Whales: From Land-Dwelling Ungulates to Giants of the Seas

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Abstract *This lecture, held on June 21, 2023, as part of the lecture series "Eine Uni – Ein Buch: 'The Whale Rider'. Eine Erkundung Neuseelands mit Witi Ihimaeras Roman", is about whales (Cetacea), which are an order of aquatic mammals that have secondarily shifted their habitat from the mainland back into the sea. In the Paleogene period, more precisely in the Eocene epoch, over 50 million years ago, the evolution of whales began from small, land-living ungulates about the size of a larger dog to today's giants of the seas weighing up to 200 tons. This development took place on the coasts of the Tethys Ocean, which at that time still lay between India and Asia, and is clearly supported by both morphological and genetic evidence. The land-sea transition is excellently documented by fossils from the Paleogene sedimentary deposits that are now exposed in the Indo-Pakistan region. Herein I will explain this evolution of whales and the complex morphological (reduction and transformation of limbs to fins, changes in bone structure) and physiological adaptations (inner ear modification for underwater hearing, modified lung breathing with blowhole, insulating fat layer and cardiovascular blood circulation system to minimise heat loss) that were necessary for this fundamental habitat change. I will also discuss how the evolution of whales is closely linked to plate tectonic, climatic and oceanographic changes through time. The first archaic whales still had fur and four limbs, and although they had a semiaquatic lifestyle, they were still able to walk on land. Modern whales evolved from these archaic whales, first the toothed whales and then the plankton-eating baleen whales, which produced the largest animals that have ever lived on our planet.*

Keywords *Cetacea; ungulates; toothed whales; baleen whales; evolution; fossil bones*

This lecture is about the evolutionary history of whales. Whales are mammals, and their ancestors once stood on solid ground, just as we do today. But that was over 50 million years ago, and herein I would like to explain the evolution of whales from land-dwelling ungulates to giants of the seas.

The entire lecture series is about the book *The Whale Rider* (1987) by Witi Ihimaera and perspectives from different scientific disciplines on the content of the book. As a geoscientist and paleontologist, I have a natural science perspective on the whole story: a whale rider can only exist if there are whales, because the whale is needed as a means of transportation for the whale rider. Whales themselves have a very long history and lived many millions of years before the Māori. According to Māori legend, without the whale, *Paikea*, the ancestor of the Māori, would not have come ashore in New Zealand on the back of a whale. The whale that *Paikea* presumably rode was probably a southern humpback whale. This is the simple connection to *The Whale Rider*: without whales, there would be no whale riding, and thus, according to Māori tradition, the settlement of New Zealand would not have been possible.

How did we find the whale, or rather, how did the whale get to us? Whales (Cetacea) are an order of aquatic mammals that have shifted their habitat from the mainland back to the sea. The evolutionary path to this point is long and complex. Since their development in the Cambrian period over 520 million years ago, vertebrates lived exclusively in the oceans until the Devonian period. Then, about 380 million years ago, in the Middle Devonian epoch, vertebrates made their way onto land and conquered the mainland as their new habitat. Aquatic fish first evolved into semi-aquatic amphibians, then into land-dwelling amniotes, a clade of four-legged animals including reptiles, birds and mammals, which can reproduce independent of water, some of which, however, later returned to the sea in several evolutionary lineages, including whales. However, whales were not the first. There were a whole series of vertebrates that returned to the sea from land as secondary aquatic amniotes. The transition of vertebrates to land required major morphological and physiological changes: breathing air through lungs instead of gills, moving on land using front and hind limbs that had been transformed from fins, supporting body weight against gravity, and other adaptations. On the way back from land to sea, many of these changes had to be reversed. For instance, after the largest mass extinction in Earth's history, 252 million years ago at the end of the Permian period, land-dwelling reptiles returned to the sea and evolved into marine reptiles such as ichthyosaurs. In the early Mesozoic era, long before whales, the oceans looked something like this: Ichthyosaurs and other marine reptiles such as plesiosaurs were top predators in the sea and fed mainly on ammonites and other cephalopods. The ichthyosaurs grew to gigantic sizes of up to 20 meters in length quite quickly in the early Triassic, within 3 million years after the end-Permian mass extinction (Sander et al. 2021). The whales, on the other hand, took almost 50 million years to reach such sizes in the Pliocene-Pleistocene after their first occurrence in the early Eocene (Sander et al. 2021). In the course of Earth's history, terrestrial vertebrates have returned to the sea several times independently of each other, such as sea turtles and whales – we will discuss this for the latter in more detail later – as well as other mammal groups such as seals and sea cows, but also birds such as penguins (Kelley and Peynson 2019). Whales evolved in the early Paleogene period, about 10 million years after the mass extinction 66 million years ago caused by the

Chicxulub meteorite impact, which wiped out the dinosaurs on land at the end of the Cretaceous period, but also the large marine reptiles in the oceans. This freed up ecological niches of apex predators in the sea, which were later occupied by whales.

How did whales return from land to the sea and become such giants, the largest animals ever on planet Earth? The evolution of whales began around 54 million years ago in the early Eocene. As geoscientists, we have a long timeline stretching back to the formation of the Earth 4.56 billion years ago and are comfortable dealing with such geological time scales. However, most people find it difficult to imagine. They may be able to calculate in human generations (30 years = one generation), but 54 million years is a very, very long time. Humans did not even exist then; our species has only been around for about 300,000 years, and the oldest hominids for a maximum of 7 million years.

In the Eocene epoch 54 million years ago, the first archaic whales began to develop, and in the Oligocene epoch about 34 million years ago, these evolved into the whales we know today, the toothed whales (Odontoceti) and the baleen whales (Mysticeti), which gave rise to the giants of the seas such as the fin whale and blue whale (Fordyce 1980; Thewissen and Williams 2002; Goldbogen et al. 2019). Here, I want to present what we know about the evolution of whales and how researchers have arrived at these conclusions. Very early on, it was assumed, including by Charles Darwin, that whales might have descended from land animals, since almost all other mammals live on land. The first mammals developed in the Upper Triassic epoch over 200 million years ago, but at that time they were still very small, about the size of rats, and lived in the shadow of the dinosaurs. It was only after the extinction of the dinosaurs at the end of the Cretaceous period, 66 million years ago, that mammals underwent a size increase and strong radiation into different orders, including whales, and for the first time, land-dwelling mammals reached hippopotamus size in the Eocene. Whales, along with sea cows, seals and sea otters, are the only group of secondary aquatic mammals that have returned to the sea (Kelley and Peynson 2019). All other mammals are land animals. This led to the assumption that whales may have descended from land animals, but until a few decades ago, this had not been well proven by fossils.

There is now a very good fossil record for the evolution of whales, which clearly shows that whales are descended from land-dwelling ungulates (Thewissen 1998; Zimmer 1999; Thewissen and Williams 2002; Gingerich 2012). Based on these fossil finds, it is possible to reconstruct an early ancestor of whales, *Indohyus*, and how it might have looked like (Thewissen et al. 2007; Fig. 1). Whales are descended from ungulates, however, not from perissodactyls (odd-toed ungulate) but rather from artiodactyls (even-toed ungulates) (Gingerich et al. 2001; Thewissen et al. 2001).

Fig. 1: Whales are descended from land-living, quadruped, wolf-sized, even-toed ungulates. Photo simulation of Indohyus, *an early land-dwelling hoofed ancestor that lived in the Indian region in the Eocene around 54 million years ago.*

Source: credit Roman Uchytel, https://uchytel.com/Indohius

It is fascinating that whales still lived on land over 54 million years ago. Based on fossil finds of early whales made in the Indo-Pakistan as well as Egyptian region, paleontologists have been able to trace and document the transition from land-dwelling ungulates to sea-dwelling whales (Thewissen 1998; Zimmer 1999; Gingerich et al. 1983 and 2001; Thewissen et al. 2001 and 2007; Thewissen and Williams 2002). The morphology of the limb bones, especially the astragalus or double-pulley ankle bone, which is part of the ankle joint and characteristic of hoofed animals, shows that whales were indeed originally hoofed animals. This becomes apparent when comparing the morphology of the astragalus of a modern antelope, a pronghorn, and fossil astragalus bones of early whales (Fig. 2).

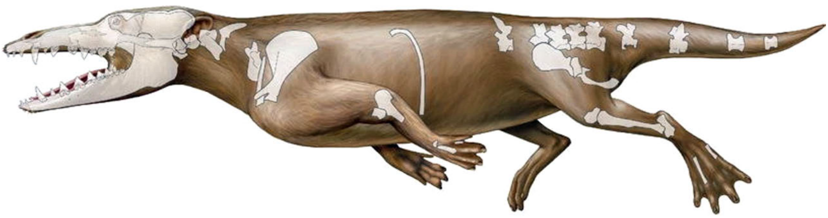
The characteristic feature of the astragalus is that it has joints at both ends of the ankle bone, which is unique to ungulates. This allows the joint surfaces of the foot and lower leg to move against each other during running movements. Early whales, such as the *Pakicetus* from the middle Eocene, also had such a double-pulley astragalus, which proves their relationship to ungulates (Gingerich et al. 2001; Fig. 3).

Pakicetus (Fig. 3) is named after Pakistan, where it was found and where this early whale lived as a semi-aquatic, probably foot-powered swimmer between 54 and 48 million years ago (Gingerich et al. 1983 and 2001; Gingerich 2012). However, it is not only the presence of a double-pulley astragalus that confirms the hoofed animal relationship of whales; this is also confirmed independently by genetic studies of modern whales and hoofed animals, which also prove a close phylogenetic relationship (Gatesy et al. 2013). This means that we have clear evidence, both genetically and morphologically, that whales are descended from land-dwelling even-toed ungulates.

Fig. 2: Photos of two fossil astragalus bones of early primitive whales from the middle Eocene, Rodhocetus balochistanensis *(left) and* Artiocetus clavis *(right), compared to the astragalus bone of a modern pronghorn (center). All three bones have the joint characteristic of ungulates at both ends of the ankle bone, thus a double-pulley ankle bone. Scale in cm.*

Source: Gingerich 2012, Fig. 10, p. 319

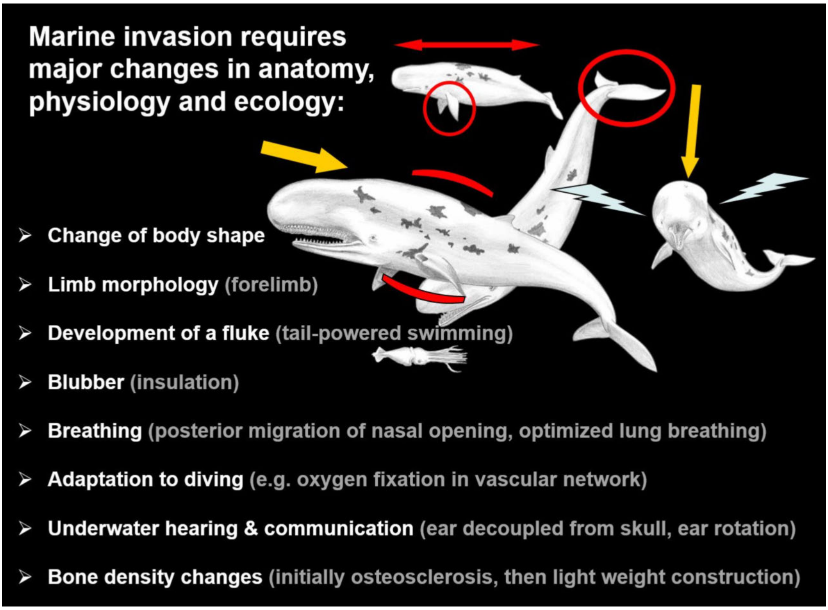
Fig. 3: Reconstruction of the first true whale, Pakicetus, *which lived about 50 million years ago in the Tethys Sea in an area that is now India and Pakistan*



Source: by John Klausmeyer of the University of Michigan Exhibit Museum in Gingerich 2012, Fig. 5, p. 314

How did a hoofed animal living on land return to the sea? This required a whole series of morphological, physiological, and ecological changes to be able to live permanently in water (Fig. 4). The body shape must be adapted, and the front limbs must be transformed into flippers, while the tail is converted into a tail fin, or fluke, to enable energy-efficient swimming to propel themselves forward. Furthermore, the skull shape changed, which was mainly controlled by diet and echolocation or filter feeding. As warm-blooded animals, whales have a body temperature of 36 °C, plus or minus two degrees, which they maintain through a layer of fat that insulates their bodies so that they do not cool down in the water. In addition, they have developed a sophisticated cardiovascular blood circulation system to minimise heat loss to the surrounding water. Since the limbs are cooler than the core of the body due to their large surface area, body heat is partially recovered via counter-flow blood circulation patterns and pathways, and heat loss is reduced by reducing blood flow to the limbs. They needed to develop an osmoregulatory system to deal with the excess salt load ingested from ambient seawater. Breathing must also be adapted. As lung breathers, whales must repeatedly surface to breathe, expelling used air at high pressure through the nostril located on the top of their head, the blowhole, and quickly inhaling fresh air. In addition, the whale's body must also withstand the hydrostatic pressure of the surrounding water, and oxygen must be kept dissolved in the blood, as whales can dive very deep. The record holder is the sperm whale, which can dive up to 3,000 meters deep and stay underwater for up to 45 minutes without breathing while hunting mainly giant squids and other deep-sea fish. Another very important adaptation to life in water is the development of underwater hearing, as sound waves travel almost five times faster underwater than in air. To achieve this, the inner ear of whales has adapted morphologically and is decoupled from the skull to enable oriented hearing underwater. This allows whales to locate their prey and orient themselves underwater. The corresponding inner ear morphology is a characteristic feature of whales.

Fig. 4: Adaptations in the body plan and metabolism of whales that are necessary for the transition from life on land to life in water



Source: modified, personal communication with Oliver Hampe

The skeleton of whales has also been adapted to life in water, and bone density has been reduced. Today's whales have relatively spongy bones, which means they are lightweight, unlike land animals, they do not have to carry their own body weight against gravity due to buoyancy in water. This is why whales suffocate agonisingly after beaching themselves on the coast, as their body weight compresses their lungs. However, the ancestor of the primitive whales that entered the water often had rather heavy limb bones because, like today's hippopotamuses, it walked on the bottom of the water (Thewissen et al. 2007). This required dense and heavy bones with a thick bone cortex, which enabled them to stay underwater in an energy-efficient manner. Thus, numerous morphological and biological adaptations are essential for survival in aquatic environments.

Where did the evolution of early whales take place? This was linked to the right environmental setting, which was controlled by plate tectonics. India, as a continent, split off from the large southern continent of Gondwana and drifted northward across the equator over many millions of years before it collided with Asia, closing the Tethys Ocean and forming the Himalayas. Just before this continent-continent collision occurred, the evolution of early whales took place between 54 and 40 million years ago in the coastal and marine areas of the Tethys Sea between India and Asia. There were various aquatic habitats, such as rivers, estuaries, and shallow shelf sea areas, where the archaic whales developed. During the Eocene epoch, whales migrated from the mainland back to the sea.

Fossil finds of early whales, such as *Pakicetus* and *Ambulocetus*, come from the Indo-Pakistan region (Gingerich et al. 1983; Thewissen et al. 1994). These early whales (Archaeoceti) provide excellent evidence of the evolution from four-legged, land-dwelling, even-toed ungulates to whales that are completely adapted to life in the sea. The front limbs are transformed into fins, the hind limbs, which are no longer needed, are reduced, and the tail is transformed into a tail fin, the fluke, which enables energy-efficient propulsion. These changes in the whales' body plan took place in a geologically short period of 10 to 15 million years, over a few tens of thousands of generations. Today's whales have only rudimentary hind limbs, while the primitive whales still had small legs with the characteristic ankle bone, which proves their ancestry from hoofed animals.

The body structure and way of life of these early whales or whale ancestors are reconstructed on the basis of fossil finds. *Indohyus*, named after India, is not yet a true whale, but represents an extinct sister group of whales (Fig. 1). It was a semi-aquatic animal that walked or waded at the bottom of water bodies, probably in the fresh water of lakes or rivers (Thewissen et al. 2007). The fossil skull of *Indohyus* has a characteristic inner ear with a relatively massive bone covering, but it is not yet completely isolated from the skull, as is typical for true whales. Only in true whales is the inner ear completely separated from the skull and connected to it only by soft tissue structures. This enables whales to hear while orienting themselves in the water. Land-dwelling vertebrates cannot do this because sound is reflected by the skull bone and causes it to vibrate. You can notice this when you cover your ears; you can still hear yourself when you speak. Another adaptation to the aquatic lifestyle of early whales can be seen in the bone microstructure of the bone wall of long bones, which is much thicker than that of land-dwelling vertebrates (Thewissen et al. 2007). This is called pachyostosis, where the bone is made denser so that the animals can stay underwater with little energy expenditure, similar to how a diver's lead belt allows them to dive easily. Sea cows also have this, but in their ribs.

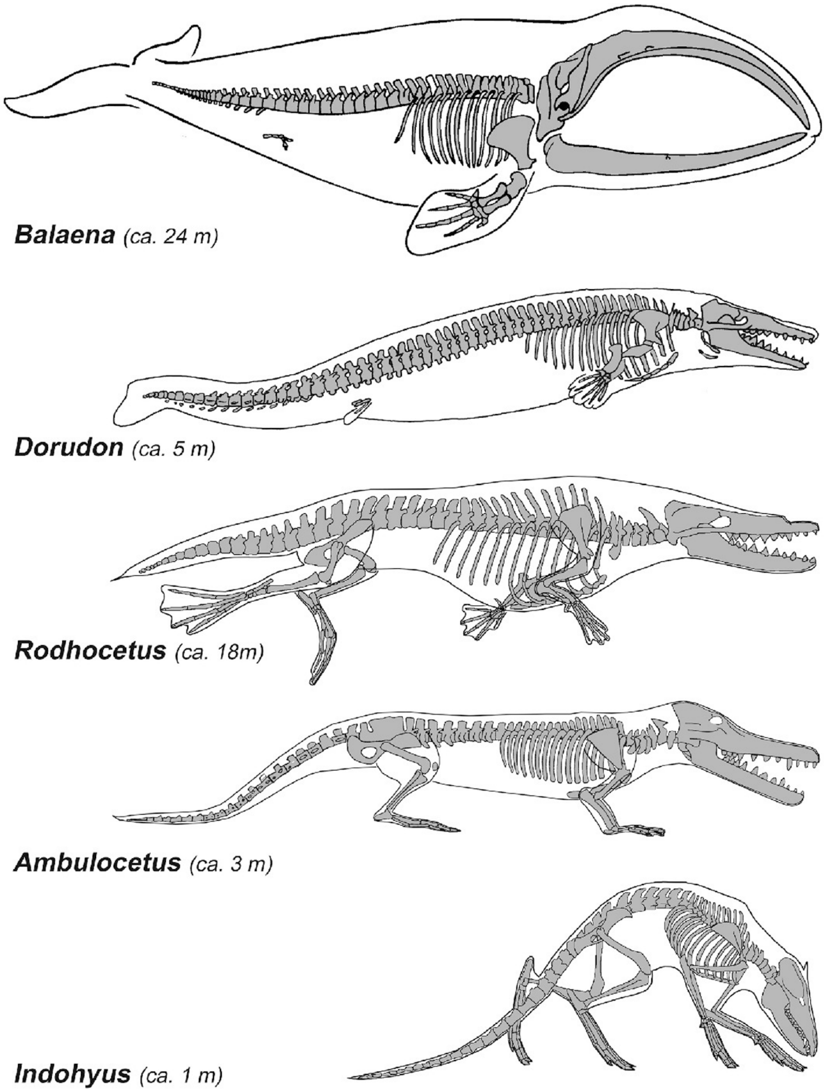
To characterise the lifestyle and habitat of early whales, the chemical composition, especially the oxygen isotope composition, of their bones and teeth can be analyzed (Roe et al. 1998; Clementz et al. 2006; Thewissen et al. 2007). These contain characteristic isotope signatures from their lifetime, which allow us to reconstruct whether the whales lived in fresh water or seawater from their fossilised skeletal remains. Low ratios of the heavy oxygen isotope ^{18}O to the light oxygen isotope ^{16}O are characteristic of freshwater and less evaporation stress, to which animals living in water are less exposed than animals living on land (Roe et al. 1998; Clementz and Koch 2001). Land animals sweat and therefore lose relatively more light oxygen than heavy oxygen via water vapour. In addition, their oxygen isotopes vary more than those of aquatic vertebrates because they are more exposed to evaporation stress (Clementz and Koch 2001). In addition, the carbon isotopes in teeth provide information about the diet of whales, e.g., whether they ate mainly land or aquatic plants. It appears that early whales ate different food than their sister group, *Indohyus* (Thewissen et al. 2007). Overall, the stable isotope data indicate an aquatic lifestyle for this early whale sister taxon, but it may still have obtained its food on land, while whales originated from an *Indohyus*-like ancestor, and these early whales consumed a diet of aquatic prey (Clementz et al. 2006; Thewissen et al. 2007).

Then came the evolutionary step to the first whales. *Pakicetus* is considered the first true whale and lived in the early to middle Eocene (Gingerich et al. 1983). Fossils of various individuals, such as skulls, teeth, and bones, have been found. *Pakicetus* still had fur, massive leg bones and, most importantly, an inner ear that was separated from the skull. This shows that it was able to hear underwater. However, it used paddle-like swimming and retained the ability to walk on land.

Over the course of evolution, the archaic whale *Pakicetus* developed into larger forms that were even more adapted to aquatic life, such as the three- to four-meter-long *Ambulocetus* (Fig. 5; Thewissen et al. 1994). *Ambulocetus* was an ambush hunter preying on other land-dwelling animals in the coastal region of Indo-Pakistan approximately 48 million years ago. However, as an aquatic carnivore, it also preyed upon fish.

The first fully marine whales, which were already more similar to today's whales, developed in the late Eocene. Fossil remains have been found in the El Fayoum Oasis in Egypt, where whales are found in the desert today. One such early toothed whale was *Dorudon*, which had already developed a fluke and whose hind limbs were severely stunted because they were no longer used (Fig. 5). These Dorudontidae were up to five meters long and belonged to the Basilosauridae family, from which modern whales later evolved. These basilosaurids never returned to land, were fish eaters, and had strong serrated teeth. Forty million years ago, they evolved into the first very large whales, up to 20 meters in length, such as *Basilosaurus isis*, the largest representative from Egypt (Voss et al. 2019; Fig. 5). Those who are linguistically inclined will surely wonder why *-saurus* (Greek *sauros*), meaning lizard, appears at the end of the name *Basilosaurus*. This was a taxonomic misidentification when this ancient whale was first named; it was previously mistakenly interpreted as a sea snake, hence the name *Basilosaurus*. Of course, it is a mammal, but the original name takes precedence in nomenclature and therefore remains in use. *Basilosaurus* and *Dorudon* were the top predators in the Eocene ocean and took on the role of marine reptiles that became extinct at the end of the Cretaceous period.

Fig. 5: Evolution of the skeleton and bauplan of early whales starting from the sister taxon Indohyus *via the first true whale,* Pakicetus *(not shown here but see Fig. 3),* Ambulocetus *and* Rodhocetus, *which could still walk on land, to fully marine whales with greatly reduced hind limbs, such as* Dorudon. *From the latter modern toothed and baleen whales descended. Fossils of the first three taxa were found in the Indo-Pakistan realm, whereas* Dorudon *was found in the Fayoum area of Egypt.*



Source: by S. Gemballa in Moormann and Scheersoi 2024, Fig. 29.4, p. 523

Fig. 6: Bizarre Eocene sandstone rocks shaped by wind and water erosion in the desert with tafoni weathering structures on their surface, UNESCO World Heritage Site Wadi Al-Hitan, Valley of the Whales, El-Fayoum Oasis, Egypt

Source: own photograph

The evolution of these early full marine whales is ironically well documented by whale fossils found in the desert in Egypt, UNESCO World Heritage Site Wadi Al-Hitan, the Valley of Whales (Helmy et al. 2023; Ibrahim et al. 2025). This is a fantastic landscape and a unique geological setting near the El-Fayoum Oasis in the northeastern Sahara. Around 40 million years ago, the archaic whales *Dorudon* and *Basilosaurus* lived alongside many other marine organisms in the Tethys Sea. But how did these whales get into the desert? Plate tectonics, sea level fluctuations, climate changes, and erosion processes all played or still do play a role. In the Eocene epoch, 40 million years ago, northern Africa was flooded by a tropical, shallow epicontinental sea, part of the Tethys, the precursor to the Mediterranean Sea. These archaic whales swam around there, and their carcasses washed up in shallow lagoons/coastal areas (Ibrahim et al. 2025). Later, the sea receded, and the marine sands and whale bones solidified to fossil-bearing sandstone layers that were later uplifted by tectonic processes, exposing the whale bones through erosion by wind and water. Today, they can thus be found in the dry desert. Bizarre weathering forms of the Eocene sandstone formations characterise this magnificent landscape (Fig. 6), which contains many significant fossils of early whales, including hundreds of whale skeletons, which is why this region has been designated a World Heritage Site. The presence of trace fossils such as fossilised traces of burrows from bivalves and crustaceans (Fig. 7; Gee et al. 2019) indicates that there used to be very shallow seawater in the coastal area of a tropical sea where the whale carcasses were beached (Ibrahim et al. 2025). Today, the fossil bones and skeletons of these whales, which have been exposed by erosion from the marine sandstone rock, can be found in the desert sand because the sea retreated and the climate in the Sahara area has become much drier in recent Earth history, forming this vast desert. Thus, now many whale fossils can be found on the surface in the desert exposed by erosion such as the vertebral spine of a *Basilosaurus* with all its vertebrae or tooth impressions of these large, ancient toothed whales, such as *Dorudon* and *Basilosaurus* (Fig. 8). There are also entire skeletons in excellent condition and some even with stomach contents, indicating that *Basilosaurus isis* fed on sympatric smaller whales such as juvenile *Dorudon atrox* and large fishes (Voss et al. 2019).

Fig. 7: Middle Eocene bioturbated sandstone rocks with trace fossils of fossilised crustacean or bivalve burrows (Gee et al. 2019), UNESCO World Heritage Site Wadi Al-Hitan, Valley of the Whales, El-Fayoum Oasis, Egypt

Source: own photograph

Important representatives of various early whales are shown in Fig. 9 together in a 'family portrait'. The first true whale was *Pakicetus*, which lived in freshwater, was semi-aquatic, but also still land-based (Gingerich et al. 1983; Thewissen et al. 2001).

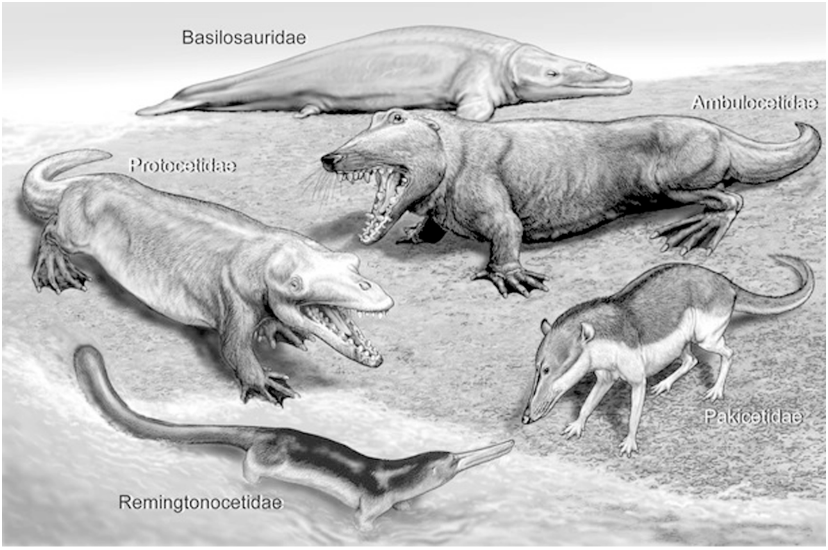
The following primitive whales, such as *Kutchicetus*, *Ambulocetus*, and *Rodhocetus*, lived increasingly aquatic and marine lives. *Dorudon*, depicted like a seal on land (Fig. 9), was one of the first fully marine whales that no longer came ashore (Thewissen and Williams 2002). These basilosaurids were fully adapted to an aquatic lifestyle, but for educational purposes, they are shown together with the other primitive whales. The transition from a land-dwelling hoofed animal to a fully aquatic marine whale took place very quickly in geological terms, within about 10 to 15 million years (Thewissen 1998; Thewissen and Williams 2002). Today's closest living relatives of whales would be hippopotamuses, while the *Indohyus*, which is not yet a true whale and therefore does not belong to the Cetacea, represents the extinct sister group of whales (Thewissen et al., 2007). All the representatives of the primitive whales or Archaeoceti up to the fully marine-adapted *Dorudon* are shown here together (Fig. 9). The subfamily Dorudontidae then gave rise to the modern whales that you know today, i.e., the toothed whales, the Odontoceti, and the baleen whales, the Mysticeti.

Fig. 8: Fossilized skeletons of basilosaurids from the middle Eocene (ca. 40 to 37 million years ago), UNESCO World Heritage Site Valley of the Whales, El-Fayoum Oasis, Egypt. The top two photographs show articulated vertebrae of Basilosaurus, a different view of the same complete skeleton. The bottom ones show impressions of teeth from Basilosaurus in the sandstone and teeth in a lower jaw.

Source: own photographs

During their evolution, whales had to undergo a wide range of morphological and physiological adaptations. These included changes in skull shape related to different feeding modes and prey sizes, as well as shifts in the position of the nose, which moved upward on the skull and became the blowhole in modern whales. Another important innovation, which only appeared in modern toothed whales, was echolocation for locating prey, which, of course, requires not only the ability to hear but also the emission of sound waves. These sound waves emitted by whales are focused by the melon, a special organ made of fat and connective tissue in the head of toothed whales, and their reflection is heard via the lower jaw. Later, baleen whales also developed intraspecific infrasonic communication. Whales have thus developed very complex adaptations for underwater hearing and communication.

Fig. 9: Paleoartistic reconstruction of early Eocene whales (Archaeocetes) that are to different degrees adapted to an aquatic lifestyle. The first fully marine archaeocete, Dorudon, *then gave rise to the modern toothed and baleen whales.*

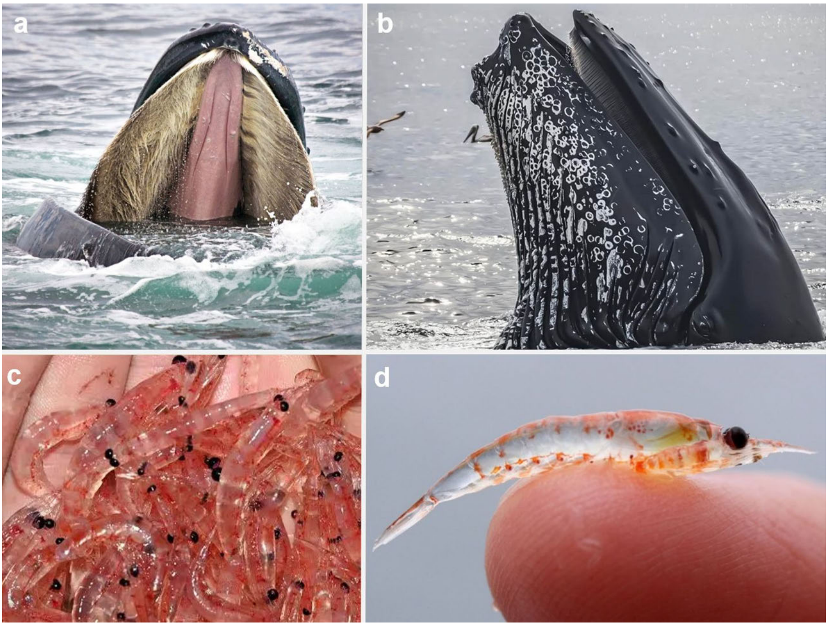


Source: Thewissen et al. 2009, Fig. 27, p. 286, licensed under CC BY 2.0

Finally, we come to the evolution of today's modern whales, which was also influenced by plate tectonic and geological processes. It is no coincidence that modern whales emerged around 35 million years ago, as their emergence is linked to the movement of continental plates and the formation of sea connections and currents (Fordyce 1980; Marx and Fordyce 2015). Both poles were ice-free throughout the Mesozoic era because there was a lot of CO_2 in the atmosphere that had been released from the Earth's mantle through volcanic activity; as a result, it was very warm, and no inland ice could form there. Today, we have reached a man-made level of 430 ppmv (National Oceanic & Atmospheric Administration). Before the industrial era, the CO_2 concentration in the atmosphere was around 280 ppmv, and this concentration has varied only a little over the last 20 million years (DeConto et al. 2008), for instance, between ice ages and interglacials. Before that, the CO_2 content in the Earth's history was significantly higher, and the climate was correspondingly warmer. Climate models show that only when the CO_2 concentration in the atmosphere falls below 750 ppmv can winter snow on continents in polar regions build up into inland ice (DeConto et al. 2008). In addition, the initially only partial glaciation of Antarctica at the beginning of the Oligocene, 34 million years ago, was initiated by the formation of the cold Antarctic Circumpolar Current. The opening of two marine straits, the Tasman Strait and the Drake Passage, separated Antarctica from Australia and South America, respectively, and the cold Antarctic Circumpolar Current thermally isolated Antarctica, preventing warm water from the tropics from reaching Antarctica (Stanley 2005). Together with the low CO_2 concentration in the atmosphere, this led to the formation of inland ice and initially only to a partial glaciation of Antarctica. Later, during the Miocene, Antarctica became completely glaciated (Stanley 2005; DeConto et al. 2008). The glaciation at the Eocene/Oligocene boundary caused cold, nutrient-rich water (minerals and nutrients brought in by glacial erosion from Antarctica) to spread around Antarctica via the polar current. This nutrient-rich, cold water provided a rich source of food for whales, namely (zoo)plankton, which flourished there. This plankton prompted a group of whales, the baleen whales, or Mysticeti, to reduce and eventually lose their teeth and instead develop baleen plates made of keratin to filter the abundant krill from the water and thus become plankton eaters (Marx and Fordyce 2015; Fig. 10).

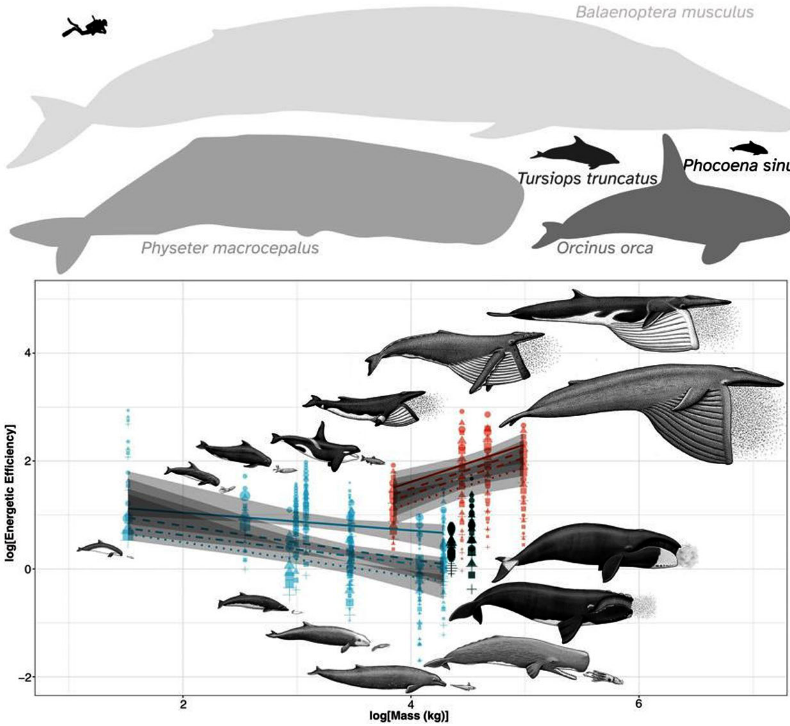
Among modern whales, toothed whales, Odontoceti, first developed. They had teeth like orcas. From toothed whales, then baleen whales evolved, which in transitional forms still had some teeth (Geisler et al. 2017; Tsai et al. 2024) but had already developed baleen to filter-feed large quantities of plankton. Early representatives of baleen whales, which lived 30 million years ago, still had teeth in the front of their jaws, which were still developed as grasping teeth, but at the back of the jaw, they were serrated and may have already functioned a little like fish traps (Geisler et al. 2017). Early baleen whales have been found at the Eocene/Oligocene boundary, i.e., during the period when the nutrient-rich, cold Antarctic Circumpolar Current formed (Fordyce 1980; Marx and Fordyce 2015). Baleen is made of keratin, just like our hair and fingernails and arranged in baleen plates which are fibrous at the ends (Fig. 10, a and b). These baleen plates are used to filter large quantities of small krill crustaceans from the seawater (Fig. 10, c and d). Krill swarms several football fields in size live in the nutrient-rich cold polar seas, which is why whales migrate there today to feed abundantly during the polar summer. With their baleen, large baleen whales can filter enormous amounts of water in record time; a fin whale, for example, can enclose around 70,000 litres in a few seconds and filter it in less than a minute through its baleen to retain only the prey. That is a volume of water heavier than the whale itself, from which it extracts around 10 kilograms of krill, depending on krill density in the water (https://baleinesendirect.org/en/une-video-inedite-du-comportement-alimentaire-de-rorquals-communs/).

Fig. 10: Humpback whale mouth with keratinous baleen plates (a). Side view of a humpback whale head (b). Krill, small marine crustaceans, form protein-rich, high-energy food for baleen whales (c). Single krill animal on a fingertip (d).



Source: (a) credit John Tunney, Shutterstock, https://www.shutterstock.com/image-photo/humpback-whale-opens-mouth-wide-show-120146803; (b) https://www.peta.de/themen/wale/; (c) credit Dan Costa, https://www.nsf.gov/science-matters/antarctic-krill-superheroes-southern-ocean#image-caption-credit-block; (d) credit Sophie Webb/NOAA, https://utopia.de/news/krill-fang-in-der-antarktis-grund-dafuer-ist-das-verrueckteste-der-geschichte_660685/

*Fig. 11: Size comparison of silhouettes of the blue whale (*Balaenoptera musculus*), the largest animal that ever lived on Earth, with other large, toothed whales such as the sperm whale (*Physeter catodon*; the largest toothed whale), killer whale (*Orcinus orca*) and two species of dolphin with a diver for scale (top). The bottom graph shows the relation between energy efficiency (related to feeding) and body mass, both on a log scale. Only filter-feeding enables the sustenance of the giant body size of baleen whales.*



Source: cutout of Burin et al. 2023, Fig. 1, p. 1788, licensed under CC BY 4.0 (top) and Goldbogen et al. 2019, Fig. 4, p. 1371 (bottom)

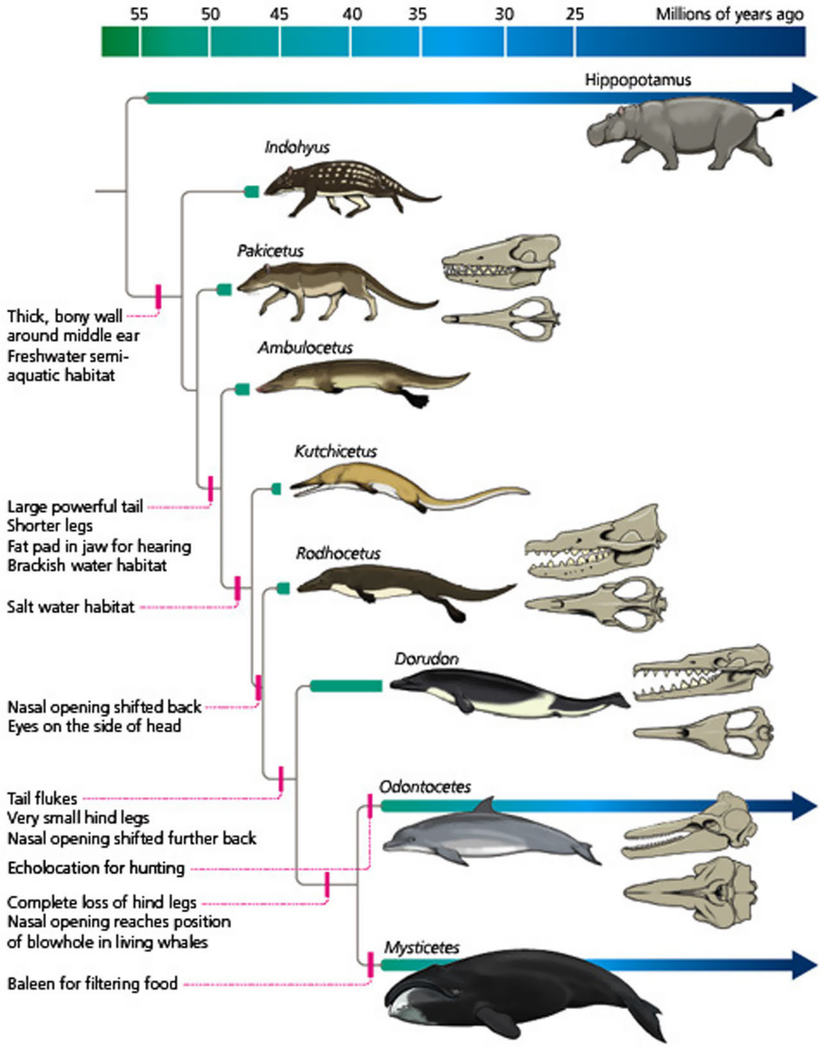
This 'bulk feeding' on zooplankton has led to these gigantic forms, especially among baleen whales (Goldbogen et al. 2019), particularly since three million years ago in the Pliocene-Pleistocene epoch, when the north pole also became ice-covered. The Arctic also had corresponding krill swarms and nutrient-rich waters from continental runoff, providing additional feeding grounds for baleen whales. The evolution of whales ultimately produced the largest animal that has ever lived on our planet, namely the blue whale (*Balaenoptera musculus*) (Fig. 11). They have been recorded as measuring up to 32 meters in length, weighing up to 200 tons, and living to a maximum age of at least 100 years. Other whales, such as the bowhead whale, even live up to 200 years old. Baleen whales migrate huge distances, thousands of kilometres from the equator to both polar regions, to feed on krill and other plankton with their baleen plates (Fig. 10). The record holder is the gray whale, with a migration distance of over 16,000 km for its round trip from pole to pole. Unfortunately, whales, especially the giants of the seas, are threatened in many ways by human hunting, pollution, ship traffic, fishing and climate change (Hersh et al. 2025).

Toothed whales can also grow quite large, such as the sperm whale, the largest odontocete, which can reach lengths of over 20 meters. It also holds the record for deep diving. It can dive over 3,000 meters in three-quarters of an hour to hunt its preferred prey, giant squid, in the deep sea. Finally, a comparison of the largest animals in Earth's history highlights both the relative smallness of humans and the immense size of the largest animal ever known: the blue whale – surpassing all dinosaurs and every other known animal in size (Fig. 11).

The baleen whales have produced the true giants of the seas. Filtering protein-rich zooplankton food such as krill (Fig. 10) has proven successful in facilitating gigantism in baleen whales (Goldbogen et al. 2019). First filter-feeding probably already evolved in the Oligocene (Geisler et al. 2017; Tsai et al. 2024) and has later led to gigantic forms in baleen whales (Marx and Fordyce 2015). But also, echolocating toothed whales evolved a wealth of behavioral diversity in foraging tactics to capture their prey that can even be culturally transmitted by social learning (Hersh et al. 2025).

Key steps in whale evolution from terrestrial, even-toed ungulates to secondary aquatic marine mammals since ca. 54 Ma in the Eocene (Fig. 12) were body plan changes (hind limb loss, fluke formation, forelimb modification to flippers, snout shape, nostril position, blubber), modifications of ear morphology (directional under water hearing) and feeding ecology (filter-feeding with baleen, search for prey using echolocation in toothed whales) (Thewissen 1998; Zimmer 1999; Thewissen and Williams 2002). Whales have an excellent fossil record that documents the transition from land-dwelling ungulates to sea-dwelling whales very well. Plate tectonics and other geological processes influenced the evolution of continents, climate, ocean currents, sea level changes, and ultimately whales. The transition from land to sea took place in coastal habitats, which also served as deposition sites for the skeletal remains of early whales. Whales live in water, die in water, and are quickly embedded in marine sediments, where they can be preserved as fossils. These fossil specimens allow paleontologists to reconstruct the evolution of whales. Fossils of archaic whales have been preserved in Eocene aquatic/marine sedimentary rocks in Indo-Pakistan, but also in Egypt, and provide evidence of the early evolution of whales from land-dwelling ungulates to fully marine whales.

Fig. 12: From hoofed land-mammals to giants of the sea. Phylogenetic evolution of whales from the sister taxon Indohyus *through the first true archaic whale* Pakicetus *to the fully marine* Dorudon, *from which the modern toothed whales (Odontocetes) and baleen whales (Mysticetes) eventually developed.*



Source: Zimmer 2013, Fig. 1.7, p. 358

Today, 89 different species and 13 families of whales still exist, mainly toothed whales, but also some baleen whales, which, as giants of the seas, are among the largest animals that have ever lived on our planet (Fig. 11; Burin et al. 2023), have important ecosystem functions as apex predators and nutrient distributors but may also help to sequester CO_2 (Pearson et al. 2023). Thus, whales were, are and will remain true giants of the sea in many aspects.

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