

## The Development of Early Terrestrial Ecosystems

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### Summary

In this review of terrestrialization by plants and animals in the early Phanerozoic, the classical idea of a major mid-Palaeozoic event is discarded in favour of gradual colonization over a long time period. Four phases of colonization of the land by plants are recognized but their limits are often difficult to define. The first, of microbial mats comprising prokaryotes and later photosynthesizing protists (algae) but with no direct fossil evidence, extends from the Precambrian and may persist in environments unsuitable for colonization by higher plants and animals today. The second, based on microfossils (spores and cuticles) possibly from plants of bryophyte aspect (if not affinity) started in the Ordovician (c. 460 Ma ago) and ended in the Lower Devonian, but was overlapped by the third phase beginning early in the Silurian (c. 430 Ma). This consisted of small plants of axial organization with terminal sporangia probably allied to the tracheophytes. The advent of taller vascular plants of varied organization around the Silurian - Devonian boundary (c. 420-400 Ma) signalled the final pioneering phase - that of major adaptive radiations on land, culminating in the appearance of extant groups, in changes in reproductive strategy and in the development of complex vegetation structure. The animal record is sparser than that of the plants, but suggests an early land fauna in the mid-Palaeozoic which differed from later terrestrial assemblages in lacking herbivores, with the first direct fossil evidence for land animals in the late Silurian.

### Introduction

Historically, the advent of vascular plants and earliest records of supposed terrestrial animals in the late Silurian and early Devonian captured the imagination as a dramatic terrestrialization event, triggered by the environmental stimuli of increasing atmospheric oxygen and decreasing ultra-violet radiation. These stimuli associated with increased ozone density supposedly allowed the migration of green algae from water on to land, bringing faunas with them (Berkner & Marshall, 1965). Certainly it is the first records of vascular plants, unequivocal indicators of terrestrialization, that have dominated the literature. It now seems likely that oxygen levels were much higher earlier in the Palaeozoic (e.g. Berner & Canfield, 1989) and that subaerial surfaces were colonized by photosynthesizing organisms throughout the Phanerozoic. Here, we summarize stages in this early greening by autotrophs which, except for Cyanobacteria and possibly green algae, have no close living counterparts (Table 1). We emphasize that they overlapped, with replacement resulting from competition as plants more finely tuned, both physiologically and anatomically, to the terrestrial environment evolved. We also review the accumulating evidence for the early stages of the invasion of the land by animals.

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millipedes, though it has been pointed out that the *Skolithos* could have been formed subaqueously and the soil developed at a later date following emergence (Wright, 1990; Chaloner, Scott & Stephenson, 1991). Body fossils of both annelids and myriapods may be represented in marine sediments in the early Palaeozoic (Conway Morris *et al.*, 1982; Mikulic, Briggs & Kluessendorf, 1985*a,b*; Robison, 1987). Work on a fauna of millipedes from the late Silurian of Stonehaven, as yet unpublished (Almond, 1989), is interesting in relation to this.

What distinguishes saltmarshes from bare muddy, sandy or rocky littoral zones is the vegetation. Saltmarshes and mangrove swamps are more stable in some ways because of the ameliorating effect of the plants. Salinity, temperature and water supply may fluctuate as much as on the bare shore, but at root, litter and substrate level these fluctuations are lessened. Because the saltmarsh/mangrove is defined by its plants, it follows that there are many different kinds throughout the world and through time. Interestingly, saltmarshes are providing a route for animals colonizing land at the present day: the talitrid amphipods, crabs, prosobranch and pulmonate gastropods, as well as for recolonization of the littoral by terrestrial insects and spiders (Little, 1990).

The Prídolf Ludford Lane biota (Jeram, Selden & Edwards, 1990) may have lived in a rhyniophytoid saltmarsh. The terrestrial animals in this biota share many similarities with later, Devonian, faunas. They comprise predatory centipedes and trigonotarbid arachnids, and are found with a restricted aquatic fauna of eurypterids, scorpions, ostracodes, fish, scolecodonts, bivalves and *Lingula*, plus *Cooksonia*, further rhyniophytoids and *Nematothallus*. Sedimentology of this Platyschisma Shale reveals that the biota was deposited in lags within dominantly intertidal and storm generated deposition. In some parts of the Platyschisma Shale, plant and animal-rich blocks of finely (tidal?) laminated siltstone form breccias within channels, giving the impression of storm-induced erosion of tidal saltmarsh. On the other hand, it is not impossible that such blocks were reworked from non-marine influenced coastal habitats.

#### **Phase 4 - Late Ludlow (Australia)/Early Gedinian (Laurentia) into Frasnian**

The advent of this final pioneering phase is marked by a major change in higher plant architecture. Innovations in growth patterns overcame the constraints of the determinate growth exhibited by rhyniophytoids and produced a change in vegetation structure as plants grew taller. Accompanying this was an increase in sporing potential, usually achieved by strobili and trusses. That there was a radical change in plant affinity at the beginning now seems less likely: the recent demonstration of tracheids in Lower Devonian *Cooksonia pertoni* strengthens the possibility that at least some of the rhyniophytoids were indeed vascular plants. However two major tracheophyte groups appear - the Zosterophyllophytina and the Drepanophycopsida (Lycophytina s.l.), while throughout the Lower Devonian there were major diversifications of vascular plants, first of the zosterophylls, and from the beginning of the Siegenian, the trimerophytes (Edwards & Davies, 1990). The large number of taxa included under 'other' alongside those conforming to the Rhyniophytina, Zosterophyllophytina and Lycophytina by Edwards & Davies in their analysis of early land plant radiations emphasizes their disparity of organization. Space does

not allow detailed description of taxa here: the reader is referred to Gensel & Andrews (1984), Hao & Beck, (1991) and Li & Edwards (1992) (Chinese plants), and Kenrick & Crane (1991) for further references. The end of the phase is more difficult to define. In terms of affinity and hence the disappearance of what might be considered the pioneering groups of vascular plants, the Zosterophyllophytina became extinct in the Frasnian as did the Drepanophycopsida although herbaceous lycophytes persist to the present day (Edwards & Berry, 1991). The barinophytes extended into the Carboniferous (Scheckler, 1984). However there were major changes around the Emsian-Eifelian boundary, when the trimerophytes disappeared, involving major evolutionary innovation with profound effects on vegetation structure and reproductive strategies. In the former the advent of the progymnosperms in the Eifelian marked the beginning of a new era - the 'upward struggle' being facilitated by the acquisition of the vascular cambium. The evolution of heterospory occurred in a number of groups with the earliest ovules recorded in the Famennian.

### *Habit of vegetation*

In the present southern hemisphere, the beginning of the phase is marked by records of *Baragwanathia* (Tims & Chambers, 1984), and in the present northern hemisphere where subsequent events are best documented, by the genus *Zosterophyllum* itself (Edwards, 1990). These two taxa exemplify the two major kinds of gross morphology in early land plants, viz. axial systems and the leafy stems typical of herbaceous lycophytes today. The erect system of *Zosterophyllum* was relatively simple, with strobili lacking bracts or leaves terminating infrequently branched or undivided naked axes, more complex (K + H) branching being confined to a presumed rhizomatous system. Anisotomy, overtopping and the development of lateral branch systems occurred in a number of groups in the Lower Devonian. In the zosterophylls, it was accompanied by more extended periods of spore production as sporangia were distributed on lateral axes, while in trimerophytes sporangia were produced in terminal clusters on lateral branches (Banks, 1980). Direct measurement of overall height is impossible for these, usually transported, fragmentary fossils. Estimates based on axis diameter (Chaloner and Sheerin, 1979) that show logarithmic progressive increase in width throughout the Devonian are translated into increase in height during this interval. Gensel & Andrews (1984) reported that Emsian *Pertica* and *Trimerophyton* may have reached 2 m in height. These increases in size were achieved only by primary growth, the first record of secondary xylem being in Eifelian progymnosperms, e.g. *Rellimia* and *Aneurophyton*.

Such heights, combined with narrow, much branched axes suggest a somewhat unstable plant in isolation and there is considerable evidence from distribution of fossils in sediments for growth in monotypic, probably clonal, stands. Direct evidence for clonality is limited (Tiffney & Niklas, 1985). The reconstruction of Emsian *Psilophyton crenulatum* (Doran, 1980) with its irregularly branching rhizome-like system, with spiny (presumably superficial) horizontal axes and naked downwardly diverted axes is similar to growth habits proposed for *Asteroxylon* and *Drepanophycus spinaeformis*. Whether or not the mat of presumed horizontal branches in *Zosterophyllum* species was subterranean is more conjectural. Such considerations are significant in terms of surface run-off and sediment binding. Evidence for *in situ* vertical 'rooting' structures is widespread in Siegenian-

Emsian fluvial sediments of the Rhenish Schiefergebirge (Schultka & Remy, 1990) although the plants themselves remain unknown. In contrast, horizontal leafy stems identified as *Drepanophycus spinaeformis* produced irregularly branched smooth axes (? adventitious roots) that penetrated fluvial sediments for many centimetres (Schweitzer, 1983; Rayner, 1984). Indeed *D. spinaeformis*, one of the most cosmopolitan Lower Devonian plants, constitutes a departure from the somewhat monotonous 'reed-stand' character of this early land vegetation, occurring in such profusion at certain German localities that it must have formed quite dense thickets of 'scramblers and trailers'. This kind of vegetation, comprising herbaceous lycophytes, was widespread globally in the Middle and early Upper Devonian. Of especial interest to this account is *Leclercqia complexa* found with arthropods at Gilboa, New York and also recorded from Europe, Kazakhstan and Australia.

Evidence for stratification in phytocommunities is seen in the Emsian of north-eastern America, where Gensel & Andrews (1984) suggested that many zosterophyllophytes, *Drepanophycus* and *Kaulangiophyton*, all with rhizomes and aerial shoots, grew in dense, low mats, while trimerophytes such as *Pertica* and *Trimerophyton* formed a second, taller layer. The advent of secondary thickening in Eifelian progymnosperms and the probable forerunners of the arborescent lycophytes (e.g. *Lepidosigillaria* and *Lepidodendropsis*) in the Givetian further increased capacity for upward growth. The earliest progymnosperms (e.g. *Aneurophyton*) were bushes, but by the end of the Devonian, *Archaeopteris* had a well developed trunk (*Callixylon*) at least 1 m wide and branching crown with a profusion of small, laminar leaves. At the same time, the arborescent lycophyte *Cyclostigma* was approaching the dimensions of Carboniferous swamp forest forms. Indeed, the presence of thin coals in both Middle and Upper Devonian points to the existence of well-developed swamp communities, the younger including large, deltaic marshes and smaller upland backswamps (Scheckler, 1986).

Throughout this period there is evidence for heterospory in dispersed spores (Chaloner & Sheerin, 1979) and from a very limited megafossil record it seems that this condition evolved separately in a number of lineages (e.g. Gensel & Andrews, 1984). The first ovules are recorded from the United States and Belgium in the Famennian (Fa2c) (Fairon-Demaret & Scheckler, 1987; Rothwell, Scheckler & Gillespie, 1989). The elimination of the free-living gametophyte reduced dependence on environmental high humidity, while food reserves of seeds would have permitted germination and establishment under vegetation cover. As regards the terrestrial ecosystem, ovules and seeds would have produced concentrated energy sources for herbivores. The Carboniferous provides the earliest evidence that plants have invaded much drier inland (upland?) areas and the arid Permian of the northern hemisphere saw the spread of such plants into the lowlands.

### *Plant ecology*

Uncertainties in reconstructions of plants, and hence vegetation structure, are matched by those attempting to place them in their habitats. Exceptions are the 'rooted' examples described above and the Rhynie Chert. Some of the former indicate that the plants (e.g. Scottish *D. spinaeformis*) were riparian, preserved following flooding and rapid burial in muds and sands. Axial megafossils of *Gosslingia breconensis* in cyclothem sequences in the Siegenian medial Lower Old

Red Sandstone facies of South Wales that are aligned in parallel with fertile regions all at the same level, again suggest that the plants, growing close to the flooding rivers, were still attached to substrate (Edwards, 1980a). At the same quarry there is some sedimentological evidence that *Tarella trowenii* colonized point bar systems, and may have been adapted for regeneration in potentially unstable/disturbed habitats (Edwards & Kenrick, 1986). *Zosterophyllum myretonianum* (Gedinnian: Angus-Edwards, 1975) is associated with lacustrine deposits as are some of the Rhenish Schiefergebirge examples (Schultka & Remy, 1990). In contrast to such examples, from Emsian records in Maine, Andrews *et al.*, (1977) reconstructed coastal marshland communities consisting of "large stands of *Psilophyton* with smaller clumps of other taxa interspersed" citing *Thursophyton*, *Psilophyton dapsile*, *Taeniocrada* and *Kaulangiophyton* as examples of the latter. By far the most comprehensive analysis to date is that of Schweitzer (1983) who combined sedimentological, palaeozoological and palaeobotanical information in the reconstruction of a range of coastal plant communities including sub- and intertidal, saltmarsh and marsh less influenced by the sea for the Lower Devonian of Rhineland.

### *Plant distribution*

The discovery of Lower Devonian gametophytes (see references in Remy & Hass, 1991; Schweitzer, 1983) demands re-evaluation of hypotheses on life-cycles of early land plants. These were previously based on extant homosporous pteridophytes where homoiohydric sporophytes capable of surviving water-stress may be limited in their distribution by desiccation sensitive, autotrophic gametophytes (Edwards, 1980b; Kenrick & Crane, 1991, but see Gray, 1985b). In the Rhynie Chert, gametangiophores possess axes with water-conducting cells, cuticles and stomata - anatomical characters that both allow identification with co-existing sporophytes (*e.g.* *Aglaophyton* and *Horneophyton*) and demonstrate homoiohydricity. In that the gametangia themselves resemble those of extant embryophytes, free water was still needed for fertilization. Thus it is possible that early land plants were not as strictly confined to humid habitats as previously thought, but because the fossil record is biased towards precisely such habitats (*e.g.* coastal, lacustrine and riparian) preservation of plants from drier ecosystems is unlikely.

Accumulating evidence suggests that in the Lower Devonian terrestrial plants were capable of reducing surface erosion and even of creating deeper physical disturbance resulting in break-up of rock. Their increase in height and branching and hence biomass would have enhanced organic matter input into soils, and this initially may have been accompanied by a decrease in rate of turnover as percentages of recalcitrant materials, particularly lignin, increased (Robinson, 1990). Little is known about the evolution of lignin decomposers: there may well have been a time lag between the introduction of the polymer in any great amounts into soils and its adoption as a fungal substrate. The roles of fungi in these early terrestrial ecosystems are largely unexplored. Of particular relevance is the hypothesis that on mineral nutritional grounds, pioneering land plants with weakly developed absorbing systems could not have survived on land in the absence of a mycorrhizal fungus (Pirozynski & Malloch, 1975). To date, although fungi are abundant in Rhynie Chert megafossils, there is little unequivocal evidence for their

trophic status. The majority appear to be decomposers, but certain cysts resemble the chlamydospores of the extant vesicular arbuscular mycorrhizal fungus *Glomus* (Stubblefield & Taylor, 1988; Taylor, 1990) while Taylor, Remy & Haas (1992) have recently described fungal parasites of algae.

The best direct evidence for Lower Devonian ecosystems comes from the Siegenian autochthonous chert deposit at Rhynie, where higher plant communities grew on sandy substrates bordering shallow pools on an alluvial flood plain. Associated with the plants are Cyanobacteria and algae, presumably colonizers of the pools and moist surfaces. The organisms are preserved as silica permineralizations produced after flooding with silica-rich water from hot springs (Trewin & Rice, 1992).

When influx was gentle, plants are preserved in growth positions but more usually they were knocked over. Some of the accumulations of fragmentary plants and plant litter are now interpreted as having been washed in during periods of flooding rather than as autochthonous peats (Clare Powell, pers. comm.) although there is also some evidence for weakly developed soils with organic matter mixed with sediment. The proximity of the hot springs and incontrovertable evidence for flooding raises the possibility that the plants were adapted to a highly stressed environment such as pertains in Yellowstone National Park, Wyoming, today. Indeed the taxa are not recorded elsewhere. Although their organization is similar to that in coeval plants, they lack the peripheral thick-walled support tissues seen in zosterophylls and *Psilophyton* that are considered possible adaptations for survival during drought conditions. Of particular relevance here is the anatomy of the first zosterophyll (*Trichopherophyton* (Lyon & Edwards, 1991)) to be described from the chert, which, like the remaining taxa probably relied for support on turgid parenchymatous tissues - tissues that would readily be decomposed in more conventional sedimentary environments. Thus differences in composition may relate to both ecology and taphonomy, the latter the best explanation for the absence of fossils with *Aglaophyton* organization elsewhere.

### *Ecology*

Food webs were evidently well developed by Gedinian times but were based on the typical decomposer/microherbivore chain such as occurs in modern soil and litter communities rather than the more familiar macroherbivore chain above ground. Evidence for this is the lack of macroherbivores in any of the known Siluro-Devonian terrestrial biotas (*i.e.* Ludford Lane, Rhynie, Alken, Gilboa, Fig. 1); only predators, decomposers, and possibly fungivores are present. This domination of ecosystems by the decomposer chain may have persisted even into the late Palaeozoic, since direct evidence of herbivory (*e.g.* chewed leaves) in the Upper Carboniferous (Scott & Taylor, 1983) is weak compared with its abundance in later eras (Chaloner, Scott & Stephenson, 1991). The difficulty of digesting lignin and other toxic by-products, together with the low nutritive value of the vegetative parts of vascular plants, may be the reason for the slow evolution of this lifestyle (Shear, 1991). Even in living animals, evidence for primary cellulases is weak and controversial (Martin, 1991); herbivores utilize an intestinal flora of symbiotic bacteria and fungi to degrade plant material before it can be absorbed by the animal.

It is a logical step therefore, from the external decomposer to the herbivore by internalizing the decomposition part of the chain. Thus the chain is short-circuited, and plant detritus reaches the ground in the form of frass rather than as newly discarded leaves *etc.* Early evidence of the decomposer chain comes from coprolites and gut contents. Lycopod tracheids have been found in the intestine of the giant Carboniferous myriapod *Arthropleura* (Rolfe & Ingham, 1967), which suggests they fed on the wood of fallen trees (Shear & Kukalová-Peck, 1990). Smaller arthropleurids are also known from the Devonian of Gilboa (Shear & Kukalová-Peck, 1990) and Onteora (Selden & Shear, 1992), New York. Coprolites have been described by a number of authors from coal balls, both from the matrix (*i.e.* peat) and within galleries in wood in a coal ball (Baxendale, 1979; Scott & Taylor, 1983). Coprolites are also known from the Lower Carboniferous of France and Scotland (Scott, 1977; Scott, Chaloner & Paterson, 1985; Rex & Galtier, 1986), the Devonian of the Welsh Borderland (see later) and the Silurian of Sweden

Period (10 <sup>6</sup> yrs BP)	Stage	Silurian and Devonian localities with terrestrial biota
375 DEVONIAN	Givetian	Gilboa, New York: lycophytes, progymnospermophytes; spiders, trigonotarbids, mites, centipedes, arthropleurids, scorpions, eurypterids; deltaic mudstone
380	Eifelian	
387	Emsian	Alken-an-der-Mosel, Germany: algae, lycophytes, rhyniophytes; eurypterids, xiphosurans, crustaceans, molluscs, fish, trigonotarbids; brackish lagoon Rheinischen Schiefergebirge, Germany: lycophytes, trimerophytes, <i>Taenioocrada</i> ; <i>Lingula</i> , ostracodes, bivalves, fish, eurypterids, trigonotarbid; flood plain Rhynie, Scotland: algae, zosterophyllophyte, rhyniophytes, <i>Asteroxylon</i> ; collembolans, trigonotarbids, mites, crustaceans; terrestrial hot spring
394	Siegenian	
401	Gedinnian	
— 410 SILURIAN	Přídolí	Ludford Lane, England: rhyniophytes, <i>Nematothallus</i> ; trigonotarbids, centipedes, eurypterids, scorpions, restricted marine fauna; sub/intertidal lag deposit
415		

Fig. 1. Stratigraphic chart showing the earliest terrestrial biotas, of late Silurian to mid-Devonian age. For details see: Gilboa - Kethley *et al.* (1989), Norton *et al.* (1988), Norton *et al.* (1989), Schawaller, Shear & Bonamo (1991), Selden, Shear & Bonamo (1991), Shear (1986), Shear & Bonamo (1988), Shear *et al.* (1984), Shear *et al.* (1987); Rhynie - Hirst (1922), Hirst & Maulik (1926); Ludford Lane - Jeram, Selden & Edwards (1990); Alken-an-der-Mosel - Størmer (1970-76); Rheinischen Schiefergebirge - Schultka (1991).

(Sherwood-Pike & Gray, 1985). Whilst the presence of coprolites gives information about the presence and activities of animals, it tells us little about what type of animal produced the coprolite or what it was actually eating, since faeces represent material rejected as food.

Actual damage to plants has been observed in the Rhynie Chert in the form of lesions to stems of *Rhynia*, as illustrated by Kevan, Chaloner & Saville (1975) and Rolfe (1985). The wounds show necrosis and hypertrophy of neighbouring cells, the darkening of some cells suggesting a chemical wound response. Various ideas have been put forward to explain the observed features: physical damage by hot water or volcanic ash, by sap-feeding arthropods, or by parasites, fungi, nematodes or mites (Rolfe, 1985). There seems little doubt that the damage occurred while the plants were alive and they continued to react to the wound. Whereas physical damage by heat or irritant ash crystals cannot be ruled out, it would be expected to occur in distinct horizons. Fungi might be expected to attack a wound already inflicted, which begs the question of what caused the original wound. There is little doubt that nematodes existed from early in the Palaeozoic though their fossil record contains many enigmas (Conway Morris, 1985). Interestingly, the mites described from the Devonian localities (Norton *et al.*, 1988, 1989; Kethley *et al.*, 1989) belong to modern families of free-living predators on nematodes and other small, soft-bodied animals, rather than plant parasites, though they may have been fungivorous (Rolfe, 1985). The highly specialized parasitic mites are the only arachnids which feed on plant material. The trigonotarbid arachnids found at all the Devonian sites (Fig. 1) bear chelicerae which belong to the typical pulmonate arachnid type (Shear *et al.*, 1987) and, whilst it is possible they could have inflicted a wound on a *Rhynia* stem, to do so would involve unnatural contortions of the animal! Their chelicera bears a fang which opposes a group of large teeth and both hand and fang bear brushes of setae; the chelicera is apparently optimized for gripping prey whilst externally digested fluids are sucked into the mouth. Suctorial mouthparts in insects and mites are highly specialized (Hughes, 1959; Shear & Kukalová-Peck, 1990) and quite unlike those seen in the Trigonotarbida. There are many ways in which delicate meristems, particularly if exposed, could have become damaged, thus invoking a wound response and the apparent presence of herbivore damage in the mature stem.

### *Spines*

The absence of fossil evidence for herbivores in these early terrestrial systems poses questions as to the functions of spines commonly found on coeval plants. The possibility that they were not so much concerned with defence, but with increasing area for light harvesting may well seem more attractive. Gensel (1991) in describing a variety of spine types in *Sawdonia acanthotheca* ranging from undivided to larger broad emergences with up to eight pointed segments suggested that they may provide a model for the evolution of the divided microphyll such as is seen in *Leclercqia*. However in *Sawdonia ornata*, the tips of the undivided spines are frequently open with dark stains, suggestive of exudation. This may merely indicate excretion of secondary metabolites, but is perhaps more suggestive of chemical defence. Further, it is difficult to apply a photosynthetic role to the unicellular, very sharply pointed spines of *Trichopherophyton* in the Rhynie Chert



(see discussion in Lyon & Edwards, 1991). On the other hand, the spines in these plants would be no defence against any of the known Devonian animals, since these animals were far too small to have grazed the plant stems.

### *Spores and sporangia as food sources*

In the absence of any documented storage organs, the sporangia of early land plants constitute their greatest concentrations of energy resources, and would thus seem prime targets/important substrates for early herbivores. The trend towards increased numbers and concentrations of sporangia would have enhanced their value. Availability of nutrients would have decreased on maturation of spores, when sporopollenin was deposited. Even so, Southward (1973) postulated that pollen feeders were the most primitive herbivores, while Chaloner showed experimentally that although the majority of spores pass undamaged through guts of locusts and millipedes some are cracked open (Chaloner, 1976; Chaloner *et al.*, 1991). Direct evidence for spore-feeding is absent, but Fanning *et al.*, (1991) in considering the functions of the prominent spines on the sporangia of *Pertonea langii*, suggested a defensive role. Indirect evidence comes from coprolites. Two coalified fusiform masses of spores have been recovered on maceration of Gedinnian sediments from the Welsh Borderland. Neither show any indications of an enclosing sporangium wall. In the first, the vast majority of spores belong to two dispersed taxa, closely related structurally, but differing markedly in size and in nature and size of ornament, and are associated with small amounts of structureless sheets or frass. The second, of almost identical shape, contains a wider range of spore taxa and much more unidentifiable debris. Unlike the first, many of the spores are damaged, and we have little doubt that this is a coprolite and may derive from a spore-feeding arthropod. The nature of the first is more conjectural. Similarities in spores and the bimodal size distribution initially suggested heterospory, but the absence of tetrads, the presence of extraneous material and the lack of a wall taken in conjunction are perhaps more indicative of a coprolite. That the product was a spore-feeder seems less likely, in the absence of spore damage. It was more probably an indiscriminate detritus-feeder that chanced upon, ate and excreted the undigested spore masses. In general, as noted above, spores in coprolites tell us little about the food of the producer. Spores were probably widespread and thickly strewn at some seasons in the Devonian litter, just as today. Any non-specific litter feeder would ingest many spores, possibly of a single species of plant, and these are likely then to pass through the gut unharmed. One can imagine evolution proceeding to the use of gut microflora or enzymes to crack spores and thence to the development of jaws for the purpose of spore feeding, or the utilization of the animal by the plant as a dispersal vector, perhaps combined with partial degradation of the sporopollenin wall to aid germination. In this context, the evidence of *Monoletes*-type seed-fern pollen between the ventral plates of Upper Carboniferous *Arthropleura* indicates the abundance of such pollen in the litter through which this animal was ploughing (Scott & Taylor, 1983).

In the Rhynie Chert, trigonotarbids are commonly found within plant stems or sporangia (Kevan, *et al.*, 1975; Rolfe, 1980; 1985). This has been given as evidence in favour of herbivory. However, many trigonotarbid fossils are moulted skins (podomeres inside abdomen for example); also, *c.* 15 dehisced

sporangia have been examined which could be shown to be in growth position and no arthropods found inside (Rolfe, 1980). Therefore, it is more likely that these relationships represent either debris of trigonotarbids and plants drifted together or animals seeking shelter inside rotten stems or sporangia, for moulting for example. Comparison of Rhynie with modern hot-spring environments such as in Yellowstone National Park, Wyoming, suggests that the Rhynie biota was not engulfed by a sudden flood of hot water but lived in close proximity to the spring and the continual flow of water deposited sinter over dead material. New areas could become engulfed occasionally, but not violently, so that most animals preserved are likely to be moulted skins rather than carcasses.

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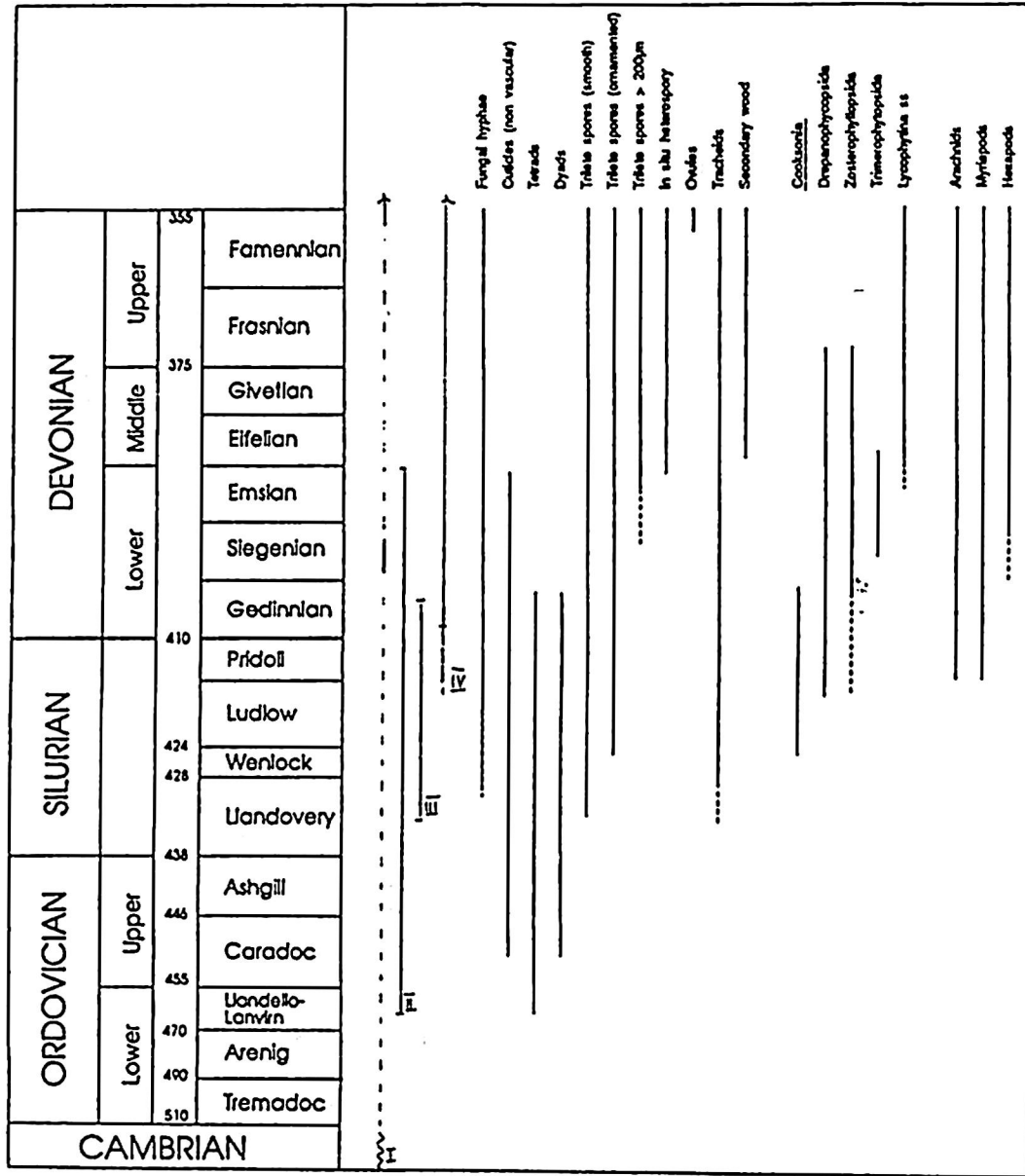


Table 1. Stratigraphic chart for most of the Lower Palaeozoic with ranges of Phases (I-IV) and key elements. Dotted lines indicate uncertainties in dating. Dashed line in Phase IV reflects discrepancy between present north and south hemispheres, and in I lack of direct fossil evidence.

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*(Based on a paper presented to the Botanical Society by Dr Dianne Edwards in February, 1992.)*

### **Phase 1 - ?Precambrian Extending into Early Phanerozoic and Later**

Current thinking favours the existence of a terrestrial ground cover in the Precambrian perhaps as early as 2,200 Ma ago, but although there appears to be good evidence for emergent subaerial surfaces with high carbon content in the Precambrian, direct fossil evidence for a covering of presumably prokaryotes has not yet been documented (see Wright, 1985; Retallack, 1990). Circumstantial evidence is based on the widespread occurrence of Cyanobacteria in the Precambrian, including inhabitants of the intertidal zone (Mendelson & Schopf, 1992), on similarities between some of the Cyanobacteria with soil- or crust-forming types today (*e.g.* *Eosynechococcus*, *Kakabekia*) and on the existence of extant microbes in a wide range of stressed environments, from deserts to sabkhas to hot springs (*e.g.* Campbell, 1979; Golubic & Campbell, 1979; Knoll, 1985). Thus it seems reasonable that the land surfaces, particularly when damp, were initially coated by photosynthesising mats of Cyanobacteria plus other prokaryotes and possibly fungi involved in decomposition, and then eventually by photosynthesising protists ('algae'), the timing of the appearance of the latter on land perhaps constrained by low ozone density (Fischer, 1965; Margulis, Walker & Rambler, 1976; Gray & Boucot, 1977). Retallack (1990, p. 366-371), in his detailed descriptions of putatively vegetated Precambrian palaeosols, listed the kinds of evidence which should be evaluated in the absence of fossils. These include the detection of wispy trace fossils, the isotope analysis and distribution of organic carbon, the profiles of minerals (such as phosphate) cycled by organisms and the detection of particular fabrics and structures that can be related to sediment binding or surface 'varnishing'. Retallack cited the 3,000 Ma Jerico Dam and the 2,200 Ma Waterval Onder palaeosols as probable Precambrian examples of soils produced by interaction between organisms and sediment on some of the above criteria, while Beeunas & Knauth (1985) cited depleted  $\delta^{13}\text{C}$  and  $\delta^{14}\text{C}$  values at one horizon in the 1,200 Ma Mescal Limestone of central Arizona as evidence for a vegetated, subaerially exposed surface.

Such surface mats would have had limited sediment binding capacities but could have encrusted a wide range of substrates. They may well have resulted in the development of very thin layers of humus with input of nitrogen locally enhanced by Cyanobacteria in moist areas, and in the creation of microenvironments for cryptozoans. This type of vegetation, as Wright (1985) emphasized, would have been outcompeted by taller plants, but persists even today in more hostile environments inaccessible to higher plants and perhaps even more importantly to 'potentially disruptive metazoans' (Knoll, 1985). In the early Palaeozoic it would have created the habitats for multicellular terrestrial green algae, postulated by Stebbins & Hill (1980) to have been ancestral to higher land plants.

#### *Terrestrial Metazoa*

Evidence for the existence of Metazoa on land during phase 1 is controversial (Robbins, Porter & Haberyan, 1985; Chaloner, Scott & Stephenson, 1991) and conjecture is rife. Shallow marine, and possibly freshwater, metazoans had become well-organized and diverse by the late Precambrian (Ediacaran faunas), and it may be from this stock that terrestrial metazoans were derived. The first fossil representatives of animal groups which are wholly terrestrial today do not provide

**Appendix**

Plant genera mentioned in the text, with their possible affinities.

**Vascular plants**

Rhyniophytina ( <i>sensu</i> Edwards & Edwards, 1986)	<i>Cooksonia pertoni</i> <i>Horneophyton</i> <i>Rhynia</i>
Zosterophyllophytina	<i>Gosslingia</i> <i>Sawdonia</i> <i>Tarella</i> <i>Trichopherophyton</i> <i>Zosterophyllum</i>
Trimerophytina	<i>Pertica</i> <i>Psilophyton</i> <i>Trimerophyton</i>
Lycophytina	
Protolpidodendrales	<i>Leclerqia</i>
Drepanophycopsida	<i>Asteroxylon</i> <i>Baragwanathia</i>
Progymnospermophyta	<i>Rellimia</i> <i>Aneurophyton</i>
Incertae sedis	<i>Barinophyton</i> <i>Kaulangiophyton</i> <i>Taeniocrada</i> <i>Thursophyton</i>
Incertae sedis - embryophyte	<i>Aglaophyton</i> <i>Pertonella</i>
Incertae sedis - non-embryophyte	<i>Nematothallus</i>



evidence for the timing of terrestrialization since these early forms may have been aquatic, and perhaps preadapted for land life. Examples are a possible oligochaete annelid from the Ordovician Trenton Limestone of Quebec (Conway Morris, Pickerell & Harland, 1982), *Aysheaia*, an onychophoran found in the undoubtedly marine Burgess Shale (Middle Cambrian, British Columbia; Whittington, 1978), myriapod-like fossils in marine Silurian (Mikulic, Briggs & Kluessendorf, 1985*a,b*) and Middle Cambrian (Robison, 1987) strata, and euthycarcinoids (early uniramians) from the Silurian of Western Australia (K.J. McNamara pers. comm.; Anderson, 1991). The existence of such pre-terrestrial forms does not of course rule out their coexistence with fully terrestrial relatives, thus, for example, it is likely that the first terrestrial scorpion lineages coexisted with their aquatic relatives for much of late Palaeozoic time (Selden & Jeram, 1989). Aquatic precursors can be suspected when cladograms predict the existence in suspiciously early times of groups presently wholly terrestrial. The most primitive metazoan group which occurs in terrestrial habitats today is the Platyhelminthes, but these animals also occur in marine, freshwater and soil habitats today, and lack a fossil record (Conway Morris, 1985), so the timing and route of their colonization is uncertain (Little, 1983; 1990).

## Phase 2 - Llanvirn into Lower Devonian

Beginning in the Llanvirn (Gray, 1991), evidence for this phase is based not on megafossils but on sporomorphs (sometimes called cryptospores) and cuticles recovered from bulk maceration of fine-grained clastic sediments. Cryptospores as defined by Richardson, Ford & Parker (1984) are tetrads, dyads and monads lacking haptotypic features (*e.g.* triletes) associated with germination. The end of the phase, marked by the disappearance of cryptospores, may be in the early Devonian, but the record is confused by reworking and the possibility that cryptospores, particularly monads, are overlooked in assemblages dominated by miospores of vascular plants.

### *Sporomorphs*

Sporopollenin-impregnated resting or dispersal units are not confined to higher plants (see *e.g.* acritarchs, prasinophycean cysts (Tappan, 1980)). Cryptospores are not algal, and while they cannot be directly attributed to a higher plant group, their distribution in certain sediments and their general similarities with bryophyte spores suggest a subaerial origin and the exploitation of wind for dispersal (Gray 1985*a*; 1991). Cryptospores thus present indirect evidence for a land vegetation for which there is little or no megafossil record. This suggests absence from vegetative organs of recalcitrant biopolymers, such as lignin, that enhance fossilization potential, and supports ecophysiology and physiognomy more similar to bryophytes than to vascular plants (Gray 1985*b*; see also Bell, 1989 'diads' in liverworts). The recent description of dyads in late Silurian elongate sporangia which are barely distinguishable from subtending unbranched axes (Fanning, Richardson & Edwards, 1991) points to very simple sporophytes. The fossils are fragmentary and it has not yet been possible to show (perhaps by ultrastructural studies) that these separating dyads are homologous with Ordovician and early Silurian permanent forms, nor indeed to determine the affinities of the late Silurian fossils. The earliest dyads and tetrads are described as 'permanent' because they do not readily separate into discrete units, and they are frequently surrounded by a resilient membraneous sac

which may be smooth or ornamented. The beginning of this phase is based on tetrads reported from the mid-Ordovician (Llanvirn) of Saudi Arabia (see Gray, 1991), while low diversity assemblages of tetrads and dyads are recovered from Caradoc sediments in the type area (Welsh Borderland; Richardson, 1988) and in the Murzuk Basin, Libya (Gray, Massa & Boucot, 1982). In the Ashgill they are also found in central Bohemia (Vavrdova, 1984), and the Appalachian region, Kentucky and Quebec in North America (see references in Gray, 1985a) and possibly South Africa (Gray, Theron & Boucot, 1986). Records of somewhat more diverse sporomorphs of greater size occur in the early Silurian of South America (Parana Basin, Brazil; Gray *et al.*, 1985), Ghana (Bär & Riegel, 1980), North Africa (Tunisia, Morocco) as well as North America and Britain. For reviews, see Gray (1985a; 1988), and Richardson & Edwards (1989). There are far too few records in the Ordovician to allow sensible assessment of the centre of origin and rate of spread of these unknown pioneer spore-producing plants. The early records occur in relatively high latitudes in Gondwana and Rhenish provinces (Libya c. 75° S; Britain c. 50° S in McKerrow & Scotese, 1990) and although there are still many Gondwana occurrences in the Ashgill and Rhuddanian, the north American records indicate migration towards the equator (*e.g.* c. 20° S).

Thus by the end of the Ordovician land surfaces over a wide geographic area were affected by this second phase of colonization. Detection of diversification typical of adaptive radiations within the Silurian is problematic because these sporomorphs possess relatively few characters, but that there was possibly gradual change in the composition of this phase of terrestrial vegetation is evident from Richardson's (1988) recent attempt to subdivide his *Nodospora* sp. A - *Dyadospora murusdensa* Assemblage zone (roughly equivalent of Gray's microfossil Assemblage Zone 1) into three, although clearly more records are needed on a global scale to substantiate it. In the late Silurian (Prídolí) although spore diversity is low compared with trilete spores, in absolute abundance cryptospores outnumber them and remain numerous in the Gedinnian, suggesting that the parent plants were still an important component of land vegetation (Fanning, Richardson & Edwards, 1991; Richardson, pers. comm.).

### *Cuticles*

In the Libyan Caradocian record, Gray, Massa & Boucot (1982) illustrated a fragment of cuticle with cellular imprints similar to examples described in the Silurian (Lang, 1937; Edwards, 1982; Edwards, Edwards & Rayner, 1982) which are attributed to *Nematothallus* Lang. Such cuticles are unequivocally derived from land plants, although the nature of the underlying tissues and indeed the affinities of the plant remain obscure. The lack of alignment of the 'cells' (alignment is characteristic of cuticles from plants with axial organization), together with their very irregular topography, suggests that the organism was thalloid, possibly encrusting mud and rock surfaces. Lang (1937) considered that the cuticles covered a plant of predominantly tubular construction, including internally ornamented tubes (Burgess & Edwards, 1991). Smooth tubes are recorded in the Ordovician, but the earliest ornamented forms occur in the late Llandovery (Pratt, Phillips & Dennison, 1978) long after the first appearance of the cuticles: more records are again required to evaluate the significance of these occurrences.

It is also tempting to link the cuticles with the sporomorph producers. The lack of permanent dyads and tetrads in the Siegenian and Emsian when cuticles remain common, is evidence against such an association, except that rates of evolution of different organs of the plant could have become uncoupled such that spores were produced as monads.

The absence of any perforations in these cuticles resembling stomata or liverwort pores (but see Edwards & Rose, 1984) suggests that their primary function may not have been to reduce evaporation, achieved in extant plants by a waxy layer within the cuticle. A superficial resilient covering could have acted as a UV or light absorbing screen, facilitated run off or deterred pathogens in the pioneering land plants, with changes of function and chemistry later.

### *Coalified fossils*

Maceration of circular, elliptical and coalified compressions with irregular outlines, just a few millimetres in diameter from Llandovery sediments (Pratt *et al.*, 1978) have yielded sheets of organic matter with possible cellular imprints and fragments of wefts of both smooth and ornamented tubes (Niklas & Smokovitis, 1983). In one example longitudinally aligned smooth tubes surround similarly orientated banded forms. Such tubes characterize the Nematophytales (Lang, 1937) although the organization of the axial fragment recovered from an irregular compression (3 x 1 mm), is unique. The authors interpreted the fragment as analogous to the conducting strand of higher plants, and argued that environment of deposition and  $\delta^{13}C$  values supported a terrestrial origin for the fragments. Relationship with the spore or spore producers remains largely conjectural.

### *Ecology*

Lack of information, because of non-preservation of the vegetative parts of the spore producers, suggests these land plants had not evolved the homoiohydric characters of vascular plants (Raven, 1984), and Gray (1985*b*) argued persuasively for a primary adaptive radiation on land of poikilohydric plants with a non-vascular grade of organization comparable with that of the bryophytes, although not necessarily directly related to that group. Whatever the affinities, it seems highly likely that terrestrial vegetation comprised a low ground cover with maintenance of high humidity just above the ground. In undisturbed areas there would have been gradual build-up of a thin layer of humus, but by comparison with soils developed under moss and lichen cover today (Wright, 1985) there would have been little mixing of rocky substrate and organic matter, and considerably less (<50%) mineral weathering, hence macronutrient production (e.g. Mg, P, K), than under vascular plants (Retallack, 1985). However, present day associations of moss and nitrogen-fixing cyanobacteria found as pioneers on virgin substrates (e.g. Surtsey in Iceland, Rodgers & Henriksson, 1976) could have increased productivity and accelerated such build-ups of humus, but we have no direct evidence for this. Gray (1985*b*) reviewed the attributes of extant bryophytes that allow them to colonize a wide range of water-stressed environments. Whether or not the earliest higher plants were highly adapted, perhaps restricted to moist environments (K-selected) or were opportunists (r-selected) cannot be determined (Selden & Edwards, 1989). Of

relevance here is Dewey's suggestion (in Boucot *et al.*, 1974) that the irregular topography of a red late Ordovician palaeosol was maintained by stabilization of the surface by clumps of non-vascular land plants, lacking any large rooting organs, and Retallack (1990) compared this with moss or lichen colonization of desert or alpine rocky substrate. The climate in this Nova Scotian example was interpreted as tropical, seasonally dry and sub-humid. It is worth emphasizing that many such palaeosols are preserved because they represent an unusual set of environmental conditions and ones which today produce somewhat stressed/hostile habitats colonized by highly adapted plants, and may be atypical of more widespread vegetation of the time.

Important in the consideration of routes onto land for animals are the various environmental scenarios developed for Precambrian to Ordovician emergent surfaces, (see *e.g.* Beerbower, 1985). Without the ameliorating effects of macrophytes, physical conditions for life would have been harsh and subject to wide fluctuations (Beerbower, 1985; Gray, 1985a; Shear, 1991). Thus the barriers to colonization were more severe for the pioneers than for later settlers. Once established, the founder biota would have provided routes and niches for organisms poorly adapted for unstable habitats. Physical factors such as temperature, water supply, solute concentration, *etc.* are unpredictable or wildly fluctuating in terrestrial habitats in contrast to their stability in the aquatic milieu. Possibly the most unstable habitat today is the marine littoral zone, and it is this area which is first encountered by animals terrestrializing directly from the sea. Littoral animals adapt to the great and rapid changes in water supply, temperature, salinity, *etc.* of the littoral zone using strategies of physiological tolerance. Such animals have proved more successful land colonizers than those which regulated their body fluids to the osmotic pressure of fresh water (Little, 1990). The regulators can be as intolerant of unstable physical conditions as are fully marine animals. In contrast, considerations of the water relations of extant halophytic vascular plants suggest that phytotransmigration would have been more readily achieved physiologically from fresh water, although this leads to problems with the generally accepted characean ancestry of land plants (see also pp.344 and 348). Fresh water characeans maintain their intracellular osmolarity constant whereas terrestrial vascular plants, many marine algae and some soil and fresh water algae tend to keep cell turgor constant when environment changes. However there is a euryhaline characean *Lamprothamnion* with the latter capability, which might exemplify the biochemical evolutionary pathway of the ancestral group (for references, see Raven, 1985). There is also the possibility that the immediate ancestors of the higher plants were themselves terrestrial (Stebbins & Hill, 1980) and were turgor regulators.

Inland habitats in the early Palaeozoic must have resembled modern deserts with their immature, mineral soils and rapid run-off. For littoral organisms to colonize such an environment requires tolerance of a somewhat greater range in temperatures but not water supply or salinity. Pioneer metazoans in these habitats are likely to have been desiccation tolerators which require high humidity for activity but can withstand (often long) periods of drying out (Selden & Edwards, 1989). Among lower metazoans, rotifers, nematodes and tardigrades undergo cryptobiosis, forming a desiccation-resistant cyst to weather extremes of drought, temperature or salinity, and this may also be the dispersal stage (see a recent review

of cryptobiosis in tardigrades: Wright, Westh & Ramlow, 1992). Nematodes and rotifers are not strictly terrestrial since whilst they are tolerant of desiccation, they are only active when in water (albeit a thin film in some situations). Tardigrades have an arthropod-like cuticle which includes a lipid layer to reduce water loss, and some species are active in air, usually in moist situations such as in moss (Wright, 1991). Many tardigrades inhabit the littoral zone, and some cosmopolitan bryophilous species have been reported from littoral habitats (Wright *et al.*, 1992). Thus it is easy to conceive of littoral tardigrades with the ability to form tuns, dispersing by wind to inland vegetated habitats typical of phase 2.

### Phase 3 - Llandovery (Upper Aeronian) to Gedinnian

Evidence for earliest part is based on spores; the first megafossils identified as the spore producers occur from the late Wenlock and plants with similar aspect persist into the Lower Devonian.

#### *The plant evidence*

The phase is characterized by the appearance of miospores - monads with well-defined, discrete trilete marks. The age of the oldest is equivocal, but probably Aeronian (Llandovery type area - Burgess, 1991; Tuscarora Formation, Pennsylvania - Strother & Traverse, 1979; western Libya - Hoffmeister, 1959), and there are convincing records in the Rhuddanian of Libya (Richardson, 1988), North America and possibly Ireland (see reviews in Gray 1985a; Richardson & MacGregor, 1986; Richardson & Edwards, 1989). The existence of *Ambitisporites vavrdovii*, which has a thin proximal exine and which when complete shows an irregular trilete crack, together with *Ambitisporites avitus* and slightly preceeding it, may be evidence of evolutionary progression from a separating 'permanent' tetrad to trilete spore with discrete trilete (Richardson, 1988). The advent of sculptured spores in the late Wenlock (Homerian) heralded a major diversification in sporomorph sculpture and structure which continued into the Lower Devonian. The Wenlock event is recorded in southern Britain, Libya and Spain, and was more or less synchronous with the appearance of fertile megafossils of plants of pteridophyte-like aspect. Earlier Llandovery-age axes are sterile (Schopf *et al.*, 1966). The Irish fossils resemble *Cooksonia* which occurs in later Silurian and early Devonian sediments, but they are devoid of any anatomical detail. *Cooksonia* itself found in the Ludlow and Prídolf of north America, Britain, Bohemia, Libya and Podolia (Richardson & Edwards, 1989; Edwards, 1990) is characterized by smooth isotomously branching axes terminated by globular or discoidal sporangia. Although no complete plants have been found, the small diameter and lengths of Silurian axes are suggestive of plants of short stature, probably rarely more than a few centimetres tall. Admittedly limited evidence (Edwards, 1990) indicates that vegetation in late Silurian Laurentia was dominated by plants of this aspect (rhyniophytoids), with variation produced by differences in sporangial shape and nature of sporangial appendages (*e.g.* Edwards & Davies, 1990; Fanning, Edwards & Richardson, 1990) and it persisted into the early Devonian. The recent demonstration of tracheids in Lower Devonian *C. pertoni* confirms its vascular status (Edwards, Davies & Axe, 1992), but tracheids have not been seen in other Devonian rhyniophytoids nor in Silurian fertile axes (Edwards & Rogerson, 1976; Niklas & Smokovitis, 1983). As the *Cooksonia* tracheids were

very small and few, failure to demonstrate them in these taxa is understandable. A growing body of evidence from late Silurian sporangia has revealed that some of the spores in the dispersed record, particularly the oldest ones (*e.g. Ambitisporites*) were indeed produced by rhyniophytoids (Fanning, Richardson & Edwards, 1991). Such information indicates that although this third phase in phytoterrestrialization comprised plants of differing affinity from earlier ones, its substrate interaction would not have been that dissimilar. The sporophytes may have been slightly taller, and would certainly have been composed of more rigid and possibly decay-delaying tissues (sterome of Edwards, Fanning & Richardson, 1986; Robinson, 1990), but equally as a result of determinate growth would not have greatly enhanced phytobiomass and build-up of humus-rich soils. Although Richardson & MacGregor (1986) were able to distinguish five spore assemblage zones in the interval between Aeronian and the end of the Silurian, there is as yet no evidence for major change in vegetation in the present northern hemisphere.

Such uniformity in terms of vegetational impact from the Ordovician to almost the end of the Silurian may well provide an explanation for Retallack's (1990) observations on similarities (except in thickness) between a late Ordovician and a late Silurian (Ludlow) palaeosol. For the former at Potter's Mill, Pennsylvania, he envisaged that the closest extant vegetation analogue would be rootless liverworts and in the Ludlow Bloomsberg Formation he recorded 'indistinct wispy bioturbations of the surface horizon', the wisps being 1-5 mm in diameter and 'irregular subhorizontal to vertical branching tubular features' filled with clay or sand, which he considered to be traces of plant rhizomes. Irregular root-like bioturbations in red beds from the Prídolf of Nova Scotia and the early Devonian of Britain are interpreted as having been produced by xeromorphic rhyniophytes growing on dry soils, comparable today with desert, alpine or open wood-land vegetation of lycophytes. In contrast, based mainly on life cycles of modern pteridophytes and on the preservation of the rhyniophytoids in marine and fluvial sediments, it has been postulated that these simple land plants colonized moist habitats in coastal areas (Edwards, 1990; Edwards, Fanning & Richardson, in press). Retallack (1990) interpreted the palaeoenvironmental setting of some Llandovery putative rhyniophytoids (Schopf *et al.*, 1966) as a salt marsh, and a similar habitat is considered below for a late Silurian biota. However, there is no direct evidence for a saltmarsh environment in the Maine sediments, the plant-bearing beds being interbedded with conglomerates that have yielded marine faunas consistent with a shallow, subtidal, quiet setting.

### *Metazoa*

A possible scenario for colonization of "turfs" of bryophyte aspect by desiccation-tolerant Metazoa has been described in phase 2 above. Once colonizers became established, more permanent plant-animal relationships were developed, including the fungivore and decomposer niches in perhaps stable humid environments beneath vegetation clumps. Evidence of soil-inhabiting Metazoa in the Ordovician was described in the Potters Mill Clay Palaeosol from the uppermost Ordovician Juniata Formation of Pennsylvania (Retallack, 1985; Retallack & Feakes, 1987). The prominent *Skolithos* and similar burrows in this formation were interpreted as resulting from the activity of vermiform metazoans, possibly earthworms or