A Brief History of Whale Evolution

As Supported By the Fossil Record

BIOB 272 – Genetics and Evolution

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December 8, 2017

Cetaceans—whales, dolphins, and porpoises—are so different from other animals that, until recently, scientists were unable to identify their closest relatives. As any elementary student knows, a whale is not a fish. That means that despite the similarities in where they live and how they look, whales are not at all like salmon or even sharks. Carolus Linnaeus, known for classifying plants and animals, noted in the 1750s that "whales breathe air through lungs not gills; are warm blooded; and have many other anatomical differences that distinguish them from fish" (Prothero, 2015). Other characteristics cetaceans share with all other mammals are: they have hair (at some point in their life), they give birth to live young, and they nurse their young with milk. This implies that whales evolved from other mammals and, because ancestral mammals were land animals, that whales had land ancestors (Thewissen & Bajpai, 2001). But before they had land ancestors they had water ancestors.

The ancestors of fish lived in water, too. Up until 375 million years ago (mya), everything other than plants and insects lived in water, but it was around that time that fish and land animals began to diverge. A series of fossils represent the fish-to-tetrapod transition that occurred during the Late Devonian Period 359-383 mya (Herron & Freeman, 2014). In search of a new food source, or to escape predators more than twice their size (Prothero, 2015), the first tetrapods pushed themselves out of the swamps and began to live on land (Switek, 2010). These creatures developed hindlimbs, forelimbs, and both pelvic and pectoral girdles (Prothero, 2015) and were the predecessors of synapsids, a lineage of amniote vertebrates that originated 306 mya, during the Late Carboniferous Period, and ultimately gave rise to mammals (Herron & Freeman, 2014). A *Dimetrodon* is an example of a synapsid, a proto-mammal. Although it looks like a reptile or dinosaur, it is distinctly pre-mammalian "by virtue of its lateral temporal fenestra" (Herron & Freeman, 2014), which is a skull feature that is not found in non-mammals.

Over the course of 100 million years, synapsids evolved into the first mammals. Around 200 mya, during the late Triassic period or the early Jurassic period, mammals begin to appear in the fossil record. At that time dinosaurs were the dominant vertebrate, and they remained so until 66 mya when a mass extinction wiped them out and "cleared the way for a major radiation of mammals" (Switek, 2010). Many modern animal lineages originated around that time—give or take 10-20 million years—including elephants, pigs, horses, and rabbits (Herron & Freeman, 2014).

Although it was a mystery for decades, the origin of whales is now one of the best documented examples of macro-evolution in the fossil record (Switek, 2010). Over the past thirty years, a combination of paleontological, geological, anatomic, and molecular data has been compiled that builds and supports the case for the evolutionary history of whales. All sources indicate that modern whales had an ancestor that lived on land 52.5 mya (Uhen, 2010). A preponderance of evidence suggests that what William H. Flower proposed to be the case in 1883 *is* true: whales are artiodactyls (Uhen, 2010). Artiodactyls are hoofed mammals, and the word itself means "even toed" (Neufeldt, 1988). The order includes swine, ruminants (cattle, buffalo, goats, deer, giraffes, camel, llama, etc.), and the hippopotamus (Herron & Freeman, 2014). Flower had speculated "based on shared characteristics of various internal organs, that cetaceans might be related to the ungulates—the hoofed mammals" (Herron & Freeman, 2014). An English comparative anatomist and surgeon, Flower recognized similarities in the soft-tissue structures (stomachs, livers, respiratory organs, and reproductive organs) of whales and artiodactyls.

Flower said as much when he delivered a lecture titled “On Whales, Past and Present, and Their Probable Origin,” but at that time, the scientific community was not inclined to agree with him (Uhen, 2010).

From the 1950s until the 1980s, most scientists thought whales had evolved from ancient, land-dwelling carnivores called mesonychids, a taxon that is now extinct; however, scientific evidence has disproven that hypothesis. Interestingly, the missing link is very much like a mesonychid. In 1979, a paleontologist found the fossil remains of *Pakicetus* in northern Pakistan (Thewissen & Bajpai, 2001). Judging by its skull, *Pakicetus* was similar to a wolf in shape and size, but he had “a prominent sigmoid process and involucrum in the ear—telltale signs that this was a cetacean” (Thewissen & Bajpai, 2001). Fossils of over a hundred Pakicetidae have been found and date to between 48-52.5 mya. *Pakicetus* was 6 feet long, had a snout with nostrils far forward, four limbs that function for walking, no tail fluke (Smithsonian Museum, 2017), and its teeth resembled that of modern meat eaters, not plant eaters. The anklebone of *Pakicetus* is a derived character used to diagnose members of the artiodactyl family (Herron & Freeman, 2014). Geological clues and geochemical tests performed on teeth indicate that the desert where *Pakicetus* was found was once a stream bed (Thewissen & Bajpai, 2001). This was the transitional fossil for which paleontologists had been searching. Since that time, hundreds of proto-whale fossils have been found (many of them in Pakistan or neighboring India), and though they are “not a series of direct ancestors and descendants, each genus represents a particular stage of whale evolution. Together they illustrate how the entire transition took place” (Switek, 2010).

The next link in the fossil record is *Ambulocetus*, which was discovered in 1994, also in Pakistan. *Ambulocetus natans* which means "walking swimming whale" lived roughly 47 mya. Some of its features are whale-like and others more representative of land mammals. *Ambulocetus* had limbs for walking with very long fingers and toes, which were probably webbed, a long snout, a spine that could undulate, and proportions similar to those of an alligator (Prothero, 2015). *Ambulocetus* fossils are found in sedimentary rock layers that have been deposited over those in which fossils of *Pakicetus* are found. Protozoa, mollusks, and vertebrates buried with *Ambulocetus* indicate that it lived in a near-shore marine environment (Thewissen & Bajpai, 2001), and from isotopic tests, it has been inferred that *Ambulocetus* had a marine diet but drank freshwater (Uhen, 2010).

In the late 1990s, another piece of the puzzle—*Remingtoncetus*—was uncovered just four kilometers from the first *Ambulocetus*, and in identical layers of sediment, which indicates it is the same age, 47 million years old (Thewissen & Bajpai, 2001). *Remingtoncetus* looked even more like a mammalian crocodile than *Ambulocetus* did, and its limbs, pelvic girdles, and axial skeleton indicate that it could both walk on land and swim in the water (Uhen, 2010). Evidence in rock layers surrounding *Remingtoncetus* indicate the animal lived in an estuary environment. It is unknown whether *Remingtoncetus* drank fresh or ocean water because teeth have not been well preserved, making isotopic testing difficult (Uhen, 2010).

The next oldest fossils in the cetacean record are from about 45 mya and come from protocetids, "early whales" (Neufeldt, 1988) called *Rodhocetus*, and were also found in Pakistan. The skull of *Rodhocetus* was larger; it had a shorter, more powerful neck (better for diving); wider rear legs that were more like flippers; stronger tail muscles; and an ear much like that of a modern day whale. That means it was capable of turning and twisting at high speeds without getting disoriented, making it agile enough to outmaneuver predatory fish (National Geographic, 2014). The skeleton of *Rodhocetus* has proportions that indicate it propelled itself with its feet and used its tail to steer (Prothero, 2015). The teeth of *Rodhocetus* reveal that it was nearly entirely aquatic (Switek, 2010). Remains of protocetids similar to *Rodhocetus* occur in the fossil record for millions of years. Then, around 40 mya, changes in the fossils of ancestral whales show that they were living their entire lives in the sea.

In 1834, the fossil remains of an ancient whale, "archaeocete", were found and delivered to anatomist Richard Harlan. He named the species *Basilosaurus*, "emperor lizard", after mistaking the specimen for a giant reptile (Prothero, 2015). Sir Richard Owen, a famous British anatomist, correctly identified the beast as a whale based on its teeth, which had multiple roots and were distinctly mammalian (Thewissen & Bajpai, 2001). He tried to rename it *Zeuglodon*, "yoked tooth", but "by the rules of naming animals, the first name is the right name, no matter how misleading it may be" (Prothero, 2015). Many more specimens were found throughout Alabama, Mississippi, and Arkansas in the 1800s (Prothero, 2015). These remains were quite a distance, in both time and space, from when and where the older fossils were discovered—circa 1990, in Pakistan. Throughout the years, species similar to *Basilosaurus* have been discovered in India, Pakistan, New Zealand, Africa (Thewissen & Bajpai, 2001), and most recently in Peru (Uhen, 2010). Once these archaeocetes were no longer bound to land, they made their way to the oceans and spread across the globe.

In the 1990s, a complete, articulated skeleton of *Basilosaurus* was found in an Egyptian desert near a place called Wadi El-Hatin, “Whale Valley”. The creature was 80 feet long and eel-like (National Geographic, 2014), its arms and hands were modified into paddles, and it had non-functional hind limbs about the size of a human arm (Prothero, 2015). The sequence of tail vertebrae in the *Basilosaurus* matches that of modern day whales which suggests it had a tailfin (Berkeley, 2017). This ancient cousin of current whale species disappeared from the fossil record 36 mya. Mysteriously the lineage appears to have died out. Perhaps *Basilosaurus* lacked the power to dive or maybe it was unable to survive the cooling of the oceans (National Geographic, 2014). Fortunately, another line was better adapted.

Whale Valley turned out to be a goldmine for ancient whale fossils. Alongside the *Basilosaurus*, in 37 million-year-old sedimentary rock layers, were dozens of smaller *Durudons* (Thewissen & Bajpai, 2001). Testing of the sediments suggest that the remains “were deposited in near-shore marine environments, including mangrove swamps, sea-grass meadows, and bays with barrier islands, as well as off shore environments such as coral reefs” (Thewissen & Bajpai, 2001). *Durudon* averaged about 16 feet in length. Their compact body size may have been an evolutionary benefit which enabled them to thrive in colder waters. 35 mya, when the monster sharks ruled the seas, *Durudon* may have moved to arctic waters where their cold-blooded predators, the *Megalodon*, could not have survived (National Geographic, 2014). In areas with few predators, these ancient whales would have been free to disperse and multiply.

The fossils mentioned are all from the Eocene Epoch, 34-56 mya. These key finds help piece together how and when whales evolved from land animals to sea dwellers. The remains of the first of these, *Pakicetus*, showed evidence of an evolutionary relationship to artiodactyls. Analysis of DNA sequences from living animals has verified that whales are not only most similar to artiodactyls, but that whales descended from them (Prothero, 2015). Whales are located next to the *Hippopotamus amphibius* on phylogenic trees, within the order Artiodactyla. The group of whales and hippos is called Whippomorpha (*Wh*ale + *hippo* + *morpha,* "shape") by molecular biologists, and Cetacodontomorpha by most other scientists (Prothero, 2015). The last common ancestor of whales and the hippopotamus can be traced back to just over 50 mya. *Indohyus*, "Indian pig", was the size of a rabbit with the body of the small deer. It has the ear of a whale; very dense skeletal bones like whales, hippos, and other aquatic animals; and teeth that prove it ate plants. This combination of features link the fossil to both groups (Prothero, 2015).

Today there are over 80 cetacean species divided into two suborders: Mysticeti and Odontoceti. Mysticeti includes the baleen whales: humpback whales; bowhead whales, which live 200 years; gray whales, known to migrate 12,000 miles; and blue whales, the largest creatures on earth. Odontoceti includes the toothed whales: dolphins, porpoises, beluga whales, sperm whales, and killer whales (National Geographic, 2014).

In the 1750s, Carolus Linnaeus recognized that whales shared characteristics with land mammals and, therefore, must be mammals. However, for 250 years, how and where whales fit among the mammals remained unclear. Fossils found during the last three decades have made it possible to explain the progression from fish to tetrapod, tetrapod to proto-mammal, proto-mammal to mammal, and finally, mammal to sea mammal. Scientists from a variety of disciplines—geology, stratigraphy, paleontology, molecular biology, anatomy, and physiology—took part in discovering and interpreting the data. The origin and speciation of whales is now well documented and well understood; the mystery is largely solved. A combination of good luck and better science has allowed the whale to find its proper branch on the tree of life—right next to the hippopotamus and among the deer, the antelope, the pig, and the peccary.

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