Terrestrialization (Precambrian–Devonian)

Advanced article

Article Contents

Paul A Selden, *University of Manchester, Manchester, UK*

The emergence of plants and animals from the sea on to land – terrestrialization – was one of the major advances in the history of life on Earth. Evidence for early colonization is poor, but the fossil record reveals that by mid-Palaeozoic times complex terrestrial ecosystems had become established.

doi: 10.1038/npg.els.0004145

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 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 more recently been shown to be illusory. Instead, it is more likely that the terrestrial habitat was colonized 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 – a fine demonstration of the Gaia hypothesis. **See also**: Fossil record

In order for plants and animals living in the sea 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. 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 colonizers 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 terrestrialization 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 internalized and valves are required to regulate air flow – stomata in plants, spiracles in insects, etc.

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 terrestrialization in the Middle Palaeozoic, the fossil record holds the only clues. Four phases of terrestrialization were recognized 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; colonizations 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 4000 Ma BP there is evidence in the form of metamorphosed sedimentary rocks of erosion by free water. Land surfaces must have been barren and desert-like, 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 the Precambrian is lacking, but Retallack (1990) has summarized ideas on the origin of life in clay soils. During the later Precambrian, it is likely that cyanobacterial crusts covered the land surface. Evidence for this is:

1. the widespread occurrence of Precambrian Cyanobacteria in better preserved, nonterrestrial environments;
2. the fact that Cyanobacteria are common on stressed land surfaces today (e.g. around hot springs, deserts and salt flats); and
3. the localized development of carbon-rich layers in Precambrian palaeosols that may represent the remains of prokaryotic mats.

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. Nevertheless, probable prokaryotic colonizers would have been extremely important in developing soil profiles and contributing towards a terrestrial environment that was amenable to later colonization by higher plants and animals. **See also**: Photosynthesis and respiration in cyanobacteria

Vascular Plants

Shear (1991) noted the important difference between an ecological concept of land plants and the vascular plants, a systematic unit known as Tracheophyta. Furthermore, there is evidence in the form of carbonized tubes of possibly vascular anatomy in non-tracheophyte plants of unknown affinity. The idea that terrestrialization 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 pretracheophytes.

In the second phase of land colonization, 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. 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 recognized, but they can only exceptionally be linked to vegetative taxa. It was also at this time that the rhyniophytoids – simple, smooth, 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 recognized 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

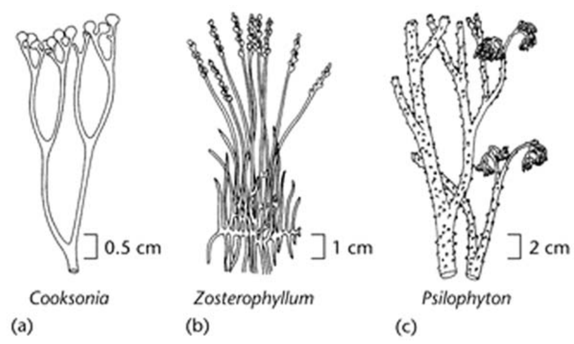

Figure 1 Reconstructions of early land plants. (a) *Cooksonia* from the Late Silurian; (b) *Zosterophyllum* from the Lower Devonian; (c) *Psilophyton* from the Lower Devonian. Note the increase in stature and complexity through time.

Silurian and Devonian Arthropod Records

There is no evidence for 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. 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 *Skolithos* burrows are evidence for vermiform animals, possibly millipedes (diplopods), apparently in terrestrial substrates. It is possible, however, that these formed subaqueously and the substrate later emerged and developed a soil.

Evidence of land animal body fossils is restricted to phase 4 (**Table 1**). The oldest land animals come from the Silurian Period (Wenlock–Ludlow Epochs) of Stonehaven, Scotland (Wilson and Anderson, 2004), and are millipedes with spiracles – openings of air-breathing organs (The record of an Ordovician orbited mite (Bernini *et al.*, 2002) is considered doubtful). Nearly as old is a biota from the earliest Pridoli Epoch at the site known as Ludford Lane (Jeram *et al.*, 1990). In sediments representing flood

Table 1 Stratigraphic chart showing the earliest terrestrial biotas, of Late Silurian to Middle Devonian age

Period (Ma BP)	Epoch or stage	Silurian and Devonian localities with terrestrial biota
Devonian		
354		
	Fammenian	
364		
	Frasnian	
370		
	Givetian	Gilboa, New York: lycopsids, progymnospermopsids; spiders, trigonotarbids, mites, chilopods, arthropleurids, scorpions, eurypterids, hexapods?; deltaic mudstone
380		
	Eifelian	
391		
	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, possible hexapods; fluvial swamp
400		
	Pragian	Rhynie, Scotland: algae, zosterophyll, rhyniopsids, *Asteroxylon*; collembolans, trigonotarbids, mites, crustaceans, chilopods, eurypterid?; terrestrial hot-spring
412		
	Lochkovian	
Silurian		
417		
	Pridoli	Ludford Lane, England: rhyniophytoids, *Cooksonia*, *Nematothallus*; trigonotarbids, chilopods, arthropleurids, euthycarcinoids, eurypterids, scorpions, restricted marine fauna; sub/intertidal lag deposit
419		
	Ludlow	
423		Stonehaven, Scotland: diplopods; braided streams
	Wenlock	
428		

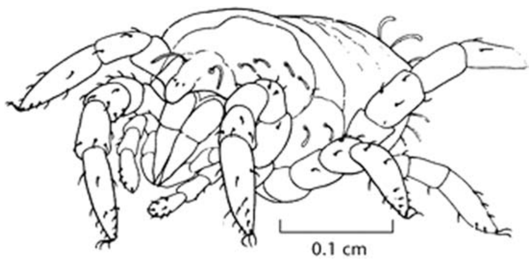

Figure 2 The mite *Protacarus crani* from the Rhynie chert. Left lateral view of holotype specimen. Reproduced from Hirst S (1923) On some arachnid remains from the Old Red Sandstone (Rynie Chert Bed, Aberdeenshire). *Annals and Magazine of Natural History* **12** : 455–474.

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 Lochkovian 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, spiders, mites, chilopods, arthropleurids and possible insects. **See also**: Rhynie chert

Thus, the earliest land animal body fossils belong to diplopods, scutigerimorph chilopods and trigonotarbid arachnids. Trigonotarbids are extinct relatives of spiders and, like them, were predators. Trigonotarbids (**Figure 3**) are found in nearly all Devonian terrestrial biotas, but true spiders did not appear until the Late Devonian at Gilboa. Scorpions were mostly aquatic at this time; their terrestrialization started in the Middle Devonian and aquatic and terrestrial scorpions existed together until the Carboniferous. Aquatic scorpions and the related eurypterids, both predatory animals, may have made excursions on to land. 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.

Scutigerimorph 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 at Gilboa and Arthropleurida at all sites. The former are predators and the latter detritivores.

Modern terrestrial ecosystems are dominated by insects and their relatives (Hexapoda). These are represented in the Devonian only by Collembola (springtails) from Rhynie. Collembola are detritivores/fungivores that occur in modern soils in enormous numbers. The evidence for Devonian true insects is equivocal. The supposed earliest insect fossil, *Gaspea*, from the Middle Devonian of Gaspé, Canada, may be a modern contaminant (Jeram *et al.*, 1990), but pieces of cuticle closely resembling that of modern primitive hexapods have been found at Ludford Lane and Gilboa. The earliest known unequivocal insect fossil comes from the Lower Carboniferous of Germany.

The earliest terrestrial animals were predominantly carnivores; there were some detritivores, but herbivores were absent. The evidence points towards a food chain based on detritivory, which is common in soils today. Modern herbivory involves gut floras that presumably evolved within detritivorous ancestors. Thus, either these Devonian localities are sampling a soil ecosystem, or else the food chain was detritivore-based. There is little evidence for herbivory

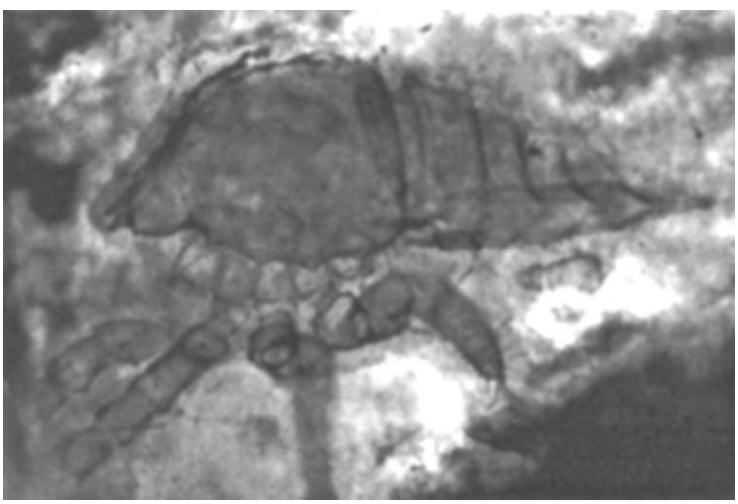

Figure 3 The trigonotarbid *Palaeocharinus* sp. in Rhynie chert. Left lateral view of approximate sagittal section, anterior to left. This specimen is < 1 mm long; Rhynie trigonotarbids range up to 5 mm in length.

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 herbivore-dominated world.

References

Bernini F, Carnevale G, Bagnoli G and Stonge S (2002) An Early Ordovician oribatid mite (Acari: Oribatida) from the island of Öland, Sweden. In: Bernini F, Nannelli R, Nuzzaci G and Lillo E de (eds) *Acarid Phylogeny and Evolution. Adaptation in Mites and Ticks*, pp. 45–47. Dordrecht, The Netherlands: Kluwer.

Edwards D and Selden PA (1993) The development of early terrestrial ecosystems. *Botanical Journal of Scotland* **46**: 337–366.

Jeram AJ, Selden PA and Edwards D (1990) Land animals in the Silurian: arachnids and myriapods from Shropshire, England. *Science Washington* **250**: 658–666.

Retallack GJ (1990) *Soils of the Past. An Introduction to Paleopedology* Boston, MA: Unwin Hyman.

Shear WA (1991) The early development of terrestrial ecosystems. *Nature* **351**: 283–289.

Wilson HM and Anderson LI (2004) Morphology and taxonomy of Paleozoic millipedes (Diplopoda: Chilognatha: Archipolypoda) from Scotland. *Journal of Paleontology* **78**: 169–184.

Further Reading

Beerbower R (1985) Early development of continental ecosystems. In: Tiffney BH (ed.) *Geological Factors and the Evolution of Plants*. New Haven, CT: Yale University Press.

Edwards D, Selden PA, Richardson JB and Axe L (1995) Coprolites as evidence for plant–animal interaction in Siluro–Devonian terrestrial ecosystems. *Nature* **377**: 329–331.

Selden PA and Edwards D (1989) Colonisation of the land. In: Allen KC and Briggs DEG (eds) *Evolution and the Fossil Record*, chap. 6, pp. 122–152. London: Belhaven.

Selden PA and Jeram AJ (1989) Palaeophysiology of terrestrialisation in the Chelicerata. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **80**: 303–310.

Selden PA and Nudds JR (2004) *Evolution of Fossil Ecosystems*. London: Manson Publishing.

Shear WA and Selden PA (2000) Rustling in the undergrowth: animals in early terrestrial ecosystems. In: Gensel PG and Edwards D (eds) *Plants Invade the Land: Evolutionary and Environmental Perspectives*. New York: Columbia University Press.

Shear WA, Selden PA, Rolfe WDI, Bonamo PM and Grierson JD (1987) New terrestrial arachnids from the Devonian of Gilboa, New York (Arachnida: Trigonotarbida). *American Museum Novitates* **2901**: 1–74.