Evolution of Whales from Land to Sea[1]

PHILIP D. GINGERICH
Ermine Cowles Case Collegiate Professor of Paleontology
University of Michigan

THE HISTORY of life on earth extends three billion years back in time, two-thirds of the history of our planet. Every individual that has ever lived is one of countless experiments matching physiology, form, and function carried out in parallel, generation by generation, since life's genesis. If the diversity of organisms living today seems overwhelming, try to comprehend the diversity of all of the organisms that have ever lived. The common man, skeptical of evolution, has my sympathy.

It hasn't been easy to make sense of the history of life. This is the task of paleontology—*paleo-ontology*—the study of "ancient being," or "ancient life." Paleontology traces its roots to Leonardo da Vinci in the fifteenth century and Conrad Gesner in the sixteenth century. Later Nicolas Steno showed that the superposition of geological layers or strata establishes the sequence of their deposition through time. Fossils can be used to recognize the layers, and superposition determines the relative ages of the fossils.

Charles Darwin is sometimes given credit for evolution as though it were something he discovered. However, by the end of the eighteenth century fossils were used routinely to organize and map geological strata. By the time of Darwin's birth in 1809 there were working geological timescales. The terms we use today to represent geological eras (fig. 1), Paleo-*zoic*, Meso-*zoic*, and Ceno-*zoic*, were introduced in 1838, 1840, and 1854, respectively, all before Darwin published the *Origin of Species*. Darwin was a geologist and paleontologist for the first half of his life, and knew there had to be an explanation for the ubiquitous evidence that fossils, recording the history of life, changed through geological time.

In the *Origin of Species*, Darwin proposed natural selection as the explanation. Ironically, many creationists seemingly accept selection

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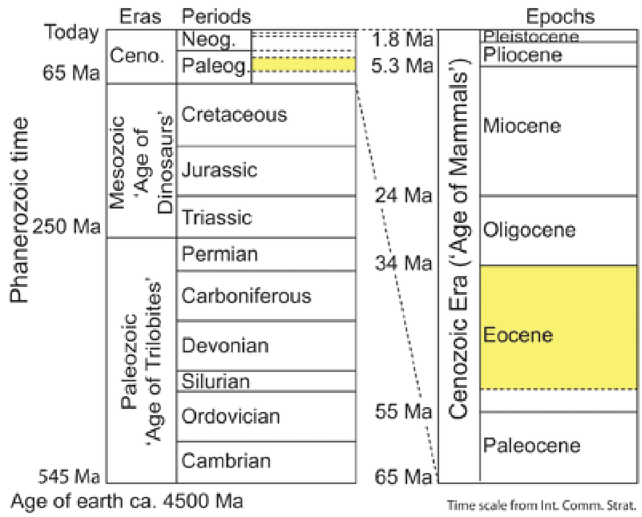

FIGURE 1. Outline of the geological time scale. The time scale is based on the succession of animal life observed during the Paleozoic, Mesozoic, and Cenozoic eras. Animals are abundantly represented by fossils through all three eras. Temporal calibration is in millions of years before present (*Ma*). Note that the Eocene epoch when archaeocete whales lived is shaded. Paleocene and Eocene epochs together are sometimes called the "greenhouse earth" part of the Cenozoic, in contrast with the following Oligocene through Pleistocene "icehouse earth" with its polar icecaps. Ancestral archaeocetes were replaced by descendant Mysticeti and Odontoceti in response to greenhouse-to-icehouse climate change.

and change on a small scale, while denying its power to produce the diversity of forms we see in the fossil record. Evidence for the geological time scale and evidence for evolution are one and the same: fossils changing through geological strata and geological time.

If fossils are plentiful and the course of life complicated, so be it. We don't have to study all lines of evidence at once. Here I will focus on whales as a case in point, documenting the changes we see through a critical twenty-million-year interval early in their evolution.

WHALE EVOLUTION

My interest in whale evolution started some thirty years ago with a chance discovery in Pakistan. A creationist caricature published in response to this work (fig. 2) made me realize that whale evolution is a hot-button issue. It also made me realize the necessity of knowing intermediate stages. How could I, or anyone, comprehend a transition as great as the evolution of whales from land to sea without the intermediate stages?

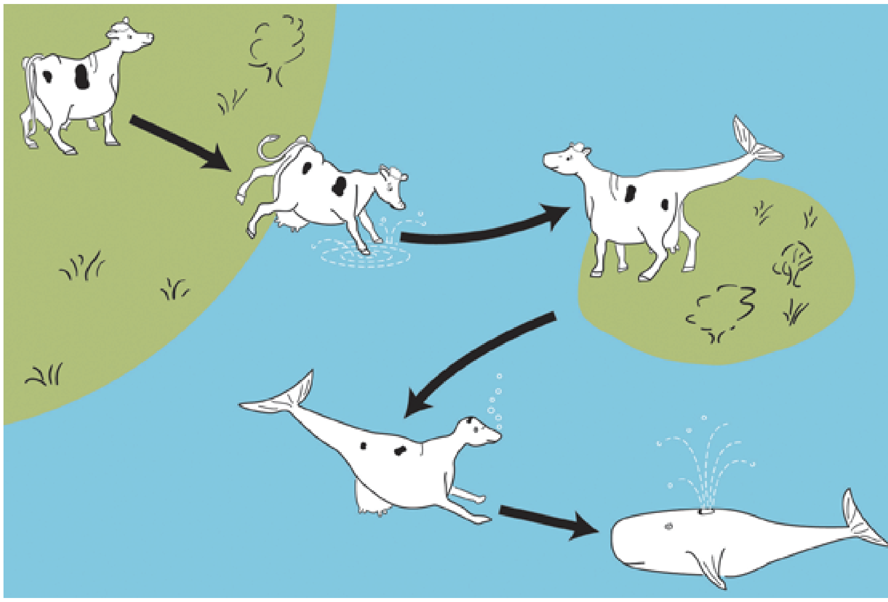

FIGURE 2. Creationist caricature of whale evolution distributed by Luther Sunderland. This appeared in 1984 following publication of our 1983 *Science* cover article on *Pakicetus*. Sunderland's point was well made: anyone expected to understand that whales evolved from early artiodactyls (ancestors of cows, sheep, deer, hippos, etc.) must be shown stages that are intermediate in time, morphology, and physiology.

Life on land seems safe. It is what we are used to. Mammals have been evolving on land for two hundred million years, through much of the Mesozoic and all of the Cenozoic. Many things have to change for a mammal to live in the sea (fig. 3). Here I will focus on the most salient characteristics and the ones most easily documented in the fossil record: modifications of the land-mammal body and its supporting skeleton to enable whales to swim efficiently in water.

Whales have three advantages for evolutionary studies: (1) they are living today so they are familiar; (2) they are large so they are easy to see and study; and (3) they live in water where they are easily buried so they have an excellent fossil record. Whale fossils change through time, documenting evolution and making the evidence accessible even for skeptics.

I should mention here that public description of the first archaic whale ever known, by Philadelphia naturalist Richard Harlan, took place in the chambers of the American Philosophical Society in 1832—more than 175 years ago. These came from the Eocene of Louisiana, and Harlan, mistaking the whale for a sea serpent, named the animal *Basilosaurus* ("king lizard"; Harlan 1834).

Function	*Land*	*Sea*	*Change*
1. Breathe	Air	Air	—
2. Nurse	Milk	Milk	—
3. Drink	Fresh water	Sea water	X
4. Eat	Plants and animals	Fish and plankton	X
5. Move	Walk, run, swim, or fly	Swim	X
6. Swim	Paddle with limbs	Push water with a tail fluke	X
7. See	Eyes and light	Ears and sound	X
8. Communicate	Sound and light	Sound	X
9. Hear	Tympanic membrane	Tympanic bone	X
10. Temp. regulation	Hair or fur	Blubber	X
11. Mate	Land	Sea	X
12. Give birth	Head first	Tail first	X

FIGURE 3. The evolution of whales from land to sea required major change in ten of the twelve physiological functions listed here. Whales continue to breathe air with lungs and nurse with mammary glands, as do land mammals.

The first one hundred years of archaeocete studies were summarized in APS member Remington Kellogg's classic *Review of the Archaeoceti* (Kellogg 1936). This was so comprehensive that it effectively stopped research on early whales for the next fifty years, because it seemed that everything was known that could be studied. Kellogg viewed archaeocetes as "descended from some primitive insectivore-creodont stock" and regarded them as "collateral derivatives of the . . . blood-related stock from which the Mysticeti and the Odontoceti sprang" (Kellogg 1936, 343). We now know that archaeocetes evolved from early Artiodactyla, not from an insectivore-creodont stock, and that they were directly ancestral to both baleen whales (Mysticeti) and toothed whales (Odontoceti; fig. 4), not collateral derivatives (Fordyce and de Muizon 2001; Gingerich 2005; Uhen 2010).

STAGES OF DISCOVERY

Pakicetus *from Pakistan*

The chance discovery that sparked my interest in whale evolution was made in the North-West Frontier Province of Pakistan, where I led an American-French team searching for Eocene land mammals. In 1977 we found these at a site of early middle Eocene age (48 Ma) near the village of Chorlakki. When we returned the next year, my colleague Jean-Louis Hartenberger noticed bone in a block of red

Order CETACEA
  Suborder MYSTICETI: latest Eocene or early Oligocene (34 Ma) to present
    Baleen whales
  Suborder ODONTOCETI: early Oligocene (34 Ma) to present
    Toothed dolphins, porpoises, and sperm whales
  Suborder ARCHAEOCETI: early to late Eocene (ca. 50 to 34 Ma)
    Family Basilosauridae
      Basilosaurus isis: late Eocene of Egypt (37 Ma)
      Dorudon atrox: late Eocene of Egypt (37 Ma)
    Family Protocetidae
      Protocetus atavus: middle Eocene of Egypt (ca. 45 Ma)
      Rodhocetus balochistanensis: middle Eocene of Pakistan (47 Ma)
      Artiocetus clavis: middle Eocene of Pakistan (47 Ma)
      Maiacetus inuus: middle Eocene of Pakistan (47 Ma)
    Family Remingtonocetidae
      Remingtonocetus harudiensis: middle Eocene of Pakistan (41 Ma)
    Family Ambulocetus
      Ambulocetus natans: middle Eocene of Pakistan (48-47 Ma)
    Family Pakicetidae
      Pakicetus attocki/inachus: middle Eocene of Pakistan (48 Ma)
      Himalayacetus subathuensis: early Eocene of India (ca. 53 Ma)

FIGURE 4. Outline classification of the mammalian order Cetacea listing one or more genera and species representing each of the five families of Archaeoceti. Three here, Pakicetidae, Protocetidae, and *Dorudon* within Basilosauridae, are generalized enough to lie on the main line of cetacean evolution, while Ambulocetidae, Remingtonocetidae, and *Basilosaurus* within Basilosauridae are specialized side branches.

conglomeratic matrix. He broke the block open and revealed the well-preserved braincase of a mammal a little larger than a wolf. We cataloged this as a "creodont skull" and borrowed it for further preparation at the University of Michigan. After it was cleaned, two things were clear: (1) the braincase was small for the size of the skull; and (2) the tympanic bulla covering the middle ear was small, but dense and whale-like. Colleagues Ewan Fordyce and Lawrence Barnes confirmed that the skull was cetacean because of the characteristic "sigmoid process" on the tympanic bulla. We named the new whale *Pakicetus inachus* (*Paki-cetus* meaning "Pakistan whale") and put it in its own subfamily or family Pakicetinae or Pakicetidae (Gingerich and Russell 1981).

The partial cranium of *Pakicetus* was the oldest evidence of whales known at the time, it came from a continental red-bed deposit that accumulated in a coastal river, it was associated with land mammals, and it had periotic ear bones showing none of the separation from surrounding skull bones necessary to hear directionally in water. Teeth and a partial jaw from the same deposit, referred to *Pakicetus*, were like those of later archaeocetes. The anterior teeth were simple and pointed, while the molar teeth still had shearing crests. We interpreted *Pakicetus* as semiaquatic, supporting the general inference that whales evolved from a terrestrial ancestor. We further suggested that whales made a gradual transition from land to sea in the early Eocene, spending progressively more time feeding on planktivorous fishes in shallow, highly productive embayments associated with closure of the ancient eastern Tethys Sea as the Indian Subcontinent became a part of Asia (Gingerich et al. 1983).

Later research on similar red-bed deposits elsewhere in Pakistan yielded postcranial bones referred to *Pakicetus*. These became controversial when they were interpreted, with little explanation, to portray *Pakicetus* as a terrestrial mammal, with running rather than swimming adaptations (Thewissen et al. 2001). Measured consideration of the evidence reveals four lines of evidence that favor interpretation of *Pakicetus* as semiaquatic rather than terrestrial: (1) the hearing mechanism of *Pakicetus* is intermediate between those of land mammals and aquatic cetaceans (Thewissen and Hussain 1993); (2) *Pakicetus* has a short ilium bone of the pelvis, and multivariate analysis of semiaquatic mammals indicates that a short ilium is the most important skeletal measure indicating aquatic adaptation (Gingerich 2003); (3) postcranial bone microstructure demonstrates that pakicetids were highly derived semiaquatic mammals (Madar 2007); and (4) finger and toe bones (not yet described) are long and slender like those of semiaquatic *Maiacetus* and *Rodhocetus*. A reconstruction of *Pakicetus* consistent with this evidence is shown in figure 5.

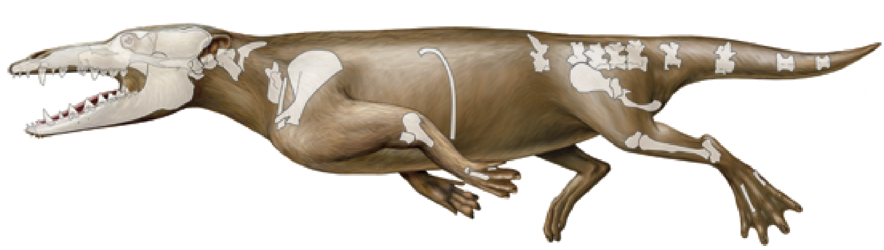

FIGURE 5. Reconstruction of the 48-million-year-old (48 Ma) pakicetid archaeocete *Pakicetus attocki* based on the isolated postcranial bones described by Madar (2007). There is no complete skeleton of *Pakicetus*, but enough is known to show that it was semiaquatic, not terrestrial, and probably a foot-powered swimmer like *Maiacetus*. Skeleton is estimated to have been about 1.4 meters long. Illustration is by John Klausmeyer, University of Michigan Exhibit Museum.

Basilosaurus *and* Dorudon *from Egypt*

The Soviet Union invaded Afghanistan in December of 1979, which soon stopped paleontological field work in neighboring parts of Pakistan. I started field work in Egypt in 1983 with the modest goal of collecting one or two comparative specimens for ongoing interpretation of fossil whales from Pakistan. The site targeted, "Zeuglodon Valley," had been known since 1905 but was rarely visited. It proved to be extraordinarily rich in exceptionally well-preserved fossil whales. I eventually gave the site an Arabic name, Wadi Hitan or Wadi Al Hitan ("Valley of Whales"), and it is now an internationally known and much-visited UNESCO World Heritage Site. Most fossils known from Wadi Al Hitan are late Eocene in age (37 Ma).

In 1983 Elwyn Simons, Holly Smith, and I collected jaws of a smaller juvenile whale and parts of the skull and jaws of a much larger adult. In 1985 we collected additional specimens, making it clear that two different genera and species were represented: the smaller was *Dorudon atrox* and the larger was *Basilosaurus isis*. Both belong to the archaeocete family Basilosauridae. By 1987 and 1989 we had read Kellogg (1936) thoroughly, and our focus was on mapping and measuring fossils in the field while looking for parts of the skeleton that weren't known to Kellogg. In 1989 another chance discovery led to a knee, the first known for a whale, on a skeleton of *Basilosaurus*. Now, knowing where to look, we soon found complete pelves and leg, ankle, foot, and toe bones of *Basilosaurus* (fig. 6; Gingerich et al. 1990).

Knowing how fast evolution can be, I thought that once legs, feet, and toes lost their function they would disappear in a few hundreds or thousands of generations (an instant to a geologist). Such change wouldn't require the million or more generations separating *Basilosaurus* from *Pakicetus* when whales first took to the water. The pelves of *Basilosaurus* didn't connect to the backbone, and its legs were small in comparison with the size of the skeleton, but the legs, feet, and toes were still present. My thoughts soon turned to Pakistan and *Pakicetus*, and to the eleven-million-year time difference separating *Pakicetus* and *Basilosaurus*. What did the legs of older *Pakicetus* and any intermediate whales look like?

We continued to work in Egypt and collected several nice skeletons of *Dorudon* in 1991 and 1993. These were the first complete skeletons of any archaeocete, and showed for the first time the number of vertebrae in an archaeocete skeleton, the size and proportions of the hands, and again the presence of reduced hind limbs and feet. Mark Uhen described and analyzed the new specimens in his Ph.D. dissertation (Uhen 2004). *Dorudon* was clearly a tail-powered swimmer like modern

FIGURE 6. Dr. B. Holly Smith searching for foot bones near the base of the tail of a *Basilosaurus isis* skeleton during a 1991 expedition in Wadi Al Hitan in Egypt. The first evidence of knees, ankles, feet, and toes in whales was found at Wadi Al Hitan. This site, with hundreds of Eocene archaic whale skeletons exposed at the surface, is now a UNESCO World Heritage Site and open-air museum. Inset shows reassembled 15-cm-long foot of a 15-meter-long *Basilosaurus* (Gingerich et al. 1990).

whales. A reconstruction of *Dorudon* consistent with the skeletal evidence is shown in figure 7.

Rodhocetus, Artiocetus, *and* Maiacetus *from Pakistan*

The Soviet invasion of Afghanistan ended in February 1989, the year we found legs, feet, and toes on *Basilosaurus*. By 1991 I was working in Pakistan again. In 1993 graduate student Xiaoyuan Zhou found the articulated skeleton of a new protocetid whale *Rodhocetus kasranii* in western Punjab Province (Gingerich et al. 1994). It had a large pelvis attached to the backbone, and one upper leg bone (femur) was complete. However, the skeleton was also frustrating because it lacked the forelimbs, lacked the hind limbs below the knee, and lacked all but the base of the tail. Several more articulated skeletons were found in the 1990s, but it wasn't until we moved our field area to eastern Balochistan Province in 2000 (fig. 8) that we found what we were seeking.

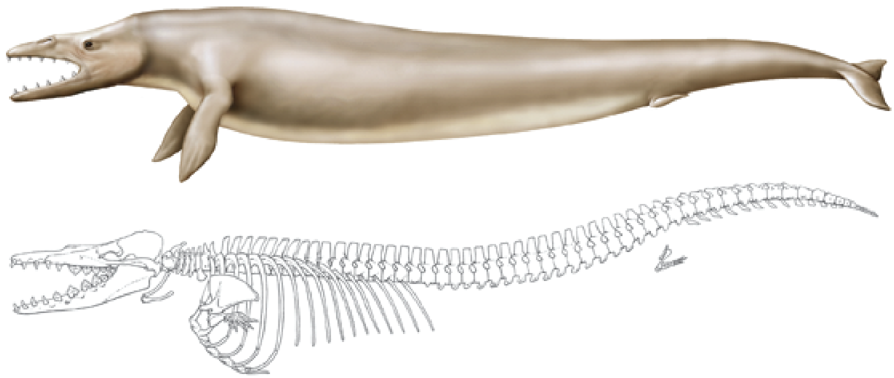

Figure 7. Reconstruction of the 37-million-year-old (37 Ma) late Eocene basilosaurid archaeocete *Dorudon atrox* from Wadi Al Hitan in Egypt. Several virtually complete skeletons are known, described by Uhen (2004). These were the first to preserve all vertebrae, complete forelimbs with hands, and *Basilosaurus*-like hind limbs. Terminal caudal vertebrae are flattened dorsoventrally like those of modern cetaceans, indicating the presence of a tail fluke. *Dorudon* was a fully aquatic tail-powered swimmer. Skeleton is 4.9 meters long. Illustration at the top is by John Klausmeyer, University of Michigan Exhibit Museum.

Figure 8. Rest during a "long march" looking for fossil-bearing strata in Balochistan Province of Pakistan. Men at left are Munir ul-Haq and Intizar Hussain Khan of the Geological Survey of Pakistan, Philip Gingerich of the University of Michigan, and Muhammad Arif of the Geological Survey of Pakistan. The three men at right are tribal guards. Photo by Iyad Zalmout.

On our first day in the field in Balochistan, graduate student Iyad Zalmout found a piece of an astragalus, and Pakistan geologist Munir ul-Haq found another. The two pieces fit together to make a complete bone, with, to my great surprise, a grooved surface or trochlea on each end. This "double-pulley" astragalus was part of a protocetid skeleton that included an exceptionally well-preserved skull. The skull and partial skeleton were eventually named *Artiocetus clavis* (Gingerich et al. 2001). A week or so later Munir ul-Haq found much of the skeleton of the protocetid *Rodhocetus balochistanensis*, and this too had a "double-pulley" astragalus. Finally, to cap the 2000 field season, Iyad Zalmout found what became the type specimen of the protocetid *Maiacetus inuus*, a female with a near-term fetus in utero (Gingerich et al. 2009). The airplane hijackings of 11 September 2001 effectively ended our Pakistan field work, but on a final 2004 expedition Zalmout and Haq found the complete skeleton of a male *Maiacetus inuus*, which is illustrated in figure 9.

For those in the know, a "double-pulley" astragalus is diagnostic of the mammalian order Artiodactyla, the group including modern cows, sheep, deer, hippos, etc. (fig. 10). Our discovery of double-pulley astragali in the skeletons of protocetid whales ended a long debate with molecular biologists, who argued that whales are genetically artiodactyls. Paleontologists like Leigh Van Valen thought whales were related to Artiodactyla, but derived the two groups independently from extinct Condylarthra (Van Valen 1966). Our finding of double-pulley astragali in skeletons of early whales meant that the relationship was much closer, as molecular biologists had inferred. Molecular phylogenies are always simple in some sense (omitting extinct relatives and optimizing resemblance among living taxa using parsimony or relative likelihood).

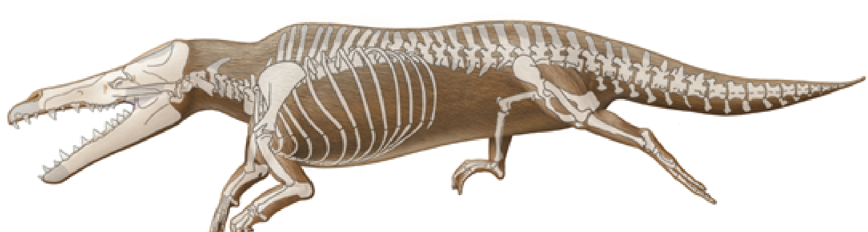

FIGURE 9. Reconstruction of the 47-million-year-old (47 Ma) protocetid archaeocete *Maiacetus inuus* based on a complete skeleton described in Gingerich et al. 2009. Terminal caudal vertebrae are not flattened dorsoventrally and *Maiacetus* clearly lacked the tail fluke of modern cetaceans. *Maiacetus* was a semiaquatic foot-powered swimmer. Skeleton is 2.6 meters long. Illustration is by John Klausmeyer, University of Michigan Exhibit Museum.

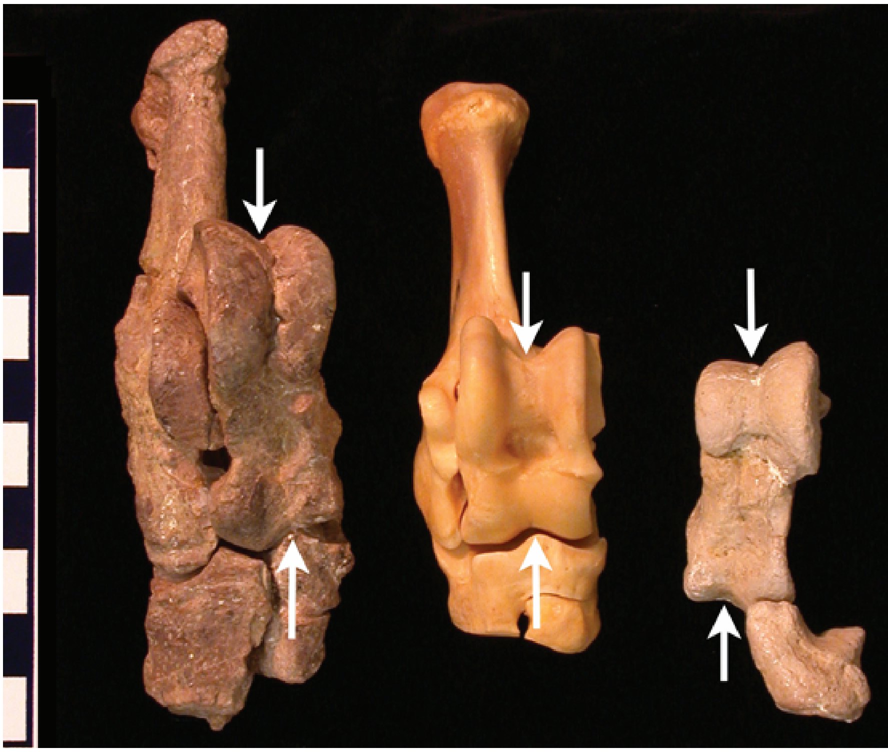

FIGURE 10. Ankle bones of middle Eocene protocetid *Rodhocetus balochistanensis* (left), modern pronghorn antelope *Antilocapra americana* (center), and middle Eocene protocetid *Artiocetus clavis* (right). Top arrow in each points to the proximal trochlea (pulley) of the astragalus bone for articulation with the tibia of the lower leg, and bottom arrow points to the distal trochlea of the astragalus for articulation with the foot. Double-pulley astragali like these are diagnostic of the mammalian order Artiodactyla (even-toed hoofed mammals), and finding such specialized astragali in early whale skeletons indicates the close relationship of whales to artiodactyls. Scale at left is in cm.

In this instance the fossil record confirmed the connection of living Cetacea (through Archaeoceti) to Artiodactyla.

STAGES OF WHALE EVOLUTION

There are many advantages to finding whole skeletons of fossil whales. These include enabling a thorough comparison of fossil whales with each other, enabling comparison with a diverse range of mammals to place the whales in behavioral and functional context, and constraining the speculation about similarities and differences that inevitably ensues when important elements are missing. Comparison of fossil whales with each

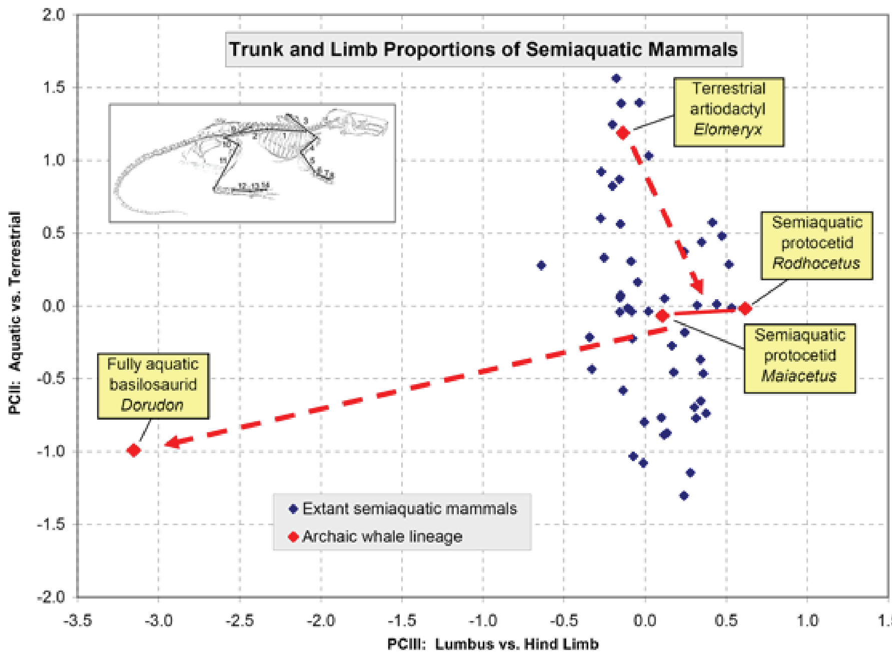

FIGURE 11. Principal components graph of 14 trunk and limb skeletal proportions (inset) for a representative sample of 50 species of extant semiaquatic mammals. PC axis I (not shown) separates species by size. PC axis II (ordinate) separates aquatic and terrestrial species. PC axis III (abscissa) separates tail-powered from foot-powered swimmers. Adding fossils, we see that whales evolved from a terrestrial early Eocene artiodactyl, represented structurally by *Elomeryx*, to middle Eocene foot-powered swimmers like *Rodhocetus* and *Maiacetus*, to middle and late Eocene tail-powered swimmers like *Dorudon* (dashed line). Inset skeleton is that of the Russian desman, a foot-powered swimmer that resembles *Rodhocetus* closely in skeletal proportions. Modern fully aquatic whales cannot be graphed because they lack the femur, tibia, and foot elements included in the analysis. However, simulation experiments making the femur, tibia, and foot progressively smaller in *Dorudon* move it farther to the left and off the chart, which gives an indication of where modern whales would lie if they could be plotted. Analysis is more fully explained in Gingerich (2003) and Gingerich et al. (2009).

other and comparison with a diverse range of mammals in functional context are illustrated in figure 11. Here the relative sizes of bones in the forelimb, torso, and hind limb for each fossil skeleton are compared with each other and simultaneously compared with proportions in a broad range of living semiaquatic mammals for which we know the mode of swimming. Possible structural ancestors of whales like *Elomeryx*, protocetid whales like *Maiacetus* and *Rodhocetus*, and basilosaurid whales like *Dorudon* separate into three seemingly discrete structural stages of whale evolution. These represent a primitive terrestrial

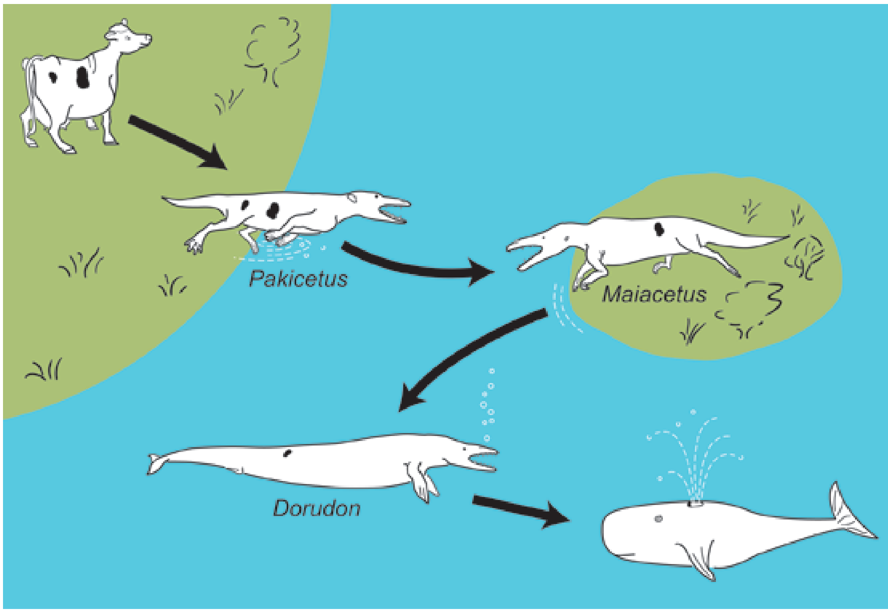

FIGURE 12. Stages in the evolution of whales from land to sea. (A) *Elomeryx* is a model artiodactyl land-mammal ancestor; (B) *Pakicetus* is a 48 Ma semiaquatic archaeocete incapable of directional hearing in water; (C) *Maiacetus* is a 47 Ma semiaquatic foot-powered swimmer with jaws and ears modified for hearing in water; (D) *Dorudon* is a 37 Ma fully aquatic tail-powered swimmer with reduced hind limbs that makes a good structural ancestor for Oligocene-to-Recent modern Odontoceti and Mysticeti.

stage, a more-advanced semiaquatic stage of foot-powered swimming, and an even more advanced fully aquatic stage of tail-powered swimming. Modern whales are fully aquatic, too; swim with a fluked tail; and have lost any trace of an external hind limb.

To understand how these stages tie together, it is useful to return to the creationist caricature of figure 2. This has been redrawn in figure 12, maintaining the spirit of the original. We now know that whales are most closely related to artiodactyl mammals living on land, not Holstein cows per se, but Holsteins can serve symbolically. The cartoon stage where whales entered the water and became semiaquatic can be represented by early middle Eocene *Pakicetus*, which lacked critical specializations for hearing in water but, to the extent it is known, had a skeleton modified for swimming. Whales probably never went through a cartoon stage combining hooves on their feet with flukes on their tails, but otherwise this advanced semiaquatic stage can be represented by middle Eocene *Maiacetus*, which had an enhanced ability to hear in water and swam with its feet, but still came out on land to give birth.

The cartoon stage with a fully aquatic whale swimming with a fluked tail is nicely represented by the late Eocene archaeocete *Dorudon*. Finally, modern whales are modern whales, differentiating into Mysticeti and Odontoceti. Thanks, creationists, for asking to see the intermediate stages.

Does the story end here? No, this is science, and the enquiring mind wants to know more. What group of early artiodactyls gave rise to whales, and can we find intermediates between terrestrial artiodactyls and *Pakicetus*? How did whales develop the specializations for hearing that first appeared in protocetids like *Maiacetus*? How did whales make the transition from foot-powered swimming in *Maiacetus* to tail-powered swimming in *Dorudon*? And how did a late Eocene *Dorudon*-like ancestor give rise to modern Mysticeti on one hand and Odontoceti on the other? When and how did whales make the physiological transitions listed in the table in figure 3? We still have much to learn!

Acknowledgments

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