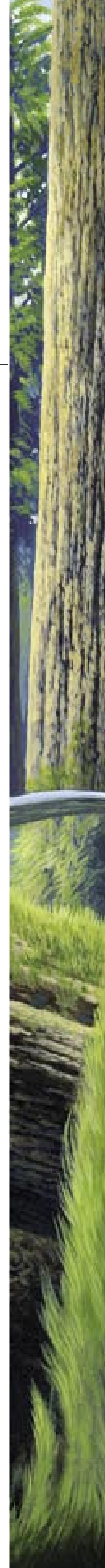
GETTING A LEG UP ON LAND

Recent fossil discoveries cast light on the evolution of four-limbed animals from fish

BY JENNIFER A. CLACK



UP FOR AIR: *Acanthostega,* an early tetrapod, surfaces in a swamp in what is now eastern Greenland, some 360 million years ago. Although this animal had four legs, they would not have been able to support its body on land. Thus, rather than limbs evolving as an adaptation to life on land, it seems that they may have initially functioned to help the animal lift its head out of oxygen-poor water to breathe. Only later did they find use ashore.

IN THE ALMOST four billion years since life on earth oozed into existence, evolution has generated some marvelous metamorphoses. One of the most spectacular is surely that which produced terrestrial creatures bearing limbs, fingers and toes from water-bound fish with fins. Today this group, the tetrapods, encompasses everything from birds and their dinosaur ancestors to lizards, snakes, turtles, frogs and mammals, including us. Some of these animals have modified or lost their limbs, but their common ancestor had them—two in front and two in back, where fins once flicked instead.

The replacement of fins with limbs was a crucial step in this transformation, but it was by no means the only one. As tetrapods ventured onto shore, they encountered challenges that no vertebrate had ever faced before—it was not just a matter of developing legs and walking away. Land is a radically different medium from water, and to conquer it, tetrapods had to evolve novel ways to breathe, hear, and contend with gravity—the list goes on. Once this extreme makeover reached completion, however, the land was theirs to exploit.

Until about 15 years ago, paleontologists understood very little about the sequence of events that made up the transition from fish to tetrapod. We knew that tetrapods had evolved from fish with fleshy fins akin to today's lungfish and coelacanth, a relation first proposed by American paleontologist Edward D. Cope in the late 19th century. But the details of this seminal shift remained hidden from view. Furthermore, estimates of when this event transpired varied wildly, ranging from 400 million to 350 million years ago, during the Devonian period. The problem was that the pertinent fossil record was sparse, consisting of essentially a single fish of this type, *Eusthenopteron,* and a single Devonian tetrapod, *Ichthyostega,* which was too advanced to elucidate tetrapod roots.

With such scant clues to work from, scientists could only speculate about the nature of the transition. Perhaps the best known of the scenarios produced by this guesswork was that championed by famed vertebrate paleontologist Alfred Sherwood Romer of Harvard University, who proposed in the 1950s that fish like *Eusthenopteron,* stranded under arid conditions, used their muscular appendages to drag themselves to a new body of water. Over time, so the idea went, those fish able to cover more ground—and thus reach ever more distant water sources—were selected for, eventually leading to the origin of true limbs. In other words, fish came out of the water before they evolved legs.

Since then, however, many more fossils documenting this transformation have come to light. These discoveries have expanded almost exponentially our understanding of this critical chapter in the history of life on earth—and turned old notions about early tetrapod evolution, diversity, biogeography and paleoecology on their heads.

Finding a Foothold

AMONG THE FIRST fossil finds to pave the way for our modern conception of tetrapod origins were those of a creature called *Acanthostega,* which lived about 360 million years ago in what is now eastern Greenland. It was first identified in 1952 by Erik Jarvik of the Swedish Museum of Natural History in Stockholm on the basis of two partial skull roofs. But not until 1987 did my colleagues and I finally find specimens revealing the postcranial skeleton of *Acanthostega.*

Although in many ways this animal proved to be exactly the kind of anatomical intermediary between fish and full-blown tetrapods that experts might have imagined, it told a different story from the one predicted. Here was a creature that had legs and feet but that was otherwise ill equipped for a terrestrial existence. *Acanthostega*'s limbs lacked proper ankles to support the animal's weight on land, looking more like paddles for swimming. And although it had lungs, its ribs were too short to prevent the collapse of the chest cavity once out of water. In fact, many of *Acanthostega*'s features were undeniably fishlike. The bones of the forearm displayed proportions reminiscent of the pectoral fin of *Eusthenopteron.* And the rear of the skeleton showed a deep, oar-shaped tail sporting long, bony rays that would have provided the scaffolding for a fin. Moreover, the beast still had gills in addition to lungs.

The piscine resemblance suggested that the limbs of *Acanthostega* were not only adapted for use in water but that this was the ancestral tetrapod condition. In other words, this animal, though clearly a tetrapod, was primarily an aquatic creature whose immediate forerunners were essentially fish that had never left the water. The discovery forced scholars to rethink the sequence in which key changes to the skeleton took place. Rather than portraying a creature like *Eusthenopteron* crawling onto land and then gaining legs and feet, as Romer postulated, the new fossils indicated that tetrapods evolved these features while they were still aquatic and only later co-opted them for walking. This, in turn, meant that researchers needed to reconsider the ecological circumstances under which limbs developed, because *Acanthostega* indicated that terrestrial demands may not have been the driving force in early tetrapod evolution.

Acanthostega took pride of place as the missing link between terrestrial vertebrates and their aquatic forebears. There was, however, one characteristic of *Acanthostega* that called to mind neither tetrapod nor fish. Each of its limbs terminated in a foot bearing eight well-formed digits, rather than the familiar five. This was quite curious, because before this discovery anatomists believed that in the transition from fish to tetrapod, the five-digit foot derived directly from the bones constituting the fin of *Eusthenopteron* or a similar creature. Ordinarily, scientists might have dismissed this as an aberrant specimen. But a mysterious partial skeleton of *Tulerpeton,* a previously known early tetrapod from Russia, had a six-digit foot. And specimens of *Ichthyostega* also found on our expedition to eastern Greenland revealed that it, too, had a foot with more than five digits.

Findings from developmental biology have helped unravel some of this mystery.

> Many of the critical innovations arose while these beasts were still largely aquatic. And the first changes appear to have been related not to locomotion but to an increased reliance on breathing air.

We now know that several genes, including the *Hox* series and *Sonic Hedgehog,* control elements of fin and limb development. The same sets of these genes occur in both fish and tetrapods, but they do different jobs in each. *Hoxd 11* and *Hoxd 13,* for instance, appear to play a more pronounced role in tetrapods, where their domains in the limb bud are enlarged and skewed relative to those in the fish fin bud. It is in these regions that the digits form. How the five-digit foot evolved from the eight-digit one of *Acanthostega* remains to be determined, but we do have a plausible explanation for why the five-digit foot became the default tetrapod pattern: it may have helped make ankle joints that are both stable enough to bear weight and flexible enough to allow the walking gait that tetrapods eventually invented.

Acanthostega also drew attention to a formerly underappreciated part of early tetrapod anatomy: the inside of the lower jaw. Fish generally have two rows of teeth along their lower jaw, with a large number of small teeth on the outer row complementing a pair of large fangs and some small teeth on the inner row. *Acanthostega* showed that early tetrapods possessed a different dental plan: a small number of larger teeth on the outer row and a reduction in the size of the teeth populating the inner row—changes that probably accompanied a shift from feed-

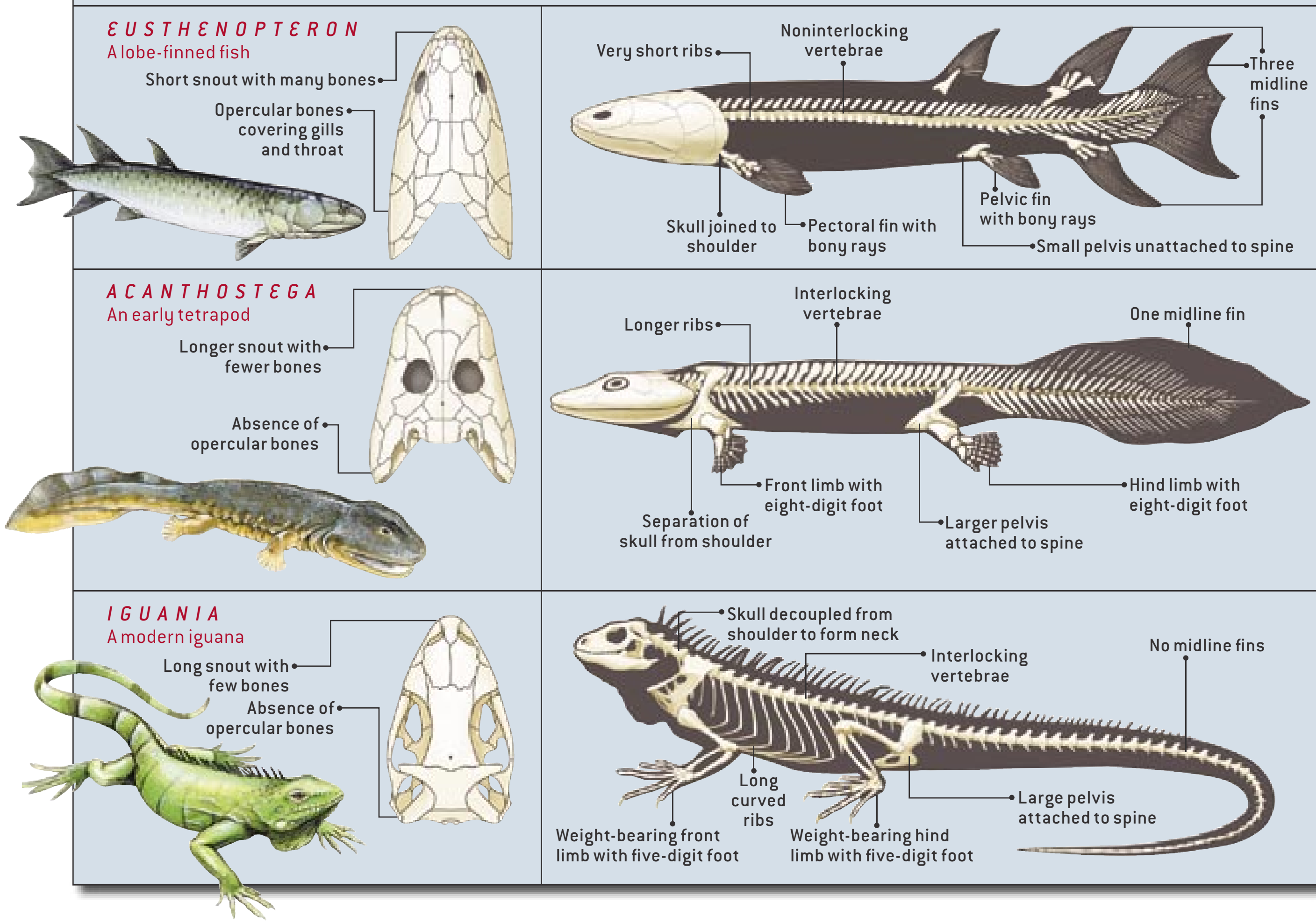
Overview/*The Origin of Tetrapods*

- The emergence of land-going vertebrates was a cornerstone event in the evolution of life on earth.
- For decades, a paltry fossil record obfuscated efforts to trace the steps that eventually produced these terrestrial tetrapods from their fish ancestors.
- Fossils recovered over the past 15 years have filled many of the gaps in the story and revolutionized what is known about tetrapod evolution, diversity, biogeography and paleoecology.
- These recent finds indicate that tetrapods evolved many of their characteristic features while they were still aquatic. They also reveal that early members of the group were more specialized and more geographically and ecologically widespread than previously thought.

RAÚL MARTÍN (*preceding pages*)

TURNING TETRAPOD

The evolution of terrestrial tetrapods from aquatic lobe-finned fish involved a radical transformation of the skeleton. Among other changes, the pectoral and pelvic fins became limbs with feet and toes, the vertebrae became interlocking, and the tail fin disappeared, as did a series of bones that joined the head to the shoulder girdle (*skeletons*). Meanwhile the snout elongated and the bones that covered the gills and throat were lost (*skulls*).



ANDREW RECHER

ing exclusively in the water to feeding on land or with the head above the water.

This insight enabled experts to recognize additional tetrapods among remains that had long sat unidentified in museum drawers. One of the most spectacular of these finds was that of a Late Devonian genus from Latvia called *Ventastega*. In the 1990s, following the discovery of *Acanthostega*, researchers realized that a lower jaw collected in 1933 was that of a tetrapod. Further excavation at the original *Ventastega* site soon yielded more material of exceptional quality, including an almost complete skull.

Meanwhile a number of near-tetrapod fish have also been unveiled, bridging the morphological gap between *Eusthenopteron* and *Acanthostega*. Two of these genera paleontologists have known about for several decades but have only recently scrutinized: 380-million- to 375-million-year-old *Panderichthys* from Europe's Baltic region, a large fish with a pointy snout and eyes that sat atop its head, and 375-million- to 370-million-year-old *Elpistostege* from Canada, which was very similar in size and shape to *Panderichthys*. Both are much closer to tetrapods than is *Eusthenopteron*. And just last year an expedition to Ellesmere Island in the Canadian Arctic led by paleontologist Neil Shubin of the University of Chicago produced some outstandingly well preserved remains of a fish that is even more tetrapodlike than either *Panderichthys* or *Elpistostege*. Shubin and his team have yet to describe and name this species formally, but it is shaping up to be a fascinating animal.

A Breath of Fresh Air

THANKS TO THESE recent finds and analyses, we now have the remains of nine genera documenting around 20 million years of early tetrapod evolution and an even clearer idea of how the rest of the vertebrate body became adapted for life on land. One of the most interesting revelations to emerge from this work is that, as in the case of limb development, many of the critical innovations arose while these beasts were still largely aquatic. And the first changes appear to have been related not to locomotion but to an increased reliance on breathing air.

Oddly enough, this ventilation shift

PRIMEVAL PROMENADE: *Ichthyostega* is the earliest known tetrapod to show adaptations for nonswimming locomotion, although it seems likely to have moved more like a seal than a typical land vertebrate. This animal also had some aquatic features, including a large tail and flipperlike hind limbs, as well as an ear that appears to have been specialized for underwater use. How *Ichthyostega* divided its time between the terrestrial and aquatic realms is uncertain. But it may have dug nests for its eggs on land and hunted and fed in the water.

RAÚL MARTÍN

may have kicked off the gradual morphing of the shoulder girdle and pectoral fins. Indeed, evolutionary biologists have struggled to explain what transitional forms like *Acanthostega* did with their proto-limbs, if not locomote. The hypothesis favored on current evidence is that as the backwardly directed fins gradually turned into sideways-facing limbs with large areas for muscle attachments, they gained in strength. And although it would be millions of years before the forelimbs developed to the point of being able to support the body on land, they may well have functioned in the interim to allow the animal to raise its head out of the water to breathe. The toes could have facilitated this activity by helping to spread the load on the limbs.

Last year Shubin's team announced the discovery of a 365-million-year-old tetrapod upper arm bone, or humerus, that has bolstered this idea. The bone, dug from a fossil-rich site in north central Pennsylvania known as Red Hill, appears to have joined the rest of the body via a hingelike joint, as opposed to the ball-and-socket variety that we and other terrestrial vertebrates have. This arrangement would not have permitted a walking gait, but it would have enabled just the kind of push-up that a tetrapod needing a gulp of air might employ. It also might have helped the animal hold its position in the water while waiting to ambush prey.

Breathing above water also required a number of changes to the skull and jaw. In the skull, the snout elongated and the bones that form it grew fewer in number and more intimately sutured together, strengthening the snout in a way that enabled the animal to lift it clear of water and into an unsupportive medium. The bones at the back of the head, for their part, became the most firmly integrated of any in the skull, providing sturdy anchors for muscles from the vertebral column that raise the head relative to the body. And the fusing of bones making up the lower jaw fortified this region, facilitating the presumed "buccal pump" mode of tetrapod ventilation. In this type of breathing, employed by modern amphibians and air-breathing fish, the mouth cavity expands and contracts like bellows to gulp air and force it into the lungs. Buccal pumping may have demanded more jaw power under the influence of gravity than in the water, where organisms are more or less weightless.

Might the strengthening of the jaws have instead come about as an adaptation for feeding on land? Possibly. The earliest tetrapods were all carnivorous, so it is unlikely that, as adults, they fed much on land during the first phases of their evolution, because the only prey they would have found there were insects and other small arthropods. The babies, on the other hand, needed just this type of prey, and they may have been the ones that initially ventured farthest out of the water to get them.

Meanwhile, farther back in the skeleton, a series of bones that joins the head to the shoulder girdle in fish disappeared. As a result, tetrapods, unlike fish, have a muscular neck that links the head to the rest of the skeleton and allows for movement of the head separate from the body. The gill system also underwent substantial renovation, losing some bones but increasing the size of the spiracle—an opening on the top of the head that led to an air-filled sac in the throat region, making the entire respiratory apparatus better suited to breathing air.

But why, after millions of years of successfully breathing underwater, did some fish begin turning to the air for their oxygen? Clues have come from the overall shape of the skull, which in all early tetrapods and near-tetrapods discovered so far is quite flat when viewed head-on. This observation, combined with paleoenvironmental data gleaned from the deposits in which the fossils have been found, suggests that these creatures were shallow-water specialists, going to low-water places to hunt for smaller fish and possibly to mate and lay their eggs. Perhaps not coincidentally, vascular plants were flourishing during the Devonian, transforming both the terrestrial and aquatic realms. For the first time, deciduous plants shed their leaves into the water with the changing seasons, creating environments that were attractive to small prey but difficult for big fish to swim in. Moreover, because warm water holds less oxygen than colder water does, these areas would have been oxygen-poor. If so, the changes to the skeleton described here may have given early tetrapods access to waters that sharks and other large fish could not reach by putting them literally head and shoulders above the competition. It was just happenstance that these same features would later come in handy ashore.

These breathing-related innovations sent tetrapods well on their way to becoming land-worthy. Getting a grip on terra firma required further modifications to the skeleton, however. An overhaul of the ear region was one such development. Many of the details of this transformation are still largely unknown. But it is clear that even in the tetrapodlike fish that still had fins, *Panderichthys* among them, the part of the skull behind the eyes had already become shorter, following a shrinking of the capsules that house the inner ears. If, as paleoenvironmental evidence suggests, *Panderichthys* dwelled in shallow tidal flats or estuaries, the reduction in the inner ear may reflect the growing influence of gravity on the vestibular system, which coordinates balance and orientation. At the same time an increase in the size of the air chamber in its throat may have aided hearing. In some modern fish this air sac "catches" sound waves, preventing them from simply passing straight through the animal's body. From there they are transmitted by the surrounding bones to the inner ear. The enlarged air chamber evident in *Panderichthys* would have been able to intercept more sound waves, thereby enhancing the animal's hearing ability.

Modifications to the ear region were also closely tied to those in the gill system. To wit: a bone known as the hyomandibula—which in fish orchestrates feeding and breathing movements—shrank in size and got lodged in a hole in the braincase, where it became the stapes. In modern tetrapods the stapes magnifies sound waves and transmits them from the eardrum across the air space in the throat to the inner ear. (In mammals, which have a unique hearing system, the stapes is one of the three ossicles making up the middle ear.) The first stage of conversion must have occurred rapidly, given that it was in place by the time of *Acanthostega*. Quite possibly it proceeded in tandem with the shift from fins to limbs with digits. But the stapes would not take on its familiar role as a component of the terrestrially adapted tympanic ear for millions of years. In the meantime, it apparently functioned in these still aquatic tetrapods as a structural component of the skull.

Taken together, these skeletal changes have necessitated a sea change in the way we regard early tetrapods. Gone are the clumsy chimeras of popular imagination, fit for neither water nor land. What were once considered evolutionary works in progress—an incompletely developed limb or ear, for example—we now know were adaptations in their own right. They were not always successful, but they were adaptations nonetheless. At each stage of this transition were innovators pushing into new niches. Some, in fact, were highly specialized to do this.

Breaking the Mold

BY AND LARGE, the limbed tetrapods and near-tetrapods unearthed thus far have been sizeable beasts, around a meter long. They preyed on a wide variety of invertebrates and fish and were probably not fussy about which ones. We are beginning to find exceptions to this generalist rule, however. One is *Livoniana,* discovered in a museum in Latvia by Per Erik Ahlberg of Sweden's Uppsala University in 2000. This animal is represented by some lower jaw fragments that exhibit a bizarre morphology: instead of the usual two rows of teeth lining each side of the jaw, it had seven rows. Exactly what *Livoniana* might have been consuming with this corn-on-the-cob dentition we do not know. But it most likely had a diet apart from that of its brethren.

Renewed work on the first known Devonian tetrapod, *Ichthyostega*, is showing that it, too, diverged from the norm—contrary to earlier preconceptions. The ear region and associated parts of the braincase of *Ichthyostega* have long baffled researchers because they display a construction unlike that of any other tetrapod or fish from any period.

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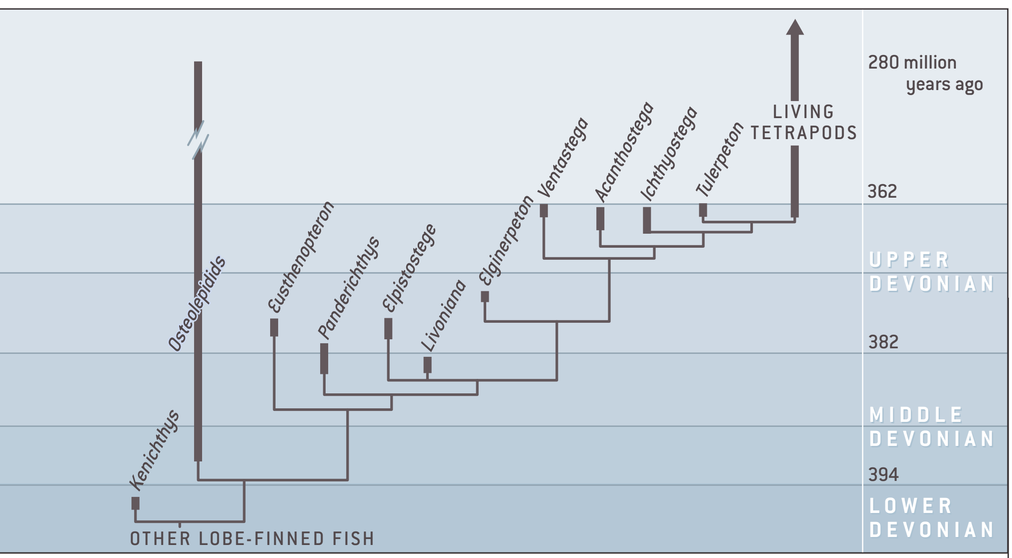
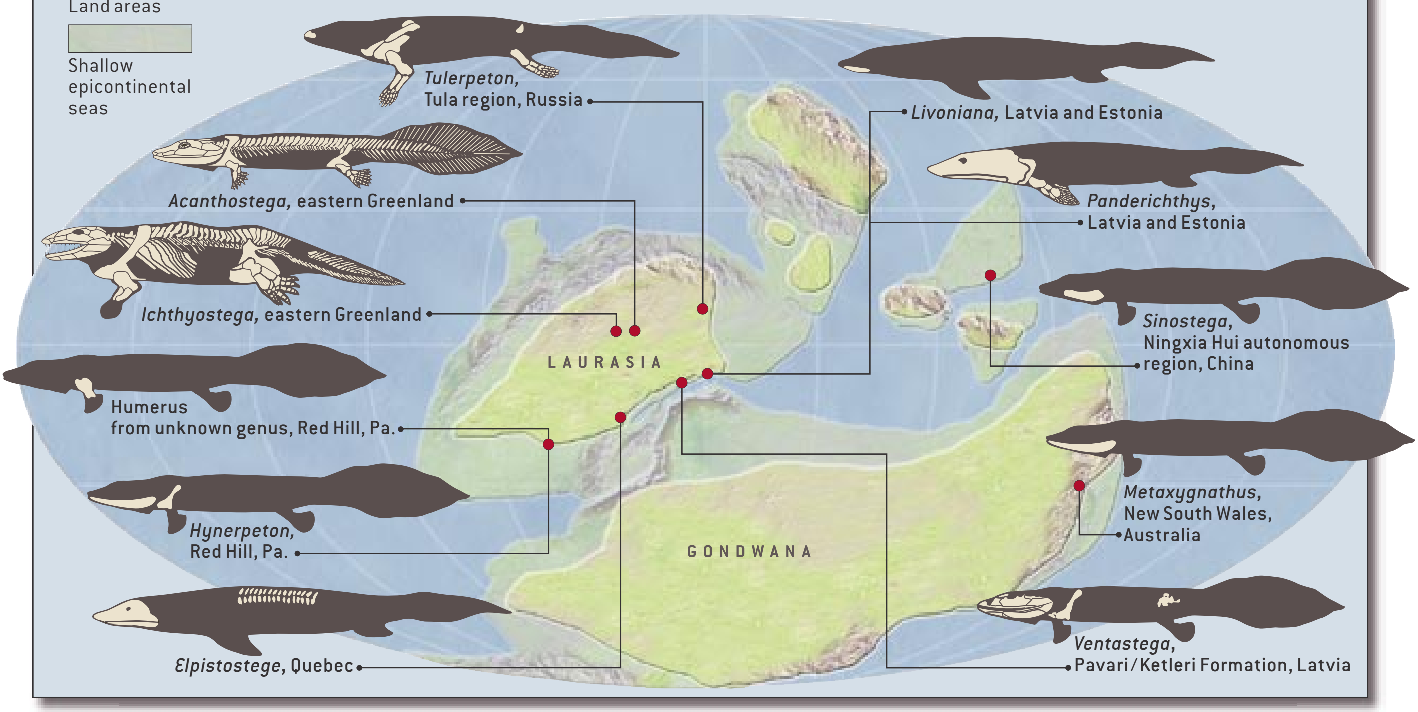


TETRAPOD RELATIONS: Tetrapods arose from lobe-finned fish like *Eusthenopteron* some 380 million to 375 million years ago, in the late Middle Devonian period.

LUCY READING-IKKANDA

DEVONIAN DISCOVERIES

Fossils of early tetrapods and near-tetrapod fish have turned up at sites as far-flung as northwestern China and the eastern U.S. As a result, it is now apparent that these animals lived throughout the tropics and subtropics of the ancient landmasses Laurasia and Gondwana. And the earliest tetrapods, it seems, inhabited freshwater and brackish water environments rather than strictly marine ones.



But with the aid of new fossils, fresh preparation of previously collected material and, crucially, CT scanning of key specimens, my colleagues and I have begun to make sense of this mysterious construction. The best interpretation seems to be that *Ichthyostega* possessed a highly specialized ear, but one that was geared for use underwater. Instead of having an eardrum, as many modern terrestrial animals do, at each side of the back of the head lay a chamber with strengthened top and side walls that was probably filled with air. Into the membranous floor of this chamber stretched a spoon-shaped and very delicate stapes, which presumably vibrated in response to sound impinging directly on the air in the chamber, transmitting these vibrations to the inner ear through a hole in the wall of the braincase. This arrangement would imply that *Ichthyostega* spent a good deal of time in water. Likewise, the animal's tail fin and flipperlike hind limbs suggest an aquatic lifestyle.

Yet other parts of the *Ichthyostega* skeleton bespeak an ability to get around on land. It had incredibly powerful shoulders and forearms. And the ribs of the chest region were very broad and overlapping, forming a corset that would have prevented the chest cavity and lungs from collapsing when on the ground. Even so, *Ichthyostega* probably did not locomote like a standard-issue land vertebrate. For one thing, its ribcage would have restricted the lateral undulation of the trunk that typically occurs in tetrapod movement. And in contrast to fish, *Acanthostega* or other early tetrapods, *Ichthyostega* had spines on its vertebrae that changed direction along the spinal column, hinting that the muscles they supported were specialized for different jobs and that it moved in a unique fashion. This multidirectional arrangement of the vertebral spines parallels that in mammals today, but it was unheard of in Devonian tetrapods until we studied *Ichthyostega*. All told, this latest evidence suggests that, rather than bending in the horizontal plane, as the body of a fish does, the body of *Ichthyostega* bent mainly in a vertical plane. The paddlelike hind limbs do not seem to have contributed much forward thrust during locomotion—the robust forelimbs and large shoulders provided that. Thus, on land *Ichthyostega* may have moved rather like a seal, first raising its back, then advancing both forelimbs simultaneously, and finally hauling the rest of its body forward.

In September, Ahlberg, Henning Blom of Uppsala University and I published a paper detailing these findings in the journal *Nature*. If we are correct, *Ichthyostega* is the earliest vertebrate on record that shows some adaptations for nonswimming locomotion. It is impossible to say with certainty what *Ichthyostega* was doing ashore. It may have been eating stranded fish there but reproducing in water, in which case it could have used its specialized ear to listen for potential mates. (This scenario implies that *Ichthyostega* was making noises as well as listening to them.) Alternatively, *Ichthyostega* may have been eating in the water and listening for prey there, whereas it was using its forelimbs to dig nests for its eggs on land. Ultimately, however,

ANDREW RECHER (*tetrapods*); LUCY READING-IKKANDA (*map*) its particular body plan was doomed, because no fossil dating later than 360 million years ago can be reliably attributed to the *Ichthyostega* lineage. No doubt there were many such superseded designs over the course of early tetrapod evolution. Further work will be needed to confirm these ideas, but the latest data demonstrate that Devonian tetrapods were more diverse than previously suspected. We are learning to expect more such surprises as these animals and their relatives become better known.

Have Legs, Will Travel

THE FOSSILS UNCOVERED over the past two decades have done more than allowed scientists to trace many of the changes to the tetrapod skeleton. They have also provided fresh insights into when and where these creatures evolved. We are now reasonably certain that tetrapods had emerged by 380 million to 375 million years ago, in the late Middle Devonian, a far tighter date range than the one researchers had previously postulated. We have also determined that the early representatives of this group were nothing if not cosmopolitan.

Devonian tetrapods were scattered across the globe, ranging from locations that are now China and Australia, where creatures known as *Sinostega* and *Metaxygnathus,* respectively, have turned up, to the eastern U.S., where the Red Hill humerus and a beast called *Hynerpeton* were found. Placing the fossil localities onto a paleogeographic map of the time, we see that these animals dwelled throughout the tropics and subtropics of a supercontinent comprising Laurasia to the north and Gondwana to the south. Their near-ubiquitous distribution in the warmer climes is a testament to how successful these creatures were.

Within these locales, Devonian tetrapods inhabited a startlingly wide range of environments. Deposits in eastern Greenland that were the first to yield such creatures indicate that the area was once a broad river basin dominated by periodic floods alternating with drier conditions. The river was unequivocally freshwater in origin and thus formed the basis for received wisdom about the environments in which tetrapods evolved. But the discoveries of such creatures as *Ventastega* and *Tulerpeton* in deposits representing settings of varying salinity have called that notion into question. The Red Hill site in Pennsylvania has proved particularly rich in providing a context for the tetrapods, yielding many fish species as well as invertebrates and plants. Like the eastern Greenland deposits, it represents a river basin. Yet paleoenvironmental studies suggest that the region had a temperate climate, rather than the monsoonal conditions associated with the Greenland finds. That is to say, early tetrapods may have been even more widespread than we thought.

Although we now have a good explanation for why the front limbs evolved the way they did, we lack one for the origin of the hind limbs because none of the fossils recovered so far contains any clues about them.

Unfinished Business

WE STILL HAVE MUCH to learn about changes in anatomy that accompanied the rise of tetrapods. Although we now have a reasonable hypothesis for why the shoulder girdle and front limbs evolved the way they did, we lack an adequate explanation for the origin of the robust hind-limb complex—the hallmark of a tetrapod—because none of the fossils recovered so far contains any clues about it. Only specimens of *Ichthyostega* and *Acanthostega* preserve this part of the anatomy, and in both these animals the hind limbs are too well formed to reveal how they took shape. Almost certainly no single scenario can account for all the stages of the transition. We also want to acquire a higher-resolution picture of the order in which the changes to the skeleton occurred, say, when the hind limb evolved relative to the forelimb and the ear.

The discovery and description of additional fossils will resolve some of these mysteries, as will insights from evolutionary developmental biology. To that end, studies of the genetic-control mechanisms governing the formation of the gill region in fish and the neck area in mammals and birds are just beginning to provide hints about which processes characterize both tetrapods and fish and which are unique to tetrapods. For example, we know that tetrapods have lost all the bones that protect the gills in fish but that the genes that govern their formation are still present in mice, where they function differently. We have also ascertained that in the neck region, the biochemical pathways that preside over the development of limbs have broken down. Although biologists can easily induce extra limbs to grow on the flank of a tetrapod, this cannot be done in the neck. Something special happened when tetrapods first evolved a neck that prevented limbs from sprouting there.

Other questions may be more difficult to answer. It would be wonderful to know which one of the many environmental contexts in which tetrapod fossils have turned up nurtured the very first members of this group (the available evidence indicates only that these animals did not debut in strictly marine settings). We would also like to comprehend fully the evolutionary pressures at work during each phase of the transition. Lacking a perfect fossil record or recourse to a time machine, we may never piece together the entire puzzle of tetrapod evolution. But with continued work, we can expect to close many of the remaining gaps in the story of how fish gained ground. SA

MORE TO EXPLORE

Gaining Ground: The Origin and Evolution of Tetrapods. Jennifer A. Clack. Indiana University Press, 2002.

The Emergence of Early Tetrapods. Jennifer A. Clack in *Paleogeography, Paleoclimatology, Paleoecology* (in press).