

COLONISATION OF THE LAND

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THE PHYSICAL ENVIRONMENT IN THE EARLY PALAEOZOIC

The image of the colonisation of the land by plants as a spectacular event, when barren wastes suddenly became verdant triggered by a change in some extrinsic environmental factor, is fading. It derived from the appearance and rapid diversification of vascular plants, unequivocal land colonisers, and, almost simultaneously, the earliest terrestrial arthropods, in the late Silurian and early Devonian. The environmental stimulus usually cited hitherto was a reduction in ultraviolet (UV) radiation due to ozone production when oxygen levels increased. A growing amount of evidence suggests that terrestrialisation was a gradual process, occurring throughout the earliest Palaeozoic, possibly with origins in the Precambrian. As the atmosphere evolved, particularly with respect to partial pressure of oxygen (P_{O_2}), so land surfaces were modified as mats of microbes and thallophytes produced substrates more convivial for colonisation by larger plants (macrophytes) and animals (Holland 1984; Retallack 1985).

Thus to define the physical parameters of atmosphere and hydrosphere associated with the colonisation of land is to trace their history throughout the early Palaeozoic. Direct evidence is lacking. Considering the hydrosphere, analysis of fluid inclusions in evaporites suggests that the major constituent composition of seawater, including Na^+ and Cl^- , has changed little over the last 900 Myr. Values from rocks as old as Permian confirm this general observation, but Silurian results are less secure (Holland *et al.* 1986). Freshwater systems may have been depleted in minerals prior to the establishment of extensive terrestrial vegetation and associated chemical weathering, even allowing for retention of some minerals within organic

material in land plants (Holland 1984). Partial pressure of atmospheric CO_2 (P_{CO_2}) may have been higher than at present, while P_{O_2} would have been lower but may have increased markedly on the advent of terrestrial higher plants, a new source of photosynthetic oxygen production. The estimated minimum P_{O_2} value of about 10% of present atmospheric level (PAL) for the early Cambrian is based on the respiratory requirements of its diverse communities of aquatic metazoans, and it may well have reached 50% PAL towards the end of the Silurian. Both P_{O_2} and P_{CO_2} could have varied considerably, but Holland *et al.* (1986) argued that the 'continuity of animal life precludes wild fluctuations'. Based on putative P_{O_2} values, the density of ozone is unlikely to have increased significantly through the Palaeozoic; reduction in UV radiation was not a trigger for the appearance of the terrestrial higher plants.

Without extensive macrophyte cover, chemical and physical properties of terrestrial substrates would have been very different (Beerbower 1985). Carbon dioxide generated in decaying vegetable matter promotes the release of major mono- and divalent cations from silicates and carbonates, thereby enhancing chemical weathering; thus early substrates would have been nutrient-poor. Low availability of potassium is indicated by the preponderance of potassium feldspars in pre-Silurian sediments. Without organic matter in the soil, there would have been no bacterial nitrogen fixation. Combined nitrogen levels would have been low, and input limited to nitrogen dissolved in rainwater. Restricted chemical weathering would have resulted in low production of clay minerals with silts predominating.

In the absence of rooted plants as windbreaks and sediment binders, erosion would have been greater, and sandy, rocky soils with high permeability and low water retention developed. The absence of abundant soil, organic matter and clays would also have limited retention of essential ions. Lack of sediment binding would have affected the nature of stream systems: braided streams would have predominated over sinuous ones, resulting in a shortage of stable moist environments such as point bars. Early terrestrial environments would consequently have been nutrient-poor, physically unstable, and subject to violent fluctuations in temperature and water content (Beerbower 1985). Exceptions may have been lowland alluvial or lacustrine areas with fine-grained water- and nutrient-retentive soils. It is in such environments that the first land plants of any size may have become established and created suitable habitats for terrestrial animals.

PHYSIOLOGICAL CONSIDERATIONS

Water

Water is essential for life: virtually all biochemical reactions work in an aqueous medium, and water is necessary for the transport of solutes.

Water is also necessary for the maintenance of cell volumes which are vital for the internal cell architecture, ensuring correct functioning of biochemical pathways, and for the turgor which provides support in plants. On land, water loss is a particular problem because water-vapour pressure is much lower in air than in the aquatic medium. Since availability of water is highly variable on land, adaptations are required to maintain a continuous supply or to reduce loss during drought periods. Water must be available in some form in every terrestrial environment for life to exist there at all, although supply may vary from the highly unpredictable flash flood in the otherwise arid hot desert to the constant humidity of the tropical forest. Indeed, if terrestrial and aquatic habitats did not interdigitate then it seems unlikely that life could ever have made the sudden leap from sea to land (Little 1983, p. 2).

All organisms can be placed into two broad categories depending on their responses to fluctuations in available water. *Homoiohydric* forms maintain an internally hydrated environment and are thus immune from external changes. *Poikilohydric* forms have no such control: intolerant examples are killed on desiccation, but tolerant forms possess ecophysiological adaptations to withstand it. Most homoiohydric plants are desiccation-tolerant.

Living terrestrial organisms can be classified into four main groups on the basis of their water relations (Little 1983, p. 3):

1. *Aquatic organisms*. Microscopic soil animals (e.g. nematodes, ostracodes, protozoans) and plants (e.g. unicellular algae) which can only survive immersed in a film of water are, strictly speaking, aquatic rather than terrestrial, and are poikilohydric and desiccation-intolerant.
2. *Cryptic forms*. These inhabit soil, leaf litter and tropical forests where a constant high humidity is assured. They differ from the first group in that the majority are macroscopic. They are intolerant of desiccation and may use behavioural adaptations to prevent it. Among animals, examples are earthworms, leeches, flatworms, slugs, woodlice, insect larvae, burrowing amphibians, and some myriapods. Plants include algae, some bryophytes and, most importantly, the gametophytes of homosporous pteridophytes. Although some of the latter may be subterranean, most require light for photosynthesis and thus live on the surface.
3. *Poikilohydric organisms with desiccation tolerance*. These, too, require high humidity for activity, but withstand desiccation by ecophysiological adaptations. The cytoplasm of some has the capacity to dry out and then rehydrate to function normally (cryptobiosis: e.g. cyanobacteria, algae, mosses and liverworts, rotifers, mites); others aestivate during dry periods (e.g. land snails, lungfish). Plants in this category are common primary colonisers of unstable environments. In some extreme instances, desiccation tolerance is exhibited by resting stages such as the seeds of angiosperms or the eggs of fairy shrimps, the organisms themselves being opportunists, flourishing and completing their life histories under ephemeral favourable conditions.

4. *Homoiohydric organisms*. These are the true conquerors of the land. As well as occupying the environments already mentioned, they have invaded a great diversity of arid niches, and created new habitats themselves. They maintain an internally hydrated environment, and include most tracheophytes, reptiles, birds, mammals, insects, arachnids, and some isopods and snails.

Homoiohydry has been achieved in plants and animals by the use of waterproof cuticle covering all aerially exposed parts. In both plants and arthropods, long-chain lipids (waxes) in the cuticle form the main impermeable barrier (for review, see Hadley 1981), and the lowest H_2O permeability coefficients recorded are of the order of 10^{-5} m s^{-1} for plant cuticles and 10^{-6} m s^{-1} for arthropod cuticles (Raven 1985). Lipids also occur in the epidermis of terrestrial vertebrates, but their waterproofing effectiveness is probably low compared to the keratinised layers in these animals. The waxes may have evolved initially as a network of patches on the cuticle to repel external water in small arthropods which obtain oxygen from air by diffusion through the cuticle. A water-impermeable cuticle may also help in maintaining internal osmotic concentration where that of the animal differs from that of the environment, thus it may have already evolved in aquatic ancestors. In plants, too, patchy wax would favour CO_2 diffusion, while its water-repellant properties would prevent the development of a water-film barrier to diffusion. Cuticles may also have conferred some protection from harmful UV radiation and from attack by fungi (and arthropods?).

Arthropod epicuticle, which contains water-repellant lipids, is rarely preserved in fossils, but in scorpions the waterproofing seems to extend into the upper part of the exocuticle, termed the hyaline exocuticle. Evidence for this comes partly from *in vivo* experiments on scorpions which indicate that water loss is not greatly increased by removal of the epicuticle (Hadley and Quinlan 1987). Hyaline exocuticle is known only from scorpions, and possibly xiphosurans and eurypterids. The presumed lipids appear to enhance the preservation potential of scorpion exocuticle when that of other arthropods oxidizes, since fossil scorpion cuticle is abundant in non-marine horizons in the Carboniferous to the virtual exclusion of all other arthropod remains (Bartram *et al.* 1987).

Water balance and transport

Primary aquatic plants may have specialised organs for attachment, but not for water absorption. The latter must have evolved in response to terrestrialisation, and the earliest were probably hair-like unicellular outgrowths (rhizoids) on horizontal underground stems (rhizomes). Compared with an extensive root system, the volume of substrate exploited by rhizomes is low and such a system is relatively inefficient. Before development of extensive plant cover, the substrate itself would have been deficient in mineral nutrients, e.g. phosphorus, and so it has been argued that the transmigrant algae, or earliest vascular plants, could have survived only in the presence

of a symbiotic fungus in the absorbing system. Today, the roots of plants colonising nutrient-poor soils commonly possess such a fungus, termed a mycorrhiza. Hair-like fungal hyphae emanating from the roots greatly increase the volume of substrate exploited for minerals, while fungal metabolism produces phosphorus- and probably nitrogen-containing compounds which are subsequently absorbed by the higher plant. In addition, organic acids derived from the fungus enhance chemical weathering of the substrate.

Water-transport systems are known only in land plants and are best developed in homoiohydric forms. Flow of water is maintained by transpiration (evaporation from aerial surfaces), and the conducting cells, initially tracheids, have implosion-resistant modifications in the form of rings or helices formed from lignin. This polymer is unknown in algae, and may also have been involved in support in the early land colonisers. Only homoiohydric plants can achieve a height greater than 2 m in air, and this is made possible by additional structural tissues, a gas-exchange regulation system, and xylem, which is dead tissue with a specific conductance to water a million times greater than that of living parenchyma (Raven 1985). This greater burden of non-photosynthetic tissues (e.g. for absorption, conduction, support, and reproduction) in larger plants would have been supported by the greater photosynthetic yields possible on land. Higher O₂ concentrations would allow their growth and maintenance.

Water loss

Water loss in animals has been studied particularly closely in some arachnids, and especially desert-dwelling forms (for a review, see Little 1983, p. 109). It is not easy to obtain data recorded under comparable conditions for all arachnids, since water loss varies according to various factors, including air humidity, temperature, wind speed, and the activity and size of animal. The lowest rates of water loss, expressed as percentage of body weight per hour at close to 0% relative humidity, are found in desert living scorpions (0.032–0.091), ticks (0.004–0.033), and Solifugae (0.090) (Little 1983, Table 6.3). Because of the waterproofing of the cuticle in terrestrial arthropods, gas exchange occurs through specialised respiratory surfaces which are internalised to reduce water loss.

The major route of water loss in plants is via open stomata (see p. 134). Opening and closure is usually related to internal concentrations of CO₂, but under extreme water stress this control is overridden and the stomata close.

Water loss during excretion is solved in terrestrial animals by the production of insoluble waste. In general, relatively insoluble and non-toxic guanine or uric acid is excreted in preference to the widespread production of highly toxic and soluble ammonia or less toxic but soluble urea of aquatic ancestors.

Osmoregulation

Life originated in saltwater, and the body fluids of organisms contain solutes in aqueous solution. Osmosis is the movement of solvent from a dilute to a more concentrated solution across a semipermeable membrane (i.e. one that is impermeable to the solute). Osmosis is passive, and can be prevented by the application of hydrostatic pressure. Thus the difference in solution concentration can be expressed as the pressure required to prevent osmosis: osmotic pressure. Alternatively, the osmotic gradient which exists across a membrane can be visualised as a gradient in the potential for chemical activity. Water will pass passively from a dilute solution with high potential to a more concentrated solution with lower potential. Plant cell walls act against the resulting increase in volume so it is useful in botany to distinguish this counteracting pressure (wall or turgor potential) from the concentration gradient (solute or osmotic potential). Animal cell membranes offer little resistance to osmosis so the osmotic pressure referred to in this context is theoretical, and generally expressed as a concentration; osmotic concentration is a better description.

Osmotic concentration can be expressed in moles per litre (molarity), moles per kilogram (molality), osmoles (Osm) per litre (osmolarity), or osmoles (Osm) per kilogram (osmolality) (for details see Rankin and Davenport 1981), and osmotic potential in bars or pascals. The concern here is the difference in concentration between the environment (salt- or freshwater) and the body fluids. Solutions of the same osmotic concentration are iso-osmotic; if one solution has a greater osmotic concentration than another then the former is hyperosmotic and the latter hypo-osmotic. Isotonic, hypertonic, and hypotonic are almost equivalent terms used in botany.

Animals

The observation that animal body fluids resemble seawater in ionic composition, together with the fact that all animal phyla occur in the sea, yet several do not occur on land or in freshwater, provides strong evidence that all are primitively marine. The osmolarity of seawater is about 1000 mOsm l^{-1} . Radiation of animals into environments of greater osmolarity (hypersaline: 1200–2300 mOsm l^{-1} ; brines: above 2300 mOsm l^{-1}) or lower osmolarity (brackish: 15–900 mOsm l^{-1} ; fresh below 15 mOsm l^{-1}) required active mechanisms for the regulation of the osmotic concentration of their body fluids (osmoregulation), or changes in metabolism to tolerate low internal osmolarity. Accordingly, the present osmotic concentration of terrestrial animals can give clues to the routes taken onto land. Crustaceans have been most intensively studied because they occur in a wide range of salinities and habitats (for a review, see Little 1983).

Most marine crustaceans are osmoconformers, that is, their haemolymph osmotic concentration is essentially the same as that of seawater. Among the vertebrates, only the hagfishes are osmoconformers. The

remaining marine fishes, and a few branchiopod crustaceans, are osmoregulators, maintaining their body fluids at concentrations well below that of seawater. Decapod crustaceans living in brackish estuaries hyporegulate or hyperregulate weakly, according to the external concentration. Shore-living crustaceans face particular problems: salinities can vary from strongly hypersaline in evaporating pools to fresh during rainstorms. Therefore, like estuarine forms, littoral crustaceans are usually weak osmoregulators but are euryhaline, i.e. tolerators of a wide range of salinities.

On the other hand, freshwater crustaceans hyperregulate, some strongly, maintaining osmotic concentrations close to that of seawater even in freshwater. Others have very weak haemolymph concentrations and their regulatory ability breaks down in brackish water; these can be termed stenohaline freshwater forms (as opposed to stenohaline marine osmoconformers), and include freshwater crayfish, amphipods, and most freshwater fish.

To summarise, freshwater-adapted animals are mainly regulators, whereas littoral and estuarine forms are tolerators of a wide range of environmental osmotic concentrations; in this respect, the tolerators are better adapted to the variable terrestrial environment.

Plants

Cell water relations in plants are fundamentally different to those in animals due to the presence of an enclosing, relatively inextensible, cellulose cell wall and an intracellular vacuole. The latter provides the opportunity for using toxic substances, such as Na^+ and Cl^- , as osmoregulatory material, isolating them from sites of general metabolic activity. When such a cell is placed in water or a hypotonic medium, water will tend to enter in response to the concentration of organic and inorganic solutes in the vacuole and cytoplasm (the osmotic potential of the cell), but as the cell increases in volume there is an opposing pressure from the cell wall (turgor potential). The resultant of these two forces is called the water potential of the cell, and at equilibrium is equivalent to the potential of the bathing medium. Such cells are said to be turgid, and this condition is essential for both metabolism and growth, and incidentally provides hydrostatic support. For most vascular plants the osmotic potential of cell contents (-7 to -20 bars), and hence the water potential, is lower than that of the soil solution, and water is taken in. Halophytes take up water because they have much lower cell osmotic potentials (see Table 6.1). Vascular plants, marine and some freshwater algae respond to changes in environmental water potential by maintaining turgor (turgor regulation) through osmotic adjustment, i.e. by removal or addition of solutes (Turner and Jones 1980). However, certain freshwater characean green algae, believed to be related to the group from which vascular plants evolved, maintain constant osmotic potential (osmolarity regulation), but not turgor. More needs to be known of the distribution of turgor and osmolarity regulation mechanisms in

Table 6.1. Ranges in approximate values of osmotic potential in ecologically different plants (from various sources).

<i>Plant group</i>	<i>Habitat</i>	<i>Osmotic potential (bars)</i>
angiosperms	freshwater	-2 to -16
	mesic meadows (herbs)	-5.5 to -20
	dry woodland (herbs)	-8 to -32
	deciduous woodland (trees)	-10 to -27
	desert	-15.5 to -40
	mangroves	-30 to -40
	saltmarshes } halophytes	-25 to -50
thalloid liverworts	moist	-5 to -15
mosses	mesic to dry	-15 to -25
	very dry	-30 to -60
algae	brown marine	-24 to -32
	green marine	-40
	green freshwater	-1.5 to -8
	diatoms freshwater	-4 to -8
cyanobacteria	freshwater	-5

pteridophytes and charophytes before hypotheses relating osmotic properties and routes on to land can be applied to plants (Raven 1985).

Temperature

Temperature, like many of the other physical properties discussed here, is far more variable and unpredictable on land than in water; in part this is because the rate of transfer of heat in air is much faster than in water. Cold temperatures tend to slow down biochemical reactions, and problems are caused by the correlation of temperature with other factors, such as water loss. Animal life in hot deserts is made possible through numerous behavioural modifications such as burrowing, nocturnal activity, and 'stilting' gaits over hot surfaces. Temperature control is also achieved in cold climates by the antifreeze properties of the haemolymph of some arthropods. Homoiothermy was made possible through the transition to land life and the greater availability of oxygen (see below) for metabolism.

Upper temperature survival limits (45–50°C) are similar in plants and animals but there are no active mechanisms for temperature control in

plants. Transpiration can reduce overheating but is of little use in xerophytes (plants adapted for life in very dry environments) which often have to endure high temperatures accompanied by water stress. Indeed, most individuals occasionally sun-scald or photosynthesise suboptimally in elevated temperatures. In contrast, certain plants can become physiologically acclimated to survive low temperature, the most important environmental factor which controls plant distribution. In some cases the cytoplasm itself may not freeze, even in temperatures as low as -40°C , but ice crystals form extracellularly. Most information comes from seed plants, particularly crops, and little is known of low-temperature responses in pteridophytes, particularly of the free-living sexual phase (gametophyte) in their life cycle. More data are available for mosses, which in the dehydrated state can survive major extremes of temperature (-100°C to $+100^{\circ}\text{C}$). They are not so tolerant when moist, except for certain boreal and arctic mosses, some of which can survive wetting by snow melt during the day and encasing in ice at -20°C overnight (Richardson 1981).

Gas exchange

There is more oxygen in air (8.65 mol m^{-3}) than in water (0.262 mol m^{-3}) and the potential flux of O_2 across a respiratory membrane is $0.17 \text{ mol m}^{-2} \text{ s}^{-1}$ in air and $4.2 \times 10^{-5} \text{ mol m}^{-2} \text{ s}^{-1}$ in water (Raven 1985). However, its availability to organisms depends on a variety of physical and biological factors; for example, since diffusion to one side of a membrane causes depletion at the other, there must be constant replenishment. For this reason, aquatic animals normally irrigate their gills mechanically by pumping water over them, by vibrating them, or by the use of ciliary currents. In air, simple diffusion is adequate for many invertebrates, but ventilation lungs occur particularly in the more active or homoiothermic animals. Other factors which govern the rate of diffusion of O_2 at the respiratory membrane are: the efficiency of oxygen-binding molecules; the circulatory system; and diffusion rates within the tissues. The effects of these factors can be measured as the percentage difference in oxygen content between the inhalent and exhalent respiratory currents, which is termed utilisation. Figures for utilisation exceed 50% (and may reach 80%) in fish and cephalopods, vary from around 30% to 75% in polychaetes and crustaceans, but are generally well below 10% in bivalves (Jones 1972). In higher vertebrates utilisation figures lie in the middle range, being around 22% in man and 31% in the pigeon. Finally, the metabolic costs of ventilation and irrigation must be considered. It is costly in energy to move large amounts of water, in contrast to the far less dense and less viscous air, yet irrigation is far more important for the supply of oxygen in aquatic animals than is ventilation in air-breathers. Particularly in small animals, the cost of supplying oxygen to muscles to improve irrigation must be carefully balanced against the improved oxygen uptake produced.

The advantages to be gained by breathing air are offset to some extent by the problem of water leakage across respiratory membranes, since the H_2O molecule is smaller than the O_2 molecule. To reduce water loss, air-breathing organs (lungs) are internalised, in contrast to gills, which are evaginations for gas exchange in water. The methods by which animals have made the transition from obtaining oxygen in water to air-breathing is the main concern here, a subject complicated by the great variety of oxygen-uptake methods employed by animals living in transitional environments.

Cutaneous gas exchange

Cutaneous respiration alone is sufficient for small, aquatic animals, but this method is also used in many other groups in conjunction with respiratory organs. Cutaneous respiration in air occurs in virtually all terrestrial animals to some degree, but is particularly well developed in the amphibians. Air-breathing amphibians utilise the skin as well as the lungs and mouth cavity for gas exchange. In some frogs, for example, the skin accounts for 30–50% of oxygen uptake, but 75–86% of carbon dioxide loss (Jones 1972). In this, as in other amphibians studied, temperature, and hence seasonality, affects the relative percentages of oxygen obtained by pulmonary, buccal, and cutaneous gas exchange. The importance of cutaneous respiration in amphibians is shown by observations reported in Jones (1972, p. 45) that some newt species utilise the skin for all oxygen uptake in air, but need to use lungs in addition when in water!

Gills

Gills are used for breathing air in many Crustacea and some amphibious fish. Terrestrial amphipods and isopods respire partly through the skin but mainly through the gills, and in isopods an additional pseudotracheal system has developed on the pleopods. The gills of air-breathing crabs remain moist in the branchial chamber, and in many species accessory lungs are also developed (see below). The gills of Palaeozoic aquatic scorpions may have been used for air-breathing since it is likely that the book-lungs of these arachnids have evolved directly from book-gills. Air-breathing by arthropod gills can be achieved simply by selective thickening of the cuticle to strengthen gill lamellae supports and the development of struts to keep the lamellae apart to allow air circulation. In fish such adaptations are not possible and additional mechanisms for oxygen uptake, or tolerance of anaerobic metabolism, are used by amphibious fish.

Lungs—the gastropods

True lungs occur in the gastropod molluscs, arthropods and vertebrates. In the gastropods, six families of prosobranchs and 30 of pulmonates have terrestrial representatives (see Little 1983, p. 34). In all these, the lung is formed from a highly vascularised part of the mantle cavity wall, and gills are reduced or lost. Secondary gills are developed in freshwater snails, and

are used together with cutaneous and pulmonary respiration in relative proportions dependent on habitat. In the terrestrial pulmonates these lungs are ventilated by air inhaled by muscular action of the mantle cavity, in contrast to the lungs of prosobranchs which rely on diffusion alone.

Crustacean lungs

The lungs of decapod crustaceans are, like those of the pulmonate molluscs, highly vascularised areas of the branchial chamber wall. There is a general trend among crabs to reduction in gill area and increase in lung area with increasing terrestrial habitat, but gills are never lost. Three respiratory strategies occur in air-breathing crabs (Greenaway 1984). In the first, appendage activity causes inhalation of air at the bases of the legs. This passes through the gills, which are stiffened to prevent collapse and facilitate drainage after emersion, and then into the lungs. In the second strategy, aerial respiration via lungs merely supplements the gills. In these crabs, water is held in the branchial chamber, and circulated by the scaphognathites (flattened branch of the maxilla) over hair patches where the water is reoxygenated before being passed back over the gills. The most highly terrestrialised 'land' crabs (e.g. *Holthuisiana*) adopt a third strategy. These crabs utilise a perfusion lung, inhaling and exhaling air by means of thoracic musculature; the gills are not used in aerial respiration.

Chelicerate respiration

Microscopic palpigrades and some mites, among the arachnids, have no specialised respiratory organs. Extant scorpions, uropygids, amblypygids, schizomids, and some spiders have only book-lungs. Most spiders, however, use book-lungs and tracheae (Little 1983, p. 114). Book-lungs are internal, lamellate structures in the opisthosoma, opening by a small pore, the stigma, and are homologous with the book-gills of aquatic chelicerates: *Limulus* and the aquatic Palaeozoic scorpions. It would appear that scorpions colonised land without the use of secondary lungs. The so-called 'gill' of the extinct eurypterids closely resembles crab lungs or isopod pseudotracheae and could not have functioned as a gill; true gills, presumed to have been present, are as yet undiscovered (Selden 1985). Sieve tracheae are developed from book-lungs and are similar to them with the exception that cylinders replace the lamellae; they occur most commonly in small spiders or those living in xeric habitats, as well as in ricinuleids and pseudoscorpions. Tube tracheae, on the other hand, are a secondary development of ramifying diverticula arising from the atrium (entrance chamber) of the book-lung; the lung itself may be lost. The fast and ferocious desert-dwelling solifugids utilise an extensive, ventilated tracheal system (tube tracheae also occur in opiliones, and some spiders and mites). Because of the morphological similarity between book-gills and book-lungs, it is not easy to distinguish them in fossils unless stigmata or similar restricted openings are present.

Uniramian respiration

Two small groups of myriapods, Pauropoda and symphyla, are small, primitive, and cannot withstand desiccation; they obtain oxygen either cutaneously or by the use of tracheae. Chilopoda and Diplopoda breathe by means of tracheae also, as do the Onychophora in spite of their flexible cuticle which lacks a wax layer. The hexapods apparently evolved on land from myriapod-like uniramians. They have a well-developed tracheal system which in pterygotes, unlike that of most myriapods and apterygotes, includes a mechanism for closure of the spiracles to reduce water loss.

Vertebrate lungs

Vertebrate lungs are generally thought to have arisen in fishes living in those freshwater environments where oxygen levels are very low. However, there is no reason why lungs could not have developed in marine, perhaps intertidal, conditions, since air-breathing occurs in gobies and blennies, and most Devonian lobe-finned fishes were marine (Thompson 1980). Many modern fishes from numerous families breathe air to supplement the poor oxygen supply in swamps and seasonally anaerobic waters. Commonly a highly vascularised part of the buccal and pharyngeal walls is used, but in some species more distal parts of the alimentary canal serve for oxygen uptake, and expired air is regurgitated or passed out through the anus. Comparison with the secondary lungs of pulmonate gastropods and decapod crustaceans is obvious. However, it is the separate pharyngeal gas bladder, which has arisen numerous times among the fishes, which eventually gave rise to the tetrapod lung. Though modern teleosts use it as a hydrostatic organ, it is quite probable that the swim bladder arose for air-breathing. In lungfish, the lung arises primitively from the ventral side of the pharynx (the teleost swim bladder is dorsal in position), and coupled with this are a series of circulatory and physiological modifications (for a review, see Little 1983, p. 183). *Neoceratodus* is essentially a gill-breather and uses its lungs only as accessory air-breathing organs. However, *Lepidosiren* and *Protopterus* are obligate air-breathers and use the much reduced gills primarily to eliminate CO₂.

The bimodal system of gas exchange of the lungfish, in which O₂ is taken up primarily by the lungs but CO₂ is expelled mainly through the gills, also occurs in amphibians. The earliest tetrapods had scaly skin, so the respiratory system of modern amphibians, utilising cutaneous, buccal, and pulmonary gas-exchange, may therefore be a secondary adaptation (Gans 1970). However, rich faunas of Lower Carboniferous tetrapods from Scotland (Milner *et al.* 1986) suggest a broad diversity of forms which probably originated in the Devonian. Modern anurans inhale air by means of a buccal pump (their dorsoventrally flattened heads may be an adaptation to increase the efficiency of this), but exhale using flank muscles; higher tetrapods have well-developed ribs (except chelonians, which use hyoid cartilages) and thoracic musculature for inhalation and exhalation

(aspiration ventilation). As soon as the tetrapod gait developed, and the body could be supported off the ground, it is likely that aspiration ventilation developed and the gills became reduced. Carbon dioxide could be lost through the skin, but there would nevertheless be a rise in P_{CO_2} in the blood (acidosis). Internal CO_2 receptors developed, which, coupled with the improvement in pulmonary breathing, would have come to control the ventilation rate, and short-term acid-base regulation to prevent harmful acidosis would thus have passed from the gills to the lungs. With the need for longer-term acid-base regulation out of water, this role passed to the kidneys, and the skin could become waterproof and scaly; this stage was apparently reached in the labyrinthodonts (Little 1983, p. 198).

Plants

For photosynthesising land plants, maintenance of a sufficient supply of CO_2 to green cells would have been the major problem (Raven 1985), there being no mechanical ventilation. Increase in area for uptake is achieved by the development of an intercellular space system with maximum exposure of the surfaces of mesophyll (photosynthetic) cells to this internal atmosphere. Such surfaces must be moist and there results a problem of excessive water loss. The latter is reduced by the internalisation of the surfaces for gas exchange and cuticularisation of the non-photosynthetic epidermis. Contact with the atmosphere is via pores with variable aperture, the stomata.

Conclusions

The major limiting factor in the change from the aquatic life to air-breathing in animals is not the supply of oxygen but the problem of CO_2 excretion in air. In tetrapods a secondary perfusion lung and bimodal gas exchange developed; a strikingly similar system occurs in land crabs, which may be considered to be at the 'lungfish level' of evolution in this comparison (Innes and Taylor 1986). Apparently, secondary lungs developed in eurypterids but this group never became fully terrestrialised (Selden 1985). In contrast, the closely related arachnids developed a diffusion lung and became terrestrial, but, as Little (1983, p. 117) pointed out, the arachnid book-lung is an inefficient organ, existing only because it evolved directly from the book-gill, and it is most improbable that it would have evolved directly in any group which originated on land. Tracheae have been developed by isopod Crustacea, arachnids, and uniramians, apparently after they emerged onto land. Because rates of water loss are high in tracheate arthropods without closeable spiracles, it is likely that emergence from the cryptozoic niche only occurred after the development of spiracular closing mechanisms; a striking parallel therefore exists between tracheates and land plants, with their stomata.

Support and locomotion

Smaller land plants, such as mosses, rely on a hydrostatic skeleton, and turgid tissues are also important for support in some vascular plants. However, most homoiohydric vascular plants also possess thick-walled structural tissues, where cell walls are composed of extra cellulose or cellulose impregnated with lignin. The latter polymer probably evolved as the rigid wall component in xylem, but its use in extraxylary structural tissues allowed the achievement of the increased height permitted by homoiohydry. In addition, there is considerable evidence in early vascular plants that support was achieved by virtue of growth in dense, monospecific stands.

Small animals such as slugs and worms can use hydrostatic skeletons on land. Arthropods and tetrapods moving onto land evolved the hanging stance for stability, and both groups developed some form of ankle joint to prevent the newly acquired plantigrade foot from twisting on the ground, and thereby being abraded and losing grip. Such skeletal adaptations are among the most useful indicators of terrestriality in fossils. Aquatic scorpions retain the digitigrade foot, for example. Arthropods become vulnerable to predation and desiccation during moulting, and it is possible that pioneer terrestrial forms returned to the water for ecdysis (Dalingwater 1985).

Sense organs

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. The stridulatory organs found on fossil trigonotarbid arachnids from the Devonian of Aberdeenshire and New York suggest their terrestrial mode of life, and their trichobothria (fine hairs which respond to air vibrations) prove it (Shear *et al.* 1987).

Digestion

Størmer (1976) emphasised the development of a preoral cavity for external digestion in terrestrial arachnids, myriapods and insects, a feature which is discernible in fossils.

Reproduction and dispersal

Organs for internal fertilisation and elaborate courtship devices are indicative of, but not exclusive to, terrestrial forms. Extant decapod Crustacea

and amphibians return to the water to breed, but the amniote egg of higher tetrapods has removed the dependence on aquatic environments in all stages in their life cycles. Insect eggs have a complex coat to prevent both drowning and water loss. In extant bryophytes and pteridophytes the male gametes are motile and require a film of water for external fertilisation. Internal fertilisation is seen in seed plants, which appeared in the Late Devonian. Dispersal in early land plants was achieved by asexual meiospores produced on the sporophyte; meiospore walls are impregnated with sporopollenin which may originally have evolved as a chemical defence against infection in algae. These protective walls also confer resistance to desiccation and possibly UV radiation in both poikilohydric bryophytes and homoiohydric pteridophytes.

THE NATURE OF THE FOSSIL EVIDENCE

Palaeontological evidence for colonisation of the land comes from two sources: external evidence from the sedimentary environment, including palaeosols and trace fossils; and morphological and anatomical evidence from the fossils themselves.

External evidence

The Rhynie Chert in Aberdeenshire (Table 6.2) is the only example of an early, autochthonous, petrified, terrestrial ecosystem, providing a unique glimpse of a wetland community in Devonian times. Its exact age remains uncertain, but is probably Pragian/Emsian. The chert comprises thin accumulations of peat showing clear evidence of fungal decomposition, separated by plants in growth position. Parts of the peat surface were covered by cyanobacterial mats, and algae also flourished in surface pools. Animal remains in the Rhynie Chert include freshwater crustaceans, predatory trigonotarbid arachnids, and rare mites and collembolans. Petrological evidence suggests that there were several periods of flooding by siliceous water, each separated by a significant time-lag. The source of the silica may have been from the weathering of volcanogenic sediments or from hot springs.

There are occasional records of plants preserved in growth position in clastic sediments. Schweitzer (1983) recorded *Sciadophyton laxum*, thought to be the gametophyte of *Zosterophyllum rhenanum*, in environments interpreted as intertidal or lower saltmarsh, in the Rhenish Lower Devonian. The associated fauna includes eurypterids and the bivalve *Modiolopsis*. Rayner (1984) illustrated Scottish Emsian *Drepanophycus spinaeformis* rooted in fluvial sediments.

Fossils are recovered from sediments deposited in continental, brackish-water and marine environments. As all these sediments are water-lain, the

Table 6.2. The three major Devonian terrestrial faunas compared. Key: Flora (not exhaustive): *L.* lycopsids, including prelycopods; *R.* rhyniophytes; *P.* progymnospermopsids; *A.* Algae; *F.* Fungi. Aquatic/amphibious fauna: *E.* eurypterids; *S.* scorpions; *X.* xiphosurids; *C.* freshwater crustaceans; *Other* includes molluscs and fish. Terrestrial fauna: *T.* trigonotarbid; *S.* spiders; *M.* mites; *P.* pseudoscorpions; *A.* arthropleurids; *C.* centipedes; *c.* collembolans. Abundance: ✓ = presence, c = common, r = rare, ? = questionable record.

Locality	Age	Lithology	Habitat	Flora					Aquatic/amphibious fauna					Terrestrial fauna						
				<i>L</i>	<i>R</i>	<i>P</i>	<i>A</i>	<i>F</i>	<i>E</i>	<i>S</i>	<i>X</i>	<i>C</i>	<i>Other</i>	<i>T</i>	<i>S</i>	<i>M</i>	<i>P</i>	<i>A</i>	<i>C</i>	<i>c</i>
Gilboa, New York	Givetian 380 Myr	Grey shale	Freshwater delta swamp	✓		✓			r	?				c	?	r	r	✓	✓	
Alken- an-der- Mosel, Germany	Emsian 390 Myr	Black shale	Brackish lagoon	✓	✓		✓		c		✓	✓	c	r	?			r		
Rhynie, Scotland	Pragian– Emsian 400 Myr	Chert	Terrestrial bog near hot spring	✓	✓		✓	✓				c		c	?	r				r

original habitats of the entombed organisms remain obscure and recognition of land colonisers is critical.

The earliest Precambrian palaeosols merely indicate emergent subaerial surfaces and are termed extinct or abiotic (Holland 1984). Later Precambrian representatives (from 2400 Myr ago onwards), with abundant disseminated carbon, may indicate the activities of microbial mats. Retallack (1985) described in detail early Palaeozoic examples and found indirect evidence of a soil fauna from bioturbation structures.

Trace fossil evidence of land life is equivocal because the crawling traces tend to be preserved in wet, cohesive sediment, and could have been made by amphibious animals, or subaqueously (see reviews by Pollard 1985; Rolfe 1980; and Selden 1984).

Morphology and anatomy

Direct comparison with living relatives can be used as a criterion of terrestriality in some fossil groups; this is only possible if extant relatives exist and the preservation of the fossils is sufficiently good to be certain of affinity. Thus Silurian *Baragwanathia*, preserved as impressions, is considered a terrestrial vascular plant because it shares sufficient morphological characters with later Lower Devonian forms which on grounds of morphology and anatomy are closely related to lycopods. Silurian *Cooksonia* on the other hand, which is known only from marine sediments, lacks cuticle, stomata, and vascular tissues. Its claim to land-plant status rests on its axial architecture and hence presumed self-supporting erect growth habit and *in situ* spores with sporopollenin. It shows little morphological similarity with extant pteridophytes. The discovery (Edwards *et al.* 1986) of support tissues (sterome) and stomata in Lower Devonian representatives establishes the land-plant status of *Cooksonia* by this time, but does nothing to confirm the affinity or habitat of Silurian examples. In the case of the earliest land plants which are morphologically completely different from later and extant groups (e.g. Rhyniophytina, Trimerophytina, Zosterophyllophytina), anatomical evidence can be used to demonstrate land status. Thus in the common coalified compression fossils of vascular plants, anatomical and biochemical adaptations associated with homoiohydry (e.g. cuticle with cutin, xylem with lignin) have high fossilisation potential and persist when all other tissues are converted to coal. Indeed, because abundant strengthening tissues may have slowed down decay as well as maintaining the integrity of the whole organ, they increase fossilisation potential. Such plants are probably preferentially represented in the fossil record, while vascular plants with hydrostatic skeletons (e.g. *Rhynia gwynne-vaughanii* from the Rhynie Chert) do not occur as compression fossils in more typical Old Red Sandstone assemblages (Edwards 1979). Similarly, poikilohydric plants, e.g. bryophytes, will also be under-represented.

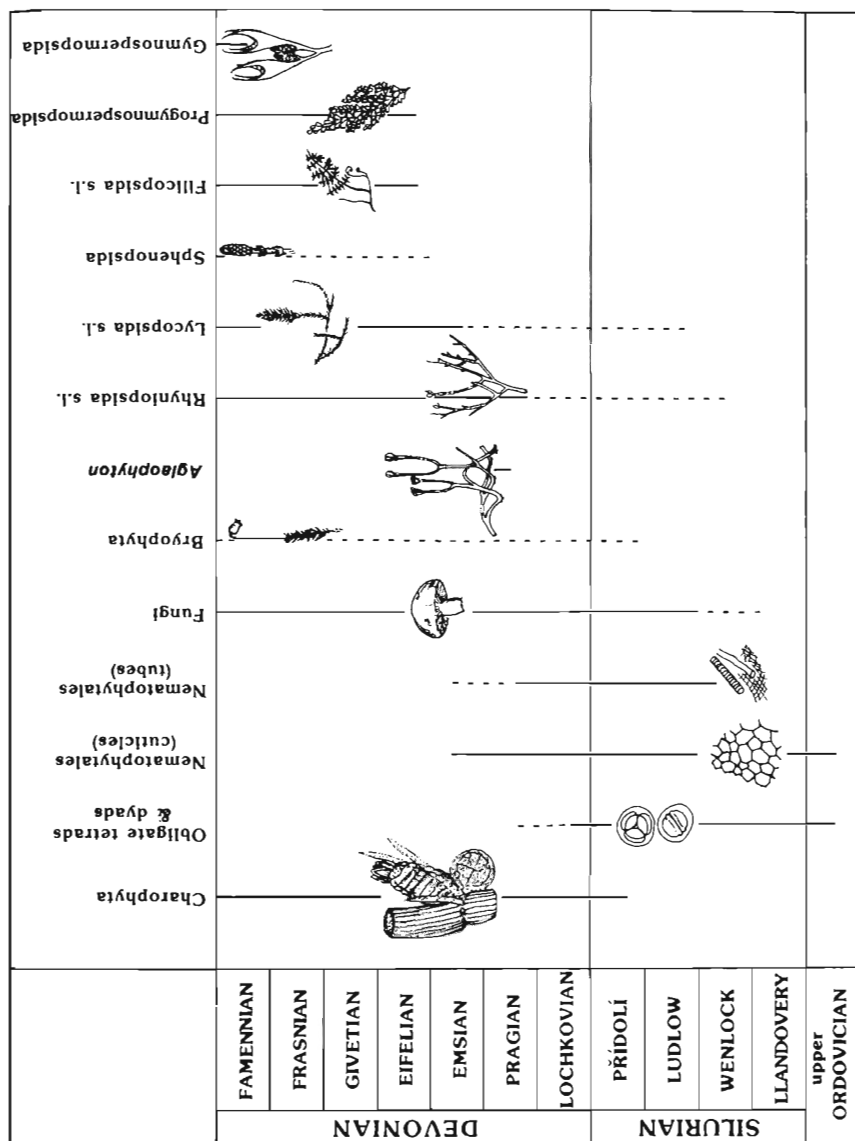


Figure 6.1. The fossil record of plant invasion of the land in Ordovician to Devonian times.

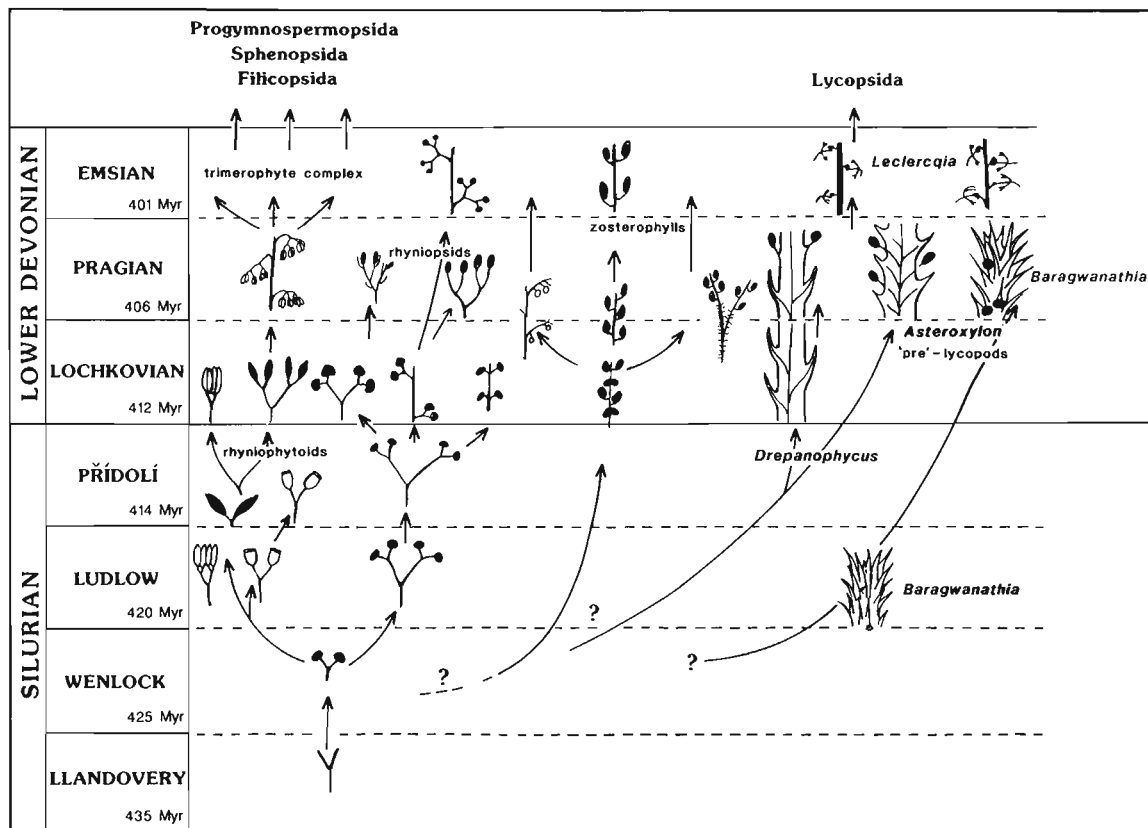


Figure 6.2. Possible phylogeny of early vascular plants during the Silurian and Devonian, showing increasing complexity of organisation.

The best three-dimensional anatomy is found in permineralisations, where cells are preserved in pyrite, calcite, or silica (Edwards 1986). In the Rhynie Chert, *Rhynia gwynne-vaughanii* has all the attributes of a vascular land plant, including an intercellular space system and rhizomes with rhizoids. The associated *Aglaophyton (Rhynia) major*, which is not very dissimilar and would undoubtedly also be placed in the Rhyniophytina were it preserved as a compression fossil, is shown to have a moss-like conducting strand and not tracheids. It thus possesses a new combination of moss and homoiohydric vascular plant characters (D.S. Edwards 1986). Similarly, while all extant scorpions are terrestrial, the presence of external gills and a digitigrade tarsus, as well as sedimentological evidence, confirms the view that early scorpions were aquatic.

The potential of microfossils in the recognition of terrestrial organisms has only recently been exploited. Spores and fragments of cuticle extend the record of land plants into the Ordovician (Figures 6.1 and 6.2), although the types of plant that produced them remain highly conjectural (Gray 1985). Micropalaeontological techniques are similarly proving extremely useful in the study of the earliest terrestrial animals (Shear *et al.* 1987).

THE FOSSIL RECORD

Plants

Colonisation of the land by animals was achieved by a number of groups at different times. In contrast, the plant story appears very simple. This may merely mask our ignorance, as the record is predominantly of vascular plants. Thus algae may have invaded the land on a number of occasions, but such attempts went unrecorded because of their low fossilisation potential. Similarities between bryophytes and tracheophytes, particularly the egg-containing apparatus (archegonium), indicate a common ancestor. Whether the presumed archegoniate intermediate migrated onto land just once, or whether it evolved on land, perhaps as a drought evader or with ecophysiological tolerance, or indeed whether there were several independent migrations from semi-aquatic forms, cannot be determined. Whatever their origins, poikilohydric bryophytes and homoiohydric tracheophytes as we know them evolved on land, and probably more or less at the same time (although the earliest moss, *Muscites*, is recorded in the Carboniferous and the liverwort *Palaviciniites* in the Upper Devonian). Possible earlier examples are the Lower Devonian *Sporogonites* with some moss characters (unbranched fertile axes, stomata immediately below the sporangium), and Přídolí *Tortilicaulis* with an unbranched twisted axis characteristic of liverworts. Evidence for diversity among the early colonisers comes from anatomically preserved plants with anomalous conducting tissues formerly considered tracheophytes (Edwards and Edwards 1986). These include

Taeniocrada dubia and *Aglaophyton major*. However, in the absence of gametophytes, relationships to archegoniates cannot be determined.

As to the tracheophytes themselves, the earliest examples with *in situ* tracheids occur in Ludlow sediments, *Cooksonia* is usually considered the earliest fertile member, but Silurian representatives, including the oldest Wenlock ones, lack cuticle, stomata, and vascular tissues (Edwards *et al.* 1983). Their claim to land-plant status rests on their axial architecture and hence presumed self-supporting erect growth habit, and *in situ* spores with sporopollenin. Support tissues and stomata in Lower Devonian representatives confirm the land-plant status, but no relationship with the tracheophytes. The earliest fertile rhyniophytes with *in situ* tracheids are Pragian, e.g. *Uskiella spargens*. They persisted in small numbers into the Emsian, but because of their predominantly determinate mode of growth, limited sporing capacity, and small size they were outcompeted by the Trimerophytina from which all major lines of vascular plants, except the club mosses, evolved.

Also present in marine Ludlow sediments from Australia is *Baragwanathia longifolia*. Anatomical and morphological features in Lower Devonian examples demonstrate lycopod affinities, although the diagnostic relationship between sporophyll and single axillary sporangium has not been demonstrated. Based on records from Old Red Sandstone localities in the present northern hemisphere (Edwards and Fanning 1985), lycopods are traditionally thought to have evolved from the Zosterophyllophytina, fertile examples of which do not appear until the Lochkovian. Thus it is possible that plants with tracheids evolved more than once (i.e. the zosterophyll and rhyniophyte lines), but it has to be emphasised that this would have occurred on land.

Spores

The earliest spores thought to derive from vascular plants or their immediate ancestors occur in Llandovery sediments. Older microfossils suggest the existence of a completely different kind of land vegetation (Gray 1985). Both bryophytes and pteridophytes possess spores with triradiate marks, and there is currently no way of distinguishing between them in the dispersed spore record. Gray argued most persuasively that the dispersed permanent (obligate) tetrads (Figures 6.1 and 6.2) found in palynomorph assemblages from late Ordovician to late Silurian sediments derive from land plants at the liverwort grade of organisation, with either ecophysiological adaptations to drought or ephemeral vegetative stages. The affinities of the tetrad producers, e.g. as bryophyte ancestors, are highly conjectural.

Nematophytale

Associated with the earliest tetrads in Ordovician sediments, and present throughout the Silurian and Lower Devonian, are fragments of cuticle with a reticulate pattern quite unlike that produced by the epidermis of vascular plants. Assuming that the functions of the cuticles are similar, these

microfossils provide the most compelling evidence for terrestrial vegetation in Ordovician times, although the nature of the organism below the cuticle still eludes us. Later in the Silurian and Devonian such cuticles are found associated with wefts of large and small tubes, some of the former possessing thickenings reminiscent of tracheids. Lang (1937), calling this thalloid organism *Nematothallus*, believed that its unique organisation indicated a new and now extinct phylum of land plants that were neither algal nor tracheophytes. Certainly the abundance of such cuticles in Lower Devonian sediments indicates that *Nematothallus* was an important coloniser of the land.

Fungi

Abundant vegetation on land would eventually have resulted in accumulation of plant matter forming substrates for exploitation by terrestrial fungi. The Rhynie Chert provides excellent examples of such saprotrophs (Stubblefield and Taylor 1988). The evolution of cutin, lignin, and sporopollenin would have presented new sources of energy for fungi. Lignin, for example, can be metabolised only by basidiomycetes and a few ascomycetes. Hyphae and spores of terrestrial Ascomycetes are recorded in the Silurian (Sherwood-Pyke and Gray 1985) and thyrlothecia typical of extant Hemisphaeriaceae in the Lower Devonian (Stubblefield and Taylor 1988). Hyphae present in an Upper Devonian wood, which shows a pattern of decay similar to that in white rot, may belong to ascomycetes but are more probably basidiomycetes. Mycorrhizal associations between Zygomycetes and higher plants are suggested by the presence of resting spores in axes of Rhynie Chert plants and *Psilophyton* (Stubblefield and Taylor 1988).

Animals

Figure 6.3 shows the fossil record of terrestrial animals, which is sparse (Rolfe 1980; 1985). There were many animal invasions of the land, at least one for each class, and numerous separate invasions within arthropod groups such as the Chelicerata and the Crustacea. The record suggests that the primary period for these terrestrialisations was the Silurian, and most terrestrial animal groups invaded the land alongside the plants. The major exception to this is the Crustacea, groups of which are attempting colonisation at the present time.

The oldest terrestrial animals may be the Siluro-Devonian kampecarid myriapods (Almond 1985), but in spite of their diplopod features, there is doubt regarding both this affinity and their terrestriality (cf. scorpions). Recent records of myriapod-like forms from undoubted marine sediments of Silurian age, Wisconsin (Mikulic *et al.* 1985), and the Cambrian of Utah (Robison 1987), suggest a long aquatic ancestry for this group. Records of other myriapod-like forms from the Siluro-Devonian generally prove, on reinvestigation, to be misidentified (e.g. *Necrogammarus*; see Selden 1986).

The oldest undoubted terrestrial animal body fossils are from the Lower Devonian Pragian–Emsian (400-Myr-old) Rhynie Chert of Aberdeen, from the Emsian (390-Myr-old) of Alken-an-der-Mosel, Germany, and the Givetian (380-Myr-old) of Gilboa, New York, all yielding comparable material (Table 6.2). Among the terrestrial invertebrates in these faunas are the earliest records of many arachnids: trigonotarbid (extinct spider

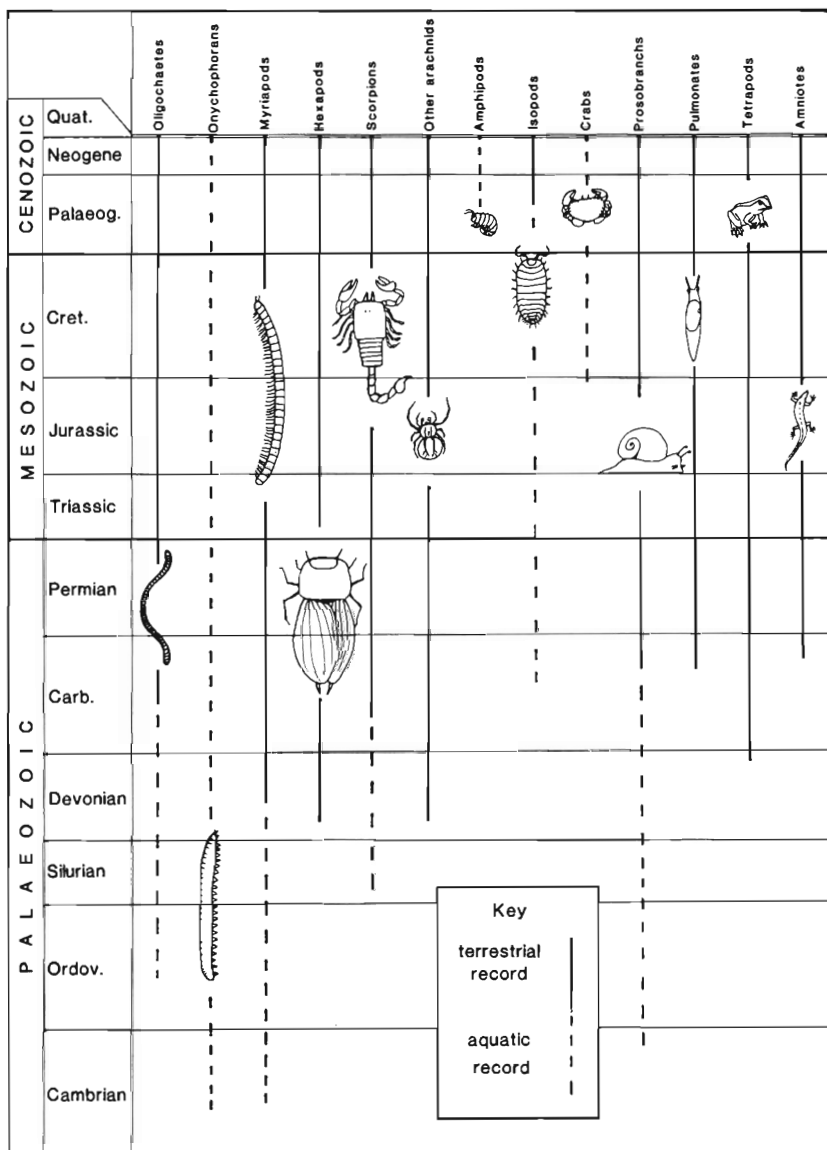


Figure 6.3. The fossil record of colonisation of the land by animals.

relatives), a possible spider, mites, a pseudoscorpion, arthropleurids, a new order of centipedes (Devonobiomorpha) among the myriapods, and collembolans. The fully terrestrialised features of these animals suggest origins in the Silurian or earlier. Thus these three faunas present glorious vistas on early land life at the start of the history of terrestrial ecosystems.

There are no records of terrestrial planarians, nemerteans or nematodes, although fossil examples of parasitic and aquatic nematodes are known (Conway Morris, 1981). Oligochaete annelids are known from the Carboniferous, and their traces (burrows and faecal pellets) occur in palaeosols from the Carboniferous onwards. Land snails, both pulmonates and heliciniid prosobranchs, are recorded from the Upper Carboniferous. They were probably established members of the land fauna by that time (Solem 1985). Crustaceans have a generally good fossil record, but the ranges of terrestrial groups are short. Amphipods first appeared in the Upper Eocene, though they may have originated in the mid- to late Mesozoic; the terrestrial talitrids have no fossil record. They may have invaded the land via newly established coastal angiosperm rain forests around Cretaceous Gondwanaland (Spicer *et al.* 1987). Isopods have a fossil record from the Upper Carboniferous and supposed origins in the Devonian, but the earliest terrestrial Oniscoidea are Eocene. Crabs and crayfish first appeared in the Jurassic; the main crab radiations were Cretaceous and Eocene. Families with terrestrial representatives first appeared in the Palaeogene but true terrestrial forms not until the late Neogene.

The oldest tetrapods are from Late Devonian (Famennian) age sediments from Australia, South America and Eurasia, but especially eastern Greenland (Clack 1988). Assuming these animals had a common ancestor, their wide geographic range suggests a long pre-Famennian history. The oldest trackway assigned to tetrapod walking is from the late Silurian/early Devonian Grampians Group of Victoria, Australia (Warren *et al.* 1986). Therefore tetrapods probably share with the arthropods a Silurian origin. However, the earliest tetrapods probably laid eggs in water like modern amphibians; for the earliest amniote we must look to the Carboniferous. However, since the palaeontological criteria for recognising it as a reptile are skeletal we still cannot be sure when the amniote egg first appeared.

ROUTES ONTO LAND

Freshwater

The habitats of the trans migrant algae were probably not streams or rivers but shallow ephemeral pools, backwater lagoons, or lakes with oscillating water levels, and were probably far commoner before the advent of extensive terrestrial vegetation (Beerbower 1985). Such transitory water bodies would have provided the stimulus for the evolution of desiccation resistant structures, e.g. sporopollenin impregnated meiospores (Raven 1984b) and cuticles.

The freshwater route was used by animals as diverse as platyhelminths, annelids, prosobranch molluscs, crayfish, some grapsid crabs, and the vertebrates (Little 1983, Table 10.1). The reasonably good correlation between osmotic concentration and routes onto land shown by crustaceans can also be demonstrated in the molluscs. The most successful are the pulmonates, which have a relatively high osmotic concentration; in contrast, the prosobranchs have a low osmotic concentration and are generally restricted to humid tropical forests where fatal desiccation is less likely (Little 1983).

The success of terrestrial vertebrates, having taken the freshwater route, contrasts with those successful invertebrate groups with largely marine ancestors. The relatively bigger tetrapods could spend longer on land without the threat of desiccation (cf. scorpions also; see Rolfe 1980). Their freshwater origins conferred the ability to osmoregulate, rather than tolerate, but their large size and waterproof skin allowed them to overcome the water problem on land. Respiratory mechanisms also give clues to the freshwater origin of vertebrates. Littoral animals need to breathe air fairly continuously for long periods while awaiting the return of the tide, so they have generally adapted pre-existing branchial structures for air-breathing. In contrast, animals in poorly oxygenated freshwater are intermittent air-breathers and so developed entirely new organs to take in large volumes of air at a time. Palaeontological evidence also points to a freshwater route for the terrestrial vertebrates.

MARINE

Estuarine, saltmarsh, and littoral environments are characterised by major fluctuations in the osmotic potential of the bathing medium. Physiology of extant plants colonising salt marshes (halophytes) is exceedingly specialised and such plants probably derive from terrestrial angiosperms. Today, pteridophytes and bryophytes (Raven 1984a) are rarely found in such stressed environments, and it seems unlikely that emergent marine or saltmarsh 'rooted' algae were the successful transmigrants. However, Schweitzer (1983) cited assemblages of early vascular plants preserved in littoral and saltmarsh environments as evidence for this route.

The marine route proved the most successful for invertebrate colonisers, and was apparently taken by nemertines, polychaetes, littorinacean prosobranchs, pulmonates, most crustaceans, chelicerates, and probably myriapods and hexapods (Little 1983, Table 10.1). Osmotic arguments favouring a marine route for Crustacea and Mollusca are particularly strong, but are less so for other groups. In particular, interstitial environments present a more gradual change in salinity from marine to terrestrial than that encountered by the epifauna. It therefore follows that among interstitial forms, such as oligochaetes and nematodes, it may be difficult to distinguish osmoregulatory ability derived from a freshwater or interstitial

ancestry. Myriapods, hexapods, and chelicerates all 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 a marine route is suggested. The arachnid conversion of the book-gill into the book-lung is a prime example of the use of an existing aquatic respiratory organ to breathe air for long periods in littoral animals. Interstitial animals, having emerged as tolerators, possibly later developed an osmoregulatory ability as well, since both oligochaetes and some insects can produce hypo-osmotic urine (Little 1983, p. 213). A marine-interstitial route can therefore be distinguished.

Land

Stebbins and Hill (1980) postulated that the higher green plants may have evolved from mats of filamentous algae inhabiting surfaces of moist soils. Physiologically, this would be plausible, but direct evidence is lacking, and the question of the migratory routes of the soil algae remains unanswered. Similarly, it is possible that the hexapods evolved from the myriapods on land, so that the problems of terrestriation had already been solved by their ancestors. Palaeontological evidence suggesting a long marine history for the myriapods, rather than their evolution from onychophoran-like forms on land, is accumulating.

EARLY LAND COMMUNITIES—AN OVERVIEW

Land surfaces in the early Palaeozoic would have been at least partially covered by microbial mats initially predominantly cyanobacterial but later with green coccoid and filamentous algae. Today such mats mainly occur on moist soils, but cyanophyte-dominated crusts also form on rock, sand and soil in dry and arid desert environments, where they accrete and bind sediments. Some of these micro-organisms would have acted as natural nitrogen fertilisers. Decaying remains would have introduced humus and promoted some chemical weathering in the substrate, and would have increased water and mineral retention, all this creating microenvironments for interstitial animals. Although such mats may have been widespread, they would have been easily disrupted and destroyed in unstable environments, and soils would have been gradually built up only in stable, perhaps low-lying areas.

Around mid-Ordovician times the microfossil record suggests a change in land vegetation, perhaps to one comprising multicellular thallophytic carpets, with nearest living examples (but not necessarily relatives) in the bryophytes (Gray 1985). From the projected size and presumed lack of rooting systems, it can be postulated that some further amelioration, and to a lesser extent stabilisation, occurred particularly in humid environ-

ments, but there was no major change in the processes operating earlier. Palaeosols are known from the late Ordovician onwards (Retallack 1985). The oldest, the Potters Mill clay palaeosol from the Ashgillian of Pennsylvania, appears to have formed in a subtropical, subhumid palaeoclimate with wet and dry seasons, and was a red-brown silt soil. Of great interest are the abundant, deep, vertical burrows, possibly made by arthropods, possibly millipedes (Retallack and Feakes 1987). Animals responsible for the palaeosol burrows may have avoided desiccation if the soil never dried out; yet the postulated wet/dry season would have encouraged cryptobiosis, and animals capable of this, such as mites and tardigrades, could have colonised the land by wind dispersal in the encysted state.

The first half of the Silurian saw the appearance of the pioneering erect pteridophyte-like plants. Initially small, of limited productivity, and lacking extensive subterranean systems, they would have made little impact on terrestrial vegetation. Suitable habitats may have been limited in number and highly stressed. This may well have depressed the vegetative and reproductive vigour of the sporophyte resulting in conservation of resources. In the surface-living gametophyte, however, in which almost all cells are photosynthetic and less energy is required for structural and conducting tissues, both vegetative and reproductive phases may have been completed quickly when moisture was available (Edwards 1979). The sporophyte then became established as a site occupier tolerant of drier conditions. The growth habit and terminal sporangia of the earliest representatives (rhyniophytes) suggest that there was a single period of spore production.

As such plants became larger and more widespread, particularly in early Devonian times, there would have been an increase in ecosystem homeostasis and a major amelioration of substrates with build-up of nutrient-rich/water-retentive humic soils. Stands of probably monotypic vegetation spreading by means of extensive rhizomatous systems would have clothed low-lying areas, with spore production occurring over much longer periods. The Rhynie Chert provides evidence of peat development. However, bearing in mind the limitations of 'external' fertilisation that characterises the pteridophytes, plants may still have been restricted to damp areas. Moderation of physical stress would have produced stable populations, however, and the potential development of food webs of increasing complexity. The oldest body fossils of land animals occur at this time, but evidence of herbivory is lacking. The development of spines on aerial surfaces of plants may have increased photosynthetic capacity, but may also have conferred protection against grazers. In the zosterophyll *Sawdonia ornata* open darkened tips to spines suggest additional chemical defence. Response to wounding, as dark-staining or necrotic areas, has been reported in Rhynie Chert plants (Kevan *et al.* 1975), but arthropod involvement is equivocal (Rolfe 1985). Regeneration of surface tissues is described in *Psilophyton dawsonii* (Banks 1981) but the cause of the wound is unknown.

In all three early terrestrial ecosystems known to date (Table 6.2),

predatory arthropods predominate; the remaining arthropods are probably detritivores or fungivores. The apparent lack of herbivory has been explained in various ways—spore-feeding (Kevan *et al.* 1975; rejected by Rolfe 1980; Shear *et al.* 1987), and differential preservation (Shear *et al.* 1987)—but this lack may not be significant. The decomposer food chain is typical of the soil fauna of the present day, the only herbivores being surface-feeding macrofauna. The paucity of detritivores in the faunas of Rhynie and Gilboa can be explained by the poor preservation or recovery of the mites, collembolans, nematodes and enchytraeids, for example, because of their small size.

Suggested causes of terrestrialisation are various: escape from predators, more abundant food supply, or the filling of vacant niches, for example, but such hypotheses are not readily testable. Chance undoubtedly played a large part. In theory, autotrophs must have preceded heterotrophs onto land, and carnivores must have followed their prey. Individual taxa moved on to land separately, but the majority appear to have made the adaptive breakthrough in mid-Palaeozoic times. It is probably realistic to envisage established communities colonising the terrestrial environment at this time, rather than pioneering species.

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