The Whale's Tale

Searching for the landlubbing ancestors of marine mammals

By RICHARD MONASTERSKY

Only 24 years after Charles Darwin rewrote the book of life with his theory of natural selection, a fellow Victorian scientist named William Flower trained this powerful new idea on one of the toughest problems in zoology: the whale. Natural historians had long before recognized that whales are mammals, but that was about as far as they had come in understanding the origins of cetaceans. How evolution had managed to craft such a unique beast presented a mystery as vast as the creature itself.

In 1883, Flower offered an idea that—on the face of it—seemed positively daft. The legless leviathans, he suggested, had evolved from mammals known as ungulates, a group whose best-known characteristic is a set of hoofed feet. In other words, dolphins, porpoises, humpbacks, orcas, and all other whales are close kin of cows, horses, pigs, and related barnyard stock.

More than a century after Flower raised his audacious hypothesis, it no longer stirs even a whiff of controversy. Dozens of scientific studies over the past 3 decades have convinced biologists that cetaceans are the progeny of hoofed mammals. Yet the whale's story is far from finished.

Two opposing groups of scientists are currently battling over the next chapter in the saga. They clash on the issue of exactly where whales fit in the tree of hoofed mammals. Far from just an arcane argument, the debate has much to say about how whales made the profound transformation from life on land to mastery of another medium.

What's more, the skirmish documents the intense Darwinian struggle shaping the science of biology as it evolves. The war over whales pits the classical techniques of studying bones and flesh against the most modern methods of genetic analysis—two approaches that lead to different versions of the whale's origin tale.

"This is one of *the* fundamental questions right now," says Patrick Luckett, an embryologist at the University of Puerto Rico in San Juan and a coeditor of the JOURNAL OF MAMMALIAN EVOLUTION. "This is something that's very interesting to evolutionary biologists because there is this continuing controversy."

The most recent genetic evidence, reported in August, provides the strongest support yet for the hypothesis that whales and hippopotamuses are first cousins. If true, this would slice these marine animals from their long-standing position on the mammal family tree and graft them onto a different branch. It would also suggest that the ancestor of whales and hippos may have ventured into the water more than 55 million years ago.

From the fossil bones, however, paleontologists see no need to cut into the mammalian tree. Hippos, they say, are only distant relatives of whales, no closer than are deer, pigs, or other even-toed ungulates.

For Charles Darwin, whales represented a major case of heartburn. The famed naturalist had no trouble envisioning whales evolving from four-legged mammals, but his audience certainly did.

In his *Origin of Species*, Darwin notes a case of a black bear swimming for hours with its mouth agape, catching aquatic insects much as a whale might feed. "I can see no difficulty in a race of bears being rendered, by natural selection, more aquatic in their structure and habits, with larger and larger mouths, till a creature was produced as monstrous as a whale," he speculated.

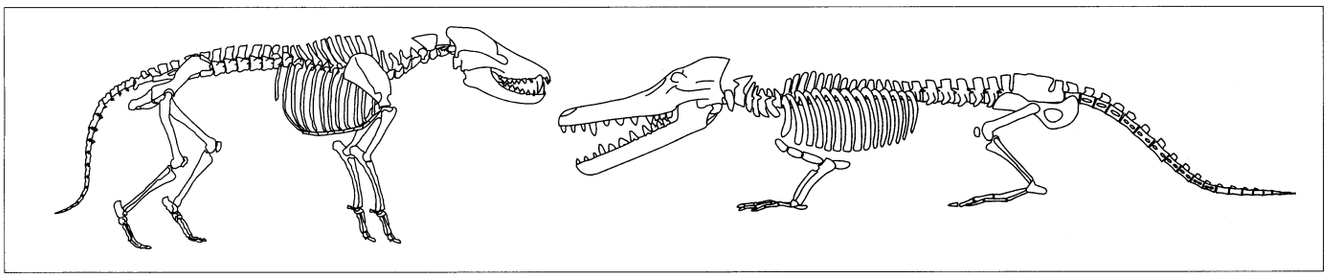
The ridicule and attacks engendered by this passage grew to such a pitch that Darwin pared it down and then deleted it altogether in later editions.

Although Darwin got the particulars wrong, his swimming-bear scenario was not far off the mark. Modern molecular biologists say that they now have the unassailable evidence to track whales' origins among four-legged mammals.

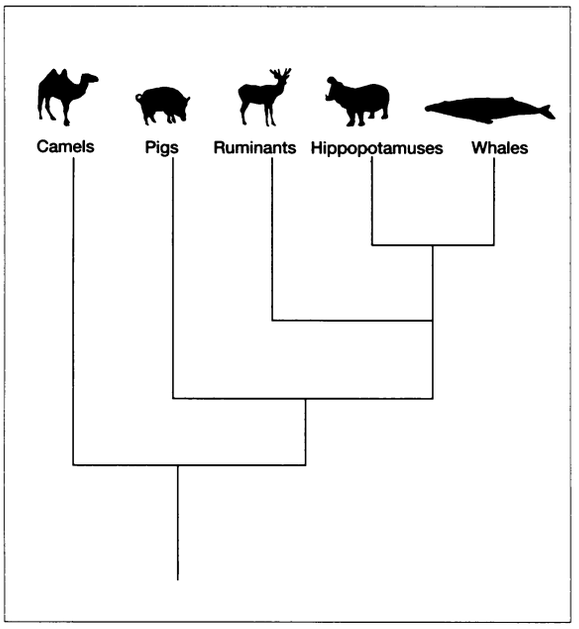
In the Aug. 31 PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES, a team of Japanese and U.S. researchers used one of the newest types of genetic analysis to track the phylogeny, or relationships, among some mammals. The group focused on whales and members of the order Artiodactyla, the group that paleontologists in recent years have considered whales' closest living relatives. Artiodactyls are hoofed animals that have an even number of toes on each foot, such as pigs, giraffes, and hippos.

Norihiro Okada of the Tokyo Institute of Technology and his colleagues examined a part of the animals' genetic code that doesn't specify instructions for any genes. Some of this so-called junk DNA is

Thewissen



Kissing cousins? Built like hoofed wolves, the extinct animals known as mesonychians (left) bear a close resemblance to fossil whales, such as an Ambulocetus natans *(right) found in 49-million-year-old rocks in Pakistan.*



Finding a new home for whales: Unique genetic elements in the DNA of mammals suggest that whales belong within the family tree (shown here) of artiodactyls, hoofed mammals with an even number of toes. Whales and hippopotamuses share four genetic elements not present in any other artiodactyl, suggesting that they are each other's closest living relatives.

made up of segments that can copy themselves and then splice the copies back into the genetic strands at various points. One group of these mobile elements consists of short interspersed elements, or SINEs; long interspersed elements, or LINEs, form another.

Such segments have been insinuating themselves into the code of life for billions of years, says Okada. "In the case of the human genome, SINEs constitute more than 10 percent of the genome, and LINEs constitute more than 15 percent," he says.

Usually harmless, these segments have an uncanny ability to co-opt the DNA-copying apparatus in cells, and they may have played a role in spawning some viruses. "Retroviruses, such as the AIDS viruses, were believed to have been generated from LINEs," says Okada.

Though SINEs and LINEs may fulfill no useful mission in the genome, these self-serving molecules turn out to have unique value in mapping the twists and turns of evolution. By looking for particular examples of these copies in specific sites of the genome, researchers can determine when various species split off from related ones.

In the recent study, Okada and his colleagues found that all artiodactyls are not equally related to whales, as paleontologists have long maintained. Instead, hippos and whales share four SINEs not present in the other artiodactyls tested—camels, pigs, deer, giraffes, and cows. Since hippos are clearly artiodactyls, whales would also deserve bona fide membership in the same order, rather than simply being cousins to artiodactyls, as paleontologists would have it.

Molecular biologists have found evidence of a link between whales and hippos before, but Okada's technique has much more power than the conventional analysis of gene sequences, says Daniel Graur of Tel Aviv University in Israel. "Okada's ruining my livelihood. He'll put me out of business," jokes Graur, who analyzes genes.

In the standard method of constructing genetic family trees, molecular biologists compare the DNA sequences of genes in several species of organisms. Because the sequences change slowly over time, they should look more similar in closely related species—deer and antelope—than they do in more distant species—deer and pig.

This technique isn't foolproof. It goes awry when the same mutation happens independently in two different species. This kind of event, a molecular version of convergent evolution, makes two animals' sequences look similar even though they may be only distantly related. What's more, a mutation in one spot can change again or even correct itself, further muddling comparisons of sequences.

Scientists who analyze gene sequences try to get around this problem by considering many different genes, each of which represents a string of hundreds to thousands of individual DNA bases—the four letters in the genetic alphabet.

In contrast to standard sequencing, analysis of SINEs and LINEs presents a nearly perfect record of evolutionary change, says Okada. In 10 years of study, he has never found an example of these elements appearing independently in the same spot or, once inserted, extracting themselves from the DNA. "I am 100 percent confident with the conclusion that the most closely related species to whales, among extant mammals, is the hippo," Okada says.

Other molecular biologists agree that the SINE and LINE data add weight to the idea of a close relationship between whales and hippos, but many say that the connection was already firmly established by conventional genetic data. "Every gene I've ever sequenced says the same thing. The molecular data is all fairly consistent," says John Gatesy of the University of Wyoming in Laramie, one of the first who reported the whale-hippo connection. Some researchers have taken to calling this the whippo hypothesis.

For molecular biologists, the whale story is one of the clearest evolutionary tales they have to tell. Sometime more than 55 million years ago, the artiodactyl ancestors of whales and hippos split off from other groups that would lead to camels, pigs, deer, and cows. The whippo lineage may have developed a watery lifestyle even before the hippos and whale branches diverged. Biologists have noted that both groups share particular aquatic adaptations, such as the ability to nurse and communicate underwater.

"There's an awful lot of people who feel the data are so strong and so compelling, there isn't any question about it," says David M. Hillis of the University of Texas at Austin.

Scientists who study whale fossils, however, have several bones to pick with that attitude.

"I think that's an unfair dismissal of the paleontological data, and it's just unwise not to consider the fact that the fossil record is in contradiction to the molecular data," says Maureen O'Leary, a paleontologist at the State University of New York at Stony Brook. One of these two sets of information is yielding the wrong answer, and scientists don't know which, she says.

The biggest problem with the molecular approach, she says, is that it considers only a few living examples of related species, leaving out the 90 percent that have gone extinct. Seen against the backdrop of a much broader array of creatures, a different pattern emerges.

Since the 1960s, paleontologists have drawn strong evolutionary connections between whales and an extinct group of ungulates called mesonychians. Looking a little like a wolf with hooves, mesonychians had an unusual set of teeth that resemble those of ancient whales. Unlike all other ungulates, which have flattened molars with cusps for grinding plants, whales and mesonychians have bladelike molars presumably useful for tearing meat.

"Whales and mesonychids among ungulates seem to be unique in that they resemble carnivorous animals," says O'Leary.

If mesonychians are the nearest known relatives to whales, however, whales couldn't fit next to hippos within the artiodactyls. The problem lies in the ankle. Mesonychians lack a specialized joint there that serves as one of the defining features of artiodactyls.

In all known members of this order, an ankle bone called the astragalus has a pulley-shaped knob at each end. That provides more freedom for flexing the foot up and down and limits twisting from side to side, says paleontologist J.G.M. Thewissen at the Northeastern Ohio Universities College of Medicine in Rootstown. Their unique astragalus helps artiodactyls bound over rough terrain without dislocating their ankles.

If the ankles of mesonychians won't give them membership among artiodactyls, then their presumed close relatives, the cetaceans, should not fit, either, reason paleontologists. One way to test this hypothesis would be to take a look at a whale astragalus, but evolution has made that difficult.

Modern whales have only vestiges of leg bones and lack astragali. Thewissen and his colleagues have therefore tried to find examples of this bone in fossils of ancient whale species that had true hind legs. "We all thought that once we had found the astragalus from a whale, we would solve the problem," says Thewissen.

He recently discovered such a key while prospecting in Pakistan for bones from the earliest known whales, members of a 50-million-year-old family called pakicetids. The key, though, turned out to have the wrong shape to unlock the solution. The pakicetid astragalus doesn't clearly resemble a mesonychid ankle or an artiodactyl ankle, Thewissen reported in the March Systematic Biology. "It's sort of a letdown," he says.

Other questions cloud the issue further. In part, Thewissen identified the Pakistani astragalus as belonging to a pakicetid whale because no other animal in those deposits could lay claim to a bone of that size. However, the astragalus was not clearly part of a pakicetid skeleton, so some paleontologists wonder whether it belonged to an animal other than an ancient whale.

How evolution led whales into the water

Paleontologists once despaired of ever tracing the evolution of whales back to the time when their ancestors walked on land. For much of this century, the fossil record had little to say about the earliest stages in this transition because the most ancient whale fossils came from animals already completely at home in the sea.

Within the past 2 decades, however, a wave of finds has helped fill in the progression from land to water. In 1983, Philip D. Gingerich of the University of Michigan in Ann Arbor and his colleagues discovered in Pakistan the skull of the earliest known whale, a 50-million-year-old animal they named *Pakicetus*. The fossils of several pakicetid whales range from wolf-size to as big as a bear, and they are found in the remains of small, ephemeral streams only about 1 meter deep.

Scientists have yet to uncover a full skeleton of one of these whales, but the animals' ears reveal clues to their lifestyle. "They tell me that they were doing something different than land mammals do," says J.G.M. Thewissen of the Northeastern Ohio Universities College of Medicine in Rootstown.

Thewissen studied the arrangement of ear bones in pakicetids in 1993 and concluded that they were best adapted to hearing through a medium much denser than air. The ears may have worked well underwater, or the animals may have listened out of the water by putting their jaws on the ground as some predators do, he says.

In 1994, Thewissen reported the discovery of a complete skeleton of a whale only slightly more recent than *Pakicetus*. This creature, which he named *Ambulocetus*, had limbs that would have been clumsy on land. Its large feet and supple spine allowed the animal to swim by flexing its hind half up and down in a precursor to the type of motion that modern whales use.

From the sedimentary deposits in which it was found, researchers can tell that *Ambulocetus* apparently lived in the ocean close to shore, perhaps near the mouths of rivers where it could get fresh water for drinking. The oxygen isotopes of its bones suggest that this species hadn't fully developed the ability to consume seawater as today's whales do. —*R.M.*

In an attempt to break the deadlock over whale origins, some of the opponents in the debate are joining forces. O'Leary and Gatesy are just starting out on a massive phylogenetic project that will combine genetic information with morphological data describing anatomical structures in fossil and living species. Once they put all the details into a database, a computer program will sort out the possible family trees relating the different animals.

As yet, the researchers have not figured out how to pull off the daunting task of pooling such dissimilar information. "There are some intricate problems with combining the molecular and morphological data into one analysis," says O'Leary.

One of the best ways to resolve the controversy, she says, would be to acquire some new information that causes one of the sides to shift its position. In some previous debates regarding the relationship between toothed and baleen whales, additional molecular analyses reversed controversial conclusions of earlier studies. On the other hand, a new whale fossil could show up with feet that belong unmistakably to an artiodactyl.

Thewissen has high hopes on the fossil front. "I think we'll have better fossils that will really bear on this question in the near future," he says.

If so, these bones could ultimately write a conclusion to the story that Darwin and Flower started more than a century ago. □