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PERSPECTIVES: EVOLUTION

The Ancestry of Whales

Kenneth D. Rose

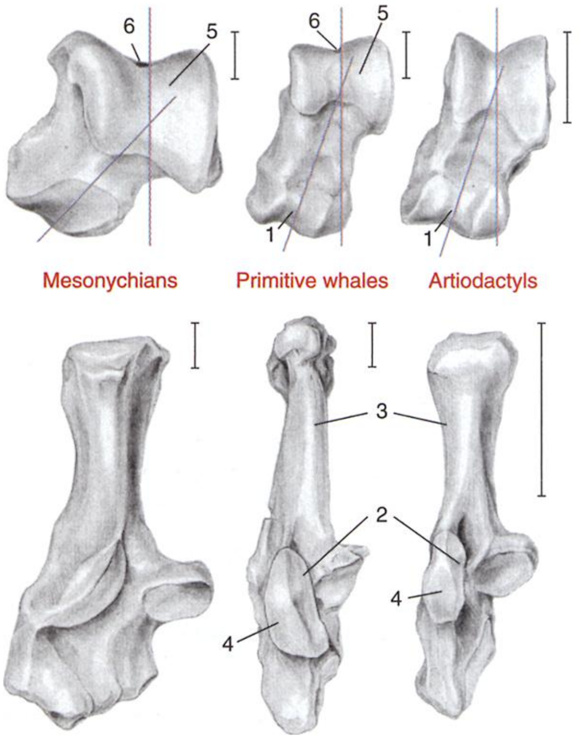
Whales are mammals that moved to the sea about 50 million years ago. Exactly how they are related to other mammals has long been one of the most vexing questions facing mammalogists and paleontologists. In the last decade, mounting evidence that whales are highly specialized ungulates (hoofed mammals) has been bolstered by the discovery of an impressive array of previously unknown fossil whales in Pakistan, India, and Egypt, which largely fill the morphological gulf between land mammals and ocean-dwelling cetaceans (whales, dolphins, and porpoises).

The move to the ocean required many adaptations to living in water, but the earliest whales still closely resembled land animals. One of the most spectacular transitional forms is the "walking whale" *Ambulocetus* from the middle Eocene (about 47 to 48 million years ago). This species had relatively well-developed limbs, paraxonic feet (where the plane of symmetry passes between the third and fourth digits), and hooflike terminal toe bones (*1*).

But fossils have failed to provide conclusive indications of the whales' closest relatives. Instead, they have sparked new controversy. Most recent morphological analyses suggest that mesonychians, an extinct group of terrestrial carnivorous ungulates, form the sister group of cetaceans (*2*, *3*). But molecular systematists maintain that cetaceans belong to the artiodactyls (even-toed ungulates such as sheep, cows, pigs, camels, deer, and hippos) and are in fact the sister group of hippopotami (*4*, *5*).

On page 2239 of this issue, Gingerich *et al.* (*6*) report important new fossil evidence—skeletons of two very primitive ancient whales with well-developed limbs from the middle Eocene of Pakistan—that goes a long way toward resolving the conflict. The fossils provide compelling morphological evidence that whales are not just related to, but descended from artiodactyls rather than mesonychians, thus bringing the morphological evidence into accord with molecular data, at least at the ordinal level.

The most important evidence comes from the shape and orientation of joint surfaces of several ankle bones in the new fossils. These specialized features, typically associated with adaptation to running, have only been observed in artiodactyls and are widely considered diagnostic of the order (see the first figure). Their presence in an animal that was probably better adapted for aquatic than terrestrial locomotion strongly suggests common heritage rather than convergent evolution.



Fossil comparison. Ankle bones of mesonychians, primitive fossil whales, and early Eocene artiodactyls; astragali above, calcanei below. Diagnostic artiodactyl traits present in early whales include a trochlea (grooved joint surface) for the navicular bone (1), modified shape and orientation of articular surfaces between the astragalus and calcaneus [(2) also present on underside of astragalus, not visible here; see supplemental fig. 3 in (*6*)], and a narrow calcaneus with an elongate heel process (3) and a large, convex fibular articulation (4). Primitive mesonychid-like traits present in ancient whales, but not in any known artiodactyl, include a shallower tibial trochlea with more rounded trochlear ridges (5) and retention of a remnant of the astragalar foramen (6), the opening of a canal through which a nerve and vessels pass in primitive mammals. Although mesonychids also have a navicular trochlea, it is much shallower and offset from the tibial trochlea at a greater angle than in primitive whales and artiodactyls. Scale bars, 1 cm.

CREDIT: E. KASMER

Ankles from primitive ancient whales have previously been reported (*7*), but the new specimens are the first that are directly associated with whale skeletons and that are well enough preserved to provide important clues to the relationship between cetaceans and artiodactyls. The specialized ankle characters mentioned above corroborate a close alliance with artiodactyls, but the new skeletons also exhibit several primitive placental traits lost in all known artiodactyls or present only in the most primitive fossil artiodactyls (see the first figure). They thus seem to superimpose artiodactyl traits on a skeletal anatomy that is in some respects more primitive than that of any known artiodactyl.

For example, the forefoot in one of the new fossils (*Rhodocetus*) is mesaxonic (the plane of symmetry passes through the large third digit). This is also the case in two of the most primitive groups of fossil artiodactyls—the early Eocene artiodactyl *Diacodexis* and some anthracotherioids (*8*, *9*)—but almost all other artiodactyls (and mesonychians) have paraxonic forefeet. In addition, the new ancient whale fossils retain a clavicle and a third trochanter on the femur, vestiges of which are found in only the most primitive

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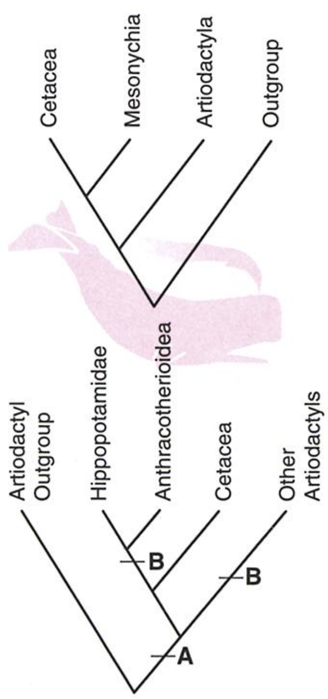
The author is in the Program for Functional Anatomy and Evolution, Johns Hopkins University School of Medicine, Baltimore, MD, 21205, USA. E-mail: kdrose@jhmi.edu

known Eocene artiodactyls (*8*, *10*, *11*). Loss of these features was long considered diagnostic of Artiodactyla. Some of them could represent character reversals or independent losses, but taken together they suggest very early divergence of cetaceans from artiodactyls.



Whales and their relations. (Top) Current hypothesis of relationships based on morphology (*3*, *4*). **(Bottom)** Possible relationships compatible with fossil and molecular data, based on the new fossil data (*6*). A, ankle specializations of ancient whales and artiodactyls; B, other artiodactyl specializations.

Despite this evidence that cetaceans evolved from artiodactyls, substantial discrepancies remain. If cetaceans belong to artiodactyls, then similarities in the cranial and dental morphologies of mesonychians and cetaceans (*2*, *3*) must be a result of convergent evolution or must have been lost in artiodactyls. Furthermore, molecular data favor a sister-group relationship between whales and hippopotami (*5*). This conflicts with the conventional view based on morphology that hippopotami are closer to other artiodactyls than they are to whales (*12*).

Can a special affinity between whales and hippopotami be reconciled with the fossil record? The existing evidence suggests that cetaceans branched very early from artiodactyls, emerging from an unknown basal artiodactyl that had a slightly more primitive ankle than any known artiodactyl, including *Diacodexis* (the oldest artiodactyl) and anthracotherioids. The latter may be ancestral to hippopotami (*13*, *14*).

It is thus conceivable that hippopotami and cetaceans are the only living members of a clade that has been separate from other artiodactyls since before the Eocene (see the second figure). Such a scenario implies that some advanced artiodactyl features evolved more than once: in the anthracotherioid-hippopotamid clade (after the cetaceans diverged) and independently in other artiodactyls.

We are rapidly filling the gaps in the cetacean transition from land to water. Also this week, Thewissen *et al.* (*15*) report slightly older whales from Pakistan that have ankle bones similar to those illustrated here, providing further evidence that this ankle morphology, shared with artiodactyls, was primitive for whales. Two other evolutionary transitions vital to our understanding of the relationship between whales and artiodactyls beg for elucidation: the precise ancestry of hippopotami and the origin of artiodactyls themselves. The answers seem likely to come only from an improved fossil record—perhaps from the same region that has yielded fossils showing that whales evolved from artiodactyls.

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PERSPECTIVES: APPLIED PHYSICS

Optics in the Nano-World

S. W. Koch and A. Knorr

Applications of optical microscopy are generally limited by the standard resolution limit set by the wavelength of visible light. The invention of near-field scanning optical microscopy (NSOM) first enabled this limit to be overcome, opening up many systems, from physics to biology, to investigation by optical microscopy. NSOM offered greatly improved spatial resolution compared with conventional optical microscopy, and the use of tunable excitation sources allowed basic spectroscopic information to be obtained. On page 2224 of this issue, Guest *et al.* (*1*) report the next major step forward in this field. The authors describe a technique that combines the high spatial resolution of NSOM with the high spectral resolution of coherent nonlinear optical spectroscopy.

Optical measurements at the nanometer scale require a light source with an illumination spot in the nanometer range. For visible-light frequencies, where the wavelength is a few hundred nanometers, conventional optical microscopy fails because the resolution is restricted to half the wavelength of the used light (*2*). To overcome this problem, the light must be localized in a spot with a diameter much smaller than the wavelength of the light. Ideally, the spot should have nanometer-scale dimensions. This can be done by applying small apertures (*3*).

The price for this high resolution is that the character of the light changes drastically when it propagates through the aperture. The localization of the light waves results in the formation of evanescent waves, which have an imaginary wave number and decay exponentially in space (in contrast to conventional light waves, which propagate freely). The intensity of an evanescent wave thus decays rapidly as the distance from the aperture increases. Therefore, the aperture has to be close to the object, often only a fraction of the wavelength away. This is the regime of near-field optics.

NSOM techniques have many applications in solid state physics, where substantial efforts are made to design electronic devices with features on the nanometer scale. Electrons can be confined in nanometer-scale structures, called quantum dots (*4*). In these structures, the matter-wave properties of the electrons are changed drastically because the spatial confinement of the electrons approaches the deBroglie wavelength. Their electronic and optical properties therefore differ qualitatively from those of the bulk material.

The atomic landscape encountered by electrons in a quantum dot can be mapped and analyzed with tunneling spectroscopy

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S. W. Koch is in the Department of Physics, Philipps University, 35032 Marburg, Germany. E-mail: stephan.w.koch@physik.uni-marburg.de A. Knorr is at the Institute for Theoretical Physics, Technical University, 10623 Berlin, Germany. E-mail: andreas.knorr@physik.tu-berlin.de