Originally published in December 2000

Fish-shaped reptiles called ichthyosaurs reigned over the oceans for as long as dinosaurs roamed the land, but only recently have paleontologists discovered why these creatures were so successful

Picture a late autumn evening some 160 million years ago, during the Jurassic time period, when dinosaurs inhabited the continents. The setting sun hardly penetrates the shimmering surface of a vast blue-green ocean, where a shadow glides silently among the dark crags of a submerged volcanic ridge. When the animal comes up for a gulp of evening air, it calls to mind a small whale—but it cannot be. The first whale will not evolve for another 100 million years. The shadow turns suddenly and now stretches more than twice the height of a human being. That realization becomes particularly chilling when its long, tooth-filled snout tears through a school of squidlike creatures.

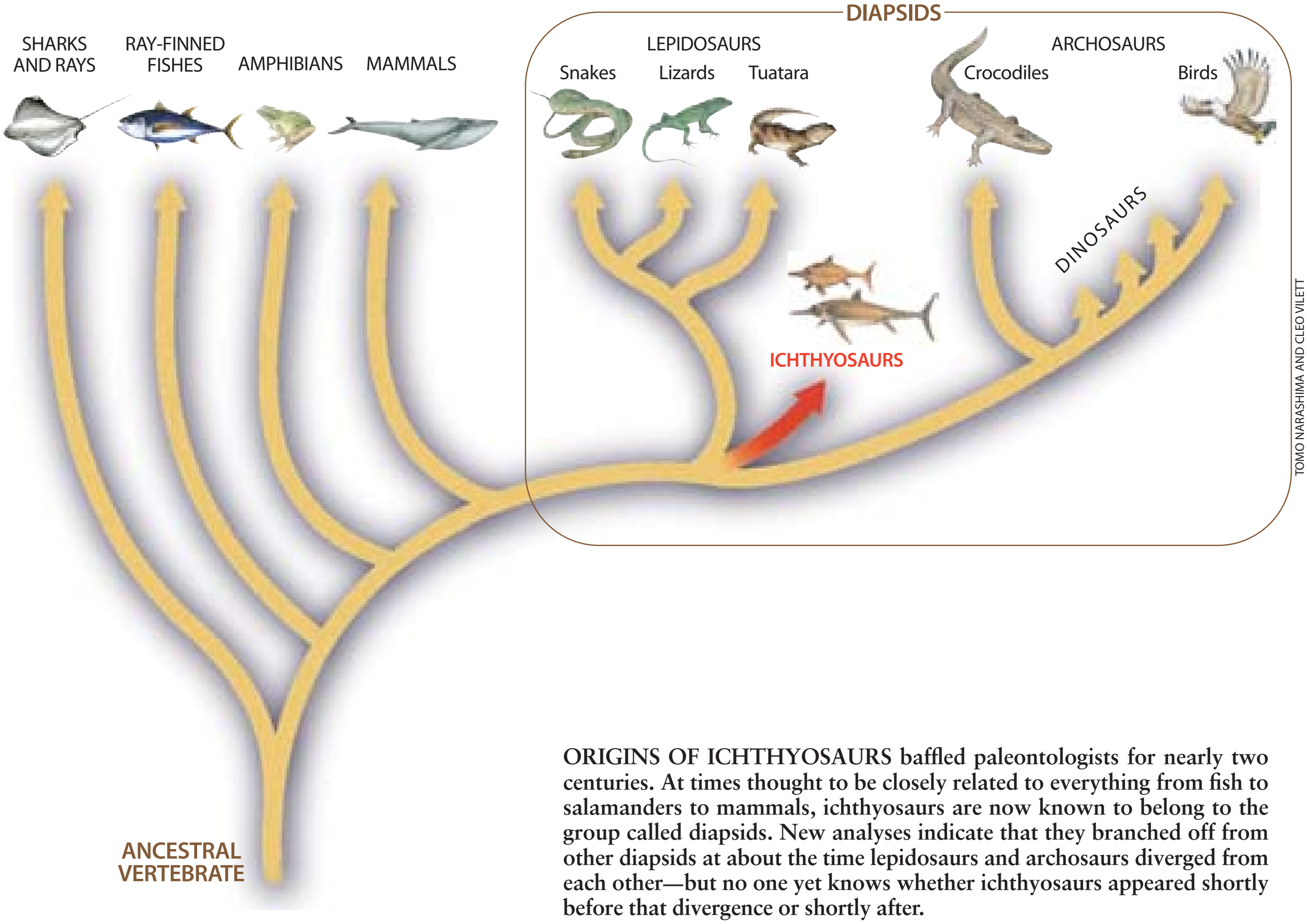
The remarkable animal is *Ophthalmosaurus*, one of more than 80 species now known to have constituted a group of sea monsters called the ichthyosaurs, or

Rulers *of the* Jurassic Seas

by Ryosuke Motani

ICHTHYOSAURS patrolled the world's oceans for 155 million years.

KAREN CARR



ORIGINS OF ICHTHYOSAURS baffled paleontologists for nearly two centuries. At times thought to be closely related to everything from fish to salamanders to mammals, ichthyosaurs are now known to belong to the group called diapsids. New analyses indicate that they branched off from other diapsids at about the time lepidosaurs and archosaurs diverged from each other—but no one yet knows whether ichthyosaurs appeared shortly before that divergence or shortly after.

fish-lizards. The smallest of these animals was no longer than a human arm; the largest exceeded 15 meters. *Ophthalmosaurus* fell into the medium-size group and was by no means the most aggressive of the lot. Its company would have been considerably more pleasant than that of a ferocious *Temnodontosaurus,* or "cutting-tooth lizard," which sometimes dined on large vertebrates.

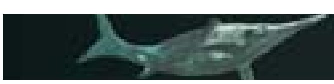
When paleontologists uncovered the first ichthyosaur fossils in the early 1800s, visions of these long-vanished beasts left them awestruck. Dinosaurs had not yet been discovered, so every unusual feature of ichthyosaurs seemed intriguing and mysterious. Examinations of the fossils revealed that ichthyosaurs evolved not from fish but from land-dwelling animals, which themselves had descended from an ancient fish. How, then, did ichthyosaurs make the transition back to life in the water? To which other animals were they most related? And why did they evolve bizarre characteristics, such as backbones that look like a stack of hockey pucks and eyes as big around as bowling balls?

Despite these compelling questions, the opportunity to unravel the enigmatic transformation from landlubbing reptiles to denizens of the open sea would have to wait almost two centuries. When dinosaurs such as *Iguanodan* grabbed the attention of paleontologists in the 1830s, the novelty of the fish-lizards faded away. Intense interest in the rulers of the Jurassic seas resurfaced only a few years ago, thanks to newly available fossils from Japan and China. Since then, fresh insights have come quickly.

Murky Origins

Although most people forgot about ichthyosaurs in the early 1800s, a few paleontologists did continue to think about them throughout the 19th century and beyond. What has been evident since their discovery is that the ichthyosaurs' adaptations for life in water made them quite successful. The widespread ages of the fossils revealed that these beasts ruled the ocean from about 245 million until about 90 million years ago—roughly the entire era that dinosaurs dominated the continents. Ichthyosaur fossils were found all over the world, a sign that they migrated extensively, just as whales do today. And despite their fishy appearance, ichthyosaurs were obviously air-breathing reptiles. They did not have gills, and the configurations of their skull and jawbones were undeniably reptilian. What is more, they had two pairs of limbs (fish have none), which implied that their ancestors once lived on land.

Paleontologists drew these conclusions based solely on the exquisite skeletons of relatively late, fish-shaped ichthyosaurs. Bone fragments of the first ichthyosaurs were not found until 1927. Somewhere along the line, those early



FACT: The smallest ichthyosaur was shorter than a human arm;

animals went on to acquire a decidedly fishy body: stocky legs morphed into flippers, and a boneless tail fluke and dorsal fin appeared. Not only were the advanced, fish-shaped ichthyosaurs made for aquatic life, they were made for life in the open ocean, far from shore. These extreme adaptations to living in water meant that most of them had lost key features—such as particular wrist and ankle bones—that would have made it possible to recognize their distant cousins on land. Without complete skeletons of the very first ichthyosaurs, paleontologists could merely speculate that they must have looked like lizards with flippers.

The early lack of evidence so confused scientists that they proposed almost every major vertebrate group—not only reptiles such as lizards and crocodiles but also amphibians and mammals—as close relatives of ichthyosaurs. As the 20th century progressed, scientists learned better how to decipher the relationships among various animal species. On applying the new skills, paleontologists started to agree that ichthyosaurs were indeed reptiles of the group Diapsida, which includes snakes, lizards, crocodiles and dinosaurs. But exactly when ichthyosaurs branched off the family tree remained uncertain—until paleontologists in Asia recently unearthed new fossils of the world's oldest ichthyosaurs.

The first big discovery occurred on the northeastern coast of Honshu, the main island of Japan. The beach is dominated by outcrops of slate, the layered black rock that is often used for the expensive ink plates of Japanese calligraphy and that also harbors bones of the oldest ichthyosaur, *Utatsusaurus*. Most *Utatsusaurus* specimens turn up fragmented and incomplete, but a group of geologists from Hokkaido University excavated two nearly complete skeletons in 1982. These specimens eventually became available for scientific study, thanks to the devotion of Nachio Minoura and his colleagues, who spent much of the next 15 years painstakingly cleaning the slate-encrusted bones. Because the bones are so fragile, they had to chip away the rock carefully with fine carbide needles as they peered through a microscope.

As the preparation neared its end in 1995, Minoura, who knew of my interest in ancient reptiles, invited me to join the research team. When I saw the skeleton for the first time, I knew that *Utatsusaurus* was exactly what paleontologists had been expecting to find for years: an ichthyosaur that looked like a lizard with flippers. Later that same year my colleague You Hailu, then at the Institute for Vertebrate Paleontology and Paleoanthropology in Beijing, showed me a second, newly discovered fossil—the world's most complete skeleton of *Chaohusaurus,* another early ichthyosaur. *Chaohusaurus* occurs in rocks the same age as those harboring remains of *Utatsusaurus,* and it, too, had been found before only in bits and pieces. The new specimen clearly revealed the outline of a slender, lizardlike body.

Utatsusaurus and *Chaohusaurus* illuminated at long last where ichthyosaurs belonged on the vertebrate family tree, because they still retained some key features of their land-dwelling ancestors. Given the configurations of the skull and limbs, my colleagues and I think that ichthyosaurs branched off from the rest of the diapsids near the separation of two major groups of living reptiles, lepidosaurs (such as snakes and lizards) and archosaurs (such as crocodiles and birds). Advancing the family-tree debate was a great achievement, but the mystery of the ichthyosaurs' evolution remained unsolved.

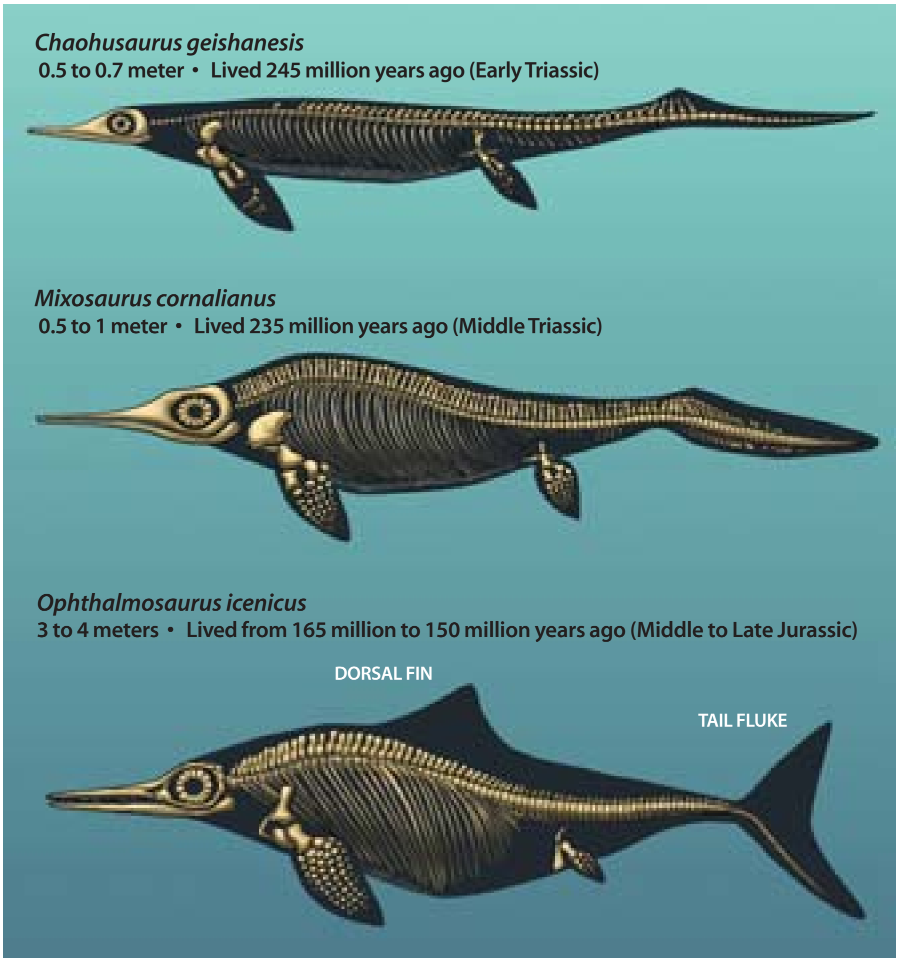
From Feet to Flippers

Perhaps the most exciting outcome of the discovery of these two Asian ichthyosaurs is that scientists can now paint a vivid picture of the elaborate adaptations that allowed their descendants to thrive in the open ocean. The most obvious transformation for aquatic life is the one from feet to flippers. In contrast to the slender bones in the front feet of most reptiles, all bones in the front "feet" of the fish-shaped ichthyosaurs are wider than they are long. What is more, they are all a similar shape. In most other four-limbed creatures it is easy to distinguish bones in the wrist (irregularly rounded) from those in the palm (long and cylindrical). Most important, the bones of fish-shaped ichthyosaurs are closely packed—without skin in between—to form a solid panel. Having all the toes enclosed in a single envelope of soft tissues would have enhanced the rigidity of the flippers, as it does in living whales, dolphins, seals and sea turtles. Such soft tissues also improve the

NEW FOSSILS of the first ichthyosaurs, including *Chaohusaurus*, have illuminated how these lizard-shaped creatures evolved into masters of the open ocean.

RYOSUKE MOTANI

the largest was longer than a typical city bus



ED HECK

ANCIENT SKELETONS have helped scientists trace how the slender, lizardlike bodies of the first ichthyosaurs (*top*) thickened into a fish shape with a dorsal fin and a tail fluke.

hydrodynamic efficiency of the flippers because they are streamlined in cross section—a shape impossible to maintain if the digits are separated.

But examination of fossils ranging from lizard- to fish-shaped—especially those of intermediate forms—revealed that the evolution from fins to feet was not a simple modification of the foot's five digits. Indeed, analyses of ichthyosaur limbs reveal a complex evolutionary process in which digits were lost, added and divided. Plotting the shape of fin skeletons along the family tree of ichthyosaurs, for example, indicates that fish-shaped ichthyosaurs lost the thumb bones present in the earliest ichthyosaurs. Additional evidence comes from studying the order in which digits became bony, or ossified, during the growth of the fish-shaped ichthyosaur *Stenopterygius,* for which we have specimens representing various growth stages. Later, additional fingers appeared on both sides of the preexisting ones, and some of them occupied the position of the lost thumb. Needless to say, evolution does not always follow a continuous, directional path from one trait to another.

Backbones Built for Swimming

The new lizard-shaped fossils have also helped resolve the origin of the skeletal structure of their fish-shaped descendants. The descendants have backbones built from concave vertebrae the shape of hockey pucks. This shape, though rare among diapsids, was always assumed to be typical of all ichthyosaurs. But the new creatures from Asia surprised paleontologists by having a much narrower backbone, composed of vertebrae shaped more like canisters of 35-millimeter film than hockey pucks. It appeared that the vertebrae grew dramatically in diameter and shortened slightly as ichthyosaurs evolved from lizard- to fish-shaped. But why?

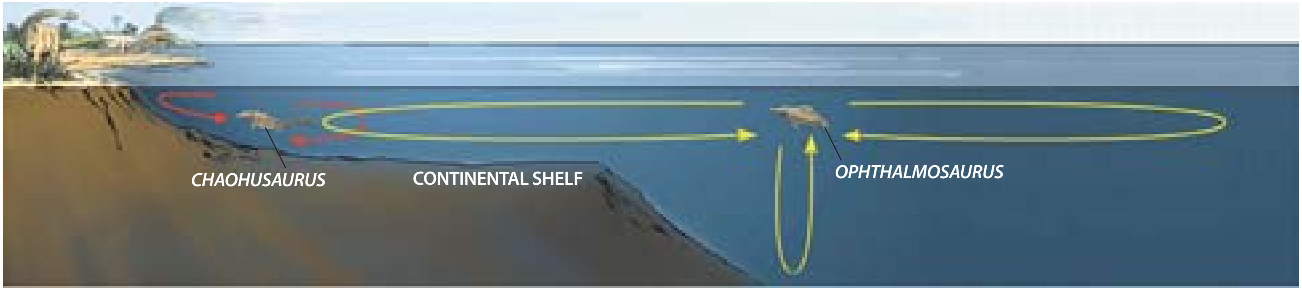
My colleagues and I found the answer in the swimming styles of living sharks. Sharks, like ichthyosaurs, come in various shapes and sizes. Cat sharks are slender and lack a tall tail fluke, also known as a caudal fin, on their lower backs, as did early ichthyosaurs. In contrast, mackerel sharks such as the great white have thick bodies and a crescent-shaped caudal fin similar to the later fish-shaped ichthyosaurs. Mackerel sharks swim by swinging only their tails, whereas cat sharks undulate their entire bodies. Undulatory swimming requires a flexible body, which cat sharks achieve by having a large number of backbone segments. They have about 40 vertebrae in the front part of their bodies—the same number scientists find in the first ichthyosaurs, represented by *Utatsusaurus* and *Chaohusaurus*. (Modern reptiles and mammals have only about 20.)

Undulatory swimmers, such as cat sharks, can maneuver and accelerate sufficiently to catch prey in the relatively shallow water above the continental shelf. Living lizards also undulate to swim, though not as efficiently as creatures that spend all their time at sea. It is logical to conclude, then, that the first ichthyosaurs—which looked like cat sharks and descended from a lizardlike ancestor—swam in the same fashion and lived in the environment above the continental shelf.

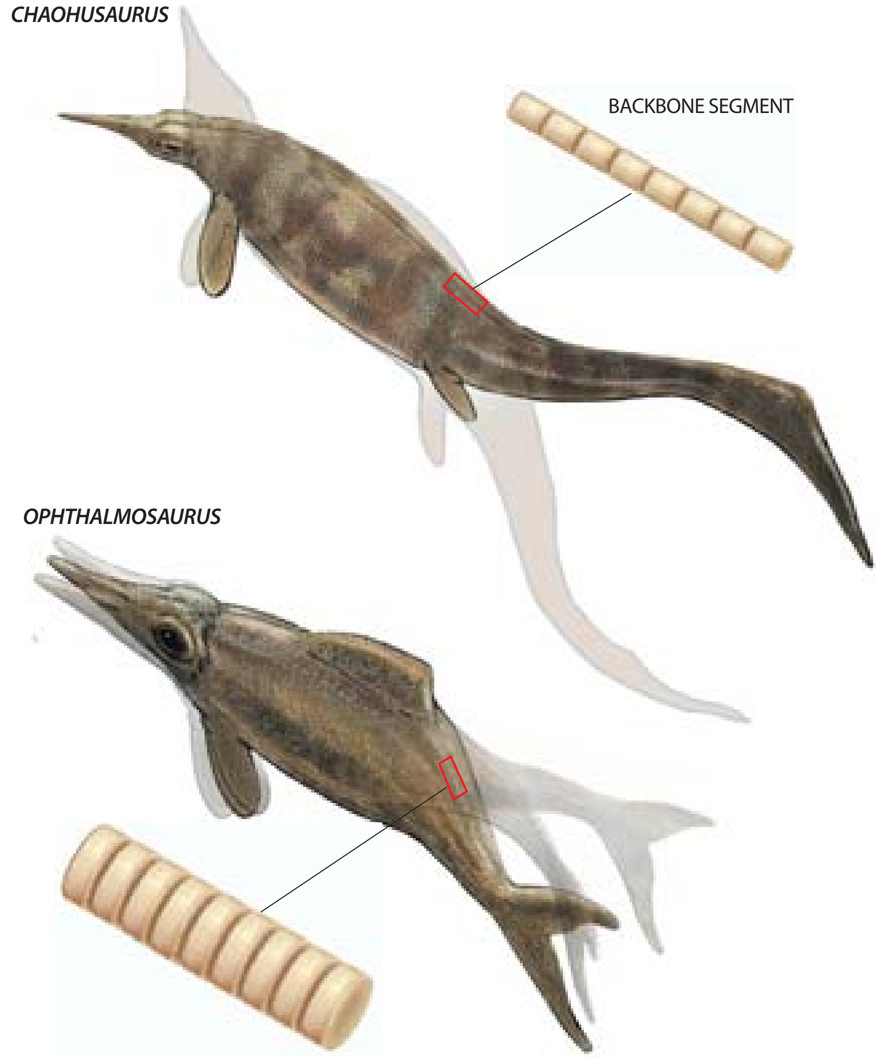
Undulatory swimming enables predators to thrive near shore, where food is abundant, but it is not the best choice for an animal that has to travel long distances to find a meal. Offshore predators, which hunt in the open ocean where food is less concentrated, need a more energy-efficient swimming style. Mackerel sharks solve this problem by having stiff bodies that do not undulate as their tails swing back and forth. A crescent-shaped caudal fin, which acts as an oscillating hydrofoil, also improves their cruising efficiency. Fish-shaped ich-

FACT: No other reptile group ever evolved a fish-shaped body

KAREN CARR



SWIMMING STYLES—and thus the habitats (*above*)—of ichthyosaurs changed as the shape of their vertebrae evolved. The narrow backbone of the first ichthyosaurs suggests that they undulated their bodies like eels (*right*). This motion allowed for the quickness and maneuverability needed for shallow-water hunting. As the backbone thickened in later ichthyosaurs, the body stiffened and so could remain still as the tail swung back and forth (*bottom*). This stillness facilitated the energy-efficient cruising needed to hunt in the open ocean.



KAREN CARR; ADRIENNE SMUCKER (*vertebrae*)

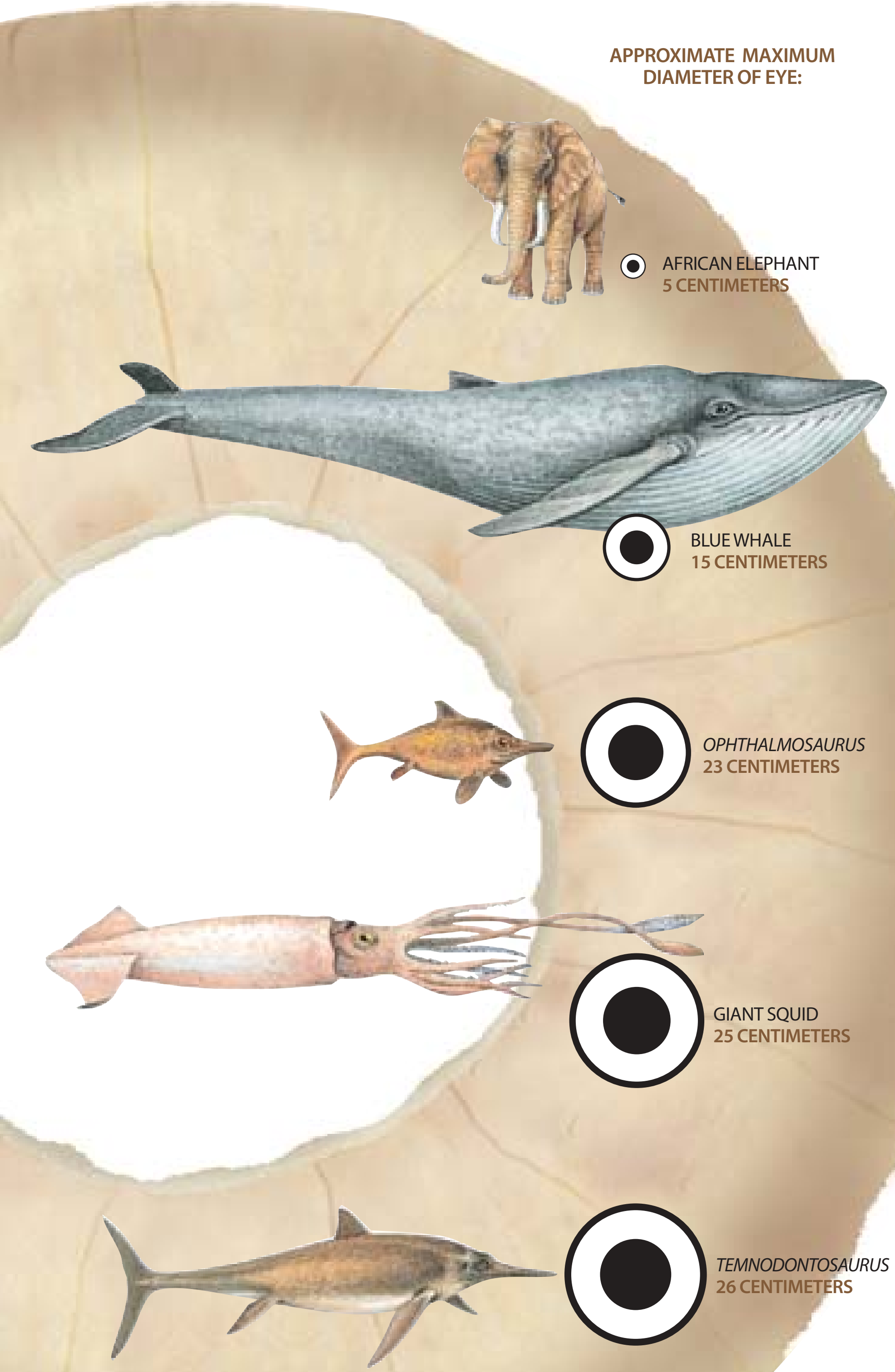
thyosaurs had such a caudal fin, and their thick body profile implies that they probably swam like mackerel sharks.

Inspecting a variety of shark species reveals that the thicker the body from top to bottom, the larger the diameter of the vertebrae in the animal's trunk. It seems that sharks and ichthyosaurs solved the flexibility problem resulting from having high numbers of body segments in similar ways. As the bodies of ichthyosaurs thickened over time, the number of vertebrae stayed about the same. To add support to the more voluminous body, the backbone became at least one and a half times thicker than those of the first ichthyosaurs. As a consequence of this thickening, the body became less flexible, and the individual vertebrae acquired their hockey-puck appearance.

Drawn to the Deep

The ichthyosaurs' invasion of open water meant not only a wider coverage of surface waters but also a deeper exploration of the marine environment. We know from the fossilized stomach contents of fish-shaped ichthyosaurs that they mostly ate squidlike creatures known as dibranchiate cephalopods. Squid-eating whales hunt anywhere from about 100 to 1,000 meters deep and sometimes down to 3,000 meters. The great range in depth is hardly surprising considering that food resources are widely scattered below about 200 meters. But to hunt down deep, whales and other air-breathing divers have to go there and get back to the surface in one breath—no easy task. Reducing energy use during swimming is one of the best ways to conserve precious oxygen stored in their bodies. Consequently, deep divers today have streamlined shapes that reduce drag—and so did fish-shaped ichthyosaurs.

Characteristics apart from diet and body shape also indicate that at least some fish-shaped ichthyosaurs were deep divers. The ability of an air-breathing diver to stay submerged depends roughly on its body size: the heavier the diver, the more oxygen it can store in its muscles, blood and certain other organs—and the slower the consumption of oxygen per unit of body mass. The evolution of a thick, stiff body increased the volume and mass of fish-shaped ichthyosaurs relative to their predecessors. Indeed, a fish-shaped ichthyosaur would have been up to six times heavier than a lizard-shaped ichthyosaur of the same body length. Fish-shaped ichthyosaurs also grew longer, further augmenting their bulk. Calculations based on the aerobic capacities of today's air-breathing divers (mostly mammals and



birds) indicate that an animal the weight of fish-shaped *Ophthalmosaurus*, which was about 950 kilograms, could hold its breath for at least 20 minutes. A conservative estimate suggests, then, that *Ophthalmosaurus* could easily have dived to 600 meters—possibly even 1,500 meters—and returned to the surface in that time span.

Bone studies also indicate that fish-shaped ichthyosaurs were deep divers. Limb bones and ribs of four-limbed terrestrial animals include a dense outer shell that enhances the strength needed to support a body on land. But that dense layer is heavy. Because aquatic vertebrates are fairly buoyant in water, they do not need the extra strength it provides. In fact, heavy bones (which are little help for oxygen storage) can impede the ability of deep divers to return to the surface. A group of French biologists has established that modern deep-diving mammals solve that problem by making the outer shell of their bones spongy and less dense. The same type of spongy layer also encases the bones of fish-shaped ichthyosaurs, which implies that they, too, benefited from lighter skeletons.

Perhaps the best evidence for the deep-diving habits of later ichthyosaurs is their remarkably large eyes, up to 23 centimeters across in the case of *Ophthalmosaurus*. Relative to body size, that fish-shaped ichthyosaur had the biggest eyes of any animal ever known.

The size of their eyes also suggests that visual capacity improved as ichthyosaurs moved up the family tree. These estimates are based on measurements of the sclerotic ring, a doughnut-shaped bone

ICHTHYOSAUR EYES were surprisingly large. Analyses of doughnut-shaped eye bones called sclerotic rings reveal that *Ophthalmosaurus* had the largest eyes relative to body size of any adult vertebrate, living or extinct, and that *Temnodontosaurus* had the biggest eyes, period. The beige shape in the background is the size of an *Ophthalmosaurus* sclerotic ring. The photograph depicts a well-preserved ring from *Stenopterygius*.

TOMO NARASHIMA (*animals*); EDWARD BELL (*sclerotic ring*); RYOSUKE MOTANI (*photograph*)

FACT: Their eyes were the largest of any animal, living or dead that was embedded in their eyes. (Humans do not have such a ring—it was lost in mammalian ancestors—but most other vertebrates have bones in their eyes.) In the case of ichthyosaurs, the ring presumably helped to maintain the shape of the eye against the forces of water passing by as the animals swam, regardless of depth.

The diameter of the sclerotic ring makes it possible to calculate the eye's minimum f-number—an index, used to rate camera lenses, for the relative brightness of an optical system. The lower the number, the brighter the image and therefore the shorter the exposure time required. Low-quality lenses have a value of f/3.5 and higher; high-quality lenses have values as low as f/1.0. The f-number for the human eye is about 2.1, whereas the number for the eye of a nocturnal cat is about 0.9. Calculations suggest that a cat would be capable of seeing at depths of 500 meters or greater in most oceans. *Ophthalmosaurus* also had a minimum f-number of about 0.9, but with its much larger eyes, it probably could outperform a cat.


RYOSUKE MOTANI

SMALL ISLAND in northeast Japan turned out to harbor two almost complete skeletons of *Utatsusaurus,* the oldest ichthyosaur.

Gone for Good

Many characteristics of ichthyosaurs—including the shape of their bodies and backbones, the size of their eyes, their aerobic capacity, and their habitat and diet—seem to have changed in a connected way during their evolution, although it is not possible to judge what is the cause and what is the effect. Such adaptations enabled ichthyosaurs to reign for 155 million years. New fossils of the earliest of these sea dwellers are now making it clear just how they evolved so successfully for aquatic life, but still no one knows why ichthyosaurs went extinct.

Loss of habitat may have clinched the final demise of lizard-shaped ichthyosaurs, whose inefficient, undulatory swimming style limited them to near-shore environments. A large-scale drop in sea level could have snuffed out these creatures along with many others by eliminating their shallow-water niche. Fish-shaped ichthyosaurs, on the other hand, could make a living in the open ocean, where they would have had a better chance of survival. Because their habitat never disappeared, something else must have eliminated them. The period of their disappearance roughly corresponds to the appearance of advanced sharks, but no one has found direct evidence of competition between the two groups.

Scientists may never fully explain the extinction of ichthyosaurs. But as paleontologists and other investigators continue to explore their evolutionary history, we are sure to learn a great deal more about how these fascinating creatures lived.

The Author

RYOSUKE MOTANI, who was born in Tokuyama, Japan, is a researcher in the department of paleobiology at the Royal Ontario Museum in Toronto. As a child he found ichthyosaurs uninteresting. ("They looked too ordinary in my picture books," he recalls.) But his view changed during his undergraduate years at the University of Tokyo, after a paleontology professor allowed him to study the only domestic reptilian fossil they had: an ichthyosaur. "I quickly fell in love with these noble beasts," he says. Motani went on to explore ichthyosaur evolution for his doctoral degree from the University of Toronto in 1997. A fellowship from the Miller Institute then took him to the University of California, Berkeley, for postdoctoral research. He moved back to Canada in September 1999.

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Ryosuke Motani's Web site: www.ucmp.berkeley.edu/people/motani/ichthyo/