Information module on *Dorudon atrox*

Cetacea includes the living mysticetes (baleen whales) and odontocetes (toothed whales), as well as the more ancient, extinct archaeocetes. The archaeocetes include the oldest whales, dating back to the earliest Eocene at 53 million years ago, the semi-aquatic ambulocetids, protocetids and remingtonocetids from the early and middle Eocene, and the basilosaurids from the early and late Eocene, which are the first of the fully aquatic whales. The basilosaurids include the gigantic, serpentine *Basilosaurus cetoides and B. isis* that are namesakes of their biological family, and the smaller, more compact *Dorudon atrox* that more closely resembles modern whales skeletally and may be close to the ancestry of the mysticetes and odontocetes.

Fossil specimens of *Dorudon*, including the first complete skeletons known for archaeocetes, were collected in abundance from localities in "Zeuglodon Valley" (Wadi Hitan, the Valley of Whales), Egypt. This is now part of the Sahara, but the localities are comprised of sedimentary rocks of the middle to late Eocene Gehannem, Birket Qarun, and Qasr el Sagha Formations, formed of mudstones, claystones, and sands deposited in lagoonal and shallow open marine settings. *Dorudon* was thought by some researchers to be a juvenile version of the more immense *Basilosaurus*, and also for a time carried the name "*Prozeuglodon*," but the name *Dorudon* was erected in the mid-1800s and has priority. As well, there is no longer any question that fossils of this whale belong in a distinct species. Although the taxon has been known for a long time, recovery of *Dorudon* fossils only began in earnest in the 1980s with the University of Michigan Museum of Paleontology (UMMP)-Cairo Geological Museum (CGM) expeditions to Wadi Hitan led by UMMP faculty-curator (now emeritus) Prof. Philip Gingerich. Subsequently, *Dorudon atrox* was described in detail by Dr. Mark Uhen, as part of his dissertation research at the University of Michigan—much of what we understand about this archaeocete whale derives from his study.

Numerous adaptations for aquatic existence are present in the skull of *Dorudon*. The cranium is elongate and low, with a long rostrum and nasal opening retracted to a position above the first premolars. Correspondingly, the conical incisors and canines are aligned anteroposteriorly, rather than in an anterior arcade, and upper and lowers interlock when the jaws are closed. This would be advantageous for seizing prey such as fish. The orbits are splayed laterally outward on each side, across a broad "frontal shield." The braincase is modest in size, requiring the development of a projecting sagittal crest to accommodate the temporalis muscles for jaw movements. Brain weight is estimated at 944 g, which when compared with estimated body mass yields a low encephalization quotient (EQ) of 0.438 (a living mammal of the size of *Dorudon* is expected to have an EQ of 1.0). This is not unexpected as many Eocene animals were less encephalized than their modern descendants. Strikingly, a number of anatomical features correlate with a superb ability to hear directionally under water and perceive higher sonic frequencies of sound-producing fish: density and swelling (pachyostosis and osteosclerosis) of the auditory bulla, presence of a conical apophysis formed by folding of the tympanic ring, associated with development of a conical tympanic ligament instead of a flat membrane, cranial asymmetry pronounced in the rostral region of the skull, isolation of the ear region from contact with the cranium, "pan-bone" thinning of the lower jaws, and inferred presence of thick mandibular fat pads. Unlike modern toothed whales, however, *Dorudon* primitively retained markedly heterodont teeth, with cheek teeth differentiated from simple anterior teeth by sporting many cusps and multiple roots. There is evidence that while it was an important marine predator in the middle and late Eocene, *Dorudon atrox* in turn was a prey item for the larger basilosaurid *Basilosaurus isis*, at least in its juvenile stages of development.

The skeleton of *Dorudon* is also well documented and reveals information about its commitment to aquatic life and mode of locomotion. The forelimbs were flattened and were probably used as steering and balancing flippers; the pelvis was disarticulated from the vertebral column, permitting the deployment of long trunk muscles to drive the tail and fluke in swimming; there are numerous, large chevron bones on the underside of the tail that would have provided greater effectiveness to tail depressor muscles; and there are osteological signs in anatomical differentiation of caudal vertebrae for the presence of a fluke. This morphology suggests oscillatory swimming in a different mode than the undulatory swimming of *Basilosaurus*, perhaps achieving speed by frequency of fluke oscillations. Also unlike *Basilosaurus*, *Dorudon* did not have pachyostotic, osteosclerotic ribs or elongate vertebrae. Similar to its larger relative, however, *Dorudon* also retained pelvic bones and mobile hindlimbs that projected from the body wall, perhaps employed as copulatory guides. The limbs would not have functioned in terrestrial walking and it is highly unlikely that *Dorudon* ever came out of the water. The loss of pelvic articulations would have allowed for a large birth canal and precocial development of large neonates that would have been able to swim immediately following their birth, as in modern whales. Vertebral formula for *Dorudon* is seven cervicals, 17 thoracics, 20 lumbars, no apparent sacrals (no articulation with pelvic bones), and 21 caudals. The relatively great length of the lumbar region, achieved by possession of a large number of individual vertebrae, is an aquatic adaptation and contributes to an adult body length of about five meters. Allometric analysis of the relationship between body length and weight in modern whales, applied to *Dorudon*, yields a body mass estimate of 2,240 kg, about the size of a modern beluga whale.

The skeletal elements of *Dorudon* were prepared, molded, and cast in the University of Michigan Museum of Paleontology's Vertebrate Preparation Lab by the Chief Preparator and a large crew of undergraduate student assistants. A highly accurate mounted skeletal replica of *Dorudon atrox* is permanently suspended above the East Atrium in the new Natural History Museum in the Biology Science Building, alongside the skeleton of *Basilosaurus isis*. Reconstruction of the specimen was done by then Assistant Preparator Jennifer Moerman (now Sontchi), an alumnus of the University of Michigan, and Exhibit Illustrator John Klausmeyer. Exhibit Preparator Dan Erickson worked with Jennifer to make the mount of the skeleton.

<u>More information about *Dorudon atrox* can be found in the following publications</u>:

Luo, Z., and P.D. Gingerich. 1999. Terrestrial Mesonychia to aquatic Cetacea: Transformation of the basicranium and evolution of hearing in whales. *University of Michigan Papers on Paleontology*, no. 31, 98 pp.

Uhen, M.D. 2004. Form, function, and anatomy of *Dorudon atrox* (Mammalia, Cetacea): An archaeocete from the middle to late Eocene of Egypt. *University of Michigan Papers on Paleontology*, no. 34, 222 pp.

Peters, S.E., M.S.M. Antar, I.S. Zalmout, and P.D. Gingerich. 2009. Sequence stratigraphic control on preservation of late Eocene whales and other vertebrates at Wadi al-Hitan, Egypt. *Palaios* 24:290-302.

Fahlke, J.M., P.D. Gingerich, R.C. Welsh, and A.R. Wood. 2011. Cranial asymmetry in Eocene archaeocete whales and the evolution of directional hearing in water. *Proceedings of the National Academy of Sciences, USA* 108:14545-14548.

Fahlke, J.M. 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.

Gingerich, P.D. 2012. Evolution of whales from land to sea. *Proceedings of the American Philosophical Society* 156:309-323.

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