Terrestrialisation (Precambrian–Devonian)

Advanced article

Article Contents

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Based in part on the previous versions of this eLS article 'Terrestrialisation (Precambrian–Devonian)' (2001, 2005, 2012).

The emergence of plants and animals from the sea on to land – terrestrialisation – was one of the major advances in the history of life on Earth. Evidence for early colonisation is poor, but the fossil record reveals that by mid-Palaeozoic times complex terrestrial ecosystems had become established. The first phase of land colonisation by organisms may have started in the Precambrian, some 2.6 Ga ago, in the form of microbially bound alluvial sands. The second phase began in earnest in Ordovician times, when early land plants, in the form of bryophyte-like spores, first appeared in the fossil record. By the Silurian, true vascular plants were present, and these green swards were inhabited by mainly detritivorous and predatory arthropods. By the late Devonian, true forests had developed, but it was not until the latest Palaeozoic that modern-type terrestrial ecosystems, with abundant herbivores in the food chain, appeared.

Introduction

Terrestrialisation – the colonisation 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 its origin and the development of multicellularity. As an event, however, it lacks the drama of the sudden appearance of terrestrial life in the fossil record that once seemed apparent but has been shown to be illusory. Instead, it is more likely that the terrestrial habitat was colonised by increasingly higher forms of life as the environment became more convivial over many millions of years. This was, for the most part, due to amelioration of the land habitat by the biota itself. **See also**: Fossil Record

In order for plants and animals living in the sea to colonise 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. As a medium for biochemical reactions, for the transport of cell solutes and for the maintenance of cell turgor, water is essential to life. It is the variability of its availability on land that is problematic for terrestrial life – inundation can be as fatal as dehydration for a land organism. Four groups of land organisms can be defined based on their management of water availability.

1. Aquatic organisms avoid the problem by living in interstitial water in soils; these include microscopic nematodes, protozoans and unicellular algae.
2. Cryptic forms differ from those in the group above in being macroscopic but similarly inhabit environments of constantly high humidity, such as soil and tropical forest litter. Included in this group are some algae and bryophytes, gametophytes of homosporous pteridophytes, earthworms, leeches, flatworms, isopods, slugs, insect larvae, some amphibians and myriapods.
3. Poikilohydric (desiccation-tolerant) organisms require high humidity to function but can tolerate desiccation by drying out and rehydrating when conditions become favourable again. Cryptobiotic Cyanobacteria, some bryophytes and algae, rotifers and mites occur in this group; also included are some vascular plants that are primary colonisers of unstable environments as well as organisms with desiccation-tolerant resting stages such as the seeds of vascular plants and the eggs of fairy shrimps.
4. 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 tracheophytes, tetrapods, insects, arachnids and some isopods and molluscs.

Another important barrier to terrestrialisation is the necessity to change from obtaining oxygen from water to breathing air. Oxygen is more abundant in air ($8.65\,\mathrm{mol\,m^{-3}}$) than in water ($0.262\,\mathrm{mol\,m^{-3}}$), but its availability to organisms depends on other factors, such as the rate of diffusion and the efficiency of oxygen-binding molecules in the blood. Many littoral plants and animals can survive out of water for periods, but organisms that spend their lives out of water require new organs of respiration: lungs rather than gills. The problem is compounded by the fact that the carbon dioxide and oxygen molecules are larger than water molecules, thus membranes for gas exchange leak water. This means that respiratory surfaces need to be internalised, and valves are required to regulate air flow – stomata in plants, spiracles in insects and so on.

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Degrees of terrestrial adaptation can be determined in living animals and plants from their anatomy and physiology, but for the sequence and timing of events during the major phase of terrestrialisation in the Middle Palaeozoic, the fossil record holds the only clues. Four phases of terrestrialisation were recognised by Edwards and Selden (1993), based mainly on the plant fossil record. Exceptional examples of invertebrate animal fossils appear in the later phases. Complex terrestrial biotas, based mainly on arthropods and plants, had developed by the Devonian period; colonisations by vertebrates, molluscs and crustaceans followed these early pioneers much later, into already well-established ecosystems. **See also**: **Adaptation and Natural Selection: Overview**; **Fossil Record: Quality**

Precambrian Land Organisms

The first seven-eighths of the history of the Earth is called the Precambrian. The early Precambrian was completely inhospitable to life, but by about 4 Ma BP there is evidence in the form of metamorphosed sedimentary rocks of erosion by free water. Land surfaces must have been barren and desertlike, with lethally high ultraviolet (UV) radiation. There was less oxygen than in the present atmosphere, but levels increased throughout the Precambrian as a result of the activity of photosynthetic organisms.

Fossil evidence of terrestrial life in this first phase of terrestrialisation is poor. During the Proterozoic, it is likely that microbial crusts were present on the land surface. Evidence for this are the widespread occurrence of Precambrian Cyanobacteria in better preserved, nonterrestrial environments; the fact that Cyanobacteria are common on stressed land surfaces today (e.g. around hot springs, deserts and salt flats) and the localised development of carbon-rich layers in Precambrian palaeosols that may represent the remains of prokaryotic mats (Labandeira, 2005; Beraldi-Campesi, 2013; Wellman and Strother, 2015).

Precambrian Metazoa are known only from the marine environment, and there is no evidence of higher plants in the fossil record until much later, in the Palaeozoic Era. Nevertheless, probable bacteria and the archaeans colonisers would have been extremely important in developing soil profiles and contributing towards a terrestrial environment that was amenable to later colonisation by higher plants and animals. **See also**: **Photosynthesis and Respiration in Cyanobacteria**

Land Plants

Shear (1991) noted the important difference between an ecological concept of land plants (Embryophyta and also lichenised fungi) and the true vascular plants (Tracheophyta) that have a water-conducting system which enables them to grow erect from the substrate. However, there is evidence in the form of carbonised tubes of possibly vascular anatomy in nontracheophyte embryophytes of unknown affinity. The idea that terrestrialisation was a single evolutionary advance in plants, wherein all the anatomical adaptations to land life appeared simultaneously in the first tracheophyte, is disappearing as a range of separate adaptations are discovered among a variety of primitive embryophytes (Cascales-Miñana *et al*., 2019).

In the second phase of land colonisation, extending from the Ordovician to the Lower Devonian, fossil evidence consists of sporopollenin-impregnated, desiccation-resistant dispersal or resting forms (sporomorphs) and plant cuticles that are presumably adapted to land life. These early forms cannot be allied with certainty to living plant groups, though some may be bryophytes and others seem to have had a thalloid form for part of their life cycle (Wellman, 2010). Such plants may have been adapted to widely fluctuating water supply and temperature: desiccation-tolerant forms, able to dry out and recover.

In the third phase, from the Lower Silurian (Llandovery) to Lower Devonian (Lochkovian), the first miospores (monads with well-defined trilete marks) are encountered. Later, these spores became sculptured, and many taxa are recognised, but they can only exceptionally be linked to vegetative taxa. It was also at this time that the rhyniophytoids – simple, smooth and upright stems branching isotomously and bearing axial globular or discoidal sporangia – originated and later proliferated. Internal anatomy of rhyniophytoids is poorly known, but tracheids have been demonstrated in *Cooksonia* (**Figure 1a**). The landscape was now taking on the appearance of a short, green turf, and presumably, animal–plant relationships were being established in these early terrestrial ecosystems. **See also**: **Coevolution**

The fourth phase can be recognised as beginning in the Late Silurian (Late Ludlow) of Australia or Early Devonian (Early Lochkovian) of Laurasia and finishing – though the end is less clear – in the Late Devonian (Frasnian). This phase was the final pioneering stage during which the major tracheophyte groups Zosterophyllophytina and Drepanophycopsida appeared, all land plants diversified (**Figure 1**) and the first body fossil evidence for land animals is found. Both of these tracheophyte groups became extinct at the end of the phase, but others persisted. Competition among new plant groups developed, and the upward struggle culminated in the tree form being established by the Late Devonian. Stratification in plant communities occurred at the same time. Heterospory and the elimination of the free gametophyte led to the seed habit by the end of the Devonian period. **See also**: **Gametophyte and Sporophyte**

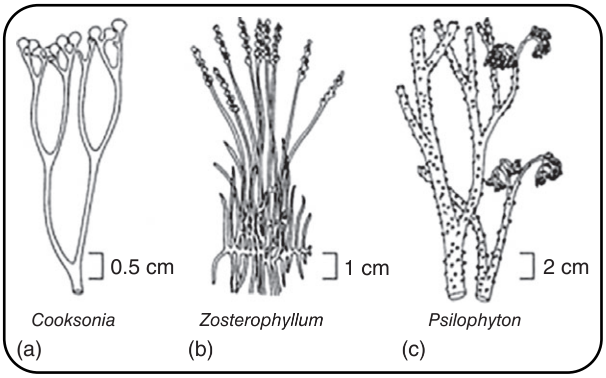

Figure 1 Reconstructions of early land plants. (a) *Cooksonia* from the Late Silurian. (b) *Zosterophyllum* from the Lower Devonian. (c) *Psilophyton* from the Lower Devonian. Note the increase in stature and complexity through time.

Silurian and Devonian Arthropod Records

Some recent research using molecular dating methods have placed the terrestrialisation of arthropods much further back in time than suggested by the fossil record. For example, the analysis by Lozano-Fernandez *et al*. (2020) placed arachnids emerging onto land in late Cambrian–early Ordovician times, while Noah *et al*. (2020) recognised numerous scenarios of multiple invasions (and returns) of the land from the sea by chelicerates.

There is no fossil evidence for metazoan animals on land during phases 1 and 2, but it is likely that animal cryptobiosis had developed in conjunction with the bryophytic swards of phase 2. Pioneer animals such as tardigrades are well adapted for life in such unstable environments. These microscopic water bears thrive in moist habitats which periodically dry up. When this occurs, they form tuns that, like seeds, provide both protection during the dry period and a dispersal mechanism. Indeed, the survival potential of tardigrades is legendary (Jönsson *et al*., 2008; Tsujimoto *et al*., 2016). The tuns of littoral tardigrades would no doubt have blown inland and rehydrated in moist habitats during this phase.

In phase 3, the only evidence of metazoan life on land comes from trace fossils. Arthropod trackways formed subaerially are known from a number of localities, but these were primarily aquatic animals, such as eurypterids, making brief excursions across mudflats and sand bars. In uppermost Ordovician rocks, palaeosols containing burrows were cited as evidence for vermiform animals, possibly millipedes (diplopods), apparently in terrestrial substrates (Retallack and Feakes, 1987). However, these have since been shown to have formed in a marginal marine environment. Similarly, trackways in the upper Ordovician Borrowdale Volcanic Group were interpreted as the result of millipede-like animals walking on land or, rather more likely, emerging from water and dying on the shoreline of the sea or a lake, hence not truly terrestrial animals (Shillito and Davies, 2018; Briggs *et al*., 2019). The oldest known terrestrial metazoan trace fossils are Silurian in age (Davies *et al*., 2010).

Evidence of land animal body fossils is restricted to phase 4 (Table **1**). A record of an Ordovician oribatid mite (Bernini *et al*., 2002) has not been generally accepted (Schaefer *et al*.,

Table 1 Stratigraphic chart showing some early terrestrial biotas with both plant and animal remains of Silurian and Devonian age

Period (Ma BP)	Epoch	Localities with terrestrial biota
Devonian		
359		
	Fammenian	Strud, Belgium: plants, eurypterids, various crustaceans, *Strudiella*, fish, tetrapods; floodplain and temporary pools
372		
	Frasnian	
383		
	Givetian	Gilboa, New York: lycopsids, progymnospermopsids; uraraneids, trigonotarbids, mites, chilopods, arthropleurids, scorpions, eurypterids, hexapods; deltaic mudstone
388		
	Eifelian	
393		
	Emsian	Alken-an-der-Mosel, Germany: algae, lycopsids, rhyniopsids; eurypterids, xiphosurans, crustaceans, molluscs, fish, trigonotarbids, arthropleurids; brackish lagoon Gaspé and New Brunswick, Canada: lycopsids, rhyniopsids, trimerophytes, zosterophylls, lycopsids; scorpions, arthropleurids, diplopods; fluvial swamp
408		
	Pragian	Rhynie, Scotland: cyanobacteria; fungi, nematophytes; algae, charophytes, zosterophyll, rhyniopsids, *Asteroxylon*; collembolans, trigonotarbids, mites, opilionids, crustaceans, chilopods, euthycarcinoids, *Rhyniognatha*; terrestrial hot spring
411		
	Lochkovian	Stonehaven, Scotland: plant fragments, crustaceans, diplopods, fish; braided streams
Silurian		
419		
	Pridoli	Ludford Lane, England: rhyniophytoids, *Cooksonia*, *Nematothallus*; trigonotarbids, chilopods, arthropleurids, euthycarcinoids, eurypterids, scorpions, restricted marine fauna; sub/intertidal lag deposit
423		
	Ludlow	Kerrera, Scotland: plant fragments, diplopods, eurypterids, fish; temporary playa lake
427		
	Wenlock	Hagshaw Hills, Scotland: eurypterids, diplopod, fish; freshwater lake
433		

2010). All of the putative records of the earliest land animal over the past few years have come from the Midland Valley of Scotland. At Stonehaven, millipedes with spiracles (openings of air-breathing organs) were reported in sedimentary rocks dating to the middle Silurian Period (*c*. 427 Ma) (Wilson and Anderson, 2004). However, more recent zircon datings of these strata have shown them to be lowermost Devonian (*c*. 414 Ma) in age (Suarez *et al*., 2017; Selden, 2019). The oldest land animal status then passed to *Casiogrammus ichthyeros* (Wilson, 2005) from the Hagshaw Hills (middle Silurian, *c*. 430–433 Ma) (Selden, 2019). However, this fossil consists simply of numerous body segments, lacking other features that would identify it as a millipede or a land animal. Further dating studies on the Scottish terrestrial deposits (Brookfield *et al*., 2020) showed that millipedes from 425 Ma rocks on the island of Kerrera are more definitively the oldest land animals at present. They occur together with fish, eurypterids and plant remains in sediments suggestive of temporary lakes (Trewin *et al*., 2012).

Nearly as old as the Kerrera millipedes is a biota from the earliest Pridoli Epoch (*c*. 423 Ma: Catlos *et al*., 2020) at the site known as Ludford Lane (Jeram *et al*., 1990). In sediments representing flood deposits apparently derived from erosion of salt marshes, fossil trigonotarbid arachnids and myriapods occur together with land plants and a restricted marine fauna. Better preserved are the trigonotarbids, mites (**Figure 2**), Collembola, crustaceans and myriapods from the Lower Devonian Rhynie chert of Scotland, preserved in terrestrial hot-spring deposits. The younger Alken-an-der-Mosel site in Germany has produced terrestrial plants and trigonotarbids together with a brackish marine fauna. The oldest land animals in North America come from late Middle Devonian strata of Gilboa, New York. This material, like that of Ludford Lane, was etched from shales using hydrofluoric acid and includes trigonotarbids, uraraneids, mites, chilopods, arthropleurids and possible insects. **See also**: **Rhynie Chert**

Thus, the earliest land animal body fossils belong to diplopods, scutigeromorph chilopods and arachnids. Trigonotarbids are extinct relatives of spiders and, like them, were predators. Enigmatic arthropod fragments from Gilboa, formerly described as trigonotarbids, then as spiders, have since been shown to belong to a group of proto-spiders called uraraneids (Selden *et al*., 2008). Trigonotarbids (**Figure 3**) are found in nearly all Devonian terrestrial biotas. Scorpions may have been aquatic at this time, though the evidence is disputed (Howard *et al*., 2019). If so, aquatic and terrestrial scorpions probably existed together until the Carboniferous. Aquatic scorpions and the related eurypterids, both predatory animals, may have made excursions onto land (Lamsdell *et al*., 2020). The oldest fossil harvestman (Opiliones) occurs at Rhynie; it appears to belong to the modern group which includes the familiar daddy long-legs (Dunlop *et al*., 2004). Two groups of mite fossils occur at Rhynie and Gilboa: oribatids, which are detritivores or fungivores in modern ecosystems, and alicorhagiids, which are known to prey on nematodes.

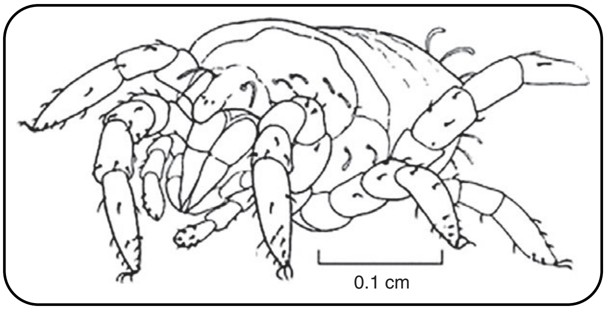

Figure 2 The mite *Protacarus crani* from the Rhynie chert. Left lateral view of holotype specimen. Hirst, S. (1923). XLVI.—On some Arachnid remains from the Old Red Sandstone (Rhynie Chert Bed, Aberdeenshire). Annals and Magazine of Natural History, 12 (70), 455–474.

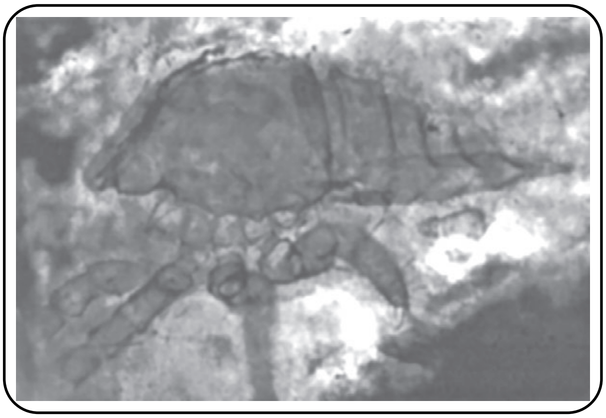

Figure 3 The trigonotarbid *Palaeocharinus* sp. in Rhynie chert. Left lateral view of approximate sagittal section, anterior to left. This specimen is <1 mm long; Rhynie trigonotarbids range up to 5 mm in length.

Scutigeromorph chilopods are long-legged, fast-running predators common in warm parts of the world today; diplopods are primarily detritivores. Extinct orders of myriapods also occur in these early terrestrial biotas: Devonobiomorpha (chilopods) at Gilboa, Arthropleurida (diplopods) at most sites and the enigmatic euthycarcinoids from Rhynie, the Upper Devonian of Belgium and elsewhere (their trackways are known from Cambrian strata), which are now considered amphibious stem-group myriapods (Gueriau *et al*., 2020).

Modern terrestrial ecosystems are dominated by insects and their relatives (Hexapoda). These are represented in the Devonian only by Collembola (springtails) in the Rhynie Chert. Collembola are detritivores/fungivores that occur in modern soils in enormous numbers. The jaw apparatus of *Rhyniognatha* from Rhynie, considered to represent the oldest true insect by Engel and Grimaldi (2004), more likely belongs to a centipede (Haug and Haug, 2017). A supposed insect fossil, *Gaspea*, from the Middle Devonian of Gaspé, Canada, is most likely a modern contaminant (Jeram *et al*., 1990). Similarly, a supposed complete insect from the Upper Devonian of Strud, Belgium (Garrouste *et al*., 2012; Gueriau *et al*., 2018), has been debunked (Hörnschemeyer *et al*., 2013; Haug and Haug, 2017). Pieces of cuticles closely resembling that of modern primitive hexapods have been found at Ludford Lane and Gilboa.

Evidence of plant–animal interaction in early terrestrial ecosystems is provided by coprolites (fossil faeces). Droppings represent the undigested parts of an animal's diet. Those described from Siluro-Devonian ecosystems show a preponderance of detritivore and fungivore producers, mainly millipedes and collembolans (Habgood *et al*., 2004; Edwards *et al*., 1995, 2020), and commonly include a large number of undigested spores.

The earliest terrestrial animals were predominantly carnivores; there were some detritivores and fungivores, but modern-style herbivores were absent. There is some evidence of animals piercing plant cells and extracting fluids, but no animals were chewing plant leaves or stems whole. Therefore, such plant organs, upon death, would be degraded by fungi and bacteria on the ground. This semidecomposed matter would have formed the food of detritivores. Evidence from coprolites and body fossils points towards a food chain based on detritivory, which is common in soils today. Modern herbivory involves symbiotic bacteria and fungi within the animals' guts that most likely evolved within detritivorous ancestors. Thus, the earliest terrestrial food chains were detritivore based. There is little evidence for modern herbivory until at least Late Carboniferous times. Aquatic tetrapods are known from the Late Devonian, but the earliest unequivocal terrestrial vertebrates are Carboniferous in age. Herbivorous tetrapods first appeared in the Late Carboniferous, but it was not until Late Permian times that a modern-type food chain had been assembled. Taking the evidence as presented, trophic relationships in early terrestrial ecosystems were radically different from those in today's more herbivore-influenced world.

Glossary

Cryptobiosis Ability of an organism to form a resting stage in order to survive unfavourable (e.g. drought) conditions.

Detritivore Animal which derives nutrition from eating plant and animal detritus, for example most millipedes (Diplopoda).

Embryophyta Taxonomic group of land plants, including bryophytes (mosses and lichens) and vascular plants (Tracheophyta).

Fungivore Animal which derives nutrition from eating fungi, for example millipedes (Diplopoda), many insect larvae and slugs.

Homoiohydric Desiccation resistance. Descriptive of organisms which maintain internal hydration, even in drought, by the use of waterproof cuticles and so on.

Littoral The seashore; living on the seashore.

Myriapoda Arthropods with many, similar segments and legs; including millipedes (Diplopoda), centipedes (Chilopoda) and arthropleurids.

Palaeosol Fossilised soil.

Poikilohydric Desiccation tolerance. Descriptive of organisms which require high humidity but tolerate desiccation and rehydrate when favourable conditions resume.

Sporomorph Plant spore or spore-like object.

Tracheophyta Land plants which have a vascular system for conducting fluids and hence are able to reach greater heights above the substrate than more primitive lands plants.

Trilete mark Triradiate feature on a plant spore through which germination occurs.

Vermiform Worm shaped.

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