

Hind limbs of Eocene Basilosaurus: evidence of feet in whales

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WHALES ARE REMARKABLE among mammals in being fully aquatic, and their transition from land to a sea is among the most interesting problems of evolution [1-3]. Most mammals use limbs, particularly hind limbs, in locomotion. Modern cetaceans live in water and lack hind limbs entirely, retaining only rod-like vestiges of pelvic bones, femora, and rarely tibiae embedded in musculature of the ventral body wall [4, 5]. Limbs are important for understanding the early evolution of whales. Hind limb buds have long been known in embryonic cetaceans up to 32-mm crown-rump length [6], and adults with externally projecting rudiments are also known [7]. We now describe evidence of functional hind limbs in a cetacean.

Basilosaurus is a large serpentine Eocene vertebrate discovered early in the 19th century when it was described as a reptile and named "king lizard" [8]. Richard Owen demonstrated the mammalian characteristics of Basilosaurus and, within mammals, its cetacean affinities [9]. Two species are known: *B. cetoides* from the late Eocene of the southeastern United States and *B. isis* from the late middle Eocene of Egypt [10, 11]. The most complete Basilosaurus specimens known previously were two partial skeletons of *B. cetoides* collected by C. Schuchert in Alabama in 1894 and 1896 for the U.S. National Museum (USNM). One of these specimens, USNM 12261, includes left and right innominate bones of the pelvis and a partial femur [12, 13]; these remains were considered vestigial and functionless [14], an interpretation consistent with loss of functional hind limbs in modern whales.

In 1987 and 1989 we mapped 243 partial skeletons of *B. isis* and 77 partial skeletons of smaller archaeocetes [15] in the desert of Zeuglodon Valley (ZV), 50 km west of Fayum oasis in north central Egypt [16]. All occur in a 90-m-thick stratigraphic section of shallow marine sandstones and shales of the Gehannam and Birket Qarun formations of late middle Eocene age [17]. Excavations in 1989 yielded several nearly complete skeletons combined in the reconstruction shown in Fig. 1A. These indicate that *B. isis* had 7 cervical, 18 thoracic, and 42 lumbar and caudal vertebrae (Fig. 2), 9 more than the number of vertebrae shown in reconstructions of *B. cetoides* [13, 14]. Limb and foot bones described here were all found in direct association with articulated skeletons of *B. isis* and undoubtedly represent this species. Specimens are conserved in the Cairo Geological Museum (CGM) and University of Michigan Museum of Paleontology (UM).

The innominate (Fig. 1B) is a straplike coossification of an elongated pubis and a relatively small ilium and ischium, each contributing to a well-defined acetabulum. The pubis and ischium surround a small obturator foramen. Left and right pubes fit together at a robust unfused midline symphysis [18]. The femur has a curved cylindrical head, a broad and high greater trochanter, considerable midshaft torsion, two flat facets for the patella, and distinct posteriorly directed medial and lateral condyles. The patella is relatively large, with a single flat femoral facet. The tibia and fibula are each only about one-half the length of the femur and are coossified at each end (Fig. 1B).

Tarsal bones exhibit a variable pattern of fusion at articulations that were probably immobile in life. Specimen UM 93231 has the astragalus, calcaneum, cuboid, and navicular coossified as one rigid bone (Fig. 1B), whereas CGM 42176 has the astragalus, navicular, ectocuneiform, and mesocuneiform fused (Fig. 3). Each specimen has a cuneiform articulating with the navicular and cuboid in the normal ectocuneiform position. A second cuneiform is much smaller and fused to the ectocuneiform as a mesocuneiform.

Basilosaurus lacks pedal digit I (hallux) entirely, and a breadlike mesocuneiform is the only remnant of digit II. Three metatarsals are known: one articulates with the distal surface of the ectocuneiform, identifying it as metatarsal III, and two articulate directly with the cuboid, identifying them as metatarsals IV and V. Metatarsal V is reduced relative to III and IV. The distal end of metatarsal III has a smooth flat surface for a proximal phalanx. The distal ends of metatarsals IV and V have more spherical surfaces for their proximal phalanges, suggesting a wider range of motion at these joints. Only one proximal phalanx is known. This fits onto metatarsal IV and has a small terminal second phalanx fused to it.

Metatarsals III and IV are the largest and longest metatarsals, making the foot paraxonic. A paraxonic pes in Cetacea is consistent with serological evidence of relationship to Artiodactyla [21] and dental evidence of derivation from mesonychid Condylarthra [22]. Artiodactyla and mesonychid Condylarthra both have a paraxonic pes [23].

The inferred posture and range of motion of the hind limb of Basilosaurus are unusual for a mammal. On each side the innominate lay in the ventral body wall with the acetabulum opening downward. The femur has two distinct patellar surfaces lying at right angles to each other, one on the distal end and the other on the anterior surface. These surfaces are flat, and indicate two distinct stable positions of the patella relative to the femur. The two surfaces join along a convex narrowly rounded edge, indicating that a transition between stable positions of the patella was possible but that intermediate positions were unstable.

Articular surfaces on the femoral condyles are directed posteriorly, indicating that the knee was always flexed to some degree. The astragalus articulates with both the tibia and fibula, but the entire tibial facet is on the medial side of the astragalus, meaning that the foot was always supinated. The posterior position of the fibular trochlea formed by the astragalus and calcaneum indicates that the ankle was normally extended. Fitting articular surfaces together, with the patella positioned on the distal articular facet of the femur, yields a posture in which the femur points almost directly forward, and the rest of the limb extends backward from the knee (Fig. 1B, solid drawings in Fig. 1, C and D). This is interpreted as the habitual resting posture of the hind limb. Hydrodynamic considerations dictate that the femur was almost entirely within the body wall, while distal elements lay flat against the body wall externally.

The cylindrical shape of the femoral head indicates limited motion at the hip joint, with the femur rotating downward and outward from its resting position. A distinct apex of the patella extends beyond its articular surface on one side only (interpreted as proximal). Patellar asymmetry and the narrowly rounded edge separating patellar surfaces on the femur suggest a stabilizing mechanism locking the knee in partial extension when the patella was pulled onto the anterior surface of the femur. This

unusual knee of *Basilosaurus* indicates a single alternative to its posture at rest. A downwardly rotated femur, extended locked knee, abducted hip, and dorsiflexed ankle are shown in open outline in Fig. 1, C and D.

Hind limbs of *Basilosaurus* appear to have been too small relative to body size (fig. 1A) to have assisted in swimming, and they could not possibly have supported the body on land. However, maintenance of some function is likely for several reasons: most bones are present; some elements are fused, but remaining joints are well formed with little suggestion of degeneracy; the patella and calcaneal tuber are large for insertion of powerful muscles; and the knee has a complex locking mechanism. The pelvis in generalized mammals supports reproductive organs in addition to its common use in locomotion. The pelvis of modern whales serves to anchor reproductive organs [5], even though functional hind limbs are lacking. Thus hind limbs on *Basilosaurus* are most plausibly interpreted as accessories facilitating reproduction. Abduction of the femur and plantar flexion of the foot, with the knee locked in extension, probably enabled hind limbs to be used as guides during copulation, which may otherwise have been difficult in a serpentine aquatic mammal.

Characteristics related to reproduction are often dimorphic in mammals, and dimorphism in a larger sample of limb elements would support the interpretation of hind limb function proposed here (lack of dimorphism would not necessarily refute it). Discovery of pelvic limbs and feet in *Basilosaurus* raises the possibility that other archaeocetes retained functional hind limbs [24]. New specimens are required to test both hypotheses. In the meantime, retention of well-formed pelvic limbs in *Basilosaurus* corroborates the morphological primitiveness of archaeocetes. Temporal and morphological intermediates are direct and important evidence of transition in evolution: an Eocene whale with functional hind limbs narrows the gap considerably between generalized Paleocene land mammals that used hind limbs in locomotion and Oligocene-Recent modern whales that lack pelvic limbs.

REFERENCES AND NOTES

[1] The oldest fossil whales are late early Eocene in age. *Pakicetus* and its relatives have teeth like later whales, but their auditory bullae are only partially modified for hearing in water and they are found in continental sediments with land mammals, suggesting that the transition had only begun [2]. Nothing is known of the postcranial skeleton of *Pakicetus*. Middle and late Eocene whales have more specialized crania and all come from marine sediments. Cetacea are classified in three suborders: Archaeoceti for archaic Eocene whales including *Basilosaurus*, Odontoceti for Oligocene-to-Recent toothed whales, and Mysticeti for Oligocene-to-Recent baleen whales [3].

[2] P. D. Gingerich et al., *Science* 220, 403 (1983).

[3] L. G. Barnes, D. P. Domning, C. E. Ray, *Mar. Mammal Sci.* 1, 17 (1985).

[4] J. Struthers, *J. Anat.* 15, 141 (1881); *ibid.* (new series), 7, 291 (1893); O. Abel, *Denkschr. Kaiserl. Akad. Wiss. Vienna Math.-Naturwiss. Kl.* 81, 139 (1908); E. Lonnberg, *Ark. Zool.* 7 (no. 10), 1 (1910); D. A. Parry, *Proc. Zool. Soc. London* 119, 51 (1949).

[5] W.M.A. de Smet, *Z Saugetierkd.* 40, 299 (1975).

- [6] G. Guldberg, *Anat. Anz.* 9, 92 (1894); H. C. Muller, *Arch. Naturgesch.* 7, 1 (1920); T. Ogawa, *Sci. Rep. Whales Res. Inst.* 8, 127 (1953).
- [7] R. C. Andrews, *Am. Mus. Novit.* 9, 1 (1921); T. Ogawa and T. Kamiya, *Sci. Rep. Whales Res. Inst.* 12, 197 (1957); T. Nemoto, *ibid.* 17, 79 (1963); S. Ohsumi, *ibid.* 19, 135 (1965). The rudimentary limb described by Andrews was said to include a femur, tibia, tarsus, and metatarsus; only two were ossified, and these are best interpreted as a femur and tibia with intervening connective cartilage. Tarsal and metatarsal bones are not found in extant whales.
- [8] R. Harlan, *Trans. Am. Philos. Soc. (new series)*, 4, 397 (1834). See Kellogg [14] for full history.
- [9] R. Owen, *Trans. Geol. Soc. London Ser. 2*, 6, 69 (1839). Owen's genus *Zeuglodon* is a junior synonym of *basilosaurus*.
- [10] *Basilosaurus cetoides* was named by Owen [9h; its age is late Jacksonian [14], correlated with Priabonian late Eocene by W. G. Siesser et al. [*Geol. Soc. Am. Bull.* 96, 827 (1985)]. *Basilosaurus isis* was named by H. J. L. Beadnell [in C. W. Andrews, *Geol. Mag. London Ser. 5*, 1, 214 (1904)]; its age is middle Mokattamian, correlated with Bartonian late middle Eocene [17]. *Basilosaurus isis* probably lived from about 42 to 40 million years before present.
- [11] L. G. Barnes and E. Mitchell, in *Evolution of African Mammals* [V. J. Maglio and H. B. S. Cooke, Eds. (Harvard Univ. Press, Cambridge, MA, 1978), pp. 582-602], provide the most recent review of Egyptian archaeocetes. They follow Kellogg [14] and place *B. isis* in *Prozeuglodon*.
- [12] F. A. Lucas, *Proc. U.S. Nat. Mus.* 23, 327 (1900).
- [13] J. W. Gidley, *ibid.* 44, 649 (1913).
- [14h R. Kellogg, *A Review of the Archaeoceti* (Carnegie Institution of Washington, Washington, DC, 1936).
- [15] These smaller archaeocetes include specimens of *Prozeuglodon atrox* described by C. W. Andrews [*A Descriptive Catalogue of the Tertiary Vertebrata of the Fayum, Egypt* (British Museum, London, 1906)]. The holotype of *P. atrox*, type species of *Prozeuglodon*, is an immature skull from Zeuglodon Valley, where immature skulls this size associated with dorudontine vertebral columns are common, and immature skulls associated with basilosaurine vertebral columns are unknown. Thus *Prozeuglodon* is almost certainly dorudontine and not basilosaurine, *P. atrox* is not a synonym of *B. isis*, and *Prozeuglodon* is not available as a distinct genus for what is here called *B. isis* [compare [11] and [14]; see also Fig. 2].
- [16] H. J. L. Beadnell, *The Topography and Geology of the Fayum Province* (Survey Department, Cairo, 1905).

[17] R. Said, *The Geology of Egypt* (Elsevier, Amsterdam, 1962); A. Strougo and M. A. Y. Haggag, *Neues Jahrb. Geol. Paleontol. Monatsh.* 1984, 46 (1984); A. Strougo and M. A. Boukhary, *Revue Micropaleontol.* 30, 122 (1987).

[18] In previous descriptions of USNM 12261, *B. cetoides*, Lucas [12] interpreted the pubic symphysis of each innominate as its posterior end. Gidley [13] and Kellogg [14] accepted this, but reversed left and right innominates. Some question remains as to which innominate is left and which is right; reversing these would have little effect on the reconstruction discussed here. Gidley confused proximal and distal ends of the partial femur, and Kellogg reversed the head and greater trochanter (most of the head is missing). In the meantime, Abel [19] interpreted the innominates as coracoids of a new Eocene bird, *Alabamomis gigantea*, and Stromer [20] compared them to innominates of the African water shrew *Potamogale*, and fancifully reconstructed ilia more than doubling their length. Innominate of *B. cetoides* are similar in length to those of *B. isis* but differ in being much broader anteroposteriorly. The partial femur of *B. cetoides* differs in having a much narrower greater trochanter.

[19] O. Abel, *Centralbl. Mineral. Geol. Palaeontol.* 1906, 456 (1906).

[20] E. Stromer, *Sitz. Bayer. Akad. Wiss. Munchen Math.-Phys. Kl.* 1921, 54 (1921).

[21] A. Boyden and D. Gemeroy, *Zoologica* 35, 145 (1950).

[22] L. Van Valen, *Am. Mus. Nat. Hist. Bull.* 132, 90 (1966).

[23] A. S. Romer, *Vertebrate Paleontology* (Univ. of Chicago Press, Chicago, 1966).

[24] We collected the proximal half of a femur and a complete patella associated with a dorudontine skeleton (ZV-72) in Zeuglodon Valley in 1989 before these elements were found with *B. isis* and before they could be positively identified. Given what we now know, these fossils show that one small archaeocete had hind limbs, but their full size, form, and possible function cannot be determined until they are better known.

[25] We thank the Egyptian Geological Survey and Mining Authority and Mme. Ferial El Bedewi, director of the Cairo Geological Museum, for support of field work. A. A. Barakat, A. A. Abd Ellatif, and W. J. Sanders helped in the field and Y. Attia and P. Chatrath provided logistical support. We thank D. C. Fisher for help in interpreting the locking knee, and P. Webb for information on swimming in anguilliform vertebrates. We thank F. Ankel-Simons, L. G. Barnes, D. L. Domning, D. C. Fisher, C. Gans, P. Myers, C. Ray, G. R. Smith, and F. C. Whitmore for reading the manuscript. Specimens were prepared by W. J. Sanders and illustrated by B. Miljour. Field research in Egypt in 1987 and 1989 was supported by the Duke University Faym Expedition and by the National Geographic Society Committee on Research and Exploration (grants 3424-86 and 4154-89).

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