

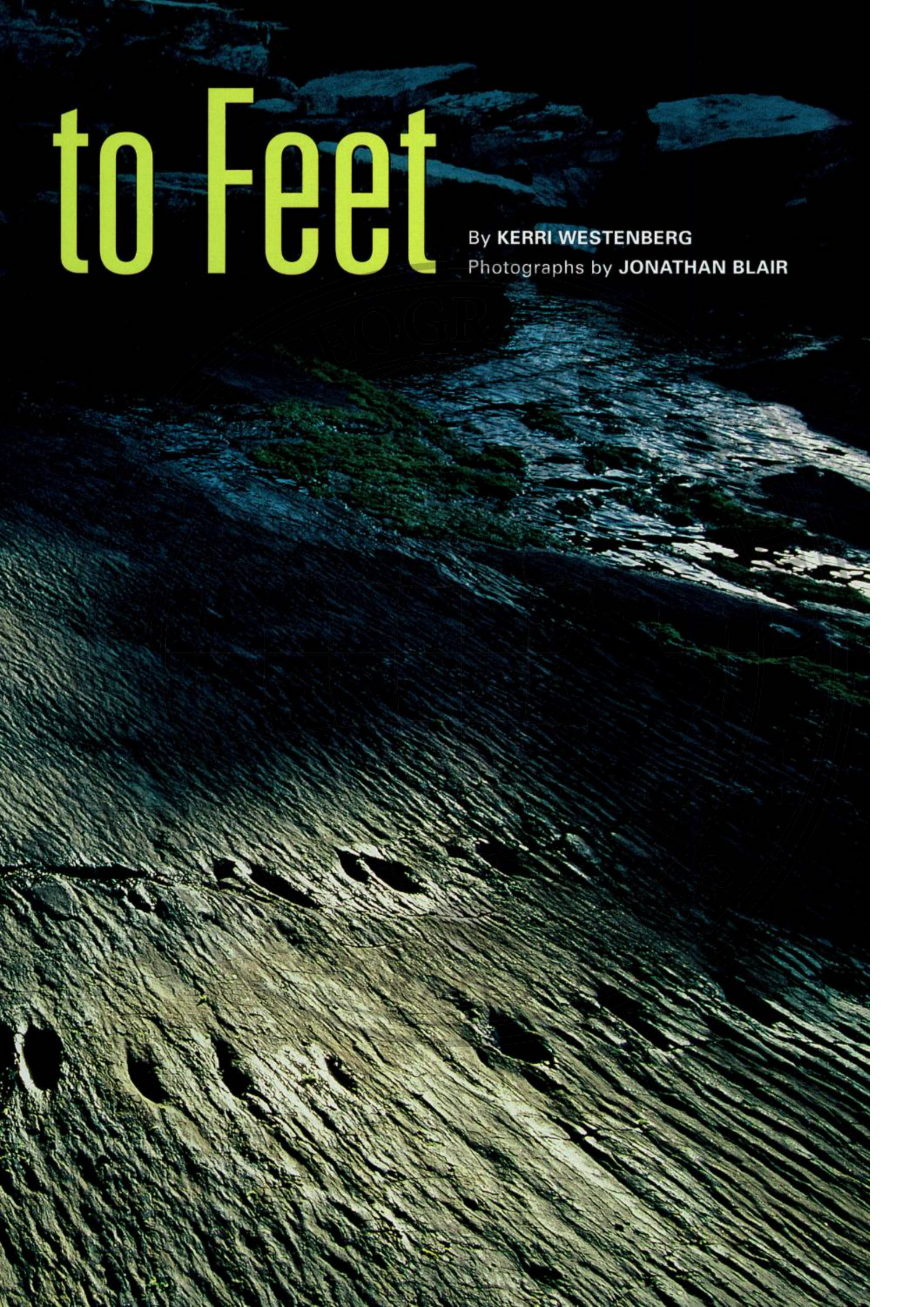
From Fins

It never walked on land. But the aquatic animal thought to have left these stone footprints in Ireland more than 365 million years ago moved through the muddy shallows on four feet—an evolutionary milestone that would change life on Earth forever. These tracks and other recent fossil finds have forced scientists to rethink when and how life came to land.

to Feet

By **KERRI WESTENBERG**

Photographs by **JONATHAN BLAIR**





"COME TO SEE our big fossils?" asks Joseph O'Shea as he greets a visitor from the red doorway of his house on Valentia Island off the remote southwest coast of Ireland. O'Shea, a whiskered, bright-eyed man in his 80s, is delighted with the unexpected company. "Never seen them myself," he says, pointing a gnarled finger across a green pasture, "but they're on the far side of that field at the edge of the sea."

Until 1992 no one had seen what has drawn me to this isolated coast just south of Dingle Bay—the fossilized footprints of a mysterious animal that lived more than 365 million years ago during the Devonian period. That year Iwan Stössel, a Swiss geology student, was walking the coast and came across this set of

150 tracks, each the size a basset hound might leave. Paleontologists call the kind of animal that made these prints a tetrapod, which translates from Greek as "four-footed." Such animals, with four limbs rather than fins, were new during the Devonian, which is known as the age of fishes because of its abundance of fish fossils. But until recently scientists could say little about tetrapod evolution. Only one nearly complete early tetrapod, a creature called *Ichthyostega*, had ever been found.

That dearth of fossils has long frustrated specialists because tetrapods supposedly made one of the greatest breakthroughs in the history of life on Earth, one that made possible the evolution of humans. By developing those four limbs they became the first large animals able to crawl out of the water, where life first

Millions of years ago
500

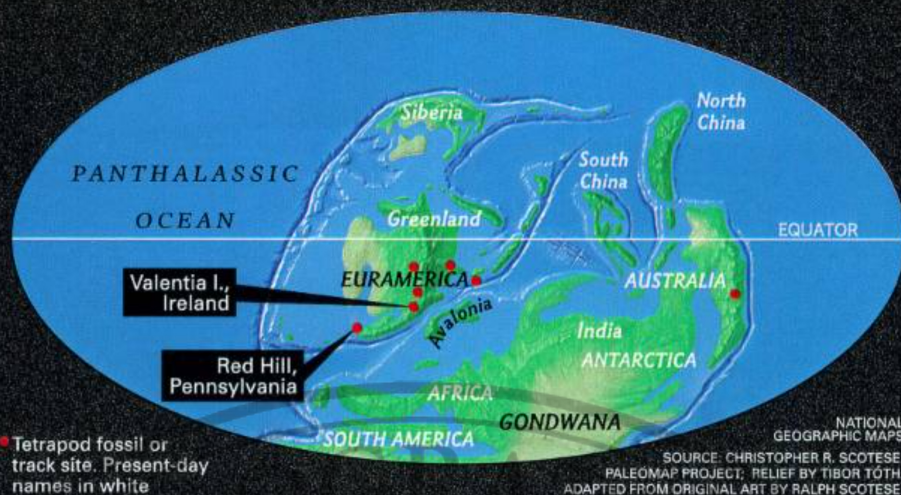
400

300

▲
Origin of
jawed fishes

Devonian World

▲
Vertebrates
established on land



Discoveries From the Devonian World

On the trail of an ancient tetrapod—the name scientists use for any animal with a backbone and four limbs—Swiss geologist Iwan Stössel (left, in plaid shirt) and friend Tom Dennehy clear rocks from the fossilized tracks on Ireland's Valentia Island. A stunned Stössel discovered the footprints in 1992. "When I saw the trackway, I knew it was important," he says. "The oldest tetrapod fossils then known were younger than these rocks." The mysterious walker, like all early tetrapods found to date (at sites shown on map above), lived in tropical wetlands during the late Devonian (time line, facing page).

evolved, onto dry land. But new fossil discoveries, such as these footprints, have suggested answers—and created controversy—about just when and how those first steps were taken.

The Valentia Island footprints are the longest of the known tetrapod trackways. Although today the Valentia tracks lie at the edge of the ocean, symbolizing the emergence of animal life from the sea, their current position is only a geologic fluke. When they were laid down, Ireland was landlocked and south of the Equator. In fact, the Valentia footprints were probably left in a shallow tropical stream.

With geologists Ken and Bettie Higgs from University College Cork, I follow Joseph O'Shea's directions, crossing the pasture and climbing down onto rocks near the shore. On a 30-foot-long ledge the tracks lay gleaming in the sun, distinct and deep and puddled with salt water. They wind across the ledge, as if the tetrapod that made them all those years ago had meandered leisurely.

I try to imagine what this animal would have looked like, but I conjure up only an unclear image of a fish with limbs. The creature left no bones, only clues that could be deduced from the tracks. Stössel, who measured the footprints, estimates the animal was more than three feet long and powered its steps with large back legs. And because the trackway showed no hint of a tail being dragged behind, scientists have concluded that this creature was not walking on dry land. Instead, it waded through shallow water with its tail buoyed up.

We linger at the shore, talking about the world this creature inhabited. At the beginning of the period 410 million years ago most of the world's landmass was divided into two continents, Euramerica and Gondwana (map, above). I could have walked from Ireland back to America. Oxygen levels were similar to those of today because plants, which produce that gas through photosynthesis, had begun colonizing land 15 million years earlier. Mats

of algae, bacteria, and fungi stretched over moist patches on the continents, while along shorelines and on floodplains grew short, stick-like plants without leaves. The only sizable animals on land were spider-like creatures that lived in the vegetated regions.

During the ensuing 50 million years, the Devonian world grew increasingly green as the interactions of plants and animals worked the rock into soils. By the end of the period the planet's two large continents were covered in places by forests of primal shrubs and trees the size of Douglas firs and were being melded

by plate tectonics into a single supercontinent.

As we look out to sea, Ken tells me that Devonian waters were filled with gigantic predatory fish with crushing jaws and protective armor made of external bone. Sharks ate their way up deep, wide rivers. The Valentia tetrapod descended from one of the fish that lived close to the river's edge in waters too shallow for the predatory giants.

Still, the Valentia tetrapod remains a phantom to me. To put flesh on the animal that made those fossil footprints, I seek out scientists specializing in the Devonian.



In Stockholm, I ask Hans Bjerring of the Swedish Museum of Natural History what the creature might have looked like. He shows me a drawing of *Ichthyostega*, discovered in Greenland in 1929 and for most of this century the sole example of early tetrapods. The drawing portrays the animal standing at the edge of a pond in a sparse landscape. The tetrapod has broad, powerful shoulders, a long, rounded tail, and short, sturdy limbs.

This representation was based on the studies of the late Erik Jarvik, who until his death last year was one of the world's leading experts on

ancient fish and an elder colleague of Bjerring's. As a young man, Jarvik had helped collect the original *Ichthyostega* specimens, and he undertook the description of the tetrapod in the early 1930s. The task took decades.

Unlike Jarvik, most specialists during that time believed the animals that evolved limbs arose from an ancient fish population that lived in lakes that dried up episodically. Those fish had to use their fins to drag themselves to other ponds. The fins eventually evolved into limbs, according to this theory.

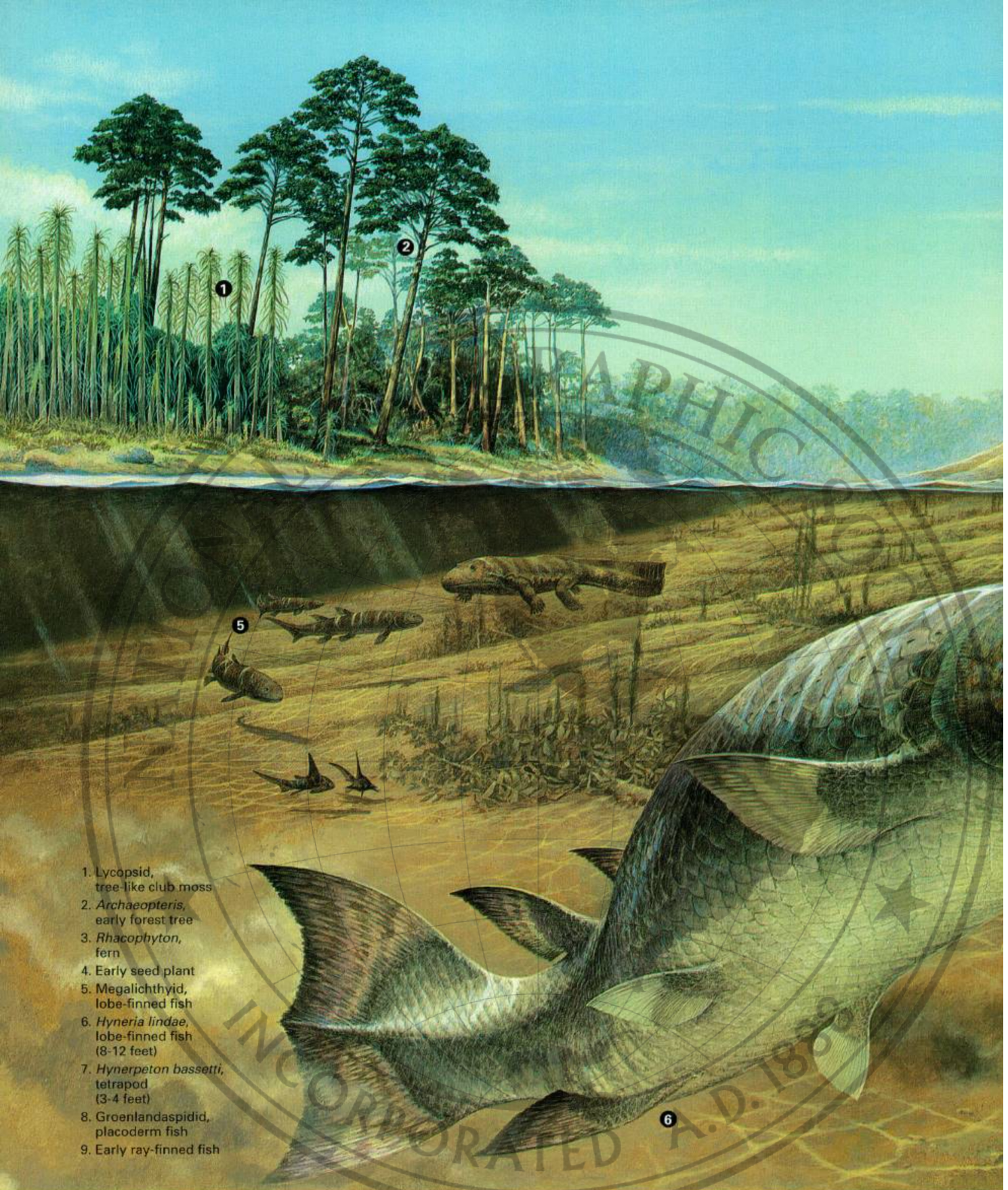
Bjerring, however, scoffs at that scenario as "hocus-pocus." He thinks that *Ichthyostega* evolved in swamps clogged with water plants. "It isn't easy to swim around thick vegetation," he explains. Fins became limbs, he maintains, because they made it easier to maneuver through the swampy mire. In fact, he doubts that *Ichthyostega* ever actually stepped foot on land. Many specialists now agree.

POWERFUL EVIDENCE that limbs evolved while tetrapods were still waterbound comes from a fossil discovered in the mountains of Greenland in 1987 by Jenny Clack, a paleontologist at Cambridge University's Museum of Zoology. That fossil of a tetrapod known as *Acanthostega* and dating from 360 million years ago emerged from a ton of rock Clack brought to her lab and painstakingly investigated for clues to the past. Among the hundreds of specimens she uncovered was the most complete Devonian tetrapod ever found, an *Acanthostega* that she affectionately calls Boris.

She leads me to the museum display case where Boris is kept. More than any artist's drawings could do, Boris lets me visualize what tetrapods looked like. Still partly encased in rock and curled up like a sleeping dog, Boris has stumpy legs, a tail almost the length of his body, and short ribs emerging from his backbone like the teeth of a comb. He also has a snout like a crocodile's and a jaw filled with sharp teeth. He seems to be smiling devilishly.

The fishy ancestry of land vertebrates can be seen in the belly fins of *Eusthenopteron*, an extinct lobe-finned fish found in Quebec's Miguasha Park. "These fins contain the same bones as our arms and legs," says paleontologist Richard Cloutier, holding the fossil.



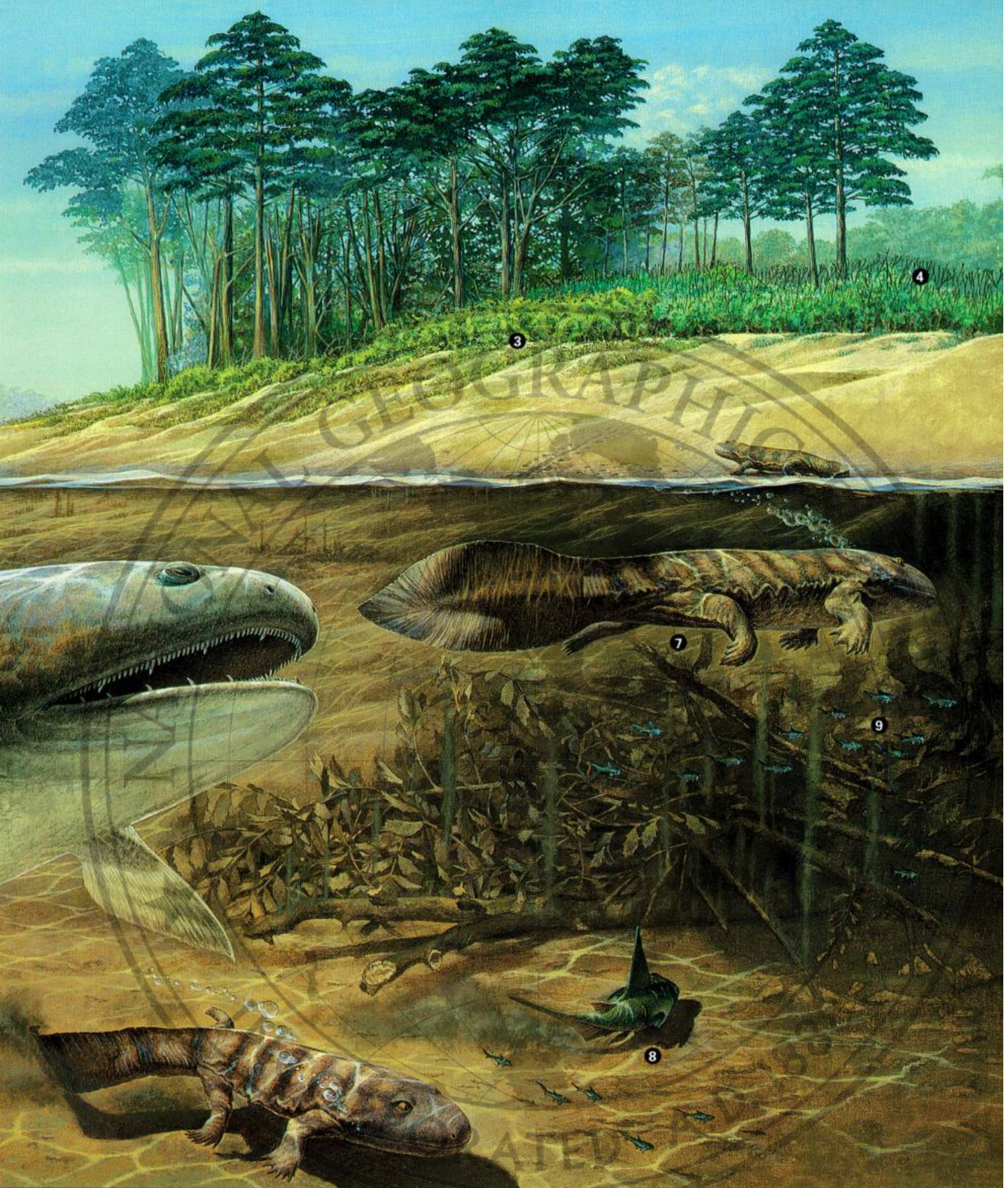


1. Lycopsid, tree-like club moss
2. *Archaeopteris*, early forest tree
3. *Rhacophyton*, fern
4. Early seed plant
5. Megalichthyid, lobe-finned fish
6. *Hyneria lindae*, lobe-finned fish (8-12 feet)
7. *Hynerpeton bassetti*, tetrapod (3-4 feet)
8. Groenlandaspisid, placoderm fish
9. Early ray-finned fish

The World Where Limbs Evolved

A 12-foot-long reason to take to the land: Devonian tetrapods like *Hynerpeton* (7) shared waterways with fearsome fish such as *Hyneria* (6). Both were discovered in the same fossil bed near Hyner, Pennsylvania, the site on which this scene is based. Early limbed vertebrates like *Hynerpeton* were built for the water. They breathed with a

fish's gills and swam with a fish's tail. Their legs helped them push aside debris or hold their place in currents. So why would tetrapods, so well suited to water, eventually turn to land? Avoiding predators was just one possible motive. A short walk might lead them to meals. Or perhaps landlocked pools offered safe places to lay their eggs.

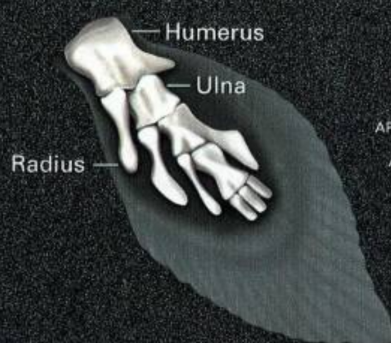


TOOL KIT FOR WALKING

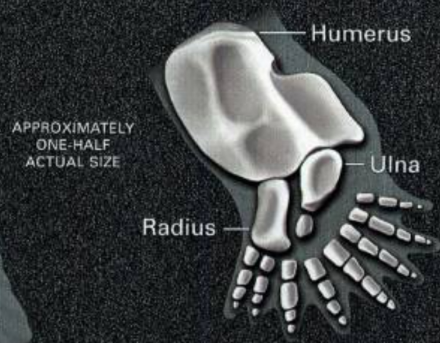
The three strong bones in all land vertebrate arms can be traced back to the fins of lobe-finned fishes. But limbs evolved at first for life in water; the arm bones of most early tetrapods (far right) were too weak to bear weight without water's buoyancy. The same parts were later adapted for walking on land.

ART BY KAZUHIKO SANO; DIAGRAMS BY JEN CHRISTIANSEN, NGS STAFF

Lobe-finned fish (*Eusthenopteron*)



Tetrapod (*Acanthostega*)



"Boris clearly didn't walk on land," says Clack. She points out the anatomical reasons for her conclusion. His wrists and ankles are too weak to support his weight on land. His ribs are too small to support the muscles needed to hold his body off the ground. His fish-like tail would have dragged on land, slowing him down or getting constantly scraped and infected. He had gills as well as lungs.



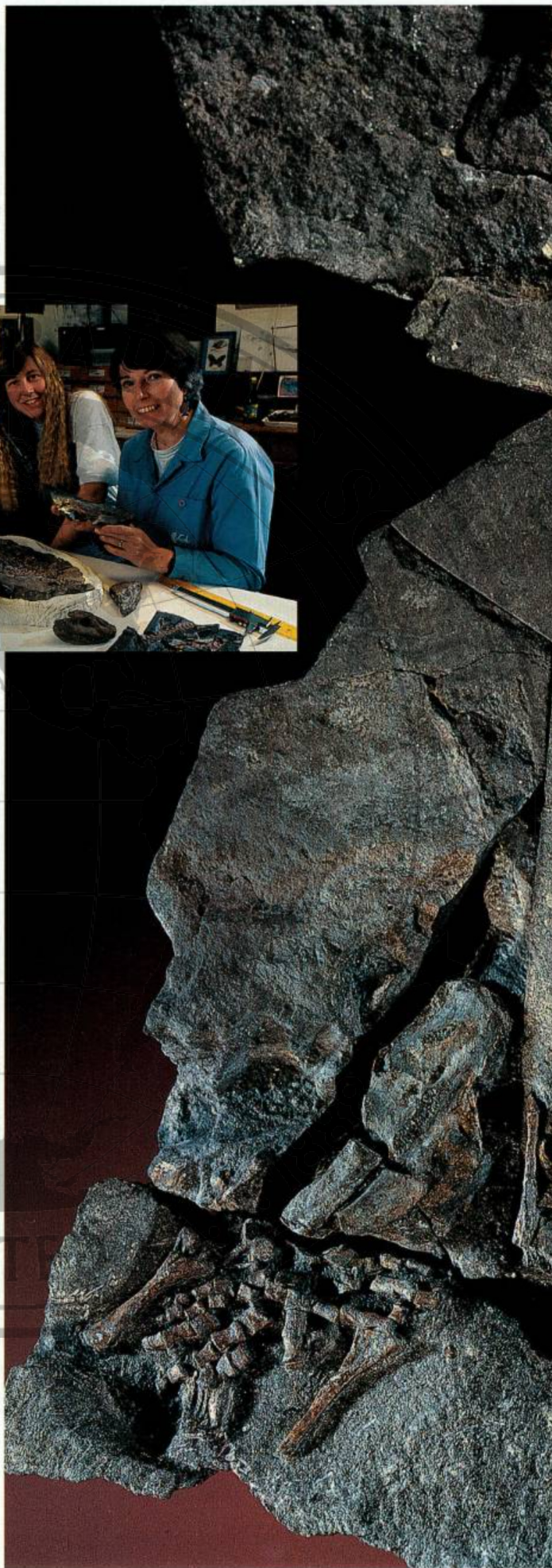
Clack shows me more evidence that Boris was a water dweller, placing the beautifully preserved skull of another *Acanthostega* in my hand. It too was collected in Greenland. She points out a series of holes, each about twice the size of the periods on this page, that run along the jawline and below the eyes.


"These holes are part of a sensory system like the type fish use today, stretching from head to tail, to detect vibrations in the water, such as those made by moving predators and prey," she explains.

Like Bjerring, Clack believes *Acanthostega* evolved its limbs and toes to maneuver in swampy waters. "If you can grasp onto vegetation, then you can hold your position in a stream," she explains. "You can feel your way through murky water. You can dig in the mud for prey. You can avoid bigger predators by crawling into plant-choked waters where swimming would have been difficult."

So must we conclude that early tetrapods never walked on land? Must the first ground-breaking ancestors of humans come from another source? Probably not.

Writer KERRI WESTENBERG secretly dreams of becoming a paleontologist. This is her first article for the GEOGRAPHIC. JONATHAN BLAIR has photographed 33 articles for the magazine on subjects as diverse as ancient extinctions, Roman ruins, and meteorites.





Part fish, part amphibian, *Acanthostega* (model, far left) is a "missing link" says Cambridge paleontologist Jenny Clack (left, in blue), who nicknamed this fossil specimen Boris. Clack returned from Greenland in 1987 with a rock that showed only the tip of an *Acanthostega* skull. Three years of cleaning by Sarah Finney, to Clack's right, revealed a surprise at the end of its arm: eight fingers instead of the five that are standard.

MODEL (FACING PAGE) BY RICHARD HAMMOND; SPECIMEN FROM GEOLOGICAL MUSEUM, UNIVERSITY OF COPENHAGEN



Land's early pioneers, ancient plants left traces beneath a sheep pasture in Rhynie, Scotland. Nigel Trewin, at far left, and Lyall Anderson, both of the University of Aberdeen, examine drill cores rich in fossils from 400-million-year-old plants. Vegetation colonized shores and wetlands millions of years before animals. The green invasion prepared the way for land vertebrates by forming swamps, spurring the evolution of legs for navigating through debris-choked water and lungs for breathing air when plant decay used up water's dissolved oxygen.

At a site called Scat Craig in northeastern Scotland, Per Ahlberg, a young paleontologist from the Natural History Museum in London, has found pieces of a new tetrapod that lived earlier in the Devonian than any other of its relatives. The animal, named *Elginerpeton* after a town near Scat Craig, confuses any simple story of how and when limbs evolved. Ahlberg takes me to the place where the perplexing fossils were found.

"We've only found parts of its jaw, pelvis, shoulder, and limbs," he says as we pull on Wellington boots and make our way down an overgrown path, crossing a cold, shallow stream. "Those pieces, however, tell us a lot. *Elginerpeton* was as large as you—five feet long, and it already had developed robust hind limbs."

Was this earliest of tetrapods a land dweller? Does *Elginerpeton*, which lived some 370 million years ago, prove that at least some tetrapods left the water during the early days of the Devonian? Not exactly.

"It had this peculiar twist to its hind limb," Ahlberg explains. "The leg stuck out sideways, like a salamander's or crocodile's, but the sole of the foot faced backward rather than down. That would be no good for walking at all, as the animal couldn't put its foot flat on the ground. But it would be ideal for paddling in water."

So why did the rest of the limb seem built for crawling on land? Ahlberg suspects that

Elginerpeton's ancestors had evolved the ability to walk—whether in water or on land—but that *Elginerpeton* itself had returned to a strictly aquatic life for unknown reasons.

Elginerpeton's ancestors may well have given rise to other tetrapods that stayed on land. In 1984 a Russian paleontologist discovered the limbs of a tetrapod called *Tulerpeton*, which seemed made for crawling. But it's difficult to say it was a land dweller because it was found surrounded by ancient fish fossils at a site that during the Devonian was a coastal lagoon.

O THER TETRAPOD FOSSILS have emerged in recent years from Latvia and Australia. But only one clear-cut candidate for a land-dwelling tetrapod has emerged—a creature named *Hynerpeton*, discovered in 1993 near the town of Hyner in north-central Pennsylvania.

"I was very lucky to find this particular bone," said Ted Daeschler, a Devonian specialist at the Academy of Natural Sciences in Philadelphia. He is holding a three-inch-long piece of *Hynerpeton*'s shoulder that only an anatomist could appreciate. Striations on that chunk of shoulder, however, revealed a lot about *Hynerpeton*'s behavior. They showed where the animal's forelimb muscles had attached to the shoulder, and judging from the size of those muscles, Daeschler believes the



SPECIMEN FROM GEOLOGICAL MUSEUM, UNIVERSITY OF COPENHAGEN

Wanted: More Bones

Theories about tetrapod origins are built on a few rare fossils. In the 12 years since this *Acanthostega* skull (above) was unearthed, the number of known tetrapods has jumped from two to eight. Per Ahlberg (right) recognized a tetrapod jaw among fish fossils at Oxford's University Museum in 1990. He tracked down matching parts in four other collections and named the long-overlooked creature *Elginerpeton*. Surprising fossils keep emerging. Ted Daeschler (below) has dug up a Devonian fish fin that may have finger-like bones.



Who walked here? A model based on known fossils and posed to fit the Valentia Island tracks suggests an answer: a tetrapod, its tail floating in water without leaving a mark. Now on dry land, these tracks foreshadow vertebrates' new world to come.

three-foot-long tetrapod had developed the most robust and muscular forelimbs of any known Devonian animal.

"No doubt about it," he says. "This animal could have done push-ups in the water or on dry land."

Hynerpeton's shoulder bone also indicates that the animal would have relied on its legs to give its body momentum, rather than strictly flexing its backbone and tail as fish do.

The only Devonian tetrapod found in the United States, *Hynerpeton* lived 365 million years ago, making it the third oldest tetrapod yet discovered. If *Hynerpeton* indeed lived on land, it would suggest that the move onto land occurred early. And while some tetrapods returned to the water, others would have thrived in their new terrestrial world. Over millions of years, in the ensuing periods known as the Carboniferous and Permian, they would have given rise to the ancestors of both dinosaurs and mammals.

Daeschler returns regularly to the site where he found *Hynerpeton's* shoulder fragment, seeking more clues to the world tetrapods pioneered. The site, called Red Hill, is a road cut bulldozed through an outcrop of the same kind of reddish sandstones that have yielded the Devonian fossils of Greenland and Europe. Its rocks span a long stretch of Devonian time, and the enormous variety of fish, arthropods, and plants it has revealed from the late Devonian makes it one of the world's most important sites from that period. Daeschler invites me to visit Red Hill for a weekend dig. Hoping I might actually find a piece of a tetrapod myself, I enthusiastically join him and two vans full of fossil hunters along Pennsylvania Route 120 on a chilly October morning.

The fossil hunters, a mixture of amateur and professional paleontologists, quickly scramble up the steep sides of the road cut. Wielding rock hammers and Swiss army knives, they begin extracting bits and pieces of Devonian fish, the most abundant fossils at Red Hill. I find nothing—not even fish teeth.

"Your eyes aren't trained to see fossils yet," Daeschler says, comforting me.

Attempting to learn, I stay close to Del Szatmary, a New Jersey police officer who has found many fossils at Red Hill. Glancing down at the base of the road cut, he spots intriguing markings on a small rock by his feet. Those markings turn out to be those of an extinct spider-like animal. Not exactly a tetrapod, the quarter-inch-long fossil nevertheless is a new species that fills an important gap in the evolutionary history of arachnids.

SPEND THE REST OF THE DAY a bit jealous. My fieldwork is nearing its end. By now I can walk a site like Red Hill and see a piece of a tree and imagine a Devonian forest there. I have no trouble envisioning Szatmary's arachnid poised on the foliage of that forest. If I could find even a toe of a tetrapod, my mind's eye could turn it into a salamander-like creature the size of a crocodile, a predator lurking in those woods.

In fact, a toe would be particularly satisfying. I have spent many hours thinking about limb parts—and even the number of digits each limb might possess: To their surprise, paleontologists have found tetrapods with as many as eight toes, confounding their assumption that five has always been the norm.

I have learned that limbs probably evolved for something totally different than what we, descendants of tetrapods, use them for. But that's how evolution works. Something evolves that solves one problem and opens up a world of new possibilities. Consider what the limbs humans inherited from tetrapods have done. They not only put our species on dry land, they also let us run, build, draw pictures, make music. In fact, some scientists argue that if tetrapods had not developed limbs, the big brain of humans would never have developed.

"What purpose would it have served?" asked Erik Jarvik in a 1980 book I'd read. "It was when the basic pattern of our five-fingered hand for some unaccountable reason was laid down . . . that the prerequisite for the origin of man and the human culture arose."

Indeed, without that fortuitous invention, old Joseph O'Shea could never have lifted his gnarled finger that sunny day in Ireland and pointed me the way to those tracks at the edge of the sea. □

