

EQUIPPING LIFE FOR LAND

WHEN THE FIRST TETRAPOD (FOUR-LEGGED) fossil was found in Upper Devonian lake and river deposits in Greenland, the animal it represented was thought to be a salamander-like amphibian, capable of crawling out of the water and walking. *Ichthyostega*, as the creature was called, seemed to combine limbs and a deep ribcage for air-breathing lungs with its many fish-like features. In effect, *Ichthyostega* appeared to fill the evolutionary gap between fishes and land-going animals.

This original theory has now been revised, however. The limbs of *Ichthyostega* and its contemporary, *Acanthostega*, were better adapted for swimming than walking. Also, these animals retained gills and may have breathed in both air and water. They were gradually adapting towards the final difficult transition from water to land.

Terrestrial vertebrates had to overcome a number of problems in order to survive. Take a fish out of water and it will soon die. It will fall on its side and flap without moving any distance. It will gasp for oxygen but its gills collapse out of water. Having no ears, it will not be able to hear anything and will become blind as the eyes dry out. The skin will lose moisture. Land-living animals also had to be able to move around. Most have evolved legs for this purpose. The first



MUDSKIPPER

The mudskipper is a modern bony fish that can leave the water to find food on exposed mudbanks, using its long, bony pectoral fins to prop itself up and wriggle across soft, wet mud. However, it has to remain wet and cannot stay out of the water for long.

terrestrial creatures, the centipede-like Ordovician arthropods, had inherited many pairs of jointed legs from their aquatic ancestors, but the vertebrates had to make the best of a very different evolutionary heritage. From paired fins, they had to evolve jointed, muscular limbs strong enough to lift the body and propel it forwards on land.

The main means of propulsion for fish is the sideways flexing of the body in a series of S-shaped waves. Although this kind of movement works



GREENLAND WATERWAYS

The oldest tetrapod fossils, of *Ichthyostega* and *Acanthostega*, have been found in late Devonian river and lake deposits from Greenland. These first four-limbed vertebrates were aquatic creatures. They used their muscular limbs, hands and feet for additional propulsion, holding on to plants and perhaps digging for shellfish. Growing to about 3 feet (1 metre) long, these early tetrapods were powerful predators, capable of attacking small fish. However, the tetrapod young were probably preyed on by fish, such as the lobe-finned fish, *Holoptychius*, the lungfish, *Dipterus* and the placoderm, *Bothriolepis*, as well as adult tetrapods.



FROM FINS TO LEGS

Terrestrial vertebrates had to evolve legs out of fins. But not all forms of fin are suitable to develop into limbs. The panderichthyids had two pairs of narrow-based fins and, as in the leg structure of most tetrapods, each of these fins was supported by a single bone that joined the shoulder or hip girdle. The girdles in turn are joined to the backbone. At the

outer end of each limb bone was a pair of wrist bones and then a number of rays (the spines of the fin). By contrast, today's true fishes have fan-shaped fins that are supported by a number of bones, and a lot of rays. Of the two types of fin, only the former, as found in the panderichthyids, was suitable to develop into a leg strong enough to lift a body.

site of Lode, in Latvia, is a remarkable animal. Along with tetrapod-like paired fins at the front and back of the body, it has a skull that is almost indistinguishable from that of the first four-legged animals, with a flat head, closely spaced eyes and a large mouth. The ribs are also joined to the backbone in the same way. When the remains of *Elpistostege*, one of the panderichthyids, was first discovered, it was thought to be a tetrapod.

effectively on land, as demonstrated by snakes, it cannot lift a body off the ground. Many land vertebrates, such as lizards, evolved a compromise solution, where the body still moves in S-shaped waves but is also lifted up onto stilt-like legs. This movement puts new pressure on the backbone, however, so land vertebrates' skeletons had to become stronger and more flexible – an evolutionary process that took a long time.

TETRAPOD ANCESTORS

So what animals did *Acanthostega* and *Ichthyostega* evolve from? Research has revealed that the panderichthyids, a group of fish with paired muscular fins, are anatomically closest to the tetrapods and are their most likely ancestors. *Panderichthys* itself, found at the late Devonian

ACANTHOSTEGA FOSSIL

By disentangling the jumbled skeletal remains of this early tetrapod fossil, scientists have revised ideas about how backboneed animals evolved for life on land. Found high on a remote mountainside in Arctic Greenland and entombed in hard sedimentary rock, the fossil required many days of careful preparation to unveil its secrets. The fossil shows that *Acanthostega* had a flattened skull with eye sockets placed close together on the top surface.



THE EARLY TETRAPODS



TREE-FERN

The few living tree-ferns look just like their Carboniferous ancestors. They are crowned with numerous fronds 10 feet (3 metres) in length that would produce an unstable plant but for the growth of massive roots.



FIRST VERTEBRATE LAND COMMUNITY

The wealth of fossils recovered from the freshwater limestone of East Kirkton in Scotland offers a remarkable glimpse of the past. A dense tropical forest of clubmosses, seed plants and tree-ferns covered the lower slopes of volcanoes and the shores of small lakes. The water was full of fish, amphibious tetrapods such as *Balanerpeton*, and eurypterids. Other tetrapods, such as *Westlothiana*, were more at home on land and had to compete with large and dangerous scorpions for food.

SOME OF THE MOST INTERESTING FOSSILS FROM the Mississippian (Lower Carboniferous) period found in recent years have come from a limestone quarry in East Kirkton, Scotland. The fossil fauna includes the first of several different early tetrapod groups: amphibians like *Balanerpeton woodi* and *Silvanerpeton*; an animal known as *Eucritta* that combined amphibian and reptilian features; and *Westlothiana lizziae*, an almost true reptile. The tetrapods of East Kirkton formed the world's oldest known vertebrate terrestrial community.

UNDER THE VOLCANO

The limestone of East Kirkton is unusual because it came from freshwater rather than saltwater, originally deposited in a small lake at the foot of volcanically active hills. The mineral-rich soils that formed on the ash and lava promoted the growth of a lush vegetation of clubmosses (lycopsids), horsetails (sphenopsids), ferns (pteridosperms) and naked seed plants (gymnosperms). The forest provided food and shelter for the variety of terrestrial animals, including vertebrate tetrapods and invertebrate scorpions,

myriapods, eurypterids and harvestmen. Storms, forest fires and even flooding periodically devastated the area, washing plant fragments and a sample of the animals into the lake where they perished and were quickly covered by a protective layer of sediment, forming well-preserved fossils.

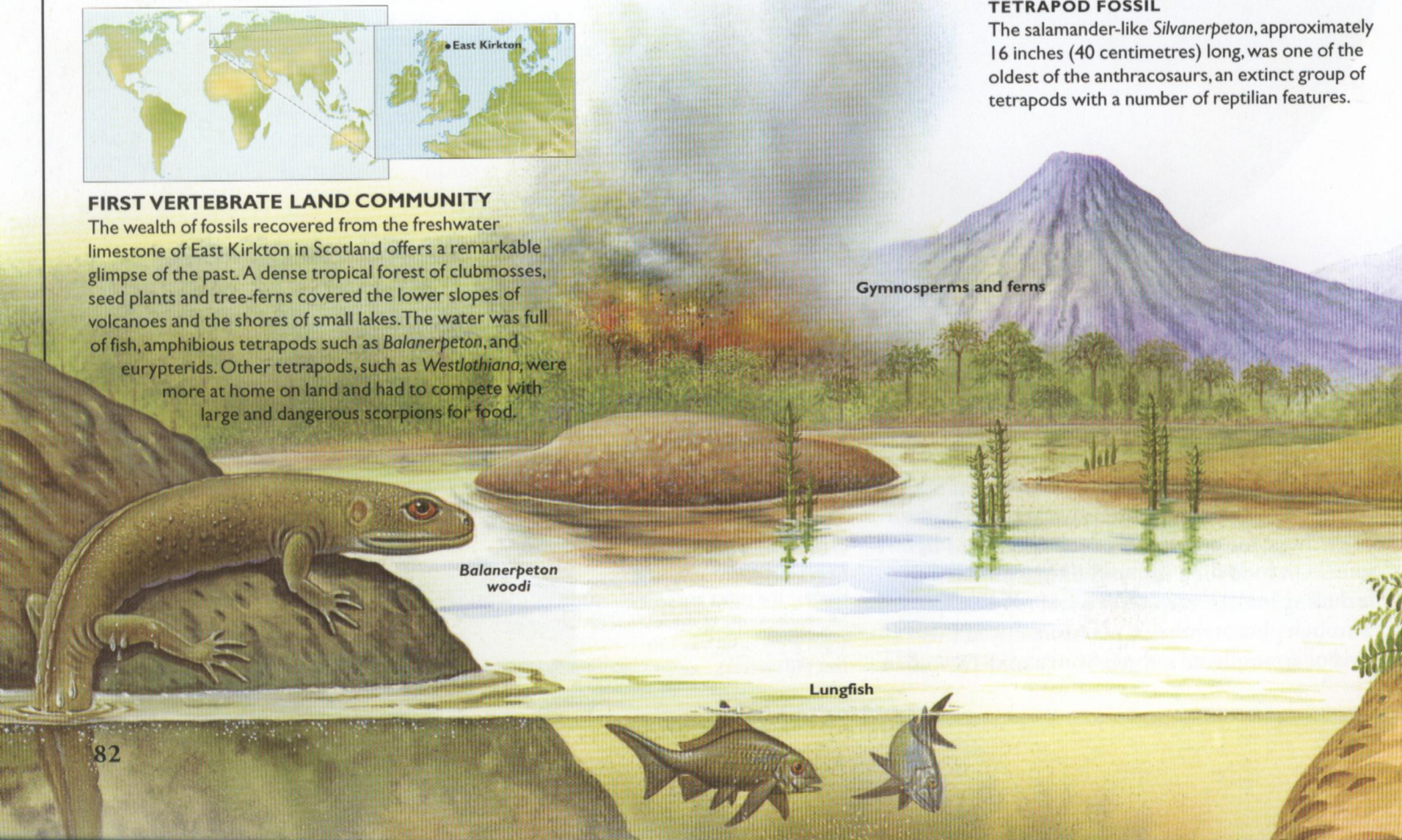
TERRESTRIAL FOOD CHAIN

The terrestrial food chain still relied on arthropod detritivores – animals that fed on rotting vegetation – such as mites and millipedes. But there were many additions to the fauna, including the oldest known harvestman (opilionid arachnid) and the first air-breathing scorpion, *Pulmonoscorpius*, a large, active predator, growing up to 28 inches



TETRAPOD FOSSIL

The salamander-like *Silvanerpeton*, approximately 16 inches (40 centimetres) long, was one of the oldest of the anthracosaurs, an extinct group of tetrapods with a number of reptilian features.



Gymnosperms and ferns

Balanerpeton woodi

Lungfish

AQUATIC LIFE

The waters of the Carboniferous lake in East Kirkton supported a remarkable variety of fish. Six species of bony (actinopterygian) fish were accompanied by two species of spiny (acanthodian) ones, as well as members of two shark families. The most probable explanation for this

impressive diversity of life is that the lake was originally linked to a much larger body of water. An infilling of volcanic ash from the surrounding area may have created a natural barrier that cut creatures off from their original habitat, trapping them without the possibility of escape.

(70 centimetres) long. Even this impressive beast was dwarfed by one of the three eurypterids known from the locality. *Hibbertopterus scouleri* looked like a huge, flattened, streamlined lobster. It had a headshield 26 inches (65 centimetres) wide and must have been around 10 feet (3 metres) long. Although it may have been the biggest arthropod ever, it only scavenged small prey.

Westlothiana lizziae, a vertebrate tetrapod that grew to 8 inches (20 centimetres) in length, was once thought to be the world's oldest reptile fossil. It turned out not to be a reptile, however, because it had a number of features, especially in the ankle and palate, more characteristic of primitive tetrapods than true egg-laying (amniote) reptiles.

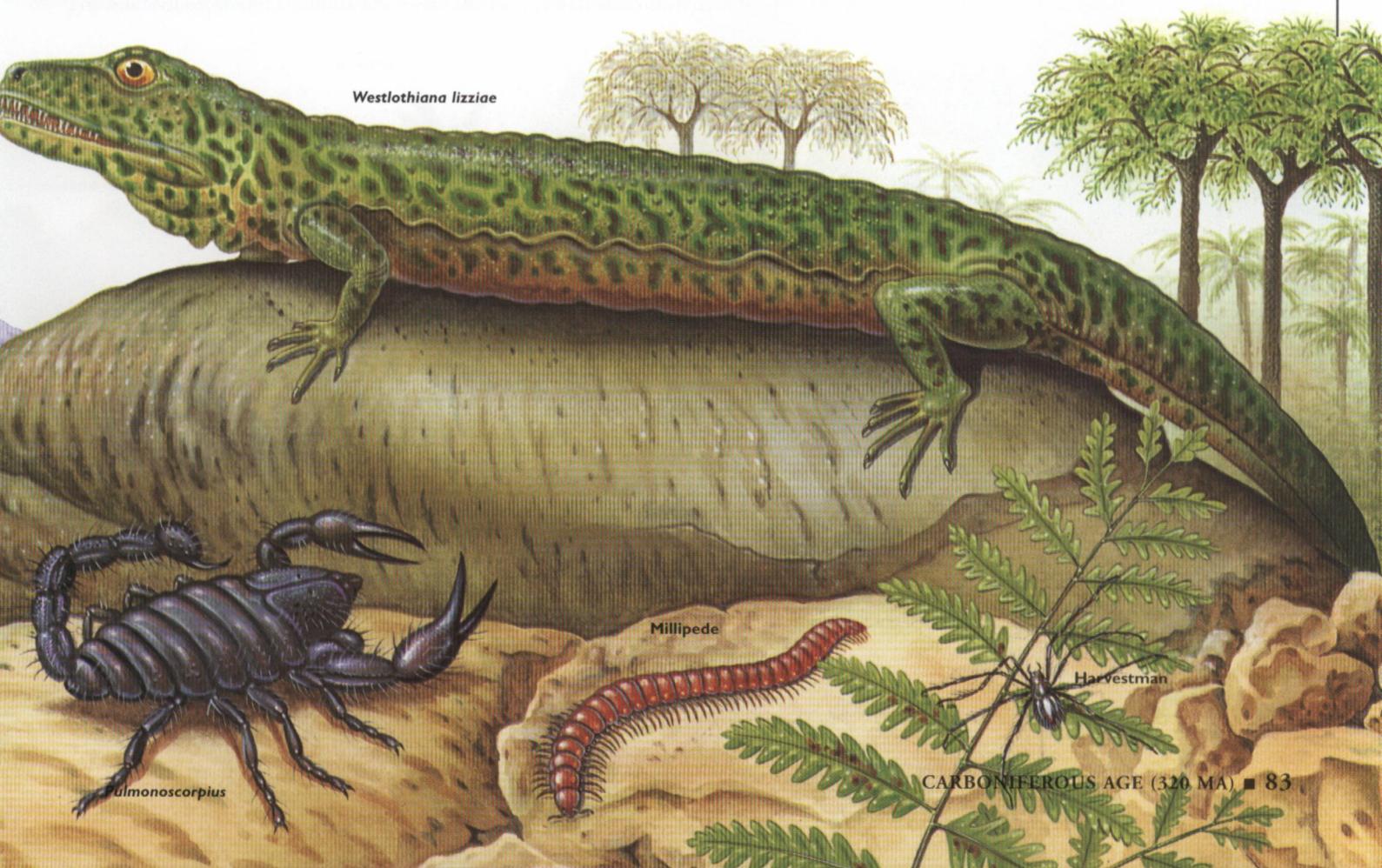
OTHER KIRKTON FINDS

Several small amphibians growing to around 20 inches (50 centimetres) were among the other vertebrates found at East Kirkton. Some, like *Balanerpeton woodi*, resembled modern salamanders. The structure of the limbs and ankles show that *Balanerpeton* lived mostly on land, but like all amphibians, it was severely constrained by the need to return to water to breed. It also shows crucial changes in skull structure that allowed the development of earbones that detect sound in air. With a mouth full of small, sharp teeth, it was an active predator on the lakeshore.

Some of the smaller reptile-like antracosaur, which grew to about 12 inches (30 centimetres), were also present. With poorly developed wrists and ankles, these creatures were really better suited to swimming than walking. Other amphibians included the *Ophiderpeton*, an unusual snake-like creature. With 200 vertebrae in its backbone, it probably grew to about 3 feet (1 metre) in length, and was another terrestrial predator.

LAND SCORPION

This well-preserved fossil from East Kirkton is of the oldest known land scorpion, *Pulmonoscorpius kirktonensis*. The scorpion's unusual structures for air-breathing, called "book-lungs", can still be found.



Westlothiana lizziae

Millipede

Harvestman

Pulmonoscorpius