The Whales of Tethys

by Philip D. Gingerich

In Greek mythology, Tethys is the wife of Oceanus and a sea goddess in her own right. About a hundred years ago, geologists appropriated her name for the ancient sea that once divided the earth's great northern and southern continents. Today the Mediterranean is a mere suggestion of what Tethys must have been in its time. Stretching from what is now Spain to Indonesia, Tethys was an ocean when trilobites and other early forms of life flourished, and it lasted more than 500 million years, through the Age of Dinosaurs and into the Age of Mammals. The inexorable drift of continental plates finally obliterated Tethys. India and central Asia converged and raised the Himalayas; Arabia pushed into western Asia and uplifted the Zagros; Africa encroached on Europe and raised the Alps. Tethyan sea sediments now lie dry and exposed in the Sahara Desert and in the folded foothills of the Himalayas and the Alps.

Extensive and relatively shallow, the waters of Tethys would have been warm and well stocked with fish and mollusks. It must also have been inviting to mammals that lived at its edge. Three hundred million years after vertebrates first colonized land, some mammals reversed their pattern and returned to Tethys. Today, the descendants of those seagoing pioneers—toothed porpoises and dolphins and the toothed and baleen whales that make up the order Cetacea—have adapted fully to life in water. All have a streamlined body, a blowhole or pair of holes on the top of the skull for breathing, simplified teeth (replaced in some by keratinous baleen), a specialized system for underwater hearing, and locomotion powered by a fluked tail instead of by limbs or flippers. These advanced cetacean features were acquired in steps over time, but the prototype was a land mammal living on the shores of Tethys.

The oldest-known fossil whales come from the Kuldana Formation, a stratum of rocks in northern Pakistan deposited by ancient rivers and sandwiched between Tethyan marine formations. In the Eocene, some fifty million years ago, Tethys could not have been far downriver from this site. In 1979, I led an international team from the United States, France, and Pakistan to search the Kuldana Formation for fossils of early land mammals. One December day, Jean-Louis Hartenberger, a rodent specialist, hammered open a rock with what looked like a small bone on its surface; the bone turned out to be a crest on the back of a beautifully complete fossil skull. Because the skull was relatively large but the braincase was small, we began to suspect that he had found an archaeocete, a member of an ancient family of whales. These now-extinct relatives of today's toothed and baleen whales had some modern features, such as a dense tympanic bone for hearing, but lacked many others, including a blowhole on the top of the skull.

When I returned to my lab at the University of Michigan, my colleagues and I removed the remaining rock from the new skull. The configuration of bones in the skull base confirmed that it was indeed an archaeocete; we named it *Pakicetus inachus*. We later speculated that this dog-sized whale first entered Tethys from its riverside home to take advantage of easy fishing in the warm waters.

Pakicetus, which lived about fifty million years ago, had not evolved the ability to hear directionally, or perhaps to hear well at all, in water, a hallmark of modern whales. Archaic features such as this, along with its discovery among remains of land animals, makes *Pakicetus* a very primitive whale indeed. In time and in its morphology, *Pakicetus* is perfectly intermediate, a missing link between earlier land mammals and later, full-fledged whales.

Our unexpected discovery and our subsequent investigation of *Pakicetus* made me realize how little was known about the

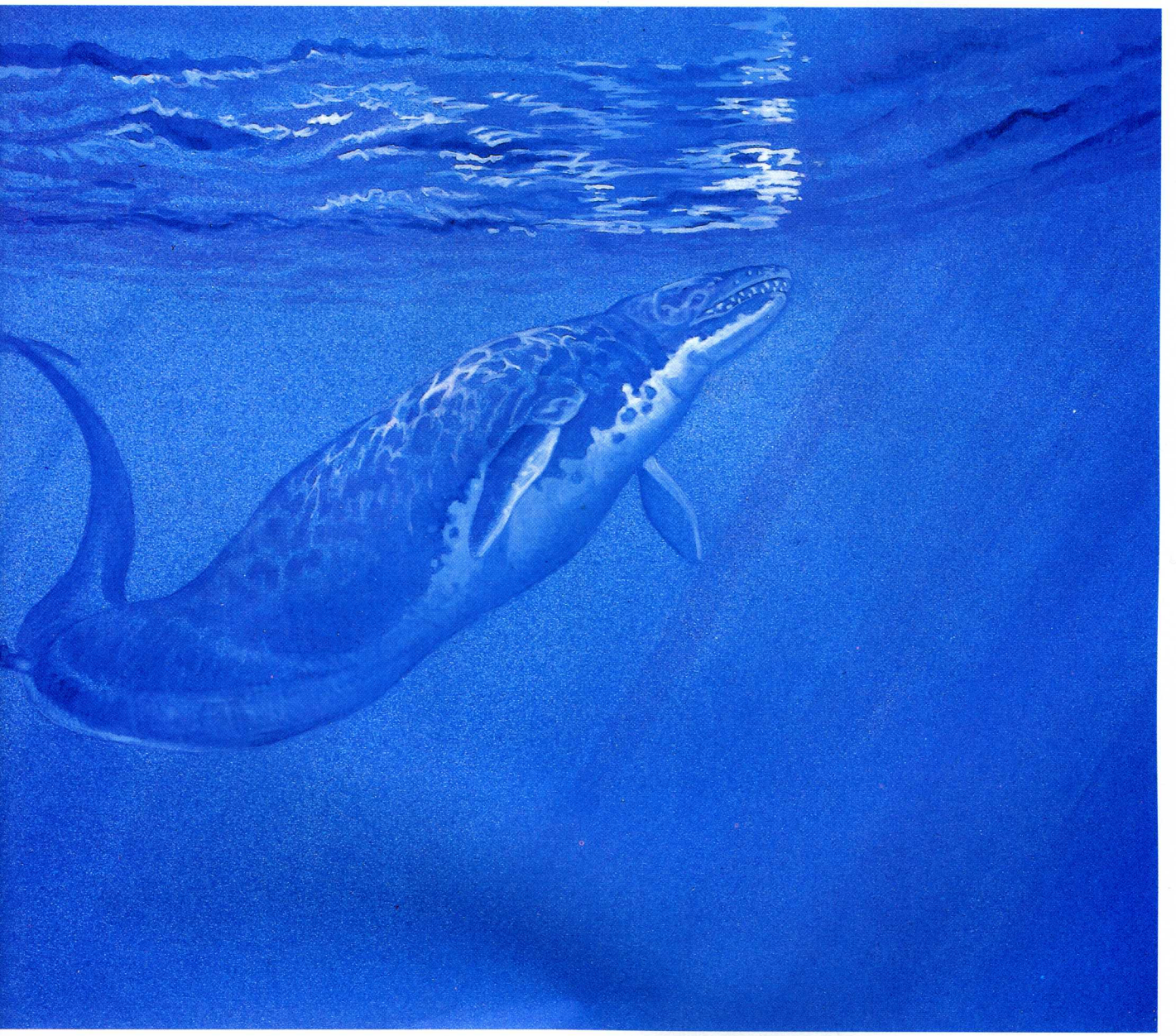
Basilosaurus, *an ancient whale that lived some forty million years ago, had front flippers and tiny but functional hind limbs, complete with thigh, femur, and three toes. It may have used its feet to guide its fifty-foot-long body during copulation. A fossil of the whale was unearthed in 1989 in what is now the Egyptian Sahara.*

transition of whales from land to sea. I also reasoned that we need not remain in the dark. After all, whales live and die in water, where they are easily buried and fossilized, and their fossils are large and relatively easy to find. Furthermore, marine rocks of Eocene age cover vast areas of the earth's surface. Since finding *Pakicetus,* my colleagues and I have been exploring whenever possible the deserts of Pakistan and Egypt for whales to fill the gaps in our knowledge. Our results have been gratifying.

In 1989, I was working with paleontologists Elwyn Simons and Holly Smith in Tethyan sediments of the Egyptian Sahara, where we found another archaeocete. In addition to a hefty, four-foot-long skull and huge ribs, we found a thigh bone, then lower leg bones, then an ankle. Finally, we also unearthed, one by one, three tiny toes. These, the first complete hind limbs and feet of an archaeocete to be discovered, belonged to the forty-million-year-old *Basilosaurus isis,* a large early whale that must have been one of the most ferocious marine carnivores of its time. Because the hind limbs (about eighteen inches long) were not connected to a sacrum in the spinal column as are the hind limbs of land mammals, *Basilosaurus* could not possibly have used its feet to lift or support its eellike, fifty-foot-long body. Yet the bones and joints are so well formed, with strong processes for the attachment of muscles, that the limbs appear to have been functional. I suspect that *Basilosaurus* used its legs and feet as guides during copulation.

Basilosaurus exhibits not only an unusually elongated shape but also oddly proportioned vertebrae that lead me to believe that it was on a side line, rather than on the main path to the evolution of modern whales. Another cetacean from the same era, found in Egypt and known as *Prozeuglodon atrox,* combines normally proportioned vertebrae with hind limbs much like those of *Basilosaurus* and is a better candidate for a direct ancestor of modern whales.

Paleontologists have long believed that because whales evolved from land mammals, they must have had hind limbs and feet early in their history. What surprised me most about finding hind limbs on *Basilosaurus* and *Prozeuglodon* was that these archaeocetes lived ten million years after *Pakicetus* and the origin of whales. Ten million years is a long time, even to a geologist, and finding hind limbs on such "late" whales means that the transition from land to sea took time—time enough to allow us to study the intermediate stages



in the fossil record. Evolution is dynamic, but change doesn't happen in a flash. Thus, we can expect to unearth many more missing links.

Further rungs in the cetacean evolutionary ladder have already come to light. Recently, paleontologists Hans Thewissen, Taseer Hussain, and Muhammad Arif were working in Pakistan when they found a partial skeleton of a brand-new species of a forty-nine-million-year-old Tethyan archaeocete, with important parts of both front and hind limbs. The femur, or thigh bone, is large, like that of a land mammal, but the feet are long, like those of a seal. The scientists named the animal *Ambulocetus natans,* "the walking whale that swam," in recognition of its amphibious nature. *Ambulocetus* was possibly like an otter or seal in its behavior. It most likely came ashore to breed and give birth. Using its flipperlike front limbs, it may have moved about on land by hitching itself forward, similar to the way a sea lion moves on land. Its hind legs and feet evidently propelled it through the water when it returned to Tethys to feed on marine fare.

The Tethyan sediments of Pakistan continue to be a mine of ancient whale remains. In December of 1992, University of Michigan graduate student Xiaoyuan Zhou found an archaeocete about forty-eight million years old in sediments that were deposited in deeper water than all older finds. It has a nearly complete vertebral column, a small femur, and short neck vertebrae, indicating some streamlining of the head and body. Land mammals and some early fossil whales have fused sacral vertebrae and therefore rather stiff hips and tails, but this creature's sacral vertebrae were not fused, giving its back and tail a flexibility approaching that of later whales. It is thus an important link in the transition to fully whalelike swimming, in which the animals undulate their body and move their fluke up and down.

In the same month, Muhammad Arif and I were again scouring the shallow Tethyan sediments of Pakistan when he found two forty-seven-million-year-old partial skulls and skeletons of a previously poorly known whale called *Indocetus*. The new fossils showed that the animal was long necked and still had long hind limbs, a rigid sacrum, and a robust tail. As in our earlier *Pakicetus,* we saw many similarities between this primitive animal and land mammals known as mesonychids. A varied group ranging from cat size to bear size, mesonychids lived between sixty and thirty-seven million years ago. They were principally carnivorous scavengers.

Was the first land mammal to return to the sea and start the wheels of whale evolution a mesonychid? This theory—originally put forth in the 1960s by Leigh Van Valen, an American Museum graduate student at the time—is based on similarities in tooth structure. Subsequent discoveries, particularly of similarities in whale and mesonychid skeletal structure, have upheld this view.

As the fossil record of early whales continues to grow, our knowledge of the evolution of advanced cetacean traits becomes clearer and more complete. Fossils contradict the notion that whales suddenly appeared full-blown, without intermediate forms. I am a skeptical soul, but I have seen a lot of Tethys and excavated a lot of whales in the past fifteen years. Intermediates, missing links, are everywhere.

Along the coast of Tethys, an ancient warm ocean that stretched from Spain to Indonesia, an undulating Basilosaurus *catches fish with its four-foot-long jaws and battery of sharp teeth.*
Painting by F. Heimberg; collection of G. Pilleri