whales would have a relatively larger  $S$  with smaller  $A$  than smaller dolphins.

When the relationships between  $S$ ,  $A$ , and  $BL$  are compared between life history stages within a species, differences between juveniles and adults are evident that would affect performance (Amano and Miyazaki, 1993; Curren et al., 1993). In neonates and prepubescent dolphins, the increase in  $S$  with respect to  $BL$  is not as rapid as observed for adults (Perrin, 1975; Amano and Miyazaki, 1993). Therefore, young animals may be at a disadvantage when swimming, thus requiring the use of free-riding behaviors to maintain speed with the parent (Lang, 1966).

The interaction between  $S$  and  $A$  as related to effectiveness of the hydrofoil design is expressed as the aspect ratio (AR). AR is calculated as  $S^2/A$  (Webb, 1975; Vogel, 1994). High AR indicates long narrow flukes, whereas low AR indicates broad flukes with a short  $S$ . High-AR hydrofoils are characteristic of relatively fast swimmers.

AR varies from 2.0 for the Amazon river dolphin (*Inia geoffrensis*) to high values of 6.1 and 6.2 for the fin whale (*Balaenoptera physalus*) and false killer whale (*Pseudorca*

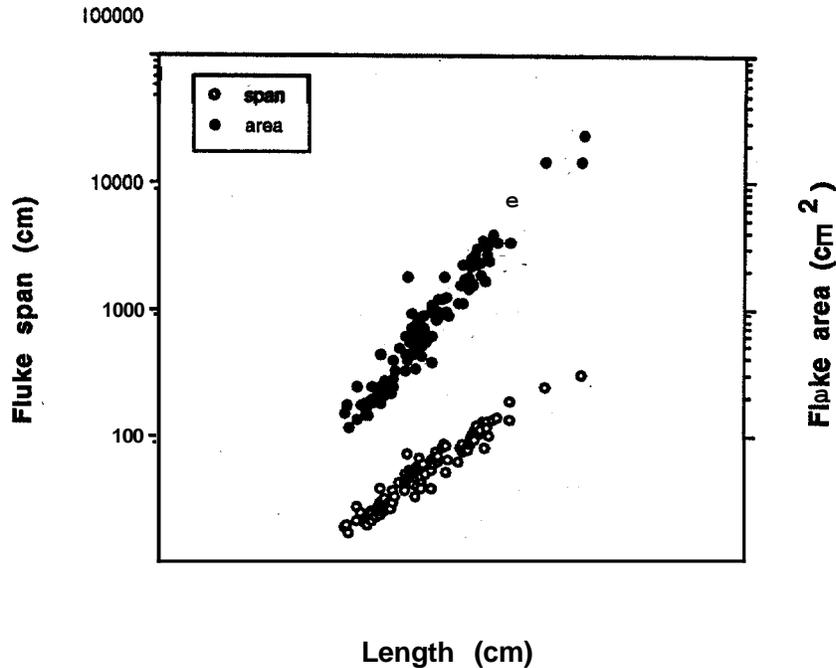


FIGURE 3. Relationship of planar surface area and fluke span versus body length. Data from Videler and Kamer-mans (1985), Bose and Lien (1989), Bose *et al.* (1990), Curren (1992), and Fish (1993b, unpublished).

*crassidens*), respectively (Bose and Lien, 1989; Fish, unpublished). These values correspond to the swimming performance in these species. *Pseudorca* moves at maximum speeds of 7.5 m/s (Fish, unpublished) with speeds in schools of 3 m/s (Norris and Prescott, 1961) and *Balaenoptera* attains maximum speeds of 10 m/s with sustained speeds of 2.5 m/s (Bose and Lien, 1989). *Inia* is relatively slower with a maximum speed of 3.9 m/s and routine speed of about 0.4–0.9 m/s (Best and da Silva, 1989).

Well-performing flukes maximize the ratio of lift ( $L$ ) to drag ( $D$ ) generated by their action (Webb, 1975). An increase in the maximum  $L/D$  with increasing size is achieved by increasing  $S$  more rapidly than the square root of  $A$ , thereby increasing  $AR$  (von Mises, 1945; Lighthill, 1977; van Dam, 1987). The lift for flukes of a given area and motion would be greatest when  $AR$  is highest (Bose *et al.*, 1990; Daniel *et al.*, 1992). The longer trailing edge of a high- $AR$  fluke increases the mass of water deflected posteriorly augmenting the thrust component. However,  $AR$  above 8–10 provides little further advantage and may be structurally limited (Webb, 1975).

Drag incurred by the flukes is inversely dependent on  $AR$  related primarily to the induced drag component (Webb, 1975). Induced drag is produced as a consequence of the lift generated by the flukes. As the flukes are canted at an angle to the water flow, lift is produced by deflection of the water and pressure difference between the dorsal and ventral surfaces of the flukes (Webb, 1975; Blake, 1983). The pressure difference produces spanwise cross flows that go around the fluke tips resulting in the formation of spiraling vortical flow. The flow is shed from the fluke tips as longitudinal tip vortices. The energy dissipated by the

vortices represents the induced drag. High AR and tapering of the flukes reduce tip vorticity and induced drag (Webb, 1975; Rayner, 1985; Webb and Burrfenil, 1990; Daniel *et al.*, 1992).

Induced drag also is limited by the sweep ( $A$ ) of the flukes. It was shown by van Dam (1987) that a tapered wing with sweptback or crescent design could reduce the induced drag by 8.8% compared with a wing with an elliptical planform. Minimal induced drag is fostered by a sweptwing planform with a root chord greater than the chord at the tips giving a triangular shape (Kiichermann, 1953; Ashenberg and Weihs, 1984). This optimal shape approximates the planform of cetacean flukes. Flukes have sweep angles ranging from lows in killer whale (*Orcinus orca*) and Dall's porpoise (*Phocoenoides dalli*) of 4.4 and 5.4°, respectively, to a maximum value of 47.4° for white-sided dolphin (*Lagenorhynchus acutus*) (Bose *et al.*, 1990; Fish, unpublished).

Sweep of the fluke together with taper has the effect of concentrating the surface area toward the trailing edge. This would effectively shift the lift distribution posterior of the center of gravity affecting pitching equilibrium (von Mises, 1945; Webb, 1975). Lighthill (1970) and Wu (1971b) suggested that a minimum in wasted energy would be realized when the pitching axis was moved to the 0.75 chord position. Proximity of the pitch axis close to the trailing edge was supported by Chopra (1975).

The sweep angle is inversely related to the aspect ratio of the flukes (Bose *et al.*, 1990; Curren *et al.*, 1993; Fig. 4). The combination of low sweep with high AR allows for high-efficiency rapid swimming (Azuma, 1983). High sweep may compensate for the reduced lift production of low-AR flukes. Highly sweptback, low-AR wings produce maximum lift

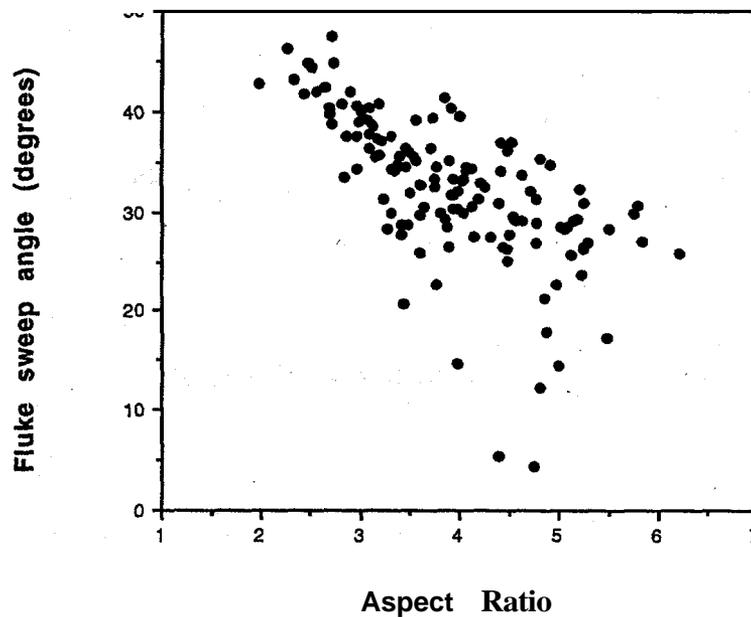


FIGURE 4. Relationship between sweep angle ( $A$ ) and aspect ratio ( $AR$ ). Data from Bose and Lien (1989). Bose *et al.* (1990), Curren (1992), and Fish (1993b, unpublished).

when operating at large angles of attack (see below), when low-sweep, high-AR designs would fail (Hurt, 1965). However, the maximum lift is reduced with increasing sweep angle for a given AR, whereas efficiency increases (Liu and Bose, 1993). Mathematical analysis by Chopra and Kambe (1977), however, found that a sweep angle exceeding about 30° leads to a reduction in efficiency. The relationship between sweep and AR also indicates a structural limitation to the strength and stiffness of the flukes (van Dam, 1987; Bose *et al.*, 1990). The ability to sustain certain loads without breaking is considered a major constraint on increasing span and AR (Daniel, 1988). Because the fibrous composition not only strengthens the flukes but also increases flexibility, extreme increase in span with increased AR, although potentially generating higher lift, would exaggerate the bending of the appendage in an oscillatory mode and reduce performance.

Flukes, however, do show some degree of both spanwise and chordwise flexibility. The center of the flukes is more rigid than the tips. During the upstrokes fluke tips are bent down slightly from the plane of the fluke and lag behind the center, whereas bending in the opposite direction occurs during the downstroke. Bose *et al.* (1990) suggested that the phase difference related to this spanwise flexibility would prevent the total loss of thrust at the end of the stroke. While the tips would be ending the stroke and effectively generating no thrust, the center would have started the next stroke and begun thrust generation. On the other hand, chordwise flexibility at the trailing edge of the flukes potentially can increase the efficiency of the flukes by up to 20% with only a moderate decrease in the overall thrust (Katz and Weihs, 1978).

Sections of the fluke along the longitudinal axis display a conventional streamlined foil profile with a rounded leading edge and long tapering trailing edge (Fig. 2). The sharp trailing edge and rounded leading edge are crucial for generating lift and minimizing drag (Lighthill, 1970; Vogel, 1994). The streamlined cross section is maintained by the core of fibrous material (Felts, 1966). The flukes are symmetrical about the chord (Lang, 1966; Bose *et al.*, 1990). In examining the flukes of the common dolphin (*Delphinus bairdi*), Lang (1966) reported that some warpage was evident. This may explain the contradictory results of Purves (1969) who noted an asymmetry in the fluke cross sections. Whereas an asymmetry would have supported thrust production through only half of the stroke cycle of the dolphin, the symmetrical design of the flukes indicates that thrust is generated on both up- and downstrokes.

For any section through the fluke in the parasagittal plane, measurements can be made on the chord ( $C$ ), maximum thickness ( $T$ ), and shoulder position ( $SP$ : distance of  $T$  from leading edge expressed as a percentage of  $C$ ) (Fig. 2).  $SP$  and the thickness ratio ( $TR = T/C$ ) indicate hydrodynamic performance relating to the generation of lift and drag for foil sections (von Mises, 1945; Hoerner, 1965). Flukes range from 25 to 40% for  $SP$  and between 0.16 and 0.25 for  $TR$  (Lang, 1966; Bose *et al.*, 1990). These sections are similar to engineered foils, which are classified by the National Advisory Committee for Aeronautics (NACA). The NACA 63-021 foil (Abbott and von Doenhoff, 1949) provides a reasonable facsimile of the fluke sections. This resemblance suggests that the flukes would be able to produce high lift with low drag at angles of attack up to 20°. This would be possible because the shape of the fluke section does not promote extremes in the chordwise pressure distribution which cause separation of flow from the foil surface and increase drag (Lang, 1966). Thus, cavitation that could damage the animal is not expected to occur even at routine swimming speeds of dolphins.

The flukes of modern cetaceans have a design to act as a hydrofoil for lift production. The combination of moderate aspect ratio, sweep, cross-sectional design, and flexibility of the flukes furnishes a morphology capable of the generation of high lift with low drag performance. To realize the potential of a lift-based propulsion, the flukes must be moved in a fashion that optimally orients the flukes into a flow.

### 3. Kinematics and Hydrodynamic Performance

#### 3.1. Propulsive Movement

Whales generate thrust exclusively with caudal flukes (Fish and Hui, 1991). The tail flukes, which act as the hydrofoil, oscillate dorsoventrally. Although different in the orientation of the hydrofoil, the propulsive motions of cetaceans are similar to those of some of the fastest marine vertebrates, including scombrid fishes and lamnid sharks. These motions are characteristic of the so-called carangiform with lunate tail or thunniform mode (Lighthill, 1969).

The posterior one-third of the body is bent to effect dorsoventral movement of the flukes (Fig. 5; Parry, 1949b; Slijper, 1961; Lang and Daybell, 1963; Videler and Kamerling, 1985; Yanov, 1991; Fish, 1993b). Although these heaving motions vertically displace the flukes through an arc, the flukes do not move as a simple pendulum. Rather, superimposed on the motion, the flukes are pitched at a joint at their base. Pitching at the base of the flukes occurs because of the double hinge mechanism of the caudal vertebrae including the "ball" vertebrae (Watson and Fordyce, 1993).

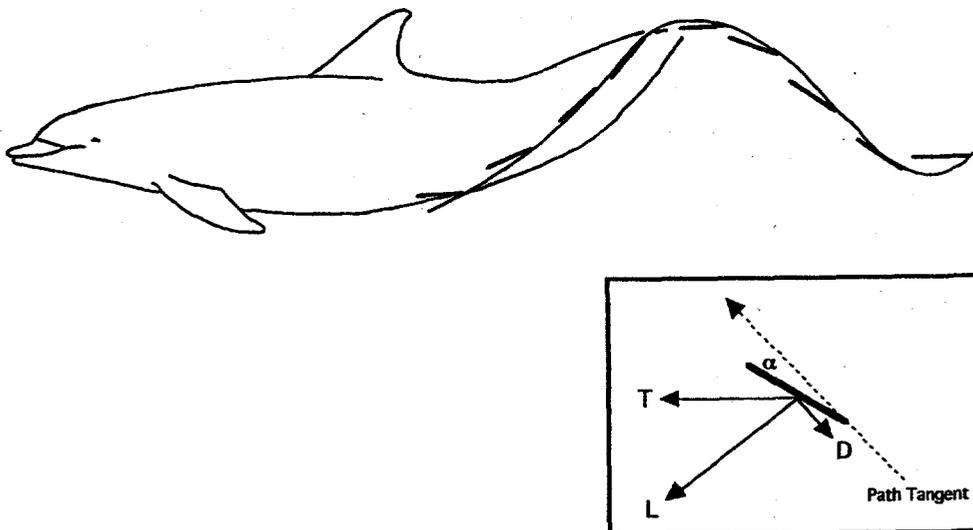


FIGURE 5. Path of oscillating dolphin flukes through a stroke cycle. The tips of the flukes move along a sinusoidal path. Fluke position along the path is illustrated as a straight line. The box shows the relationship between the tangent to the path of the flukes and the angle of attack,  $\alpha$ . From Fish (1993b).

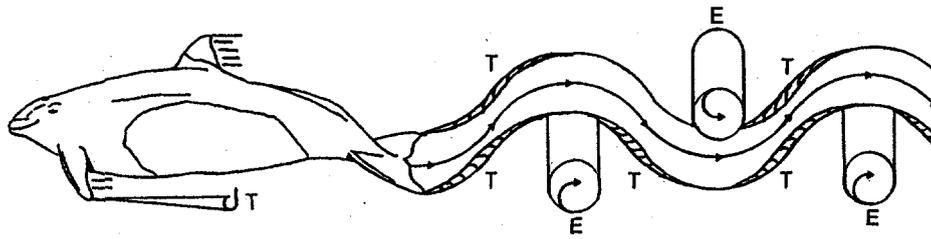


FIGURE 6. Pattern of vorticity shed in wake of dolphin. Tip vortices (T) and trailing edge vortices (E) generated from the flukes are shown. From Fish (1993a).

The heaving and pitching motions of the flukes result in a varying angle (pitch angle) between the flukes and the horizontal plane (Figs. 5, 6). At its maximum vertical displacement, the flukes have a pitch angle of zero so that the axis of the fluke chord is parallel to the axis of progression (i.e., horizontal when the animal is swimming at constant depth). This orientation effectively minimizes the drag on the flukes but generates no thrust. As the flukes are downswept, the pitch angle increases by flexion at the peduncle-fluke junction. Through the middle of the downward excursion of the stroke, the pitch angle is maintained at a maximum (Fig. 5). The end of the stroke is accompanied by a decrease in the pitch angle with the flukes again oriented parallel to the direction of forward progression. The average pitch angles for the harbor porpoise (*Phocoena phocoena*) and white-sided dolphin (*Lagenorhynchus acutus*) were 34 and 33°, respectively (Curren *et al.*, 1994).

The ability to rotate the flukes about a pitching axis allows for control of angle of attack. Angle of attack is defined as the angle between the tangent of the fluke's path and the axis of the fluke's chord (Fig. 5) (Fierstine and Walters, 1968; Fish, 1993b). Maintenance of a positive angle of attack ensures thrust generation throughout the majority of the stroke cycle (Lang and Daybell, 1963; Lighthill, 1969, 1970; Videler and Kamermans, 1985; Go-forth, 1990).

The magnitude of the attack angle will affect the propulsive efficiency and the thrust generated in lift-based swimming (Webb, 1975). As angle of attack is increased for a hydrofoil, there is increase in both lift and drag. Lift will increase faster than the drag with increasing angle of attack up to a critical level. Further increase of angle of attack leads to an increase in drag and precipitous loss of lift in a condition called *stall*. Stall is caused by separation of the flow from the foil surface, which is unavoidable at a critical angle of attack.

Angle of attack of oscillating dolphin flukes increases rapidly at the initiation of up- and downstrokes reaching a maximum within the first third of the stroke (Fish, 1993b). Maximum angle of attack varies indirectly with swimming speed in bottlenose dolphins (*Tursiops truncatus*). Maximum values ranging from 12 to 21° for *Tursiops* and 22.5 to 24° for *Lagenorhynchus* were reported by Fish (1993b) and Lang and Daybell (1963), respectively. Such ranges are below the 30° angle for an oscillating foil at which stall occurs (Triantafyllou and Triantafyllou, 1995).

Maximum heave amplitude is confined to the tips of the flukes. At low swimming speeds (<2.2 m/s for *Lagenorhynchus*), heave amplitude appears to increase with speed (Curren *et al.*, 1994). Heave amplitude, however, is independent of swimming speed at rou-

tine and sprint speeds (Fish, 1993b). Maximum heave amplitude remains a constant proportion of body length at approximately **20%**.

Alternatively, the stroke frequency varies directly with swimming speed. Maximum frequency corresponds to tailbeat frequency at maximum voluntary muscular effort for dolphins (Goforth, 1990). The positive linear relationship of frequency with swimming speed for *Tursiops* is consistent with observations on other marine mammals and fish that use hydrofoil propulsion (Webb, 1975; Feldkamp, 1987; Fish *et al.*, 1988). Modulation of frequency with constant amplitude would prevent excessive distortion of the body, which would increase overall drag and decrease locomotor efficiency. This trend differs from semiaquatic paddlers, which modulate amplitude and maintain a constant frequency to achieve higher swimming speeds (Williams, 1983; Fish, 1984).

Flukes follow a sinusoidal pathway (Fig. 5) that is symmetrical about the longitudinal axis of the body and in time (Videler and Kamermans, 1985; Goforth, 1990; Fish, 1993b). Previously it was assumed that cetaceans swam with an asymmetrical propulsive stroke. This assumption was predicated on differences in the epaxial and hypaxial muscle masses (Purves, 1963). Parry (1949a) was able to confirm differences in stroke duration between upstroke and downstroke from counts of **film** frames of a dolphin swimming away from a camera. Unfortunately, the film records of the swimming dolphin showed that the animal was giving birth at the time. However, control of the flukes does permit variable movements during up- and downstrokes so that a stroke cycle can be divided into power and recovery phases (Purves, 1963).

As already discussed, the propulsive movements of cetaceans are confined to the posterior one-third of the body, with the greatest amplitude at the flukes (Fish and Hui, 1991). This action restricts thrust production to the flukes. By restricting bending to the peduncle and base of the flukes, this permits rotational motion to maintain a positive angle of attack to the oncoming flow (Webb, 1975). Thus, the flukes are able to produce a high lift and nearly continuous thrust over the entire stroke cycle (Fish, 1992). Such movements, classified as thunniform swimming, will engender high performance in thrust production and efficiency.

### 3.2. Thrust Production and Efficiency

Although measurements and calculations of lift and drag performance by static hydrofoils and wings permit a rudimentary understanding of the development of thrust by flukes, such estimates are not directly translated to thrust production by the flukes because of their oscillatory motions. To comprehend the dynamic production of lift-based thrust, hydromechanical models were employed (Lighthill, 1969; Wu, 1971b; Chopra and Kambe, 1977). Because the flukes are connected to the body by a narrow attachment, the caudal peduncle, that oscillates in the direction of its minimum resistance, the flukes are essentially separated from the body (Lighthill, 1969, 1970; Fish and Hui, 1991). This allows analysis of thrust production by the flukes to be made separate of the body and its actions.

Estimates of thrust based on the motion of the flukes alone have been used to independently assess the drag related to body form and swimming motions. A number of studies have used kinematic data (Noms and Prescott, 1961; Lang and Daybell, 1963; Fish, 1993b) to help develop hydromechanical models based on oscillating plates or hydrofoils

(Parry, 1949a; Lighthill, 1969, 1970; Wu, 1971b; Chopra and Kambe, 1977; Yates, 1983; Romanenko, 1995).

As the flukes oscillate ventrally, they are pitched at a positive angle of attack to the oncoming flow. The angle of attack and fluke velocity are determined by the vertical velocity of the flukes and horizontal velocity of the body. The streamlines of fluid are deflected above and below the flukes imparting a higher velocity to the upper flow. By the Bernoulli theorem, a pressure difference results with a lower pressure on the dorsal aspect of the flukes. The net pressure produces a pressure force that is resolved into drag tangent to the axis of motion of the flukes and a lift perpendicular to the axis of motion (Webb, 1975). The center of lift is relatively near the leading edge at or anterior to the maximum thickness (Vogel, 1994). The pressure force is reversed on the upstroke.

The orientation of the flukes throughout the stroke produces lift directed forward and upward during the downstroke and forward and downward during the upstroke. The anteriorly directed component from the mean forward tilt of lift represents the thrust (Daniel *et al.*, 1992). Thrust from lift increases directly with increases in angle of attack. However, low angles of attack increase hydromechanical efficiency while reducing the probability of stalling and decreased thrust production (Chopra, 1976).

Lift also depends on the frequency of oscillation of the flukes. Thrust increases with frequency whereas efficiency decreases (Daniel, 1991). The reciprocating action of the flukes means that the flow pattern is reversed through the stroke, and because the water has inertia, the flow pattern will take time to redevelop potentially affecting performance (Wu, 1971b; Daniel, 1991; Daniel *et al.*, 1992). The importance of the oscillatory motion to thrust generation and efficiency is determined by the reduced frequency parameter, which is the ratio of oscillatory to forward motion (Daniel *et al.*, 1992). A reduced frequency less than 0.1 indicates nearly steady motion (Yates, 1983; Daniel *et al.*, 1992). High values of reduced frequency indicate the dominance of unsteady effects, which incur lower lift than steady motion (Lighthill, 1970). Reduced frequencies of 0.51–1.15 for *Tursiops* and 0.4 for *Lagenorhynchus* were reported by Fish (1993b) and Webb (1975), respectively, indicating the dominance of unsteady effects.

Unsteady effects may contribute to thrust production by increasing the relative velocity and thus the lift (Daniel *et al.*, 1992). In addition, accelerational flows fostered by the unsteady effects may generate thrust.

As thrust from lift is produced, momentum is transferred from the flukes to the water. The momentum is proportional to the mass of the affected water and velocity of the flukes. The water is pushed back in a direction opposite to the swimming direction with a net rate of change of momentum that according to Newton's third law is equal and opposite to the thrust (Wu, 1971a; Chopra, 1975; Videler, 1993). The thrust produced balances the viscous and pressure drag of the body and flukes.

The momentum imparted to the fluid is concentrated in a jet of fluid directed on average opposite to the swimming direction (Wu, 1971a; Rayner, 1985; Videler, 1993). The jet induces the resting water around it to generate a vortex wake. A wake is necessary to produce thrust. The wake is visualized as a trail of connected alternating clockwise and anti-clockwise vortex rings with the jet directed through the center of the rings (Fig. 6). This vortex pattern is generated at the bottom and top of the stroke as vortices shed from the fluke with opposite circulation (Vogel, 1994). Tip vortices that roll off the fluke tips connect the shed vortices to form the ring.

In addition to the lift, leading edge suction contributes to thrust (Lighthill, 1970; Chopra and Kambe, 1977; Ahmadi and Widnall, 1986). A suction is created as the flow becomes highly accelerated as it moves around a **sharp** corner (Yates, 1983). The high acceleration locally decreases the pressure and produces the suction. **At** the trailing edge where vorticity is shed, flow around the edge is forbidden (Videler, 1993; Vogel, 1994). The rounded leading edge promotes the suction force (Lighthill, 1970; Wu, 1971b). The effect of leading edge suction is to tilt the pressure force forward by an angle equal to the angle of attack (Weihs, personal communication). The total lift force, which is typically normal to the fluke axis, is tilted perpendicular to the direction of fluke motion and thus increases the thrust component. However, excessive leading edge suction could induce stalling via boundary layer separation and reduce thrust. The lunate configuration of the leading edge of the flukes reduces leading edge suction without a decrease in total thrust (Chopra and Kambe, 1977; van Dam, 1987).

Efficiency **is** defined as the ratio of the mean thrust power required to overcome the drag on the animal divided by the mean rate at which the **animal** is doing work against the surrounding water (Lighthill, 1970). Efficient **thrust** production requires high lift production while minimizing energy **loss** into the wake (Blake, 1983).

Wu (1971b) estimated that the propulsive efficiency of a dolphin could be **as high as** 0.99. This efficiency was assumed to be an overestimate because Wu used a two-dimensional analysis that underestimated trailing vorticity and wake energy **loss** (Ahmadi and Widnall, 1986; Karpouzian *et al.*, 1990). Competing three-dimensional models of lunate tail swimming predict efficiencies lower than 0.99 but above 0.7 (Chopra and Kambe, 1977; Yates, 1983; Bose and Lien, 1989; Karpouzian *et al.*, 1990; Fish, 1993b, 1996). Efficiencies in this range **are** considered good, because few engineered propellers achieve efficiencies higher than 0.7 (Liu and Bose, 1993). The high efficiencies associated with swimming by dolphins are dependent on a fluke design that enhances high thrust with reduced drag and on fluke oscillation that maintains continuous thrust production (Fish, 1992).

The design and mechanics of flukes of modern cetaceans have produced a highly efficient propulsor for large thrust production. However, the ancestors of cetaceans were terrestrial (Gingerich *et al.*, 1983; Thewissen *et al.*, 1994) and would not have developed flukes prior to entering the water. How then did flukes evolve, and what were the transitional stages and their levels of performance?

#### 4. Evolution

The evolution of cetacean flukes has been a matter of speculation for over 100 years (Flower, 1883; Howell, 1930). The soft tissue composition of the flukes has left no record of how **or** why they arose and how they may have evolved to the high-efficiency and large-thrust-generating propulsive structures. **This** is contradictory to the situation for ichthyosaurs, which are another highly derived secondarily aquatic vertebrate with a high-aspect-ratio caudal propulsor (Motani *et al.*, 1996). These extinct marine reptiles left not only a rich store of fossilized skeletons, but in a number of cases, particularly during the Jurassic, they fortuitously left imprints of lunate tail fins. The recent discovery of a Lower Triassic ichthyosaur, *Chensaurus chaoxianensis*, with an elongate body and caudal fin shape allowed investigators to construct a possible pathway examining the transition from

anguilliform, through subcarangiform to more derived thunniform swimmers (Motani *et al.*, 1996).

Despite recent discoveries of early cetaceans, such as *Pakicetus*, *Ambulocetus*, and *Rodhocetus* (Gingerich *et al.*, 1983, 1994; Thewissen *et al.*, 1994, 1996a), there still remains a paucity of tangible physical evidence on the evolution of the flukes. Tail vertebrae in these fossils are lacking or incomplete, especially for the most terminal portions. To **this** add that (1) modern cetacean species exhibit the highly derived thunniform swimming mode and design, (2) **no** series of intermediate fluke designs exist, and (3) they are phylogenetically disjunct from their closest living relative (i.e., ungulates), which have specialized for terrestrial locomotion; thus, little direct information is available to answer the evolutionary questions regarding the transition of the flukes.

Substitutes to direct observations of morphological transition in fossil lineages are the use of ontogenetic information and the use of model specimens. By examining embryonic development within an individual, the ontogeny can be used as an additional character for understanding the phylogenetic framework. Similarities between ontogenetic and phylogenetic sequences reflect a possible pathway related to shared developmental patterns. Such inferences have been used previously to lend support to the evolution of complex anatomical changes (Rowe, 1996) and have been suggested as a means of reconstructing design modifications in the flukes of whales (Folkens and Barnes, 1984). Alternatively, a model can be constructed that draws **on** the swimming performance of modern species as analogues of the primitive intermediate forms (Fish, 1996). By testing living organisms of similar mechanical design to extinct species, performance characteristics can be examined to judge their importance in order to construct a mechanically plausible evolutionary scenario. Because the mechanics of swimming is used to generate the model, the modern species chosen need not be closely related to the group of interest or to each other. Lauder (1995) justified this technique of using extant surrogates to determine performance in extinct forms from a different clade.

#### 4.1. Ontogeny

Despite their importance to the evolution and locomotion of whales, development of the flukes has been largely overlooked. The ontogeny of the flukes was the **main** focus of study over 100 years ago (Flower, 1883; Ryder, 1885; Howell, 1930). The argument at that time was whether the flukes represented a secondarily acquired structure or were the vestiges of the hind limbs. Morphologists of the time including Huxley, Flower, and Owen supported the former view, while Ryder defended the idea that the flukes were integumentary limb-folds that had migrated caudally (Flower, 1883; Ryder, 1885; Howell, 1930).

Much of the evidence quoted by Ryder (1885) was based on the assumption that whales had a seal-like ancestor that used its hind flippers for propulsion similar to modern seals. With the hind limbs extended posteriorly, these limbs were believed to have fused to the body rendering them immobile and eventually causing the muscles and bones of the pelvis and extremities to atrophy. However, the integument of the feet would be in position on the lateral aspect of the tail to form the rudiments of flukes. In addition, the flukes would develop as folds distally rather than **as** lateral ridges extending the entire length of the tail.

Ryder's scenario has been discounted and the flukes are considered to represent mere-

ly outgrowths of the skin and connective tissue of the tail (Slijper, 1979). The occurrence of whales exhibiting external hind limbs (Andrews, 1921), the presence of embryonic limb buds anterior of the tail (Rice and Wolman, 1971; Slijper, 1979), and fossil cetaceans with mobile but reduced hind limbs (Gingerich *et al.*, 1990, 1994) indicate separate ontogenies of the flukes and the hind limbs.

Initially, the tail in cetacean embryos is drawn out to a point with no trace of flukes. For example, in *Stenella attenuata*, the absence of flukes occurs in embryos approximately 45 mm in total length (Meyer *et al.*, 1995; Penn, 1997). By 63 mm, flukes appear as a diamond or spadelike design with rounded edges (Perrin, 1997). This stage is reached in the gray whale (*Eschrichtius robustus*) at a size of 120 mm, which is estimated to be an age of 87 days (Rice and Wolman, 1971). When the *Stenella* fetus has reached a size of 165 mm, the flukes have expanded laterally reminiscent of the fluke shape of slow-swimming species. *Stenella* exhibits a deeply notched, lunate fluke design similar to adults by 225 mm (Meyer *et al.*, 1995).

Examination of other whale embryos showed similar developmental patterns (Ryder, 1885; Rice and Wolman, 1971). Such patterns possibly reflect the evolutionary transition of cetacean flukes. This developmental-transitional sequence is displayed in Fig. 7 as a reproduction of the figure original provided by Ryder (1885). Such a generalized sequence, although theoretically possible, is conjectural as a reconstruction of the evolution of flukes (Folkens and Barnes, 1984).

## 4.2 Functional Model

Prior to the evolution of flukes, the ancestors of modern cetaceans would have needed extensive changes not only to their morphology but also to the mechanism used to pro-

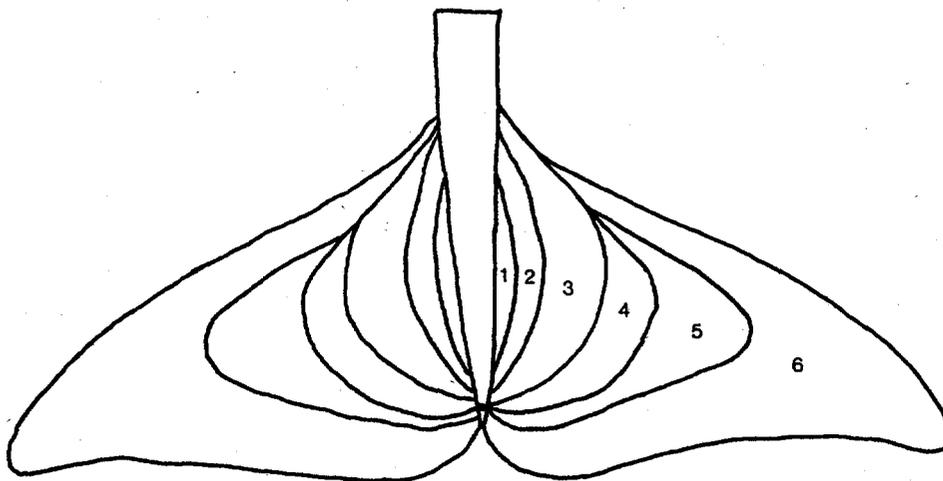


FIGURE 7. Successive contours of six stages of fluke development redrawn from Ryder (1885). Fluke outlines were compiled from different sources and scaled to equivalent size.

duce thrust for swimming (Fish, 1996; Thewissen *et al.*, 1996a). This is no trivial matter in that the swimming modes of terrestrial and semiaquatic ancestors would have used not only different appendages from the flukes of cetaceans, but also the force necessary to generate thrust would have had different derivations (Howell, 1930; Fish, 1992, 1996).

Paddling using alternate motions of the legs is the primitive mode of aquatic propulsion in mammals (Williams, 1983; Rayner, 1985; Fish, 1992, 1993a,c). Combinations of forefeet, hind feet, or all four feet are used to generate thrust (Tarasoff *et al.*, 1972; Williams, 1983, 1989; Fish, 1984, 1993c). The stroke cycle is composed of power and recovery phases.

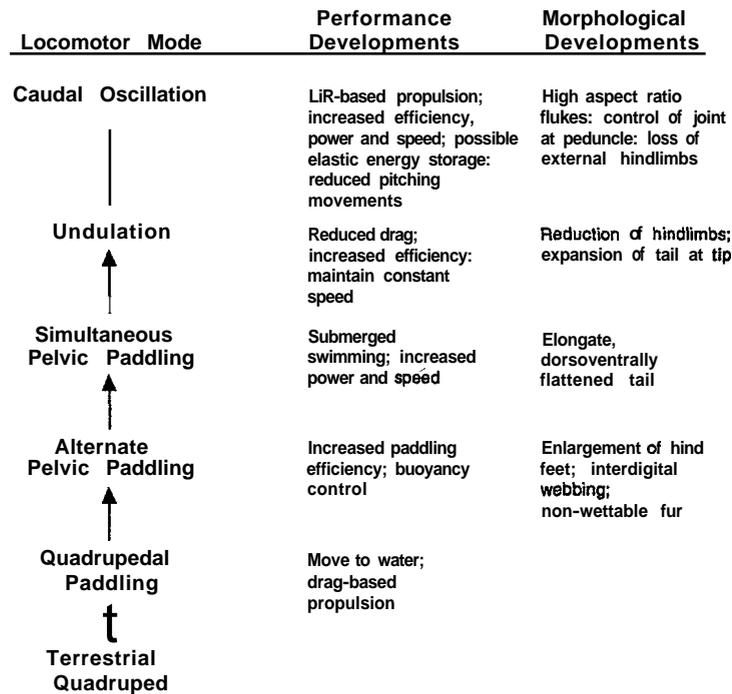
During the power phase the foot is stroked posteriorly while the digits are abducted (spread) to maximize the planar area by the inclusion of interdigital webbing or lateral fringe hairs. The increased area and movement of the foot produces a drag with an anteriorly directed component. Thus, thrust for the animal is generated from the integration of the drag component from all paddling feet. This drag-based mechanism is analogous to paddling a canoe or rowing a boat.

During recovery, the foot is repositioned without generating thrust. Despite adduction of the digits and other conformational changes that reduce the area of the limb during recovery, some posteriorly oriented drag will be generated that reduces the net thrust (Fish, 1984). As a result, drag-based paddling has a low mechanical efficiency of < 40% (Fish, 1993a). Therefore, more energy is required to produce the same thrust by paddling than by lift-based propulsion (Weihs and Webb, 1983). Propulsors using lift can be twice as effective in generating thrust and may be up to five times more effective (Weihs, 1989).

How then could lift-based swimming with flukes have evolved from an inefficient drag-based limbed propulsion? To address this question, as well as the evolution of the derived swimming modes for other aquatic clades, Fish (1993a, 1996) developed a functional model based on kinematics, energetics, and hydrodynamics of swimming in modern mammals. The underlying assumption of the model is that neuromotor patterns for locomotion are conservative (Jenkins and Goslow, 1983; Smith, 1994). The idea of conservatism permits large-scale changes in swimming kinematics and performance with only slight modification of the neuromotor pattern originating from terrestrial locomotion. Therefore, despite the dissimilarities between the motions of the body and appendages for drag-based and lift-based aquatic propulsion, the modes can be related as modifications for swimming from the neuromotor patterns associated with terrestrial gaits (Fish, 1996). Symmetrical terrestrial gaits, such as walk and trot, are the basis of paddling modes; whereas lift-based swimming arises from asymmetrical gaits, such as gallops and bound, which utilize spinal flexion in concert with simultaneous limb motion for rapid progression (Rayner, 1985; Williams, 1989; Fish, 1993a, 1994, 1996; Gutmann, 1994).

A subset of the model by Fish (1996) pertinent to the present discussion is shown in Fig. 8. The model assumes that the terrestrial ancestor to cetaceans (i.e., mesonychian condylarths) would first swim using a modified quadrupedal gait by paddling with all four limbs as has been overly characterized as a "dog paddle." Mesonychians were terrestrial and displayed a morphology for cursorial locomotion (Gingerich *et al.*, 1994; Thewissen, 1994; O'Leary and Rose, 1995). In addition, lift provided by the paddling motions of the forelimbs would aid in maintaining trim to keep the nares above the water surface for continuous respiration (Fish, 1993c).

With adaptation to a semiaquatic existence, a shift to exclusive use of the hind limbs for paddling would occur. Pelvic paddling prevents mechanical and hydrodynamic inter-



**FIGURE 8.** Functional model showing changes in swimming mode, performance, and morphology associated with increasing aquatic habits within the cetacean lineage.

ference between ipsilateral limbs and frees the forelimbs for tactile reception, prey capture, food manipulation, maneuverability, and locomotor stabilization (Fish, 1993c, 1996). Abandonment of forelimb use for propulsion and trim control would be compensated by the acquisition of enlarged hind feet and nonwettable fur. Increased thrust would have been fostered by elongation of the digits and addition of interdigital webbing permitting an increased foot area to affect a larger mass of water (Fish, 1984). Air entrapped in the fur in conjunction with the air in the lungs would maintain a positive buoyancy to prevent submergence of respiratory openings and provide a nearly horizontal trim for improved streamlining (Fish, 1993c). In addition, the nonwettable fur increases the insulation over the body to reduce heat loss to the highly thermally conductive aquatic environment.

Increased buoyancy, however, would eventually be a disadvantage as the cetacean ancestors commenced underwater foraging. The greater up-force would have made it difficult and energetically demanding to submerge. To generate sufficient force for diving to counteract the positive buoyancy, simultaneous strokes of the hind limbs could have been used to submerge to a sufficient depth where compression of the air in the fur and lungs would reduce the up-force. In addition, the simultaneous strokes increase speed when submerged, particularly in pursuit of prey. Such a swimming pattern is used when diving by otters (Tarasoff *et al.*, 1972; Williams, 1989; Fish, 1994). Because this swimming mode represents a modified bounding gait, the motion of the limbs is coordinated with flexion

and extension of the spine (Fish, 1994). As observed for the river otter (*Lutra canadensis*), the tail displays an undulatory pattern that has the capability of thrust generation,

The addition of the tail in thrust generation becomes important to maintain speed underwater, because the simultaneous strokes of the limbs will incur periods of no thrust and increase drag when both feet are in the recovery phase of the stroke. Undulatory movements of the tail can generate nearly continuous thrust over the stroke cycle reducing accelerations and increasing efficiency (Fish, 1993a). For *Lutra*, undulation will be limited because the tail tapers posteriorly. Increased thrust production from tail undulation is facilitated by expansion of the tail tip perpendicular to the plane of motion. This morphology is displayed by the giant river otter (*Pteronura brasiliensis*), which possesses webbed hind feet and a broad, flattened tail (Howell, 1930; Chanin, 1985). From a film by Cousteau and Cousteau, Fish (1994) made observations of swimming *Pteronura* that showed the otter to rapidly swim submerged by simultaneous strokes of the hind limbs and undulation of the tail in the vertical plane. The morphology and swimming mode of *Pteronura* suggest an intermediate design between drag-based paddling and lift-based undulation (Howell, 1930; Sanderson, 1956) and a modern analogue of the primitive cetacean (Flower, 1883).

As suggested from the swimming patterns of otters, the transition from paddling to axial undulation required the presence of a long tail. This has been a long-held view (Flower, 1883; Ryder, 1885), although there has never been a mechanism to explain the tail's occurrence. One possible explanation for the possession of a long tail may be its use for thermoregulation in warm climates. The high surface-to-volume ratio and elaborate vascularization of mammalian tails act as effective thermoregulatory devices for the control of body insulation by regional heterothermia (Fish, 1979; Hickman, 1979). In warm climates where low insulation is warranted, a long tail would be an advantage to prevent overheating by elimination of excess metabolic heat to the environment. Indeed, cetaceans originated in tropical and subtropical climates where a long tail for temperature regulation would be advantageous (Barnes et al., 1985; Fordyce, 1992; Gingerich et al., 1994; Thewissen et al., 1994).

In the final stages of the sequence, undulation of the tail would replace limb propulsion (Fish, 1993a, 1996). By removing the appendages from propulsion, drag is reduced, thrust can be continuously generated, and efficiency is increased. Further increase in performance using caudal undulation is achieved by expanding the tail distally, which would culminate in the rapid evolution of high-efficiency caudal hydrofoils (i.e., flukes) (Webb and Buffrénil, 1990; Fish, 1993a, 1994, 1996; Gutmann, 1994). The inclusion of a joint at the base of the flukes to control pitch would complete the transition to lift-based propulsion. The implication of the model is that the orientation and propulsive movements of the flukes are the evolutionary result of axial motions associated with terrestrial gaits.

When early archeocetes are examined with respect to the functional model, the morphology of these early whales suggests changes corresponding to the proposed sequence. *Pukicetus inachus* from the early Eocene is recognized as the oldest and most primitive cetacean known (Gingerich et al., 1983; Thewissen, 1994). Although only the cranial and jaw structures have been described, *Pukicetus* does exhibit some features associated with movement into water and submerged foraging, including its ear structure and dentition (Gingerich et al., 1983; Thewissen and Hussain, 1993). The degree of aquatic adaptation in *Pukicetus*, however, indicates that this species was amphibious and as such most likely would have propelled itself by paddling.

Further evolution toward increased aquatic habits is displayed by *Ambulocetus natans*, which had well-developed limbs and a prominent tail (Thewissen *et al.*, 1994). This early semiaquatic cetacean appears to occupy a place on the functional model where propulsion is achieved by a combination of simultaneous pelvic paddling and caudal undulation (Fig. 8). The hind foot of *Ambulocetus* had elongate metapodials and phalanges, indicating increased surface area for paddling (Thewissen *et al.*, 1994). The spine was considered primarily restricted to movement in the sagittal plane (Thewissen *et al.*, 1996a). The tail of *Ambulocetus* was long and powerful and was composed of few (possibly 15) long caudal vertebrae similar to those of mesonychians (Thewissen *et al.*, 1996a). The length of the tail suggested to Thewissen *et al.* (1996a) that a well-developed hydrofoil was lacking. The bending moments for such a tail would be effectively too low to move fully developed flukes. Compared with *Ambulocetus*, modern cetaceans have short caudal vertebrae providing better leverage for the longitudinal muscles.

Thewissen and Fish (1997) considered *Ambulocetus* to be analogous in swimming performance to *Pteronura*. As such, the tail of *Ambulocetus* may have supported at least a rudimentary lateral flange to increase thrust production by caudal undulation. Flower (1883) suggested that an ancestral cetacean would show similarities with *Pteronura*. However, Ryder (1885) argued against any analogy with *Pteronura* on ontogenetic grounds. He cited that the lateral ridges extended the entire length of the tail of *Pteronura*, whereas embryonic cetaceans showed fluke folds developed only at the tail tip. In addition, Thewissen *et al.* (1996a) suggested that *Ambulocetus* was an ambush hunter, relying on burst swimming to capture prey, rather than an agile pursuit predator like otters. Despite such differences, otters represent a suitable model for swimming performance in early cetaceans based on their similar morphology.

Flukes apparently evolved by the middle of the Eocene as observed indirectly from the fossils in the various cetacean families. In the Protocetidae, *Rodhocetus kasrani* displayed a number of spinal characteristics associated with generating large forces from dorsoventral movements of the tail, including robust vertebrae with high neural spines and unfused sacral vertebrae (Gingerich *et al.*, 1994). In addition, the femur was markedly reduced indicating a reduction or abandonment of paddling and perhaps terrestrial movements. Based on examination of oxygen isotopes, the protocetid *Indocetus* ingested sea water and lived in a neritic habitat similar to modern cetaceans (Thewissen *et al.*, 1996b). Because the Protocetidae were marine pursuit hunters (Thewissen *et al.*, 1996a), fluke swimming would be required for sustained locomotion in the open ocean, particularly where prey is dispersed widely (Webb, 1984).

By the end of the Eocene and throughout the Oligocene, swimming was exclusively with flukes with the hind limbs being inconsequential or absent (Gingerich *et al.*, 1990). The rapid radiation of cetaceans with increasing body size favored mechanisms that maximized swimming performance (Webb and Buffr n il, 1990; Fordyce, 1992).

The inference from the ontogenetic data and functional model is that in early cetaceans the flukes would have been represented by small rounded, lateral outgrowths toward the tip of the tail. Such a structural modification would have been advantageous for the small ancestral cetaceans. As cetaceans became larger and more proficient in the water, the outgrowths would have expanded farther, increasing the propulsive surface area to compensate for the increased drag. The flukes would have evolved into their present form as speed and efficiency increased.

## 5. Summary and Conclusions

The flukes of modern cetaceans are high-performance oscillatory propulsors with a design to produce high lift for thrust generation with low drag and high efficiency. The collagenous internal structure provides the framework for a flexible hydrofoil with relatively high aspect ratio and moderate sweepback. The evolutionary sequence by which flukes arose is still speculative, because there is no direct evidence that reveals origin. The ontogeny of the flukes suggests a derivation from lateral integumentary folds at the end of the tail. Using modern analogues of transitional stages with increasingly aquatic habits, a functional model proposes that ancestral cetaceans had long tails that were used for swimming in conjunction with modified terrestrial gaits of the limbs. Flukes would have developed to increase power output and efficiency by lift-based propulsion as the inefficient drag-based paddling was abandoned. Recent fossil discoveries of early cetaceans support this scenario. However, until impressions of flukes early in their evolution are unearthed, this inquiry will never be fully resolved.

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