

Evolution & Behavior

A four-legged ancestor led the way for early whales dispersal

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ABSTRACT

The discovery of a four-legged whale in nearly 43 million years old marine deposits of coastal Peru provides insights on the early dispersal of modern whales, dolphins and porpoises' ancestors to the Americas. We could assess timing of this dispersal, the route taken, and the locomotion abilities, of these early, hoofed-bearing amphibious whales.



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The whales, dolphins, and porpoises (generally called “[cetaceans](#)”) that we know today are fully aquatic mammals, spending their entire life in the water. Whereas the forelimbs of these hydrodynamic animals are transformed into flippers, mostly used for steering, their hind limbs are highly reduced, and they predominantly rely on oscillations of their caudal fluke for swimming. Discovered in deposits from South Asia dated to about 50 million years ago (Ma), the earliest cetaceans were very different: small, [four-legged hoofed mammals](#) only spent part of their time in the water, either to hide from terrestrial predators or to search for aquatic prey. Although retaining the ability to move on land, some early, quadrupedal whales gradually acquired adaptations for a more efficient underwater locomotion, including longer toes and fingers on

large, webbed feet and hands. These acquisitions helped them dispersing westward, from their area of origin (India and Pakistan) to the northern coast of Africa.

Due to a scantier fossil record on both sides of the Atlantic Ocean, the colonization, more than 41 Ma, of the New World by these amphibious whales (called [protocetids](#)) remained poorly understood. When did they reach this continent? Which marine 'route' did they take? What were their locomotion abilities? We recently uncovered a whale fossil from the [middle Eocene](#) of Peru which provided us with some new clues.

In 2011, our international team discovered the skeleton of an ancient whale in Peru's coastal desert

([Pisco Basin](#)). The first elements appearing at the surface were the mandibles with teeth. Further excavation revealed forelimb elements, then vertebrae, the hip, and finally the femur, the tibia, and many foot bones. We realized that we just found one of these four-legged whale skeletons, the first for South America and the most complete outside South Asia, even including one of the kneecaps! Sediment blocks containing the skeleton were then brought to the *Museo de Historia Natural*, in Lima, where the bones were freed from their rock matrix, before being studied.

While confirming its attribution to the family Protocetidae, the study of this skeleton revealed several anatomical differences with other members of the family, leading to the description of a new genus and species: *Peregocetus pacificus* (namely the traveling whale that reached the Pacific Ocean). Besides, its geological age of nearly 43 Ma makes this protocetid the oldest for the Americas. The new find thus indicates that four-legged whales reached the New World less than 10 million years after their emergence in South Asia and that they may have taken a southern route, across the South Atlantic, at a time when the distance between Africa and South America was two times shorter than nowadays. The completeness of *Peregocetus*' skeleton also provides clues about the walking and swimming abilities of this ancient whale. The morphology of its hips (tightly attached to the sacrum), proportions of limbs, and indications for the presence of small hooves (yes, a hoofed whale!) at the end of individual toes and fingers all support the idea that this large, 3.5 to 4 meters long animal could occasionally return to the shore, maybe to give birth,

for a nap, or social interactions. On the aquatic side, in addition to the large, webbed feet and hands indicating that limbs were still involved in underwater locomotion, part of the tail vertebrae of *Peregocetus* are strikingly similar to those of semi-aquatic mammals like otters. All these elements point to an otter-like swimming technique, combining movements of the feet with vertical undulations of the tail. Together with westward-running surface currents, such a contribution of the tail most likely helped *Peregocetus*' ancestors to swim across the South Atlantic and colonize the Americas.

More derived protocetids will lose the firm connection between hip and vertebral column, a feature that certainly prevented them from walking on land. Then protocetids' descendants, [basilosaurids](#), will greatly reduce their hindlimbs, being the first fully marine cetaceans, using a powerful caudal fluke for moving in the water. About 37 Ma, basilosaurids will give rise to the first modern cetaceans, the [mysticetes](#) (baleen whales and relatives) and [odontocetes](#) (echolocating toothed whales).

Although this new four-legged whale from the Eocene of Peru brings new light on the way early cetaceans dispersed to the New World, we lack its skull and the tip of its tail! New fieldwork in the fossil-rich Pisco Basin may lead to the discovery of new *Peregocetus* skeletons; those may eventually provide further clues on the presence (or absence) of a proto-fluke at the end of the tail of this hoofed whale.