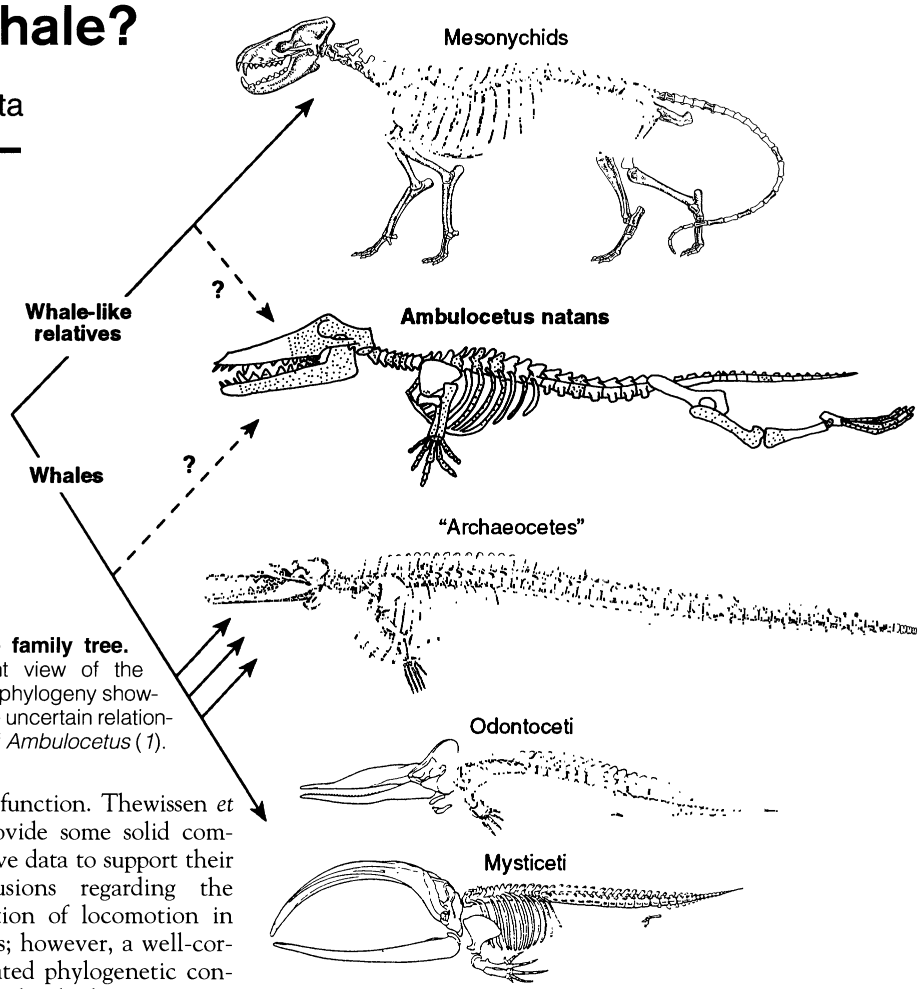
What Is a Whale?

Annalisa Berta

Paleontologists dream about discovering morphologic intermediates in the fossil record. Such discoveries are rare and exciting when they occur. On page 210 of this issue Thewissen *et al.* (*1*) describe a skeleton with limbs and feet of a whale from 52 million-year-old sediments in Pakistan. The authors provide some evidence for the seemingly preposterous conclusion that archaic whales were capable of walking on land. This conclusion, however, is more reasonable when the ancestry of whales is considered.

The closest relatives of whales are an extinct group of ungulates, mesonychid condylarths (*2, 3*). Although modern whales lack grinding teeth and hooves, a number of shared derived features found in the Cete (mesonychids + whales) strongly ally them with higher ungulates, specifically artiodactyls (*4*). Thewissen *et al.* in reporting their new whale describe it as a new genus and species, *Ambulocetus natans*, belonging to the archaeocete whale family Protocetidae. Archaeocetes are a "scrapbasket" group of extinct Eocene whales that together with the two living whale lineages, the toothed whales (Odontoceti) and the baleen whales (Mysticeti), comprise the mammalian order Cetacea.



Whale family tree. Current view of the whale phylogeny showing the uncertain relationship of *Ambulocetus* (*1*).

By the standard of many archaeocetes, *Ambulocetus* is very well known, consisting of a partially articulated skeleton with skull, vertebrae, ribs, and limbs. Modern whales lack hindlimbs (though they may be present in embryos), retaining only vestiges of pelvic bones and hindlimb elements embedded in the musculature of the body wall (*5*). The discovery of partial hindlimbs and feet in *Ambulocetus* invites functional explanation for their use in locomotion. Thewissen *et al.* suggest that *Ambulocetus* swam by undulating the vertebral column and paddling with the hindlimbs, combining aspects of modern seals and otters, rather than by vertical movements of the tail fluke, as is the case in modern whales. Although our knowledge of the skeletal anatomy of archaeocetes is poor, interestingly, prior interpretations of archaeocete hindlimbs have not always invoked their use in locomotion. For example, the very reduced hindlimbs of another archaeocete, *Basilosaurus isis*, were interpreted as copulatory guides (*5*), but could just as reasonably be interpreted as vestigial structures without a function. Thewissen *et al.* provide some solid comparative data to support their conclusions regarding the evolution of locomotion in whales; however, a well-corroborated phylogenetic context with which to interpret these character transformations would greatly enhance its utility. For example, since the pelvic girdle is not preserved, there is no direct evidence in *Ambulocetus* for a connection between the hindlimb and the axial skeleton. This hinders interpretations of locomotion in this animal, since many of the muscles that support and move the hindlimb originate on the pelvis.

Many questions surround the base of whale evolution. First, relationships among archaic whales—the archaeocetes—are unresolved, as Thewissen *et al.* mention; some archaeocetes are more closely allied with mysticetes than with each other (*6*). Because of this, identification of *Ambulocetus* as an archaeocete somewhat obscures its relationship to other whales. A second question is whether *Ambulocetus* is, in fact, strictly speaking, a whale, or whether it is just a close relative of whales (see figure). The answer depends on how "whale" is defined.

Whales can be defined in several different ways, emphasizing either possession of certain characters (character-based definition) or with respect to common ancestry (stem-, node-, and apomorphy-based definitions) (*7, 8*). Character-based definitions are problematic. For example, how can whales be defined as lacking hindlimbs, since some whales (for example, several archaeocetes) possess them? Another problem arises considering that discoveries of ostensible whales occur fairly regularly (*9, 10*), with new combinations of characters making it difficult to decide whether they are whales following a strictly character-based definition. A more reasonable solution is to use a phylogenetic definition, that is, one based on common ancestry. In the previous example, because archaeocetes are more closely related to modern whales than they are to mesonychids, *Ambulocetus* is a whale by virtue of its inclusion in that lineage. Evidence to support the inclusion of *Ambulocetus* in the whale lineage comes from derived characters that it shares with modern whales. There have been few attempts to provide a phylogenetic definition for whales. Prothero *et al.* (*4*), as part of a larger phylogenetic analysis on ungulates, provided the following derived characters to unite whales and distinguish them from the closely related mesonychids: (i) all incisors parallel with toothrow, (ii) medial lambdoidal crest semicircular, (iii) nasals retracted, (iv) protocones small, and (v) accessory cusps large. Characters (i), (ii), and (iii) are not preserved in *Ambulocetus*,

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leaving dental features to support its identification as a whale. In this context, note that several early whales from the Eocene of Pakistan, *Gandakasia* and *Ichthylestes*, known only from teeth, were originally described as mesonychids (*11*). Rather than use Prothero's definition of a whale, Thewissen *et al.* use other characters to establish *Ambulocetus* as a whale, including an inflated ectotympanic that is poorly attached to the skull and bears a sigmoid process, reduced zygomatic arch, long narrow muzzle, broad supraorbital process, and teeth that resemble other archeocetes. Before these purported whale characters can be used in a phylogenetic definition of whales, however, the possibility that some of them may have a broader distribution (for example, in mesonychids) needs to be examined.

While the study of Thewissen *et al.* provides new information at the base of whale evolution, recent molecular data have challenged traditional views of later whale evolution. According to Milinkovitch *et al.* (*12*), data from mitochondrial DNA suggest that odontocete whales might not be a monophyletic group; that is, they do not comprise a lineage that includes the common ancestor and all of its descendants. A closer relationship is suggested between the sperm whales and the baleen whales than between the sperm whales and other alleged odontocetes. These molecular results have intriguing evolutionary implications (*13*). Either baleen whales secondarily lost the ability to navigate using echolocation or, alternatively, echolocation in whales may have evolved twice, once within the sperm whale + baleen whale clade and once within other odontocetes. The molecular view of odontocetes as a nonmonophyletic group is not supported by morphologic evidence, although few studies have addressed the problem using comprehensive data sets (including both fossil and recent taxa) and rigorous phylogenetic methods (*14, 15*).

Molecular as well as morphologic studies compel us to reexamine whale phylogeny. Although its relationship to other whales is uncertain, *Ambulocetus natans* is a whale, using a definition based on ancestry. This discovery is significant in providing a more complete picture of morphologic diversity at the base of whale evolution, particularly in documenting the locomotory transition in whales from land to the sea. More importantly, perhaps, it directs us to what is most needed now, an expanded study of the phylogenetic relationships of all whales and their close relatives, including extinct as well as recent taxa.

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What Are We? Where Did We Come From? Where Are We Going?

Luke O'Neill, Michael Murphy, Richard B. Gallagher

If an angel appeared before you and granted the answer to one question, what would that question be? If your burning desire is to know whether there is intelligent life elsewhere in the universe, you are in good company. A group of eminent physicists, chemists, and biologists agree that this is *the* "angel question." It remains, for the time being, unanswerable, but questions almost as fanciful—what are we, where did we come from, and where are we going—are at least beginning to be tackled in a meaningful scientific way. These were the themes that dominated a recent meeting in Dublin (*1*), held to commemorate the series of lectures given in Trinity College 50 years ago by Erwin Schrödinger.

Those original Schrödinger lectures, entitled "What Is Life?", electrified public audiences in Dublin half a century ago and, when published by Cambridge University Press in 1944, had a major influence on the development of molecular biology. In them, Schrödinger put forward two propositions. First, "order from order": Inspired by studies of Delbrück on the rate of mutation in fruit flies exposed to x-rays, he discussed the physical nature of the gene and the mechanism of heredity. His suggestion of it being an aperiodic crystal was a remarkably prophetic description of the structure of DNA. Second, "order from disorder": an outline of how living organisms maintain order while being displaced from equilibrium, a feat made possible by the metabolism of food or, as Schrödinger termed it, negative entropy. Speakers at the 50th anniversary meeting were invited to speculate on the future of biology in the spirit of Schrödinger's original lectures.

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What Are We?

Genetically, that is, in terms of information content, humans are 99 percent identical to chimpanzees. Indeed, argues Jared Diamond, a visitor from outer space would classify humans as a third species of chimpanzee, not with the separate classification that we award ourselves. How, then, did we become so successful? What sets us apart from other species? Diamond, professor of biology at the University of California, Los Angeles, proposed that it is human inventiveness, a talent developed as a consequence of the acquisition of language. The first signs of inventiveness appeared around 50,000 years ago, judging from the evidence of elaborate tools, art, and burial of the dead. It is possible that changes in the voice box facilitating efficient transmission of information allowed this development of inventiveness. It was pointed out by Stephen Jay Gould (Harvard University) that early language would have had a selective value that could have been co-opted by early man in acquiring inventiveness, so language and inventiveness probably coevolved. John Maynard Smith (University