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Ancient toothed whales

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Archaeocetes ('ancient whales') were amphibious and aquatic mammals that inhabited the estuaries, seas and oceans of the Eocene. Evolving from primitive hoofed mammals, most probably during the Palaeocene, they developed a variety of body shapes and feeding styles, and gave rise to the toothed and baleen whales of today. While the most primitive archaeocetes lacked aquatic specializations and probably only foraged at the water's edge, later types became committed to an aquatic life. By the end of the Eocene, archaeocetes were fully marine and sometimes enormous in size. Archaeocete diversity is often understated and only in the past two decades have palaeontologists come to appreciate the variation exhibited by this group. New details provided by new types of archaeocete fossils have helped to piece together the complex story of cetacean (i.e. whale) origins and early evolution.

The oldest known archaeocetes – the pakicetids *Pakicetus*, *Ichthyolestes* and *Nalacetus* – are from the early Eocene. *Himalayacetus*, a small Indian form based on a supposedly early Eocene lower jaw, was described in 1998 as the oldest known archaeocete. However, this has been contested and *Himalayacetus* may be actually middle Eocene in age. All early archaeocetes are unique to India and Pakistan, suggesting southern Asia as a centre of origin for the group. A supposed early Eocene archaeocete scapula from the English London Clay, named *Anglocetus beatsoni* Tarlo, was later shown to be from a turtle.

By the late middle Eocene, seal-like archaeocetes had spread to Africa and North America. This distribution indicates that these forms were now able to disperse from the shallow marine shelf regions inhabited by earlier types and could cross oceans, an idea supported by their morphology and perhaps also by

isotopic data (see below). Fully aquatic archaeocetes – the basilosaurids and dorudontids – first appeared at the end of the middle Eocene and by the late Eocene their fossils occur throughout the Northern Hemisphere and as far south as New Zealand.

There is no evidence that archaeocetes survived beyond the Eocene, except in the form of their modified odontocete (toothed whale) and mysticete (baleen whale) descendants. Several post-Eocene cetaceans previously suggested to be late-surviving archaeocetes, such as *Kekenodon* from New Zealand, are instead primitive toothed mysticetes.

Controversial origins

Cetaceans are clearly placental mammals and there is good evidence, both morphological and genetic, that all cetaceans share the same ancestor. Living cetaceans are highly modified compared to their terrestrial relatives. Consequently, determining to which group cetaceans might be most closely related has long been problematical. Multiple lines of evidence, including soft tissue anatomy, tooth microstructure, embryology and blood composition, indicate that cetaceans are part of the hoofed mammal, or ungulate, group. Primitive archaeocetes, some of which had hoof-like toe bones, confirm this view. Among living ungulates, cetaceans share several soft-tissue features with even-toed ungulates (artiodactyls), the group that includes the hippopotamuses, pigs, camels and antelopes.

Until very recently, it was thought that whales were most likely descended from the mesonychians, a group of vaguely dog-like ungulates that thrived during the Palaeogene, as both mesonychians and archaeocetes share features of the skull and teeth.

However, genetic evidence contradicts this model, and molecular biologists have consistently found that cetaceans are not simply closely related to artiodactyls; they are artiodactyls and, more specifically, are most closely related to hippos. This idea was resisted initially by most palaeontologists, as the morphological evidence for an affinity between archaeocetes and mesonychians appeared quite good. The resulting controversy was dubbed the 'whippo' debate and molecular biologists even gave a new name, the Whippomorpha, to the supposed cetacean-hippo clade.

Fossil discoveries made since 1998 have now led palaeontologists to also doubt the idea that cetaceans descend from mesonychians. Associated skeletons of primitive archaeocetes described in 2001 finally revealed that the earliest cetaceans were artiodactyl-like terrestrial running animals with the long, slim limb bones and pulley-like ankle bones of artiodactyls. This provides strong support for the view that cetaceans and artiodactyls are each other's closest relatives, and that primitive members of both groups were morphologically similar. However, the fossils do not demonstrate an inclusion of cetaceans within Artiodactyla, nor for the monophyly of 'whippomorphs'. Because the most primitive artiodactyls may include the ancestors of hippos, the close affinity that primitive artiodactyls have with the archaeocetes is not inconsistent with the molecular evidence.

Archaeocete morphology

Spanning as they do the transition from terrestrial to aquatic mammals, archaeocetes are morphologically diverse, and derived forms differ markedly from basal ones. However, a number of features are common to all archaeocetes and appear to be derived characters that separate cetaceans from all other ungulates.

Archaeocetes in general possessed elongate, narrow jaws equipped with long pointed incisors (Figs 1–3). This morphology is one of the defining characters of cetaceans. The muscles involved in closing the jaws and in chewing were larger in archaeocetes than in

Fig. 1. Reconstructed skeleton of the middle Eocene archaeocete *Rodhocetus* from Pakistan, highlighting the main differences between primitive archaeocetes and modern cetaceans. Total length 3 m. Redrawn from Gingerich *et al.* (2001).

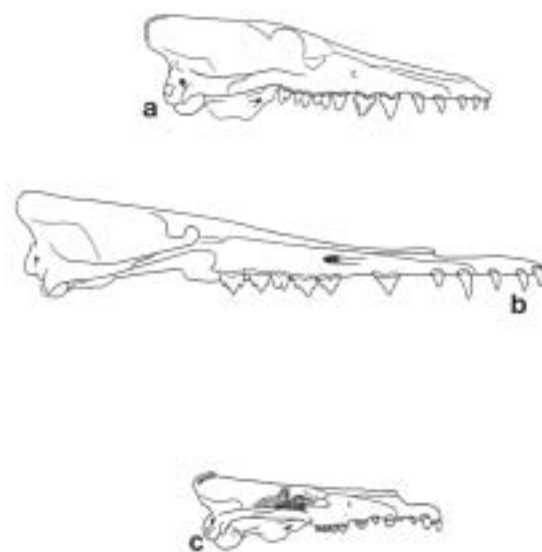
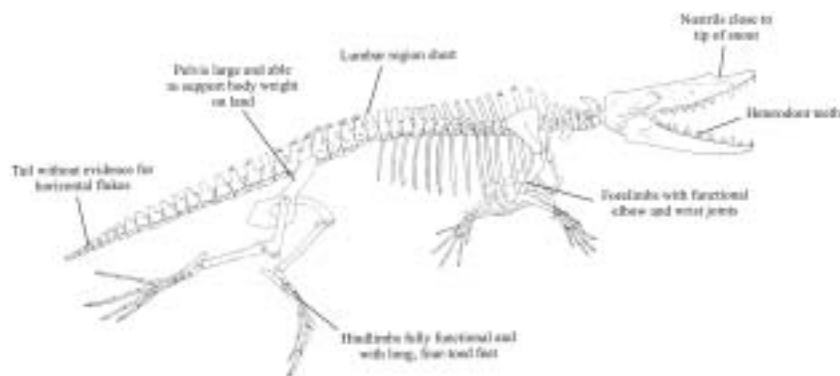


Fig. 2. Archaeocete skull diversity. **a.** The pakicetid *Pakicetus* (early Eocene of Pakistan). **b.** The remingtonocetid *Remingtonocetus* (middle Eocene of India). **c.** The protocetid *Artiocetus* (middle Eocene of Pakistan). Note the anteriorly located nostrils in the pakicetid and the remarkably elongate rostrum of the remingtonocetid. Redrawn from Kumar & Sahni (1986), Thewissen *et al.* (2001) and Gingerich *et al.* (2001). Not drawn to the same scale throughout.

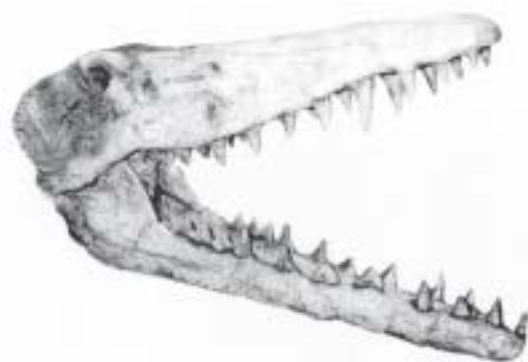
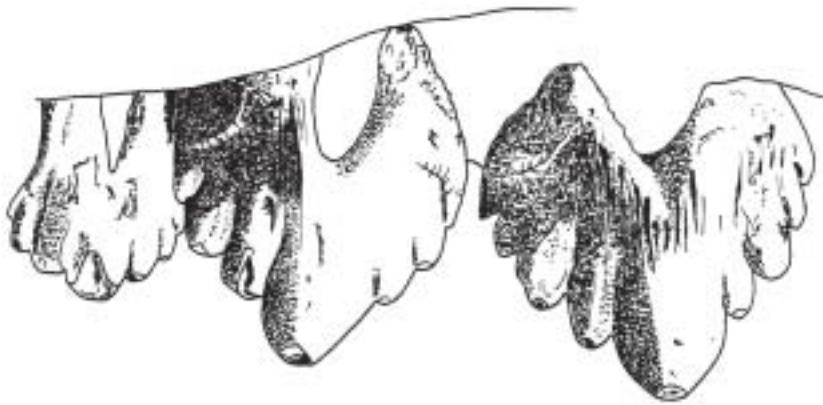


Fig. 3. Reconstructed replica skull of *Ambulocetus natans* from the middle Eocene of Pakistan. Note the crocodile-like proportions, orbits located high on the head and conical anterior teeth.

modern whales, and the teeth of some archaeocete groups indicate that crushing and chewing were still important. Unlike modern cetaceans, archaeocetes grew two sets of teeth during their life (though there is one possible exception, discussed below) and were heterodont. Reduction of the chewing teeth occurred during archaeocete evolution, and the loss of various cusps on the premolars and molars help to characterise the group. In the archaeocete groups Remingtonocetidae, Basilosauridae and Dorudontidae



the premolar and molar teeth were multi-cusped, laterally compressed blades suited for slicing, and not for chewing (Fig. 4).

In modern cetaceans the hollow region in the lower jaw (the mandibular foramen) is particularly large compared to that of other mammals. This houses a structure, the fat pad, which conducts

Fig. 4. First molar (at far left) and last two premolars of the dorudontid *Zygorhiza kochii* from the late Eocene of the USA, seen in lingual (inside) view. Redrawn from Kellogg (1936).

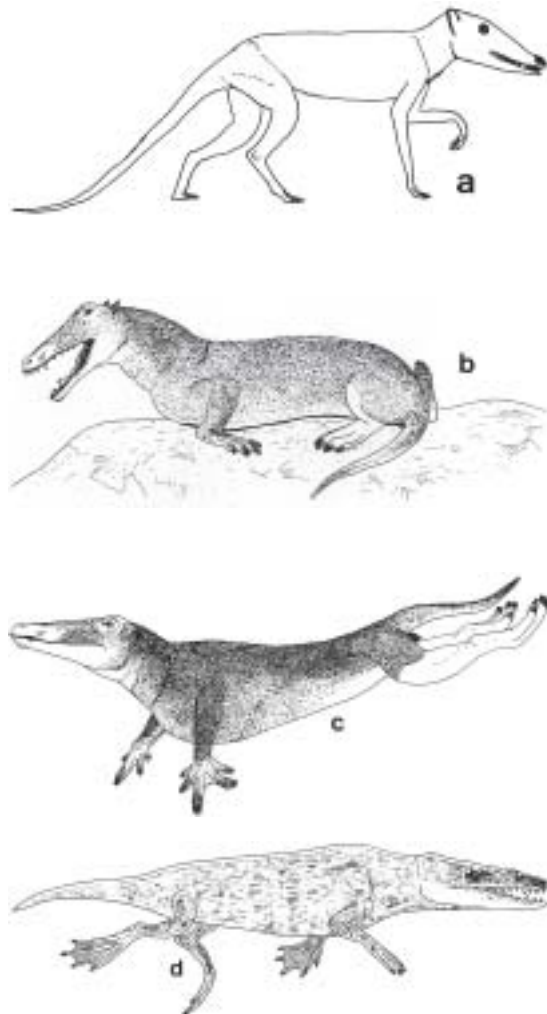


Fig. 5. Life restorations of three primitive archaeocetes, all of which are from Pakistan. **a.** Early Eocene *Pakicetus* (total length 2 m). **b.** Middle Eocene *Ambulocetus* (total length 3 m). **c.** *Ambulocetus* in hypothetical swimming pose. **d.** Middle Eocene *Rodhocetus* (total length 3 m).

sounds from the lower jaw to the middle ear. The most basal archaeocetes, the pakicetids, had very small mandibular foramina and probably lacked a fat pad. However, these features were present in later archaeocetes. Modern cetaceans also exhibit enlarged, dense-boned middle ear bones that are rotated in position relative to those of terrestrial mammals. While derived archaeocetes possess ear bones of this type, pakicetids had middle ear bones intermediate between those of terrestrial ungulates and derived archaeocetes. The middle ears of basilosaurids and dorudontids have features indicative of high-frequency hearing.

In modern cetaceans, the tympanic bullae (bowl-shaped skull bones attached to the underside of the back of the skull) are only loosely connected to the other skull bones and are acoustically isolated from the rest of the skull by air-filled pouches. All cetaceans, even pakicetids, have tympanic bullae formed from very dense bone, but the pakicetids lacked air-filled pouches and their bullae were firmly connected to the other skull bones. Pakicetids therefore show that the advanced underwater hearing style of modern cetaceans was not present in the earliest cetaceans. There is no evidence that archaeocetes possessed a melon, the lens-shaped structure in the forehead probably used in focusing outgoing sounds, nor are their skull bones asymmetrical or telescoped backwards as they are in modern cetaceans.

In modern cetaceans, the elbow and wrist joints are largely immobile. Similarly restricted degrees of motion appear to have been present in basilosaurids and dorudontids. In contrast, the forelimbs of more primitive archaeocetes still had flexible elbows and wrists, and appear suited for weight bearing (Figs 1, 5). A peculiarly reduced forelimb with a fused elbow joint is seen in the Egyptian dorudontid *Ancalocetus*. Like modern cetaceans, basilosaurids and dorudontids (excepting *Ancalocetus*) possessed an expanded fan-shaped scapula.

While ambulocetids and remingtonocetids had elongate neck vertebrae, these were shorter in protocetids, and shorter still in basilosaurids and dorudontids. In contrast to some modern cetaceans, the neck vertebrae of archaeocetes were never fused together. A substantial reduction of the pelvis occurred during archaeocete evolution, but, unlike modern whales, all archaeocetes possessed external hind limbs. Protocetids and remingtonocetids had large pelvic girdles and robust hind limbs, and *Ambulocetus* had particularly large, long-toed feet. In the details of their internal structure and relative size, the hind limb bones of these archaeocetes recall those of otters and sea lions, and suggest that they supported the weight of their owners when on land.

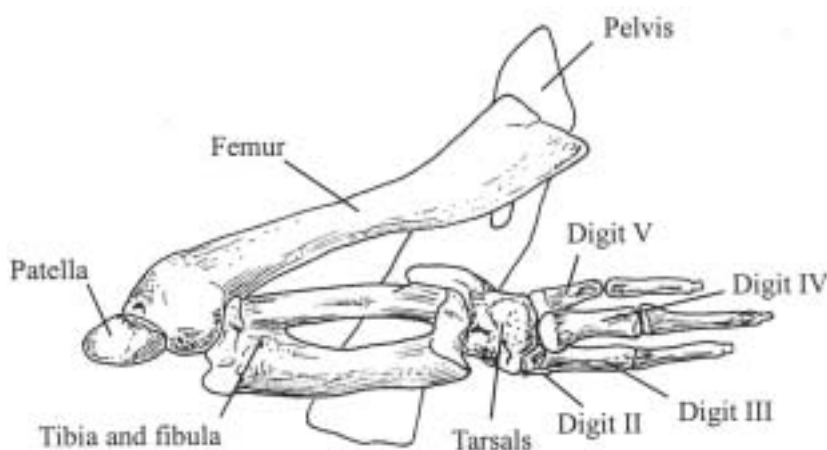


Fig. 6. The hindlimb and pelvis of *Basilosaurus isis* from the late Eocene of Egypt. Though tiny in proportion to the body (see Fig. 8A), these hindlimbs were still four-toed and with a functional knee joint (redrawn after Gingerich *et al.*, 1990).

Basilosaurids were shown in 1990 to have possessed diminutive four-toed hind limbs (Fig. 6), despite traditional interpretations that regarded them as being devoid of such external appendages. Dorudontids are also known to have possessed hind limbs. It now seems likely that external hind limbs were still present in primitive mysticetes and odontocetes. In modern cetaceans, the pelvis has no connection with the vertebral column. This was also true of advanced archaeocetes. Conversely, primitive types possessed a connection of four vertebrae, a condition retained in protocetids such as *Rodhocetus* from middle Eocene Pakistan. Other protocetids were intermediate. For example, *Protocetus* from the middle Eocene of Egypt and *Natchitochia* from the middle Eocene of the USA had only one sacral vertebra.

Toward the tip of the cetacean tail, the cross-sectional shape of the vertebrae changes from round to square. The square distal vertebrae are those to which the tail flukes are connected. Among archaeocetes, such square vertebrae are seen in basilosaurids and dorudontids, but not in more primitive types. The reduced hindlimbs and much enlarged tails of advanced archaeocetes are in keeping with a caudal oscillation swimming style similar, to that seen in living cetaceans.

Archaeocete diversity

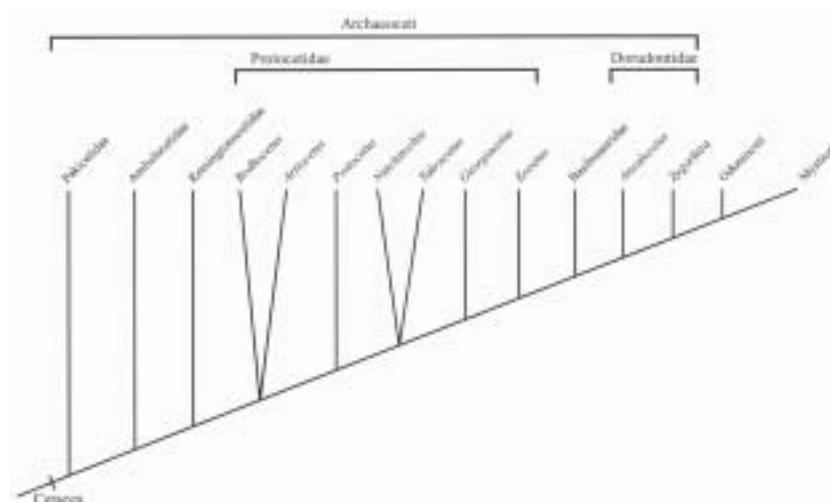
To date the most primitive cetaceans are the pakicetids from the early Eocene of India and Pakistan. In all known aspects of morphology pakicetids are clearly less derived than later cetaceans. Pakicetids were small and did not exceed 2 m in total length. A peculiar feature of their skulls were dorsally-directed eye sockets located near the midline of the skull (Fig. 2). Though pakicetid fossils were first collected in the 1940s, they were not recognized as primitive cetaceans until 1980. While often reconstructed as seal-like proto-whales, new material

shows that they were predominantly terrestrial, and much like primitive artiodactyls in morphology, and probably lifestyle. Pakicetid fossils are mostly known from rocks deposited in shallow freshwater environments.

Ambulocetus natans Thewissen *et al.*, a long-skulled amphibious archaeocete from the middle Eocene of Pakistan (Fig. 5B), was first described in 1994 and has added a new chapter to our understanding of early cetacean evolution. Importantly, the best-known *Ambulocetus* specimen includes substantial postcranial material. The robust vertebral column was clearly highly mobile in the dorsoventral plane and the feet were very large. These features indicate that *Ambulocetus* swam by flexing its back up and down while using its feet for propulsion (Fig. 5C). This method of swimming, called spinal undulation, would appear to be antecedent to the caudal oscillation swimming style developed later on. *Ambulocetus* and the tooth-based genus *Gandakasia*, also from the middle Eocene of Pakistan, are grouped together in the Ambulocetidae. *Himalayacetus* is also probably an ambulocetid.

Protocetids appear to have been the first cetaceans capable of crossing wide oceanic barriers and, until the discovery of pakicetids in the 1980s, were the most primitive cetaceans known. Most were larger than earlier archaeocetes, in some cases exceeding 5 m in length, and in the largest forms the skull was almost a metre long. Protocetids had smaller hindlimbs than ambulocetids and remingtonocetids, though these probably still functioned in terrestrial locomotion. Even primitive protocetids had large, powerful tails and may have employed caudal oscillation while swimming. The slim jaws and pointed teeth of most protocetid genera suggest that they were predators of fish. However, *Takracetus* from the middle Eocene of Pakistan, had a broader rostrum and may have been able to catch larger prey, perhaps includ-

Fig. 7. Cladogram depicting the archaeocete groups and the specific taxa mentioned in this article. Note that Protocetidae, Dorudontidae and Archaeoceti itself are all paraphyletic grades and not clades. Diagram by Stig Walsh.





ing cephalopods. By the protocetid stage of archaeocete evolution, the nostrils had migrated dorsally and were now above the canine or premolar teeth.

Two large, advanced protocetids, *Eocetus* from the middle Eocene of Africa and North America, and *Georgiacetus* from the middle Eocene of North America, share features of the teeth and vertebrae with basilosaurids and dorudontids. This indicates that the Protocetidae are a grade, not a clade. Indeed, Archaeoceti itself is clearly paraphyletic because, in traditional classifications, it excludes its two descendant clades Odontoceti and Mysticeti (Fig. 7). However, it remains a convenient term for those cetaceans that are not odontocetes or mysticetes.

Remingtonocetids were first recognized as a distinct group in 1986. Their exact relationship to other cetaceans remains unclear but they were probably related to protocetids. Their exceptionally long-snouted skulls (Fig. 2) are unusual in having small orbits and enlarged middle ears widely separated by a broad cranium. These features suggest that remingtonocetids relied more on hearing than on sight. Their name means 'Remington's whales' and honours Remington Kellogg (see 'Suggestions for further reading'). Kellogg's name is also commemorated in *Kelloggia*, an Oligocene odontocete from western Asia.

Unlike other archaeocetes, basilosaurids and dorudontids share with advanced cetaceans a rotated pelvis and the loss of the third upper molar. Their often huge body size, loss of the sacrum and reduced hindlimbs indicate that they were unable to move on land. *Basilosaurus*, one of the most famous of fossil mammals, was a long-bodied basilosaurid that inhabited the middle and late Eocene shallow seas of North America, Africa, southern Asia and possibly Europe. Perhaps reaching 20 m in length, it was first de-

scribed in 1834 and thought to be an immense reptile, hence the name ('king lizard'). In 1842 Richard Owen recognized that *Basilosaurus* was a mammal and renamed it *Zeuglodon* ('yoke tooth'). *Basilosaurus* is unique in its remarkably elongate lumbar and cau-

Fig. 8. *Basilosaurus* is the largest and best known archaeocete. **a.** Skeleton of *B. cetoides* from the late Eocene of the USA (total length 20 m). Redrawn from Kellogg (1936). **b.** Life restoration of *B. cetoides*.



Fig. 9. Skeletal reconstruction of the dorudontid *Zygorhiza kochii* from the late Eocene of the USA. The animal may not have been as dorsoventrally flexible as depicted here. Total length 6 m. Diagram by Ken Carpenter, used with permission of the artist.



dal vertebrae. These would have given it a very long body compared to other archaeocetes, suggesting that dorsoventral undulation was important in its swimming style (Fig. 8).

Dorudontids, unlike basilosaurids, were proportioned much like modern cetaceans (Fig. 9). All dorudontids were morphologically similar, and they almost certainly include the ancestors of odontocetes and mysticetes. Like odontocetes and mysticetes, the dorudontid *Chrysoctetus* from the late Eocene of the USA appears to have lacked deciduous teeth and therefore appears to have been especially close to the ancestry of these advanced cetaceans.

Archaeocete lifestyle and ecology

Primitive archaeocetes like pakicetids may have scavenged on seashores and fished in shallow water. Conversely, protocetids might have lived like sea lions, while basilosaurids and dorudontids were probably not unlike living predatory cetaceans in their ecology. Though archaeocetes have traditionally been regarded as generalized and rather clumsy predators of slow-moving fish, recent discoveries suggest intriguing specializations among the different lineages. Pakicetid skeletal morphology remains poorly understood, but their delicate incisors indicate that they picked up small prey animals. Ambulocetids, with their dorsally located eye sockets and extensive bony palates, have been regarded as mammalian analogues of amphibious predatory crocodiles. Like a crocodile, *Ambulocetus* could have remained hidden with all but its eyes projecting above the water surface. Its elongate, tubular rostrum may have been well able to resist the struggles of large prey animals.

Oxygen isotope analysis of well-preserved archaeocete teeth may provide some insight into archaeocete lifestyles, though this area is fraught with controversy. By studying the isotopes preserved in the tooth phosphate, it has been suggested that pakicetids and ambulocetids only ingested freshwater and that protocetids ingested saltwater. Because *Ambulocetus* probably inhabited marine environments, the freshwater isotopic signature of its tooth phosphate may suggest that it sought out freshwater when in need of a drink or, alternatively, that only adults inhabited marine environments.

Basilosaurids and dorudontids were all similar in skull morphology. Their robust incisors and canines,

and worn tips to their serrated premolars and molars, indicate that they preyed on vertebrates including large fish. How *Basilosaurus* swam has been the subject of debate and it has been argued that its large vertebrae were buoyant and that it was therefore a surface-dwelling animal, largely unable to dive. Its dense-boned ribs with their expanded club-like ends may have helped it to remain stable.

If basilosaurids and dorudontids were fully aquatic, they perhaps gave birth to large precocial babies in secluded waters, as some cetaceans do today. Early archaeocetes conceivably gave birth on beaches and may have been behaviourally similar to seals and sea lions. However, we know nothing of archaeocete social behaviour. The complex social behaviour often associated with cetaceans is in fact largely unique to a few select groups of odontocetes and there is no reason to predict the presence of these sorts of behaviours in archaeocetes.

Suggestions for further reading

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