SINCLAIR STAMMERS/SPL/GETTY

BEASTS FROM THE DEEP

Ichthyosaurs were some of the largest and most mysterious predators to ever prowl the oceans. Now, the giant reptiles are starting to give up their secrets.

BY TRACI WATSON

Valentin Fischer had always wanted to study fossils, perhaps dinosaurs or extinct mammals. Instead, when he was in graduate school, Fischer ended up sorting through a pile of bones belonging to ancient marine reptiles known as ichthyosaurs — a group that had been mostly ignored by modern palaeontologists. It was not exactly his dream job.

"I said, 'Ohhh, ichthyosaurs, so boring'," recalls Fischer. "They all look the same. It's always a pointy snout and big eyes."

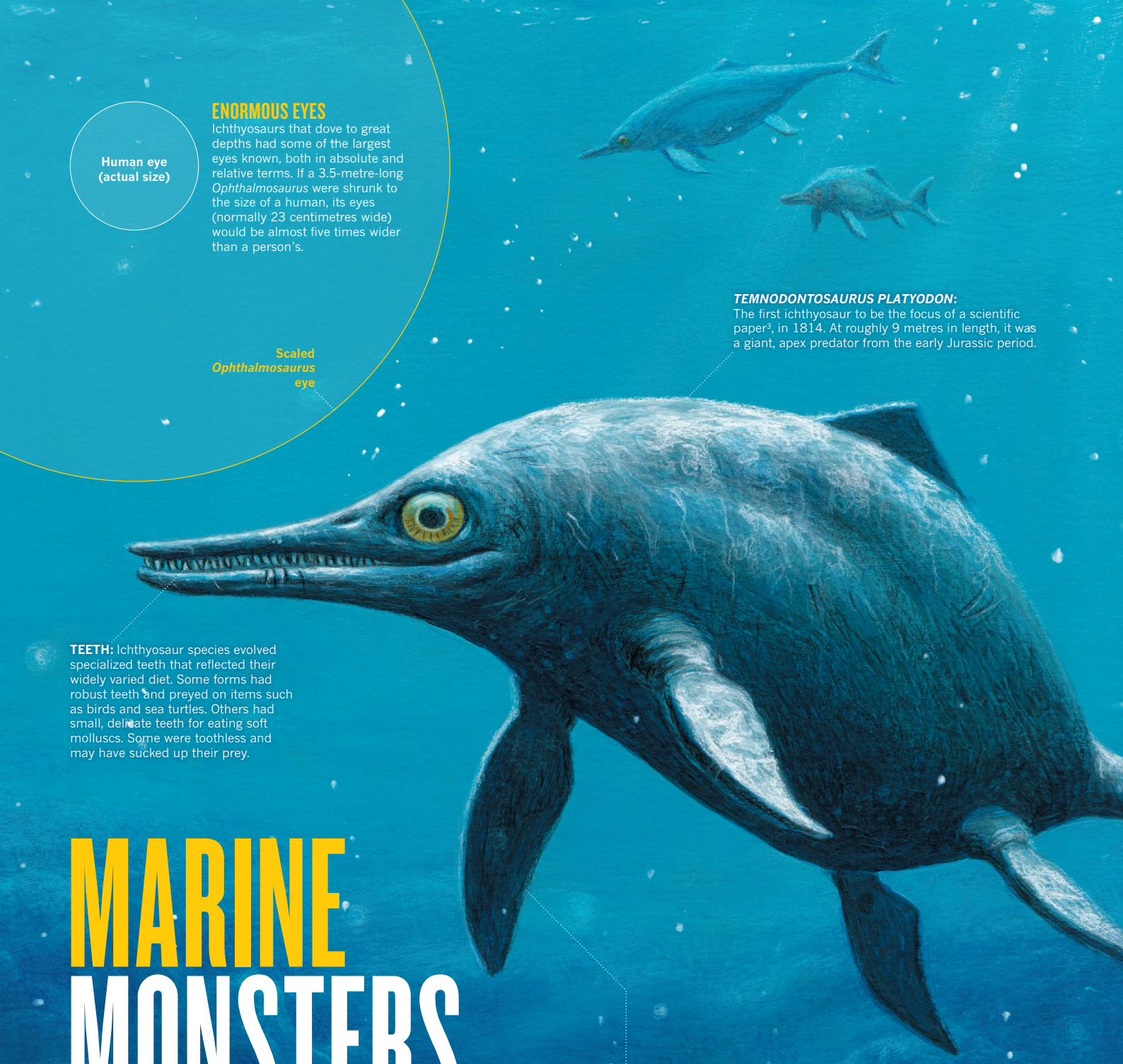
Fischer put his feelings aside and dutifully began combing through the fossils stored in a research centre in provincial France. Among the specimens stashed in plastic boxes was an ichthyosaur skull that had been partially destroyed by ants and tree roots while buried underground. When Fischer cleaned up the skull, he realized that it was probably a species new to science.

As discoveries started to pile up, he got hooked. Fischer, now at the University of Liège, Belgium, and his colleagues have since described seven surprising new ichthyosaurs, ranging from a tuna-sized reptile with thin, sharp teeth[1] to an animal as big as a killer whale, with a beak like that of a swordfish[2].

Many ichthyosaurs had sharp conical teeth to help them catch fast-moving prey.

Fischer is part of an ichthyosaur renaissance that is sweeping palaeontology. After ignoring them for decades, more and more researchers have started to focus on the reptiles, which were among the top predators in the seas for some 150 million years during the days of the dinosaurs (see 'Marine monsters').

And that renewed interest has brought a slew of discoveries. In the two centuries leading up to 2000, researchers identified roughly 80 species of ichthyosaur and close relatives. In the past 17 years, they've added another 20–30, says vertebrate palaeontologist Ryosuke Motani



ENORMOUS EYES

Ichthyosaurs that dove to great depths had some of the largest eyes known, both in absolute and relative terms. If a 3.5-metre-long *Ophthalmosaurus* were shrunk to the size of a human, its eyes (normally 23 centimetres wide) would be almost five times wider than a person's.

***TEMNODONTOSAURUS PLATYODON*:** The first ichthyosaur to be the focus of a scientific paper[3], in 1814. At roughly 9 metres in length, it was a giant, apex predator from the early Jurassic period.

TEETH: Ichthyosaur species evolved specialized teeth that reflected their widely varied diet. Some forms had robust teeth and preyed on items such as birds and sea turtles. Others had small, delicate teeth for eating soft molluscs. Some were toothless and may have sucked up their prey.

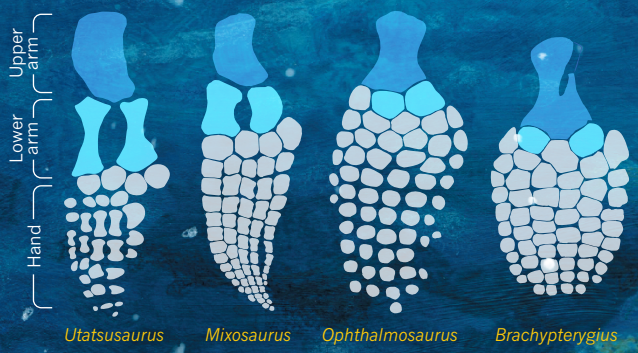
MARINE MONSTERS

Ancient aquatic reptiles called ichthyosaurs ruled the seas for much of the Mesozoic era, when dinosaurs reigned. These marine creatures evolved from land-dwelling reptiles and quickly diversified in the early Triassic period into a vast variety of agile swimmers, including some that were the biggest marine predators of their time.

BY RICHARD MONASTERSKY AND TRACI WATSON
ILLUSTRATION BY ESTHER VAN HULSEN
DESIGN BY WES FERNANDES

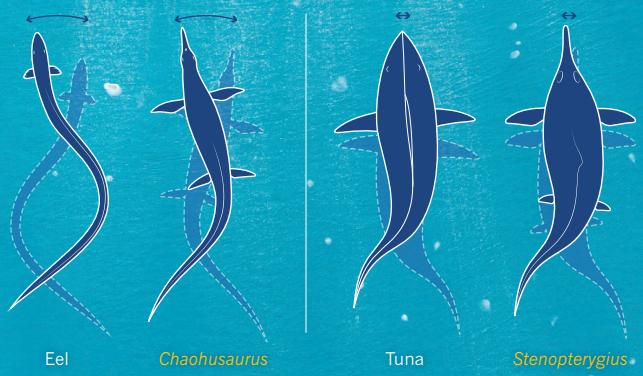
FOREFINS

The front flippers of ichthyosaurs evolved from limbs originally fit for walking on land. Over time, the bones of the lower arm shortened, and new digits appeared on the 'hand', which became more paddle-shaped.

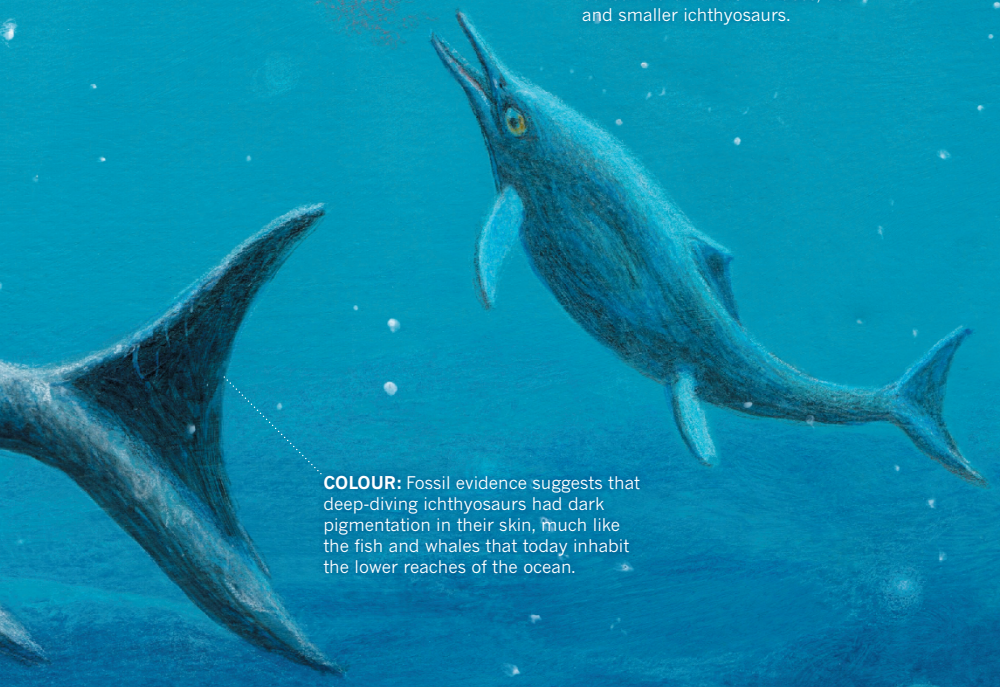


SWIMMING STYLES

Early ichthyosaurs undulated from side to side similarly to eels, whereas later species had stiffer backbones and moved more like tuna, which increased their speed.



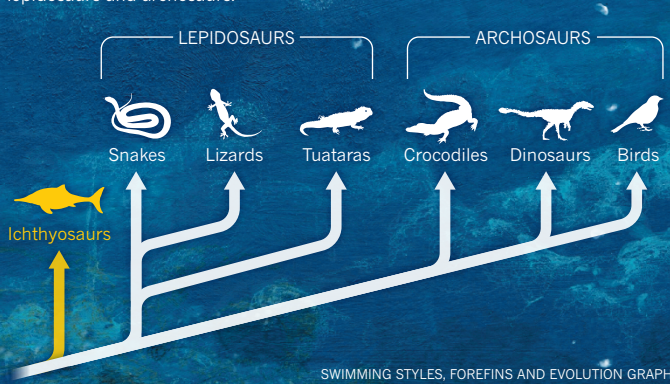
PREY: Stomach contents of fossil ichthyosaurs show that some dined on ancient squid-like creatures called belemnites, whereas others consumed different molluscs, fish and smaller ichthyosaurs.



COLOUR: Fossil evidence suggests that deep-diving ichthyosaurs had dark pigmentation in their skin, much like the fish and whales that today inhabit the lower reaches of the ocean.

EVOLUTION

The ancestors of ichthyosaurs remain unknown, but analysis of fossils suggests that they diverged from other reptiles before the evolutionary split between lepidosaurs and archosaurs.



SWIMMING STYLES, FOREFINS AND EVOLUTION GRAPHIC ADAPTED FROM RYOSUKE MOTANI.

THE LONG REIGN

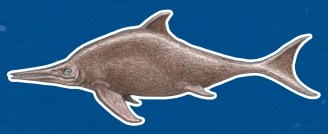
Ichthyosaurs had an amazingly successful run, enduring from nearly 250 million to 94 million years ago. Over that time, they evolved a huge range of body shapes and sizes. Some were adapted to deep diving; others prowled shallower, coastal waters.

◂ Millions of years ago (Mya)

Upper Cretaceous

100 Mya

Lower Cretaceous



Platypterygius australis: Grew to about 7 metres. Bite marks on some bones may reflect fighting between members of the species.

Ophthalmosaurus: Large eyes and other evidence suggest that this genus was able to swim to great depths.

150 Mya

Upper Jurassic

Middle Jurassic

Excalibosaurus: With its long upper jaw, this genus may have hunted by whipping its head back and forth, like modern swordfish.

Lower Jurassic

200 Mya

Upper Triassic

Shonisaurus sikanniensis: This giant species from the Triassic grew to more than 20 metres long and was apparently toothless in adulthood. It may have fed by sucking up prey.

Middle Triassic

Mixosaurus: In this genus of small early ichthyosaurs, some were shorter than 2 metres.

Lower Triassic

of the University of California, Davis, and the number of papers on the animals has soared.

"There are more people working on ichthyosaurs right now than I have seen for my entire career," says Judy Massare of the State University of New York College at Brockport, who began studying the animals in the 1980s.

The swell of research is starting to answer key questions about ichthyosaurs, such as how and where they originated and how quickly they came to rule the oceans. The group was even more diverse than once thought, ranging from early near-shore creatures that undulated like eels to giants that cruised the open ocean by swishing their powerful tails. "They could go anywhere, just like whales," Motani says. The biggest ones rivalled blue whales (*Balaenoptera musculus*) in length and were the largest predators in the Triassic seas.

The work is also revealing the last chapters of the ichthyosaur story, which culminated with the animals' extinction during the Upper Cretaceous, some 30 million years before dinosaurs disappeared. Some scholars now argue that the 'fish-lizards' were vanquished in part by the era's drastic environmental shifts. That's a form of redemption for ichthyosaurs; an old theory had suggested that they vanished when more capable predators, such as swift sharks, emerged and eclipsed them.

And palaeontologists point to one more reason to focus on ichthyosaurs: because their distant ancestors were land reptiles, the creatures offer a particularly dramatic example of one of the biggest evolutionary makeovers evident in the fossil record, says vertebrate palaeontologist Stephen Brusatte of the University of Edinburgh, UK. "They totally changed their bodies, biologies and behaviours in order to live in the water."

FISHY START

The word 'dinosaur' hadn't even been coined when a weird skeleton appeared along the southwestern English coast in the early nineteenth century. The bones caught the eyes of celebrated fossil hunter Mary Anning, then no older than 13, and her brother. Their fossil fetched them £23, a substantial sum at the time, and inspired the first scientific paper[3] devoted to ichthyosaurs. The paper, published by British surgeon Everard Home in 1814, erroneously called the animal a "fish … not of the family of sharks or rays". Other naturalists soon recognized the fossils as reptiles.

The leading lights of natural history marvelled at these creatures. Frenchman Georges Cuvier, considered the father of vertebrate palaeontology, called them "incredible", and held up ichthyosaurs as support for his theory that catastrophic mass extinctions have plagued Earth. British geologist Charles Lyell, meanwhile, suggested that ichthyosaurs could reappear when Earth's climate cycled through a favourable phase.

Then came the discovery of monstrous land animals, many of which were armed with rows of fierce teeth. This group, named dinosaurs, captivated the public and scientists alike. According to Fischer, they "kicked ichthyosaurs off the pedestal of glory". The fossils of the marine reptiles piled up unstudied in museums, and their life story was left incomplete.

Today's renaissance in ichthyosaur research is filling in the gaps, especially the fish-lizards' origins. It took massive anatomical change to mould fully aquatic animals out of land reptiles. Their arms shrank and their hands enlarged, forming seaworthy flippers. They developed the ability to hold their breath for long stretches, even up to 20 minutes. Many evolved huge eyes — larger than footballs, in one species — for peering through the dark depths.

Researchers suspect that those changes took place not long before or after an apocalyptic mass extinction that wiped out 80% of Earth's marine species at the end of the Permian period[4]. But until the past few years, they have lacked fossils to illustrate much of that transition.

One of the early forms helping to fill in that gap is an animal that Motani calls "the most bizarre" early ichthyosaur ever seen, which he and his colleagues discovered in a Chinese limestone quarry[5]. It had a head the size of an orange and a torso encased by wide slabs of bone, earning it the scientific name *Sclerocormus parviceps*, or 'stiff-trunk small-skull'. It dates to 248 million years ago, only 4 million years after the end-Permian extinction. A nearby quarry yielded a snub-nosed fish-lizard of roughly the same age, *Cartorhynchus lenticarpus*[6]. About as long as a rainbow trout (*Oncorhynchus mykiss*), this primitive ichthyosaur may have heaved itself around on land atop its big flippers in much the same way that sea turtles do.

These early animals weren't direct ancestors of the fish-shaped ichthyosaurs. But they are still "a big step forward in understanding where ichthyosaurs came from", says Erin Maxwell, a palaeontologist at the Stuttgart State Museum of Natural History in Germany. The fossils show, for example, that ichthyosaurs originated in what is now the eastern part of south China. At the time, it was one of the few places in the world where land plants flourished. Decaying vegetation would have enriched the nearby seas, Motani says, and eventually, "seafood looked attractive to animals that happened to live near the coastline".

The land-worthy flippers of *Cartorhynchus* led Motani to argue that it had recent ancestors that were terrestrial, or at least amphibious. That would make it a close relative of the land-based or amphibious ancestor of all ichthyosaurs. He interprets the heavy bones of both *Sclerocormus* and *Cartorhynchus* as evidence of a bottom-dwelling lifestyle. Other animals that moved from land to sea also went through a bottom-dwelling phase, Motani says, and with his new finds, "we have proof that ichthyosaurs went through that heavy stage, and were most likely bottom feeders" — unlike the later ichthyosaurs, which were creatures of the open ocean.

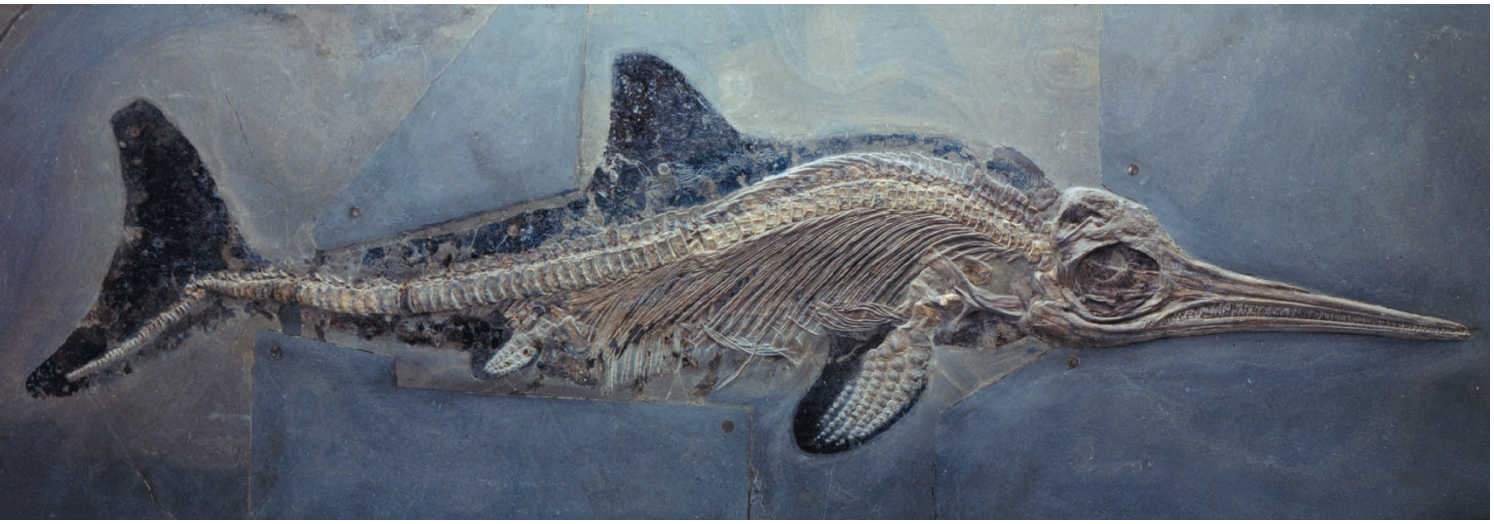
> "ONCE THESE THINGS HIT THE WATER, THEY JUST WENT NUTS."

Other researchers agree that the Chinese fossils provide a valuable window into the transformation from landlubber to sea creature. The discoveries are "some of the most interesting reptile fossils that have been found recently", Brusatte says. "They are giving us a glimpse of what it actually took to turn a land-living reptile into something semi-aquatic and then something that looked like a fish."

Proper ichthyosaurs, which boast long snouts and kinked tails to distinguish them from their primitive forebears, appeared during the early Triassic and quickly took over their new environment. Discoveries over the past few years have revealed the wide variety of fish-lizards that emerged at the same time as *Cartorhynchus* or soon after.

Take the killer-whale-sized *Thalattoarchon saurophagis*, or 'lizard-eating ruler of the seas', which was spotted in Nevada 20 years ago but not fully excavated[7] until 2008. Its sharp teeth reveal it as a "large meat-eater or flesh-tearer" that preyed on fish and other ichthyosaurs, says vertebrate palaeontologist Martin Sander of the University of Bonn in Germany and the Natural History Museum of Los Angeles County, who helped to describe the animal. During its reign in the early Middle Triassic, only 8 million years after the end-Permian extinction, it "basically ate anything it wanted to", Sander says.

On Norway's Spitsbergen Island north of the Arctic Circle, researchers have hacked away the permafrost to reveal large, primitive ichthyosaurs that seem to date to the very early Triassic. The finds have yet to be identified, but they help to show that "once these things hit the water, they just went nuts", says Patrick Druckenmiller, a palaeontologist at the University of Alaska Fairbanks and part of the Spitsbergen team. The presence of large predators at this time suggests that creatures of all sizes and lifestyles restocked the oceans



FIELD MUSEUM LIBRARY/GETTY

Like many later ichthyosaurs, *Stenopterygius quadriscissus* lived in the open ocean. Black marks around fossil show the outline of the preserved skin.

after the devastation of the end-Permian extinction.

After their initial burst of evolution, ichthyosaurs went through some tough times. In the later Triassic, many species died out during one or more mass extinctions that also claimed large fractions of species on land and in the oceans.

After this, the ichthyosaur's story gets complicated. Palaeontologists had long thought that the group was hit by a major loss of biodiversity in the Jurassic and never really recovered. The fossil record suggested that only a handful of species, all similar in appearance and lifestyle, limped across the Jurassic–Cretaceous boundary 145 million years ago. Then the whole group went extinct midway through the Cretaceous, while dinosaurs thrived for another 30 million years or so, until an asteroid strike wiped them out. The lack of diversity among ichthyosaur species could have hampered their ability to compete against sharks and other emerging predators in the seas.

But finds in the past few years have called that whole story into question. New fossil discoveries show that many more species thrived during the Cretaceous than previously recognized. These species also had more diverse body types and food sources than researchers thought.

Ichthyosaurs' reputation has risen in good part because of Fischer's work — not at sweaty dig sites but in hushed museums. "I am very bad at finding fossils in the field," Fischer confesses. "The only ichthyosaur I've found, ever, is a single vertebra." But the hundreds of museum specimens that he has scrutinized — some of them left unexamined for a century — have yielded a bounty of Cretaceous novelties. In just over a decade, Fischer's team and other groups have reported at least nine new species from this period.

Fischer and his colleagues estimate that the number of known ichthyosaur species was just as high during parts of the early Cretaceous as during spans of the Jurassic. It turns out that the fish-shaped reptiles called parvipelvians, the only group of ichthyosaurs to endure from the Triassic into the Cretaceous, had a greater range of shapes during the middle of the early Cretaceous than at any other time in their history[8]. "The diversity of ichthyosaurs in the Cretaceous, in particular, is even higher than we ever thought it was", says Fischer's co-author Darren Naish, a vertebrate palaeontologist at the University of Southampton, UK. He calls it a "Cretaceous ichthyosaur revolution".

Then, according to Fischer's analysis, a one-two punch hit the ichthyosaurs. A good number of species went extinct roughly 100 million years ago, and the few survivors followed their relatives some 5 million to 6 million years later. To understand why, Fischer looked to environmental factors. He noticed a correlation between climate and extinctions: the greater the temperature fluctuation in a given period, the more species of ichthyosaurs winked out.

Other scientists agree that climate disruptions could have played a big part in the animals' disappearance. Climate volatility "is a much better hypothesis than any proposed so far. It matches what we know about extinction risk in large predators today," Maxwell says.

The mid-Cretaceous was a difficult time in the oceans. Ichthyosaurs died out when sea levels were high and marine oxygen levels were low. Many other ocean groups, such as ammonites, were going downhill fast during the same period. Ichthyosaurs, then, might be "just a small facet of something more important", Fischer says. He's now looking at whether other marine predators during the Cretaceous followed the ichthyosaur pattern.

Fischer's results are not universally accepted. Motani, for example, thinks that Fischer's scenario is plausible, but he takes issue with the statistical methods that Fischer uses to date ichthyosaurs' extinction. Fischer places the reptiles' disappearance close to 94 million years ago, but if the creatures went extinct at a different time, the correlation between their fate and climate volatility would not be as strong. Fischer stands by his conclusions, however, and says that the fossil record for marine reptiles actually improves during the Cretaceous, which adds confidence to conclusions about ichthyosaurs during that period.

The debate over ichthyosaurs' final days will continue to rage, as scientists strive to understand the forces behind the mysterious extinction of a successful group. Researchers also hope to understand what befell the ichthyosaurs that died out at the end of the Triassic. More fossils would help. So would techniques that have already been deployed to better date the sediments containing ichthyosaurs, enabling researchers to pinpoint species' histories with higher precision.

The new debates and competition characterizing the field do not perturb Motani. He has no yearning for the lonely days when he was one of so few ichthyosaur specialists that journals struggled to peer-review his manuscripts. On the contrary, he is glad that more scientists are pursuing the animals he regards as "beautiful, and beautifully adapted". To Motani and other partisans, ichthyosaurs are finally getting the attention they've long deserved. ■

Traci Watson *is a freelance journalist in Washington, DC.*

1. Fischer, V., Masure, E., Arkhangelsky, M. S. & Godefroit, P. *J. Vertebr. Paleontol.* **31,** 1010–1025 (2011).
2. Martin, J. E., Fischer, V., Vincent, P. & Suan, G. *Palaeontology* **55,** 995–1005 (2012).
3. Home, E. *Phil. Trans. R. Soc. Lond.* **104,** 571–577 (1814).
4. Stanley, S. M. *Proc. Natl Acad. Sci. USA* **113,** E6325–E6334 (2016).
5. Jiang, D.-Y. *et al. Sci. Rep.* **6,** 26232 (2016).
6. Motani, R. *et al. Nature* **517,** 485–488 (2015).
7. Fröbisch, N. B., Fröbisch, J., Sander, P. M., Schmitz, L. & Rieppel, O. *Proc. Natl Acad. Sci. USA* **110,** 1393–1397 (2013).
8. Fischer, V., Bardet, N., Benson, R. B., Arkhangelsky, M. S. & Friedman, M. *Nature Commun.* **7,** 10825 (2016).