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Could land-based early photosynthesizing ecosystems have bioengineered the planet in mid-Palaeozoic times?

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Abstract:

The Ordovician and Silurian periods were times of major geological activity as regards palaeogeography, volcanism and climate change, the last of these evidenced by a series of cooling episodes and glaciations that climaxed in the Late Ordovician Hirnantian. The presence of cryptospores in the Darriwilian (Mid Ordovician) marked the advent of higher plants on land. A critical survey of direct (mega- and microfossils) and some indirect evidence in succeeding rocks indicates the presence of algae, bacteria, cyanobacteria, fungi, probable lichens, cryptophytes and basal tracheophytes. Similar associations of photosynthesizers and decomposers today in cryptogamic covers, e.g. biological crusts, except that bryophytes replace cryptophytes (basal embryophytes) and tracheophytes are absent. Thus extant cryptogamic covers, which make significant contributions today to global carbon and nitrogen fixation and prevention of erosion, provide an excellent analogue for the impacts of early land vegetation on both lithosphere and atmosphere. As a prerequisite to assessing impacts in Ordovician-Silurian times, with particular consideration of parameters used by climate modellers, the effects of a number of abiotic factors on the growth and survival of extant cryptogamic ground covers and their environmental impacts are reviewed. Factors include photosynthetically active radiation, ultraviolet radiation, temperature, water, oxygen, carbon dioxide, nitrogen, phosphorus, iron, surface roughness and albedo. A survey of the nature and extent of weathering facilitated by such vegetation concludes that it was limited based on depth of weathering when compared with that from rooted tracheophytes today, with minor effects on carbon dioxide drawdown. Since global net productivity from Ordovician–Silurian cryptogamic covers was very probably lower than today, and while the small fraction of intractable material in their organic carbon would have resulted in a more rapid turnover of terrestrial biomass, we conclude that there was decreased possibility of long term organic carbon burial. Hence there would have been very limited increase in atmospheric oxygen and decrease in carbon dioxide resulting from carbon burial.

Key words: cryptogamic covers, atmospheric evolution, climate models, rock weathering, volcanism, palaeogeography.

THE colonization of Earth’s subaerial surfaces by embryophytes is celebrated as a major event in the history of life – an event which not only greened the planet, but resulted in changes in atmosphere and lithosphere while ameliorating the latter, creating habitats for animals. Sixty years ago this bench mark tended to be equated with the advent, close to the Silurian/Devonian boundary, of vascular plants (tracheophytes) and their subsequent radiations/diversifications (e.g. Berkner and Marshall 1965), but it is now appreciated that the green revolution began much earlier and is marked, currently in the Mid Ordovician, by the appearance in palynological assemblages of spores of non-tracheophytic embryophytes (Rubinstein *et al.* 2010). Much credit for raising awareness and significance of such spores is due to the late Jane Gray, who advocated their bryophyte affinity and grade of organization, with inferences for their palaeoecology and physiology (Gray 1984), even though their architecture, tissue construction and life histories had next to no foundation in the fossil record. Initially she had subdivided the time interval into Microfossil Assemblage Zones I-III based on the appearance and relative frequencies of cryptospores and trilete spores (Gray 1985) and subsequently placed these in her mid Ordovician–Permian Palaeophytic Era (Gray 1993: Table 1). Evolutionary Level I in the Epeirophytic Era —Phycomycophytic (Precambrian-mid Ordovician) included algae, cyanobacteria, lichens, fungi but not embryophytes. Gray emphasized that level II included elements of I plus bryophytes or bryophyte-like plants that 'necessarily prepared the way for the development of vascular plants' (Gray 1993:159) that characterized levels III and IV.

Equally appropriate to the hypothesis to be tested here was the approach by Bateman (1991) who had subdivided the time interval into three phases:-

1, biochemical (*c.* 2000 Ma – Ordovician) when fundamental chemical pathways in algae and bacteria were established in aqueous environments;
2, anatomical (Ordovician – Silurian) which saw the emergence of most lineages and alternation of generations, based on turgor stabilized tissues;
3, morphological (Devonian acme) which was marked by disparity and increase in size.

Here we would also emphasize that in consideration of the impact of vegetation through time, changes in composition transcend taxonomic boundaries as ecosystems became cumulatively more complex. We put forward the proposition that the land was colonized from at least the Mid Ordovician to almost the end of the Silurian by a community that was a complex of varying proportions of (non-cyano) bacteria, cyanobacteria, algae, cryptophytes (basal embryophytes cf. bryophytes; *sensu* Edwards *et al*. 2014), basal tracheophytes, fungi and lichens, sometimes known in extant analogues as biological crusts etc., but here we use the term cryptogamic covers (CCs) (Elbert *et al.* 2012; see also LePage and Pfefferkorn 2000). Although today these communities flourish in environments where the amplitude and frequency of extremes of temperature and water availability preclude or greatly restrict the occurrence of vascular plants, this does not mean that CCs did not modify their environment. We would advocate that in the mid-Palaeozoic CCs also modified their environment, at least locally and, were eventually replaced by vascular plants in most habitats. In this paper we evaluate their ecological roles in CO_2 and N_2 fixation and hence soil fertility through, in part, nutrient availability from weathering and N_2 fixation, water retention, stabilization/erosion (local effects) and, via photosynthesis and weathering, atmospheric/climate changes (global effects).

Such potentially global impacts require an understanding of the physical world in Ordovician through Silurian times as sources of alternative drivers to global change.

ORDOVICIAN–SILURIAN WORLD

Climate and sea level

Atmospheric ρCO_2 was a major driver of Phanerozoic climate (Royer *et al.* 2004). Climate models indicate very high ρCO_2 values (8–20 PAL (Pre-Industrial Atmospheric Level)) in the early Palaeozoic before a large drop in the Devonian-Carboniferous in response to weathering induced by large vascular plants on continents (e.g. Berner 1991, 1994, 2006a, 2006b; Berner and Kothavala 2001; Fig. 1). Such high values, indicative of a greenhouse world, have to be reconciled with at least temporary falls to ρCO_2 <8 PAL required for late Ordovician glaciation(s) to occur. Among the physical parameters used in model simulations to reduce

ρCO_2 are continental silicate weathering, degassing fluxes from volcanism and orogenesis, and evolving palaeogeography with associated changes in sea level and ocean circulation (e.g. Berner models, Herrmann *et al.* 2004a; Nardin *et al.* 2011; Goddéris *et al.* 2014; Pohl *et al.* 2014). A long term cooling trend from the Cambrian to modern equatorial temperatures for mid-late Ordovican seawater is predicted from $\delta^{18}O$ stable isotopes (Trotter *et al.* 2008). Among few values reconstructed from $\delta^{13}C$ for atmospheric ρCO_2, ~16 PAL was reported from the late Ordovician (Yapp and Poths 1992).

Globally high sea levels in the Ordovician, which submerged continental margins in mid-low latitudes under vast areas of epeiric seas, reached a Palaeozoic maximum in the Late Ordovician (early Katian ~225 m above present day; Haq and Schutter 2008; Fig. 2A-C). With reduced land surface areas, low albedo would feed back to high temperatures. The Hirnantian climax of late Ordovician glaciation(s) was accompanied by a sharp sea level fall of 50-100 m (Brenchley 2004). Herrmann *et al.* (2004b)'s model simulations indicate that for ice sheets to form and glaciation to occur, even with reduced ρCO_2 to PAL 8, both a fall in sea level and reduction in poleward heat transport through ocean circulation would be necessary. Early Silurian post-glacial transgression re-flooded the continental shelves as another long-term deepening trend culminated in a mid-Silurian high before steady decline through into the early Devonian (Emsian; Haq and Schutter 2008; Fig.2D-F).

Palaeogeography and volcanism

Ordovician palaeogeography has the south pole on the drifting Gondwanan supercontinent, most continents also in the southern hemisphere and oceans covering northern temperate and high latitudes, and the north pole (Fig. 2; ~95 % of northern hemisphere covered by oceans in the mid-late Ordovician: Pohl *et al.* 2014). Ordovician–early Devonian closure of the Iapetus Ocean and the Tornquist Sea led to volcanic island arc/microplate–continent collision as opposed to true continent–continent collision (van Staal and Hatcher 2010) to form the Caledonide mountain chain and extensive terrestrial environments on the Old Red Sandstone continent (Laurussia; Fig. 2). While Iapetus was still wide, early Ordovician subduction and arc volcanism on both sides produced early Taconian (Laurentia), Penobscottian (Gondwana) and Finnmarkian (Baltica) orogenic events, with extensive peri-cratonic arc systems fringing both Laurentia and Gondwana through the Ordovician (van Staal and Hatcher 2010). During the closure of Iapetus, Avalonia, which formed part of a ribbon-like continent of arc terranes including Ganderia, joined with Baltica before collision with Laurentia took place in early Silurian times (Llandovery-Wenlock; Soper and Woodcock 1990; Cocks and Torsvik 2002; van Staal and Hatcher 2010). The Avalonian continent, Baltica and Siberia had drifted north into temperate to low latitudes with Iapetus closure, the formation of Laurussia and opening of the Rheic Ocean, while Gondwana moved southwards and rotated clockwise (Fig. 2). On Gondwana, Ocloyic/Famatinian orogenesis resulted from subduction related magmatism along the proto-Andean margin of South America (e.g. González-Menéndez *et al.* 2013). Remnants of mountain chains associated with Early Palaeozoic orogenesis via continental drift, preserved in many present day continents (Eurasia, North and South America, Australia and Antarctica; van Staal and Hatcher 2010), would have had much greater topographical significance in mid-Palaeozoic times.

Explosive volcanism, preserved as tephra layers (bentonites and tonsteins) in the rock record, has a peak of abundance in the Ordovician-Silurian (Kolata *et al.* 1996; Histon *et al.* 2007; Sell 2011; Fig. 3). Extensive volcanic activity in continental and volcanic arc settings associated with Iapetus closure is evidenced by K-bentonites in Ordovican-Silurian deep marine successions in Laurentia, Baltica and Avalonia (Fig. 3). In the Precordillera of

Argentina, intense arc-magmatism also on the southern margin of Iapetus is indicated by widespread and numerous Gondwanan K-bentonites from Early to Mid Ordovician (Floian-Darriwilian; Fig.3; Huff *et al.*1998). This concentrated volcanic activity corresponds to model estimates of volcanic rocks comprising 10.5-13.5 % of total continental surface between Late Ordovician and Early Devonian, and contributing 33 % of ρCO_2 consumption through weathering in the Late Ordovician (Nardin *et al.* 2011; cf. ~30 % today). Enhanced volcanic weathering leading to a large and rapid fall in seawater $^{87}Sr/^{86}Sr$ in the Mid–Late Ordovician (late Darriwilian–early Sandbian), and continuing through to the end of the Ordovician may have provided a major sink for ρCO_2 (Young *et al.* 2009), via the generalised equation (Raven and Edwards 2001): $1\ CaMg(SiO_3)_2 + 4\ CO_2\downarrow + 6\ H_2O \rightarrow 1\ Ca^{2+} + 1\ Mg^{2+} + 4\ HCO_3^- + 2\ Si(OH)_4$. A cluster of very large eruptions across 1-2 m.y. in the late Ordovician (basal Katian) spread ash across wide areas of N America (Deicke, Millbrig, Kinnekulle K-bentonites; $>2 \times 10^6$ km^2) and central-north Europe ($<7 \times 10^5$ km^2), and K-bentonites are also recorded at this time in S China successions (Fig. 3; Huff *et al.* 1992, 2010; Kolata *et al.* 1998; Histon *et al.* 2007; Sell *et al.* 2013). These occur shortly before the start of the early Katian GICE (Guttenberg) prominent carbon stable isotope excursion (Bergström *et al.* 2010). The effects of explosive volcanic activity introducing ash into the water column, as well as ocean anoxia and heavy metals, have been suggested as the most likely explanations for teratological effects widely recorded among Ordovician to early Devonian acritarchs and chitinozoans (Munnecke *et al.* 2012; Delabroye *et al.* 2012).

Glaciations

Major explosive events are known to result in global cooling on a historical scale as a result of oxidation of volcanic sulfur gases to sulfuric acid aerosols that backscatter and absorb incoming solar radiation (e.g. Chenoweth 2001). Arc volcanism is typically less frequent than non-arc but more violent, increasing in SO_2 outgassing with explosivity (Bluth *et al.* 1993). Larger, super-eruptions (>450 km^3) have occurred at a frequency of 100-200 000 years, most recently at 26 000 BP (Oruanui eruption at Taupo, NZ; Self 2006). Four Late Cretaceous and Pliocene episodes of widespread explosive volcanism interpreted from tephra in marine drill cores correlate with glacial episodes and have been implicated as causal in climate cooling (Sell 2011).

Late Ordovician-Silurian glaciations span a period when atmospheric ρCO_2 was relatively elevated (<15 PAL; Berner and Kothavala 2001; Nardin *et al.* 2011). Since temperature and ρCO_2 are positively correlated this apparent anomaly may be explained by short term perturbation beyond the resolution of global climate models (Berner and Kothavala 2001), contributed to by lower solar luminosity that raised the CO_2-threshold for ice formation (Royer 2006). The short-lived glacial maximum of the late Ordovician Hirnantian glaciation corresponds to sea level fall, mass extinction events and the major HICE stable carbon and oxygen isotope excursions (Brenchley 2004). Arguably however this represents the culmination of much longer term climate cooling (Frakes and Francis 1988; Trotter *et al.* 2008; Veizer *et al.* 1999), with ρCO_2 drawdown resulting from increased volcanic weathering up to the onset of Ordovician glaciation (Kump *et al.* 1999; Young *et al.* 2009; Lefebvre *et al.* 2010). Buggisch *et al.* (2010) proposed that a single very large late Ordovician (earliest Katian) volcanic eruption (Deicke K-bentonite) provided the trigger for glaciation. Model simulations for the Palaeozoic, based on an absence of land plants, indicate a cooling of 3^oC in from Mid-Ordovician to early Silurian in response to enhanced weathering of fresh volcanic rocks (highest in the Late Ordovician) combined with the effects on overall continental silicate weathering of continental plate movements and changing sea levels (Nardin *et al.* 2011). Notably, however, palaeogeographical effects were considered more important than volcanism through this period in controlling ρCO_2 drawdown (Nardin *et* *al.* 2011; Goddéris *et al.* 2014). By contrast, models for the Devonian include land plant cover, which reduced albedo and led to warming that countered increased continental silicate weathering and resulted in CO_2 drawdown without temperature change (Le Hir *et al.* 2011).

Palaeoclimatic cooling and ρCO_2 drawdown have been linked with oceanic anoxia, deposition of black shales and C sequestration (e.g. Page *et al.* 2007). Black shale successions are common from late Mid-Ordovician to Late Silurian and include notably organic C-rich de-glacial black shales deposited during transgression by eutrophic epeiric seas (e.g. Luning *et al.* 2000; Page *et al.* 2007; Edwards *et al.* 2009; McLaughlin *et al.* 2012; Fig. 4). Based on a variety of facies indicators, including black shale horizons, sea level curves and carbon stable isotope records, Cherns and Wheeley (2009) interpreted multiple climatic cooling events from late Cambrian through to late Silurian. Testing of the periodicity of these events against long term eccentricity predictions indicated that orbital forcing of climate was probable (Cherns *et al.* 2013). Facies evidence for glacial deposits on Gondwana from late Ordovician (Sandbian) through to early Silurian (Llandovery/Wenlock; Grahn and Caputo 1992; Diaz-Martinez and Grahn 2007; Fig. 4) supports long term climatic cooling and recovery. Silurian climates returned to greenhouse conditions, while sea levels rose to a maximum in the late Llandovery (Telychian; Loydell 1998) although not approaching those heights reached in the Ordovician. Following this, through overall shallowing up to Iapetus closure, further cooling events are interpreted for lowstands in Silurian sea level cycles that correspond to C stable isotope excursions and biotic events (Fig. 4; Johnson 2006; Cherns *et al.* 2013). In the Appalachian foreland basin, Silurian sea level falls and positive C stable isotope excursions correlate with onset of reducing, sulfidic conditions in an anoxic basin, Fe mineralization and spread of grey to black pyritic shales from basin across to shelf (McLaughlin *et al.* 2012).

FOSSIL EVIDENCE FOR PRE-DEVONIAN PHYTOTERRESTRIALIZATION (EXCLUDING EUTRACHEOPHYTES)

Megafossils

a) Extensive patches (thalli), mostly with irregular margins, comprising coalified compressions (incrustations). Some of the most important localities yielding such megafossils as well as palynomorphs in the Lower Silurian are in the Massanutten Sandstones in the Tuscarora Formation (Rhuddanian/Llandovery) exposed in Passage Creek, Virginia (e.g. Pratt *et al.* 1978, Tomescu and Rothwell 2006). The sediments were deposited on river plains with fossils formed on overbank deposits. The organisms, some possibly preserved in growth position, were thought to have colonized drier areas in riverine wetlands, because pre-burial cracks, indicating subaerial exposure, characterize many of the coalified compressions.

The fossils, often covering bedding planes, are isodiametric black patches up to 10 cm in diameter, most with irregular outlines and some with smooth curves possibly representing the limits of the organisms; irregular projections on one side of the fossil may indicate penetration of the sediment. Strap-shaped forms also occur.

Tomescu and Rothwell (2006) illustrated five types of internally stratified organization, with layers differing in thickness, degree of folding, variations in their brown colour reflecting density (some were termed diaphanous), and repeated composition of layers. Some may comprise filaments rather than laminae, and it was an example of the former that later received more detailed examination (Tomescu *et al.* 2006; 2009a). Bleaching had revealed parallel spaces and opaque linear structures embedded in their hundreds in amorphous material. The linear structures (filaments) were resolved as comprising one to four tightly packed trichomes whose spherical cells were replaced aggregates of iron oxide crystals. More diffuse crystalline deposits around the filaments were interpreted as demonstrating the possible existence of sheaths in addition to the amorphous extracellular matrix. The overall colony was strap-shaped and sinuous. From dimensions and organization the fossil was considered cyanobacterial and of possible oscillatorian affinity and assigned to a new genus *Prattella massanuttense* (Tomescu *et al.* 2009a); the possibility that these organisms were diazotrophic is considered under Nitrogen below. The same authors (Tomescu *et al.* 2008) used scanning electron microscopy to demonstrate rod-shaped bacteria, also potential diazotrophs, within the coalified extracellular material surrounding the filaments.

Thus based on their anatomical investigations, Tomescu and colleagues had demonstrated that thalloid coalified compressions were of diverse origin whose affinities were investigated by two further approaches. The first involved experimental fossilization of a variety of organisms in an attempt to detect what structures might survive taphonomic processes to become Silurian fossils (Tomescu *et al.* 2010). Subjects included cyanobacteria, red, brown and green algae, lichens and bryophytes. The procedure involved compressing the organisms in a sandwich of wetted filter and waxed paper and further compression (using clamps) at 130ºC using a clothing iron. Sections of embedded material showed that the major lineages remained clearly identifiable, but there was variation in the distribution of internal structure ranging from those almost unaltered (e.g. the brown alga *Fucus*, red alga *Mazzaella*, lichen *Parmotrema*) to those where cellular construction was no longer visible (e.g. the green alga *Spirogyra,* ascocarps and basidiocarps of fungi, the lichen *Palligera*, the bryophytes *Marchantia* and *Anthoceros*). Intermediate preservation was noted in cyanobacterium *Nostoc*, and the liverworts *Pellia* and *Conocephalum*. The authors themselves appreciated that their simulation of fossilization processes was far removed from actual diagenesis, which would have involved intense pressures and high temperatures over considerable time intervals, but thought that, with refinement, it might provide more insightful interpretations of the structures seen in the fossils.

A more conventional approach involved carbon isotope analyses on coal scraped from thalloid compressions and contemporaneous Ordovician and Silurian rocks in the Appalachians, including the localities in the Tuscarora Formation, and comparisons with isotopic values from extant plants including those for liverworts corrected for life in Ordovician/Silurian times of postulated high atmospheric CO_2 (Tomescu *et al.* 2009b). They demonstrated that the signatures recovered from organic matter in the Rhuddanian Massanutan sandstones at the heavier ends of their ranges overlapped with those predicted for liverworts, with the inference that some of the encrustations might represent the fossilized remains of that group. Freshwater algae today, however, have a range of carbon isotope ratios encompassing the lower and higher values of those measured or predicted for extant liverworts. Overall the remains were considered to have values consistent with a terrestrial origin, but an aquatic origin cannot be ruled out (see under ‘CO_2’ below).

Although very fragmentary remains/encrustations are recorded throughout the Silurian there are only two further comprehensive investigations on their nature with discussions on their affinities. Lang (1937) placed many of his Přídolí examples in his new genus *Nematothallus*. He showed that they comprised four elements: a cuticular layer with reticulate (pseudocellular) patterning that covered two associations of tubes and numerous isolated spores. Branching was rare in all tubes and septa not recorded. Wefts of the wider tubes (12-40 µm diameter) sometimes contained examples (c. 12 µm diameter) with internal, narrow, annular wall thickenings (2.5-5.0 µm apart). The smaller tubes (c. 2.5 µm diameter) were always smooth-walled. It was impossible to reconstruct the three dimensional organization in these compressions but their consistent association in many examples persuaded Lang that the organism had a thallus in which wefts of fine tubes were sandwiched between the uppermost peripheral pseudocellular cuticle and more deeply seated wefts of wide and small tubes. Such layers may have differentially been preserved and separated on decay thus accounting for the frequent presence particularly of cuticles and tubes in palynological preparations. Lang deliberated on the processes involved in the production of the pseudocellular patterning on the resilient cuticles, be it produced by the dilated ends of tubes at right angles to the surface or the points of contact of the underlying mesh with the cuticle, but in 1945 concluded that the cuticle with internally projecting flanges represented the remains of a cellular sheet in which the inner periclinal walls and wider limits of the anticlinal walls were not preserved. Based on the consistent association of spores with tubes, he was convinced that, even though the former varied in shape and size, they were part of the reproductive cycle of the organism.

As to affinities, Lang, comparing the associations of tubes with those seen in *Prototaxites* and the frequent co-occurrences of the two genera in assemblages in the Welsh Borderland Přídolí and Lochkovian, concluded that the two might be related, with *Nematothallus* possibly the ‘leafy’ appendages of *Prototaxites* stems and trunks, and he placed them in a new ‘class’ Nematophytales. The affinities of *Prototaxites* had been debated very soon after it was so misnamed (Dawson 1859, Carruthers 1872). Carruthers favoured algal affinities with the browns most likely based on the size of specimens and complexity of their tissues. This was at odds with the terrestrial status proposed by Dawson and reinforced by Lang (1937) on the presence of cuticle and spores. Indeed Lang was of the opinion that the nematophytes were a unique group of land plants neither close to algae or tracheophytes, but with some characteristics of both. Recently discovered charcoalified mesofossils from the Lochkovian of the Welsh Borderland have revealed the three dimensional construction of the thallus (Edwards *et al.* 2013). It was stratified with a superficial, usually uniseriate upper cortex, the outermost layer of which gives rise to the cuticle with reticulate patterning. It covered a palisade zone of wider tubes with occasional septa and a basal zone of narrow randomly interwoven and infrequently branched tubes. Although spores were occasionally found adhering to the tissues, the authors considered it unlikely they had been produced by the organism, and that the banded tubes, when present, were interpreted as contaminants, possibly involved in the degradation of tissues. In addition to the thalli with the imperforate cuticles, others, of similar internal construction, had perforated surfaces with papillae or protruding hyphae. Isolated 'cuticles' of this type, when found in palynological assemblages, had been called *Cosmochlaena* (Edwards 1986).

Edwards *et al.* (2013a) interpreted such thalli as made of fungal hyphae, and from the complexity of organization as closest to those of lichenised fungi, although a photobiont could not be identified. The recovery of cuticles and sheets of cells from the upper Ordovician of Libya (Gray *et al.* 1982; Fig. 4) extends the record of this kind of organization in deep time (see below) although whether or not to use the genus *Nematothallus* as defined by Lang in this context has been debated (e.g. Edwards 1982) and deemed inadvisable by Strother (1993). He had earlier described (Strother 1988) four different types of thalloid compressions with tubular construction from the late Wenlock – early Ludlow Broomsburg Formation in Pennsylvania and described three new species, viz. *N. taenia* (thalli: narrow sinuous strap-shaped; 1-2 cm long; tubes: unbranched 6-10 µm wide; longitudinal alignment), *N. elliptica* (thalli: circular to elliptical; <1 cm wide; tubes: unbranched 3-13 µm wide extend to margins and *N. lobata* (thalli: irregular lobed with shallow concave depressions; 1-2 cm maximum length), plus *N. cf. pseudo-vasculosa* (thalli: ovate (11x17 mm) with circular indentations (3 mm wide): tubes of two types (*c.* 15 µm, *c.* 4.0 µm); embedded in an amorphous matrix. He initially concluded that the generic name was better confined to thalloid fossils of tubular construction, because the cuticles were frequently absent from Lang's material. In 1993, he elevated Lang's Nematophytales to the level of phylum as suggested by Burgess and Edwards (1988) and created the Nematothallaceae to distinguish thalloid from axial (e.g. *Prototaxites*) members. Lang's *Nematothallus pseudo-vasculosa* was chosen as the types species, although the lectotype selected from Lang's material possessed differentially thickened tubes, but no cuticular layer. He altered Lang's diagnosis of the species to omit the latter as well as cuticularised spores, and emphasized that some species might lack the differentially thickened tubes.

It would clearly be impossible to undertake anatomical investigations on all coalified encrustations in Mid-Palaeozoic rocks and also unwise to conclude that all belonged to the nematophytes or bacteria. Indeed Strother introduced the possibility that some were the remains of thalloid gametophytes such as are present in major clades of liverworts and hornworts today (Strother 2010). A liverwort-like dorsi-ventral thallus has been proposed for the last common ancestor of present-day land plants (Mishler and Churchill 1985) although, based on the nature of the gametophyte apical cell in extant basal liverworts and mosses, Ligrone *et al.* (2012) advocated leafless axial organization in the archetypal gametophyte. To date there is no direct fossil evidence compatible with either hypothesis in pre-Devonian rocks.

b) *Axial fossils.* No axial compression fossils have been recorded in Ordovician rocks. The earliest examples named *Eohostimella heathana* comprise isotomously branching axes of essentially tubular construction preserved in marine rocks in Maine dated by invertebrates as upper Llandovery (Schopf *et al.* 1966). Unlike *Hostinella*, which lacks any enations, the surfaces of the axes were covered by minute spinose appendages (up to 0.3 μm). These were borne on a coalified cylinder (100-300 μm thick) filled with sediment: no vascular tissues were recorded. The fragments, up to 35 mm long and varying in width between one and two millimetres were thought to derive from, at least in part, an erect plant, because they extended through several bedding planes. Such orientation of transported material in marine rocks makes such an inference questionable as indeed are the affinities of the fossils. The first record of fertile bifurcating axial plants comes from the late Wenlock (Homerian) of Ireland (Fig. 4). The fragments are very small with axis diameter rarely exceeding a millimeter (range 0.3-1.7 mm) and the terminal sporangia being short and wide conform to Lang's 1937 definition of *Cooksonia* (Edwards *et al.* 1983). In outline, some of the sporangia resemble *Cooksonia pertoni* and others, e.g. *C. hemisphaerica,* (Fig. 4) but they are usually somewhat smaller. It is impossible to estimate the height of a complete plant: the longest fragment is 15 mm and branches three times, while a 13.5 mm long example branches twice. The basal parts of the plant are unknown and the fossils lack anatomy.

The earliest records of axial fossils in Gondwana (from the Kirusillas Formation near Cochabamba, Bolivia) are in rocks dated by graptolites as late Wenlock – early Ludlow. Initial description by Toro *et al.* (1997) indicated the presence of *Cooksonia*, *Rhynia*, *Zosterophyllum* and *Drepanophycus*, but subsequent recollection at the locality uncovered bedding planes with abundant unidentifiable coalified debris and probable coprolites as described by Edwards *et al.* (2001). However loose blocks further down the hillside were full of very short lengths of narrow, parallel-sided axes and occasional forking ones similar to later *Hostinella*, but much smaller. Traces of longitudinally aligned superficial cells, some with iron oxide infill were present, but tracheids were not observed. None of the material was fertile. By contrast, in the slightly younger Early Ludlow to early Přídolí Lipeon Formation in southern Bolivia near Tarija, well preserved rhyniophytes, including *Cooksonia* cf *caledonica* (*C. caledonica* is now known as *Aberlemnia* Gonez and Gerrienne 2010), diverse isolated rhyniophytoid sporangia as well as abundant smooth axes some with branching typical of

Hostinella, were preserved in a shallow water marine setting (Edwards *et al.* 2001). Also present were quite diverse small, irregularly branching fragments possibly the tips of algae such as *Buthotrephis* or *Hungerfordia.*

The disparity in sporangial morphology is similar to that in Přídolí and Lochkovian assemblages in the Welsh Borderland and comparisons were made with *Steganotheca*, *Tarrantia*, *Cooksonia hemisphaerica*, *C. cambrensis* and *Culullitheca* but unequivocal assignation proved impossible (e.g. Fanning *et al.* 1990, 1992). At the Jarcas locality diameter of the sterile axes reached 1.3 mm, but was usually less than a millimetre. The most complete specimen, comprising an axis subtending three lateral branches on one side, one of which branched dichotomously a further two times, was tentatively interpreted as a creeping rhizome bearing upright stems. The biggest fertile specimen at this locality was 5 cm long and 0.7 to 0.2 mm wide and branched at least twice with two axes terminating in sporangia.

Similar grades of organization and sizes of plants were recorded in the Ludlow of the developing palaeocontinent Laurussia and in the Bohemian and Libyan assemblages of north Gondwana (Obrhel 1968; Daber 1971). In South Wales, *Cooksonia pertoni* was found in the Gorstian (Upper Ludlow) along with *Hostinella* (Edwards *et al.* 1979), while in the Ludfordian these taxa occurred with *Steganotheca* (Edwards and Rogerson 1979) from the locality that had produced an unbranched sterile axis with the earliest to date record of *in situ* tracheids (Edwards and Davies 1976). However, that vascular tissues had evolved by this time is evidenced by discoveries in the Ludlow of both zosterophyll (Kotyk *et al.* 2002) and lycopsid (Tims 1980; Fig. 4) clades of Canada and Australia respectively. Such fossils mark a radical change in plant architecture as plants were released from the constraints of determinate growth and limits on reproductive capacity imposed by terminal sporangia production. The resulting increase in biomass above ground produced by increased branching and laminar light harvesting capability, initially via microphylls, increased the potential for export of metabolite for further innovation and investment in underground systems such as more extensive rhizomes and roots.

The Prototaxites *complex.* (See also p. xx). In addition to the very well defined axial fragments of embryophytic derivation, there are numerous roughly cylindrical/axial compressions in Ludlow and Přídolí rocks of southern Britain that possess a usually greater thickness of coal and pronounced surface striations. These have been frequently assigned to *Prototaxites* and occasional more detailed anatomical investigation has revealed the diagnostic two systems of tubes (e.g. Lang 1937). They are however considerably smaller than the Emsian examples from the type and other localities, where they attained tree trunk size dimensions (Dawson 1859, 1871; Fig. 4). The earliest convincing examples are recorded in the Llandovery Denbyshire Grits, north Wales (Hicks 1881) where two sizes of tubes are described from irregularly shaped fragments, some parallel-sided. Such fragments are small with dimensions more typical of later Silurian records than Devonian ones. A possibly earlier (Lower Llandovery) member of the prototaxalean complex was described by Niklas and Smocovitis (1983), although anatomy came from an elongate fragment within an irregularly shaped coalified compression. It comprised longitudinally aligned smooth tubes surrounding differentially thickened ones (banded tubes). Niklas and Smocovitis included comparisons with nematophytes in their somewhat inconclusive discussions on affinities: the description of banded tubes in organisms (*Nematosketum*, Burgess and Edwards 1988) with typical construction otherwise very similar to that in *Prototaxites*, reinforces placement in the prototaxalean/nematophyte complex. *Prototaxites* itself has not been recorded as a megafossil in the Ordovician.

Microfossils

Spores. An assemblage of spores recovered from the early mid Ordovician (Dapingian: 473-471 Ma) Zanjon Formation in Argentina (Rubinstein *et al.* 2010; Fig. 4) is commonly regarded as the oldest evidence for terrestrial vegetation. Similar but not identical, and far more convincing, spores have been described from younger Ordovician, Silurian and Lower Devonian assemblages, and are distinguished from the trilete spores (monads) that characterize vascular plants by their distinctive configurations including dyads and tetrads and have been named cryptospores because the producers were conjectural (Richardson *et al.* 1984). That they derived from land plants is evidenced by (1) their size and general morphology, (2) their occurrence in both continental and marine rocks, (3) their resilience through time, and (4) geochemical analyses that indicate similar wall compositions to extant land plant spores. That they were produced from plants with relationships to bryophytes is evidenced by (1) liberation of mature spores as permanent tetrads (e.g. the liverworts *Sphaenocarpos, Riccia*), (2) lamellate ultrastructure of their walls albeit recorded in dyads (e.g. Taylor 1995; Wellman *et al.* 2003), (3) molecular studies that indicate that bryophytes are paraphyletic to the vascular plants and that liverworts are sister group to all other land plants (e.g. Kenrick and Crane 1997; Cox *et al.* 2014) and (4) the nature of tissues in extant bryophytes that reduces the likelihood of their preservation and accounts for the lack of megafossils in the coeval rocks. Indeed the first indication that the parent plants were embryophytes comes from fragments of wall or cuticles in contact with masses of tetrads in the mid-Ordovician (Llanvirn) of Oman (Wellman *et al.* 2003; Fig. 4), while spores in better preserved sporangia are found in Upper Silurian and Lochkovian localities (for review see Edwards *et al.* 2014).

The oldest cryptospore assemblage is preserved in marginal marine/estuarine sequences and was dated by chitinozoans (Rubinstein *et al.* 2010). Described as moderately diverse, it contained three monad and two tetrad taxa. *Sphaerasacus glabellus* is an enveloped smooth-walled spherical monad, also recorded from the late Ordovician and early Silurian. Naked hilate monads included *Chomotriletes*? sp with ornament on the distal surface comprising convolute muri resembling fingerprints. Laevigate examples were too poorly preserved to allow assignment to a species of *Laevolancis*. The two tetrad taxa comprised naked *Tetrahedraletes* cf *medinensis* and a new taxon, in which a tetrad of laevigate spores with equatorial thickenings is surrounded by a loose crumpled, but smooth, envelope. The authors accepted the spores as derived from liverworts.

Slightly younger (by 8-12 million years) late Mid Ordovician (Darriwilian) assemblages from the Czech Republic (Vavrdova 1990) and Saudi Arabia (Strother *et al.* 1996) showed limited increased diversity including both naked and enveloped (rare) tetrads including *Stegamibiquadrilla contenta* with microregulate-semipunctate ornament as well as, for the first time, naked and enveloped permanent dyads.

Larger numbers of the latter characterized assemblages from the type Caradoc succession (Sandbian–mid Katian) in southern Britain. Wellman (1996) described at least 16 taxa in the assemblages including well preserved, but rare, laevigate monads with intact hila assignable to *Laevolancis*. Assemblages of similar composition occurred throughout the upper Ordovician and Silurian with increase in numbers of smooth laevigate *Laevolancis* types in the basal Llandovery and ornamented forms in the Wenlock. However, in a mid Katian assemblage recovered from a core through the Qasim Formation in Saudi Arabia (Steemans *et al.* 2009), trilete monads are reported for the first time (Fig. 4). The previous earliest convincing record was of smooth forms in the basal Silurian (Llandovery: Hoffmeister 1959). Amongst abundant cryptospores, Steemans *et al.* 2009 illustrated seven species of trilete examples, - two smooth, the remaining five with an ornament of verrucae and/or muri. All types have been found in *Cooksonia pertoni*. Isolated ornamented forms had previously been recorded in Wenlock and younger rocks. Such data extend the record of vascular plants into the Ordovician, but their spores did not dominate assemblages of palynomorphs in terms of taxa and numbers until the Devonian. Almost all cryptospores disappeared at the end of the Lochkovian. Numbers of permanent tetrads and dyads had declined during the Silurian, but hilate monads continued in comparatively large numbers into the Lochkovian (Richardson 2007) when, at least in the Welsh Borderland, crassitate spores characteristic of basal tracheophytes, such as *Cooksonia*, were replaced by retusoid examples characteristic of zosterophyllls.

Footnote. Records of palynomorphs with some characteristics of cryptospores have been recovered from Mid and Late Cambrian rocks from the USA (Strother and Beck 2000; Strother *et al.* 2004; Taylor and Strother 2009). Dominant elements from the older strata are clusters of dyads and tetrads ’not substantially different’ from cryptospores. Walls are mostly smooth, but some are gemmate or scabrate and spores may be enveloped. Strother *et al.* (2004) concluded that they derived from an extinct terrestrial flora intermediate between chlorophytes (*s.l.*) and embryophytes. Their credentials as cryptospores were queried as they appeared to lack clear tetrahedral symmetry and there were variable numbers of units in some polyads (Wellman 2003). Similar clusters were reported by Taylor and Strother (2009) as part of a far more detailed account based on Upper Cambrian examples of enveloped polyads, described as synoecosporal packets. The basic unit of each packet comprised a dyad and there were 2 to 4 dyads in each packet. Groups of packets containing variable numbers of dyads were surrounded by a further synoecosporal wall. The basic unit of the dyad comprised at least two laminae close to the spore lumen. Such configurations are not compatible with the tetrads and dyads assumed produced by meiosis in later examples (see Edwards *et al.* 2014).

Whether or not they represent a further extinct group and one which colonized land surfaces remains open to questions.

Fungi. Palynological preparations from Ordovician into Lower Devonian rocks frequently contain small fragments of tubes or filaments which from their dimensions and cellular characteristics might well belong to fungi. The best preserved come from the near shore, Upper Silurian Burgsvik Sandstone, Gotland and are associated with pellet-like masses interpreted as coprolites (frass) produced by microarthropods and multicellular spores (Sherwood-Pike and Gray 1985). Most of the hyphae have roughened, granulate surfaces, verticillate branching and have perforate septa. The lateral branches are flask-shaped (ampulliform) structures compared with the conidiophores of Fungi Imperfectae, allied to the terrestrial ascomycetes. Burgess and Edwards (1991) had isolated similar material from Wenlock to Lower Devonian localities and named examples with granules clustered around branches as *Ornatifilum granulatum*. Their preparations included smooth walled tubes, also recorded from the Upper Ordovician, in which septa were absent and branching rare. A new species, *O. lornensis* was described from the Lower Old Red Sandstone of Scotland (Wellman 1995), and broadly similar remains were recorded from a number of older Silurian localities in the Midland Valley. Such records demonstrate the probable existence of fungi in terrestrial vegetation during the Ordovician-Silurian time interval but little more.

The mid-Ordovician record of glomalean fungi from Wisconsin USA (Redecker *et al.* 2000, Redecker and Graham 2002) is based on wefts of occasionally branching non-septate hyphae containing spherical to subspherical spores all of which terminate hyphae. Thus the spores resemble those of glomelean fungi and particularly the genus *Glomus*. Similar configurations of spores and hyphae were compared with those in present day arbuscular mycorrhizal fungi, and raised the possibility that such symbolic associations were present with coeval land plants. The problem with this record rests on its syngenicity, not its biogenicity. The fungi were preserved in limestones laid down in a 'preserved shallow marine' environment. The researchers took the precaution of isolating non-weathered rock, not contaminated with roots of extant plants and found no modern material in their macerates. However they did not produce or examine petrological sections of the matrix, which is a dolomite, a post-depositional replacement of limestone and as such a porous rock, into which extant Glomeromycota may have percolated or even colonized surfaces with bacteria and fungi when the rock was redeposited. Thus further evidence is required to demonstrate the syngenicity of the fungi.

That fungi were present throughout this time interval seems likely as molecular evidence suggests that all major fungal lineages had diverged at least 1000 m.y. ago (Heckman *et al.* 2001). Evidence from Precambrian fossils is controversial e.g. *Eomycetopsis* has been reinterpreted as a cyanobacterial sheath (for references see Taylor *et al.* 2015, Butterfield this volume?).

The Prototaxites complex. P*rototaxites* has already been included as an axial fossil in the Silurian based on much smaller representatives than the Emsian examples that attained tree-trunk dimensions (Dawson 1859, 1871). Here it is included as a fungus as originally hypothesized by Church (1919) and more recently by Hueber (2001) based on a very thorough examination of material from the Emsian type locality. Hueber favourably compared the various kinds of tubes in *Prototaxites* with hyphae present in the Holobasidiomycetes and placed the fossils in a new order, the Prototaxales. His conclusions on the reproductive structures are less compelling. His hypothetical reconstructions are based on poorly preserved structures interpreted as inflated sterigmata, each bearing a speculum, but no spores. These were repeatedly observed at the concentric growth increments interpreted as remains of a hymenium. The status of *Prototaxites* as a land plant (Dawson 1871, Lang 1937, Hotton *et al.* 2001) is no longer questioned, thus dismissing questions of affinity with algae. The recent suggestion that the 'trunks' were concentric mats of marchantioid liverworts presumably produced by rolling down a slope with the larger tubes equivalent to rhizoids (Graham *et al*. 2010) has been widely criticized, both as physically impossible (Boyce and Hotton 2010) and on anatomical grounds (Taylor *et al.* 2010).

Boyce *et al.* (2007) had earlier produced δ^{13}C isotope values both from *Prototaxites* and co-occurring vascular plants and showed considerable variation in values ranging from -15.6‰ to -26.6‰, which is within the range likely for CCs in the mid-Palaeozoic (-15 to -30 ‰; see under 'CO_2' below) in *Prototaxites* which strongly suggested heterotrophic nutrition on isotopically distinct subtrates as is seen in fungi. Carbon isotope values for *Prototaxites* produced by Graham *et al.* (2010) appeared to show a signature similar to that measured in experiments on *Marchantia*, but these are not thought meaningful because no allowance was made for both differences in atmospheric δ^{13}C in Devonian times and the type of medium used in their cultures. Finally narrow intact axial structures with prototaxalian anatomy recovered from Lochkovian rocks (Edwards and Axe 2012) were interpreted as cords or rhizomorphs and show no liverwort features.

Such discussions on affinity are clearly important considerations on carbon cycling. Indeed the identity of *Prototaxites* as a heterotrophic organism raises major questions on suitable nutrient sources for such a potentially gigantic sporophore. Such issues were addressed by Selosse (2002), who then advocated a lichen-type symbiosis for *Prototaxites* purely on energy relationships. A similar affinity has more recently been postulated by Retallack and Landing (2014) on anatomical grounds, but the cortical nests of coccoid algae are not, as the author admitted, very well preserved and thus do not provide unequivocal evidence for a photobiont.

How plausible is photosynthetic energization of *Prototaxites*? The very low surface area per unit volume or dry matter of *Prototaxites* means that, even at the higher atmospheric CO_2 in the mid-Palaeozoic, intercellular gas spaces are essential to attain a CO_2 assimilation rate that uses a substantial fraction of the photons that can be absorbed from full sunlight (Raven 1986; Raven and Edwards 2014). Extant terrestrial photosynthetic embryophytes with similar dimensions and surface area per unit volume to *Prototaxites* are all homoiohydric, e.g. the cactus *Carnegeia gigantea* with Crassulacean Acid Metabolism (Bronson *et al.* 2011). Raven (1986) points out that the structures and functions required for homoiohydry occur in fungi, albeit in a diversity of species in this large and diverse Kingdom. However, there is no direct evidence in *Prototaxites* of the occurrence of these attributes, i.e. dead water-conducting cells, intercellular gas spaces, hydrophobin-like hydrophobic proteins as a cuticle analogue, and, perhaps less plausibly, nematode- and protest-trapping machinery based on constriction of a ring of three cells (20-30 μm in diameter) by rapid cell turgor increase as a prototype for stomata (Raven 1986; Yang *et al*. 2007). Finally, homoiohydric *Prototaxites* exhibiting facultative Crassulacean Acid Metabolism could explain the range of natural abundance carbon isotope ratios in *Prototaxites* (Boyce *et al.* 2007), i.e. -15.6 ‰ to -26 ‰, with the lower (more negative) values relating to C_3 expression and the higher values involving expression of Crassulacean Acid Metabolism (Raven and Spicer 1996). However, the absence of evidence of homoiohydry in *Prototaxites* (see above), and the absence of evidence of Crassulacean Acid Metabolism in the Palaeozoic (Raven and Spicer 1996), make this explanation of the carbon isotope ratios of *Prototaxites* unlikely.

EVIDENCE FOR LICHENS IN PRE-DEVONIAN ROCKS

First, that lichens were present in the Lower Devonian is evidenced by silicified *Winfrenatia reticulata,* which shows a consistent structural association between fungal hyphae and cyanobacterial photobiont, in the Pragian Rhynie Chert (Taylor *et al.* 1995; 1997), although it differs from any extant forms in comprising an association of possibly two cyanobacteria and a mycobiont of uncertain affinity (Karatygin *et al.* 2009). Preservation of photobionts is more conjectural in the coalified specimens assigned to two species of lichens with stratified organization from the early Lochkovian of the Welsh Borderland (Honegger *et al.* 2013). The generic names *Chlorolichenomycetes* and *Cyanolichenomycetes* reflect the affinities of the photobiont. *Nematothallus* and *Cosmochlaina* differ from these taxa in their possession of a stratified thallus in which a palisade tissue of wide tubes is sandwiched between an upper superficial cortex, which decomposes to leave *Nematothallus* cuticles, and basal wefts of small tubes (Edwards *et al.* 2013). However a *Nematothallus* ‘cuticular’ patterning was recorded in *Chlorolichenomycetes* and the authors concluded that *Nematothallus* and other similar organisms with stratified thalli were best assigned to lichens, and from their complexity with the lichenised ascomycetes and more precisely to Pezizomycotina. Earlier, Kerp and Kring (in Steur and van der Brugghen 1998) commented on anatomical similarities between *Leptogium lichenoides* and *Nematothallus*. As is discussed below, calibrated molecular clock outcomes suggest that ascomycetous lichen fungi (the commonest lichens today) originated in the early Carboniferous.

As mentioned earlier, *Nematothallus* cuticles and fragments of tubes (hyphae) are common constituents of palynomorph assemblages and extend the range of the genus into the Ordovician (e.g. Caradoc (Katian or Sandbian), Gray *et al.* 1982), with the inference that thalloid organisms comprised principally of fungal hyphae were present on land from the mid-Ordovician, and their organization into complex tissue-like systems best fits lichenised fungi. Wefts of unbranched, non-septate tubes recovered from Mid-Cambrian rocks were considered by Strother *et al.* (2004) as indistinguishable from those Strother had also isolated from Silurian strata. This led to the inference that nematophytes and even possibly *Nematothallus* existed some 45 million years before these records in the Ordovician, but more compelling evidence from this is needed to confirm nematophytes on land in mid Cambrian times.

There are no further body fossils in the early Palaeozoic that have been unequivocally identified as lichens. Yuan *et al.* (2005) described as lichen-like associations of filamentous, ?non-septate, hyphae with ensheathed clusters of coccoid cyanobacteria or possibly green algae preserved in phosphorite in the Cambrian Doushantuo Formation (635–551 million years ago) of Southern China. The fossils, found in rocks originally described as marine, showed only little contact between fungus and presumed photobiont, and lacked any structured organization characteristic of lichens, although three-dimensional reconstruction was impossible. Fungal hyphae were common in the matrix and the authors postulated that such associations in which a number of hyphae enveloped coccoids might represent early stages towards the fungal/photoautoph symbiosis, beginning with facultative interactions between the two groups. A further inconsistency lies in the dimensions of the hyphae which are much smaller than in fungi, but are characteristic of active bacterial filaments (Honegger *et al.* 2013). Although Retallack (2014) describes the fossils as glomeromycotan lichens their location in a marine environment or possibly an isolated non-marine basin (Bristow et al 2009) would seem unlikely because of the logistics of transfer of nutrients in fluids between two separate organisms with limited contact. Yuan *et al.* had compared pyriform structures attached to the hyphae as similar to spores in glomaleans, but much smaller. In a separate evolutionary scenario, Pirozynski and Malloch (1975) had hypothesized that symbiotic associations between a semi-aquatic green alga and aquatic oomycote were essential for the successful colonization of the terrestrial environment.

Further claims for the presence of lichens in the Cambrian and Ordovician times were based on impressions/moulds on surfaces of putative palaeosols (Retallack 2009, 2011). *Farghera robusta* was described on surfaces of the Cambrian/Ordovician Grindstone Range Sandstone of South Australia, and associated with the ichnospecies *Rivularites repertus* (Retallack 2009). The cracked and pustulate surfaces of the latter closely resemble predominantly desert substrates today, which are too dry to support vascular plants. Petrographic thin sections showed branching structures that were compared with the cyanobacterial cords, fungal hyphae and lichen rhizines seen today in biological crusts of desert and tundra. *Farghera robusta* was diagnosed as comprising 2-4 times dichotomously and pseudomonopodially branching thalli (1-3 mm wide) with rounded tips and 1 mm wide marginal threads, which tapered and branched downwards. It was the latter feature, together with the prevailing environmental conditions, which led Retallack to conclude an affinity with lichens and especially with lichenised members of the Ascomycota (e.g. *Xanthoparmelia reptans*) possessing marginal rhizines. Much rarer impressions were tentatively and inconclusively compared with gametophytes and sporangia and fungi of land plants.

Based on similar sedimentary evidence, Retallack (2014) had concluded that palaeosols were associated with the 550 Ma Ediacaran communities of South Australia, and hypothesized, somewhat controversially, that several well-known members of the intensively investigated assemblages were lichens or microbial associations forming solid crusts, rather than marine metazoans or protists (Retallack 1994, 2007, 2013). Segmented examples, including *Dickinsonia* with associated burrows and traces ('Autozoan'), were interpreted either as instead of its rhizomes or mycelia organized into cords or rhizomorphs of lichens. Relief was accounted for by the presence of fungal chitin. Discoidal fossils, e.g. *Cyclomedusa*, *Aspidella*, were interpreted as microbial communities colonizing solid surfaces. *Aspidella* (as well as *Charnia*) in Newfoundland ediacaran assemblages had earlier been posited to have lived saprotrophically in marine habitats on sulfate-reducing bacteria, but was described as fungus-like, because it did not possess characters diagnostic of any living lineage, and hence had no affinities with the crown group (Peterson *et al.* 2003). Similar arguments might be used to refute Retallack's contention of lichen affinities based on the Australian material, for which there is complete absence of any morphological, anatomical or reproductive characters diagnostic of lichens or indeed fungi as recorded in the crown group.

EVIDENCE FOR PRE-DEVONIAN BRYOPHYTES

There is no unequivocal megafossil evidence for bryophytes in the Ordovician and Silurian. Fossils from the Chinese Neoproterozoic (*Longfengshania*, Zhang 1988) and Cambrian (*Parafunaria*, Yang *et al.* 2004) are described as bryophyte-like on very tenuous comparative morphology. Přídolí *Tortilicaulis transwallensis* was originally discussed as such (Edwards 1979) based on twisting in unbranched fertile axes, but later Lochkovian specimens possessed spores typical of vascular plants and dichotomous branching in the diagnostic twisted axes (Edwards *et al.*1994). However, a number of highly fragmented plant remains recovered in palynological preparations from Mid Ordovician into the Lower Devonian have been considered favourably as evidence for mosses and liverworts based on superficial resemblances by Professor Linda Graham and her team. To mimic taphonomic processes, extant bryophytes were exposed to prolonged acid-hydrolysis at high temperatures, followed by treatment with HCl and HF to simulate extraction procedures. Such studies have demonstrated the resilience of the cell walls impregnated by auto-fluorescent polyphenolic compounds in certain tissues of both gametophytes and sporophytes (Kroken *et al.* 1996). The patterning of cells in fragments of sporangial walls of *Sphagnum* were compared favourably with the patterning of cell outlines in cuticles and sheets of *Nematothallus* recovered from Ordovician to Lower Devonian rocks, but recent work (Edwards *et al.* 2013) has revealed their connection to hyphae of the reconstructed *Nematothallus*. Similarly the recent discovery of the tissues below the perforated, sometimes papillate cuticles called *Cosmochlaina* are again indicative of a hyphal construction with some hyphae penetrating the perforations (Edwards *et al.* 2013). This negates the hypothesis that the cuticles represent the lower epidermis of a marchantioid liverwort with the perforations representing the bases of rhizoids (Graham *et al.* 2004). Finally, remnants of the calyptra covering the sporangia of the moss *Polytrichum* recovered after acetolysis and rotting that comprised bundles of rows of elongate thick-walled cells with distinctive swollen junctions were compared with isolated tubes and wefts of tubes isolated from Silurian and Lower Devonian rocks (Kodner and Graham 2001). The wefts of tubes from *Polytrichum ohioense* are very similar, except for branches, to those recorded in *Nematothallus* thalli. The rare, very thick-walled isolated tube (Edwards 1982) illustrated for comparison with that from *P. commune* lacks swellings and has recently been found associated with wefts of narrow thin-walled hyphae (work in progress). The thin walled branched tube (named *Ornatifilum lornensis*) illustrated from Wellman's studies of plant debris from the Lower Old Red Sandstone of Scotland where it was considered as part of a complex of probably hyphal filaments with phialides and conidiophores comparable with those in extant ascomycotous fungi (Wellman 1995). Thus such highly questionable affinities taken collectively do not add up to unequivocal evidence for bryophytes in Ordovician, Silurian and Devonian rocks (e.g. Graham *et al.* 2014, p. 22).

Retallack's (2001) claim that ichnotaxa (burrows) and palaeosols in the Upper Ordovician Juniata Formation (Pennsylvania) provided the earliest evidence for plant-animal interaction on land in a liverwort-millipede polsterland community living on flood plains in a semi-arid topical setting has recently been challenged on sedimentological grounds by Davies *et al.* (2010), who interpret the sedimentology as from a marginal marine environment of deposition. Retallack had speculated that plants must have been present to support the animal community (most likely millipedes) as evidenced by burrows in the palaeosols and coprolites in the burrows, and although there is no evidence of liverworts in the strata, the presence of tetrads in coeval rocks made these, in his opinion, the most likely candidates.

EVIDENCE FROM SEDIMENTOLOGY FOR PRE-DEVONIAN VEGETATION

Davies and Gibling have published a series of papers in which they relate changes in fluvial facies from the base of the Cambrian to the end of the Devonian (e.g. Davies and Gibling 2010a, b, 2012; Davies *et al.* 2011). Their case histories were based mainly in North America and Europe. They divided the time interval into five stages (VS2-5) which reflect the changing composition of vegetation on land and discussed the interrelationships between vegetation and changes in fluvial style. A recent change in the timing of first records of major innovation somewhat modifies their conclusions. The first embryophytes as recorded by the appearance of cryptospores (cryptophytes) occurs in the Dapingian (Mid Ordovician) but the range of the earliest trilete spores, regarded as deriving from tracheophytes, is extended into the Katian (Upper Ordovician). There is a change in vegetational composition in the Ludlow in that the small rhyniophytes/rhynophytoids known from megafossils as old as the Wenlock are replaced in the Ludlow by the much larger tracheophytes that characterize the Pragian in Arctic Canada (Kotyk *et al.* 2002) and Australia (Tims 1980). Vegetational stages VS3 and

VS4 show ever increasing contributions of mudstones in fluvial and coastal deposits interpreted as indicating increased upland weathering of the baffling and binding of small grains in sediments in the lowlands. The beginnings of very limited changes in architectural style as evidenced by lateral accretion and hence meandering and bank stabilization are recorded in the Přdol of southern Britain. This is not unexpected. Although there is a change in the taxonomic composition of vegetation in VS3 and 4, the earliest tracheophytes, as marked by the appearance of trilete spores were probably very small and of similar architecture to some cryptophytes with similar impact on substrate, although we have absolutely no direct evidence on the nature of the basal regions of the plants. Thus the distinction between VS3 and 4 based on biological relationships seems unnecessary, merely indicating a change in affinities of the components of the CCs. Comparisons between the fluvial styles of late Silurian and Lochkovian sequences in Arctic Canada and southern Britain are of particular interest, because assemblages in the latter are dominated by rhynophytes/rhyniophytoids (axial tissues with terminal sporangia) except for Mid to Upper Lochkovian *Zosterophyllum*. By contrast, the Canadian Silurian assemblage is dominated by zosterophylls, which are related to later Pragian representatives which possess extensive creeping rhizomes with downwardly branching rooting structures at intervals (Gensel *et al.* 2001, Kotyk *et al.* 2002). In the intervening Přídolí interval there is a marked difference in fluvial deposition between the two areas in that calcic vertisols are not recorded in Canada (Miall and Gibling 1978) where aeolian deposits and evaporates indicate an arid climate. In the Anglo Welsh region there are abundant calcic vertisols linked to deposition in a monsoonal climate, high annual rainfall, strong seasonality between wet and dry periods (Love and Williams 2000), indicative of climate not vegetation control on sedimentation. Vegetational Stage 5 is thus transitional between the CCs of little impact on fluvial architecture and the first larger plants with extensive rooting systems, the earliest best known from the Givetian, Eifelian plant records being rare. Its members show a wide range of adaptations to facilitate anchorage and exploitation of a greater volume of soil for water and mineral nutrients. The plants themselves might have had substantial aerial biomass and basal regions colonizing soil surfaces or penetrating the substrate. Limited superficial rhizomatous systems are best known from the Rhynie Chert with rhizoids preserved on lower surfaces. Very rare examples of ‘uprooted’ almost intact plants preserved in clastic rocks show tufted rooting structures (e.g. Pragian zosterophylls, Arctic Canada; Basinger *et al.* 1996). Adventitous rooting systems are known from (pre) lycophytes, e.g. *Asteroxylon* and *Drepanophycus* and these penetrate several centimetres of soil (Kidston and Lang 1920) or sediment (Rayner 1984).

INTERACTIONS OF CRYPTOGAMIC COVERS (CCs) WITH ABIOTIC FACTORS RELEVANT TO GROWTH, SURVIVAL AND IMPACT ON THE ENVIRONMENT

Modellers (e.g. Herrmann *et al.* 2004*a*, *b*; Nardin *et al.* 2011; Goddéris *et al*. 2014; Pohl *et al.* 2014) use a number of physical parameters in their reconstruction of past climates that can be modified by the performance of land vegetation and its environmental consequences. These physical factors and the availability of essential nutrient elements are reviewed here. As background, we first describe the composition of CCs in the mid-Palaeozoic and today, the latter providing information on how photosynthetic organisms interact with the environment, which can inform analysis of how the mid-Palaeozoic CCs might have performed.

Composition of CCs in the mid-Palaeozoic

The fossil record provided information on cryptophytes, cyanobacterial mats, fungi including lichened examples, and early tracheophytes probably of the architecture exemplified by *Cooksonia*, although initially lacking the strengthening tissues (Edwards *et al.* 1986). Younger anatomically preserved cryptophytes, include those with branching sporophytes but the majority are preserved as sporangia and older examples are represented by spores indicating again a predominance of parenchyma dominated tissues as is seen in bryophytes.

There is very limited fossil evidence for cyanobacteria, but Sanchez-Baracaldo *et al.* (2014) have demonstrated that organisms like the non-heterocystous diazotrophic *Collema* and heterocystous diazotrophic *Nostoc* first occurred not later than the Neoproterozoic. Similarly, although there are no fossil records of terrestrial eukaryotic algae, molecular studies and fossils of aquatic algae show that green algae of the Chlorophyta *sensu stricto* (free-living Chlorophyceae, Trebouxiophyceae and Ulvophyceae, and lichenised Trebouxiophyceae and Ulvophyceae), all with desiccation tolerant representatives in CCs today, would have been present (Lewis and Lewis 2005; Raven and Edwards 2014). Among the non-photosynthetic biotas the occurrence of Archaea and non-cyanobacterial Bacteria seems inevitable. For fungi, calibrated molecular clock data (Lücking *et al.* 2009; Prieto and Wedin 2013) suggest the occurrence of Mucoromycotina, Glomeromycotina and Basidiomycotina and at least basal Ascomycotina in the mid-Palaeozoic, although lichenised Ascomycotina, comprising the majority of extant lichens, did not occur until the early Carboniferous. This means that any lichens in the mid-Palaeozoic would have been like *Winfrenatia* and or would have been basidiolichens.

Thus, taxonomically, apart from basal embryophytes replacing bryophytes, tissue composition, physiognomy, habitat interactions and land vegetation during this time interval would have analogues in cryptogamic ground covers today, but excluding those which are epiphytic.

Composition of CCs today

Photosynthetic members today include Cyanobacteria (free-living, such as the non-heterocystous diazotrophic *Collema* and heterocystous diazotrophic *Nostoc*, and in *Nostoc* in cyanolichens), Chlorophyta *sensu stricto* (free-living Chlorophyceae, Trebouxiophyceae and Ulvophyceae, and lichenised Trebouxiophyceae and Ulvophyceae), and Streptophyta (algae, as free-living Charophyceae, and the non-vascular embryophytic hornworts, liverworts and mosses) (Housman *et al.* 2006; Thomas and Dougill 2007; Belhuis *et al.* 2010; Gadd and Raven 2010; Fučiková *et al.* 2014; Raven and Edwards 2014). Non-photosynthetic biota associated with the photosynthetic members of CCs include Archaea, non-cyanobacterial Bacteria and non-lichenised Fungi forming mycorrhizal associations (Mucoromycota, Glomeromycota, Ascomycota, Basidiomycota (Smith and Read 2008; Bidartondo and Duckett 2010; Gadd and Raven 2010; Pressel *et al.* 2010; Bidartondo *et al.* 2011; Field *et al.* 2015; Rimington *et al.* 2015). All of the Glomeromycota are symbiotic, associated with a cyanobacterium as *Geosiphon*, or as arbuscular mycorrhizas with non-vascular embryophytes such as liverworts in the Marchantiopsida as well as vascular embryophytes (Smith and Read 2008; Bidartondo and Duckett 2010; Gadd and Raven 2010; Pressel *et al.* 2010; Bidartondo *et al.* 2011;Field *et al.* 2015; Rimington *et al.* 2015). Members of the other three fungal phyla also form mycorrhizal symbioses with non-vascular embryophytes, with Mucoromycotina forming symbioses with the basal clade (the Haplomitropsida) of liverworts, the basal clade of embryophytes (Smith and Read 2008; Bidartondo and Duckett 2010; Humphreys *et al.* 2010; Pressel *et al.* 2010; Bidartondo *et al.* 2011; Field *et al.* 2015; Rimington *et al.* 2015), as well as vascular embryophytes (Smith and Read 2008; Rimington *et al.* 2015).

Relevant abiotic factors and interactions with CCs: physical factors

Photosynthetically active radiation: effects on CCs. The increase in solar energy output with time (the 'Faint Young Sun') means that the flux of photosynthetically active radiation (PAR) incident on the top of the Earth's atmosphere was a few percent less than today; this means that there were more days per year, and shorter photoperiods and scotoperiods (Raven and Edwards 2014). There was a significantly lower daily integral of PAR (faint young sun plus shorter photoperiod), and a slightly lower yearly integral PAR (faint young sun). None of these differences should have posed significant problems for the photosynthetic elements relative to PAR (Raven and Edwards 2014). The global impact of clouds as PAR screens and PAR reflectors would probably have been the same as today, but the incidence of cloud in the past is not well constrained.

Photosynthetically active radiation: effects of CCs. It is unlikely that CCs influenced cloudiness. One possibility relates to those of saline inland habitats producing high concentrations of compatible solutes. If one of these compatible solutes was dimethylsulfoniopropionate (DMSP), it would break down to produce the volatile dimethylsulfide (DMS), and hence SO_2 and H_2SO_4 (Charlson *et al.* 1987). H_2SO_4 forms cloud condensation nuclei, and thus clouds (Charlson *et al.* 1987); DMSP-producing organisms in these saline habitats could increase Earth's albedo. The original CLAW (Charlson – Lovelock – Andreae – Warren hypothesis (Charlson *et al.* 1987) may have over-estimated the importance of biogenic atmospheric H_2SO_4 and hence its potential to have Gaia-like effects on cloudiness and Earth Surface Temperature (Tyrell 2013). Most of the probable contributors to pre-tracheophyte dominance CCs, i.e. Cyanobacteria; Chlorophyta, predominantly the Trebouxiophyceae, but also Charophyceae, Chlorophyceae and Ulvophyceae; Embryophyta; associated Fungi, Archaea and Bacteria (Fučiková *et al.* 2014;

Raven and Edwards 2014) are not known as major producers of DMSP, and hence DMS, unlike marine members of the Haptophyta and Dinophyta.

Ultraviolet radiation: effects on CCs. UVB (and UVA) probably had a slightly higher flux incident on the top of the Earth's atmosphere than occurs today, so slightly greater flux at the Earth's surface assuming the same cloud cover and (for UVB) O_3 content of the stratosphere. Assuming similar UV screening by the organisms to that occurring today, there is more potential for damage to nucleic acids, proteins and phenolics by UVB (less damage by UVA), and also more potential for a small contribution to photosynthesis from UVA, despite its shorter wavelength range (320-400 nm) than the normally accepted 400-700 nm range for PAR (Cockell and Knowland 1999). Photosynthetic organisms also have mechanisms that repair at least some of the damage caused by UVB (Sinha and Häder 2002). UVB and/or UVA-screening compounds that restrict the UV flux to the interior of cells occur in many organisms; both extracellular in sheaths (e.g. scytonemin in cyanobacteria) or cell walls (e.g. of mosses) and soluble intracellular UV screening compounds occur in components of CCs, of which cyanobacteria and mosses are the best-investigated examples (Cockell and Knowland 1999; Clarke and Robinson 2008; Varnali and Edwards 2010).The small optical thickness of many components of CCs restricts their capacity to screen UVB (Raven 1991; Garcia-Pichel 1994). It would be unwise, in the present state of knowledge, to suggest which of the taxa comprising CCs is most UVB-resistant.

Ultraviolet radiation: effects of CCs. The effect of CCs on the UVB flux reaching the surface of vegetation is probably minimal. The production of stratospheric O_3-destroying volatile chloro- and bromo-carbons today involves volcanism and, predominantly, biosynthesis by marine micro-organisms (Watling and Harper 1998; Keppler *et al.* 2000). Sources of chloro- and bromo-carbons on land today that involve biology are wildfire and wood-rotting fungi, and also abiological degradation of organic matter (Watling and Harper 1998; Keppler *et al.* 2000). The involvement of CCs in the present day production of volatile halocarbons is probably negligible, although the production of halocarbons by those on saline environments needs investigation. Denitrifying Archaea and Bacteria produce N_2O that is known to destroy stratospheric O_3 (Portmann *et al.* 2012).

Before there was a significant tracheophyte contribution to terrestrial vegetation there would have been no wood, so the abiotic and fungal contributions to volatile halocarbon production would have been less than today, and the overall contribution of terrestrial biota to global biological production of halocarbons would probably have been less than that today, assuming a similar flux from the ocean to that found today.

Temperature: effects on CCs. Today, mosses, trebouxiophycean alga such as *Coccomyxa* and *Prasiola*, free-living Cyanobacteria and lichens are common on (relatively) snow-free terrestrial polar habitats with (on the Antarctic continent) only two species of vascular plant (Broady 1996; Robinson *et al.* 2003; Konrat *et al.* 2008; Geffert *et al.* 2013). Some terrestrial cyanobacteria and trebouxiophycean green algae are tolerant of high temperatures for growth, and many components are tolerant of lower and higher temperatures when desiccated than they are when growing (Sand-Jensen and Jesperson 2012). These distribution and laboratory data show a wider range of tolerance of temperature by cryoptophytes than by tracheophytes. So, CCs with their present temperature tolerance should have coped with essentially all terrestrial habitats in the early and mid-Palaeozoic before there was a significant tracheophyte component in the vegetation.

Temperature: effects of CCs. If the CLAW hypothesis survived further scrutiny for cryptophytes (Tyrrell 2013) and caused a global increase in cloud cover, it would result in decreasing incoming short-wave, including near infrared, solar radiation incident on the Earth's surface and hence decrease Earth surface temperature.

Surface roughness: effects on CCs. Low surface roughness allows a thicker atmospheric diffusion boundary layer over the vegetation (Jones 2014). This means a lower diffusive conductance for ecophysiologically important gases such as CO_2, O_2 and H_2O vapour, as well as for conductive exchange of heat (a small component relative to radiative and convective heat exchange) (Jones 2014). Low surface roughness means that plant factors regulating gas exchange become relatively less important (Kellner 2001; Rice and Schneider 2004; Jones 2014).

Surface roughness: effects of CCs. The mechanical properties of CCs restrict the extent to which an organism can grow in height without support from surrounding cryptophytes. Although the polytrichaceous moss *Dawsonia* can grow to 0.5 m above surrounding vegetation, this occurs in sheltered (from wind) conditions under much taller tracheophyte vegetation. With a smaller height range among CCs in the open habitats of the early- and mid-Palaeozoic with no tall tracheophyte vegetation there would have been a smaller surface roughness than in much of the tracheophyte-containing vegetation today (see Thomas and Dougill 2007; Jones 2014).

Albedo: effects on CCs. A high albedo of CCs vegetation in the PAR range (400-700 nm) decreases the PAR incident on photosynthetic pigments, and so decreases the rate of photosynthesis at relatively low PARs, and also decreases the potential for photodamage at high PARs, for a given external radiation field (Jones 2014). The lower absorptance of PAR (and near infrared) means that there is less photon energy dissipated as sensible heat (lower plant temperature) and/or as latent heat of evaporation of water, and hence decreased water vapour loss in transpiration (Jones 2014). A higher cryptophyte albedo in the UVB means less potential for UVB damage in a given radiation environment (Jones 2014).

Albedo: effects of cryptophytes. Components of the CCs lack the highly reflective cuticle found in some desert tracheophytes, so the maximum albedo by CCs is less than that of tracheophyte vegetation (Jones 2014). Aside from this, depending on the reflective properties of the substrate, CCs can have a higher or lower albedo than adjacent unvegetated area, with effects on temperature of the vegetation relative to unvegetated areas (Tsoar and Karnieli 1995; Jones 2014).

Relevant abiotic factors and interactions with CCs: nutrient chemicals that regulate the physical environment

Water: effects on CCs. Members of the CCs are at the poikilohydric end of the poikilohydry-homoiohydry continuum, and many are at the desiccation-tolerant end of the desiccation-tolerant – desiccation-intolerant continuum (Table 3.2 of Raven and Edwards 2014). They have a limited capacity to restrict water loss, but are generally tolerant of desiccation when not growing. Cyanobacteria and cyanolichens, and embryophytes, can only rehydrate from liquid water; some terrestrial green algae, and chlorolichens, can rehydrate from water vapour, within certain limits of relative humidity (Raven and Edwards 2014). Photosynthesis may be restricted by CO_2 supply when there is a thick water layer over the organism as a result of the low diffusivity of CO_2 in water; especially a problem for bryophytes and some trebouxiophyceans (e.g. those in some lichens) that lack CO_2 concentrating mechanisms (CCMs), assuming the distribution of CCMs was the same as today (see below under carbon dioxide). Cyanobacteria almost certainly had CCMs in the mid-Palaeozoic; this is probably not the case for trebouxiophyceans (Meyer *et al.* 2008; Raven *et al.* 2012; Meyer and

Griffiths 2013; Raven and Beardall 2014). Extant hornworts that have CCMs only acquired these in the past 10 m.y. (Villarreal and Renner 2012; Meyer and Griffiths 2013). Problems with CO_2 supply are partly offset by the high atmospheric CO_2 in the Ordovician (and the rest of the lower- and mid-Palaeozoic). The presence of CCMs could increase nitrogen use efficiency (mol carbon assimilated in growth per unit nitrogen in the organism per unit time) and water use efficiency (mol carbon assimilated in growth per unit water lost under emersed conditions) in the growth of cryptophytes (Surif and Raven 1989, 1990).

The distribution and tolerance data discussed above for "Temperature" (Broady 1996; Robinson *et al.* 2003; Konrat *et al.* 2008; Sand-Jensen and Jesperson 2012; Geffert *et al.* 2013) are also relevant to the range of water availabilities tolerated by extant members, and hence their ability to colonise a great range of habitats before the advent of tracheophytes were a significant component of the terrestrial vegetation.

Water: effects of CCs. Bog-producing bryophytes create an extra-plant water store, but this only occurs in habitats that have high precipitation:evaporation ratios. If the CLAW hypothesis survived further scrutiny for these communities (Tyrrell 2013), it could alter rainfall patterns, but this would not necessarily be to the advantage of the producer organisms.

Oxygen: effects on CCs. While some estimates of O_2 suggest values of 75 % or higher of the PAL, others (Bergman *et al.* 2004) suggest values closer to 25 % of PAL. This latter, lower, value would mean that there was less stratospheric O_3 and hence more UVB reaching the Earth's surface (see above under Ultraviolet Radiation). Atmospheric O_2 at 25 % of PAL would also have meant less production of oxidised non-N_2 forms of N by lightning, as well as less effect of O_2 on Rubisco carboxylase in organisms relying on diffusive CO_2 entry in photosynthesis, as a result of the higher atmospheric CO_2:O_2 than is the case today (Harfort *et* *al.* 2007). The lower O_2 levels would have meant that maintaining the rate per unit biomass at levels found in extant organisms of enzymes with low O_2 for low-affinity oxygenases used in production of some defence compounds (possibly including, in embryophytes, precursors of lignin) would have involved a compensation increase in O_2-saturated enzyme activity, and a corresponding increase in enzyme protein content (Raven and Edwards 2014).

There is no charcoal as an indicator of wildfire before 419 Ma and there were no significant tracheophyte contributions to vegetation (Glasspool *et al.* 2004; Glasspool and Scott 2010). This absence could be the result of a low vegetation standing crop (see "Effects of CCs" below), and an oxygen concentration that, at the lower end of the range of estimates, would not be able to support wildfire (Glasspool *et al.* 2004; Glasspool and Scott 2010).

Oxygen: effects of CCs. A role for CCs in atmospheric oxygenation depends on whether there was sufficient burial of organic carbon produced, and insufficient oxidation of ferrous iron and of sulfide to remove the oxygen equivalent to the organic carbon burial. As discussed on p. xx, the small standing biomass (about 1 % of present terrestrial vegetation biomass) with its rapid turnover (perhaps due to the lack of recalcitrant organic matter in the organisms) allows rapid turnover of this biomass, and the small standing biomass was unlikely to have allowed sufficient organic carbon burial to significantly alter the atmospheric oxygen content.

Carbon dioxide: effects on CCs. Studies on photosynthesis in components of present day cryptophyte vegetation show that some rely on diffusive CO_2 entry while others have CO_2 concentrating mechanisms (CCMs) (Meyer *et al.* 2008; Raven *et al.* 2012; Meyer and Griffiths 2013; Raven and Edwards 2014). Organisms relying on diffusive CO_2 entry are some free-living and lichenised trebouxiophycean green algae, liverworts, mosses and some hornworts. Organisms with CCMs are free-living and lichenised cyanobacteria, some free-living and lichenised trebouxiophycean green algae and some hornworts. Members of other classes of green algae found in CCs (Charophyceae, Chlorophyceae and Ulvophyceae) do not seem to have been examined as to their mechanism of inorganic carbon acquisition. Under water availability conditions giving no, or thin, surface water films but without restrictions on photosynthetic capacity by loss of intracellular water, organisms lacking CCMs have their photosynthetic rate increased by additional CO_2 relative to the rate with 40 Pa CO_2 (the present atmospheric level of PAL), while organisms with CCMs are CO_2-saturated when CO_2 is at the PAL (Surif and Raven 1989, 1990).

There are probably fewer organisms with CCMs in the CCs in the early and mid-Palaeozoic with CO_2 concentrations of around 10-fold the PAL (Bergman *et al.* 2004). The beta-Cyanobacteria, whose Form IB Rubisco has a low CO_2 affinity and low CO_2/O_2 selectivity, would almost certainly have had CCMs, while the extant hornworts with CCMs have only acquired them over the last 100 Ma, i.e. a similar time interval to that of the origin and diversification of C_4 flowering plants (Raven *et al* 2012; Villarreal and Renner 2012). While the nutrients nitrogen and phosphorus could well have been limiting for the terrestrial flora before tracheophyte dominance, work on eukaryotic algae shows that CCMs are retained at higher CO_2 concentrations for growth under nitrogen and (often) phosphorus limitation than is the case for growth under nitrogen and phosphorus-replete conditions (Raven and Beardall 2014). Extant cyanobacteria do not repress their CCMs when grown in early Devonian CO_2 concentrations (Raven *et al.* 2012). The timing of the origin of CCMs in eukaryotic algae is unresolved (Raven *et al.* 2012; Meyer and Griffiths 2013), but it is likely that CCMs had not evolved in the early to mid-Palaeozoic. Regardless of the presence or absence of CCMs, all elements of the cryptophyte vegetation would probably have been CO_2-saturated under water availability conditions giving no, or thin, surface water films but without restrictions on photosynthetic capacity by loss of intracellular water. Thicker surface films of dew or rainwater (relatively low pH; air-equilibrium CO_2 and little or no HCO_3^-)

would have been more likely to limit the rate of photosynthesis than the same thickness of water that had been involved in weathering of silicate and/or carbonate rocks.

The argument here requires that (1) the water had been able to re-equilibrate with the atmosphere to replace CO_2 used in weathering, and (2) the photosynthetic organisms have HCO_3^- transporters as part of CCMs (cyanobacteria), or in the absence of CCMs, have extracellular carbonic anhydrase converting HCO_3^- into CO_2, with the CO_2 consumed in photosynthesis after diffusive entry.

The natural abundance of stable carbon isotopes in organic material in fossils of photosynthetic organism has been used to support the suggestion that the organisms were terrestrial (Tomescu *et al.* 2009a; Raven and Edwards 2014), and their possible phylogenetic relationships (Fletcher *et al.* 2004; Raven and Edwards 2014). However, the range of carbon isotope ratios for extant organisms in aquatic habitats extends from higher values than occur in terrestrial organisms to lower values than found in terrestrial organisms (Raven and Edwards 2014). Even allowing for the probable absence of CCMs from eukaryotic members of CCs in the mid-Palaeozoic, with corresponding decreased (i.e. to lower) $\delta^{13}C$ values of those eukaryotes that today have CCMs, the cyanobacteria would still have had CCMs and relatively positive $\delta^{13}C$ values (Raven *et al.* 2012; Meyer and Griffiths 2013; Raven and Edwards 2014; see Appendix to Fletcher *et al.* 2004, Figure 6.2 of Lakatos *et al.* 2007). This makes the natural abundance of stable isotopes an inappropriate indicator of habitat of phylogenetic affiliations unless a lot of additional information is available.

Carbon dioxide: effects of CCs. Drawdown of atmospheric carbon dioxide by CCs in the lower- and mid-Palaeozoic depends on the extent of burial of organic carbon produced in CCs photosynthesis, and the extent of CCs-induced weathering of, especially, silicates. Silicate weathering is particularly important because of the incomplete reversal of CO_2

drawdown by marine processes, by contrast with carbonate weathering that can be offset by marine processes in < 1 Ma). Such areas are explored further below.

Relevant abiotic factors and interactions with CCs: chemicals acting mainly as plant nutrients

Nitrogen: effects on CCs. Atmospheric N_2 is generally assumed to be relatively constant over billions of years. N_2 is the major contributor to total atmospheric pressure today, and recent application of Lyell's (1851) suggested method of estimating total atmospheric pressure from raindrop impact structures gave a value of 0.5 – 2.0 of the present value in the Archaean (Som *et al*. 2012). There are no such estimates for the early- and mid-Palaeozoic.

Nitrogen is an essential element for all organisms. CCs are unable to use N_2 to supply the N needed for growth, with the exception of diazotrophs such as some Cyanobacteria (free-living and in symbiosis) and some other Bacteria, and Archaea. The CC cyanobacteria include *Collema*, a non-heterocystous filamentous organism morphologically similar to *Oscillatoria*, and the free-living and lichenised heterocystous filamentous *Nostoc* that occurs not only on land but also in fresh waters (Housman *et al.* 2006; Belhuis *et al.* 2010). Apart from biological N_2 fixation, non-N_2 N in the oxidised form (NO, NO_2, HNO_3) is made available from lightning and, in two order of magnitude smaller amounts globally but perhaps locally important, terrestrial volcanism (Mather *et al.* 2004a,b). Assuming similar frequency of lightning, the lower atmospheric O_2 (25 % of PAL) and N_2 (assumed to be the PAL) partial pressures in the early- and mid-Palaeozoic would result in rates of production of NO, NO_2, HNO_3 that were 25 % of those occurring today (Bergman *et al.* 2004).

There is negligible non-N_2 N in igneous rocks. This is also the case for sedimentary rocks, with exception of highly localised cases from the Pleistocene (guano; coprolites; Chile Saltpetre), biogenic non-N_2 N involving birds and mammals.

Diazotrophy requires more Fe (invariably), Mo (usually) and P (frequently) per unit biomass than does growth on non-N_2 N. Fe would have been less available in the higher-O_2 early- and mid-Palaeozoic than through most of the Proterozoic, while Mo would have been more available.

Nitrogen: effects of CCs. CCs would not have had a significant effect on the quantity of atmospheric N_2. Depending on the extent of waterlogging, denitrifying Archaea and Bacteria would have contributed to atmospheric N_2O and hence stratospheric O_3 destruction. Diazotrophy would have increased the quantity of non-N_2 N in the terrestrial biosphere. Ascomycota and, especially, Basidiomycota, as ectomycorrhizas in certain seed plants are able to access N from recalcitrant high molecular mass organic complexes in soil (Smith and Read 2008). Whether these two fungal clades in association with extant bryophytes have similar functions has not been investigated. The non-vascular embryophyte mycorrhizas (Glomeromycota in the Marchantopsida; Mucoromycotina in the Haplomitropsida) have been shown to enhance uptake of ammonium, but more recalcitrant N forms have not been tested (Humphreys *et al.* 2010; Field *et al.* 2012; Field *et al.* 2015).

Phosphorus: effects on CCs. The essential element P occurs as apatite in igneous rocks, and from apatite and phosphorites in sedimentary rocks, with localized concentrations of phosphorites that are commercially viable as sources of rock phosphate for production of P fertilizers and other uses from 2.1 Ga onwards (Papineau 2010). However, the concentration of dissolved inorganic orthophosphate in equilibrium with P in rocks is very low.

Phosphorus: effects of CCs. Biological weathering increases the concentration of dissolved inorganic orthophosphate in solution. Particularly important is the production and secretion of citrate by CCs and by plants roots (Neaman *et al.* 2005; Lambers *et al.* 2008; Lenton *et al.* 2012; Porada *et al.* 2014). This releases P as dissolved inorganic orthophosphate by anion exchange from P bound to Fe_2O_3 and Al_2O_3 and P from apatite. Increased citrate secretion as a response to P limitation, both in very P-depleted soils and from volcanic soils where P is not readily available, occurs in a variety of flowering plants; no other embryophytes, or other cryptophytes, seem to have been examined for this response. However, it is known that the moss *Physcomitrella patens* secretes citrate as well as glycerate, malate and succinate, and showed that the moss increased P weathering from granite and andesite 60-fold (Lenton *et al.* 2012).

Granted the occurrence of low concentrations of dissolved inorganic orthophosphate in the soil solution, rhizines/rhizoids/root hairs and mycorrhizal fungi increase the volume of soil explored, and then exploited, for dissolved inorganic orthophosphate at a lower resource cost per unit of soil than normal rooting structures. Of these the glomeromycote arbuscular-vesicular (AM) mycorrhizas have particular advantages over rhizines/rhizoids/root hairs for minimizing resource input per unit soil explored in terms of their smaller radius, longer lifetime, and greater volume of soil explored (Smith and Read 2008). AMs are very common among extant vascular plants, but basal embryophytes, and especially mosses, have no, or non-glomeromycote, as well as glomeromycote, fungal associates in parallel with their rhizoids. Many thalloid liverworts have glomeromycote AMs (Smith and Read 2008; Bidartondo and Duckett 2010; Humphreys *et al.* 2010; Bidartondo *et al.* 2011; Field *et al.* 2015; Rimington *et al.* 2015). The fungi involved in these non-glomeromycote symbioses are members of the mucoromycotes, ascomycotes and basidiomycotes. The Mucoromycotina form associations with basal liverworts, some lycopods and a fern, while Ascomycota and

Basidiomycota occur in some bryophytes and in seed plants as ericoid and ectomycorrhizas (Smith and Read 2008; Bidartondo and Duckett 2010; Bidartondo *et al.* 2011; Field *et al.* 2012; Field *et al.* 2015; Rimington *et al.* 2015). These non-vascular embryophyte mycorrhizas have been shown to enhance uptake of inorganic orthophosphate (Humphreys *et al.* 2010; Field *et al.* 2012; Field *et al.* 2015); no attempts seem to have been made to determine if the mycorrhizas of non-vascular embryophytes can access organic P or insoluble metal Ca, Al, Fe) complexes of phosphate.

Once a terrestrial biosphere has been established the turnover of organisms produces phosphate esters in the soil; these cannot be taken up, and are converted into dissolved inorganic orthophosphate by extracellular phosphatases that have been characterized from marine and freshwater Cyanobacteria and algae, lichens and flowering plants. In the chlorolichen *Cladonia portentosa* (Hogan *et al.* 2010) its expression is increased by phosphorus deficiency, as is the case for other organisms. Bacteria associated with the chlorolichen *Lobaria pulmonaria* can, from genomic evidence, produce proteins associated with phosphorus mobilization (Grube *et al.* 2015).

Iron: effects on CCs. Fe deficiency decreases the growth of all organisms, but has a particular impact on diazotrophic organisms (Kustka *et al.* 2003). Fe is a relatively abundant element, but has limited availability from oxygenated environments due to the very low solubility of the predominant redox state of Fe (Fe^{3+}) in these conditions (Raven and Edwards 2001; Raven 2013).

Iron: effects of CCs. Aquatic cyanobacteria produce and secrete siderophores, organic compounds that chelate Fe^{3+}; the Fe^{3+}-containing siderophore can then be taken up by the producer cyanobacteria, as well as by other (cheating, rather than chelating) organisms (Raven and Edwards 2001; Kustka *et al.* 2003). A few algae, and some Fungi, also secrete siderophores (Raven 2013). A number of aquatic algae have surface reductases that convert extracellular Fe^{3+} to extracellular Fe^{2+}; the Fe^{2+} can then be taken up by the algal cells (Raven and Edwards 2001; Raven 2013). Cryptophytes do not seem to have been physiologically examined for either of these two mechanisms of Fe acquisition, although there is genomic evidence for siderophore production by bacteria associated with the chlorolichen *Lobaria pulmonaria* (Grube *et al.* 2015). Lenton *et al.* (2012) showed that the moss *Physcomitrella patens* increased Fe weathering from granite 170-fold and from andesite 360-fold relative to controls lacking the moss but, apparently, not sterile. However, the closed system used in this investigation means that the solution surrounding the grains of rock rapidly becomes saturated with Fe, so pH increases and the rate of dissolution declines.

ESTIMATES OF NET PRIMARY PRODUCTIVITY, BIOMASS AND BIOLOGICAL NITROGEN FIXATION OF MID-PALAEOZOIC CCs AS A BASIS FOR MODELLING OF THEIR GLOBAL IMPACT

Here estimates of extant global net primary productivity, biomass and biological nitrogen fixation resulting from CCs are used to suggest values for net primary productivity, biomass and biological nitrogen fixation before there was a significant tracheophyte contribution to terrestrial vegetation. Such estimates of the global contribution of mid-Palaeozoic CCs are needed for modelling of their possible global impact on atmospheric composition and weathering.

Contribution of extant CCs to global terrestrial net primary productivity and biological nitrogen fixation

Globally, CCs (cryptogamic ground covers plus cryptogamic plant covers, i.e. epiphytic on tracheophytes) today convert some 0.32 Pmol C from carbon dioxide to organic carbon per year; this is some 7 % of the net primary productivity of terrestrial vegetation (Belnap 2012; Elbert *et al.* 2012). An even more extreme difference occurs for the biomass, as organic C content of CCs (0.41 Pmol C) and total terrestrial vegetation (39-54 Pmol C) today (Elbert *et al.* 2012). Elbert *et al.* (2012) divided the C-based biomass by the C-based net primary productivity to yield a turnover time for the C in biomass, giving values of 1.2 years for (with a smaller content of refractory organic matter) and 10 years for total terrestrial vegetation (with more refractory organic material); both of these are much larger than the 2-20 days for oceanic phytoplankton.

The free-living and lichenised Cyanobacteria, and diazotrophic Archaea and non-cyanobacterial Bacteria (see next paragraph), in CCs (again, cryptogamic ground covers plus cryptogamic plant covers) account for 3.9 TMol non-N_2 N production by biological nitrogen fixation, which is nearly half of nitrogen fixation on land (Elbert *et al.* 2012).

Possible global terrestrial net primary productivity and biological nitrogen fixation in the mid-Palaeozoic before a significant contribution from tracheophytes

In considering what global CO_2 and N_2 assimilation could have occurred on land in the early and mid-Palaeozoic before tracheophytes became significant contributors, we can consider present day global estimates for cryptogamic ground cover and the area occupied by this cover. For carbon we use the values from Elbert *et al.* (2012), with further details of upper limits on the estimates and sensitivity analysis in Porada *et al.* (2013) and Porada *et al.* (2014). From Table S1a of Elbert *et al.* (2012), the global net carbon assimilation by cryptogamic ground cover today is 0.20 Pmol C per year out of a total for cryptogamic ground cover plus cryptogamic plant cover of 0.32 Pmol C. The total area of cryptogamic ground cover today is $68.38.10^{12}$ m^2 (Table S1a of Elbert *et al.* 2012), compared with a total land surface area of $153.0.10^{12}$ m^2. The 80 % of the land surface that is vegetated in today's glaciated world (from USGS) then has an area of $122.4.10^{12}$ m^2, so that the cryptogamic ground cover occupies 55% of the vegetated land area. This fraction is not, of course, to the exclusion of co-occurring tracheophytes, especially in extratropical forest, and to a decreasing extent in the order steppe, tundra and desert. Assuming that these biomes occurred in the same fractions of area in pre-tracheophyte times in the early and mid-Palaeozoic with glaciation to the same extent as today, and that the C assimilation per unit area is the same as today, global primary productivity on the land surface would have been 0.36 Pmol C per year. This compares with a global C assimilation on land today (tracheophytes plus cryptogamic ground cover of 4.7 Pmol C per year. The present day value is 4.7/0.36 or 13 times the value estimated for CCs with no significant tracheophytes, remembering the assumptions made and the comments in Porada et al. (2013) and Porada et al. (2014).

Of course, there are many assumptions in relating cryptogamic ground cover today to that in pre-tracheophyte times. Examples are the effects of the higher CO_2 concentrations in the early and mid-Palaeozoic, the absence of shading of that component of cryptogamic ground under tracheophytes in forest, and to a lesser extent in steppe, communities, and the absence of the significant tracheophyte contribution to pedogenesis. Nevertheless, the calculations are likely to be correct in indicating much lower total net primary productivity in times before there was a significant tracheophyte contribution than is the case today, with very low terrestrial primary productivity in the Ordovician and Early Silurian, based on $\delta^{13}C$ data (Jones *et al.* 2015).

Turning to terrestrial biomass before there was a significant contribution by tracheophytes, we start with the extant 0.41 Pmol C for biomass of CCs, including cryptogamic ground cover and cryptogamic plant cover. The downward correction of 0.41 Pmol C for including only cryptogamic ground cover (separate values not given) is probably similar to the upward correction of 0.41 Pg C for the larger land area available to cryptophytes when there was a negligible tracheophyte contribution. Thus the value of 0.41 Pg C for global terrestrial C-based biomass of vegetation can be taken to hold for global terrestrial vegetation biomass dominated by cryptophytes. The low global biomass and rapid turnover of organic C in vegetation before there was a significant tracheophyte contribution are two factors militating against large-scale burial of organic C from pre-tracheophyte vegetation.

For the role of CCs today (ground cover plus plant cover) in biological nitrogen fixation, Elbert *et al.* (2012; Table S1b) cite a global value of 3.5 Tmol N per year, which is about 46 % of total global nitrogen fixation each year on land. The global value for cryptogamic ground cover alone is 2.4 Tmol N per year. Correcting for the larger ground area available to cryptophytes in pre-tracheophyte times (1.79-fold), this gives a value for pre-tracheophyte biological N fixation on land of 4.2 Tmol N per year. This value is subject, like the estimate of net primary productivity cited above, to a number of caveats. Porada *et al.* (2014) use the alternative approach of scaling estimates of net C assimilation (Elbert *et al.* 2012; Porada *et al.* 2013) for the C:N:P ratio of CC vegetation to give values for the range of nitrogen and phosphorus uptake of 0.25 – 2.5 Tmol N per year and 0.015 – 0.15 Tmol P per year. For cryptogamic ground cover the extant range is 0.17 - 1.7 Tmol N per year and 0.011 – 0.11 Tmol P per year. Correcting for the larger ground area available to cryptophytes in pre-tracheophyte times (1.79-fold), this gives pre-tracheophyte values of 0.30 – 3.0 Tmol N per year and 0.019 – 0.19 Tmol P per year.

Conclusions

The influence of CCs before there was a significant contribution of tracheophytes in the mid-Palaeozoic was probably more local rather than global. The impact of weathering by CCs in the supply of phosphorus and iron, even with as large an area of CCs as in present day vegetation, would be significantly less than what is seen today because of the very limited depth of weathering. The lower global net primary productivity in the mid-Palaeozoic than today, plus the small fraction of intractable material in the organic carbon produced by CCs, means a more rapid turnover of terrestrial biomass than occurs today; the result is a smaller global standing biomass in the mid-Palaeozoic, with a correspondingly smaller possibility of long-term organic carbon burial with a corresponding increase in atmospheric oxygen.

VEGETATION AND ROCK WEATHERING BEFORE EUTRACHEOPHYTES

Many hypotheses relating to global climate change in the Ordovician involve increases in rock weathering with resultant drawdown of atmospheric carbon dioxide and associated cooling. Exceptions emphasize, *inter alia*, the importance of continental positions, their movement and, in particular, the location of a pole on the supercontinent, Gondwana (e.g. Caputo and Crowell 1985, Crowley and Baum 1991). More recently, Pohl *et al.* (2014) posited that changes in continental configurations during the Middle and Upper Ordovician had produced a 95 % oceanic Northern Hemisphere with consequences for oceanic heat transport which could have been sufficient to account for decreases in temperature even in the absence of CO_2 drawdown. A particularly comprehensive and critical review of contemporary differing approaches relating to climate modelling was provided by Boucot and Gray (2001).

The weathering hypothesis requires generation of fresh rock and, as outlined earlier, the Ordovician-Silurian was a period of intense volcanic activity (Huff *et al.* 2010; Sell 2013). Evidence for terrestrial weathering comes from a post Lower Ordovician substantial decrease in sea water of ^{87}Sr/^{86}Sr ratios, considered a proxy for global silicate weathering flux, attributable to tectonic activity (e.g. the Taconic orogeny) and the weathering of fresh continental basalt beginning in the Darriwilian (Shields *et al.* 2003; Young *et al.* 2009), as well as increase in fine-grained sediments in the rock record (Davies *et al.* 2011). The extent of *terrestrial* magma production is difficult to quantify. Only one in ten volcanoes today is terrestrial and 85 % by volume of products occur in the sea (e.g. Mitchell 2012). Most ash falls are preserved in oceans regardless of source (Huff *et al.* 2010) and there are relatively few records of oxidized basalts indicative of terrestrial lavas. There have been attempts to correlate major eruptive episodes/tectonic activity with marine carbon isotope excursions in the late Ordovician (Sandbian GICE, Hirnantian HICE; Buggisch *et al.* 2010) and refinement of their dating reinforces coincidences (Sell *et al.* 2013). Quantitative approaches to assessment of contributions of abiotic weathering involve not only extent and nature of substrate but physical parameters such as temperature, moisture/precipitation, aspect, atmospheric CO_2 and latitude, which also affect plant distribution and productivity. Latitude is particularly important as continents moved into the inter-tropical convergence zone (e.g. Nardin *et al.* 2011 attributed 33 % of weathering in the Hirnantian to fresh magma weathering, the rest to plate movements). It has long been speculated that land surfaces before the advent of tracheophytes were not barren (See Berner 1992 for references), with 'vegetation' ranging from microbial crusts to lichens and bryophytes (e.g. Gray 1985, 1993;

Beerbower 1985; Wellman 1999; LePage and Pfefferkorn 2000), although Nardin *et al.* (2011) modelled them as rocky deserts, and Jones *et al.* (2015) used $\delta^{13}C$ data to suggest a very limited terrestrial primary productivity in the Ordovician and Early Silurian.. Attempts at quantification were initially limited to field observations and measurements but have now been extended to laboratory experiments. For example, an increase in thickness of a weathering rind on the surface of a Hawaiian basalt under a lichen was later attributed to accumulation of dust around the thalli, and although Berner and Cochran (1998) demonstrated some chemical weathering associated with lichens this was much less than that associated with plant roots. Colonization by higher plants (e.g. ferns and angiosperms) tends to concentrate in crevasses where the nitrogen deficient substrate characteristic of basalts is enhanced by dust and accumulation of water. The actual surfaces of the basalt of pahoehoe type tend to be smooth and glassy, relatively dense and impermeable, and apart from lichens and very occasionally mosses are devoid of vegetation over long periods. Only on removal of the rind does agricultural cultivation become possible. The rough rubbly clinkers of a'a lava flows tend to be highly porous and often too dry for colonization. Although intrinsically high in mineral nutrients, lavas are generally inhospitable substrates for colonization. It has recently been shown that regeneration of trees on lavas in the Central Oregon Cascades, USA, was facilitated by the introduction of ash, with greater mineral accessibility introduced either by wind or flooding episodes (Deligne *et al.* 2013). This introduces the relative importance of ash, plus other constituents of pyroclastic flows, and lava in consideration of vegetation-mediated weathering both today and in mid-Palaeozoic times. The substrates may be broadly similar in chemical composition depending on type of eruption, but differ in physical properties, particularly permeability, water storage and susceptibility to erosion. Thus the small grain size of ash (<2 mm, decreasing rapidly in grain size away from the volcano; e.g. Mt St Helens, Sarna-Wojcicki *et al.* 1981) facilitates more rapid chemical weathering and is water rich, but more susceptible to air borne redistribution (Deligne *et al.* 2013). Although today lavas are commoner around volcanic eruptions than pyroclastic activity, ashes have received more attention because ash-derived soils are amongst the most fertile today (Ugolini and Dahlgren 2002). However fertility results from a combination of successive ash flows and interbedded organic material produced from decaying vegetation which is exploited for nitrogen by rooted vascular plants on recolonization, thus compensating for its deficiency in the mineral nutrient ash.

Successive layers of CCs would not allow such recycling, and perhaps account for their absence in recolonization of recent ash falls e.g. in Mount St Helens, Surtsey, Ksudach volcanoes, where angiosperms are usually the primary colonisers (e.g. del Moral and Grishin 1985, 1999; del Moral and Wood 1993; Grishin *et al.* 1996; Fridriksson and Magnussen 1992). Unpublished images and observations by Professor Katharine Cashman (Bristol University) are intriguing in that in Iceland today ash surfaces alongside ± contemporary basalts are conspicuously absent. She attributes this to the readily erodible (and possibly low pH?) of fresh ash with the possibility that when consolidation has occurred, much of the mineral nutrients may have been chemically weathered. By contrast, Parnell and Foster (2012) noting the coincidence of high ashfalls and the beginnings of land vegetation, emphasized the importance of ash with its high nutrient content, especially of phosphorus, and good drainage to colonization. As evidence they cited the high concentration of plant spores and ‘symbiotic nitrogen fixing fungi’ in ash today.

The timing of colonization, although negligible on a geological scale, has relevance to discussions here. Delays following eruptions caused by instability and possibly toxicity (low pH) would have allowed abiotic chemical weathering as well as ameliorating the substrate. Relevant literature searches covering almost all latitudes and involving both distribution of CCs and their roles in recolonization reveal little directly relevant information except to demonstrate complexity in responses, relating to climate, substrate type and aspect/landscape. Lichens (del Moral and Grishin 1999) tend to dominate on dry substrates particularly at high elevation and latitude while mosses and liverworts are also recorded at lower latitudes, such as recorded on the thick deposits of pumice on Soufriére, St Vincent and on Mt Pelée (Beard 1976). Most field surveys relating to colonization were made some time (tens to hundreds of years) after eruptions and hence are dominated by records of angiosperms (usually trees). On a shorter timescale, del Moral and Grishin wrote that 'succession has not recapitulated phylogeny' when commenting on the absence of lichens, fungi and cyanobacteria and the sporadic occurrence of mosses among the vascular plants on Mount St Helens, although lichens and bryophytes were recorded on Sakurajima volcano in SW Japan (Tagawa *et al.* 1985). On Ksudach volcano, Kamchatka Peninsula, Grishin *et al.* (1996) in a survey encompassing the hundred years since eruption reported that the immediate pioneers were angiosperm herbs, but after 20-30 years 9 species of lichens were growing on the high altitude deepest, nutrient poor, acidic, rapidly draining pumice deposits to the exclusion of angiosperms. The most in depth study based on Katmai volcano, Alaska, which has been monitored since eruption in 1912, involved both field and laboratory studies (Griggs, 1933). For at least eleven years, ash, similar in chemical composition to granite, but with low K and P content, was barren, but then colonized by fertile leafy jungermannalian liverworts, *Lophozia bicrenata* and more importantly *Cephalozia byssaca* (now *C. bicrenata*)to the exclusion of almost all other plant species, although microscopic examination revealed fragments of moss protonema (but no fertile specimens), green algae and fungal hyphae, but no cyanobacteria, as had been recorded as pioneers on Krakatau, which lacked liverworts (Tagawa *et al.* 1985). Apart from minute quantities in rainfall, Gribbs found no other nitrogen sources,nor any indications of organic matter in the substrate, and speculated the possibility of a symbiosis with a fungus. More than 75 years later, an ascomycete has been demonstrated in *Cephalosia* (Pressel *et al.* 2010) and the basidiomycete, *Sebacina,* in *L. bicrenata*. (Bidartondo and Duckett 2010). Such fungi can access recalcitrant organic nitrogen, presumably recycling it from decaying liverworts (Smith and Read 2008). Although the liverworts reproduced prolifically, subsequent moss colonizers were less successful and exhibited stunted growth. Vascular plants were represented by rare willow seedlings. Similarly exhaustive studies have not yet been undertaken on Iceland where CCs extend over considerable areas – and would provide an excellent outdoors laboratory for weathering and development of soils on a variety of magmatic substrates (work in progress at NHM)

Quantitative laboratory approaches

More quantitative approaches via experiment and modelling have involved estimates of microbial soil respiration, extent of mineral weathering and microcosm experiments involving modern analogues of rooted and non-rooted ecosystems. Thus, for example, Keller and Wood (1993) argued that pre-vascular plant subaerial surfaces would have hosted algae and lichens, and from modelling respiration values in the vadose zone beneath, would have produced levels of carbonic acid and weathered minerals similar to those in similar habitats in post Silurian times, even at today's atmospheric CO_2 values. In an alternative approach Yapp and Poths (1994) measured the $Fe(CO_3)OH$ component of goethite in an Upper Ordovician oolitic limestone which has been subjected to tropical chemical weathering, used this as a measure of the atmospheric CO_2 present at the time of goethite crystallization and derived values of microbial respiration. They concluded that the pre-vascular plant biota was as productive as extant tropical/temperate examples thus indicating significant biologically mediated chemical weathering on land, but did not extrapolate as to whether this would have been sufficient to drawn down atmospheric CO_2 to levels that initiated glaciation, as was achieved by Lenton *et al.* (2012; Fig. 1). Various models had suggested that glaciation became possible at values lower than c. 8 PAL and, based on scenarios in which biotic silicate weathering was not included, modelled values at 460 Ma predicted atmospheric CO_2 as c. 16 PAL (e.g. Herrmann *et al.* 2004b).

Lenton *et al.* (2012) cultured fragments of the moss, *Physcomitella patens* in water with fragments of basalt and andesite and then measured abundances of Ca, K, Fe, Al, K and P in the medium as indications of chemical weathering. The enhanced silicate weathering values over background abiotic effects were considered similar to those from vascular plants, and when incorporated into an adapted version of their COPSE model, the predicted CO_2 value for 460 Myr ago dropped to 8.4 PAL with global temp c. 17ºC; such values are around the threshold for glaciation, and are consistent with a global cooling episode. Further, Lenton *et al.* (2012) suggested that phosphorus released by moss-induced weathering is enhanced by a factor of 60 compared with controls lacking moss. However, this enhancement is derived from the sum of the measured phosphorus in the leachate and an assumed (from the literature) phosphorus uptake into the moss; it would have been helpful to have direct measurements. Granted increased phosphorus weathering (see also Porada *et al.* 2014), when this phosphorus was washed into seas it would have increased productivity and eventually led to burial of carbon as recorded in marine carbon isotope excursions, e.g. Guttenberg (GICE) and Hirnantian (HICE), and hence further cooling. Periodicity could have resulted from exhaustion of terrestrial, and hence marine, phosphate, with subsequent increased phosphate input from volcanicity, and from glaciation followed by deglaciation. Mid–Late Ordovician phosphate-rich limestones on Laurentia associated with upwelling and high $\delta^{13}C$ (GICE; Lavoie and Asselin 1998; Pope and Steffen 2003; Cherns and Wheeley 2007), as also seen at each end of the Proterozoic (Papineau 2010), deserve further attention in this respect.

Such microcosm experiments can always be criticized as regards procedural detail and difficulties of scaling up globally. A major problem with the measurements in Lenton *et al.* (2012) is that these relate to grain-scale weathering, while what moves to the ocean reflects landscape scale processes. Moulton *et al.* (2000) found that silicate weathering from a western Icelandic landscape vegetated by small trees was 5-6 times that from a landscape partially vegetated with mosses and lichens. The choice of a moss by Lenton *et al.(*2012), although understandable as a complete genomic sequence is known in *Physcomitella patens*, is unfortunate as compared with other postulated members of CCs as contact with substrate is low in the field compared, say, with thalloid liverworts. Baars *et al.* (2008) used the latter (*Conocephalum conicum*) in less well controlled (as regards temperature and light regimes) microcosm experiments in which trays containing algae/bacteria, bryophytes, *Psilotum* (a non-rooted tracheophyte) and *Equisetum* (a rooted tracheophyte) were grown on trays in cabinets approaching ambient (360 ppm) and c.10 PAL (3500 ppm), and the leachate containing inorganic carbon species and organic acids (negligible amounts) was collected and analysed. Elevated carbon dioxide concentrations were recorded in leachates only in the elevated CO_2 cabinets and in the leachate from *Equisetum*, and this was the only solution to produce very minor erosion on basalt tiles. The trays in the bryophyte cabinets were dominated by the liverwort, which thrived under the elevated CO_2. Organic matter had been kept to a minimum in trays to keep down soil respiration. Such data provide support for Berner’s contention that rooted tracheophytes were most important for CO_2 drawdown, a conclusion substantiated by Quirk *et al.* (in press) in experiments based on the thalloid, basal liverwort *Marchantia paleacea*, which may be colonised by the glomeromycotean arbuscular mycorrhizal fungus. They grew the liverwort with and without the symbiont for 12 months at three CO_2 levels (200, 450 and 1200ppm) on a free-draining substrate comprising quartz and *Sphagnum* peat under which were situated mesh bags containing chips of basalt of uniform size. Interspersed in the basalt were slides bearing flakes of biotite and phlogopite. Trenches developed on the latter below fungal hyphae and liverwort rhizoids provided information on extent and depth of interaction with substrate while analysis of the mineral content of the solution and liverwort tissues compared with the plant-free controls indicated the amounts of Ca, Mg and P liberated from the basalt.

Results showed that liverworts with and without symbionts increased Ca release three to five fold compared with controls, the greatest effect being at ambient CO_2 while P weathering was amplified 11 fold under liverworts with symbionts compared with seven fold in fungus free liverworts, the effects being greater at ambient and high CO_2. These figures are substantially lower than those obtained by Lenton *et al.* (2012). Similar experiments involving saplings of trees hosting a variety of types of mycorrhiza, showed that, although at the hyphal/rhizoid level, the penetration of substrate surfaces was similar to that recorded for root hairs of the trees the depth of substrate exploited was substantially greater in the latter, leading to the conclusion that amplification of weathering under liverworts would have been about 5 % relative to forests today.

We have no evidence for liverworts similar to extant forms, let alone evidence of symbionts, in the Ordovician and Silurian. Arbuscular mycorrhizas were present in at least two taxa in the Lower Devonian Rhynie Chert (Taylor *et al.* 2015), although extent of hyphal interaction with the substrate is unknown. It does seem likely that there were thalloid basal bryophytes in the CCs that would have produced effects on weathering at least comparable to those produced by liverworts lacking symbionts in the above experiments, but in the absence of rooted tracheophytes we agree with Quirk *et al*. (2012) that it would be too little to cause the drawdown of CO_2 resulting in Ordovician-Silurian glaciations.

CONCLUSIONS

The limited direct evidence outlined above plus inferences from extant vegetation provide data to support the existence and biological consequences of a land surface in the in the mid Ordovician to end of Silurian dominated by CCs*,* but their impacts on lithosphere and atmosphere remain conjectural. Considering the distribution of terrestrial vegetation today, it seems likely that areas occupied by all categories of vegetation (e.g. Matthews 1984) would be suitable habitats for the various elements in CCs in the mid-Palaeozoic, the major exception in terms of habitat being epiphytic substrates. Calculations of current vegetated areas based on satellite data (e.g. ESA, GLOBCOVER; USGS, GLCC) indicate c. 80 % coverage, and c. 87 % in an ice free world*.* Directly comparable estimates for the mid-Palaeozoic are highly speculative because the interval was one of great geological upheaval with limited data on climate controls such as continental sizes and configuration, latitudinal position (temperature, precipitation, seasonality), ocean circulation and topography, with additional inputs from orbital forcing of climate. These geological and astronomical inputs to environmental conditions would have evolved throughout the time, as would the composition of vegetation itself. However it seems reasonable to assume, based on the ecological tolerances of elements of the CCs today in a wide range of habitats hostile to tracheophytes, that they were widespread in these and more equable habitats dominated by modern vascular plants. Their composition, reflecting ecological responses to substrate, temperature and water availability, is impossible to quantify. An interesting approach was adopted by Strother (2010), who estimated the proportions of axial and thalloid fossils on bedding planes. Using seven slabs collected by Lang (1937), he estimated 50 % of the surface was occupied by incrustation and 1 % by axial fossils. These fossils were allochthonous and preserved in fluvial rocks with all the limitations of sorting during transport, but may approximate to the extent of contact between organism and substrate in habitats in the catchment area. Tomescu and Rothwell (2006) reported that some of these incrustations (no embryophytic axial fossils were present) were autochthonous and almost covered overbank, floodplain deposits. Such analyses also draw attention to the fact that our megafossil evidence during this time interval derives from marginal depositional settings, be they shallow marine, coastal plain or proximal fluvial facies. Thus the vegetation that was fossilized would have been growing on substrates dominated by sands and muds, which would have been impoverished in mineral nutrients as a result of hinterland weathering. Thus drawdown of CO_2 via rock weathering would have been lower than that on fresh magma. Such substrates have so far been overlooked in empirical activities. As to the magma itself, the extent of volcanism on land and the relative proportions of lava and ash as well as the contribution of weathering of ancient cratons remain imponderables.

Such uncertainties and gaps in knowledge make it impossible to answer our initial question as to whether photosynthesizing land vegetation bioengineered the planet in mid-Palaeozoic times, although our conclusions on interactions of extant CCs with abiotic factors indicate minimal effects on a global scale. However, there is a developing scenario of evolutionary changes in the composition of CCs and the emergence of tracheophytes of ever increasing complexity and stature such that by the end of the Silurian homoiohydric, photosynthesizing tracheophytes with underground rooting structures had become established, heralding the beginnings of a vegetation with far more profound impacts on the nature of terrestrial ecosystems particularly relating to atmospheric changes.

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REFERENCES

BAARS, C., JONES, T. H. and EDWARDS, D. 2008. Microcosm studies of the role of land plants in elevating soil carbon dioxide and chemical weathering. *Global biogeochemical cycles*, **22,** doi: 10.1029/2008GB003228.

BASINGER, J. F., KOTYK, M. E. and GENSEL, P. G. 1996.Early land plant from the Late Silurian-Early Devonian of Bathurst Island, Canadian Archipelago. *Geological Survey of Canada*, *Current Research* ***1996B***, 51-60.

BATEMAN, R. M. 1991. Palaeoecology. 34-116. *In* CLEAL, C. J. (ed.). *Plant fossils in geological*. *investigation*. *The Palaeozoic.* Horwood Press, Chichester UK.

BEARD, J. S. 1976. The progress of plant succession on the Soufriére of Mt. Vincent: observations in 1972. *Vegetatio*, **31**, 69-77.

BEERBOWER, R. 1985. Early development of continental ecosystems. 47-91. *In* TIFFNEY, B.H. (ed.). Yale University Press, New Haven and London. **5**.

BELNAP, J. 2012. Unexpected uptake. *Nature Geoscience*, **5,** 443-444.

BELHUIS, H., SEVERIN, I., CONFURIUS-GUNS, U., WOLLENZIEN, U. I. A. and STAL, L. J. 2010. Horizontal transfer of the nitrogen fixation gene cluster in the cyanobacterium *Microcoleus chthonoplastes. ISME Journal*, **4,** 121-130.

BENNETT, P. and SIEGEL, D. I. 1987. Increased solubility of quartz in water due to complexing by organic compounds. *Nature,* **326**, 684-686.

BERGMAN, N. M., LENTON, T. M. and WATSON, A. J. 2004. COPSE: A new model of biogeochemical cycles over Phanerozoic time. *American Journal of Science*, **304**, 397-437.

BERGSTRÖM, S. M., SCHMITZ, B., SALTZMAN, M. R. and HUFF, W. D. 2010. The Upper Ordovician Guttenberg $\delta^{13}C$ excursion (GICE) in North America and Baltoscandia: Occurrence, chronostratigraphic significance, and paleoenvironmental relationships. 37-67. *In* FINNEY, S.C. and BERRY, W. B. N. (eds). *The Ordovician Earth System. Geological Society of America Special Papers*, **466**, Boulder, Colorado, USA. viii + 193 pp.

BERKNER, L.V. and MARSHALL, L. C. 1965. NAS Symposium on the Evolution of the Earth's Atmosphere: HISTORY OF MAJOR ATMOSPHERIC COMPONENTS. *Proceedings of the National Academy of Sciences of the United States of America*, **53**, 1215.

BERNER, R. A. 1991. A model for atmospheric CO_2 over Phanerozoic time. *American Journal of Science;(United States)*, **291**, 339-376.

--- 1992. Weathering, plants, and the long term carbon cycle. *Geochimica et Cosmochimica Acta*, **56**, 3225-3231.

--- 1994. GEOCARB II: A revised model of atmospheric CO_2 over Phanerozoic time. *American Journal of Science;(United States)*, **294**, 56-91.

--- 2006*a*. GEOCARBSULF: a combined model for Phanerozoic atmospheric O_2 and CO_2. *Geochimica et Cosmochimica Acta*, **70**, 5653-5664.

---. 2006*b*. Inclusion of the weathering of volcanic rocks in the GEOCARBSULF model *American Journal of Science*, **306**, 295-302.

--- and CANFIELD, D. E. 1989. A new model for atmospheric oxygen over Phanerozoic time. *American Journal of Science*, **289**: 333-361.

--- and COCHRAN, M. F. 1998. Plant-induced weathering of Hawaiian basalts. *Journal of Sedimentary Research*, **68**, 723-726.

--- and KOTHAVALA, Z. 2001. GEOCARB III: a revised model of atmospheric CO_2 over Phanerozoic time. *American Journal of Science*, **301**, 182-204.

BIDARTONDO, M. I. and DUCKETT, J. G. 2010. Conservative ecological and evolutionary patterns in liverwort-fungal symbioses. *Proceedings of the Royal Society B*, **277,** 485-492.

---, READ, D. J., TRAPPE, J. M., MERCKX, V., LIGRONE, R. and DUCKETT, J. G. 2011. The dawn of symbiosis between plants and fungi. *Biology Letters*, **7**, 574-577.

BLUTH, G. J. S., SCHNETZLER, C. C., KRUEGER, A. J. and WALTER, L. S. 1993. The contribution of explosive volcanism to global atmospheric sulfur concentrations. *Nature*, **366**, 327-9.

BOUCOT, A. J. and GRAY, J. 2001. A critique of Phanerozoic climatic models involving changes in the CO_2 content of the atmosphere. *Earth Science Review*, **56**, 1-159.

BOYCE, C.K. and HOTTON, C.L. 2010. “*Prototaxites* was not a taphonomic artefact”. *American Journal of Botany*, **97**, 1073.

BOYCE, C.K., HOTTON, C.L., FOGEL, M.L., CODY, G.D., HAZEN, R.M., KNOLL, A.K. and HUEBER, F.M. 2007. Devonian heterogeneity recorded by a giant fungus. *Geology*, **35**, 399-402.

BRENCHLEY, P. J. 2004. End Ordovician glaciation. 81-83. *In* WEBBY, B. D., DROSER, M. L., PARIS, F. and PERCIVAL, I. G. (eds) *The great Ordovician biodiversification event.* Columbia University Press, NY, x + 484 pp.

BRIDGE, J. S. 2006. Fluvial facies models: recent developments. *In* POSAMENTIER, H. W. and WALTER, R. G. (eds) *Facies Models Revisited*. *SEPM Special Publication* **84**, 85-170.

BRISTOW, T. F., KENNEDY, M. J., DERKOWSKI, A., DROSER, M. L., LIANG, G., and CREASER, R. A. 2009. Mineralogical constraints on the paleoenvironments of the

Ediacaran Doushantuo Formation. *Proceedings of the National Academy of Sciences*, **106**, 13190-13195.

BROADY, P. A. 1996. Diversity, distribution and dispersal of Antarctic terrestrial algae. *Biodiversity and conservation, **5**,* 1307-1335.

BRONSON, D. R., ENGLISH, N. B., DETTMAN, D. L.and WILLIAMS, D. G. 2011. Seasonal photosynthetic gas exchange and water use efficiency in a constitutive Crassulacean Acid Metabolism plant, the giant Saguaro cactus (*Carnegeia gigantea*). *Oecologia* **167**: 861-871.

BUGGISCH, W., JOACHIMSKI, M. M., LEHNERT, O., BERGSTRÖM, S. M., REPETSKI, J. E. and WEBERS, G. F. 2010. Did intense volcanism trigger the first Late Ordovician icehouse? *Geology*, **38**, 327-330.

BURGESS, N. D. and EDWARDS, D. 1988. A new Palaeozoic plant closely allied to *Prototaxites* Dawson. *Botanical Journal of the Linnean Society*, **97**, 189-203.

---. and --- 1991. Classification of uppermost Ordovician to Lower Devonian tubular and filamentous macerals from the Anglo-Welsh Basin. *Botanical Journal of the Linnean Society*, **106**, 41-66.

BUTTERFIELD, N. J., KNOLL, A. H., SWETT, K. 1988. Exceptional preservation of fossils in an upper Proterozoic shale. *Nature*, **344**, 424-427.

CAPUTO, M. V. and CROWELL, J. C. 1985. Migration of glacial centers across Gondwana during Paleozoic Era. *Bulletin of the Geological Society of America*, **96**, 1020-1036.

CARRUTHERS, W. 1872. On the history, histological structure and affinities of *Nematophycus logani*, Carruthers (*Prototaxites logani,* Dawson), an alga of Devonian age. *Monthly Microscopical Journal*, **8**, 160-172.

CHARLSON, R. J., LOVELOCK, J. E., ANDREAE, M. O. and WARREN, S. G. 1987. Oceanic phytoplankton, atmospheric sulfur, cloud albedo and climate. Nature **326**: 655-661.

CHENOWETH, M. 2001. Two major volcanic cooling episodes derived from global marine air temperature, AD 1807–1827. *Geophysical Research Letters*, **28**, 2963-2966.

CHERNS, L. and WHEELEY, J. R. 2007. A pre-Hirnantian (Late Ordovician) interval of global cooling – The Boda event re-assessed. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **251**, 449-460.

--- and --- 2009. Early Palaeozoic cooling events: peri-Gondwana and beyond. 257-278. *In* BASSETT, M. G. (ed.) *Early Palaeozoic Peri-Gondwana Terranes; new insights from tectonics and biogeography*. *Geological Society, London, Special Publication*, **325**, 287 pp.

---, ---, POPOV, L., GHOBADI POUR, M., OWENS, R. M. and HEMSLEY, A. R. 2013. Long-period orbital climate forcing in the early Palaeozoic? *Journal of the Geological Society*, **170**, 707-710.

CHURCH, A. H. 1919. *Thalassiophyta* and the subaerial transmigration. *Oxford Botanical Memoirs***, 3**, 1-95. Oxford University Press.

CLARKE, L. J. and ROBINSON, S. A. 2008. Cell wall-bound ultraviolet screening compounds explain the high tolerance of the Antarctic moss, *Ceratodon purpureus*. *New Phytologist*, **179,** 776-783.

COCKS, L. R. M. and TORSVIK, T. H. 2002. Earth geography from 500 to 400 million years ago: a faunal and palaeomagnetic review. *Journal of the Geological Society*, **159**, 631-644.

COCKELL, C. S. and KNOWLAND, J. 1999. Ultraviolet radiation screening compounds. *Biological Reviews of the Cambridge Philosophical Society*, **74**, 311-345.

COX, C. T., LI, B., FOSTER, P. G., EMBLEY, Y. M. and CIVAN, P. 2014. Conflicting phylogenies for early land plants are caused by composition biases among synonymous substitutions. *Systematic Biology*, **63**, 272-279.

CROWLEY, T. J. and BAUM, S. K. 1991. Towards reconciliation of Late Ordovician (440Ma) glaciations with very high CO_2 levels. *Journal of Geophysical Research*, **96**, 22597-26610.

DABER, R. 1971. *Cooksonia,* one of the most ancient psilophytes, widely distributed but rare. *Botanique (Nagpur),* **2**, 35-40.

DAVIES, N. S. and GIBLING, M. B. 2010*a*. Paleozoic vegetation and the Siluro-Devonian rise of fluvial lateral accretion sets. *Geology* **38**, 51-54.

--- and --- 2010*b*. Cambrian to Devonian evolution of alluvial systems: the sedimentological impact of the earliest land plants. *Earth Science Reviews*, **98**, 171-200.

---, RYGEL, M. C. and GIBLING, M. B. 2010. Marine influence on the Upper Ordovician Juriata Formation (Potters Mills, Pennsylvania): implications for the history of life on land. *Palaios*, **25**, 527-539.

---, RYGEL, M. C. and GIBLING, M. B. 2010. The sedimentary record of Carboniferous rivers: continuing influence of land plant evolution on alluvial processes and Palaeozoic ecosystems. *Earth Science Reviews*, **120**, 40-79.

---, GIBLING, M. R. and RYGEL, M. C. 2011. Alluvial facies evolution during the Palaeozoic greening of the continents: cell studies, conceptual models and modern analogues. *Sedimentology*, **58**, 220-258.

DAWSON, J. W. 1859. On fossil plants from the Devonian rocks of Canada. *Quarterly Journal of the Geological Society of London*, **15**, 477-488.

DAWSON, J. W. 1871. Report on the fossil land plants of the Devonian and Upper Silurian formations of Canada. Geological Survey of Canada Publication, 428, 1-92.

del MORAL, R. and GRISHIN, S. Y. 1999. Volcanic disturbances and ecosystem recovery. 137-160. *In* WALKER L. R. (ed.). *Ecosystems of disturbed ground.* Elsevier

--- and WOOD, D. M. 1993. Early primary succession on the volcano Mount St Helens. *Journal of Vegetational Science*, **4**, 223-234.

DELABROYE, A., MUNNECKE, A., SERVAIS, T., VANDENBROUCKE, T. R. and VECOLI, M. 2012. Abnormal forms of acritarchs (phytoplankton) in the upper Hirnantian (Upper Ordovician) of Anticosti Island, Canada. *Review of Palaeobotany and Palynology*, **173**, 46-56.

DELIGNE, N. I., CASHMAN, K. V. and ROERING, J. J. 2013. After the lava flow: the importance of external soil sources for plant colonization of recent lava flows in the central Oregon Cascades, USA. *Geomorphology*, **202**, 15-32.

DIAZ-MARTINEZ, E. and GRAHN, Y. 2007. Early Silurian glaciations along the western margins of Gondwana (Peru, Bolivia and northern Argentina): palaeogeographic and geodynamic sitting. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology.* **245**, 62-81.

DOTT, R. H., Jr 2003. The importance of aeolian abrasion in supermature quartz sandstones and the paradox of weathering on vegetation-free landscapes. *Journal of Geology*, **111**, 387-405.

EDWARDS, D. 1979. A late Silurian flora from the Lower Old Red Sandstone of southwest Dyfed. *Palaeontology*, 22, 23-52.

--- 1982. Fragmentary non-vascular plant microfossils from the late Silurian of Wales. *Botanical Journal of the Linnean Society*, **84**, 223-256.

--- 1986. Dispersed cuticles of putative non-vascular plants from the Lower Devonian of Britain. *Botanical Journal of the Linnean Society*, **93**, 259-275.

--- and AXE, L. 2012. Evidence for a fungal affinity for *Nematasketum*, a close ally of *Prototaxites*. *Botanical Journal of the Linnean Society*, **168**, 1-18.

--- and DAVIES, E. C. W. 1976. Oldest recorded *in situ* tracheids. *Nature*, **263**, 494-495.

--- and KENRICK, P. 2015. The early evolution of land plants, from fossils to genomics: a commentary on Lang (1937) ‘On the plant-remains from the Downtonian of England and Wales’. *Philosophical Transactions of the Royal Society B*, **370**, 20140343 doi:0.1098/rstb.2014.0343

--- and ROGERSON, E. C. W. 1979. New records of fertile Rhyniophytina from the late Silurian of Wales. *Geological Magazine*, **116**, 93-98.

---, BASSETT, M. G. and ROGERSON, E. C. W. 1979. The earliest vascular plants land plants: continuing the search for proof. *Lethaia*, **12**, 313-324.

---, FANNING, U. and RICHARDSON, J. 1986. Stomata and sterome in early land plants. *Nature*, **323**, 438-440.

---, FEEHAN, J. and SMITH, D.G. 1983. A late Wenlock flora from Co. Tipperary, Ireland. *Botanical Journal of the Linnean Society*, **86**, 19-36.

---, MOREL, E.M., PAREDES, F., GANUZA, D.G. and ZÚÑIGA, A. 2001. Plant assemblages from the Silurian of southern Bolivia and their palaeogeographical significance. *Botanical Journal of the Linnean Society*, **135**, 229-250.

---., AXE, L., POIRE, D. G., MOREL, E. M., BASSETT, M. G. and CINGOLANI, C. A. 2009. Enigmatic fossils from the Upper Silurian of Bolivia: evidence for marine productivity in high-latitude Gondwana. 177-200. *In* BASSETT, M. G. (ed.) *Early Palaeozoic Peri-Gondwana Terranes; new insights from tectonics and biogeography*. *Geological Society, London, Special Publications*, **325**, 287 pp.

---, AXE, L. and HONEGGER, R. 2013. Contributions to the diversity in cryptogamic covers in the mid-Palaeozoic: *Nematothallus* revisited. *Botanical Journal of the Linnean Society*, **173**, 505-534.

---, MORRIS, J.L., RICHARDSON, J.B. and KENRICK, P. 2014. Tansley Review. Cryptospores and cryptophytes reveal hidden diversity in early land floras. *New Phytologist*, **202**, 50-78.

ELBERT, W., WEBER, B., BURROWS, S., STEINKAMP, J., BÜDEL, B., MEINRAT, O. A. and PÖSCHL, U. 2012. Contribution of cryptogamic covers to the global cycles of carbon and nitrogen. *Nature Geoscience*, **5**, 459-462.

FANNING, U., EDWARDS, D. and RICHARDSON, J. 1990. Further evidence for diversity in late Silurian land vegetation. *Journal of the Geological Society*, **147**, 725-728.

--- 1992. A diverse assemblage of early land plants from the Lower Devonian of the Welsh Borderland. *Botanical Journal of the Linnean Society*, **109**, 161-188.

FIELD, K. J., LEAKE, J. R., TILLE, S., BIDARTONDO, M.I. and BEERLING, D. J. 2012. Contrasting arbuscular mycorrhizal efficiency of vascular and non-vascular land plants to a simulated Palaeozoic CO_2 decline. *Nature Communications*, **3,** doi: 10,1038/ncomms1831.

---, RIMINGTON, W. R., BIDARTONDO, M. I., ALLINSON, K. E., BEERLING, D. J., CAMERON, D. D., DUCKETT, J. G., LEAKE, J. R. and PRESSEL, S. 2015. First evidence of mutualism between ancient plant lineages (Haplomitropspida liverworts) and Mucoromycotina fungi and its response to simulated Palaeozoic changes in atmospheric CO_2. *New Phytologist*, **205,** 763-756.

FLETCHER, B. J., BEERLING, D. J. and CHALONER, W. G. 2004. Stable carbon isotopes and the metabolism of the terrestrial Devonian organism *Spongiophyton. Geobiology,* **2,** 108-119.

FRAKES, L. A. and FRANCIS, J. E. 1988. A Guide to Phanerozoic Cold Polar Climates from High-Latitude Ice-Rafting in the Cretaceous. *Nature*, **333**, 547-549.

FRIDRIKSSON, S. and MAGNUSSEN. B. 1992. Development of the ecosystem on Surtsey with reference to Anak Krakatau. *GeoJournal*, **28**, 287-291.

FUČIKOVÁ, K., LEWIS, P. O. and LEWIS, L. A. 2014 Widespread desert affiliation of trebouxiophycean algae (Trebouxiophyceae, Chlorophyta) including discovery of three new desert genera. *Phycological Research*, **62**, 294-305.

GADD, G.M. and RAVEN, J.A. 2010. Geomicrobiology of eukaryotic organisms. *Geomicrobiology Journal*, **27**, 491-519.

GARCIA-PICHEL, F, 1994. A model for internal self-shading of planktonic organisms and its implications for the usefulness of ultraviolet sunscreens. *Limnology and Oceanography* **39,** 1704-1717.

GEFFERT, J.L., FROHM, J-P., BARTHLOTT, W. and MUTKE, J. 2013. Global moss diversity: spatial and taxonomic patterns. *Journal of Bryology*, **35**, 1-11.

GENSEL, P., CHALONER, W. G. and FORBES, W. H. 1991. *Sporogeophyton* from the late Lower Devonian of New Brunswick and Quebec, Canada. *Palaeontology*, **34**, 149-168.

---, KOTYK, M. E. and BASINGER, J. F. 2001. Morphology of above- and below-ground structures in Early Devonian (Pragian-Emsian) plants. 83-102. *In*: GENSEL, P. G. and EDWARDS, D. (eds). *Plants Invade the Land:_Evolutionary and Environmental Perspectives*. Columbia University Press, New York.

GLASSPOOL, I. J. and SCOTT, A. C. 2010. Phanerozoic concentrations of atmospheric oxygen reconstructed from sedimentary charcoal. *Nature Geoscience*, **3**, 627-630.

---, EDWARDS, D. and AXE, L. 2004. Charcoal in the Silurian as evidence of the earliest wildfire. *Geology*, **32**, 381-383.

GODDÉRIS, Y., DONNADIEU, Y., LE HIR, G., LEFEBVRE, V. and NARDIN, E. 2014. The role of palaeogeography in the Phanerozoic history of atmospheric CO< sub> 2</sub> and climate. *Earth-Science Reviews*, **128**, 122-138.

GONEZ, P., GERRIENNE, P. 2010. *Aberlemnia caledonica* gen. et comb. nov., a new name for *Cooksonia caledonica* Edwards 1970. *Review of Palaeobotany and Palynology*, **163**, 64-72.

GONZÁLEZ-MENÉNDEZ, L., GALLASTEGUI, G., CUESTA, A., HEREDIA, N. and RUBIO-ORDÓÑEZ, A. 2013. Petrogenesis of Early Paleozoic basalts and gabbros in the western Cuyania terrane: Constraints on the tectonic setting of the southwestern Gondwana margin (Sierra del Tigre, Andean Argentine Precordillera). *Gondwana Research*, **24**, 359-376.

GRAHAM, L. E., WILCOX, L. W., COOK, M. E. and GENSEL, P. G. 2004. Resistant tissues of marchantioid liverworts resemble enigmatic Early Paleozoic microfossils. *Proceedings of the National Academy of Sciences*, **101**, 11025-11029.

---, LEWIS, L. A., TAYLOR, W., WELLMAN, C. and COOK, M. 2014. Early terrestrialisation: transition from algal to bryophyte grade. 9-28. *In* HANSON, D.T. and RICE, S.K. (eds). Photosynthesis in bryophytes and early land plants. Springer, Dordrecht, Heidelberg, New York, London.

---, COOK, M. E., HANSON, D. T., PIGG, K. B. and GRAHAM, J. M. 2010. Structural physiological and carbon isotope evidence that the enigmatic Paleozoic fossil *Prototaxites* formed from rolled liverwort mats. *American Journal of Botany*, **97**, 268-275.

GRAHN, Y. and CAPUTO, M. V. 1992. Early Silurian glaciations. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **99**, 9-15.

GRAY, J. 1984. Ordovician-Silurian land plants: the interdependence of ecology and evolution. 281-295. *In*: BASSETT, M. G. and LAWSON, J. D. (eds). Autecology of Silurian Organisms. *Special Papers in Palaeontology*, **32.**

---. 1985. The microfossil record of early land plants: advances in understanding of early terrestrialisation, 1970-1984. *Philosophical Transactions of the Royal Society of London*, *B*, **309**, 167-195.

---. 1993. Major Paleozoic land plant evolutionary bio-events. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **104**, 153-169.

---, MASSA. D. and BOUCOT, A. J. 1982. Caradocian land plant microfossils from Libya. *Geology*, **10**, 197-201.

GRIGGS, R. F. 1933. The colonization of the Katmai ash, a new and 'inorganic' soil. *American Journal of Botany*, **20**, 92-113.

GRISHIN, S. Y., del MORAL, R., KRISTOV, P. and VERKHOLAT, V. P. 1996. Succession following the catastrophic eruption of Ksudach volcano (Kamchatka 1907). *Vegetatio*, **127**, 129-153.

GRUBE, M., CERNOVA, T., SOH, J., FUCHS, S., ASCHENBRENNER, I., LASSEK, C., WEGNER, U., BECHERM, D., RIEDEL, K., STENSEN, C.W. and BERG, C. 2015. Exploring functional contexts of symbiotic sustain within lichen-associated bacteria by comparative omics. *The ISME Journal*, **9**, 412-424.

HAQ, B. U. and SCHUTTER, S. R. 2008. A chronology of Paleozoic sea-level changes. *Science*, **322**, 64-68.

HARFOOT, M. B., BEERLING, D. J., LOMAX, B. H. and PYLE, J. A. 2007. A two-dimensional atmospheric chemistry modelling of Earth's Phanerozoic O_3 and near-surface ultraviolet radiation history. *Journal of Geophysical Research*, **112,** D07308, doi: 10.1029/2006JD007372.

HECKMAN, D. S., GEISER, D. M., EIDELL, B. R., STAUFFER, R. L., KARDOS, N. L. and HEDGES, S. B. 2001. Molecular evidence for the colonization of land by fungi and plants. *Science*, **293**, 1129-1133.

HERRMANN, A. D., HAUPT, B. J., PATZKOWSKY, M. E., SEIDOV, D. and SLINGERLAND, R. L. 2004a. Response of Late Ordovician paleoceanography to changes in sea level, continental drift, and atmospheric pCO_2: potential causes for long-term cooling and glaciation. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **210**, 385-401.

HERRMANN, A. D., PATZKOWSKY, M. E. and POLLARD, D. 2004b. The impact of paleogeography, pCO_2, poleward ocean heat transport and sea level change on global cooling during the Late Ordovician. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **206**, 59-74.

HICKS, H.1881. On the discovery of some remains of plants at the base of the Denbighshire Grits, near Corwen, North Wales. *Quarterly Journal of the Geological Society*, **37**, 482-496.

HISTON, K., KLEIN, P., SCHÖNLAUB, H. P. and HUFF, W. D. 2007. Lower Palaeozoic K-bentonites from the Carnic Alps, Austria. *Austrian Journal of Earth Sciences*, **100**, 26-42.

HOFFMEISTER, W. S. 1959. Lower Silurian plant spores from Libya. *Micropalaeontology,* **5**, 331-334.

HOGAN, E. J., MINULINA, G., SHEPHERD, L. J., LEITH, I. D. and CRITTENDEN, P. D. 2010. Responses of phosphomonoesterase activity in the lichen *Cladonia portentosa* to nitrogen and phosphorus enrichment in a field manipulation study. *New Phytologist*, **186**, 926-933.

HONEGGER, R., EDWARDS, D. and AXE, L. 2013a. The earliest records of internally stratified cyanobacterial and algal lichens from the Lower Devonian of the Welsh Borderland. *New Phytologist*, **197**, 264-275.

---, AXE, L. and EDWARDS, D. 2013b. Bacterial epibionts and endolichenic actinobacteria and fungi in the Lower Devonian lichen Chlorolichenomycites salopensis. *Fungal biology*, **117**, 512-518.

HOTTON, C. L., HUEBER, F. M., GRIFFING, D. H. and BRIDGE, J. S. 2001. Early terrestrial plant environments: an example from the Emsian of Gaspé, Canada. 179-212. *In*: GENSEL, P.G. and EDWARDS, D. (eds). *Plants Invade the Land: Evolutionary and Environmental Perspectives.* Columbia University Press, New York.

HOUSMAN, D. C., POWERS, H. H., COLLINS, A. D. and BELNAP, J. 2006, Carbon and nitrogen fixation differ between successional stages of biological soil crusts in the Colorado Plateau and Chihuahuan Desert. *Journal of Arid Environments*, **66,** 620-634.

HUEBER F. M. 2001. Rotted wood-alga-fungus: the history and life of *Prototaxites* Dawson 1859. *Review of Palaeobotany and Palynology*, **116**, 123-158.

HUFF, W. D., BERGSTRÖM, S. M. and KOLATA, D. R. 1992. Gigantic Ordovician volcanic ash fall in North America and Europe: Biological, tectonomagmatic, and event-stratigraphic significance. *Geology*, **20**, 875-878.

---., ---, ---, CINGOLANI, C. A. and ASTINI, R. A. 1998. Ordovician K-bentonites in the Argentine Precordillera: relations to Gondwana margin evolution. *Geological Society, London, Special Publications*, **142**, 107-126.

---, --- and ---. 2010. Ordovician explosive volcanism. 13-28. *In* FINNEY, S. C. and BERRY, W. B. N. (eds). *The Ordovician Earth System*. *Geological Society of America Special Paper*, **466**, Boulder, Colorado, USA, viii + 193 pp.

HUMPHREYS, C. P., FRANKS, P. J., REES, M., BIDARTONDO, M. I., LEAKE, J. R. and BEERLING, D. J. 2010. Mutualistic mycorrhiza-like symbiosis in the most ancient group of land plants. *Nature Communications*, **1,** 103, doi:10.1038/ncomms1105.

JOHNSON, M. E. 2006. Relationship of Silurian sea-level fluctuations to oceanic episodes and events. *GFF*, **128**, 115-121.

JOHNSON, M. J., STALLARD, R. F. and LUNDBERG, N. 1991. Controls on the composition of fluvial sands from a tropical weathering environments. Sands of the Orinoco River drainage basin, Venezuela and Colombia. *Geological Society of America Bulletin*, **103**, 1622-1627.

JONES, D. S., CREEL, R. C., RIOS, B. and RAMOS, D. P. S. 2015. Chemostratigraphy of an Ordovician-Silurian carbonate platform: δ^{13}C records below glacioeustatic exposure surfaces. *Geology*, **43**, 59-62.

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JONES, H.G. 2014. *Plants and microclimate. A quantitative approach to environmental plant physiology*. Third edition. Cambridge University Press, Cambridge, UK. 407pp.

KARATYGIN, I. V., SNIGIREVSKAYA, N. S. and DEMCHENKO, K. N. 2009. Species of the genus *Glomites* as plant mycobionts in Early Devonian ecosystems. *Paleontological Journal*, **40**, 572-579.

KELLER, C. K and WOOD, B. D. 1993. Possibility of chemical weathering before the advent of vascular land plants. *Nature*, **364**, 223-225.

KELLNER, E. 2001. Surface energy fluxes and control of evaporation from a Swedish *Sphagnum* mire. *Agricultural and Forest Meteorology*, **10**, 101-123.

KENRICK, P. and CRANE, P. 1997. The origin and early evolution of plants on land. *Nature*, **389**, 33-39

KEPPLER, F., EIDEN, R., NIEDAN, U., PROCHT, J. and SCHÖLER, H. F. 2000. Halocarbons produced by natural oxidation processes of degradation of organic matter. *Nature*, **403**, 298-301.

KIDSTON, R. and LANG, W. H. 1920. On Old Red Sandstone plants showing structure, from the Rhynie Chert Bed, Aberdeenshire. Part III. *Asteroxylon mackiei*, Kidston and Lang. *Transactions of the Royal Society of Edinburgh,* **52**, 643-680.

KODNER, R.B. and GRAHAM, L.E. 2001. High-temperature, acid-hydrolyzed remains of *Polytrichum* (Musci, Polytrichaceae) resemble enigmatic Silurian-Devonian tubular microfossils. *American Journal of Botany*, **88**, 462-466.

KOLATA, D. R., HUFF, W. D. and BERGSTROM, S. M. 1996. *Ordovician K-bentonites of eastern North America*. *Geological Society of America Special Paper* **313**, Boulder, Colorado, USA, 84 pp.

KOLATA, D. R., HUFF, W. D. and BERGSTRÖM, S. M. 1998. Nature and regional significance of unconformities associated with the Middle Ordovician Hagan K-bentonite complex in the North American midcontinent. *Geological Society of America Bulletin*, **110**, 723-739.

KONRAT, M. VON., HOGBERG, A., SÖDERSTROM, L., MUTKE, J., RENNER, H., GRADSTEIN, R., ENGEL, J., ZHU, R-L. and PICKERING, J. 2008. Early land plants today: Global patterns of liverwort diversity, distribution and floristic knowledge. 425-438. *In* MOHAMMED, M., BAKI, B.B., NASUVULHAQ-BOYCE, A. AND LEE, P.K.Y. (eds). *Bryophytes in the New Millenium*, University of Malaysia, Kuala Lumpur, Malaysia.

KOTYK, M. E., BASINGER, J. F., GENSEL, P. G., and de FREITAS, T. A. 2002. Morphologically complex plant macrofossils from the Late Silurian of Arctic Canada. *American Journal of Botany*, **89**, 1004-1013.

KROKEN, S.B., GRAHAM, L.E. and COOK, M.E. 1996. Occurrence and evolutionary significance of resistant cell walls in charophytes and bryophytes. *American Journal of Botany*, **83**, 1241-1254.

KUMP, L. R., ARTHUR, M. A., PATZKOWSKY, M. E., GIBBS, M. T., PINKUS, D. S. and SHEEHAN, P. M. 1999. A weathering hypothesis for glaciation at high atmospheric pCO_2 during the Late Ordovician. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **152**, 173-187.

KUSTKA, A., SAÑUDO-WILHELMY, S., CARPENTER, E. J., CAPONE, D. G. and RAVEN, J. A. 2003. A revised estimate of the iron use efficiency of nitrogen fixation, with special reference to the marine cyanobacterium *Trichodesmium* spp. (Cyanophyta). *Journal of Phycology*, **39**, 12-25.

LAKATOS, M., HARTARD, B and MÁGUAS, C. 2007. The stable isotopes δ^{13}C and δ^{18}O of lichens can be used as tracers of microenvironmental carbon and water sources. 77-92. *In* DAWSON, T. E. AND SIEGWOLF, R. T. W. (eds). *Stable Isotopes as Indicators of Ecological Change,* Elsevier, Amsterdam.

LAMBERS, H., RAVEN, J. A., SHAVER, G. and SMITH, S. E. 2008. Plant nutrient strategies change with soil age. *Trends in Ecology and Evolution*, **23**, 95-103.

LANG, W.H. 1937. On the plant-remains from the Downtonian of England and Wales. *Philosophical Transactions of the Royal Society of London*, *B*, **227**, 245-291.

LANG, W.H. 1945. *Pachytheca* and some anomalous early plants (*Prototaxites, Nematothallus, Parka, Foerstia, Orvillea* n.g.). *Journal of the Linnean Society, Botany*, **52**, 535-552.

LAVOIE, D. and ASSELIN, E. 1998. Upper Ordovician facies in the Lac Saint-Jean outlier, Quebec (eastern Canada): palaeoenvironmental significance for Late Ordovician oceanography. *Sedimentology*, **45**, 817-832.

LE HERON, D. P. GHIENNE, J.-F. EL HOURCHA, M., KHOUKHI, Y. and RUBINO, J.-L. 2007. Maximum extent of ice sheets in Morocco during the late Ordovician glaciation. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **245**, 200-226.

LE HIR, G., DONNADIEU, Y., GODDÉRIS, Y., MEYER-BERTHAUD, B., RAMSTEIN, G. and BLAKEY, R. C. 2011. The climate change caused by the land plant invasion in the Devonian. *Earth and Planetary Science Letters*, **310**, 203-212.

LEFEBVRE, V., SERVAIS, T., FRANÇOIS, L. and AVERBUCH, O. 2010. Did a Katian large igneous province trigger the Late Ordovician glaciation?: A hypothesis tested with a carbon cycle model. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **296**, 310-319.

LEHNERT, O., MÄNNIK, P., JOACHIMSKI, M.M., CALNER, M. and FOYDA, J. 2010. Palaeoclimate perturbations before the Sheinwoodian glaciation: a trigger for extinctions during the 'Ireviken Event'. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **296**, 320-331.

LENTON, T. M., CROUCH, M. N., JOHNSON, M., PIRES, N. and DOLAN, L. 2012. First plants cooled the Ordovician. *Nature Geoscience*, **5,** 86-89.

LEPAGE, B. A. and PFEFFERKORN. H. W. 2000. Did ground cover change over geological time? 171-182. *In* GASTALDO, R. A. and DIMICHELE, W. A. (eds). *Phanerozoic terrestrial ecosystems*. *Special papers of the Paleontological Society*. **6**.

LEWIS, L. A. and LEWIS, P. O. 2005. Unearthing the molecular phylodiversity of desert soil green algae (Chlorophyta) *Systematic Biology*, **54**, 936-947.

LIGRONE, R., DUCKETT, J. G., RENZAGLIA, K. S. 2012. Major transitions in the evolution of early land plants: a bryological perspective. *Annals of Botany*, **109**, 851-871.

LOVE, S. E. and WILLIAMS, B. P. J. 2000. Sedimentology, cyclicity and floor plain architecture in the Lower Old Red Sandstone of SW Wales. 371-388. *In* FRIEND, P. F. and WILLIAM, B. P. J. (eds), *New Perspectives on the Old Red Sandstone. Geological Society of London Special Publication*, **180**,

LOYDELL, D. K. 1998. Early Silurian sea-level changes. *Geological Magazine*, **135**, 447-471.

LÜCKING, R., HUHNDORF, S., PFISTER, D. H., RIVAS PLATA, E and LUMBSCH, H. T. (2009) Fungi evolved right on track. *Mycologia*, **101,** 810-822.

LUNING, S., LOYDELL, D., SUTCLIFFE, O., SALEM, A. A., ZANELLA, E., CRAIG, J. and HARPER, D. 2000. Silurian--Lower Devonian black shales in Morocco: Which are the organically richest horizons? *Journal of Petroleum Geology*, **23**, 293-311.

MATHER, T.A., PYLE, D.M. and ALLEN, A.G. 2004a. Volcanic source for fixed nitrogen in the early Earth's atmosphere. *Geology*, **32**, 905-908.

---, ALLEN, A.G., DAVISON, B.M., PYLE, D.M., OPPENHEIMER, C. and MCGONIGLE, A.J.S. 2004b. Nitric acid from volcanoes. *Earth and Planetary Science Letters*, **218**, 17-30.

MATTHEWS, E. 1984. Prescription of land-surface boundary conditions in GISS GCM 11: a simple method based on fine-resolution data bases. *NASA Technical Memo*, **89096**, 1-21 June.

MCLAUGHLIN, P. I., EMSBO, P. and BRETT, C. E. 2012. Beyond black shales: The sedimentary and stable isotope records of oceanic anoxic events in a dominantly oxic basin (Silurian; Appalachian Basin, USA). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **367**, 153-177.

MEYER, M. and GRIFFITHS, H. 2013. Origins and diversity of eukaryotic CO_2-concentrating mechanisms: lessons for the future. *Journal of Experimental Botany*, **64**, 769-786.

---, SEIBT, U. and GRIFFITHS, H. 2008. To concentrate or ventilate? Carbon acquisition, isotope discrimination and physiological ecology of early land plant life forms. *Philosophical Transactions of the Royal Society of London B*, **367**, 2367-2778.

MIALL, A. D. and GIBLING, M. R. 1978. The Siluro-Devonian clastic wedge of Somerset Island, Arctic Canada, and some regional palaeogeographic implications. *Sedimentary Geology*, **21**, 85-127.

MISHLER, B. D. and CHURCHILL, S. P. 1985. Transition to a land flora: phylogenetic relationships of the green algae and bryophytes. *Cladistics*, **1**, 305-328.

MITCHELL, N. 2012. Submarine volcanism: Hot, cracking rocks deep down. *Nature Geoscience*, **5**, 444-445.

MOULTON, K. L., WEST, J. and BERNER, R.A. 2000. Solute flux and mineral mass balance approaches to the quantification of plant effects on silicate weathering. *American Journal of Science*, **300,** 539-570.

MOUNTNEY, N. P. and RUSSELL, A. J. 2006. Coastal aeolian dune development Solheimasandier, southern Iceland. *Sedimentary Geology*, **192**, 167-181.

MUNNECKE, A., DELABROYE, A., SERVAIS, T., VANDENBROUCKE, T. R. and VECOLI, M. 2012. Systematic occurrences of malformed (teratological) acritarchs in the run-up of Early Palaeozoic $\delta^{13}C$ isotope excursions. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **367**, 137-146.

NARDIN, E., GODDÉRIS, Y., DONNADIEU, Y., Le HIR, G., BAKEY, R. C., PUCÉAT, E. and ARETZ, M. 2014. Modelling the early Paleozoic long-term climatic trend. *Bulletin of the Geological Society of America*, **123**, 1181-1192.

NEAMAN, A., CHOROVER, J. and BRANTLEY, S.L. 2005. Implications of the evolution of organic acid moieties for basalt weathering over geological time. *American Journal of Science*, **305**, 147-185.

NIKLAS, K. J. and SMOCOVITIS, V. 1983. Evidence for a conducting strand in early Silurian (Llandoverian) plants: implications for the evolution of the land plants. *Paleobiology*, **9**, 126-137.

OBRHEL, J. 1968. Die Silur- und Devonflora des Barrandiums. *Paläontologische Abhandlungen Berlin*, **2**, 635-793.

PAGE, A., ZALASIEWICZ, J., WILLIAMS, M. and POPOV, L. 2007. Were transgressive black shales a negative feedback modulating glacioeustasy in the Early Palaeozoic Icehouse? 123-156. *In* WILLIAMS, M., HAYWOOD, A. M., GREGORY, F. J. and SCHMIDT, D. N. (eds). *Deep-time perspectives on climate change: marrying the signal from computer models and biological proxies* The Micropalaeontological Society, Special Publications, **2**, The Geological Society, London, vi + 589 pp.

PAPINEAU, D. 2010. Global biogeochemical changes at both ends of the Proterozoic: insights from phosphorites. *Astrobiology*, **10,** 165-181.

PARNELL, J. and FOSTER, S. 2012. Ordovician ash geochemistry and the establishment of land plants. *Geochemical Transactions*, 13:7

PETERSON, K. J., WAGGONER, B. and HAGADORN, J. W. 2003. A fungal analog for Newfoundland edicarian fossils? *Integrative and Comparative Biology*, **43**, 127-136.

PIROZYNSKI, K. A. and MALLOCH, D. W. 1975. The origin of land plants: a matter of mycotrophism. *BioSystems*, **6**, 153-164.

POHL, A., DONNADIEU, Y., LE HIR, G., BUONCRISTIANI, J.-F. and VENNIN, E. 2014. Effect of the Ordovician paleogeography on the (in) stability of the climate. *Climate of the Past*, **10**, 2053-2066.

POPE, M. C. and STEFFEN, J. B. 2003. Widespread, prolonged late Middle Ordovician upwelling in North America: a proxy record of glaciation? *Geology*, **31**, 63-66.

PORADA, P., WEBER, B., ELBERT, W., PÖSCHL, U. and KLEIDON, A. 2013. Estimating global carbon uptake by lichens and bryophytes with a process-based model. *Biogeosciences*, **10,** 6989-7033.

---, ---, ---, --- and --- 2014. Estimating impacts of lichens and bryophytes on global biogeochemical cycles. *Global Biogeochemical Cycles*, **28,** 71-85.

PORTMANN, R.W., DANIEL, J. S. and RAVISHANKARA, A. R. 2012. Stratospheric ozone depletion due to nitrous oxide: influence of other gases. *Philosophical Transactions of the Royal Society of London B*, **367**, 1256-1261.

PRATT, I. M., PHILLIPS, T. L. and DENNISON, J. M. 1978. Evidence of non-vascular land plants from the early Silurian (Llandoverian) of Virginia, U.S.A. *Review of Palaeobotany and Palynology*, **25**, 121-149.

PRESSEL, S., BIDARTONDO, M. I., LIGRONE, R. and DUCKETT, J. G. 2010. Fungal symbioses in bryophytes: new insights in the twenty first century. *Phytotaxa*, **9**, 238-253.

PRIETO, M. and WEDIN, M. 2013. Dating the diversification of the major lineages of Ascomycota (Fungi). *PLoS ONE*, **8,** e65576.

QIU, Y-L., WANG, B., CHEN, Z., DOMBROVSKA, O., LEE. J., KENT, L., LI, R., JABSON, R. W. and HENDRY, T. A. 2007. A non-flowering land plant phylogeny inferred from nucleotide sequences of seven chloroplast, mitochondrial, and nuclear genes. *International Journal of Plant Sciences*, **168**, 691-708.

QUIRK, J., BEERLING, D. J., BANWART, S. A., KAKONYI, G., ROMERO-GONZALEZ, M. E. and LEAKE, J. R. 2012. Evolution of trees and mycorrhizal fungi intensifies silicate mineral weathering. *Biology letters*, **8**, 1006-1011.

RAVEN, J. A. 1986. Evolution of plant life forms. 421-492. *In* GIVNISH, T. J. (ed), *On the Economy of Plant Form and Function*.

--- 1991. Responses of aquatic photosynthetic organisms to increased solar UVB. *Journal of Photochemistry and Photobiology B: Biology,* **9,** 239-244.

--- 2013. Iron acquisition and allocation by stramenopile algae. *Journal of Experimental Botany*, **64**, 2119-2127.

--- and BEARDALL, J. 2014. CO_2 concentrating mechanisms and environmental change. *Aquatic Botany*, **118,** 24-37.

---. and EDWARDS, D. 2001. Roots: evolutionary origins and biogeochemical significance. *Journal of Experimental Botany*, **52** (supplement), 381-401.

--- and --- 2014. Photosynthesis in early land plants: adaptations to the terrestrial environment. 29-58. *In* HANSON D. T and RICE S. K. (eds). *Photosynthesis in Bryophytes and Early Land Plants, Advances in Photosynthesis and Respiration*. Springer, Dordrecht.

--- and SPICER, R. A. 1996. The evolution of Crassulacean Acid Metabolism. 360-385. *In* WINTER, K. and SMITH, J. A. C. (eds). *Crassulacean Acid Metabolism: Biochemistry, Ecophysiology and Evolution.* Springer, Heidelberg.

---, GIORDANO, M., BEARDALL, J. and MABERLY, S. C. 2012. Algal evolution in relation to atmospheric CO_2: carboxylases, carbon-concentrating mechanisms and carbon oxidation cycles. *Philosophical Transactions of the Royal Society of London B*, **367**, 493-507.

RAYNER, R. J. 1984. New finds of *Drepanophycus spinaeformis* Göppert from the Lower Devonian of Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **75**, 353-363.

REDECKER, D., KODNER, R. and GRAHAM, L. E. 2000. Glomalean fungi from the Ordovician. *Science*, **289**, 1920-1921.

--- and GRAHAM, L.E. 2002. *Palaeoglomus grayi* from the Ordovician. *Mycotaxon*, **84**, 33-37.

RETALLACK, G. J. 1994. Were the Ediacaran fossils lichens? *Paleobiology*, **20**, 523-544.

---. 2000. Ordovician life on land and Early Paleozoic global change. *Palaeontological Society Papers*, **6**, 21-45.

--- 2001. *Scoyenia* burrows from Ordovician palaeosols of the Juniata Formation in Pennsylvania. *Palaeontology*, **44**, 209-235.

--- 2007. Decay, growth and burial compaction of *Dickinsonia*, an iconic ediacaran fossils. *Alcheringa*, **31**, 215-240.

--- 2009. Cambrian-Ordovician non-marine fossils from South Australia. *Alcheringa*, **33**, 355-391.

--- 2011. Problematic megafossils in Cambrian palaeosols of South Australia. *Palaeontology*, **54**, 1223-1242.

--- 2013. Ediacaran life on land. *Nature*, **493**, 89-92.

--- 2014. Precambrian life on land. *The Palaeobotanist*, **63**, 1-15.

--- and LANDING, E. 2014. Affinities and architecture of Devonian trunks of *Prototaxites loganii*. *Mycologia*, **106**, 1143-1156.

RICE, S.K. and SCHNEIDER, N. 2004. Cushion size, surface roughness and the control of water balance and carbon flux in the cushion moss *Leucobryum glaucum* (Leucobryaceae). *American Journal of Botany*, **91**, 1164-1172.

RICHARDSON, J. B. 2007. Cryptospores and miospores, their distribution patterns in the Lower Old Red Sandstone of the Anglo-Welsh Basin, and the habitat of their parent plants. *Bulletin of Geosciences*, **82**, 355-364.

---, FORD, J. H. and PARKER, F. 1984. Miospores, correlation and age of some Scottish Lower Old Red Sandstone sediments from the Strathmore region (Fife and Angus). *Journal of Micropalaeontology*, **3**, 109-124.

RIMINGTON, W. R., PRESSEL, S., DUCKETT, J. G. and BIDARTONDO, M. I. 2015. Fungal associations of basal vascular plants: reopening a closed book? *New Phytologist* **205,** 1394-1398.

ROBINSON, S. A., WASLEY, J. and TOBIN, A. K. 2003. Living on the edge: plants and global change in continental and maritime Antarctica. *Global Change Biology*, **9**, 1681-1717.

ROYER, D. L. 2006. CO_2-forced climate thresholds during the Phanerozoic. *Geochimica et Cosmochimica Acta*, **70**, 5665-5675.

---, BERNER, R. A. and BEERLING, D. J. 2001. Phanerozoic atmospheric CO_2 change: evaluating geochemical and paleobiological approaches. *Earth-Science Reviews*, **54**, 349-392.

---, ---, MONTAÑEZ, I. P., TABOR, N. J. and BEERLING, D. J. 2004. CO_2 as a primary driver of Phanerozoic climate. *GSA today*, **14**, 4-10.

RUBINSTEIN, C. V., GERRIENNE, P., de la PLUENTE, S., ASTINI, R. A. and STEEMANS, P. 2010. Early Middle Ordovician evidence for land plants in Argentina (eastern Gondwana). *New Phytologist*, **188**, 365-369.

SÁNCHEZ-BARACALDO, P, RIDGWELL, A. and RAVEN, J. A. (2014) A Neoproterozoic transition in the marine nitrogen cycle. *Current Biology*, **24,** 652-657.

SAND-JENSEN, K. and JESPERSON, T. S. 2012. Tolerance of the widespread cyanobacterium *Nostoc commune* to extreme variations ($-269 – 105^{o}$ C), pH and salt concentration. *Oecologia*, **169**, 331-339.

SARNA-WOJCICKI, A.M., SHIPLEY, S., WAITT, R.B., DZURISIN, D. and WOOD, S.H. 1981. Areal distribution, thickness, mass, volume, and grain size of air-fall ash from six major eruptions of 1980. 577-600. *In* LIPMAN, P. W. and MULLINEAUX, D. R.

(eds). *The 1980 eruptions of Mount St. Helens, Washington*. *U.S. Geological Survey Professional Paper* **1250**.

SCHOPF, J. M., MENCHER, E., BOUCOT, A. J. and ANDREWS, H. N. 1966. Erect plants in the early Silurian of Maine. *U.S. Geological Survey*, *Professional Paper 550-D*, D69-D75.

SELF, S. 2006. The effects and consequences of very large explosive volcanic eruptions. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, **364**, 2073-2097.

SELL, B., AINSAAR, L. and LESLIE, S. 2013. Precise timing of the Late Ordovician (Sandbian) super-eruptions and associated environmental, biological, and climatological events. *Journal of the Geological Society*, **170**, 711-714.

SELL, B. K. 2011. Intense volcanism and Ordovician icehouse climate. 527-536. *In* GUTIÉRREZ-MARCO, J. C., RÁBANO, I. and GARCÍA-BELLIDO, D. (eds). *Ordovician of the World*. *Cuadernos del Museo Geominero*, **14**, Instituto Geológico y Minero de España, Madrid, 682 pp.

SELOSSE, M.-A. 2002. *Prototaxites*: a 400 myr old giant fossil, a saprophytic holobasidiomycete, or a lichen? *Mycological Research*, **106**, 641-644.

SHERWOOD-PIKE, M. A. and GRAY, J. 1985. Silurian fungal remains: probable records of the Class Ascomycetes. *Lethaia*, **18**, 1-20.

SHIELDS, G. A. 2007. A normalized seawater strontium isotope curve: possible implications for Neoproterozoic-Cambrian weathering rates and the further oxygenation of the Earth. *eEarth*, **2**, 35-42.

---, CARDEN, G. A., VEITZER, J., MEIDLA, T., RONG, J. and LI, R. 2003. Sr, C and O isotope geochemistry of Ordovician brachiopods: a major isotopic event around the Middle-Late Ordovician transition. *Geochimica et Cosmochimica Acta*, **67**, 2005-2025.

SINHA, R. P. and HÄDER, D-P. 2002. UV-induced DNA damage and repair: a review. *Photochemical and Photobiological Sciences*, **1**, 225-236.

SMITH, S. E. and READ, D. J. 2008. *Mycorrhizal Symbiosis*. San Diego, California: Academic Press.

SOM, S.M., CATLING, D. C., HARNMEIJER, J. P., POLIKVA, P. M. and BUICK, R. 2012. Air density 27 billion years ago limited to less than twice modern levels by fossil raindrop imprints. *Nature*, **484,** 359-362.

SOPER, N. J. and WOODCOCK, N. H. 1990. Silurian collision and sediment dispersal patterns in southern Britain. *Geological Magazine*, **127**, 527-542.

STAAL, C. R. VAN and HATCHER, R. D. 2010. Global setting of Ordovician orogenesis. 1-11. *In* FINNEY, S. C. and BERRY, W. B. N. (eds). *The Ordovician Earth System.*

Geological Society of America Special Paper, **466**, Boulder, Colorado, USA. viii + 193 pp.

STEEMANS, P., Le HÉRISSÉ, A., MELVIN, J., MILLER, M. A., PARIS, F., VERNIERS, J. and WELLMAN, C. H. 2009. Origin and radiation of the earliest vascular plants. *Science*, **324**, 353.

STEUR, H. and van der BRUGGHEN, W. 1998. *Nematothallus*: een raadselachtige plant uit het Siluur en het Vroeg-Devoon. *Grandboor Hamer*, **52**, 28-35.

STIVALETTA, N., BARBIERI, R., CEVENINI, F. and LOPEZ-GARCIA, P. 2011. Physicochemical conditions and microbial diversity associated with the evaporite deposits in the Laguna de la Piedra (Salar de Atacama, Chile). *Geomicrobiology Journal*, **28**, 83-95

STROTHER, P. K. 1988. New species of *Nematothallus* from the Silurian Bloomsburg Formation of Pennsylvania. *Journal of Paleontology*, **62**, 967-982.

--- 1993. Clarification of the genus *Nematothallus* Lang. *Journal of Paleontology*, **67**, 1090-1094.

--- 2010. Thalloid carbonacerous incrustations and the asynchronous evolution of embryophyte characters during the Early Palaeozoic. *International Journal of Coal* Geology, **83**, 154-161.

--- and BECK, J. H. 2000. Spore-like micofossils from Middle Cambrian strata: expanding the meaning of the term cryptospore. 413-424. *In* HARLEY, M. M., MORTON, C. M. and BLACKMORE, S. (eds). Pollen and spores. Morphology and biology. Royal Botanic Gardens, Kew. London.

---, AL-HAJRI, S. and TRAVERSE, A. 1996. New evidence for land plants from the lower Middle Ordovician of Saudi Arabia. *Geology*, **24**, 55-58.

---, WOOD, G., TAYLOR, W. and BECK, J. 2004. Middle Cambrian cryptospores and the origin of land plants. *Memoirs of the Association of the Australasian Palaeontologists*, **29**, 99-113.

SURIF, M. B. and RAVEN J. A. 1989. Exogenous inorganic carbon sources for photosynthesis in seawater by members of the Fucales and Laminariales (Phaeophyta): ecological and taxonomic implications. *Oecologia*, **78**, 97-105.

--- and --- 1990. Photosynthetic gas exchange under emerged conditions in eulittoral and normally submersed members of the Fucales and Laminariales: interpretation in relation to C isotope fractionation and N and water use efficiency. *Oecologia*, **82**, 68-80.

TAGAWA, H., SUZUKI, E., PARTOMIHARDJO, T., and SURIADARMA, A. 1985, Vegetation and succession on the Krakatau Islands, Indonesia. *Vegetatio*, **60**, 131-145.

TAYLOR, T.N., HASS, H. and KERP, H. 1997. A cyanolichen from the Lower Devonian Rhynie Chert. *American Journal of Botany*, **84**, 992-1004.

---, HASS, H., REMY, W. and KERP, H. 1995. The oldest fossil lichen. *Nature*, **378**, 244.

---, TAYLOR, E. L., DECOMBEIX, A.-L., SCHWENDEMANN, A., SERBET, R., ESCAPA, I. and KRINGS, M. 2010. The enigmatic Devonian fossil *Prototaxites* is not a rolled-up liverwort mat: comment on the paper by Graham *et al.* (AJB#97: 268-275). *American Journal of Botany*, **97**, 1075-1078.

TAYLOR, W.A. 1995. Spores in earliest land plants. *Nature*, 373, 391-392.

--- and STROTHER, P. K. 2009. Ultrastructure, morphology and topology of Cambrian palynomorphs from the Lone Rock Formation, Wisconsin, USA. *Review of Palaeobotany and Palynology*, **153**, 296-309.

THOMAS, A. D. and DOUGILL, A. J. 2007. Spatial and temporal distribution of cyanobacterial soil crusts in the Kalahari: implications for soil surface properties. *Geomorphology*, **85**, 17-20.

TIMS, J. D. 1980. *The early land flora of Victoria*. Unpublished PhD thesis. University of Melbourne, Australia.

TOMESCU, A.M.F. and ROTHWELL, G.W. 2006. Wetlands before tracheophytes: thalloid terrestrial communities of the Early Silurian Passage Creek biota (Virginia). 41-56. *In*

GREB, S. F. and DIMICHELE, W. A. (eds). *Wetlands Through Time. Geological Society of America, Special Paper*, **399**. Boulder, Colorado.

---, --- and HONEGGER, R. 2006. Cyanobacterial macrophytes in an Early Silurian (Llandovery) continental biota: Passage Creek, Lower Massanutten Sandstone, Virginia, USA. *Lethaia*, **39**, 329-338.

---, --- and ---. 2008. Earliest fossil record of bacterial – cyanobacterial mat consortia: the early Silurian Passage Creek biota (440Ma, Virginia, USA). *Geobiology*, **6**, 120-124.

---, --- and ---. 2009*a*. A new genus and species of filamentous microfossil of cyanobacterial affinity from Early Silurian fluvial environments (lower Massanutten Sandstone, Virginia, USA). *Botanical Journal of the Linnean Society*, **160**, 284-289.

---, PRATT, L. M., ROTHWELL, G. W., STROTHER, P. K. and NADON, G. C. 2009*b*. Carbon isotopes support the presence of extensive land floras pre-dating the origin of vascular plants. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **283**, 46-59.

---, TATE, R. W., MACK, N. G. and CALDER, V. J. 2010. Simulating fossilization to resolve the taxonomic affinities of thalloid fossils in Early Silurian (*ca.* 425Ma) terrestrial assemblages. *In* Bibliotheca lichenologica. NASH III, T.H. *et al.* (eds). Stuttgart. J. Cramer in der Gebrüder Borntrager Verlagsbuchhandlung **105**, 183-190.

TORO, M., CHAMON, O., SALGUERO, R. and VARGAS, C. 1997. Las plantas de la Formacion Kirusillas (Silurico) en la region de La Angostura Departamento de

Cochabamba. *Memorias del XII Congreso Geologico de Bolivia - Tarija, Bolivia*, 523-529.

TROTTER, J. A., WILLIAMS, I. S., BARNES, C. R., LÉCUYER, C. and NICOLL, R. S. 2008. Did cooling oceans trigger Ordovician biodiversification? Evidence from conodont thermometry. *Science*, **321**, 550-554.

TSOAR, H. and KARNIELI, A. 1995. What determines the spectral reflectance of the Negev-Sinai sand dunes? *International Journal of Remote Sensing*, **17**, 513-525.

TYRRELL, T. 2013. *On Gaia: A Critical Investigation of the Relationship between Life and Earth*. Princeton University Press, Princeton, NJ, USA. 320pp.

UGOLINI, F.C. and DAHLGREN, R.A. 2002. Soil development in volcanic ash. *Global environmental research*, **6**, 69-81.

VARNALI, T. and EDWARDS, H.G.M. 2010. Iron-scytonemin complexes: DFT calculations on new UV protectants for terrestrial cyanobacteria and astrobiological implications. *Astrobiology*, **10,** 711-716.

VAVRDOVA, M. 1990. Coenobial acritarchs and other palynomorphs from the Arenig/Llanvirn boundary, Prague Basin. *Vestnik Ustredniho Ustava Geologickeho*, **65**, 237-242

.

VEIZER, J., ALA, D., AZMY, K., BRUCKSCHEN, P., BUHL, D., BRUHN, F., CARDEN, G. A., DIENER, A., EBNETH, S. and GODDÉRIS, Y. 1999. ^{87}Sr/^{86}Sr, δ^{13}C and δ^{18}O evolution of Phanerozoic seawater. *Chemical geology*, **161**, 59-88.

VILLARREAL, J.C. and RENNER, S.S. 2012. Hornwort pyrenoids, carbon-concentrating structures, evolved and were lost at least five times during the last 100 million years. *Proceedings of the National Academy of Science of the USA*, **109**, 18873-18878.

WATLING, R. and HARPER, D. B. 1998. Chloromethane production by wood-rotting fungi and an estimate of the global flux to the atmosphere. *Mycological Research,* **102**, 769-787.

WELLMAN, C. H. 1995. "Phytodebris" from Scottish Silurian and Lower Devonian continental deposits. *Review of Palaeobotany and Palynology*, **84**, 255-279.

--- 1996. Cryptospores from the type area of the Caradoc Series in southern Britain. *Special Papers in Palaeontology*, **55**, 103-136.

--- 1999. Ordovician land plants: evidence and interpretation. 275–277. *In* KRAFT, P. and FATKA, O. (eds). *Quo Vadis Ordovician?* 8th International Symposium on the Ordovician System, Prague. *Acta Universitatis Carolinae, Geologica*, **43**.

--- 2003. Dating the origin of land plants. 119-141.*In* DONOGHUE, P. C. J. and SMITH, M. P. (eds). *Telling the evolutionary time scale: molecular clocks and the fossil record. CRC Press, London*.

---, OSTERLOFF, P. L. and MOHIUDDIN, U. 2003. Fragments of the earliest land plants. *Nature*, **425**, 282-285.

WU, M. Y., ZHAO, Y. L., TONG, J. N. and YANG, R. D. 2011. New macro algal fossils of the Kiali Biota in Guizhou Province, China. *Science China Earth Sciences*, **54**, 93-100.

YANG, R.-D., MAO, J-R., ZHANG, W.-H., JING, L.-J.and GAO, H. 2004. Bryophyte-like fossil (*Parafunaria sinensis*) from Early-Middle Cambrian Kaili Formation of Guizhou Province, China. *Journal of Integrative Plant Biology* (formerly *Acta Botanica Sinica*) , **46**, 180-185.

---, ---, ---, --- and --- 2004. Bryophyte-like fossil (*Parafunaria sinensis*) from Early-Middle Cambrian Kaili Formation of Guizhou Province, China. *Journal of Integrative Plant Biology* (formerly *Acta Botanica Sinica*), **46**, 180-185.

YANG, Y., ZANG, E., AN, Z., LI, X. 2007. Evolution of the nematode-trapping cells of predatory fungi of the Orbilliaceae based on sequences from rRNA-encoding DNA and multiprotein sequences. *Proceedings of the National Academy of Science USA*, **104,** 8379-8384.

YAPP, C. J. and POTHS, H. 1992. Ancient atmospheric CO2 inferred from natural geothites. *Nature* **355**, 342-344.

--- and --- 1994. Productivity of pre-vascular continental biota inferred from the Fe(CO_2)OH contents of goethite. *Nature*, **368**, 49-51.

YOUNG, S. A., SALTZMAN, M. R., FOLAND, K. A., LINDER, J. S. and KUMP, L. R. 2009. A major drop in seawater 87Sr/86Sr during the Middle Ordovician (Darriwilian): Links to volcanism and climate? *Geology*, **37**, 951-954.

YUAN, X., XIAO, S. and TAYLOR, T. N. 2005. Lichen-like symbiosis 600 million years ago. *Science*, **308**, 1017-1020.

ZHANG, Z.-Y. 1988. *Longfengshania* Du emend: an earliest record of bryophyte-like fossils. *Acta Palaeontologica Sinica*, **27**, 416-426 (In Russian with English abstract).

FIGURE CAPTIONS

Figure 1. A, Palaeozoic atmospheric oxygen (%) and B, carbon dioxide (ppm): predictions and proxies (CO_2), with key interval of mid Ordovician – early Devonian highlighted. Amended from figures kindly supplied by Lenton. A, O_2 predictions in the Berner and Canfield (1989) model [dotted line] and the COPSE model of Bergman *et al.* (2004) with standard fire feedback [dash-dot line] or strong fire feedback [dashes]. B, CO_2 predictions from the 'GEOCARB II' model of Berner (1994; dotted line) and the COPSE model of Bergman *et al.* (2004; dashed line), proxies of palaeosols (black rectangles) and stomatal indices/ratios (open rectangles) from the data compilation of Royer *et al.* (2001).

Figure 2. Palaeogeographic reconstructions A-F from early Ordovician to early Devonian, tilted to show palaeogeographic S pole on Gondwana (Paleoglobe maps, www.globalgeology.com); A, Early Ordovician (Tremadoc–Arenig), B, Mid Ordovician (Llanvirn–Llandeilo, C, Late Ordovician (Caradoc-Ashgill), D, Early Silurian (Rhuddanian/Aeronian–Telychian), E, Late Silurian (Homerian–Ludfordian), F, Early Devonian (Lockhovian–Emsian). Climatic zones indicated for A, C, and E; palaeocontinents and oceans labelled on B, D. Shading distinguishes areas of continental seas and oceans, relief of volcanic arcs, lowland areas, mountain ranges. Palaeogeographical changes driven by break-up of Gondwana, evolution of Iapetus and Rheic oceans, formation of Laurussia and growth of the Appalachian–Caledonide and Famatinian mountain ranges.

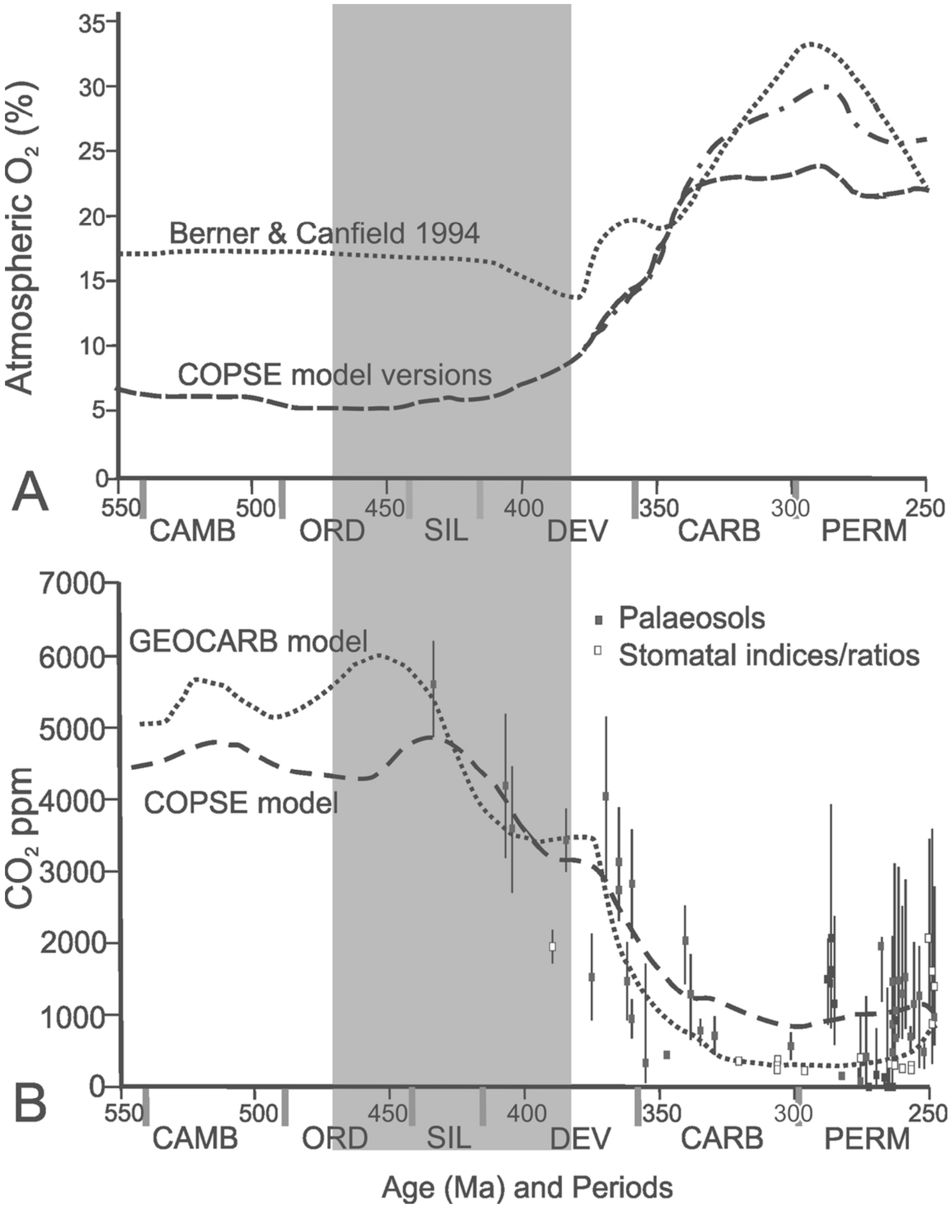
Figure 3. Distribution of Ordovician–Silurian explosive volcanism as recorded by K-bentonites in successions from high to low palaeolatitude palaeocontinents: Gondwana, Perigondwanan terranes (Podolia/Carnic Alps), Avalonia, Baltica, S.

China, Laurentia (Scotland/Ireland and N. America). (Data compilation, amended from and supplementing Histon *et al.* 2007, Huff *et al.* 2010).

Figure 4. Lower Ordovician–Lower Devonian fossil record of early terrestrial plants (* first records) shown against multiple cooling events interpreted before and after the Hirnantian glacial climax, on the basis of sedimentary facies (glaciogenic deposits/periglacial geomorphology, black shales with ‘hot’ horizons - white zigzags, cool-water carbonates and carbonate mud mounds: G, pG Gondwana,Perigondwana, A Avalonia, B Baltica, L, K Laurentia, Kazakhstan), in combination with the $\delta^{13}C_{carb}$ record and sea level curves (global, Baltica; amended from Cherns *et al.* 2013, fig. 1).

TABLE CAPTIONS

Table 1. Gray’s (1993) Microfossil Assemblage Zones I-III based on the appearance and relative frequencies of cryptospores and trilete spores.



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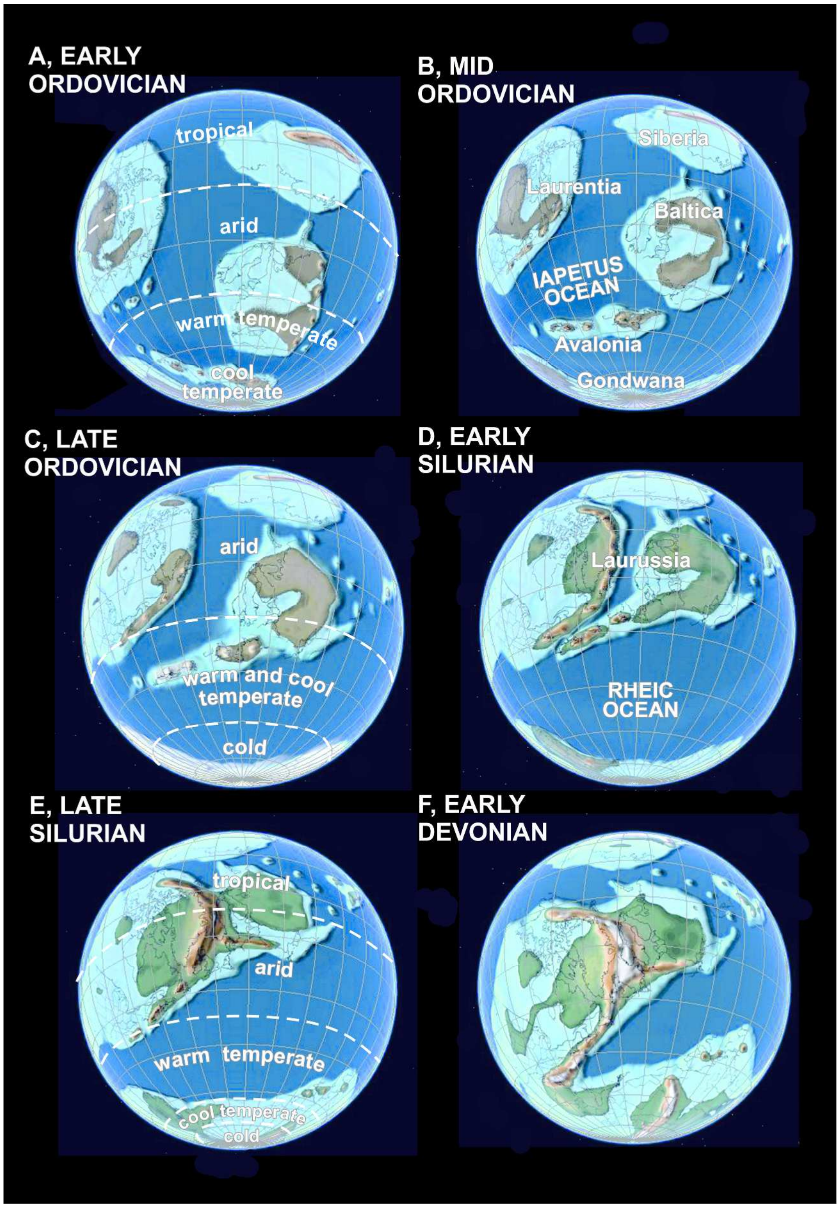

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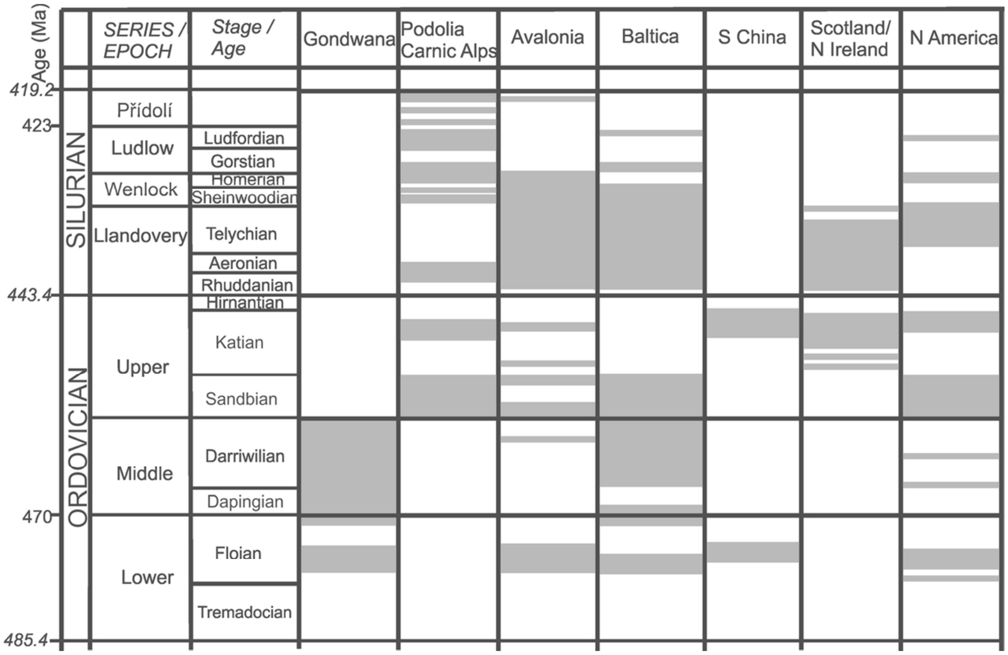
239x344mm (300 x 300 DPI)



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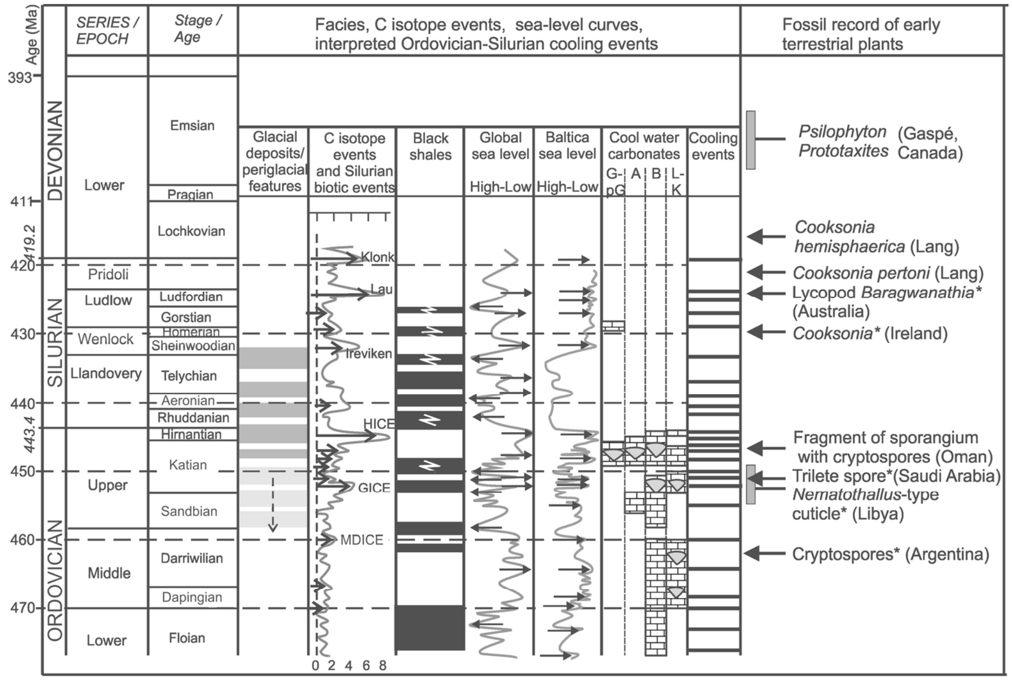

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145x128mm (300 x 300 DPI)

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Epoch/Evolutionary level II	Eoembryophytic	Mid Ordovician–pre-latest Early Silurian
Epoch/Evolutionary level III	Eotracheophytic	Latest Early Silurian–early Lochkovian
Epoch/Evolutionary level IV	Eutracheophytic	Late Lochkovian–mid Pragian