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Land Animals, Origins of

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Glossary

Coprolite Fossil feces are called coprolites.
Cryptobiosis The ability of an animal to enter a state of reduced metabolism in order to overcome adverse environmental conditions.
Detritivore An organism which eats detritus is called a detritivore.
Epifauna Organisms which live above (i.e., not within) the substrate are called epifauna.
Hexapoda Hexapoda is a group of arthropods including insects, springtails, and their close relatives.
Interstitial Living between grains of sediment is called interstitial.
Isotonic Solutions with the same concentration of solute, so that osmosis does not occur.
Metazoa Multicellular animals are called Metazoa.
Osmosis The passage of water from a solution of higher concentration to one of lower concentration is called osmosis.
Phylum (pl. phyla) A major group of animals with a distinctive body plan; e.g., Arthropoda, Mollusca.
Tetrapod A vertebrate animal with legs (rather than fins) is called a tetrapod.

Introduction

Terrestrialization – the colonization of the land habitat from the sea by plants and animals – was the third most important event in the history of life on Earth, after the origin of life and the development of multicellularity. Here, we look particularly at the origin of land animals. For many people, that brings to mind fish acquiring legs and crawling out of the mud for the first time onto dry land. However, the first tetrapods were preceded onto land by invertebrate animals many millions of years previously. Moreover, what constitutes a terrestrial animal? How much of its life cycle must it spend on land to be considered part of the terrestrial fauna?

There is no doubt that land animals originated in the sea; the isotonicity between the solute concentrations of animal cells and sea water is a testament to this. Osmotic concentration in terrestrial animals is a useful clue to the route they took onto land. Not many animals have managed to move from the sea to the land: of over 30 phyla, only the vertebrates, arthropods, mollusks, and annelids have significant numbers of macroscopic terrestrial representatives. A greater number of phyla include very few terrestrial species (e.g., platyhelminths; Figure 1), cryptobiotic representatives, or internal parasites on terrestrial organisms. The body plans of some highly successful marine phyla have apparently precluded their terrestrialization; these include the sipunculid, echiuroid, and priapulid worms; cnidarians; lophophorates; chaetognaths; pogonophores; hemichordates; and echinoderms. No phylum originated on land, and no major terrestrial taxon has become extinct, as far as we know.

Physiology

In order for marine animals to colonize the land, a number of physiological barriers need to be overcome. These include: changes to methods of respiration, water management and osmoregulation, digestion, temperature control, reproduction, dispersal, sensory perception, and support and locomotion. Water is essential to life, as a medium for biochemical reactions, and for the transport of cell solutes, for example. It is the variability of its availability on land that is problematic for terrestrial life – inundation can be as fatal as dehydration for a

Figure 1 Terrestrial flatworm (Platyhelminthes: *Bipalium* cf. *rauchi*, Singapore); © the author.

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Figure 2 Salamander (Tetrapoda, Lissamphibia: *Salamandra atra*, Switzerland); © the author.

Figure 3 Millipede (Diplopoda: *Anadenobolus monilicornis*, Barbados); © the author.

land animal. Four groups of land animals can be defined based on their management of water availability.

- Aquatic organisms avoid the problem by living in interstitial water in soils; these include microscopic nematodes, protozoans, and micro-arthropods.
- Cryptic forms differ from those in the first group in being larger, but similarly inhabit environments of constantly high humidity, such as soil and tropical forest litter. Included in this group are earthworms, leeches, flatworms (Figure 1), isopods, slugs, insect larvae, some amphibians (Figure 2), and myriapods (Figure 3).
- Poikilohydric (desiccation-tolerant) animals require high humidity to function, but can tolerate desiccation by drying out and rehydrating when conditions become favorable again. Cryptobiotic rotifers, mites, and tardigrades occur in this group; also included are animals with desiccation-tolerant resting stages such as the eggs of fairy shrimps.
- Homoiohydric organisms have achieved the true conquest of the land by the use of waterproof cuticles, transport systems, and osmoregulation. In this group are most tetrapods, insects (Figures 4 and 5), arachnids (Figures 6 and 7), and some isopods and mollusks (Figure 8).

Another important barrier to terrestrialization is the necessity to change from obtaining oxygen from water to

Figure 4 Beetle (Hexapoda, Coleoptera: *Stenocara gracilipes*, Namibia); © the author.

Figure 5 Butterfly (Hexapoda, Lepidoptera: *Neptis* sp., Yunnan, China); © the author.

Figure 6 Spider (Arachnida, Araneae: *Lasiodora* sp., Brazil); © the author.

Figure 7 Scorpion eating a cricket (Arachnida, Scorpionida: *Isometrus maculatus*, Singapore); © the author.

Figure 8 Land snail (Pulmonata: *Helix pomatia*, Italy); © the author.

Figure 9 Land crab (Crustacea, Decapoda: Trinidad); © the author.

Figure 10 Lizard (Amniota, Squamata: *Agama aculeata*, Namibia); © the author.

breathing air. Oxygen is more abundant in air (8.65 mol m^{-3}) than in water (0.262 mol m^{-3}), but its availability to animals depends on other factors, such as the rate of diffusion and the efficiency of oxygen-binding molecules in the blood. Many littoral animals can survive out of water for periods, but those that spend their whole lives out of water need lungs rather than gills. The problem is compounded by the fact that the CO_2 and O_2 molecules are larger than the H_2O molecule, thus membranes for gas exchange leak water. This means that respiratory surfaces need to be internalized and valves are required to regulate air flow, spiracles in insects, for example, so that water is not lost.

For support and locomotion on land, small animals such as slugs and worms can use their hydrostatic skeletons, but larger arthropods and tetrapods have evolved a hanging stance for stability, and both groups developed an ankle joint to prevent the newly acquired plantigrade foot from twisting on the ground. Eyes used in air differ from aquatic visual organs because of the differences in refractive index of the two media, and organs of hearing used in air are capable of perceiving higher-frequency sounds than in water. Reproduction and dispersal is much easier in the sea, where gametes can be simply released into the water, and larvae disperse in ocean currents. On land, internal fertilization and courtship is the norm. Crabs (Figure 9) and amphibians (Figure 2), for example, need to find water to breed, but the amniote egg of higher tetrapods (Figures 10 and 11) has removed the dependence on aquatic environments. Insect eggs have a complex coat to prevent both drowning and water loss.

Terrestrial adaptations can be determined in living animals from their anatomy and physiology, but to determine the sequence and timing of events during the major phase of terrestrialization in the Palaeozoic, the fossil record holds the only clues. Complex terrestrial biotas, based mainly on arthropods and plants, had developed by the Devonian period; colonizations by vertebrates, mollusks, and crustaceans followed these early pioneers much later, into already well-established ecosystems.

Figure 11 Armadillo (Amniota, Mammalia: *Dasypus novemcinctus*, Arkansas, USA); © the author.

The Fossil Record

Fossil evidence for the colonization of the land by animals (Figure 12) comes from two sources: indirect evidence from the sedimentary environment, such as fossil soils or traces of terrestrial organic molecules, and trace fossils; and direct morphological evidence from the fossils themselves. Trace fossils are evidence of the existence of organisms without any actual remains; examples include fossil footprints and trackways, worm trails, feeding structures, burrows and nests, resting traces, and chemical signatures. Body fossils, as the name implies, are actual remains of the organism, though these need not consist of the original material, which may have been replaced by other substances and, indeed, impressions of the animal's body in the sediment are also included here.

Trace Fossils

Fossil trackways indicating that aquatic animals hauled themselves out of the water and across subaerially exposed sediments date back to the latest Cambrian period (ca. 488 Ma: MacNaughton *et al.,* 2002). However, whether these animals were habitually terrestrial or were aquatic animals sprinting from one pool to another to survive desiccation is not clear. Moreover, evidence for the sediment being exposed to the air (e.g., mud cracks) does not necessarily tell us whether the tracks were made under water and then exposed, or the mud was already drying and cracking when the trackway was made (Braddy, 2004). Nevertheless, a Cambro-Ordovician origin of terrestrial animals was suggested by Rota-Stabelli *et al.* (2013) using molecular clock analyses of extant Ecdysozoa.

Many of the early Paleozoic trackways have been ascribed to myriapod-like animals, but it would be unwise to accept them as explicit evidence for the existence of myriapods (millipedes, Figure 2, and centipedes, Figure 13) as we know them. It is conceivable that there were other extinct arthropods around at this time with multiple limbs capable of leaving such impressions (see discussion in Dunlop *et al.,* 2013).

Body Fossils

While with trace fossils, sedimentological evidence is used to reveal terrestriality, to interpret body fossils, we need to find morphology that indicates land life unequivocally. For example, a lung is clearly a terrestrial adaptation; but legs need not be: they occur in amphibians, for example. Similarly, it is unwise to assume that a fossil is of a terrestrial animal just because its modern relatives live on land today. For example, while all modern onychophorans live in damp forests, their Paleozoic relatives were marine.

The earliest multicellular animals on land may well have been tardigrades. These tiny 'water bears' are extremophiles; that is, they can live in environments which would be lethal to other animals, including deep oceans, under ice, the tops of the highest mountains, hot springs, and they can even survive the vacuum of space (Jönsson *et al.,* 2008)! These tiny animals undergo cryptobiosis: if the environment becomes extreme, they metamorphose into cyst-like tuns, from which they emerge when circumstances become favorable again. Their oldest fossils are Cambrian in age (ca. 509 Ma: Müller *et al.,* 1995), from marine sediments. However, their propensity to form tuns, which can then be dispersed by the wind, means that they would have easily accessed emergent land surfaces, and likely survived there. Unfortunately, their small size means that they are rare as fossils, and the oldest terrestrial tardigrade fossil comes from amber of Cretaceous age (ca. 80 Ma: Cooper, 1964).

Excluding a very dubious record of an Ordovician mite, the oldest metazoan fossils that can confidently be considered terrestrial are millipedes from the Silurian (ca. 428 Ma) of Scotland (Wilson and Anderson, 2004). This fossil, *Pneumodesmus newmani*, shows spiracles along the side of the body; these are openings of the tracheal system by which the animal would have breathed air. Thus, there is direct morphological evidence of terrestriality. Coprolites occur in rocks of late Silurian age of the Welsh Borderland which have been attributed to detritivorous animals, probably millipedes (Edwards *et al.,* 1995). A few scorpion fossils are known from rocks of middle and late Silurian age (ca. 430–420 Ma). For example, *Dolichophonus loudonensis*, also from Scotland (Laurie, 2012) is the oldest known arachnid, and is about the same age as *Pneumodesmus*. However, there has been a debate for many years about whether the early scorpions were terrestrial or aquatic. An aquatic mode of life for early scorpions was the prevailing opinion for most of the twentieth century but, more recently, this has been questioned because of the lack of obvious morphological evidence. Some, younger, scorpion fossils do seem to have had gills, but it has been argued that these animals migrated into the freshwater habitat from the land. So, it seems that, based on trackways, coprolites, and body fossils, millipedes were the earliest recognizable animals on land.

Ludford Lane

Not far behind the millipedes, in terms of their fossil record, came the centipedes (Figure 13) and arachnids (Figures 6 and 7). Late Silurian fossils from the ca. 419 Ma locality at Ludford Lane, Shropshire, England, consist of tiny pieces of cuticle which are extracted from the sediment using acid (Figure 14). These

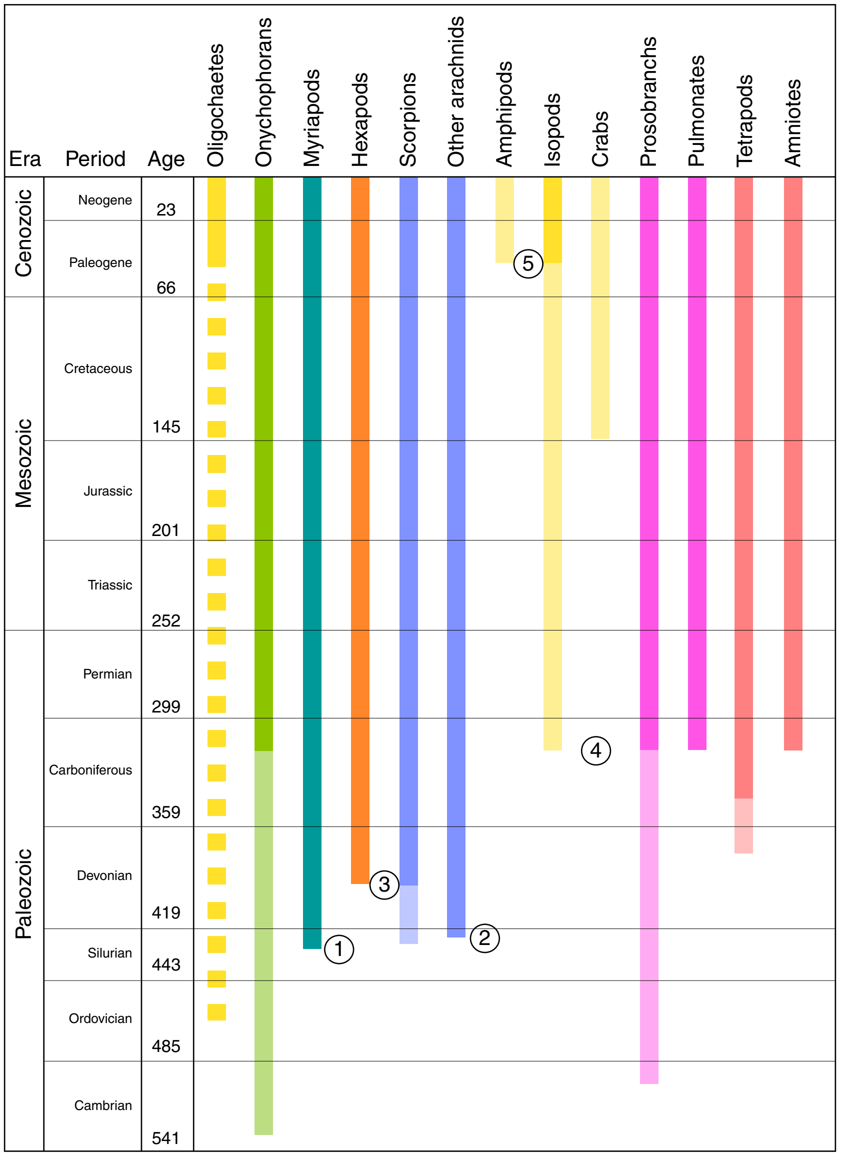

Figure 12 The body fossil record of terrestrial animals. Lighter colors refer to earlier aquatic record; dashed line refers to uncorroborated fossil record. Numbered points refer to important localities in the record of terrestrial animals: (1) Stonehaven, Scotland (earliest land animal, a millipede); (2) Ludford Lane, England (early terrestrial biota, including arachnids and myriapods); (3) Rhynie Chert, Scotland (early terrestrial biota); (4) Late Carboniferous sites such as Mazon Creek, Illinois; (5) Baltic amber; © the author.

fragments include the oldest centipede (**Figure 15**), probably related to the modern House centipede *Scutigera* (Jeram *et al.*, 1990; Shear *et al.*, 1998). Scutigeromorphs (e.g., **Figure 13**) are thought to be fairly primitive among centipedes. There is also a millipede belonging to the extinct arthropleurids (Shear and Selden, 1995). Also at Ludford Lane is the oldest non-scorpion arachnid, belonging to the extinct spider-like trigonotarbids (**Figure 16**). Younger trigonotarbids show book lungs, indicating true terrestriality, so this habitat is also assumed for the Ludford Lane fossil too. The detritivore coprolites, mentioned above, come from this famous locality.

Ludford Lane presents a very early terrestrial ecosystem based on detritus feeders (e.g., millipedes), which were preyed upon by carnivores (e.g., centipedes, arachnids). There is no evidence for herbivorous animals, as we would understand them today: i.e., animals chewing leaves and other green parts of plants. It appears that this type of food web prevailed until the late Paleozoic, by which time the symbiotic fungi and bacteria in the guts of herbivores had developed to allow internal decomposition of green plants (Shear and Selden, 2001).

Rhynie Chert

Returning to Scotland, the next youngest locality bearing terrestrial animals is of early Devonian age: the Rhynie and Windyfield cherts of Aberdeenshire, Scotland, of ca. 410 Ma age. These two adjacent localities preserve an entire terrestrial ecosystem of early plants and animals, in extraordinary

Figure 13 Centipede (Chilopoda: *Thereuropoda longicornis*, Taiwan); © the author.

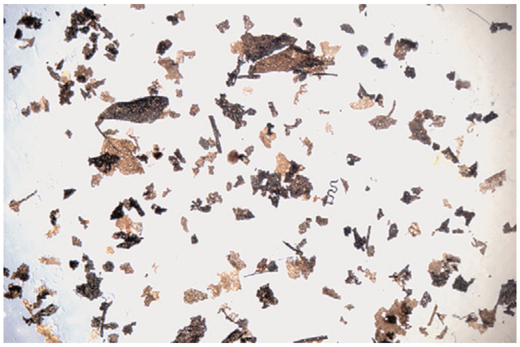

Figure 14 Minute fragments of plant and arthropod cuticle derived by maceration of Ludford Lane sedimentary rocks (Silurian, Ludford Lane, Shropshire, UK) in hydrofluoric acid; © the author.

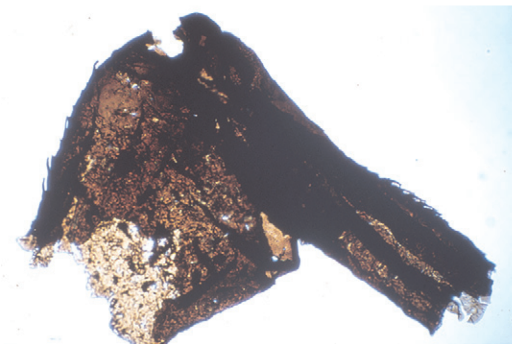

Figure 15 Knee joint of a scutigeromorph centipede (Silurian, Ludford Lane, Shropshire, UK); © the author.

Figure 16 *Palaeotarbus jerami*, the oldest known trigonotarbid arachnid (Silurian, Ludford Lane, Shropshire, UK); © the author.

Figure 17 Piece of Rhynie Chert (Devonian, Aberdeenshire, Scotland) packed with rhizomes of early land plants; © the author.

three-dimensional detail, in siliceous rock produced by a Devonian hot spring (**Figure 17**). More trigonotarbid arachnids occur here (**Figure 18**), as well as the oldest mites, for example, *Protacarus crani*, the harvestman *Eophalangium sheari* (Dunlop *et al.*, 2004). Also of significance in the Rhynie fauna are the oldest hexapods (including insects). There is a springtail, *Rhyniella praecursor* (Hirst and Maulik, 1926; Scourfield, 1940), and also the oldest true insect, *Rhyniognatha hirsti*, known only from its mandibles (Engel and Grimaldi, 2004). To complete the fauna known from Rhynie and Windyfield, there are enigmatic euthycarcinoids, centipedes, and another possible hexapod (Fayers and Trewin, 2005).

Gilboa

The Middle Devonian (ca. 390 Ma) Gilboa, New York, locality records the oldest terrestrial fossils in North America. It has

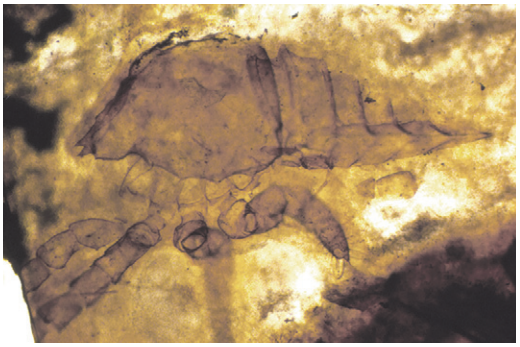

Figure 18 *Palaeocharinus*, a trigonotarbid arachnid from the Rhynie Chert (Devonian, Aberdeenshire, Scotland); © the author.

yielded trigonotarbid arachnids, as well as oribatid and alicorhagiid mites, the oldest pseudoscorpion, and the enigmatic uraraneid arachnids. *Attercopus fimbriunguis* was originally thought to be an odd trigonotarbid (Shear *et al.*, 1987), but was later reinterpreted as the oldest spider (Selden *et al.*, 1991). More recently, it was shown to be an extinct, spider-like animal, and named as a new arachnid order: Uraraneida (Selden and Shear, 2008). *Attercopus* produced silk, but lacked the typical spinneret organs which define true spiders. The Gilboa locality also has centipedes, including another scutigeromorph (Shear and Bonamo, 1988; Shear *et al.*, 1998).

Younger Records

Fossil insects from the Devonian are surprisingly rare. The record of a bristletail from Gaspé, Canada (Labandeira *et al.*, 1988) has been seriously questioned as to whether it is a real fossil or a modern contaminant (Jeram *et al.*, 1990). More recently, Garrouste *et al.* (2012) reported the discovery of a terrestrial insect, *Strudiella devonica*, from the late Devonian (ca. 365 Ma) of Belgium. This find, too, has been disputed (Hörnschemeyer *et al.*, 2013). So, it appears that hexapods, including the insects, did not become common in the fossil record until later in the Paleozoic.

Crustaceans did not get onto land until much later, and even today only a few groups are fully terrestrial. The oldest terrestrial isopods are known as fossils from Eocene (ca. 49 Ma) Baltic amber; the oldest known amphipods are even younger, Miocene in age (ca. 16 Ma), from Mexican amber; and land crabs date back only to Quaternary times (ca. 3–2 Ma).

The review so far has dealt mainly with arthropods. Having a fairly tough cuticle, these fossilize fairly readily, unlike earthworms, for example. It was also in the Devonian that the first vertebrates began to attempt terrestrialization. Tetrapods (limbed vertebrates) had evolved by Devonian times and there was a high diversity, but they are thought to have been aquatic, similar to salamanders of today (Clack, 2009). Following the Devonian, there is a barren time period known as Romer's Gap (after the vertebrate paleontologist A. S. Romer who first recognized it), which stretches from ca. 360–345 Ma into the early Carboniferous period. The first tetrapod fossils to appear after Romer's Gap include terrestrial forms; however, fossils are now appearing which hint at morphological adaptations for land life, at least, from within this gap (Clack and Finney, 2005).

Routes onto Land

It has already been hinted that animals adapted to the extremes of life on the seashore are already pre-adapted to life on land. This route proved the most successful for invertebrate colonizers, and was apparently taken by nemertines, polychaetes, many land mollusks, most crustaceans, chelicerates, and probably myriapods and hexapods (Little, 1983). Evidence comes from study of the osmoregulation abilities of the living animals; that for a marine route onto land for Crustacea and Mollusca is strong, but is less so for other groups. Interstitial environments allow a more gradual transition in salinity from marine to terrestrial than that encountered by the epifauna. Arthropods show relatively high osmotic concentrations which, in the case of the relatively small myriapods and hexapods, can be compared with the high osmotic concentrations in small crustaceans, and so a marine route is suggested. Conversion of the book-gill into the book-lung in arachnids is a good example of the use of an existing aquatic respiratory organ to breathe air.

A freshwater route onto land was apparently used by platyhelminths, annelids, prosobranch mollusks, crayfish, some crabs, and vertebrates (Little, 1983). The correlation between osmotic concentration and routes onto land shown by crustaceans can also be seen in the mollusks. The most successful are the pulmonates (slugs and snails), which have a relatively high osmotic concentration; in contrast, prosobranchs have a low osmotic concentration and are generally restricted to humid tropical forests where fatal desiccation is less likely.

The success of terrestrial vertebrates, having taken the freshwater route onto land, contrasts with those successful invertebrate groups with largely marine ancestors. The larger tetrapods could spend longer on land without the threat of desiccation because of their relatively low surface area to body mass ratio. Also, freshwater origins conferred the ability to osmoregulate efficiently, and a large size and waterproof skin allowed them to overcome the problem of water availability on land. Littoral animals need to breathe air fairly continuously for long periods while awaiting the return of the tide, so many have adapted pre-existing gill structures for air breathing. In contrast, animals in poorly oxygenated freshwater are intermittent air-breathers (e.g., coming to the surface to gulp air) and so many developed new organs to take in large volumes of air at a time. Palaeontological evidence also points to a freshwater route for the terrestrial vertebrates.

Some animal groups evolved from already terrestrial ancestor; hexapods for example, for whom the problems of terrestrialization had already been solved by their ancestors.

Conclusion

It seems likely that, among metazoans, small, cryptobiotic animals were the first to reach land from the sea. Fossil evidence for this is, however, sparse. The oldest recorded land animals are millipedes, which would have lived on detritus from early land plants. There is evidence for these in the form of body fossils and traces fossils (coprolites). Other arthropods followed, with tetrapods emerging later, possibly within the barren period known as Romer's Gap (ca. 360–345 Ma).

Once on land, animals went on to do quite remarkable things. A number of groups took to the trees, which had appeared in Devonian times, and later the air between the trees. As insects took to the skies, so their main predators, the spiders, followed them up with their elaborate webs. The tetrapods then took to the air: pterosaurs and birds, and later, bats. Finally, many land animals returned to the water; freshwater insects, for example, and marine mammals: the whales and dolphins.

See also: Complexity, the Role of Oxygen in Evolution of. Fungal Evolution: Aquatic–Terrestrial Transitions. Metazoans, Origins of

References

Braddy, S.J., 2004. Ichnological evidence for the arthropod invasion of land. Fossils and Strata 51, 136–140.
Clack, J.A., 2009. The fin to limb transition: New data, interpretations, and hypotheses from paleontology and developmental biology. Annual Review of Earth and Planetary Sciences 37, 163–179.
Clack, J.A., Finney, S.M., 2005. *Pederpes finneyae*, an articulated tetrapod from the Tournaisian of western Scotland. Journal of Systematic Palaeontology 2, 311–346.
Cooper, K.W., 1964. The first fossil tardigrade: *Beorn leggi* Cooper, from Cretaceous amber. Psyche 71, 41–48.
Dunlop, J.A., Anderson, L.I., Kerp, H., Hass, H., 2004. A harvestman (Arachnida: Opiliones) from the Early Devonian Rhynie cherts, Aberdeenshire, Scotland. Transactions of the Royal Society of Edinburgh, Earth Sciences 94, 341–354.
Dunlop, J.A., Scholtz, G., Selden, P.A., 2013. Water-to-land transitions. In: Minelli, A., Boxshall, G., Fusco, G. (Eds.), Arthropod Biology and Evolution. Berlin & Heidelberg: Springer, pp. 417–439.
Edwards, D., Selden, P.A., Richardson, J., 1995. Coprolites as evidence for plant–animal interaction in Siluro-Devonian terrestrial ecosystems. Nature 377, 329–331.
Engel, M.S., Grimaldi, D.A., 2004. New light shed on the oldest insect. Nature 427, 627–630.
Fayers, S.R., Trewin, N.H., 2005. A hexapod from the early Devonian Windyfield chert, Rhynie, Scotland. Palaeontology 48, 1117–1130.
Garrouste, R., Clément, G., Nel, P., *et al.*, 2012. A complete insect from the Late Devonian period. Nature 488, 82–85.
Hirst, S., Maulik, S., 1926. On some arthropod remains from the Rhynie chert (Old Red Sandstone). Geological Magazine 63, 69–71.
Hörnschemeyer, T.T., Haug, J.T.J., Bethoux, O.O., *et al.*, 2013. Is *Strudiella* a Devonian insect? Nature 494, E3–E5.
Jeram, A.J., Selden, P.A., Edwards, D., 1990. Land animals in the Silurian: Arachnids and Myriapods from Shropshire, England. Science 250, 658–661.
Jönsson, K.I., Rabbow, E., Schill, R.O., Harms-Ringdahl, M., Rettberg, P., 2008. Tardigrades survive exposure to space in low earth orbit. Current Biology 18, R729–R731.
Labandeira, C.C., Beall, B.S., Hueber, F.M., 1988. Early insect diversification: Evidence from a Lower Devonian bristletail from Quebec. Science 242, 913–916.
Laurie, M., 2012. XIX. – On a Silurian scorpion and some additional eurypterid remains from the Pentland Hills. Transactions of the Royal Society of Edinburgh 39, 575–590.
Little, C., 1983. The Colonisation of Land: Origins and Adaptations of Terrestrial Animals. Cambridge: Cambridge University Press.
MacNaughton, R.B., Cole, J.M., Dalrymple, R.W., *et al.*, 2002. First steps on land: Arthropod trackways in Cambrian–Ordovician eolian sandstone, southeastern Ontario, Canada. Geology 30, 391–394.
Müller, K.J., Walossek, D., Zakharov, A., 1995. "Orsten" type phosphatized soft-integument preservation and a new record from the Middle Cambrian Kuonamka Formation in Siberia. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 197, 101–118.
Rota-Stabelli, O., Daley, A.C., Pisani, D., 2013. Molecular timetrees reveal a cambrian colonization of land and a new scenario for ecdysozoan evolution. Current Biology 23, 392–398.
Scourfield, D.J., 1940. The oldest known fossil insect (*Rhyniella praecursor* Hirst & Maulik)—further details from additional specimens. Proceedings of the Linnean Society of London 152, 113–131.
Selden, P.A., Shear, W.A., 2008. Fossil evidence for the origin of spider spinnerets, and a proposed arachnid order. Proceedings of the National Academy of Sciences of the United States of America 105, 20781–20785.
Selden, P.A., Shear, W.A., Bonamo, P.M., 1991. A spider and other arachnids from the Devonian of New York, and reinterpretations of Devonian Araneae. Palaeontology 34, 241–281.
Shear, W.A., Bonamo, P.M., 1988. Devonobiomorpha, a new order of Centipeds (Chilopoda) from the Middle Devonian of Gilboa, New York State, USA, and the phylogeny of centiped orders. American Museum Novitates 2927, 1–30.
Shear, W.A., Jeram, A.J., Selden, P., 1998. Centiped legs (Arthropoda, Chilopoda, Scutigeromorpha) from the Silurian and Devonian of Britain and the Devonian of North America. American Museum Novitates 3231, 1–16.
Shear, W.A., Selden, P.A., 1995. *Eoarthropleura* (Arthropoda, Arthropleurida) from the Silurian of Britain and the devonian of North America. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 196, 347–375.
Shear, W.A., Selden, P.A., 2001. Rustling in the undergrowth: Animals in early terrestrial ecosystems. In: Gensel, P.G., Edwards, D. (Eds.), Plants Invade the Land: Evolutionary and Environmental Perspectives. New York: Columbia University Press, pp. 29–51.
Shear, W.A., Selden, P.A., Rolfe, W.D.I., Bonamo, P.M., Grierson, J.D., 1987. New terrestrial arachnids from the Devonian of Gilboa, New York (Arachnida, Trigonotarbida). American Museum Novitates 2901, 1–74.
Wilson, H.M., Anderson, L.I., 2004. Morphology and taxonomy of Paleozoic millipedes (Diplopoda: Chilognatha: Archipolypoda). from Scotland. Journal of Paleontology 78, 169–184.