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Transitions from Drag-based to Lift-based Propulsion in Mammalian Swimming[1]

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SYNOPSIS. The evolution of fully aquatic mammals from quadrupedal, terrestrial mammals was associated with changes in morphology and swimming mode. Drag is minimized by streamlining body shape and appendages. Improvement in speed, thrust production and efficiency is accomplished by a change of swimming mode. Terrestrial and semiaquatic mammals employ drag-based propulsion with paddling appendages, whereas fully aquatic mammals use lift-based propulsion with oscillating hydrofoils. Aerobic efficiencies are low for drag-based swimming, but reach a maximum of 30% for lift-based propulsion. Propulsive efficiency is over 80% for lift-based swimming while only 33% for paddling. In addition to swimming mode, the transition to high performance propulsion was associated with a shift from surface to submerged swimming providing a reduction in transport costs. The evolution of aquatic mammals from terrestrial ancestors required increased swimming performance with minimal compromise to terrestrial movement. Examination of modern analogs to transitional swimming stages suggests that only slight modification to the neuromotor pattern used for terrestrial locomotion is required to allow for a change to lift-based propulsion.

INTRODUCTION

Numerous paleontological, morphological, and molecular studies have focused on the phylogenetic relationships both within clades of aquatic mammals and with their terrestrial ancestors (Barnes *et al.*, 1985; Wyss, 1988, 1989; Berta, 1991; Milinkovitch *et al.*, 1993; Adachi and Hasegawa, 1995). Such studies were helpful in producing phylogenies and in elucidating the historical sequence of structural changes. However, phylogenetic studies are limited and lack a functional approach to determine the causal reasons for evolutionary change (Lauder, 1990). Functional analysis provides an understanding at a mechanistic level through measures of performance (i.e., exercise metabolism, locomotor kinematics, maximal swimming speed). For aquatic mammals and their transitional forms, functional analysis is therefore necessary to determine the possible environmental factors that produced the various aquatic adaptations.

The similarity in morphology and swimming mode between fish and cetaceans is the quintessential example of evolutionary convergence (Howell, 1930; Fish, 1993*a*). This familiar textbook example illustrates how similar functional requirements are met by organisms that do not share a single clade. Such convergence, with its resulting homoplasy, is associated with similar constraints imposed on animals by the physical environment and with selection for adaptations for effective swimming (Fish, 1993*a*).

Adaptations associated with increased aquatic behavior and swimming performance evolved independently in several clades of mammals (*i.e.*, Cetacea, Pinnipedia, Sirenia). Modern groups of aquatic mammals display swimming adaptations that optimize use of energy by reduction in drag and improvement in thrust production

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and efficiency (Lang, 1966; Williams, 1989; Fish, 1993*a*, b). Drag is minimized by streamlining the body and appendages (Webb, 1975; Fish, 1993*a*). Thrust and efficiency are maximized by swimming modes that use a lift-based oscillating hydrofoil (*i.e.,* cetacean flukes, phocid hindflippers, otariid foreflippers). Alternatively, less aquatically adapted terrestrial and semiaquatic mammals employ drag-based paddling (Howell, 1930; Williams, 1983; Fish, 1992, 1993*c*); this form of propulsion is considered of lower performance and more primitive than the lift-based mode (Tarasoff ***et al.,*** 1972; Baudinette and Gill, 1985; Williams, 1989; Fish, 1993*a*).

The evolution of highly derived aquatic morphologies and lift-based swimming modes represents the culmination of a sequence of transitional stages from terrestrial quadrupeds to fully aquatic mammals (Howell, 1930; Barnes ***et al.,*** 1985; Gingerich ***et*** al., 1990, 1994; Fish, 1992). The intermediates between fully aquatic mammals and their terrestrial ancestors were believed to be semiaquatic that swam by paddling (Barnes ***et*** al., 1985; Thewissen ***et al.,*** 1994). In that the kinematics and mechanics of thrust generation differs between drag-based and lift-based propulsion, how was the transition in swimming mode achieved in the evolution of aquatic mammals? In answering this question, clues may be elucidated as to what selection forces and intermediate morphological stages were required in the transition toward increased aquatic behavior.

Body Design

Body design has been one of the principle morphological parameters examined as an index of adaptation to the aquatic environment. Body shape is associated with the amount of force required to overcome drag (resistive force); a factor influenced by the flow pattern around the body. Since drag is equal to thrust (propulsive force) when the body is moving at constant velocity, body shape has been used to characterize the swimming performance of animals.

The most general index of body design used to estimate hydrodynamic performance (*i.e.,* swimming speed) is fineness ratio (FR), where FR is body length/maximum thickness. The optimal FR, which provides the minimum drag for the maximum volume, is 4.5 (von Mises, 1945). However, FR can vary from 3 to 7 with only a 10% increase in drag (Webb, 1975).

Use of FR as an index of locomotor performance is limited. Mammals have FRs within the range of reduced drag regardless of aquatic ability (Fish, 1993*a*). Sirenians have FRs which span the optimal value of 4.5. Although able to sprint at speeds of 6 m/sec, these herbivores swim slowly at 0.6–0.8 dsec (Hartman, 1979; Nishiwaki and Marsh, 1985). Fish (1993*a*) suggested that FR for sirenians may be associated with a body design to limit heat loss by a thermally sensitive aquatic species with low metabolism. High values of FR in mustelids may be more an indication of a body originally designed for hunting in burrows than for swimming (Williams, 1983, 1989). The greatest range of FR (4–11) is found in the cetacean family Delphinidae from Dall's porpoise (*Phocoenoides dalli*) to the northern right whale dolphin (***Lissodelphis borealis)*** (Fish, 1993*a*). Despite the divergence in FR, these two species are considered among the fastest dolphins with maximum speeds exceeding 8 dsec (Winn and Olla, 1979).

A better indicator of swimming performance based on design is streamlining by the possession of a fusiform body. The fusiform shape is characterized by a rounded leading edge with a long tapering tail. Streamlining minimizes drag by reducing the magnitude of the pressure gradient over the body allowing water to flow over the surface without separation (Vogel, 1994). Unfortunately, the extent of streamlining in mammals is not easily measured. Profiles of dolphins and sea lions were compared with two-dimensional airfoils (Hertel, 1966; Feldkamp, 1987*a*). However, such matches only reflect a crude resemblance and are not exact due to the three-dimensional configuration of the animal and its deviation from the smooth fusiform shape.

Swimming Mode Mechanics and Diversity

Aside from body design, swimming modes determine how effectively an animal

TABLE 1. ***Swimming modes exhibited by modern mammals.***

Mode	Thrust force	Representative genera	Habits
Quadrupedal paddling	Drag	***Didelphis, Canis, Elephas, Mustela***	terrestrial, semiaquatic
Alternate pectoral paddling	Drag	***Mustela, Thalarctos***	semiaquatic
Alternate pelvic paddling	Drag	***Castor, Chironectes, Hydromys, Ondatra***	semiaquatic
Alternate pelvic rowing	Drag	***Ondatra***	semiaquatic
Simultaneous pelvic paddling	Drag	***Lutra***	semiaquatic
Pectoral rowing	Drag	***Ornithorynchus***	semiaquatic
Lateral undulation	Acceleration reaction	***Potomogale***	semiaquatic
Dorsoventral undulation	Acceleration reaction	***Enhydra, Lutra***	semiaquatic, aquatic
Pelvic oscillation	Lift	***Odobenus, Phoca***	aquatic
Pectoral oscillation	Lift	***Zalophus***	aquatic
Caudal oscillation	Lift	***Trichechus, Tursiops***	aquatic

moves through water (Fish, 1993*a*). Two distinct swimming modes are exhibited by mammals, drag-based and lift-based propulsion. Drag-based swimming is considered a primitive, low performance mode, whereas lift-based propulsion is a high performance, derived mode based on undulation of the body (Howell, 1930; Fish, 1993*a*).

Drag-based propulsion is used by a variety of terrestrial and semiaquatic mammals (Howell, 1930; Fish, 1993*a*). The limbs are oriented in either the vertical parasagittal plane (paddling) or the horizontal plane (rowing), and strokes of the paired appendages are either alternate or simultaneous (Table 1). Stroke cycle is divided into power and recovery phases (Fish, 1984). During the power phase, the posterior sweep of the foot generates drag which is used to provide an anterior thrust for the animal (Fig. 1). Paddle area is increased by abduction of the digits and interdigital webbing or fringe hairs (Howell, 1930; Fish, 1984, 1993*c*). The recovery phase repositions the foot and incurs a non-thrust generating drag. To prevent negating the thrust during the recovery phase, drag on the foot is reduced by adducting the digits to reduce paddle area (Fish, 1984).

Highly derived aquatic mammals produce lift to generate thrust (Fig. 1). Lift is generated by oscillating a hydrofoil (***i.e.,*** flukes, flippers) at a controlled angle of attack (Lighthill, 1969; Feldkamp, 1987*b*; Fish ***et*** *al.,* 1988; Fish, 1993*b*). Lift is directed perpendicular to the pathway traversed by the hydrofoil and can be resolved into an anteriorly directed thrust force (Weihs and Webb, 1983; Fish, 1993*a*). Thrust is generated continuously throughout a stroke cycle. Although some drag is produced by the hydrofoil, it is small compared to the lift. The high lift-to-drag ratio is a function of the high aspect ratio (span^2/planar area) of the hydrofoil (Feldkamp, 1987*a*; Fish ***et*** *al.,* 1988; Fish, 1993*a*, ***b).***

Cetaceans and sirenians are caudal oscillators (Fish, 1993*a*). This mode also is described as thunniform or carangiform with lunate tail (Lighthill, 1969; Webb, 1975; Lindsey, 1978) similar to certain fast swimming fish. Unlike fish, the mammals move their propulsive flukes in the sagittal plane (Hartman, 1979; Nishiwaki and Marsh, 1985; Fish and Hui, 1991). Angle of attack is controlled by a joint at the base of the flukes to maximize thrust throughout the stroke. The Otariidae, including sea lions and fur seals, use foreflippers as oscillatory hydrofoils (English, 1976; Feldkamp, 1987*a*, ***b).*** The stroke is described as pectoral oscillation (Fish, 1993*a*) and as subaqueous flight similar to swimming by penguins and sea turtles (Baudinette and Gill, 1985; Feldkamp, 1987*b*). Phocid seals and the walrus use pelvic oscillation for swimming. The posterior body is laterally undulated moving the paired hindflippers in the horizontal plane (Backhouse, 1961; Ray, 1963; Tarasoff ***et*** *al.,* 1972; Gordon, 1981; Fish ***et*** *al.,* 1988). Ankle joints con-

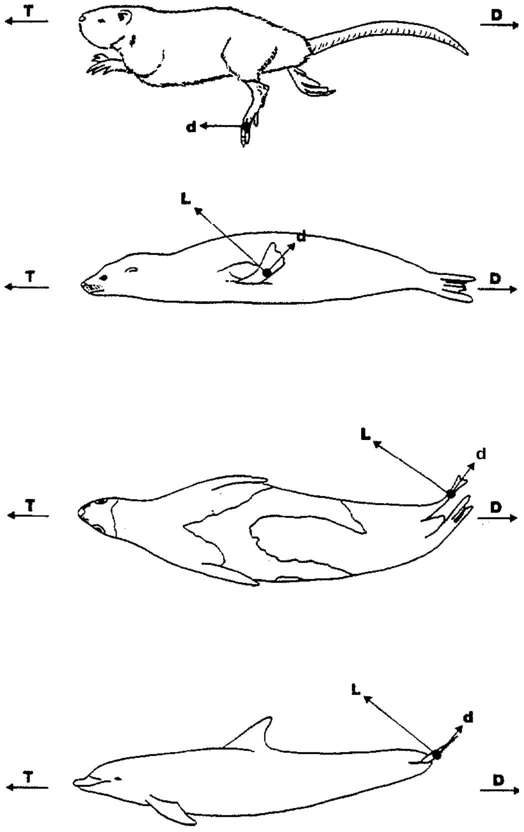

FIG. 1. Major forces associated with propulsive modes. From the top, animals and propulsive modes shown are (1) muskrat (*Ondatra* ***zibethicus*****):** paddling, (2) sea lion (*Zalophus californianus*): pectoral oscillation, (3) harp seal (*Phoca groenlandica*): pelvic oscillation, and (4) bottlenose dolphin ***(Tursiops*** *truncatus)***:** caudal oscillation. To swim at a constant velocity, an animal must generate a thrust force (T) equal and opposite to a drag force (D). Paddling is a drag-based swimming mode. The posterior sweep of the hind feet of the muskrat generates a drag force (d) which contributes to T. Using lift-based propulsive modes, the foreflippers of the sea lion, hind flippers of the harp seal, and caudal flukes of the dolphin act as hydrofoils to generate T. Lift derived from movement of the hydrofoil is resolved into an anteriorly directed thrust force. The drag associated with the hydrofoil (d) is produced mainly from frictional and induced drag components and is small relative to the lift force. (From Fish, 1993*a*.)

trol the angle of attack, analogous to cetaceans and thunniform fish.

Intermediate between drag-based and lift-based propulsion is the undulatory mode (Webb, 1988). The African otter shrew (***Potamogale***) may swim by laterally undulating a deeply compressed tail (Walker, 1975). Lateral undulations of the compressed tail of the muskrat (***Ondatra***) provided a maximum of 2% of the thrust, which was produced mainly by paddling of the hindfeet (Fish, 1982*a*). Otters are reported to propel themselves by dorsoventrally undulating the body and tail (Kenyon, 1969; Tarasoff ***et*** *al.,* 1972; Williams, 1989). Fish (1994) demonstrated in the river otter, ***Lutra canadensis,*** that simultaneous paddling by the hindfeet is integral to the undulatory mode.

SWIMMING MODE ENERGETIC PERFORMANCE

If aquatic mammals are adapted to swim in a manner that minimizes energy expenditure, there should be distinct metabolic and hydrodynamic advantages to propulsive modes employed by the most derived species. To understand the performance associated with increasing aquatic habits, the energetics of swimming can be examined by comparing efficiencies with regard to propulsive modes and morphologies of a wide variety of mammals. Maximization of thrust production and increased efficiency are highly associated with swimming modes (Rayner, 1985; Fish, 1992).

Efficiency can relate active metabolism with total mechanical work and propulsive power output (Fish, 1993*a*). There is a paucity of data on efficiency because studies of swimming performance rarely examine both metabolism and mechanical work. Aerobic efficiency (η_a) is power output (thrust power) divided by aerobically supplied power input (active metabolic rate); that is the ratio of power expended in doing useful work (i.e., move the animal forward through the water) to potential power available to perform work. Propulsive efficiency (η_p) is the ratio of thrust power to rate of total mechanical work produced. Drag power may be substituted for the thrust power when the animal is swimming steadily. However, use of drag values may give an underestimate of efficiency, because propulsive movements can increase total drag on the animal.

Comparison of efficiencies between different aquatic species show that lift-based modes are higher than drag-based paddling

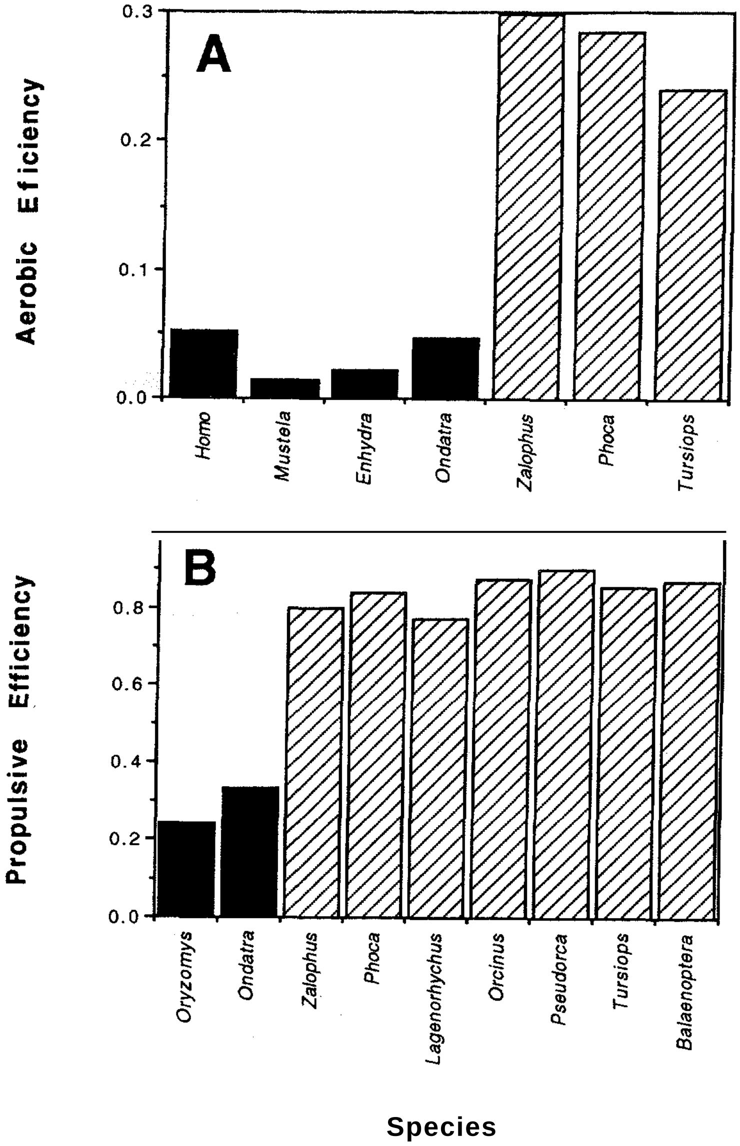

FIG. 2. Comparison of efficiencies between drag-based (black bars) and lift-based (hatched bars) swimming modes. Aerobic efficiencies are displayed in A; propulsive efficiencies in B. Data from DiPrampero *et al.*, (1974). Webb (1975), Williams (1983, 1989); Fish (1984, 1985, 1992, 1993*b*, unpublished data), Feldkamp (1987*a*), Fish *et al.*, (1988), Bose and Lien (1989). Williams *et al.*, (1992).

(Fig. 2). Values of η_a for paddling mammals are no better than 5%, whereas lift-based swimming typically reach 20% with a maximum value for sea lions of 30%. A similar trend is exhibited for η_p (Fig. 2). Paddlers had maximum reported values for η_p of 33%. The η_p of lift-based swimmers is at least 80%. No data are available for the undulatory swimming in mammals, but estimates of η_p for trout by Webb (1978) give an intermediate value of 67%.

Cost of Transport (CT) can be used to assess the efficiency of different swimming modes independent of power output (Schmidt-Nielsen, 1972; Williams, 1989; Fish, 1992). CT is the metabolic cost to

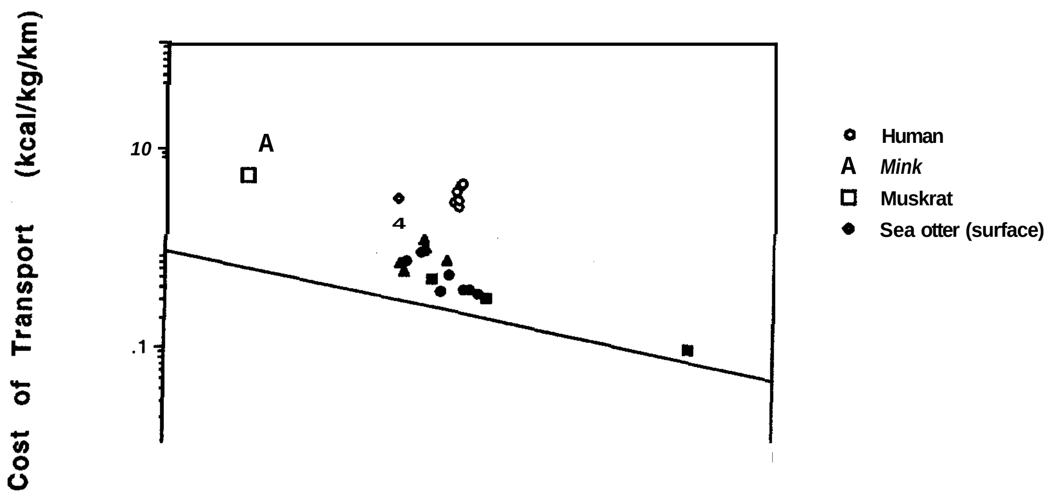

FIG. 3. Relationship between Cost of Transport (CT) and body mass. Open symbols represent CT values for drag-based propulsion when surface swimming; closed symbols represent undulatory and lift-based propulsion during submerged swimming. The solid line represents the extrapolated minimum CT for fish (Davis *et al.*, 1985). Data from Costello and Whittow (1975); Kruse (1975); Øritsland and Ronald (1975); P. E. DiPrampero, personal communication (1979); Fish (1982); Sumich (1983); Williams (1983); Innes (1984); Davis *et al.* (1985); Worthy *et* al. (1987); Feldkamp (1987*a*); Williams (1989); Williams et al. (1992).

move a unit mass a given distance and CT is inversely proportional to efficiency (Tucker, 1970). Drag-based swimmers have higher values of CT compared to lift-based swimmers of similar body mass (Fig. 3). Compared to the extrapolated line for minimum CT of fish (Davis *et al.*, 1985), paddling mammals have values of CT 10–25 times greater than fish of similar mass; whereas lift-based swimmers are only 1.9–4.6 times greater. A particularly significant data set was collected by Williams (1989) on sea otters showing the energetic advantage of shifting from paddling at the water surface to submerged swimming using undulation. CT of surface paddling was 69% greater than submerged swimming.

Association Between Terrestrial and Aquatic Movements

Neuromotor patterns for locomotion appear to be conservative (Jenkins and Goslow, 1983; Goslow *et al.*, 1989; Smith, 1994) and are independent of changes in morphology and functional role (Smith, 1994). Kinematics and electromyographic analysis of terrestrial locomotion in the reptile *Varanus* and mammal ***Didelphis*** showed similar activity patterns between homologous muscles with the same attachment sites (Jenkins and Goslow, 1983). Furthermore, homologous muscles with different attachments had similar activity patterns. Neuromotor conservation was demonstrated also between walking and flight (Goslow *et al.*, 1989; Dial *et al.*, 1991). Although muscles have been functionally reorganized for flight, several muscles have similar timing patterns in their respective locomotor cycle with walking gaits (Dial *et al.*, 1991).

The basis for conservation of neuromotor pattern is the existence of central pattern generators. Central pattern generators are neural networks in the central nervous system that govern specific, repetitive motions by providing the correct timing for muscular contraction (Grillner, 1975, 1996; Peters, 1983; Pearson, 1993). Motor patterns are executed without peripheral feedback, although afferent feedback can modify the motor programming and its output (Pearson, 1993).

The rhythmic nature of the central pat-

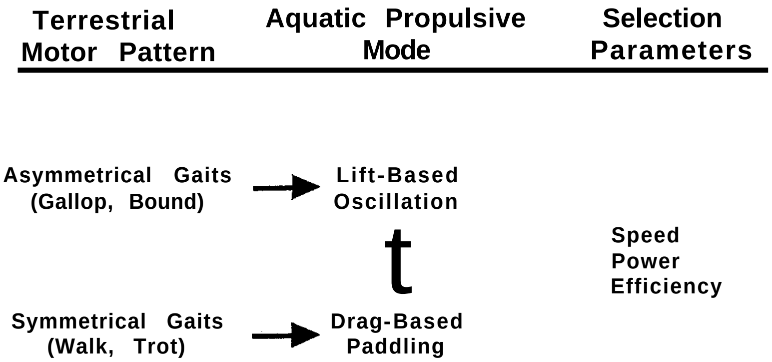

FIG. **4.** **Association between terrestrial and aquatic propulsive mode in relation** to **selection parameters for enhance performance in swimming.**

tern generator is considered important in the automatic movements associated with locomotion (Grillner and Wallen, **1985;** Pearson, **1993;** Stein ***et*** *al.,* **1995).** Central pattern generators have been demonstrated for walking and running in mammals and birds, flight in birds, and swimming in fish and reptiles. The diversity of vertebrates and locomotor behaviors linked with central pattern generators alludes to the generality of these neural networks.

Despite dissimilarities in kinematics and performance between drag-based and lift-based propulsion, these modes can be linked through the conservation of primitive neuromotor patterns associated with terrestrial gaits (Fig. **4).** Symmetrical terrestrial gaits such as walks are the basis for drag-based swimming in mammals. Examination of swimming by semiaquatic and terrestrial mammals show that they quadrupedally paddle in gaits reminiscent of a diagonal sequence run, trot, and lateral sequence singlefoot (Fig. **5;** Williams, **1983;** Fish, **1993*c*).** The "dog paddle" is actually a modified lateral sequence run (personal observation). In humans, the crawl stroke with a two-beat kick is similar to a diagonal sequence run, although this stroke may be modified to adjust for buoyancy (Costill ***et*** *al.,* **1992).** Bipedal paddling is an adjustment of the quadrupedal gait by removal of fore- or hindlimbs movements during swimming. Semiaquatic mammals use bipedal paddling to reduce interference between ipsolateral limbs and increase swimming efficiency (Fish, **1993*c*).**

Lift-based oscillatory modes arise primarily from asymmetrical terrestrial gaits (Fig. **4).** Such land-based gaits may be the most economical high-speed gaits, because of potential recycling of elastic strain energy (Alexander, **1988).** Energy economy by storage and recovery of elastic energy in a flexing body has been the focus of some work on dolphin swimming mechanics (Bennett ***et*** *al.,* **1987;** Blickhan and Cheng, **1994;** Pabst, **1996).** The undulatory mode begins as a bound or half bound using powerful simultaneous strokes of the forelimbs and hindlimbs enhanced by spinal flexion (Fish, **1994).** After an initial acceleration, only hindlimbs were used. This mode is associated with rapid swimming matching the use of asymmetrical gaits at high speeds on land. The sea otter, ***Enhydra lutris,*** uses spinal flexion in concert with simultaneous strokes of the hindfeet (Kenyon, **1969;** Tarasoff ***et al.,*** **1968;** Williams, **1989),** but the short tail precludes thrust generation by this structure, necessitating enlargement and use of the hindlimbs as propulsors. For river otters, ***Lutra canadenesis,*** simultaneous strokes of the hindlimbs generate a thrust-producing travelling wave in the body and tail (Fish, **1994).** Fish **(1994)** hypothesized that use of undulatory motions in conjunction with abandonment of limbs and distal expansion of the tail would increase swimming performance. This would have culminated in the evolution of a high-efficiency caudal hydrofoil with a lift-based oscillatory mode as displayed by cetaceans and sirenians. It is interesting that ancestral ce-

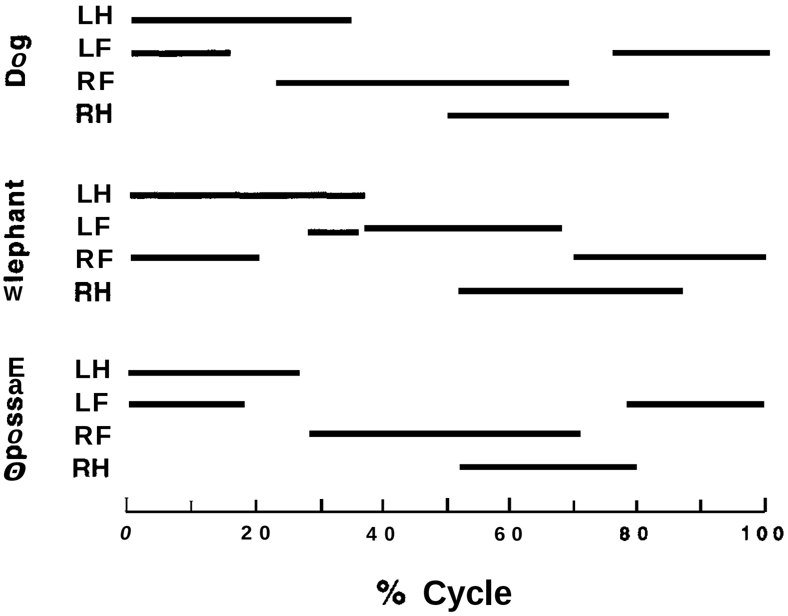

FIG. 5. Gait diagrams for three terrestrial mammals swimming quadrupedally. Mammals include dog (*Canis familiaris*), elephant ***(Elephas maximus)***, and opossum ***(Didelphis virginiana)***. Horizontal bars indicate the time as a percent of cycle of power phase for the left hindfoot (LH), left forefoot (LF), right forefoot (RF), and right hindfoot (RH). Opossum swam using a modified diagonal sequence run; elephant and dog swam with a running lateral sequence run. Data from Fish (personal observation, 1993*b*).

taceans had long, robust tails (Gingerich ***et*** *al.*, 1994; Thewissen ***et al.,*** 1994).

In the absence of an elongate tail, lift-based propulsion is confined to oscillation of the limbs as in pinnipeds. Sea lions swim by simultaneous motions of the foreflippers (Feldkamp, 1987*b*) which may have developed from a rowing posture using a modified bound. Indeed at fast terrestrial speeds (2.6 m/sec), New Zealand fur seals (***Arctocephalus forsteri***) use a bound (Beentjes, 1990).

Pelvic oscillations by both phocids and odobenids indicates use of similar motor patterns, although this may have been from different evolutionary pathways. The relationship among pinnipeds is still controversial (***i.e.,*** monophyletic versus polyphyletic; Barnes ***et*** *al.*, 1985; Wyss, 1988, 1989). The hindflippers alternate through power and recovery phases during the stroke cycle (Ray, 1963; Tarasoff ***et*** *al.*, 1972; Gordon, 1981; Fish ***et*** *al.*, 1988). This motion suggests a motor pattern based on an asymmetrical gait. ***Odobenus*** uses a lateral sequence walk on land. Its ability to use all the flippers in a walking gait are a consequence of the orientation of the hindflippers. The hindflippers can be rotated under the body, similar to otariids seals. Phocid seals can not position the hindflippers as in otariids and odobenids. Aquatic motions of phocids have no similarity with their terrestrial motions. The hindlimbs are not used in terrestrial locomotion, but dragged passively (Tarasoff ***et*** *al.*, 1972).

TRANSITION MODEL

How did propulsive modes change in the evolution of the most derived aquatic mammals? To deal with this question, a model is proposed that demonstrates how transition in swimming mode may have occurred through the various intermediate forms (Fig. ***6).*** The problem of examining transition from terrestrial to semiaquatic to fully aquatic is that rarely is there a complete set of extant intermediate forms to evaluate performance within the clade. Although a number of important transitional fossils

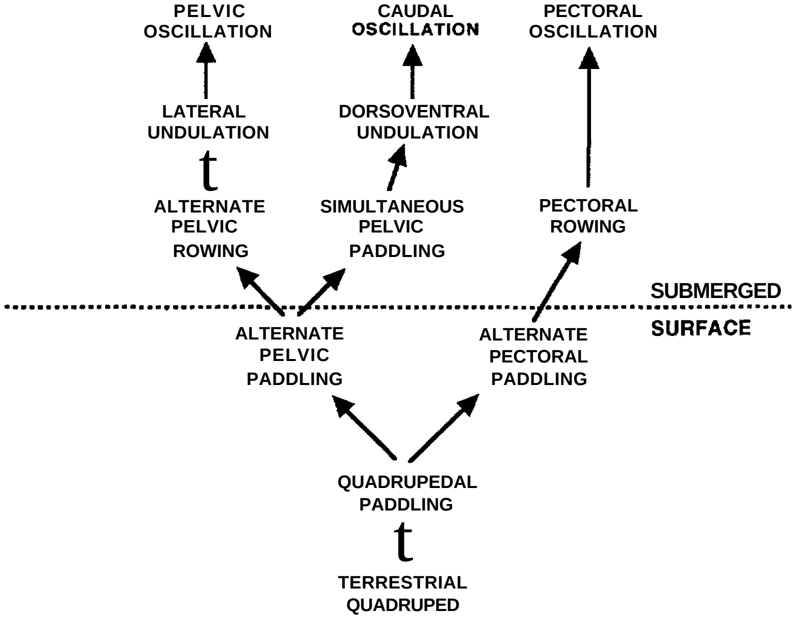

FIG. *6*. Model for sequence of transitions in swimming mode from drag-based paddling to lift-based oscillation. Dashed line indicates change from surface to submerged swimming.

have been described recently (Gingerich ***et*** *al.,* 1983, 1990, 1994; Barnes ***et*** al., 1985; Berta ***et*** *al.,* 1989; Berta and Ray, 1990; Thewissen ***et*** *al.,* 1994), information is limited on how the shift from paddle propulsion to lift-based propulsive modes may have occurred. The model, therefore, draws on the performance of modern species as analogs of the primitive intermediate forms. Lauder (1995) justified this technique **of** using modern analogs to determine performance in extinct forms from a different clade.

The model assumes that an ancestral terrestrial mammal would first swim by paddling quadrupedally using a terrestrial symmetrical gait (Rayner, 1985; Fish, 1993*a*). This swimming mode would have allowed the forelimbs to generate lift to keep the nares above the water surface for continued respiration. The addition of a non-wettable fur provides a positive buoyancy to semiaquatic mammals allowing them to float at the water surface. Non-wettable fur could have uncoupled buoyancy control for breathing from swimming movements (Fish, 1993*c*). Without the need to generate lift, a more effective bipedal paddling mode, using either forelimbs or hindlimbs, could be employed. Bipedal paddling prevents mechanical and hydrodynamic interference between the limbs and frees one set of limbs for locomotor stabilization, maneuverability, tactile reception, and food capture and processing.

With the development of semiaquatic habits using pectoral paddling or pelvic paddling, there would be limb specializations for increased thrust production and stability in water. These specializations would include (1) development of short, robust humerus and femur, (2) elongation of digits, ***(3)*** increased propulsive foot area by addition of interdigital webbing or fringe hairs, and (4) increased bone density for buoyancy control (Tarasoff ***et*** *al.,* 1972; Stein, 1981, 1989; Wyss, 1988; Berta and Ray, 1990; Fish and Stein, 1991; Thewissen ***et*** *al.*, 1994).

Underwater foraging would necessitate a change in mode to compensate for the positive buoyancy from the animal and its fur (see section below on Swimming depth and mode transition). By re-orienting the limbs and moving them in a rowing motion, thrust can be generated while simultaneously exerting a downward force. Mizelle (1935) noted that muskrats change from paddling with the hindfeet at the surface to rowing when submerged. In rowing, the symmetrical terrestrial gaits are modified to limb motions restricted to the horizontal plane. Another mechanism to generate force to counteract buoyancy would be to increase thrust by diving with simultaneous strokes of the paired limbs. Once submerged to a sufficient depth compression of the air entrapped in fur would reduce the buoyancy on the animal. Enhancement of this action would be facilitated by undulation of the tail as is seen in river otters (Tarasoff ***et al.,*** 1972; Fish, 1994).

In the evolution to a highly aquatic lifestyle, buoyancy control for diving could be effected by abandoning fur for blubber. This change reduces maintenance cost for grooming and allows the animal to more easily maintain neutral buoyancy at depth. The exception is the sea otter which spends a significant amount of time grooming its fur and maintains its buoyancy with enlarged lungs (Kooyman, 1989; Williams, 1989).

Selection for increased energy efficiency and higher swimming speeds would have facilitated the evolution of lift-based propulsion once semiaquatic mammals had adapted the drag-based modes for submerged swimming (Fig. 6). Pelvic oscillation would have originated from pelvic rowing. These modes show similarities in the alternating movements of the hindlimbs which each experience power and recovery phases as the limbs move in a horizontal plane. It is anticipated that an intermediate form using lateral undulations of the body with rowing action from the hindlimbs would have occurred in the transitional sequence. Although no modem analog of this swimming mode exists, Berta ***et al.,*** (1989) stated that in an the early fossil pinniped, ***Enaliarctos mealsi,*** the lumbar vertebrae allowed swimming by lateral movements of the trunk along with limbed propulsion. Pectoral oscillation also would have had its origin from rowing. The motion of the forelimbs in the power phase of the stroke would not only be directed posteriorly but ventrally as well. Simultaneous strokes of the forelimbs in conjunction with modifications of the limbs into winglike structures (Wyss, 1988) would have led to a change from drag-based to lift-based propulsion. The pectoral oscillatory stroke of sea lions, ***Zulophus,*** has a distinct paddling phase interposed between power and recovery phases (Feldkamp, 1987*b*).

The sequence by which caudal oscillation arose goes from simultaneous pelvic paddling through undulation of the body and tail. Such intermediate states were demonstrated from subsurface swimming in otters by Williams (1989) and Fish (1994). Likewise fossil evidence from early whales indicates the importance of the combination of hindlimb paddling and spinal undulation (Gingerich ***et al.,*** 1994; Thewissen ***et al.,*** 1994). Spinal undulation evolved before development of a tail fluke as indicated by the fossil ***Ambulocetus natans*** (Thewissen ***et al.,*** 1994). Eventually by eliminating use of inefficient paddling appendages, the undulatory mode would dominate and improve performance. The addition of caudal flukes would further enhance performance in the final transition to lift-based swimming. The presence of a long robust tail is a precondition for the development of this mode.

SWIMMING DEPTH AND MODE TRANSITION

While performance in regard to efficiency, speed, and thrust production are important in the evolution of swimming modes, swimming depth is a major factor in the effectiveness **of** the modes. This is no incidental statement in that mammals as obligate air-breathers must return to the water surface. Swimming at the air-water interface comes with an additional cost in the drag (Lang and Daybell, 1963; Hertel, 1966; Fish, 1982; Williams, 1989). Surface swimming can augment drag by as much as five times (Hertel, 1966). Increased drag at the surface, termed wave drag, results from construction of waves with energy lost to the water as potential energy in lifting it vertically (Vogel, 1994).

Alternate pectoral and alternate pelvic paddling modes appear to work well at the surface, where orientation of the limbs helps to maintain stability (Fish and Stein, 1991) and the propulsive forces from the limbs are effectively applied without surface interference. Simultaneous paddling and rowing are utilized by semiaquatic mammals when submerged. These modes are associated with force production to counteract buoyancy and increased speed. Otters paddle with an alternating stroke at the water surface, but switch to simultaneous strokes with body and tail undulations when moving quickly underwater (Williams, 1989; Fish, 1994). Oscillatory movements by derived aquatic mammals are more effective underwater. While submerged, these modes would be prevented from displacing water vertically and losing energy to wave drag.

Speed, in addition to energy economy, is impacted negatively by swimming at the water surface. Interaction of waves generated by the swimming animal sets a limit to maximum speed, referred to as "hull speed." Hull speed was original used to measure the performance of ships, but has been applied to animal systems (Prange and Schmidt-Nielsen, 1970; Aigeldinger and Fish, 1995). Hull speed is directly related to hull or body length and is due to the constructive interference of the diverging waves set up at the bow and stem. As speed increases, the wavelength of the system increases until the wavelength of the bow wave matches body length. The animal becomes trapped in the wave trough limiting further increases in speed (Vogel, 1994). An animal would have to literally swim uphill to swim faster, which is energetically costly (Prange and Schmidt-Nielsen, 1970).

Mammals rarely exceed hull speed when swimming at the surface (Aigeldinger and Fish, 1995). Competitive human swimmers reach hull speed at their maximum swimming speed (Kolmogorov and Duplishcheva, 1992; Videler, 1993).

Mammals that swim submerged are not subjected to the same speed limitation as surface swimmers. If a dolphin like *Tursiops* with a body length of 2.6 m (Fish, 19936) were limited to hull speed, its predicted maximum speed would be only 2 dsec. However, ***Tursiops*** has been reported to swim up to 15 dsec (Lockyer and Morris, 1987; Fish, 1993*b*). By swimming at a depth greater than three body diameters (Hertel, 1966), there is no effect due to wave drag and limitations of hull speed which could impede an animal's forward progress. Alternatively by leaving the water altogether by porpoising, marine mammals can maintain high speed with reduced energy costs (Au and Weihs, 1980).

CONCLUDING REMARKS

Semiaquatic mammals occupy the intermediate position between aquatic and terrestrial environments. Compared to mammals specialized for land or water, semiaquatic mammals are in the evolutionarily more precarious position of being unable to specialize in their locomotor performance in either environment. However, it was these intermediate animals that would give rise to more derived aquatic mammals. Swimming behaviors of modern analogs of these primitive intermediates best represent the original transitional stage. Comparison of modern semiaquatic mammals with fully aquatic mammals indicates which potential selection factors and mechanical constraints may have directed the evolutionary course of derived aquatic forms.

The secondary radiation of mammals into aquatic habitats was possible through a combination of behavioral, physiological, and morphological adaptations. The interaction between the habits of mammalian swimmers and the aqueous environment has produced different solutions for effective aquatic locomotion by various morphological designs and propulsive modes. Evolutionary transition from terrestrial to fully aquatic habits was accompanied by increased swimming performance by submerged swimming, streamlined body designs, and lift-based propulsive modes, which fosters increased speed, efficiency, and thrust production while reducing drag and cost of transport.

It is expected that swimming modes associated with semiaquatic and fully aquatic mammals originated from terrestrial gaits. Primitive quadrupedal and bipedal paddling represent modified symmetrical gaits, whereas rapid asymmetrical gaits were combined with oscillating hydrofoils. The transitional sequence of swimming mode with increasing aquatic habits corresponds directly to the continuum of terrestrial gaits associated with increasing speed. The idea that neuromotor patterns are conservative is the foundation to the terrestrial-aquatic transition. This conservatism permits large scale changes in swimming kinematics and performance with only slight modification of the neuromotor pattern originating from terrestrial locomotion. Grillner (1996) noted that "evolution rarely throws out a good design but instead modifies and embellishes on what already exists."

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