

## Locomotor evolution in the earliest cetaceans: functional model, modern analogues, and paleontological evidence

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**Abstract.**—We discuss a model for the origin of cetacean swimming that is based on hydrodynamic and kinematic data of modern mammalian swimmers. The model suggests that modern otters (*Mustelidae: Lutrinae*) display several of the locomotor modes that early cetaceans used at different stages in the transition from land to water. We use mustelids and other amphibious mammals to analyze the morphology of the Eocene cetacean *Ambulocetus natans*, and we conclude that *Ambulocetus* may have locomoted by a combination of pelvic paddling and dorsoventral undulations of the tail, and that its locomotor mode in water resembled that of the modern otter *Lutra* most closely. We also suggest that cetacean locomotion may have resembled that of the freshwater otter *Pteronura* at a stage beyond *Ambulocetus*.

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Accepted. 7 July 1997

### Introduction

The locomotor morphology of terrestrial mammals is very different from that of aquatic mammals. The musculoskeletal system of swimming mammals displays conspicuous specializations that can be considered as adaptations for life in the water. These adaptations are the result of dramatic morphological evolution that has made it impossible for the most specialized secondarily aquatic mammals, cetaceans and sirenians, to locomote on land.

Cetaceans descended from terrestrial mammals, and their amphibious ancestors must have had morphologies consistent with land and aquatic-locomotion. Both ancestors (land mammals) and descendants (marine cetaceans) of these amphibious taxa must have been morphologically very different from these amphibious whale intermediates. The terrestrial relatives of cetaceans, mesonychians, did not resemble early cetaceans in their locomotor morphology. The postcranial skeleton of mesonychians shows that they were cursors to varying degrees (Zhou et al. 1992; O'Leary and Rose 1995).

In spite of the locomotor changes that early cetaceans underwent, few authors in the paleontological literature have analyzed these changes, and it has commonly been assumed

that when the earliest whales had adopted modern ways of swimming. In spite of noting differences in overall morphology and muscle development, Kellogg (1936) proposed that late Eocene *Basilosaurus* had a tail fluke and implied that it swam by dorsoventral oscillation (p. 286), the locomotor mode of all modern cetaceans. Barnes and Mitchell (1970) reconstructed *Basilosaurus* with a broad horizontal tail fluke, and Uhen (1991) found that vertebral dimensions of *Basilosaurus* indicated that it swam similarly to modern cetaceans. Gingerich et al. (1994) concluded that dorsoventral oscillations of the tail were the mode of locomotion for the protocetid cetacean *Rodhocetus kasrani*.

One of the few cetaceans for which a different means of aquatic locomotion has been proposed is *Ambulocetus nantans*, an Eocene cetacean from Pakistan (Thewissen et al. 1994, 1996). Most of the limb skeleton of this taxon is known and is very different in shape from that of all other known cetaceans. On the basis of overall morphology, Thewissen et al. (1994, 1996) concluded that the power stroke of *Ambulocetus* during swimming resulted mainly from strokes of the feet, and not from strokes of the tail. Propulsive strokes were probably in the dorsoventral plane, similar to modern cetaceans.

In contrast to the paleontological literature, the zoological literature has extensively addressed **changing** function of aquatic locomotion in early cetacean evolution. Howell (1930 p. 21) **discussed** the evolving locomotor patterns in aquatic mammals and stated that "there **seems** to be a decided tendency for aquatic **mammals** to develop **as** the primary means of locomotion a single organ or pair of organs." Howell (1930) also made a distinction between (modern) cetaceans with a fusiform body and those with an anguilliform body (such **as** *Basilosaurus*), and suggested that the latter type swam differently. Slijper (1946) studied spinal morphology of cetaceans and concluded that Eocene cetaceans and mysticetes used undulating locomotor patterns, whereas odontocetes employed more oscillating patterns, but he did not base these conclusions on observations of actual swimming cetaceans.

Locomotor patterns in semiaquatic and aquatic mammals have been studied in mustelid carnivores (Tarasoff et al. 1972; Williams 1983, 1989; Fish 1994), the rodent *Ondatra* (Fish 1982a,b, 1984), dideiphid marsupials (Fish 1993a), talpid moles (Hickman 1984), and delphinid cetaceans (Slijper 1961; Fish and Hui 1991; Fish 1993c). These analyses are based on kinematic data of swimming behavior and **on** hydrodynamic principles. They commonly did not involve morphological analyses, **the** focus of **this** paper. Williams (1989) and Fish (1993b) discussed the kinematics and energetics of several swimming modes **of** semiaquatic mammals, and Fish (1996) put the transition of drag-based to lift-based forms of aquatic locomotion in an *evolutionary* perspective. Fish's (1996) model summarized the evolution of the three most-derived modes of aquatic locomotion in mammals (lateral pelvic oscillation in phocid seals, pectoral oscillation in otariid sea lions, and dorsoventral caudal oscillation in cetaceans). According to **this** model, cetacean locomotion went through the following stages: quadrupedal paddling, alternate pelvic paddling, simultaneous pelvic paddling, dorsoventral undulation, and caudal oscillation. Each of these locomotor modes is used by a number of modern mammals that compose a locomotor

guild. If the model is valid, members of these guilds can be used as functional analogues for the stages of cetacean swimming. Among the three terminal locomotor stages, the sequence leading to cetaceans can best be studied using modern analogues, because a variety of modern mammals of diverse phylogenetic background are members of each guild.

This paper will modify Fish's (1996) model and develop a morphological context for the part of the model that relates to cetacean origins (**Fig. 1**). We here propose morphological correlates for the different locomotor stages and test these with the use **of** quantitative and qualitative morphological data from the skeleton. Although the morphology of mammalian swimmers has been extensively studied (e.g., Howell 1930; Slijper 1936), there has been very little explicit work relating morphology to swimming modes.

The model as discussed here differs from that of Fish (1996) in *two* important respects. We do not differentiate between the **two** pelvic paddling modes, as these are not distinct morphologically. On the other hand, we do distinguish **two** distinct modes of dorsoventral undulation, one that is propelled by the feet (pelvic undulation, as discussed by Fish, 1996) and one that is driven by the tail (caudal undulation).

Once the morphological context for the model is established, we test the model by considering the morphology of one early cetacean, *Ambulocefus natans*. *Ambulocefus* is the most primitive cetacean for **which** much of the postcranial skeleton is known (Thewissen 1994). It is also one of the few archaic cetaceans for which most of the limb skeleton **is** known. If cetacean locomotor evolution passed through the stages identified in **Fig. 1** and if *Ambulocefus* is a **good** model for the ancestor of modern cetaceans, *Ambulocetus* must have displayed a locomotor pattern that is typical for one of these stages, and a modern mammal could be a locomotor analogue for *Ambulocetus*. Thewissen et al. (1994) did not identify a modern mammal as a locomotor analogue of *Ambulocefus*, instead **noting** that its locomotor pattern combined aspects of seals, otters, and cetaceans. Thewissen et al. (1996) proposed that *Ambulocetus's* swimming was

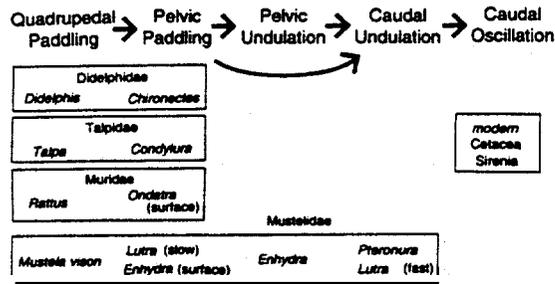


FIGURE 1. Model for the locomotor stages that cetaceans passed through in their evolution, modified from a model developed by Fish (1996). Whereas Fish's model distinguished two pelvic paddling stages, we recognize only one on the basis of morphological attributes. Fish specified the "dorsoventral undulation" mode based on the locomotor behavior of *Enhydra*, but we distinguish "pelvic undulation" and "caudal undulation," and propose that the swimming mode of *Enhydra* (pelvic undulation) may not have been a necessary intermediate for the origin of cetacean locomotion. Clades of modern mammals with locomotor behaviors in these categories are also listed.

most similar to that of *Enhydra*. Fish (1996) used data on *Enhydra* from Williams (1989) to characterize his dorsoventral undulation stage. However, *Enhydra* is a pelvic undulator and we propose below that cetacean ancestors may not have gone through a pelvic undulation stage (see Fig. 1).

#### Locomotor Model

**Quadrupedal Paddling.**—Mammals that occasionally enter the water almost invariably swim by alternating strokes of the four limbs (Fig. 1). Examples of well-studied quadrupedal paddlers are minks (*Mustela vison*) (Williams 1983), North American opossums (*Didelphis*), (Fish 1993a), and domestic dogs (Fish 1996). Exact patterns of footfall have not been determined for many quadrupedal paddlers, but Williams (1983) and Fish (1993a) interpreted the swimming patterns as a modified terrestrial gait.

**Pelvic Paddling.**—More aquatic members of clades that include quadrupedal paddlers commonly swim by alternate beats of their hind limbs only (alternating pelvic paddling) and do not use the forelimbs for aquatic propulsion. Examples include river otters (*Lutra canadensis*) (Tarasoff et al. 1972; Fish 1994), the South American opossum *Chironectes* (Fish 1993a), and the muskrat, *Ondatra* (Mizelle

1936; Fish 1982a,b, 1984). Terrestrial moles (*Scalopus*, *Talpa*) swim by paddling with all four feet, but the more aquatic star-nosed mole, *Condylura*, abandons this gait for pelvic paddling during fast swimming (Hickman 1984).

*Lutra canadensis* swims using a variety of paddling modes (including quadrupedal and forelimb-only), but during rectilinear surface swimming it usually paddles by alternating strokes of the hind limbs (Fish 1994). Forelimbs are not involved in locomotion during this locomotor pattern. The locomotor cycle for each limb can be divided into a power stroke and a recovery stroke. During the former, the hip is extended (distal femur moves caudally), the knee is extended, and the heel is plantarflexed while the foot is splayed out. The opposite motions occur in the recovery stroke, where the surface area of the foot is reduced by half to minimize drag (Fish 1984). A similar sequence occurs in *Chironectes*: the toes are abducted and extended throughout the power stroke and propulsive force is provided by extension at the hip and by knee extension (Fish 1993a). Abducting the toes will greatly enlarge the surface area of the feet if the toes are elongate and webbed.

Williams (1989) concluded that the shift from quadrupedal to pelvic paddling in mustelids minimizes the disruption of the boundary layer (between water and body) by the forelimbs. Disruption of the boundary layer would lead to increased drag (Webb 1988) and slow the animal down. Restricting paddling to one pair of extremities might also limit interference between fore- and hind limbs (Fish 1993a) and has been shown to increase aerobic efficiency (Fish 1982, 1993a; Williams 1983).

There is no sharp functional distinction between simultaneous pelvic paddling and dorsoventral undulation. In the latter, flexion and extension of the back provide the main propulsive force, but limb movements are similar. Consistent with this, Fish (1994) suggested that downward motions of the tail in paddling otters provide some thrust during the recovery stroke of the feet.

**Pelvic undulation in the Dorsoventral Plane.**—During this mode of locomotion, waves travel through the vertebral column and swing a hy-

drofoil at the feet **through the water**. Undulation mainly occurs in submerged **swimming**. Williams (1989) described the transition between pelvic paddling and undulation in sea otters (*Enhydra*). She noted that the trunk of the animal remains rigid during surface swimming, but that the subsurface undulations allow greater speeds in spite of reduced stroke frequency. The hind limb muscles provide thrust in paddling sea otters, but during undulation, the hind limbs and tail passively trail the undulations of the vertebral column. Overall, the shift from paddling to undulation improves performance, as indicated by lowered use of oxygen (Williams 1989).

Paddling relies on drag forces: propulsion is provided during the power stroke in paddlers, but not during the recovery stroke (Fish 1984). Undulation, in contrast, is a lift-based propulsive mode: it lacks a recovery stroke and thus minimizes accelerations and decelerations of the body throughout the propulsive cycle (Fish 1984).

The tail of *Lutra* acts as a hydrofoil and provides some lift, but the main propelling organs are the feet, which act as paddles (Fish 1994). In *Enhydra*, the hydrofoil has shifted from the tail to the feet. The main forces involved in foot movements are thus different; in *Lutra* they are drag forces, whereas in *Enhydra* lift is important.

**Caudal Undulation in the Dorsovenral Plane.**—As in pelvic undulation, the propulsive force in caudal undulation is provided by flexion and extension of the lumbar and caudal vertebral column. Unlike in pelvic undulation, the hydrofoil in caudal undulation is located at the tail. Undulation is rare among mammals, but Fish (1994) noted that *Lutra* mainly undulates under water and remarked that this mode might also be practiced by the Brazilian river otter, *Pteronura*. In *Lutra*, the tail, powered by lumbosacral flexors, can provide thrust during the recovery stroke during paddling. The tail thus acts as a hydrofoil, but the main propulsive force is still provided by the feet. *Lutra* therefore represents the transition between pelvic paddling and pelvic dorsoventral undulation.

Fish (1996) suggested that cetaceans went through a stage where they were pelvic un-

dulators propelled by the feet acting as a hydrofoil, similar to *Enhydra*. On the other hand, it is also possible that cetaceans went from a pelvic paddling stage, similar to *Lutra*, directly to a caudal undulating stage by enhancing the caudal hydrofoil and reducing the pelvic paddling motions. *Pteronura* could be an adequate model for this type of locomotion. Caudal dorsoventral undulation is thus a swimming mode that may have preceded dorsoventral oscillation, the cetacean mode of swimming. We here expand Fish's (1996) model to include caudal dorsoventral undulation (Fig. 1).

**Caudal Oscillation.**—All modern cetaceans swim by dorsoventral oscillations of their tail flukes. These movements are powered by the muscles of the back and abdomen and thrust is provided on both the upstroke and downstroke. Fish (1993c) and Fish and Hui (1991) reviewed the kinematics of swimming in small cetaceans.

In undulation and oscillation, sinusoidal waves run through the body of the swimmer. In undulation, different sections of the body are in different phases of the sinusoid, whereas in oscillation, the entire body is in the same phase of a sinusoid, and the motions resemble a standing wave. Undulation and oscillation are common swimming modes in fish, and there is a clear correlation between these locomotor modes and body shapes (Motani et al. 1996). These body shapes have been arranged in a graded morphological series that ranges from anguilliform, to subcarangiform, to carangiform, and finally thunniform (see, e.g., reviews by Lighthill 1969; Webb and Blake 1985; Webb 1988). Locomotor modes change gradually along this ciine, with undulating movements (defined as waves that travel through the body and that propel it) decreasing, and oscillations increasing. Cetacean morphology is not unlike that of thunniform fish (Webb and Blake 1983).

No mammalian group includes living taxa that document the transition from undulatory to oscillatory modes. Slijper (1946) suggested that mysticetes might swim by undulatory movements, but there is no experimental evidence supporting this.

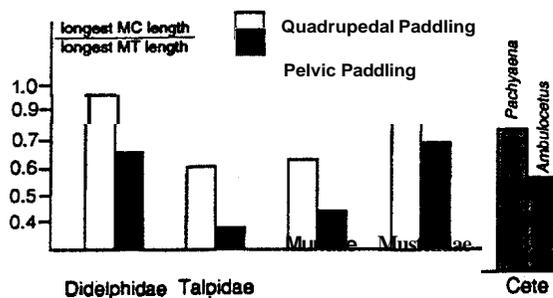


FIGURE 2. Comparison of relative metatarsal length (longest metacarpal/longest metatarsal) as an indicator of foot length in quadrupedal paddlers and pelvic paddlers of four modern clades. Ratios for extinct *Ambulocetus natans* and *Pachyaena ossifraga* are also shown (sources respectively Thewissen et al. 1996 and O'Leary and Rose 1995). Genera included are those listed in Fig. 1.

#### Testing the Model: Swimming in *Ambulocetus natans*

The fossil record documents the locomotor morphology of several cetaceans that are very different from modern forms. Among these, *Ambulocetus* is furthest removed from modern cetaceans morphologically. The search for a locomotor mode that is different from that of modern cetaceans is thus most promising in this taxon.

It is not likely that *Ambulocetus* was a quadrupedal paddler. Most quadrupedal paddlers are terrestrial animals, and they lack specific morphological specializations for swimming. Pelvic paddlers display elongated feet when compared with their terrestrial relatives (Howell 1930; Stein 1981; Fish 1984), and this is borne out by comparison of relative hind foot length (Fig. 2). The hind-limb paddler of four pairs of closely related swimmers has longer metatarsals than the quadrupedal paddler. This suggests that foot length covaries with locomotor behavior. However, it is clear that the phylogenetic history of a clade matters since the metapodial length ratio differs vastly between the different clades. For instance, some quadrupedal paddlers (e.g., *Rattus*) have lower ratios than some bipedal paddlers (e.g., *Lutra*).

The ratio for *Ambulocetus* is much smaller than that for its terrestrial relatives, the mesonychians (*Pachyaena* [Zhou et al. 1994; O'Leary and Rose 1995]). We interpret the metatarsal elongation of *Ambulocetus* as an ad-

aptation for generating propulsion with its feet during swimming. A similar conclusion was reached by Thewissen et al. (1994, 1996) based on the morphology of individual limb elements.

It is unlikely that *Ambulocetus* was a caudal oscillator. Modifications of the mammalian body plan associated with caudal oscillation might include the shape of the hydrofoil on the tail. There are hydrodynamic implications of hydrofoil shape in cetaceans (Webb 1988; Bose et al. 1990), but because the flukes do not fossilize these cannot be evaluated in cetacean evolution. During oscillation, spinal movements are concentrated in one part of the body, and vertebral modifications are to be expected in the area of rotation. Crovetto (1991) and Watson and Fordyce (1993) documented changes in vertebral body shape and intervertebral disc in the region of greatest oscillation in dolphins. Reduction of tail length can also be expected, as a shorter stalk can provide greater moments.

On the basis of length of the caudal vertebrae, Thewissen et al. (1996) inferred that the tail of *Ambulocetus* was long and robust. A long tail implies that a fluke at the distal part of the tail would have a poor lever arm (Thewissen et al. 1996) and would not be an efficient hydrofoil. In contrast to the long vertebrae in the tail of *Ambulocetus*, tail vertebrae of the modern cetaceans are relatively short. It remains possible that the tail of *Ambulocetus* provided some propulsion (see below), but it is unlikely to have matched the propulsive force generated by a fluke.

*Ambulocetus* was not a quadrupedal paddler or caudal oscillator. This implies that it used an intermediate mode of locomotion and was different in this respect from modern cetaceans. If cetaceans went through the locomotor stages predicted by the proposed model, then *Ambulocetus's* swimming may have included pelvic paddling, pelvic undulation, or caudal undulation. The morphology of *Ambulocetus* could then be consistent with that of lutrines using these locomotor modes. Comparing lutrine morphology with that of *Ambulocetus* can then be used to evaluate the hypotheses predicted by the model.

The morphology of the propulsor (paddle

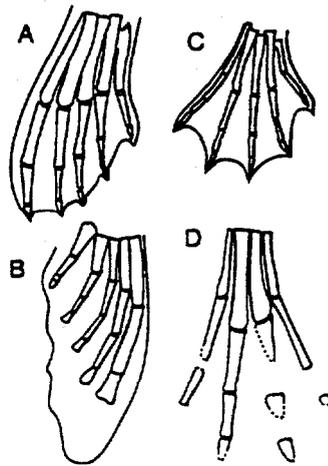


FIGURE 3. Examples of lift-based (A,B) and drag-based (C) propulsors, showing the similarity of *Ambulocetus's* foot (D) to a drag-based propulsor. Figured are dorsal views of right foot of the sea otter *Enhydra* (A), right hand of sea lion *Zalophus* (B), right foot of river otter *Lutra canadensis* (C), and right foot of cetacean *Ambulocetus* (after Thewissen et al. 1996) (D).

or hydrofoil) is an important indicator of these intermediate locomotor modes. The transition from hind-limb paddling modes of locomotion to foot- or tail-based undulatory modes involves the development of a hydrofoil and the shift from drag-based to lift-based propulsion. Optimal propulsor shape for a drag-based paddle is very different from that of a lift-based hydrofoil (Blake 1981; Webb 1988; Webb and Buffrénil 1990). Drag-based propulsors consist of a flat plane that is held normal to the direction of movement (Webb and Blake 1985). The optimal propulsor of this type has the shape of a high triangle with a narrow stalk (Webb 1988). The efficiency of a lift-based propulsor (hydrofoil) depends on its aspect ratio: the ratio width/length, where width is measured perpendicular to the flow. Efficient hydrofoils have a high aspect ratio. This ratio often cannot be calculated in fossils because the position of the hydrofoil during locomotion is not known. Overall, hydrofoils tend to be narrow and end in a pointed tip laterally (Webb 1988) and their shape is highly asymmetrical (Fig. 3A,B). These shape differences can be used to evaluate propulsive forces generated by the foot. Propulsor shape within mustelids can serve to illustrate this. *Enhydra* not only has disproportionately long

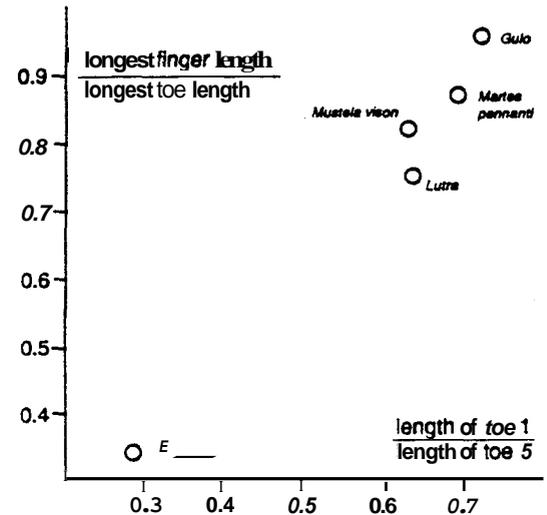


FIGURE 4. Foot size and shape in mustelids. Symmetry of the foot (ratio of the lengths of the first and fifth digits) is plotted against the relative length of the longest digit (longest finger/longest toe). *Pteronura* and *Ambulocetus* cannot be plotted because none of the investigated specimens had a full complement of hand and foot bones.

feet (Fig. 4, y-axis), but these are also highly asymmetrical (x-axis), unlike other mustelids, whereas those of *Lutra* are more symmetrical and function as paddles.

The feet of *Ambulocetus* had the shape of a high triangle (Fig. 3D), and the axis of the foot is between third and fourth digit, as in its terrestrial relatives, the mesonychians (*Mesonyx* and *Pachyaena* [O'Leary and Rose 1995]). *Ambulocetus's* feet are larger than those of mesonychians and have longer central digits, as indicated by metatarsal length (Fig. 5). The first digit of *Ambulocetus* was absent and the second and fifth digit are similar in robustness and length of preserved elements. *Ambulocetus's* feet also closely match those of drag-based mustelids such as *Mustela vison* and *Lutra*, in that the central digits are longer than digits II and V (Fig. 5). This suggests that the feet of *Ambulocetus* used a drag-based locomotor mode in water. This is unlike the lift-based hydrofoil of *Enhydra*, in which toe (and metatarsal) length diminish from digit V to I (Figs. 3A, 5). This suggests that *Ambulocetus* was not a pelvic undulator. Aquatic locomotor evolution from mesonychians to *Ambulocetus* is thus best compared with modern analogues such as *Mustela vison*, *Lutra*, and *Pteronura*.

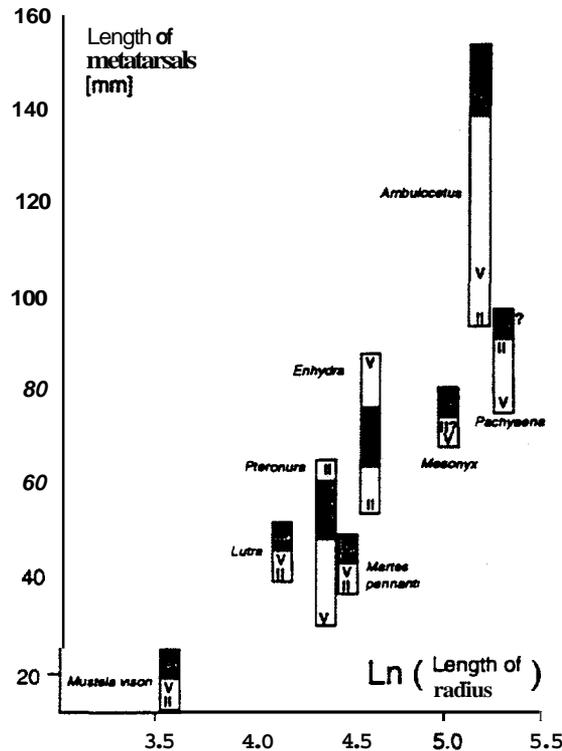


FIGURE 5. Metatarsal lengths for mustelids and Cete (cetaceans and mesonychians) as plotted against an estimator of body size (Ln radius length). Nonspecialized mustelids and cetans have metatarsals II and V that are not greatly different in length from central digits (III and IV, grey), which are the longest. This morphology is found in taxa that are mainly terrestrial (Mustelidae: *Mustela vison*, *Martes pennanti*; Cete: *Mesonyx obtusidens* [Scott 1888]; *Pachyaena ossifraga* [O'Leary and Rose 1995]). Longer central digits are found in groups with paddles that lack a pedal hydrofoil (*Lutra canadensis*, *Ambulocetus nantans*). A pedal hydrofoil is present in *Enhydra*, which has very large and proportionally unusual feet.

In addition to being propelled by the feet, *Ambulocetus* also had a powerful tail, as in *Pteronura* and *Lutra*. The tail of *Pteronura* is as long as in *Lutra*, 125% of the thoracolumbar length, versus 64% in *Enhydra*. The tail of *Pteronura* is probably more involved in propulsion than that of *Lutra*, since the transverse processes of the proximal caudal vertebrae are larger for insertion of the flexors and extensors of the tail. In addition, the fleshy part of the distal tail of *Pteronura* is laterally expanded (see Redford and Eisenberg 1992: Plate 8). This is consistent with the morphology of individual vertebrae. Figure 6 shows that the length of the third caudal vertebra increases in

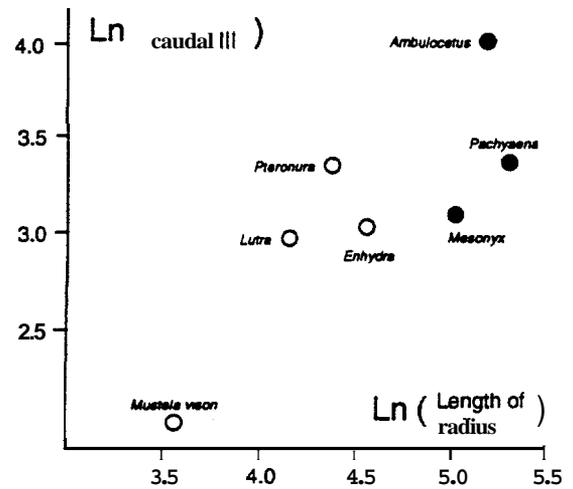


FIGURE 6. Length of caudal vertebra III in mustelids (open circles), mesonychians, and *Ambulocetus*. *Enhydra*'s tail is short and not used for propulsion, whereas the tail does provide lift in *Lutra* and *Pteronura*. Similarly, the tail vertebrae of mesonychians (*Mesonyx* [Scott 1888]; *Pachyaena* [Zhou et al. 1992]) are shorter than those of cetaceans, consistent with the presumed absence of tail-based propulsion in mesonychians. In the fossil taxa, (black circles), caudal vertebra III was not always preserved and values for a nearby proximal caudal vertebra were substituted.

size from *Mustela vison* to *Lutra* and *Pteronura*. Body size as well as tail-produced lift also increase along this series. On the other hand, *Enhydra* is larger than *Pteronura* and has a shorter third caudal vertebra, consistent with the trivial role of the tail in propulsion in *Enhydra*. This pattern is consistent with that in cetaceans, where *Ambulocetus*'s tail (as based on the third caudal vertebra) is much larger and more powerful than that of its terrestrial relatives, *Mesonyx* and *Pachyaena* (Fig. 6). It is likely that the tail provided some propulsion in *Ambulocetus*, although it was not the main propulsor. The exact surface areas of tail and feet of *Ambulocetus* cannot be determined at this point, and their relative contributions to propulsion are thus unknown, but it seems likely that the feet were more important. It is clear that, based on present evidence, *Ambulocetus* is most similar in locomotor morphology to *Lutra* suggesting that the taxon probably used pelvic paddling and caudal undulating in swimming. The swimming behavior of *Pteronura* has not been analyzed in detail, but this taxon might also be a good analogue for *Ambulocetus*'s locomotion.

The locomotor skeleton of *Arnbuloceetus* differs from that of mesonychians (Scott 1888; Zhou et al. 1992; O'Leary and Rose 1995) in the presence of much larger feet and a stronger tail. Both are consistent with improved aquatic locomotion, pelvic paddling, and caudal undulating. Given that modern cetaceans swim by means of caudal oscillation, it can be expected (Fig. 1) that the caudal undulation component was increased in those cetaceans that are intermediate between *Arnbuloceetus* and modern whales. Subsequently, caudal oscillation replaced caudal undulation in cetacean evolution. Cetacean skeletons intermediate between *Arnbuloceetus* and Neogene whales are rare, but one of the more complete is that of middle Eocene *Rodhocetus kasrani* (Gingerich et al. 1994). Consistent with the results of this paper, *Rodhocetus* probably had small feet (the feet are not preserved, but the pelvis and femur are) and a strong tail. Gingerich et al. (1994) proposed that *Rodhocetus* had a fluke, but this remains to be confirmed by recovery of distal caudal vertebrae.

In spite of the similarity between *Ambuloceetus* and lutrines, there also are obvious differences. Otters are agile hunters that display a variety of swimming modes and commonly chase prey. *Arnbuloceetus* was probably not a pursuit hunter, but rather an ambush hunter, relying on sudden bursts of movement to secure prey (Thewissen et al. 1996). *Ambuloceetus* lacked the agility and sustained speed of lutrines and its swimming was probably not related to chasing prey, and this may be reflected in the morphology of the skeleton. It is possible that ambush hunting in the earliest cetaceans represents a phylogenetic constraint and was present in the mesonychian ancestors of cetaceans.

### Conclusions

We conclude that the paleontological evidence is consistent with a model for the origin of cetacean locomotion as initially proposed by Fish and modified in Figure 1. Lutrines are the best extant functional models for early cetacean locomotion and that the locomotor morphology of *Ambuloceetus* may have been most similar to that of *Lutra* or (less likely) *Pteronura*. This does not imply that *Ambuloce-*

*tus* was ancestral to all later cetaceans; a comprehensive phylogenetic analysis of early cetaceans has yet to be undertaken (Thewissen 1994). It also does not imply that all early cetaceans swam similarly. Our study does not encompass locomotor diversity across all Eocene cetaceans, instead focusing on one transitional taxon for which the osteology is well known.

On the other hand, locomotor patterns are remarkably stable within higher clades. Members of extant groups are mostly restricted to minor variations of one locomotor pattern: all sirenians and cetaceans are caudal oscillators, all phocids and odobenids are pelvic oscillators, and all otariids are pectoral oscillators (Fish 1996). This suggests that selection for enhanced swimming was severely constrained by existing morphologies and that phylogeny, possibly through conservative neuromuscular patterns, plays a major part in determining locomotor patterns. This further emphasizes the need to study locomotor morphology in a rigorous phylogenetic context. Mustelids do display a remarkable variety of locomotor modes, from quadrupedal paddling to dorsoventral undulation. Nevertheless, all these modes are part of the same transformational series (Fig. 1).

There is rapid evolution of locomotor modes in most mammalian clades—cetaceans may have evolved caudal oscillation in approximately four million years (Gingerich et al. 1994). It is thus surprising that the entire range of swimming modes is still represented among modern lutrines, a subfamily that is approximately as old as pinnipeds (late Oligocene). It is possible that body size was an important factor since locomotor specializations tend to be more pronounced in larger taxa (Webb and Buffrenil 1990). Body sizes may have strongly constrained the evolution of pinnipeds, cetaceans, and sirenians, as all three of these clades radiated at body sizes much larger than lutrines did.

### Acknowledgments

Financial support for this work was provided by the National Geographic Society (5536-95) and the National Science Foundation (EAR-9526686) to Thewissen and by the Office

of Naval Research (N00014-95-1-1045) to Fish. We thank P. Lemelin, S. Madar, M. Uhen, and T. Williams for reading and commenting on the manuscript.

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