The Origin of Whales and the Power of Independent Evidence
Raymond Sutera

[How in the world could a whale evolve from some land-dwelling four-legged animal? On the basis of a number of other apparent transitions between other groups of animals, inferred from a number of intermediate forms, along with several other lines of evidence, it has long been asserted by scientists that whales HAD to do this too, that in fact ALL living things have evolved from earlier forms over vast periods of time. Dissenters have pointed out the many unique features of whales, perfectly adapted to their very special oceanic niche, and have claimed that there is no way such magnificent creatures could have developed by gradual changes over time from a totally different kind of animal. This view has been seemingly confirmed by the absence of any fossils which might be considered as intermediates, or transitionals, between any land-dwelling ancestors and the whales of today. Therefore, they must have been specially created by an "intelligent designer".

However, as you may have already learned, such appeal to some supernatural explanation for any natural phenomenon cannot be used in any scientific argument, simply because, whether such a cause exists or not, it cannot be disproven by any scientific testing. In this article, Raymond Sutera examines the issue of whale origins, and demonstrates one of science's greatest tools for measuring the strength of a concept: multiple independent lines of evidence. L. Flammer, ed.]

... Of course, for many years the fossil record for the whales was quite spotty, but now there are numerous transitional forms that illustrate the pathway of whale evolution.

Recent discoveries of fossil whales provide the evidence that will convince an honest skeptic. However, evolutionary biology predicts more than just the existence of fossil ancestors with certain characteristics — it also predicts that all other biological disciplines should also reveal patterns of similarity among whales, their ancestors, and other mammals correlated with evolutionary relatedness between groups. It should be no surprise that this is what we find, and since the findings in one biological discipline, say biochemistry, is derived without reference to the findings in another, say comparative anatomy, scientists consider these different fields to provide independent evidence of the evolution of whales. As expected, these independent lines of evidence all confirm the pattern of whale evolution that we would anticipate in the fossil record.

To illustrate this approach, I will present the evidence from multiple fields for the origin of the whales from terrestrial mammals. This paper will examine mutually reinforcing evidence from nine independent areas of research. Of course, as a starting point, we need to describe what makes a whale a whale.

What is a whale?

A whale is first and foremost, a mammal — a warm-blooded vertebrate that uses its high metabolism to generate heat and regulate its internal temperature. Female whales bear live young, which they nurse from mammary glands. Although adult whales have no covering of body hair, they acquire body hair temporarily as fetuses, and some adult whales have sensory bristles around their mouths. These features are unequivocally mammalian.

But a whale is a very specialized mammal with many unique characters that are not shared with other mammals — many of these are not even shared with other marine mammals such as sirenians (manatees and dugongs) and pinnipeds (seals, sea lions, and walruses). For example, whales have streamlined bodies that are thick and rounded, unlike the generally slim, elongated bodies of fishes. A whale's tail has horizontal flukes, which are its sole means of propulsion through the water. The dorsal fin is stiffened by connective tissue, but is fleshy and entirely without supporting bones.

The neck vertebrae of the whale are shortened and at least partly fused into a single bony mass. The vertebrae behind the neck are numerous and very similar to one another; the bony processes that connect the vertebrae are greatly reduced, allowing the back to be very flexible and to produce powerful thrusts from the tail flukes. The flippers that allow the whale to steer are composed of flattened and shortened arm bones, flat, disk-like wrist bones, and multiple elongated fingers. The elbow joint is virtually immobile, making the flipper rigid. In the shoulder girdle, the shoulder blade is flattened, and there is no clavicle. A few species of whales still possess a vestigial pelvis, and some have greatly reduced and nonfunctional hindlimbs.

The rib cage is very mobile — in some species, the ribs are entirely separated from the vertebral column — which allows the chest to expand greatly when the whale is breathing in and allows the thorax to compress at depth when the whale is diving deeply.

The skull also has a set of features unique among mammals. The jaws extend forward, giving whales their characteristically long head, and the two front-most bones of the upper jaw (the maxillary and premaxillary) are "telescoped" rearward, sometimes entirely covering the top of the skull. The rearward migration of these bones is the process by which the nasal openings have moved to the top of the skull, creating blowholes and shifting the brain and the auditory apparatus to the back of the skull. The odontocetes (toothed whales) have a single blowhole, while the mysticetes (baleen whales) have paired blowholes.

In the odontocetes, there is a pronounced asymmetry in the telescoped bones and the blowhole that provides a natural means of classification. Although teeth often occur in fetal mysticetes, only odontocetes exhibit teeth as adults. These teeth are always simple cones or pegs; they are not differentiated by region or function as teeth are in other mammals. (Whales cannot chew their food; it is ground up instead in a forestomach, or muscular crop, containing stones.)

Unlike the rest of the mammals, whales have no tear glands, no skin glands, and no olfactory sense. Their hearing is acute but the ear has no external opening. Hearing occurs via vibrations transmitted to a heavy, shell-like bone formed by fusion of skull bones (the periotic and auditory bullae).

These, then, are the major features of whales. Some clearly show the distinctive adaptations imposed on whales by their commitment to marine living; others clearly link the whales to their terrestrial ancestors. Others show the traces of descent from a terrestrial ancestor in common with several ancient and modern species. From all these features together, we can reconstruct the pathway that whale evolution took from a terrestrial ancestor to a modern whale confined to deep oceans.

Thinking about the ancestry of the whale

In 1693, John Ray recorded his realization that whales are mammals based on the similarity of whales to terrestrial mammals (Barnes 1984). The pre-Darwinian scientific discussion revolved around whether whales were descended from or ancestral to terrestrial mammals. Darwin (1859) suggested that whales arose from bears, sketching a scenario in which selective pressures might cause bears to evolve into whales; embarrassed by criticism, he removed his hypothetical swimming bears from later editions of the *Origin* (Gould 1995).

Later, Flower (1883) recognized that the whales have persistent rudimentary and vestigial features characteristic of terrestrial mammals, thus confirming that the direction of descent was from terrestrial to marine species. On the basis of morphology, Flower also linked whales with the ungulates [hooved mammals]; he seems to have been the first person to do so.

Early in the 20th century, Eberhard Fraas and Charles Andrews suggested that creodonts (primitive carnivores, now extinct) were the ancestors of whales (Barnes 1984). Later, WD Matthew of the American Museum of Natural History postulated that whales descended from insectivores, but his idea never gained much support (Barnes 1984). Later still, Everhard Johannes Slijper tried to combine the two ideas, claiming that whales descended from what

Barnes aptly called "creodonts-*cum*-insectivores". However, no such animal has ever been found. More recently, Van Valen (1966) and Szalay (1969) associated early whales with mesonychid condylarths (a now-extinct group of primitive carnivorous ungulates, none bigger than a wolf) on the basis of dental characters. More recent evidence confirms their assessment. Thus Flower was basically right.

The evidence

The evidence that whales descended from terrestrial mammals is here divided into nine independent parts: paleontological, morphological, molecular biological, vestigial, embryological, geochemical, paleoenvironmental, paleobiogeographical, and chronological. Although my summary of the evidence is not exhaustive, it shows that the current view of whale evolution is supported by scientific research in several distinct disciplines.

1. *Paleontological evidence*

The paleontological evidence comes from studying the fossil sequence from terrestrial mammals through more and more whale-like forms until the appearance of modern whales. Although the early whales (Archaeocetes) exhibit greater diversity than I have space to discuss here, the examples in this section represent the trends that we see in this taxon. Although there are two modern suborders of whales (Odontocetes and Mysticetes), this discussion will focus on the origin of the whales as an order of mammals, and set aside the issues related to the diversification into suborders.

Sinonyx

We start with *Sinonyx*, a wolf-sized mesonychid (a primitive ungulate from the order Condylarthra, which gave rise to artiodactyls, perissodactyls, proboscideans, and so on) from the late Paleocene, about 60 million years ago. The characters that link *Sinonyx* to the whales, thus indicating that they are relatives, include an elongated muzzle, an enlarged jugular foramen, and a short basicranium (Zhou and others 1995). The tooth count was the primitive mammalian number (44); the teeth were differentiated as are the heterodont teeth of today's mammals. The molars were very narrow shearing teeth, especially in the lower jaw, but possessed multiple cusps. The elongation of the muzzle is often associated with hunting fish — all fish-hunting whales, as well as dolphins, have elongated muzzles. These features were atypical of mesonychids, indicating that *Sinonyx* was already developing the adaptations that later became the basis of the whales' specialized way of life.

Pakicetus

The next fossil in the sequence, *Pakicetus*, is the oldest cetacean, and the first known archaeocete. It is from the early Eocene of Pakistan, about 52 million years ago (Gingerich and others 1983). Although it is known only from fragmentary skull remains, those remains are very diagnostic, and they are definitely intermediate between *Sinonyx* and later whales. This is especially the case for the teeth. The upper and lower molars, which have multiple cusps, are still similar to those of *Sinonyx*, but the premolars have become simple triangular teeth composed of a single cusp serrated on its front and back edges. The teeth of later whales show even more simplification into simple serrated triangles, like those of carnivorous sharks, indicating that *Pakicetus*'s teeth were adapted to hunting fish.

A well-preserved cranium shows that *Pakicetus* was definitely a cetacean with a narrow braincase, a high, narrow sagittal crest, and prominent lambdoidal crests. Gingerich and others (1983) reconstructed a composite skull that was about 35 centimeters long. *Pakicetus* did not hear well underwater. Its skull had neither dense tympanic bullae nor sinuses isolating the left auditory area from the right one — an adaptation of later whales that allows directional hearing under water and prevents transmission of sounds through the skull (Gingerich and others 1983). All living whales have foam-filled sinuses along with dense tympanic bullae that create an impedance contrast so they can separate sounds arriving from different directions. There is also no evidence in *Pakicetus* of vascularization of the middle ear, which is necessary to regulate the pressure within the middle ear during diving (Gingerich and others 1983). Therefore, *Pakicetus* was probably incapable of achieving dives of any significant depth. This paleontological assessment of the ecological niche of *Pakicetus* is entirely consistent with the geochemical and paleoenvironmental evidence. When it came to hearing, *Pakicetus* was more terrestrial than aquatic, but the shape of its skull was definitely cetacean, and its teeth were between the ancestral and modern states.

Ambulocetus

In the same area that *Pakicetus* was found, but in sediments about 120 meters higher, Thewissen and colleagues (1994) discovered *Ambulocetus natans*, "the walking whale that swims", in 1992. Dating from the early to middle Eocene, about 50 million years ago, *Ambulocetus* is a truly amazing fossil. It was clearly a cetacean, but it also had functional legs and a skeleton that still allowed some degree of terrestrial walking. The conclusion that *Ambulocetus* could walk by using the hind limbs is supported by its having a large, stout femur. However, because the femur did not have the requisite large attachment points for walking muscles, it could not have been a very efficient walker. Probably it could walk only in the way that modern sea lions can walk — by rotating the hind feet forward and waddling along the ground with the assistance of their forefeet and spinal flexion. When walking, its huge front feet must have pointed laterally to a fair degree since, if they had pointed forward, they would have interfered with each other.

The forelimbs were also intermediate in both structure and function. The ulna and the radius were strong and capable of carrying the weight of the animal on land. The strong elbow was strong but it was inclined rearward, making possible rearward thrusts of the forearm for swimming. However, the wrists, unlike those of modern whales, were flexible.

It is obvious from the anatomy of the spinal column that *Ambulocetus* must have swum with its spine swaying up and down, propelled by its back feet, oriented to the rear. As with other aquatic mammals using this method of swimming, the back feet were quite large. Unusually, the toes of the back feet terminated in *hooves*, thus advertising the ungulate ancestry of the animal. The only tail vertebra found is long, making it likely that the tail was also long. The cervical vertebrae were relatively long, compared to those of modern whales; *Ambulocetus* must have had a flexible neck.

Ambulocetus' skull was quite cetacean (Novacek 1994). It had a long muzzle, teeth that were very similar to later archaeocetes, a reduced zygomatic arch, and a tympanic bulla (which supports the eardrum) that was poorly attached to the skull. Although *Ambulocetus* apparently lacked a blowhole, the other skull features qualify *Ambulocetus* as a cetacean. The post-cranial features are clearly in transitional adaptation to the aquatic environment. Thus *Ambulocetus* is best described as an amphibious, sea-lion–sized fish-eater that was not yet totally disconnected from the terrestrial life of its ancestors.

Rodhocetus

In the middle Eocene (46–7 million years ago) *Rodhocetus* took all of these changes even further, yet still retained a number of primitive terrestrial features (Gingerich and others 1994). It is the earliest archaeocete of which all of the thoracic, lumbar, and sacral vertebrae have been preserved. The lumbar vertebrae had higher neural spines than in earlier whales. The size of these extensions on the top of the vertebrae where muscles are attached indicate that *Rodhocetus* had developed a powerful tail for swimming.

Elsewhere along the spine, the four large sacral vertebrae were unfused. This gave the spine more flexibility and allowed a more powerful thrust while swimming. It is also likely that *Rodhocetus* had a tail fluke, although such a feature is not preserved in the known fossils: it possessed features — shortened cervical vertebrae, heavy and robust proximal tail vertebrae, and large dorsal spines on the lumbar vertebrae for large tail and other axial muscle attachments — that are associated in modern whales with the development and use of tail flukes. All in all, *Rodhocetus* must have been a very good tail-swimmer, and it is the earliest fossil whale committed to this manner of swimming.

The pelvis of *Rodhocetus* was smaller than that of its predecessors, but it was still connected to the sacral vertebrae, meaning that *Rodhocetus* could still walk on land to some degree. However, the ilium of the pelvis was short compared to that of the mesonychids, making for a less powerful muscular thrust from the hip during walking, and the femur was about 1/3 shorter than *Ambulocetus*', so *Rodhocetus* probably could not get around as well on land as its predecessors (Gingerich and others 1994).

Rodhocetus' skull was rather large compared to the rest of the skeleton. The premaxillae and dentaries had

extended forward even more than its predecessors', elongating the skull and making it even more cetacean. The molars have higher crowns than in earlier whales and are greatly simplified. The lower molars are higher than they are wide. There is a reduced differentiation among the teeth. For the first time, the nostrils have moved back along the snout and are located above the canine teeth, showing blowhole evolution. The auditory bullae are large and made of dense bone (characteristics unique to cetaceans), but they apparently did not contain the sinuses typical of later whales, making it questionable whether *Rodhocetus* possessed directional hearing underwater.

Overall, *Rodhocetus* showed improvements over earlier whales by virtue of its deep, slim thorax, longer head, greater vertebral flexibility, and expanded tail-related musculature. The increase in flexibility and strength in the back and tail with the accompanying decrease in the strength and size of the limbs indicated that it was a good tail-swimmer with a reduced ability to walk on land.

Basilosaurus

The particularly well-known fossil whale *Basilosaurus* represents the next evolutionary grade in whale evolution (Gingerich 1994). It lived during the late Eocene and latest part of the middle Eocene (35–45 million years ago). *Basilosaurus* was a long, thin, serpentine animal that was originally thought to have been the remains of a sea serpent (hence it is name, which actually means "king lizard"). Its extreme body length (about 15 meters) appears to be due to a feature unique among whales; its 67 vertebrae are so long compared to other whales of the time and to modern whales that it probably represents a specialization that sets it apart from the lineage that gave rise to modern whales.

What makes *Basilosaurus* a particularly interesting whale, however, is the distinctive anatomy of its hind limbs (Gingerich and others 1990). It had a nearly complete pelvic girdle and set of hindlimb bones. The limbs were too small for effective propulsion, less than 60 cm long on this 15-meter–long animal, and the pelvic girdle was completely isolated from the spine so that weight-bearing was impossible. Reconstructions of the animal have placed its legs external to the body — a configuration that would represent an important intermediate form in whale evolution.

Although no tail fluke has ever been found (since tail flukes contain no bones and are unlikely to fossilize), Gingerich and others (1990) noted that *Basilosaurus*' vertebral column shares characteristics of whales that do have tail flukes. The tail and cervical vertebrae are shorter than those of the thoracic and lumbar regions, and Gingerich and others (1990) take these vertebral proportions as evidence that *Basilosaurus* probably also had a tail fluke.

Further evidence that *Basilosaurus* spent most of its time in the water comes from another important change in the skull. This animal had a large single nostril that had migrated a short distance back to a point corresponding to the back third of the dental array. The movement from the forward extreme of the snout to the a position nearer the top of the head is characteristic of only those mammals that live in marine or aquatic environments.

Dorudon

Dorudon was a contemporary of *Basilosaurus* in the late Eocene (about 40 million years ago) and probably represents the group most likely to be ancestral to modern whales (Gingerich 1994). *Dorudon* lacked the elongated vertebrae of *Basilosaurus* and was much smaller (about 4–5 meters in length). *Dorudon*'s dentition was similar to *Basilosaurus*'; its cranium, compared to the skulls of *Basilosaurus* and the previous whales, was somewhat vaulted (Kellogg 1936). *Dorudon* also did not yet have the skull anatomy that indicates the presence of the apparatus necessary for echolocation (Barnes 1984).

Basilosaurus and *Dorudon* were fully aquatic whales (like *Basilosaurus*, *Dorudon* had very small hind limbs that may have projected slightly beyond the body wall). They were no longer tied to the land; in fact, they would not have been able to move around on land at all. Their size and their lack of limbs that could support their weight made them obligate aquatic mammals, a trend that is elaborated and reinforced by subsequent whale taxa.

Clearly, even if we look only at the paleontological evidence, the [dissenters'] claim of "No fossil intermediates!" is wrong. In fact, in the case of whales, we have several, beautifully arranged in morphological and chronological order.

In summarizing the paleontological evidence, we have noted the consistent changes that indicate a series of adaptations from more terrestrial to more aquatic environments as we move from the most ancestral to the most recent species. These changes affect the shape of the skull, the shape of the teeth, the position of the nostrils, the size and structure of both the forelimbs and the hindlimbs, the size and shape of the tail, and the structure of the middle ear as it relates to directional hearing underwater and diving. The paleontological evidence records a history of increasing adaptation to life in the water — not just to any way of life in the water, but to life as lived by contemporary whales.

2. Morphological evidence
The examination of the morphological characteristics shared by the fossil whales and living ungulates makes their common ancestry even clearer. For example, the anatomy of the foot of *Basilosaurus* allies whales with artiodactyls [even-toed ungulates] (Gingerich and others 1990). The axis of foot symmetry in these fossil whales falls between the 3rd and 4th digits. This arrangement is called paraxonic and is characteristic of the artiodactyls, whales, and condylarths, and is rarely found in other groups (Wyss 1990).

Another example involves the incus (the "anvil" of the middle ear). The incus of *Pakicetus*, preserved in at least one specimen, is morphologically intermediate in all characters between the incus of modern whales and that of modern artiodactyls (Thewissen and Hussain 1993). Additionally, the joint between the malleus (hammer) and incus of most mammals is oriented at an angle between the middle and the front of the animal (rostromedially), while in modern whales and in ungulates, it is oriented at an angle between the side and the front (rostrolaterally). In *Pakicetus*, the first fossil cetacean, the joint is oriented rostrally (intermediate in position between the ancestral and derived conditions). Thus the joint has clearly rotated toward the middle from the ancestral condition in terrestrial mammals (Thewissen and Hussain 1993); *Pakicetus* provides us with a snapshot of the transition.

3. Molecular biological evidence
The hypothesis that whales are descended from terrestrial mammals predicts that living whales and closely related living terrestrial mammals should show similarities in their molecular biology roughly in proportion to the recency of their common ancestor. That is, whales should be more similar in their molecular biology to groups of animals with which they share a more recent common ancestor than to other animals that exhibit convergent similarities in morphology, ecology, or behavior. In contrast, [supernatural explanations lack] any scientific basis for predicting what the patterns of similarity should be, for there is no scientific way to predict how [such supernatural forces could] distribute molecular similarities among species.

Molecular studies by Goodman and others (1985) show that whales are more closely related to the ungulates than they are to all other mammals — a result consistent with evolutionary expectations. These studies examined myoglobin, lens *alpha*-crystallin A, and cytochrome *c* in a study of 46 different species of mammals. Miyamoto and Goodman (1986) later expanded the number of protein sequences by including *alpha*- and *beta*- hemoglobins and ribonuclease; they also increased the number of mammals included in the study to 72. The results were the same: the whales clearly are included among the ungulates. Other molecular studies on a variety of genes, proteins, and enzymes by Irwin and others (1991), Irwin and Arnason (1994), Milinkovitch (1992), Graur and Higgins (1994), Gatesy and others (1996), and Shimamura and others (1997) also identified the whales as closely related to the artiodactyls, although there are differences in the details among the studies.

By placing whales close to, and even firmly within, the Artiodactyls, these molecular studies confirm the predictions made by evolutionary theory. This pattern of biochemical similarities *must* be present if the whales and the ungulates, especially the Artiodactyls, share a close common ancestor. The fact that these similarities *are* present is therefore strong evidence for the common ancestry of whales and ungulates.

4. Vestigial evidence

The vestigial features of whales tell us two things. They tell us that whales, like so many other organisms, have features that make no sense from a design perspective — they have no current function, they require energy to produce and maintain, and they may be deleterious to the organism. They also tell us that whales carry a piece of their evolutionary past with them, highlighting a history of a terrestrial ancestry.

Modern whales often retain rod-like vestiges of pelvic bones, femora, and tibiae, all embedded within the musculature of their body walls. These bones are more pronounced in earlier species and less pronounced in later species. As the example of *Basilosaurus* shows, whales of intermediate age have intermediate-sized vestigial pelves and rear limb bones.

Whales also retain a number of vestigial structures in their organs of sensation. Modern whales have only vestigial olfactory nerves. Furthermore, in modern whales the auditory meatus (the exterior opening of the ear canal) is closed. In many, it is merely the size of a thin piece of string, about 1 mm in diameter, and often pinched off about midway. All whales have a number of small muscles devoted to nonexistent external ears, which are apparently a vestige of a time when they were able to move their ears — a behavior typically used by land animals for directional hearing.

The diaphragm in whales is vestigial and has very little muscle. Whales use the outward movement of the ribs to fill their lungs with air. Finally, Gould (1983) reported several occurrences of captured sperm whales with visible, protruding hind limbs. Similarly, dolphins have been spotted with tiny pelvic fins, although they probably were not supported by limb bones as in those rare sperm whales. And some whales, such as belugas, possess rudimentary ear pinnae — a feature that can serve no purpose in an animal with no external ear and that can reduce the animal's swimming efficiency by increasing hydrodynamic drag while swimming.

Although this list is by no means exhaustive, it is nonetheless clear that the whales have a wealth of vestigial features left over from their terrestrial ancestors.

5. Embryological evidence

Like the vestigial features, the embryological features also tells us two things. First, the whale embryo develops a number of features that it later abandons before it attains its final form. How can [the dissenters] explain such seemingly nonsensical process, building structures only to abandon them or to destroy them later? Darwin (1859) asked the same question. Would it not make more sense to have embryos attain their adult forms quickly and directly? It seems unreasonable for a [supernatural designer] ... to send the embryo along such a tortuous pathway, but evolution requires that new features are built on the foundation of previous features that it would modify or discard later.

Second, the embryology of the whale, examined in detail, also provides evidence for its terrestrial ancestry. As embryos no less than as adult animals, whales are junkyards, as it were, of old, discarded features that are of no further use to them. Many whales, while still in the womb, begin to develop body hair. Yet no modern whales retain any body hair after birth, except for some snout hairs and hairs around their blowholes used as sensory bristles in a few species. The fact that whales possess the genes for producing body hair shows that their ancestors had body hair. In other words, their ancestors were ordinary mammals.

In many embryonic whales, external hind limb buds are visible for a time but then disappear as the whale grows larger. Also visible in the embryo are rudimentary ear pinnae, which disappear before birth (except in those that carry them as rare atavisms). And, in some whales, the olfactory lobes of the brain exist only in the fetus. The whale embryo starts off with its nostrils in the usual place for mammals, at the tip of the snout. But during development, the nostrils migrate to their final place at the top of the head to form the blowhole (or blowholes).

We can also understand evolution *within* the whales via their embryology. We know that the baleen whales evolved from the toothed whales: some embryos of the baleen whales begin to develop teeth. As with body hair, the teeth disappear before birth. Since there is no use for teeth in the womb, only inheritance from a common ancestor makes any sense; there [seems to be] no reason for [a supernatural designer] to provide embryonic whales with teeth. So

we have yet another independent field in complete accord with the overall thesis — that whales possess features that connect them with terrestrial mammalian ancestors, in particular the hoofed mammals.

6. Geochemical evidence

The earliest whales lived in freshwater habitats, but the ancestors of modern whales moved into saltwater habitats and thus had to adapt to drinking salt water. Since fresh water and salt water have somewhat different isotopic ratios of oxygen, we can predict that the transition will be recorded in the whales' skeletal remains — the most enduring of which are the teeth. Sure enough, fossil teeth from the earliest whales have lower ratios of heavy oxygen to light oxygen, indicating that the animals drank fresh water (Thewissen and others 1996). Later fossil whale teeth have higher ratios of heavy oxygen to light oxygen, indicating that they drank salt water. This absolutely reinforces the inference drawn from all the other evidence discussed here: the ancestors of modern whales adapted from terrestrial habitats to saltwater habitats by way of freshwater habitats.

7. Paleoenvironmental evidence

Evolution makes other predictions about the history of taxa based on the "big-picture" view of the fossils in a larger, environmental, context. The sequence of whale fossils and their changes should also relate to changes observed in the fossil records of other organisms at the same time and in similar environments. The fossils of other organisms associated with the whale fossils indicate the environment that the whales lived in. Furthermore, this evidence should be consistent with the evidence from the other areas of study. We should expect to find evidence for a series of transitional environments, from fully terrestrial to fully marine, occupied by the series of whale species in the fossil record.

The morphology of *Sinonyx* indicates that it was fully terrestrial. It should be no surprise, therefore, that its fossils are found associated with the fossils of other terrestrial animals. *Pakicetus* probably spent a lot of time in the water in search of food. Although the mammalian fauna found with *Pakicetus* consists of rodents, bats, various artiodactyls, perissodactyls and probiscideans, and even a primate (Gingerich and others 1983), there are also aquatic animals such as snails, fish, turtles and crocodilians. Moreover, the sediment associated with *Pakicetus* shows evidence of streaming or flowing, usually associated with soils that are carried by water. The paleoenvironmental evidence thus clearly shows that *Pakicetus* lived in the low-lying wet terrestrial environment, making occasional excursions into fresh water. Interestingly, both deciduous and permanent teeth of the animal are found in these sediments with about the same frequency, supporting the idea that *Pakicetus* gave birth on the land.

The sediments in which *Ambulocetus* was found contain leaf impressions as well as fossils of the turret-snail *Turritella* and other marine mollusks. Clearly, the presence of such fossils must mean that the *Ambulocetus* fossil was found in what was once a shallow sea — although leaves can be washed into the sea and fossilize there, marine mollusks would not be found on the land.

Rodhocetus is found in green shales deposited in the deep-neritic zone (equivalent to the outer part of the continental shelf). Because green shales are associated with fairly low-oxygen bottom waters, *Rodhocetus* must have lived at a greater water depth than any previous cetacean. The fact that it is found in association with planktonic foraminiferans and other microfossils agrees with this determination of water depth. *Basilosaurus* and *Dorudon* have been found in a variety of sediment types (Kellogg 1936), indicating that they were wide-ranging and capable of living in deep as well as shallow water.

From the paleoenvironmental evidence, we can clearly see that, as whales evolved, they made their way into deeper water and became progressively liberated from the terrestrial and near-shore environments.

8. Paleobiogeographic evidence

The geographic evidence is also consistent with the expected distributional patterns for the whale's first appearance and later geographic expansion. We would expect terrestrial species to have a more restricted geographic distribution than marine species, which have essentially the whole ocean as their geographic range. The range of *Sinonyx* is restricted to central Asia. Specimens of *Pakicetus* have only been found in Pakistan; *Ambulocetus* and *Rodhocetus* seem to be similarly restricted. In contrast, *Basilosaurus* and *Dorudon*, representing the whales more

adapted to living in the open sea, are found in a much wider area. Their fossils have been found as far away from southern Asia as Georgia, Louisiana, and British Columbia.

During the Eocene, most of the areas in which fossils of the later whales have been found were fairly close to one another. In fact, most of them are along the outer margin of an ancient sea called the *Tethys*, the remnants of which today are the Mediterranean, the Caspian, the Black, and the Aral Seas. The biogeographic distribution of fossil whales matches the pattern predicted by evolution: whales are initially found in a rather small geographic area and did not become distributed throughout the world until after they evolved into fully aquatic animals that were no longer tied to the land.

9. Chronological evidence

The final strand of evidence in our mutually consistent picture of whale origins comes from a consideration of why the whales originated *when* they did. Evolution is a response to environmental challenges and opportunities. During the early Cenozoic, mammals were presented with a new set of opportunities for radiation and diversification due, in part, to the vacuum left by mass extinctions at the close of the Cretaceous Period. Because the reptiles no longer predominated, there were new ways in which mammals could make a living.

In the specific case of whales, the swimming reptiles of the world's oceans could no longer keep the mammals at bay. Before the late-Cretaceous extinctions, the Mesozoic marine reptiles such as the plesiosaurs, ichthyosaurs, mosasaurs, and marine crocodiles might well have feasted upon any mammal that strayed off shore in search of food. Once those predators were gone, the evolution quickly produced mammals, including whales, that were as at home in the seas as they once were on land. The transition took some 10–15 million years to produce fully aquatic, deep-diving whales with directional underwater hearing. Evolution predicts that whales could not have successfully appeared and radiated before the Eocene, and that mammals should have radiated into marine environments as they did into a wide variety of other environments vacated by the reptiles at the end of the Cretaceous.

Conclusion

Taken together, all of this evidence points to only one conclusion — that whales evolved from terrestrial mammals. We have seen that there are nine independent areas of study that provide evidence that whales share a common ancestor with hoofed mammals. The power of evidence from independent areas of study that support the same conclusion makes refutation by [dissenters, for any number of mostly supernatural reasons, seem] entirely unreasonable. The only plausible scientific conclusion is that whales did evolve from terrestrial mammals. So no matter how much [the dissenters claim] how impossible it is for land-dwelling, furry mammals to evolve into fully aquatic whales, the evidence itself [collectively argues otherwise]. This is the power of using mutually reinforcing, independent lines of evidence. I hope that [this approach will stimulate a more objective review of the alternative ideas, and promote a serious reconsideration of the evidence supporting] evolutionary thinking [by] the general public. This is how real science works, and we must emphasize the process of scientific inference as we point out the conclusions that scientists draw from the evidence — that the concordant predictions from independent fields of scientific study confirm the same pattern of whale ancestry.

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References

Barnes LG. Search for the first whale. *Oceans* 1984 March–April; 17 (2): 20–3.

Darwin CR. *On the Origin of Species.* New York: Random House, 1859.

Flower WH. On the arrangement of the orders and families of existing Mammalia. *Proceedings of the Zoological Society of London* 1883 Aug; 1: 178–86.

Gatesy J, Hayashi C, Cronin MA, Arctander P. Evidence from milk casein genes that cetaceans are close relatives of hippopotamid artiodactyls. *Molecular Biology and Evolution* 1996; 13 (7): 954–63.

Gingerich P. The whales of Tethys. *Natural History* 1994 April; 103 (4): 86–8.

Gingerich P, Raza SM, Arif M, Anwar M, Zhou X. New whale from the Eocene of Pakistan and the origin of cetacean swimming. *Nature* 1994; 368: 844–7.

Gingerich P, Smith BH, Simons EL. Hind limbs of Eocene *Basilosaurus*: evidence of feet in whales. *Science* 1990; 249: 154–7.

Gingerich, Philip D. and Uhen M. *Ancalecetus simonsi*, a new dorudontine archaeocete (Mammalia, Cetacea) from the early late Eocene of Wadi Hitan, Egypt." *Contributions from the University of Michigan Museum of Paleontology* 1996; 29(13): 359-401.

Gingerich P, Wells NA, Russell DE, Shah SMI. Origin of whales in epicontinental remnant seas: new evidence from the early Eocene of Pakistan, *Science* 1983; 220: 403–6.

Goodman M, Czelusniak J, Beeber J. Phylogeny of primates and other eutherian orders: a cladistic analysis using amino acid and nucleotide sequence data. *Cladistics* 1985; 1 (2): 171–85.

Gould SJ. Hen's teeth and horse's toes. In: *Hen's Teeth and Horse's Toes*. Norton: New York, 1983. p 177–86.

Gould SJ. Hooking leviathan by its past. In: *Dinosaur in a Haystack*, New York: Harmony Books, 1995. p 359–76.

Graur D, Higgins DG. Molecular evidence for the inclusion of cetaceans within the order Artiodactyla. *Molecular Biology and Evolution* 1994; 11 (3): 357–64.

Irwin DM, Arnason U. Cytochrome *b* gene of marine mammals: phylogeny and evolution. *Journal of Mammalian Evolution* 1994; 2 (1): 37–55.

Irwin DM, Kochner TD, Wilson AC. Evolution of the cytochrome *b* gene of mammals. *Journal of Molecular Evolution* 1991; 32: 128-44.

Kellogg R. *A Review of the Archaeoceti*. Washington DC: Carnegie Institute, 1936.

Matthews LH. *The Natural History of the Whale*. New York: Columbia University Press, 1978.

Milinkovitch MC. DNA-DNA hybridizations support ungulate ancestry of cetacea. *Journal of Evolutionary Biology* 1992; 5: 149–60

Milinkovitch MC, Orti G, Meyer A. Revised phylogeny of whales suggested by mitochondrial ribosomal DNA sequences. *Nature* 1993; 361: 346–8.

Miyamoto MM, Goodman M. Biomolecular systematics of eutherian mammals: phylogenetic patterns and classification. *Systematic Zoology* 1986; 35 (2):230–40.

Novacek M. Mammalian phylogeny: shaking the tree. *Nature* 1992; 356: 121–5.

Novacek M. Whales leave the beach. *Nature* 1994; 368: 807.

Shimamura M, Yasue H, Ohshima K, Abe H, Kato H, Kishiro T, Goto M, Munechika I, Okada N. Molecular evidence from retroposons that whales form a clade within even-toed ungulates. *Nature* 1997; 388: 666–9.

Szalay FS. Origin and evolution of function of the mesonychid condylarth feeding mechanism. *Evolution* 1969; 23: 703–20.

Thewissen JGM, Hussain ST. Origin of underwater hearing in whales. *Nature* 1993; 361: 444–5.

Thewissen JGM, Hussain ST, Arif M. Fossil evidence for the origin of aquatic locomotion in Archaeocete whales. *Science* 1994; 263: 210–2.

Thewissen JGM, Roe LJ, O'Neill JR, Hussain ST, Sahni A, Bajpal S. Evolution of cetacean osmoregulation. *Nature* 1996; 381: 379–80.

Van Valen L. Deltatheridia, a new order of mammals. *Bulletin of the American Museum of Natural History* 1966; 132: 1–126.

Wyss A. Clues to the origin of whales. *Nature* 1990; 347: 428–9.

Zhou X, Zhai R, Gingerich P, Chen L. Skull of a new Mesonychid (Mammalia, Mesonychia) from the late Paleocene of China. *Journal of Vertebrate Paleontology* 1995; 15 (2): 387–400.