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Progress on the Origin of Whales

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Whales are often in the news, and I think this is because we somehow see ourselves in them. We see the mystery of our intelligence in the mystery of their intelligence. We see the mystery of our origin in the mystery of theirs. And whales are literally 'extraterrestrials,' having moved from land to sea, which heightens their interest too. The most recent news about whales stems from a discovery we made last year in Pakistan. This was published in *Science* where it was featured on the cover (Fig. 1). We were able to report a long-sought breakthrough in understanding the origin of whales.

We see the mystery of our intelligence in the mystery of their intelligence

There are some eighteen major groups or 'orders' of mammals living today. One of these is Primates, including lemurs, monkeys, apes, and us. Another is Artiodactyla, including the even-toed or split-hoofed plant-eaters like cows, deer, hippopotami, etc. A third is Cetacea, including all of the great whales and the smaller dolphins and porpoises. Surprisingly, few of the eighteen orders can be traced back to any common ancestry in the fossil record. We know they are related, but our theories of genealogy depend more on inference than on direct fossil evidence.

Figure 1. Reconstruction of Rodhocetus *from the early middle Eocene showing the hoofs it retained on the middle digits of the hand, and its long, delicate webbed feet. Body proportions suggest that it lived much like sea lions do today, feeding in the sea but still coming onto land to breed and give birth. Painting is by John Klausmeyer of the U-M Exhibit Museum.*

Inference of horizontal 'sister' relationships of living animals is the stock in trade of molecular biologists specializing in phylogeny. Paleontology, in contrast, is a much more historical science and we are primarily interested in vertical ancestry and descent through time. When fossils are missing we have to admit that we just do not yet know how a group originated. Molecular biologists have become insistent in recent years that whales are most closely related to plant-eating artiodactyls and to hippos in particular. Paleontologists have generally accepted a distant relationship to artiodactyls, but have drawn the connection through a group of extinct Paleocene-Eocene meat-eating mammals called mesonychids.

When proponents of different methods cannot agree, everyone suffers, because there is no way to know who is

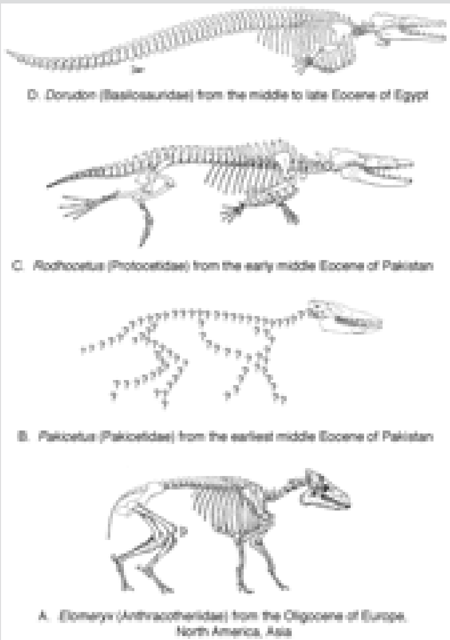

Figure 2. Four stages in the evolution of whales from even-toed artiodactyls. A, early land-dwelling anthracotheriids ('coal beasts') are now thought to be close to the origin of both whales and hippos. B, pakicetids are a critical stage in the transition from land to sea but lack associated skeletons. C, protocetids are now, as of 2001, known from complete skeletons showing that their ankle was artiodactyl-like, while the foot as a whole shows they were predominantly aquatic. D, basilosaurids such as Dorudon *are known from complete skeletons from Egypt showing that they were fully aquatic and could not have supported their weight on land.* Dorudon *was the subject of a 1996 Ph.D. dissertation in Geological Sciences by Mark Uhen. Animals shown here range from two to five meters in body length. Drawings are adapted from Scott, 1894; Gingerich, 1983; Gingerich et al., 2001; and Gingerich and Uhen, 1996). Undergraduate Doug Boyer drew the skeletal reconstruction of* Rodhocetus.

right and who is wrong. Mesonychids are extinct and cannot be analyzed by molecular genetic methods, so the only way to test whether whales are related to artiodactyls through mesonychids or through hippos is to find fossils tracing whales back in time. This is more easily postulated than done, as I can illustrate by summarizing where we stand after some 25 years spent tracing the early evolution of whales.

What I outline here is based on twenty U-M fossil-collecting expeditions to Pakistan and Egypt. These have involved many U-M students over the years, and international experience for students has always been part of their rationale. The Egyptian interlude was dictated by the Soviet invasion of Afghanistan, which made field work in the tribal areas of Pakistan impossible. As of this writing, war in Afghanistan has again delayed our field work.

Whales or Cetacea are marine mammals that look and live like fish. Whales differ of course in being warm-blooded and nursing their young like we do. A whale's body is virtually all head and tail, separated by a short neck and thorax. The front limbs are modified into flippers extending from the sides of the body. The hind limbs have completely vanished externally. Whale tails are muscular and have a broad, horizontal 'fluke' at the end. This is the hydrofoil that propels a whale as it is forced up and down through the water. Fish are similar, but propel themselves by side-to-side movements of a vertical tail. Neither moves like a land mammal!

There are two kinds of whales living today: toothed whales and baleen whales. Both can be traced from the present back to the Oligocene, when modern patterns of ocean circulation, heat transport, and upwelling were established. Whales from the Eocene belong to a third group of ancestral Archaeoceti or archaic whales, which are both older and more primitive in numerous ways. It is useful to recognize three progressively older and more primitive stages within Archaeoceti: Basilosauridae, Protocetidae, and Pakicetidae (Fig. 2).

The first archaeocete was described from North America in 1834, when it was thought to be a giant marine reptile and named *Basilosaurus* ('king lizard'). Backbones of *Basilosaurus* are shaped like thick foot-long logs and pretty much all look the same. This modularity had great potential, and in the 1840s the German showman Albert

Koch exhibited a 114-foot version called '*Hydrargos sillimanii*' on Broadway and elsewhere for a 25¢ admission fee. Koch's *Basilosaurus* was named for Benjamin Silliman, Yale's then widely known professor of chemistry and natural history, and founder of the venerable *American Journal of Science*. This gave *Hydrargos* some temporary scientific respectability, but the number of backbones and the true length of the skeleton were not known until the 1980s when we found and mapped dozens of good *Basilosaurus* skeletons in the Western Desert of Egypt. None were complete, but careful construction of a composite indicated that *Basilosaurus* had 66-68 backbones in a skeleton totaling 'only' 18 m or 58-60 ft in length. To our astonishment, we also found that *Basilosaurus* and its close relative *Dorudon* (Fig. 2D) retained functional hind limbs with feet and toes, which raised the possibility that older archaeocetes might retain distinctive ankle bones enabling us to tell whether they evolved from mesonychids or from hippo-like artiodactyls.

Once we found and documented good skeletons of basilosaurids, the next challenge was to understand protocetids. These are primitive in retaining a backbone with a bony connection to the pelvis and hind limbs, meaning that they could still support their weight on land. Our Pakistan field work in the 1990s focused on protocetids, and yielded many skulls and partial skeletons representing a surprising diversity of forms. The new skeletons were frustrating though because all were missing their fore- and hind limbs and most of the tail, which seem to have been removed by scavengers before burial. There is just no substitute for finding limbs and tails together with skulls and backbones, and in 1999 I realized that we had to search for whales in different environments if we were going to find hands and feet.

Thus in 2000 we concentrated field work in a new area on the west side of the Sulaiman Range, in the highlands of eastern Balochistan. We moved here expecting that paleogeographically we would be farther off the Indo-Pakistan subcontinent and farther out in Tethys, finding fewer whales in deeper water, and hoping that these would be less disturbed by scavengers. Only one of these expectations turned out to be true, but it was the one that really mattered! We are now working in shallower water closer to shore (its own tectonic and paleogeographic mystery), but we are finding whales at the same rate and these are virtually undisturbed by scavengers.

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Figure 3. Photo comparison of ankle bones of the primitive protocetids Rodhocetus *(left) and* Artiocetus *(right) with those of a modern pronghorn (center). The* Rodhocetus *and pronghorn ankles are from the right foot, while that of* Artiocetus *is from the left foot. Note the 'double-pulley' structure of the astragalus bone (arrows) connecting the foot to the lower leg, and the notched cuboid (asterisk) below the astragalus, which together are diagnostic of artiodactyls.*

The first of the whales found in 2000 was located our first morning in the field when graduate student Iyad Zalmout called me to look at bone fragments weathering out on the surface. Geological Survey of Pakistan [GSP] geologist Munir ul-Haq and I joined him. Iyad gave me a grooved piece of bone he had already recognized as the body of a left astragalus, a critical ankle bone for testing how closely whales are related to artiodactyls. At the same time Munir picked up another that I thought was the similarly-grooved body of the right astragalus. I worried for five minutes about why the symmetry seemed distorted, and then realized that, miraculously, the two pieces fit together to make a single complete astragalus. It was grooved on both ends because it was a 'double-pulley' astragalus characteristic of artiodactyls (Fig. 3). Excavation revealed much of the rest of the skeleton, including the best protocetid skull ever found. This belonged to a new whale that we named *Artiocetus* to emphasize the resemblance of its ankle to that of artiodactyls. The most complete hands and feet were found later and belonged to a different whale called *Rodhocetus* (Fig. 2C).

The most primitive group of archaic whales is Pakicetidae named for the earliest middle Eocene whale, *Pakicetus* (Fig. 2B), that we found in Pakistan in the 1970s. There are not as yet any associated skeletons of Pakicetidae, so it is impossible to know how aquatic *Pakicetus* may have been. A study by J. G. M. Thewissen and others published in *Nature* recently claimed that *Pakicetus* was a terrestrial runner, based on isolated bones found in a quarry where pakicetid and land mammal bones are mixed together–circumstances unlikely to convince many skeptics. The oldest pakicetid, *Himalayacetus*, was found in marine strata, so it is hard to understand how *Pakicetus* could have been terrestrial. Such an interpretation also contradicts aquatic features of the ears and skull bones in the original specimen of *Pakicetus* that first indicated a relationship to whales.

Why is what we found in 2000 so important? The skeletons we found are paleontological 'Rosetta stones' in the sense that each combines clear evidence of whales with clear evidence of artiodactyls *preserved in the very same skeleton*. These skeletons resemble archaic whales because they have the distinctive skulls and teeth of archaeocetes, and they resemble artiodactyls because they have the distinctive ankle structure of artiodactyls. The evolutionary line connecting whales and artiodactyls did not go through carnivorous mesonychids. Further, the hand and foot bones of *Rodhocetus* resemble anthracothere or 'coal-beast' artiodactyls in particular (Fig. 2A). Anthracotheres are the group of artiodactyls that hippos are thought to have been derived from, which suddenly makes a 'sister' relationship of whales and hippos plausible. Thus it appears that our molecular colleagues were right all along and the fossil record is now saying the same thing. Whales are derived from artiodactyls, and we can move on to focus on when and where and how whales became aquatic, and how herbivorous anthracotheres became carnivorous whales. Finding an articulated skeleton of a pakicetid would be a good place to start.

What does it take to carry out a successful expedition in Pakistan? There are five co-authors on our 2001 *Science* report: me, Munir, Iyad, Intizar Hussain Khan, and M. Sadiq Malkani. We were the scientists in the field making the discoveries, but there were a lot more people involved before the *Science* report came out. A proposal to work where we did was developed with the advice of the Director General, Mr. S. Hasan Gauhar, and three Directors at GSP headquarters in Quetta, Messrs. Abdul Latif Khan, S. Ghazanfar Abbas, and Dr. Imran Khan. Balochistan is virtually all tribal, and foreigners must be cleared by national and provincial security bureaus. On the road and in the field we five geologists moved with three drivers, three cooks, and at least one 'levi' guard in each car, making a field party of fourteen or more. Help for supplying the camp with water or excavating whales was always hired locally. Security is a big concern and camping involved finding suitable walled enclosures surrounding schools, medical dispensaries, or government rest houses where cars, equipment, and people could be protected at night.

Fossil skeletons were removed from the field in 40-50 kg blocks of rock tightly bandaged in burlap and plaster. These were shipped by air to Michigan, where William Sanders and undergraduate assistant Joseph Groenke in the Museum of Paleontology opened the bandaged specimens and prepared them for study.

Figure 4. Tea in the field with drivers and guards at the end of a successful day! Graduate student Iyad Zalmout is standing; GSP geologist Munir ul-Haq, who spent winter term 2001 in Ann Arbor, is in the cap at left; and Muhammad Arif, who spent the summer of 2000 here is second from right.

We are greatly indebted to William Sanders for making the most of fossils that did not always look like much when they were collected. Technical illustrations for the Science paper were prepared by Museum artist Bonnie Miljour and by undergraduate Doug Boyer. The Science cover illustration was prepared by John Klausmeyer, and casts for exhibition were prepared by Dan Erickson of the of the U-M Exhibit Museum. When you add eight manuscript reviewers, the work became a collective effort of some three dozen collaborators! Thanks too to the National Geographic Society and the National Science Foundation for providing field and laboratory funds making this collaboration possible.