Information module on *Basilosaurus isis*

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Modern cetaceans (whales and dolphins) are divided into Mysticeti, or baleen whales, and Odontoceti, or toothed whales. They are characterized by loss of functional, external hindlimbs, disarticulation of pelvic elements from the vertebral column, transformation of forelimbs into steering flippers, oscillatory or undulatory swimming modes using the torso and a caudal fluke for propulsion, compression or fusion of neck vertebrae to stabilize the head in swimming, streamlining of the body, and retraction of the nasal opening to the top of the head to form a blowhole.

These modern cetacean groups were preceded by, and evolved from, a more primitive group of whales called the "Archaeoceti." A prominent group of archaeocete whales exhibiting adaptations for a fully aquatic life and signs of gigantism was the Basilosauridae, named for its best documented genus, *Basilosaurus*. Fossils of this genus were originally discovered in the southern United States in the early 1800s and initially identified as belonging to a giant reptile, hence the misleading meaning of its name, "king lizard." Soon thereafter, however, the British anatomist Richard Owen correctly identified it as a whale. Several species belong to this genus, including *Basilosaurus cetoides* from the New World and *B. isis* from North Africa and the Middle East. *Basilosaurus isis* has been known since the late 1800s, but the most substantial documentation and collections of the species were not made until University of Michigan paleontologist Philip Gingerich began leading research programs into the western Sahara of Egypt, in the Valley of the Whales (Zeuglodon Valley or Wadi Hitan), in the 1980s. Fossils of *B. isis* are best represented in middle-to-late Eocene shallow marine sediments of the Gehannam and Birket Qarun Formations of Egypt, dated to ca. 38-36.5 Myr. This led to identification of hundreds of individuals of the species in situ and collection of abundant specimens, including a number of nearly complete skeletons. One of these was used to construct a beautiful cast replica that is displayed in the University of Michigan Museum of Natural History.

The recovery of well-preserved examples of all parts of the skeletal anatomy of *B. isis* provides a comprehensive understanding of its behavior and adaptations to life in the seas. *Basilosaurus* was an impressively large (15-18 meters in length), serpentine archaeocete. It had seven neck vertebrae, compressed but not fused, 18 trunk vertebrae, and 42 posterior back and tail vertebrae, many of which were impressively elongate. Cross-sectional observations on these large vertebrae indicate that their outer surfaces are formed of recurrent coarse layers of cortical bone, suggesting that skeletons rapidly grew to great length. Features of the posteriormost caudal (tail) vertebrae are consistent with the presence of a small fluke, and it is likely that swimming involved a great degree of undulatory movement of the body. The forelimbs are compressed, with an immobile wrist and fingers but freely mobile elbow. They probably acted as steering flippers. Ribs are heavy and enlarged, which would have helped ballast the animal and maintain trim in swimming. Although the pelvic elements (innominates) were not attached to the vertebral column and therefore could not bear weight for walking, relatively very small hindlimbs projected outside the body. Though the ankle bones were fused, the ankle remained capable of movement on the lower leg, the knee joint had a large patella and could be flexed and extended, and the upper leg could be rotated on the innominates. Toes III-V were present and toe II existed as a tiny vestigial element. The regularity of the hindlimb elements and their mobility suggest that they were functional, though they were inadequate for walking or swimming. It has been hypothesized that they were used as copulatory guides in mating, and

there is congruent evidence that male individuals had larger legs than females. The skull is primitive compared with modern whales in retaining different tooth types (heterodonty), having a relatively small braincase, and limiting posterior retraction of the nasal opening only as far as the canine position on the rostrum. Nonetheless, it housed an impressive battery of teeth, including large premolars with multiple denticles or cuspules capable of shearing, crushing, and puncturing food. Given the magnitude of force that the cranium probably produced, the capability of the tooth battery for seizing and dismembering prey items, and its massive body size, *Basilosaurus* was undoubtedly the apex predator of the oceans during its time. Taphonomic study of stomach contents and the remains of other animals in the *Basilosaurus* ecosystem show a wide range of prey items, including bony fish, sharks, sea cows, turtles, and other archaeocetes. Bite marks on skulls of juvenile individuals of the archaeocete species *Dorudon atrox* indicate hunting, rather than scavenging, behavior. Study of features of the ear region and lower jaw show that *Basilosaurus* possessed an excellent ability to hear directionally under water, though there is no indication for echolocation.

More information about *Basilosaurus isis* can be found in the following publications:

Gingerich, P.D., B.H. Smith, and E.L. Simons. 1990. Hind limbs of Eocene *Basilosaurus*: Evidence of feet in whales. *Science* 249:154-157.

Zalmout, I.S., H.A. Mustafa, and P.D. Gingerich. 2000. Priabonian *Basilosaurus isis* (Cetacea) from the Wadi Esh-Shallala Formation: First marine mammal from the Eocene of Jordan. *Journal of Vertebrate Paleontology* 20:201-204, doi:10.1671/0272-4634(2000)020[0201:PCICFT]2.0.C);2.

Gingerich, P.D. 2008. A century of research in Egypt; pp. 107-124 in J.G. Fleagle and C.C. Gilbert (eds.), *Elwyn Simons: A Search for Origins*. Springer, New York.

Fahlke, J. 2012. Bite marks revisited—evidence for middle-to-late Eocene *Basilosaurus isis* predation on *Dorudon atrox* (both Cetacea, Basilosauridae). *Palaeontologia Electronica* 15, Issue 3; 32A, 16p.; palaeo-electronica.org/content/2012-issue-3-articles/339-archaeocete-predation.

Houssaye, A., P. Tafforeau, C. de Muizon, and P.D. Gingerich. Transition of Eocene whales from land to sea: Evidence from bone microstructure. *PLoS One* 10 (2):e0118409. doi:10.1371/journal.pone.0118409.

Voss, M., M.S.M. Antar, I.S. Zalmout, and P.D. Gingerich. 2019. Stomach contents of the archaeocete *Basilosaurus isis*: Apex predator in oceans of the late Eocene. *PLoS One* 14(1):e0209021. https://doi.org/10.1371/journal.pone.0209021.

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