Strangers on the shore

They came crawling out of the oceans 450 million years ago, leaving footprints in the sand. But just what were they?

Ken McNamara and Paul Selden

THE first steps taken by an animal on to land was one of the most significant events in the history of life on Earth. But the process of pinpointing the time when footsteps were made and discovering the type of animal that made them is fraught with problems. For a long time we have lived happily with the idea that the sequence of colonisation of land from the sea and rivers paralleled the evolutionary tree of life—first the land was colonised by plants, then by small herbivorous animals that grazed on the plants and finally by larger, carnivorous animals that fed on the herbivores. But a series of recent fossil finds dating from between 450 and 370 million years ago reveals a more complex sequence of events.

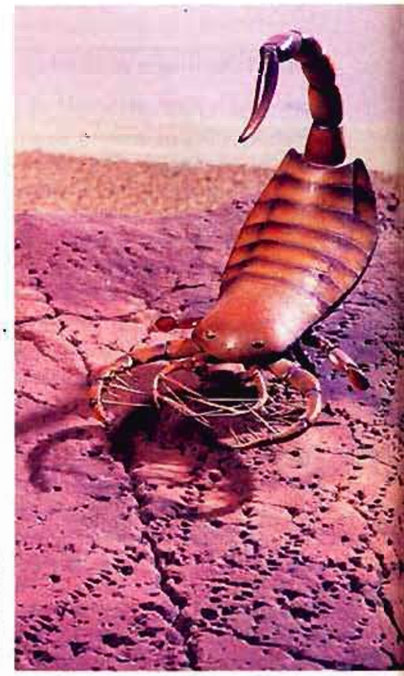
One of the first problems in trying to sort out which animals first colonised land stems from the nature of the fossil record. Moving from a watery environment, which was very conducive to fossilisation, early animals arrived on a bare, hostile surface. The land was whipped by winds, and constantly shifting rivers and sandstorms repeatedly covered, uncovered and moved dead bodies. The rocky, sandblasted "soils" were low in organic matter, and thus in cohesion. These were hardly ideal conditions for fossils to form. But at a few sites, a number of fortuitous circumstances, such as rapid burial in sediments and quick mineralisation, combined to preserve the remains of an animal's body, or the burrows and trails left behind as it moved about on land. These fossils allow us to glimpse the first attempts at colonisation of the land by animals.

One important question is whether the land the animals first walked on supported plant life. The early fossil record of land plants, however, is almost as indecipherable as that of the first animals. The earliest evidence comes from spores that Jane Gray, of the University of Oregon, and colleagues found in 1982 in Libya. These were preserved in rocks from the Ordovician period that may be up to 470 millions year old, and resemble the spores of some "lower" plants, such as living bryophytes (mosses and liverworts). This suggests that some of the earliest land plants were liverwort-like and able to withstand long periods of drought. The only earlier evidence of life on land before this is in the form of mats of bacteria and algae, which

Kristine Brimmell/Western Australia Museum

Clues to the past: the Murchison river in Western Australia has exposed fossil evidence of some of the first animals to step on the land

Early coloniser: the fossilised remains of a scorpion-like eurypterid (left) found in New York State, and a reconstruction (below) of the one that left the distinctive trackways at Kalbarri



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have recently come to light in 1200 million-year-old cherts found by Robert Horodyski in Arizona ("When algal mats ruled the land", *New Scientist*, 2 January 1993).

Some of the earliest evidence for terrestrial animals comes from fossil soils in Pennsylvania dating from about 450 million years ago during the late Ordovician. Greg Retallack and Carolyn Feakes of the University of Oregon found deep, vertical burrows, ranging from 2 to 21 millimetres in diameter, which they believe were made by soil animals, possibly millipedes. Other, indirect, evidence for terrestrial animals comes from late Silurian deposits in Sweden, where Gray and Martha Sherwood-Pike, also of the University of Oregon, found fossilised faecal pellets dating from 410 million years ago that contain remains of fungi. This implies the existence of a fungivorous microarthropod such as a mite or millipede that fed on the decomposing remains of simple land plants: a decomposer rather than a herbivore.

The simplistic view of the progressive colonisation of land by organisms from successively higher levels in the food chain must be modified to take account of such decomposers. These creatures would have played a vital role in soil production. By breaking down dead plants, they would have added nitrate and phosphate into the upper layers of the soil, thereby providing the necessary conditions for colonisation by "higher" plants—the vascular plants equipped with tissue that allows them to conduct water and other nutrients taken in through roots to the rest of the plant, and frees them from the need to live in wet habitats.

The earliest known vascular plants are all from about 420 million years ago during the late Silurian. These were plants such as *Baragwanathia*, *Salopella* and *Hedeia*, which consisted largely of a branched stem and, sometimes, small spine-like "leaves". Perhaps the most primitive-looking of all the plants was *Cooksonia*—which looked rather like a stumpy sort of sedge with a simple stem and no leaves. Doubts about the terrestrial status of *Cooksonia* were dispelled only recently by Dianne Edwards and colleagues from the University of Wales, Cardiff, when they found water-conducting vessels (tracheids) and stomata in *Cooksonia* from late Silurian rocks in Shropshire.

Baragwanathia, which resembles a club moss in form, and *Cooksonia* are usually preserved in marine sediments, which suggests that these plants grew near the shore. The extent to which inland sites were vegetated at this time is unknown. But we do know that around 400 million years ago there was a rich flora and fauna—including fairy shrimps, spider-like trigonotarbids, mites and springtails, and the simple, early vascular plants *Rhynia* and *Aglaophyton*—occupying a well-established hot-spring ecosystem at Rhynie, a classic early Devonian site in Aberdeenshire that was definitely inland.

So it seems likely that though the land was probably green when the first animals emerged from the water, it was hardly a place of bountiful food supply. Fossil evidence indicates little in the way of substantial plant life that could support herbivores. In which case, why did it take about 100 million years from the first major explosion of life in the seas some 540 million years ago, at the beginning of the Cambrian period, for animals to pluck up the courage to move on to land?

Pressing problems

They must have faced immense problems: a terrestrial environment is hostile to organisms adapted to living in water. The transition to a dry terrestrial habitat, where diurnal temperature changes were much greater than in aquatic environments, the unpredictable water supply and the necessity for respiration in air, required profound physiological changes.

One of the most pressing problems for a potential terrestrial animal was avoiding desiccation. The fossilised traces of the 450 million-year-old millipede burrows found by Retallack and Feakes in Pennsylvania point to arthropods being the first group of animals to colonise the land. Perhaps these early terrestrial colonisers coped with problems of temperature and desiccation by burrowing in the "soil". Any animal that already possessed characteristics which suited them to terrestrial conditions in some way would have been the ones most likely to succeed in the terrestrial lottery.

Another reason for the success of arthropods would lay in their tough cuticle, which had evolved at the beginning of the Cambrian period some 540 million years ago. In addition to providing defence, this exoskeleton gave strength to the body

'What were these animals doing walking around on Kalbarri's sandy river flats? We believe predators were the driving force behind the colonisation'

for moving and feeding. On land, it helped overcome the impact of gravity—a major concern to any animal moving from water to land as anyone who has ever crawled out of the sea after a long swim can testify. Without strengthened legs, movement on land would have proved difficult (even now, the limbs of land arthropods are vulnerable to mechanical failure during times of moulting while the new cuticle is hardening). Equally important was the ability of arthropods to secrete a waterproof outer layer on their cuticle to prevent water loss.

Direct evidence for arthropods emerging from water has been uncovered at Kalbarri in Western Australia, where the Murchison river flows through a deep gorge and has exposed 420 million-year-old late Silurian sandstones formed from sands deposited by an ancient river and by the wind. At various levels in the gorge, the surfaces of red sandstones, often covered by shallow-water ripple marks, are crossed by a wide range of trackways. The most spectacular are those which, together with Nigel Trewin of the University of Aberdeen, we interpret as being made by eurypterids. These extinct arthropods, related to and resembling scorpions (hence their common name sea scorpions) grew to 2 metres in length. Their distinctive tracks are up to 20 centimetres across and in places extend for many metres. The form and number of the individual footprints clearly points to the tracks being made by eurypterids. These arthropods possessed six pairs of appendages, but usually only three pairs functioned as legs for walking, with the hindmost pair commonly paddle-shaped for swimming. The front three pairs of appendages were adapted for feeding. In some species they evolved into pincers and in others into ferocious-looking cage-like structures.

While it is relatively straightforward to ascribe the eurypterid tracks to their producers, many other tracks at Kalbarri are not so easy to identify. One set appears to belong to an animal of perhaps 5 to 6 centimetres long that had 10 or 11 pairs of legs. We believe these tracks were made by a euthycarcinoid—the only arthropod to have yielded a body fossil so far in these deposits (see "Is Australian fossil the ancestor of all insects?", *New Scientist*, 17 August 1991). It appears that the euthycarcinoids, a group until recently considered to be entirely aquatic, were amphibious.

These extinct arthropods, resembling a multilegged cockroach, were most closely related to the centipedes and insects. Their presence in rocks of this antiquity has also pushed back the age of euthycarcinoids by about 120 million years, and suggests the euthycarcinoids may have, after all, been the ancestors of hexapods, the group that contains insects. Until recently, it was thought myriapods (the group that contains centipedes and millipedes) gave rise to hexapods because the earliest known euthycarcinoid was 310 million years old, while the first insect dates from about 370 million years ago.

Predators at large

So, what were the various animals doing walking around on Kalbarri's sandy river flats? Often, interpretations of the evolution of organisms into major new ecological niches suffer from what can only be termed the *Star Trek* syndrome: the implication that the species are "boldly evolving where no species has evolved before". In other words, there is a vacant ecological niche, so it must be filled. In the case of these early arthropods it was one thing to have a vacant niche to evolve into, another to possess the morphological and physiological adaptations needed to cope with the effects of gravity, low oxygen levels,

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Multilegged tracks at Kalbarri: the culprit would seem to be the euthycarcinoid (right) with its 11 pairs of legs

large diurnal temperature ranges and the ever-present danger of desiccation. If there was little in the way of plants to attract animals on to the land, we must turn to other causes.

In recent years, palaeontologists have recognised predation as an important driving force in the evolution of a number of marine invertebrates, in particular sea urchins, barnacles and some molluscs. We believe predators were also the driving force behind the colonisation of land. In addition to eurypterids and numerous other arthropod predators that flourished in the seas, lakes and rivers, a major new group of predators were evolving in the oceans and rivers at the time—the fishes. The great explosion in diversity of fishes took place between 400 and 420 million years ago. The appearance of this new group of predators, many of which would have fed upon aquatic arthropods, would have increased the predation pressure felt by some of the small arthropods.


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Creepie oldie: a 414 million-year-old trigonotarbid

This would explain the various trackways at Kalbarri. Many were made by animals moving from one pool to another as the water dried up in the dry seasons. In such a situation, with density of animals increasing in the pools as the water levels shrank, predation levels would have been very high. The stomach contents of eurypterids from elsewhere show them to have been carnivores, and they would have followed the euthycarcinoids and smaller arthropods out of the water hoping for a meal. The longer any small arthropod could survive out of water and outrun any eurypterid predator, the better its reproductive chances—and the more likely that its genes would flourish.

While the burrows in Pennsylvania provide indirect evidence of the existence on land of soil animals as early as 450 million years ago, a number of new discoveries of body fossils suggest it was between 420 and 380 million years ago, during the late Silurian and early Devonian, that the major colonisation of the land by animals took place.

The oldest body fossils of land animals, dated at 414 million years old, were found in 1990 at Ludlow on the Welsh Borders ("Oldest creepies crawled the land in Shropshire", *New Scientist*, 10 November 1990). The famous Ludlow Bone Bed has yielded fragments of fish and other fossils for many years, but in 1990 Andrew Jeram, then at the University of Manchester, discovered a large quantity of arthropod cuticle in rocks just above the bone bed. On sorting the mass of tiny leg and body segments and a little articulated material from the muddy siltstone, Jeram identified the fragments as belonging to at least two sorts of extinct centipedes and a trigonotarbid arachnid—a group of extinct arthropods that possessed six pairs of appendages, four pairs for walking and two pairs for feeding. They differ from spiders in lacking silk-producing spinnerets, and have armour plates on their abdomens.

How can palaeontologists be so certain that the Ludlow remains are of terrestrial animals? First, all trigonotarbids found at other undoubtedly terrestrial sites, such as Rhynie in Scotland and the 375 million-year-old site at Gilboa in New York State, bear structures called book-lungs. These distinctive air-breathing organs are possessed by spiders today, suggesting that trigonotarbids were also air-breathers. Secondly, all modern centipedes are terrestrial, and the structure of the legs of the two Ludlow centipedes is that of an animal which moved on land, not in water. Thirdly, land plants were also found with the remains, including *Cooksonia*.

Rhynie and Gilboa are rich sources of terrestrial body fossils from the late Silurian and early Devonian periods. At Gilboa centipedes, trigonotarbids, mites, pseudoscorpions and the earliest known spider, *Attercopus*, have been found, while the 395 million-year-old deposits at Rhynie have yielded springtails, mites and trigonotarbids. An interesting fact to emerge from the fossils found at all three sites is that early terrestrial arthropods were predominantly carnivorous. No herbivores are known. The predators probably fed mainly on microarthropod decomposers, such as mites, millipedes and soft-bodied worms, that were rarely preserved but which probably comprised a substantial part of the fauna that inhabited the soil.


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Petrified at Rhynie: the "macaroni" is in fact fossilised stems of early land plants from 395 million years ago

Strangely, there is little evidence of herbivory in the fossil record until well into the Carboniferous period, about 330 million years ago. It is only in fossilised leaves of this age and younger that there is unequivocal evidence of the kind of damage caused by animals. William Shear of Hampden-Sydney College, Virginia, who has done much of the work on the Gilboa arthropods, has suggested that by-products

Conquering a new land—plants or animals first?

THE success of predatory arthropods in colonising virtually barren landscapes, analogous to the situation on Earth about 420 million years ago during the Silurian, is seen today in the sequence of ecological succession at sites such as Mount St Helens and Krakatoa, following violent volcanic explosions.

Zoological expeditions to the Krakatoa islands in 1984 and 1985, led by Ian Thornton of La Trobe University, Victoria, revealed that arthropods quickly colonised areas of the bare lava formed from volcanic activity in the 1950s and 1970s, well before any plant became established. Thornton found arachnids, springtails and a range of insect groups.

Just two months after the explosion of Mount St Helens in 1980, long before any plant life had become established, 43 species of spiders had arrived by "ballooning"—floating through the air on gossamer threads. Similarly, crickets and wolf spiders are among the first colonisers on newly formed lava flows on Hawaii, arriving well before plants.

Springtails, present in some of the earliest terrestrial fossil deposits, are known to be very early, opportunistic colonisers of new islands. On both Krakatoa and the volcanic island of Surtsey in the North Atlantic, springtails were present at a very early stage. The early arachnids and springtails on these islands quickly established an "aeolian" ecosystem, existing on other windborne arthropods, either as scavengers or predators.

Consequently, the ability of arthropods to establish ecosystems in regions devoid of plant life supports the view that the earliest terrestrial ecosystems on Earth may have involved arthropods and "lower" plants, such as liverworts and mosses, to the exclusion of "higher" plants. Furthermore, the evolution of the "higher" vascular plants may have postdated the conquest of land by animals. Herbivorous animals that fed on the higher plants may have been the last to arrive on the scene.


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Krakatoa: arthropods show their ability to establish a foothold in regions devoid of life

from the synthesis of lignin, which was present in early vascular plants, were toxic to early terrestrial animals. True herbivory only really evolved when animals developed enzymes and a gut microflora of symbiotic bacteria which could bypass the decomposer and break up fresh plant material, returning it to the ground as excrement.

A second group of animals to step on to land during the late Silurian and early Devonian were the tetrapods—the first terrestrial vertebrates which had four limbs and had evolved from the crossopterygian fish with its four body fins. Anne Warren and colleagues at La Trobe University, Victoria, have found tetrapod trackways in the Grampians hills about 250 kilometres from Melbourne, dating from about 385 million years ago.

Driven to land

We believe their appearance on land may have again been driven by predators because the timing corresponds to the rapid expansion in the diversity of fishes. The fact that one of the most abundant groups—the placoderm fishes—evolved a heavy armour to protect themselves in the early Devonian supports the argument for high levels of predators within the aquatic environment. John Long of the Western Australian Museum, Perth, found stunning fossil evidence of this recently in Devonian rocks in the Kimberley region of Western Australia. It was a specimen of the predatory crossopterygian fish *Onychodus* preserved with a smaller placoderm in its mouth. It is presumed that the *Onychodus* choked to death on its meal. Devonian rocks elsewhere have yielded other fossilised examples of fish predation. So, for fishes that evolved fins capable of supporting the body weight out of the water and were able to breathe air, the land would have offered a refuge from the predation pressures present in the seas, lakes and rivers.

The earliest skeletal remains of tetrapods are known from younger rocks than those in which tracks are preserved. Per Ahlberg at the University of Oxford has recently identified a tibia, humerus and incomplete jaws of a tetrapod from late Devonian rocks, some 370 million years old, near Elgin in Scotland. There is no doubt that these early tetrapods had well developed legs with digits (up to eight on each forelimb in *Acanthostega*, seven in *Ichthyostega* and six in *Tulerpeton*).

Mike Coates and Jennifer Clack of the University of Cambridge, however, have recently questioned if some of these early tetrapods preserved in late Devonian rocks in Greenland, were fully terrestrial animals. From their analysis of well-preserved material they have discovered that *Acanthostega* retained fish-like internal gills and other structures associated with aquatic respiration. Coates and Clack suggest that the legs may well have evolved primarily for use in water. The forelimbs were, they believe, more likely to have been paddle-like. Furthermore, compressed lower leg bones in *Ichthyostega* closely resemble the pectoral flippers of whales, while the fossilised remains of *Tulerpeton* are only found in marine sediments far from the shoreline. But these well-developed legs, like the hard exoskeleton of arthropods, meant that tetrapods were superbly equipped for life on land.

For those animals able to withstand the rigours of a non-aqueous existence, the land was the way out. Here, at least early on, was a host of new niches to be exploited, free from the great pressure of predation existing in the seas, lakes and rivers. When all the morphological, physiological and environmental problems of a terrestrial existence were solved, it may have taken only the build-up of sufficient aquatic predation pressure to lead to the conquest of the land. Who knows, maybe animals didn't jump—perhaps they were pushed. □

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