The contents of this primer on Whale Origins is primarily taken from the website of The Thewissen Lab. Thie information here has been compiled from the extensive research of J.G.M. Thewissan. Additional information was taken from the website of Dr. Philip D. Gingerrich as noted.

The Primer of Whale Evolution

The original authors of the information within this primer are documented in full at The Thewissen Lab website. <http://www.neoucom.edu/DEPTS/ANAT/Thewissen/> All pictures on Dr.Thewissen’s website are public access, but the source must be identified immediately near the place where it is used (i.e., on the same webpage, or in the caption of the figure used).

Information taken from a source other than The Thewissen Lab will be cited under the title.

All information compiled by Sharon Green

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# Whale Ancestors

Scientists have long known that cetaceans (whales, dolphins, and porpoises) descended from four-footed land mammals.  Cetaceans still have some features of land mammals; they use lungs to breathe air and give birth to young that are nursed by milk produced by the mother.  Modern cetaceans cannot live on land, and look very different from land mammals in most respects.

Cetaceans evolved rapidly, and the entire transition from land mammal to obligate marine whale took less than 8 million years.  These Eocene cetaceans are often called archaeocetes, and they can be divided into six families: [Pakicetidae](http://www.neoucom.edu/DEPTS/ANAT/Thewissen/whale_origins/whales/Pakicetid.html), [Ambulocetidae](http://www.neoucom.edu/DEPTS/ANAT/Thewissen/whale_origins/whales/Ambulocet.html), [Remingtonocetidae](http://www.neoucom.edu/DEPTS/ANAT/Thewissen/whale_origins/whales/Remi.html), [Protocetidae](http://www.neoucom.edu/DEPTS/ANAT/Thewissen/whale_origins/whales/Protocet.html), [Dorudontidae, and Basilosauridae](http://www.neoucom.edu/DEPTS/ANAT/Thewissen/whale_origins/whales/BasilAndDor.html).  It is only since the 1990’s that relatively complete skeletons of the archaeocetes have been found in abundance and that the transition from land-to-water could be studied in detail.

Until the early years of the 21st century, most paleontologists thought that cetaceans were most closely related to mesonychians (The Mesonychian Hypothesis). Mesonychians are an extinct (Paleocene-Oligocene) group of hoofed mammals from the Northern Hemisphere. They varied in size from that of a weasel to a grizzly bear, and may have eaten carrion or meat. Unlike paleontologists, most scientists studying DNA were of a different opinion. They considered hippopotamids as the closest relatives to cetaceans (The Hippopotamid Hypothesis). Hippopotamids (including the recent Hippo and the Pygmy Hippo) are included in a group of mammals called even-toed ungulates or artiodactyls. Other artiodactyls are: pigs, peccaries, camels, llamas, giraffes, deer, goats, sheep, cattle, and antelopes.

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| http://www.neoucom.edu/DEPTS/ANAT/Thewissen/whale_origins/whales/Images/mesonychian.gif | Skeleton of a mesonychian. |

Dr. Thewissen’s website <http://140.220.1.9/DEPTS/ANAT/whaleorigins.htm>

**Pakicetidae   
The First Whales**

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| http://www.calaveras.k12.ca.us/07%20Schools/TMS/krikkers/Evolution/Resources%20for%20whale%20data%20table/Pakice9.jpg |
| A reconstruction of *Pakicetus*, based on the skeletons below.  This reconstruction can be used freely, but this statement has to be added to its caption:  Illustration by Carl Buell, and taken from <http://www.neoucom.edu/Depts/Anat/Thewissen/whale_origins/whales/Pakicetid.html>. |

Pakicetids were the first cetaceans, their fossils are only found in [northern Pakistan](http://www.neoucom.edu/DEPTS/ANAT/Thewissen/Pakistan.html) and [western India](http://www.neoucom.edu/DEPTS/ANAT/Thewissen/India.html), and the best fossils are from a locality in the Kala Chitta Hills in Punjab, Pakistan. The Indian subcontinent is probably the region where cetaceans originated. Pakicetids did not look like whales at all, and resembled land mammals. However, the skulls of pakicetids have an ear region that is highly unusual in shape, and only resembles that of modern and fossil whales. These features are diagnostic for cetaceans, they are found in all cetaceans, and in no other animals. These features are main why pakicetids are considered whales. In many other features, pakicetids are also similar to some whales, but those features are not shared by all whales. An example of the latter is the dentition. Pakiceid teeth look a lot like those of fossil whales, but are unlike those of modern whales. Pakicetids did not live in the sea. The rocks in which their fossils are preserved indicate that the bones were buried in a shallow stream, and that the climate was hot and dry. It is likely that pakicetids waded in these streams. Their bones are unusually thick, possibly an adaptation to make the animal heavier counteracting the buoyancy of the

water

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| Photograph (above) of bones of *Pakicetus* (large animal) and *Ichthyolestes* (small animal), (from the Thewissen website: <http://140.220.1.9/DEPTS/ANAT/Thewissen/publ.html>) and a line drawing of the same skeletons.  The hammer indicates the size of the skeletons, and shows that *Pakicetus* was approximately as large as a wolf, and *Ichthyolestes* is as large as a fox. All pictures on Dr.Thewissen’s website are public access, but the source must be identified immediately near the place where it is used |

The family Pakicetidae (pakicetids in English) consists of three genera, *Pakicetus*, *Nalacetus*, and *Ichthyolestes*. Of these, *Pakicetus* was the largest, and *Ichthyolestes* the smallest. In overall shape, these three are not very different. The skeleton of pakicetids was described by Thewissen et al. (2001). In evolution, pakicetids were followed by [ambulocetids](http://www.neoucom.edu/DEPTS/ANAT/Thewissen/whale_origins/whales/Ambulocet.html" \o "Ambulocetids).

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| C:\Users\Sharon\Documents\Kenan\Whale Origins P_files\HANS1.jpg | The skulls of two pakicetid whales flank the skull of a modern coyote ( *Ichthyolestes*on the left, *Pakicetus*on the right). These skulls were described by Thewissen et al. (2001). |

Pakicetid fossils were important in determining what whales were related to, and they were used to rebuke the idea that whales were closely related to an extinct group of hoofed mammals called mesonychians. These fossils confirmed what was already suggested by scientists studying the DNA of modern whales: that whales’ closest relatives are even-toed ungulates (artiodactyls, such as pig, hippo, camel, deer, and cows) Current research in the Thewissen lab attempts to determine how sound was transmitted through the pakicetid [ear](http://www.neoucom.edu/DEPTS/ANAT/Thewissen/whale_origins/os/hearing.html) and how pakicetids l[locomoted in water and on land](http://www.neoucom.edu/DEPTS/ANAT/Thewissen/whale_origins/os/Locomotion.html).   
  
Some publications on pakicetids from our lab:   
Maas, M.C. and J. G. M. Thewissen. 1995. Enamel microstructure of *Pakicetus* (Mammalia: Archaeoceti). Journal of Paleontology, 69:1154-1163.   
Thewissen, J. G. M., and S. T. Hussain. 1998. Systematic review of the Pakicetidae, Early and middle Eocene Cetacea (Mammalia) from Pakistan and India. Bulletin of the Carnegie Museum 34:220-238.   
Thewissen, J. G. M., E.M. Williams, L.J. Roe, and S.T. Hussain. 2001. Skeletons of terrestrial cetaceans and the relationship of whales to artiodactyls. Nature, 413:277-281.

High-resolution versions of these images can be found at URL: <http://www.neoucom.edu/Depts/Anat/Thewissen/publ.html>

# Ambulocetidae  The First Costal Whales

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| http://www.neoucom.edu/DEPTS/ANAT/Thewissen/whale_origins/whales/Images/ambulocetidae.jpg | The skeleton of Ambulocetus natans (approximately 12 feet long)  To see a flesh-and-blood reconstruction go to [Carl Buell's painting](http://www.neoucom.edu/DEPTS/ANAT/Thewissen/whale_origins/whales/CarlBuellPainting.html). |

Ambulocetids are large, powerful animals, with short limbs, but big feet, and a strong tail. They are only found in northern Pakistan and western India in rocks that indicate that the environment was nearshore marine and swampy. These rocks cannot be dated with great accuracy, but they are clearly younger than the sediments in which [pakicetids](http://www.neoucom.edu/DEPTS/ANAT/Thewissen/whale_origins/whales/Pakicetid.html) are found. Although ambulocetids could walk on land as well as swim, it is clear that they were not fast on either terrain. The post-cranial skeleton of ambulocetids is well known thanks to the discovery of a very complete skeleton of the species Ambulocetus natans. The name of this whale means “the walking and swimming whale,” and indicates that it was amphibious. Ambulocetus was first described by Thewissen et al. (1994), and later, in more detail, by Thewissen et al. (1996)

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| http://www.neoucom.edu/DEPTS/ANAT/Thewissen/whale_origins/whales/Images/AmbulocetusBonesPhoto.jpg | The bones of Ambulocetus natans arranged in its approximate body shape. These are the original fossils, all pertaining to a single individual. Note hammer for scale. |

Three genera of whales make up the family Ambulocetidae: Ambulocetus, Gandakasia, and Himalayacetus. Gandakasiaand Himalayacetusare only known from a single lower jaw fragment each, and cannot be compared in detail with Ambulocetus.

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| http://www.neoucom.edu/DEPTS/ANAT/Thewissen/whale_origins/whales/Images/Ambulomouth.gif | Head of *Ambulocetus* as drawn by Marion Lipka |

Some publications on ambulocetids:   
Thewissen, J.G.M., S.T. Hussain, and M. Arif. 1994. Fossil evidence for the origin of aquatic locomotion in archaeocete whales. Science 263:210-212.   
Thewissen, J.G.M., S. I. Madar, and S. T. Hussain. 1996. Ambulocetus natans, an Eocene cetacean (Mammalia) from Pakistan. Courier Forschungs-Institut Senckenberg, 190:1-86.   
Thewissen, J.G.M., and F. E. Fish. 1997. Locomotor evolution in the earliest cetaceans: functional model, modern analogues, and paleontological evidence. Paleobiology 23:482-490.   
Madar, S.I., J. G. M. Thewissen, and S. T. Hussain. 2002. Additional holotype remains of Ambulocetus natans (Cetacea, Ambulocetidae), and their implications for locomotion in early whales. Journal of Vertebrate Paleontology 22:405-422.

All pictures on Dr.Thewissen’s website are public access, but the source must be identified immediately near the place where it is used (i.e., on the same webpage, or in the caption of the figure used).

***Rodhocetus***

Reprinted from the website of Dr. PHILIP D. GINGERICH

<http://www-personal.umich.edu/~gingeric/PDGwhales/Whales.htm>

A.B.: Princeton University 1968  
M.Phil.: Yale University 1972  
Ph.D.: Yale University 1974

Ermine Cowles Case Collegiate Professor of Paleontology  
Professor of [Geological Sciences](http://www.geo.lsa.umich.edu/)  
Professor of [Biology](http://www.eeb.lsa.umich.edu/default.asp)  
Professor of [Anthropology](http://www.lsa.umich.edu/anthro/index.html)  
Director, [Museum of Paleontology](http://www.paleontology.lsa.umich.edu/) — [The University of Michigan](http://www.umich.edu/)

The mammalian order Cetacea is divided into three suborders: (1) Oligocene to Recent Odontoceti or 'toothed whales'— living today; (2) Oligocene to Recent Mysticeti or 'baleen whales'— living today; and (3) older and more primitive Eocene Archaeoceti or 'archaic whales'— which evolved from land mammals and gave rise to later odontocetes and mysticetes. My research on the origin and early evolution of whales is focused on archaeocetes. I have been fortunate to work with many colleagues on this in Egypt, Jordan, Pakistan, and India, (see co-authors in the publication list below). The stages of early whale evolution that we have documented are shown here in Figure 1. We have found and collected virtually complete skeletons of middle-to-late Eocene Basilosauridae (Dorudon and Basilosaurus), exceptionally complete skeletons of middle Eocene Protocetidae (especially Rodhocetus and Artiocetus), and a partial skull of earliest middle Eocene Pakicetidae (Pakicetus). Recovery of diagnostic ankle bones in the skeletons of primitive protocetids during our field work in Pakistan in 2000 confirmed their derivation from Artiodactyla (the mammalian order including cows, deer, hippos, etc.), and showed convincingly that whales did not originate from mesonychid condylarths as Van Valen hypothesized (and we had expected).

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| http://www-personal.umich.edu/~gingeric/PDGwhales/PDGanthtodoruskel.jpgFigure 1. Skeletons of the archaeocetes Dorudon atrox and Rodhocetus balochistanensis compared to that of Elomeryx armatus, which is here taken as a model for the extinct group of artiodactyls (Anthracotheriidae, s.l.) that we now think may have given rise to archaic whales. Pakicetushas a distinctive skull and lower jaw, but is not demonstrably different from early protocetids postcranially. Note changes in body proportions and elongation of feet for foot-powered swimming in Rodhocetus, then later reduction of the hind limbs and feet as the tail-powered swimming of modern cetaceans evolved in Dorudon.  A. Elomeryx drawing from W. B. Scott, first published in 1894. B. Pakicetus skull from Gingerich et al. (1983). Terrestrial interpretation is pure speculation: what little is known of the skeleton resembles Rodhocetus.C. Rodhocetus skeletal reconstruction from Gingerich et al. (2001). D. Dorudon skeletal reconstruction from Gingerich and Uhen (1996). Figure may be reproduced for non-profit educational use. |

Field Work in Pakistan again (1991-present)

Our first important find when we returned to Pakistan in the 1990s was an unusually complete skeleton that we named Rodhocetus kasranii (Gingerich et al., 1994). This came from the flank of the Rodho ('bald') part of the Zinda Pir anticlinorium on the east side of the Sulaiman Range. Rodhocetus is interesting and important in having a large pelvis connected to the vertebral column, but the sacral vertebrae in this connection are no longer completely fused, and Rodhocetus kasranii appears to be an intermediate showing how the sacrum became disarticulated to make the back flexible as it is in tail-powered swimmers like Dorudon and later whales. The femur is preserved on one side of the original Rodhocetus kasranii skeleton, but with this exception, the forelimbs are missing, the hind limbs are missing, and most of the tail is missing.

Continued work on the east side of the Sulaiman Range in Pakistan yielded many additional archaeocetes, including Takracetus simus, Gaviacetus razai, Dalanistes ahmedi, Qaisracetus arifi, Andrewsiphius sloani, Babiacetus indicus, Basilosaurus drazindai, and Basiloterus hussaini (Gingerich et al., 1995, 1997, 2001). However, these specimens generally lack forelimbs, hind limbs, and tails. Our inability to find limbs and tails was so frustrating that in 2000 we moved from this area, where fossil-bearing strata are beautifully exposed, to the west side of the Sulaiman Range in Balochistan Province. Previously, no fossil whales had been found on the west side of the Sulaiman Range, and the strata that interest us are not nearly so well exposed there (Fig. 6).

We have had very good luck finding well-preserved archaeocetes on the west side of the Sulaiman Range in Pakistan. The most notable were described and named Artiocetus clavis and Rodhocetus balochistanensis (Figs. 7-8; see Gingerich et al., 2001). These are the first early archaeocetes to preserve ankle bones in association with skulls and skeletons, and the first to show that early whales had distinctively artiodactyl-like ankles. Thus the earlier idea that whales evolved from mesonychid condylarths is no longer tenable and we expect that the ancestor was instead something like an anthracotheriid artiodactyl (e.g., Elomeryx in Fig. 1). From the point of view of the fossil record, the 'sister-group' relationship of whales and hippos promoted by molecular phylogeneticists is now plausible, though still tenuous and unproven.

Combining what we know of the skeletons of Rodhocetus kasranii and Rodhocetus balochistanensis, it is possible to make a composite restoration of the latter, which is the reconstruction shown in Figure 1C.

**Basilosaurids and Dorudontids**

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| http://www.neoucom.edu/DEPTS/ANAT/Thewissen/whale_origins/whales/Images/whalebones1.jpg | Reconstruction of *Basilosaurus cetoides*(top) and *Zygorhiza kochii* (not to scale). There are several inaccuracies in this old reconstruction (Kellogg, 1936), such as the exact number of vertebrae and the shape of the forelimbs. Discovery of new specimens has made it possible to correct these. |
| http://www.neoucom.edu/DEPTS/ANAT/Thewissen/whale_origins/whales/Images/whalebones2.jpg |

Basilosaurids and dorudontids lived in the late Eocene, approximately 35 and 41 million years ago. They are mainly known from the eastern United States and from Egypt, but were probably worldwide in their distribution. Basilosaurids were enormous (possibly up to 60 feet long) and had long snake-like bodies. They had a tailfluke, but they probably swam using sinuous movements with their bodies. it is not clear whether that was the main propulsive organ. Fossilized stomach contents in one *Basilosaurus* indicates that it ate fish, including sharks. Dorudontids are closely related to basilosaurids but were proportionally more like dolphins. They probably swam using their fluke. Both basilosaurids and dorudontids had complete hindlimbs, that included a mobile knee and several toes. However these extremities were tiny, so small that they were certainly not important in aquatic propulsion.

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| http://www.neoucom.edu/DEPTS/ANAT/Thewissen/whale_origins/whales/Images/dorudontid.jpg | http://www.neoucom.edu/DEPTS/ANAT/Thewissen/whale_origins/whales/Images/dorudontid_2.jpg |
| Two skull views of a dorudontid in the Natural History Museum of London | |

For more information on basilosaurids and dorudontids, visit <http://www.archaeocete.org/>

Further Reading:

All pictures on Dr.Thewissen’s website are public access, but the source must be identified immediately near the place where it is used (i.e., on the same webpage, or in the caption of the figure used).