Walking with whales

Christian de Muizon

Whales must have evolved from land-based mammals, but fossil evidence of some of the steps in between has been patchy. Newly discovered skeletons with legs fill in the gaps.

On page 277 of this issue, Thewissen and colleagues[1] describe their discovery of partial fossil skeletons from the earliest cetaceans — a group of mammals that today consists of whales, porpoises and dolphins. The fossils, which are some 50 million years old and were found in Pakistan, take us a huge step forwards in understanding the origins and evolutionary relationships of whales. Until now, the limbs of all known early cetaceans reflected an amphibious or wholly aquatic lifestyle[2–6]. But the newly discovered fossils show that the first whales were fully terrestrial, and were even efficient runners. They also reveal that cetaceans are more closely related to the oldest known even-toed ungulates — a group of hoofed mammals that includes cows, hippos, pigs, camels and giraffes — than to any other mammals. These conclusions are based on solid anatomical data, and contradict the previous hypotheses of both palaeontologists and molecular biologists[7–10].

All of the mammals that existed in the early Tertiary — some 65–50 million years ago — lived on land. So it has always been clear that aquatic cetaceans must have evolved from terrestrial mammals and returned to the water, and the forelimbs of recent cetaceans still have the same general pattern as that of land mammals. However, modern cetaceans are highly specialized, with numerous adaptations that allow them to swim, dive and feed. Their bodies are elongated and streamlined; the shape of the tail is modified into a propulsive fluke; and the limbs are much reduced in size. The forelimbs are flippers with rigid elbows and an increased number of phalanges (part of the finger bone), and function mainly in steering and stabilizing. The hindlimbs and pelvis are internal, and have no role in swimming.

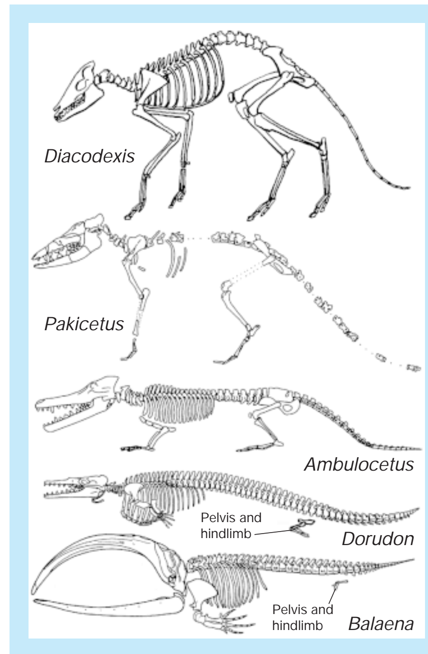

Figure 1 **The evolutionary route to a whale.** ***Diacodexis*[13] was a primitive even-toed ungulate (hoofed mammal); *Pakicetus* is one of the terrestrial cetaceans described by Thewissen *et al.*[1]; *Ambulocetus*[14] was amphibious; *Dorudon* (modified from ref. 15) was a fully aquatic archaeocete (early cetacean), but retained an articulated elbow and vestigial hindlimbs; and *Balaena* is a recent whale[16]. Skeletons are not drawn to scale.**

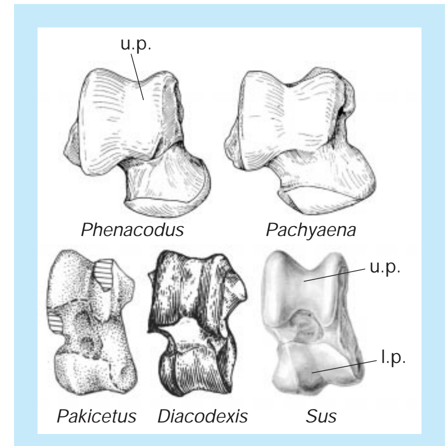

Figure 2 **Ankle bones (astragali) of hoofed mammals and primitive whales. *Phenacodus*[17], a primitive ungulate, had an unspecialized ankle bone that resembles that of *Pachyaena*[17], a mesonychian ungulate from 50 million years ago. The double-pulleyed astragali of *Pakicetus* (one of the fossil cetaceans described by Thewissen *et al.*[1]), *Diacodexis*[18] (the oldest known even-toed ungulate), and *Sus*[17] (the pig) indicate a close relationship between these species. Bones are not shown to scale. u.p., upper pulley, articulates with tibia. l.p., lower pulley, articulates with distal ankle bones.**

What was the evolutionary path from the earliest land mammals to modern, aquatic whales? Pakicetids, which existed in the early Eocene epoch, some 50 million years ago, are the earliest known cetaceans. But, until now, only the skulls of these animals had been described. Cetaceans from the middle Eocene, 45 million years ago, have been known for more than a century[11], but here, too, few limb remains were discovered, until about 20 years ago. Since then, numerous fossils from North America, Pakistan and Egypt have revealed that these early cetaceans had mobile elbows and external hindlimbs with articulated knees[2–7] (Fig. 1). However, they were already fully aquatic, except for

Box 1 Further finds from Pakistan

A report in this week's *Science* by Gingerich *et al.*[19] fleshes out the picture of early whale evolution with a description of two new species from 47-million-year-old rocks in Pakistan. One represents a new genus; the other, a close relative, is a species of the previously known genus *Rodhocetus*. Both belonged to the family Protocetidae, a group of extinct whales somewhat more aquatic in their adaptations than the pakicetids described elsewhere in this issue by Thewissen and colleagues[1].

Like the previously described *Ambulocetus*, the newly discovered protocetids had well-developed limbs with large hands and feet. Gingerich *et al.* suggest that although these creatures could have moved about on land, the limbs would have functioned as paddles. In life, the animals, which would have weighed between 400 and 500 kilograms, might have lived and moved like large sea lions. The most striking features of these protocetids are their astragali, which look remarkably like those of artiodactyls and reaffirm the close relationship between artiodactyls and whales. However, the absence of a formal phylogenetic analysis means that the researchers were unable to test the competing hypotheses of whale relationships. **Henry Gee**

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Ambulocetus, which was amphibious — much like sea lions. So there was no detailed information about the anatomy of the cetaceans' terrestrial ancestor.

Recent cetaceans are very different to other mammals, so another question that has dogged this field is that of which group of mammals contains their closest relatives — which is their 'sister group'? The cranial and skeletal anatomy of cetaceans is highly modified compared with that of land mammals, and fossils of early cetaceans are so rare and generally incomplete, that the affinities of the group are difficult to establish. On the basis of tooth and ear morphology, palaeontologists contend that cetaceans are most closely related to the mesonychians[7,8] — a group of extinct ungulates from the early Tertiary. But molecular biologists favour hippos — which form one of the families of modern even-toed ungulates (artiodactyls)[9,10] — as the sister group.

Thewissen and colleagues' discovery[1] allows us to address both of these problems. The newly found fossils include several skulls and postcranial bones from two early pakicetid species — which, it seems, had the head of a primitive cetacean (as indicated by the ear region) and the body of an artiodactyl. All the postcranial bones indicate that pakicetids were land mammals, and it is likely that they would have been thought of as some primitive terrestrial artiodactyl if they had been found without their skulls. Many of the fossils' features — including the length of the cervical vertebrae, the relatively rigid articulations of the lumbar vertebrae, and the long, slender limb bones — indicate that the animals were runners, moving with only their digits touching the ground.

But the most eloquent information provided by the fossils[1] comes from the ankle bones, particularly the astralagus (Fig. 2). This has two pulleys, which connect to both the tibia and the more distal ankle bones and allow a great deal of flexibility. This type of morphology is an adaptation for running. It was once thought to be unique to artiodactyls, but it is now clear that it also occurred in cetaceans. So, for the first time, morphological evidence shows that artiodactyls are the closest relatives of the cetaceans (also see Box 1).

This means that artiodactyls and cetaceans form the two branches of a larger group, the cetartiodactyls[12]. Thewissen and colleagues' studies also exclude the mesonychians from this larger group, in part because these ungulates do not have a double-pulleyed astragalus. Mesonychians are an unspecialized group of primitive ungulates, and perhaps some of them should be included in other groups of mammals. Cetaceans and some mesonychians have dental similarities and an elongated skull, but these features are probably the result of convergent evolution.

The authors' analysis also indicates that no one recent artiodactyl family is more closely related than another to cetaceans — in other words, hippos are not the extant sister group of the cetaceans. The closest fossil relatives of the cetaceans were probably the earliest known artiodactyls, such as *Diacodexis* (see Fig. 1).

Thewissen *et al.*'s discovery[1] of these terrestrial cetaceans is one of the most important events in the past century of vertebrate palaeontology. Only a very few fossils, such as these, reveal a link between two groups of vertebrates that are hugely different in terms of shape yet closely related in terms of evolution. When there is a drastic shift in habitat — such as from land to water — the morphology of the newly adapted animals is generally so greatly modified, because of the high selective pressure, that any resemblance to the original ancestor is quickly obliterated. But the new fossils[1] superbly document the link between modern whales and their land-based forebears, and should take their place among other famous 'intermediates', such as the most primitive bird, *Archaeopteryx*, and the early hominid *Australopithecus*. ■

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Surface physics

A new crack at friction

David A. Kessler

One of the dirty little secrets of physics is that there is no generally accepted explanation of the basic laws of friction. An advance in the theory of cracks will stimulate fresh thinking on the question.

Friction is a ubiquitous feature of everyday life. Without it, we couldn't walk, tyres wouldn't roll, and ballpoint pens would fail to write. But what is friction, and how does it act?

The basic properties are simple to grasp. To move a solid object from rest on top of a solid surface, a minimum force has to be applied to overcome the force of friction. This force is proportional to the compressive force pushing the two surfaces together, in this case the weight of the object. Intriguingly, this minimum force is independent of the area of contact between the body and the surface. So the friction force on a rectangular solid resting on a table is the same whichever face is in contact with the surface. These laws have been known since the mid 1700s and are attributed to the French physicists Guillaume Amontons (1663–1705) and Charles Augustin de Coulomb (1736–1806). It is one of the dirty little secrets of physics that while we physicists can tell you a lot about quarks, quasars and other exotica, there is still no universally accepted explanation of the basic laws of friction. On page 285 of this issue, Gerde and Marder[1] offer a theory of surface cracks that may lead to a better understanding of surface friction.

The standard picture of friction[2] (dating from as recently as the 1960s) is that the solid surfaces are not really planar, but are rough on a microscopic scale. The presence of these tiny surface features, or asperities as they are known, prevents the surfaces from coming into full contact. So the true contact area is much smaller than its apparent value, and is proportional to the compressive force between the surfaces, in much the same way that the contact area between a car tyre and the road increases when you load your car. Problems have arisen when physicists tried to confirm this picture using calculation from first principles. The goal is to construct, either analytically or on the computer, a solid body and surface from atoms with prescribed interactions, and calculate the friction force directly. But previous attempts at this found that the two surfaces ride freely on top of each other because of the mismatch between the asperities on the two surfaces, so there is no friction.

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