

Chapter 3

Photosynthesis in Early Land Plants: Adapting to the Terrestrial Environment

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Summary

The embryophytic land plants evolved from charophycean green algae, one of the three clades of green algae which are important components of the microflora of present-day terrestrial habitats. The earliest embryophytes are recognised in the fossil record from their characteristic spores, with little evidence as to their vegetative structure. These earliest

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embryophytes presumably resemble the extant terrestrial green algae in being desiccation tolerant and poikilohydric. Only the embryophytes subsequently developed the homoiohydric which characterised the organism which today contribute most of the biomass and primary productivity on land, and allowed many of the organisms to become desiccation intolerant in the vegetative phase. Pre-Carboniferous land plant fossils have very few examples of bryophytes other than spores: exceptions are the Middle Devonian *Metzgeriothallus* and the Upper Devonian *Pallaviciniites*. Many of the other fossils are recognisable as polysporangio-phytes, including vascular plants. Homoiohydricity in some of these plants is shown by the occurrence of cuticle and stomata, although there is no fossil evidence bearing on desiccation tolerance/intolerance. In addition to the embryophytes there are many other fossils, e.g. *Pachytheca*, *Parka*, *Protosalvinia*, *Prototaxites* and *Spongiophyton*, which are probably photosynthetic organisms, but are not readily classified: algae, bryophytes and lichens have been suggested, in addition to the possibility that some represent terrestrial fungi. The high atmospheric CO₂ concentrations in the early Phanerozoic would have permitted higher rates of photosynthesis than occurs today on the basis of the surface area of the plant exposed to the gas phase because large concentration gradients from the atmosphere to the carboxylase driving diffusive entry of CO₂ are possible. Relatively complex morphologies (several layers of photosynthetic structures) and/or anatomy (ventilation within the organisms using gas spaces) are required if the light-harvesting capacity is to be matched by the CO₂ assimilation capacity.

I. Introduction

The extant land flora ranges in complexity, as judged by the number of kinds of cells in the organism, from unicellular and colonial cyanobacteria and (mainly) green eukaryotic algae (free living and lichenized) to bryophytes and vascular plants (Bell and Mooers 1997). The homoiohydric and (generally) desiccation intolerant (see Definitions) seed plants, with sexual reproduction independent of liquid water on the above-ground plant surface are the most successful components of the extant land flora as judged by the number of described species and their global productivity and biomass. However, the ‘lower’ land plants, i.e. cyanobacteria, eukaryotic algae and embryophytes of the

bryophyte and pteridophyte grades, are significant components of extant terrestrial vegetation, and are more representative of the degree of complexity of the earliest photosynthetic organisms on land. In seeking present day analogues of the plants represented by the early fossils of photosynthetic organisms on land it is important to take into account differences between the present and past environments.

II. Extant Terrestrial Cyanobacteria, Algae and Embryophytes

Many higher taxa of algae, and cyanobacteria, have terrestrial representatives (Table 3.1; van den Hoek et al. 1995; Graham and Wilcox 2000; Lewis and Lewis 2005). ‘Terrestrial’ here includes epi-, endo- and hypolithic algae as well as those living on finer-grained substrates, such as soil and desert sand (Lewis and Lewis 2005; Cardon et al. 2008; Cockell et al. 2009). The embryophytes are, apparently, ancestrally terrestrial: at least the earliest knowledge we have of them is of aurally dispersed meiospores

Abbreviations: CAM – Crassulacean Acid Metabolism; CCM – CO₂ concentrating mechanism; $\delta^{13}\text{C}$ – quantitative measure of the stable carbon isotope ratio relative to the standard carbon in the VPDB (Vienna Pee Dee Belemnite). $\delta^{13}\text{C} = \{[(^{13}\text{C}/^{12}\text{C})_{\text{sample}} / (^{13}\text{C}/^{12}\text{C})_{\text{standard}}] - 1\} \times 1,000$; Ga – 10⁹ years; Ma – 10⁶ years; Rubisco – Ribulose Bisphosphate Carboxylase-Oxygenase

Table 3.1. Characteristics of cyanobacterial and algae related to the evolution of complex life on land^a.

Taxon	Lifeform	Terrestrial	Desiccation tolerant	Oldest fossils	References
Cyanobacteria	Unicellular, colonial, multicellular	<i>Nostoc</i> , many lichenized	Yes	2.13 Ga (biomarkers), 2.45 Ga (O ₂)	Tomitani et al. (2006) and Rasmussen et al. (2008)
Chlorophyta	Unicellular, colonial	No	No	1.3 Ga	Teyssèdre (2006) and Becker and Marin (2009)
Prasinophyceae	Unicellular, colonial, multicellular	<i>Fritschiella</i>	Yes	(450 Ma) ^b	Lewis and Lewis (2005), Gray et al. (2007), Becker and Marin (2009), Caisova et al. (2011), and Lüttge and Büdel (2009)
Chlorophyta	Unicellular, colonial, multicellular	<i>Prasiola</i> , <i>Trebouxia</i> many lichenized	Yes	450 Ma	Dereenne et al. (1992), Senousy et al. (2004), Lewis and Lewis (2005), Gray et al. (2007), Zhang et al. (2007), Bescker and Marin (2009), and Lüttge and Büdel (2009)
Trebouxiophyceae ^b	Unicellular, colonial, multicellular	<i>Trentopohlia</i>	Yes	540 Ma	Org et al. (1992), Gupta and Agrawal (2004), Lewis and Lewis (2005), Rindi et al. (2009a, b), and Lüttge and Büdel (2009)
Chlorophyta	Colonial, coenocytic, multicellular	<i>Klebsormidium</i>	Yes	450 Ma	Lewis and Lewis (2005), Becker and Marin (2009), and Karsten et al. (2010)
Charophyceae	Unicellular colonial multicellular	<i>Porphyridium</i> ; <i>Porphyra</i> high Intertidal	Yes	475 Ma	Oliver et al. (2005), Rubinstein et al. (2010), Wellman (2010), and Brown and Lemmon (2011)
Streptophyta	Multicellular	<i>Bostrychia</i> , <i>Caloglossa</i> , <i>Catanelia</i> high Intertidal	Yes; bryophytes > non-seed vascular plants > seed plants	1.2 Ga	Cole and Sheath (1990) and Butterfield (2000)
Embryophytes	Unicellular, multicellular	Some diatoms	Yes	540 Ma (570 Ma?)	Cole and Sheath (1990) and Yuan et al. (2011)
Rhodophyta	Unicellular, multicellular	Some diatoms	Yes (resting cells)	120 Ma	Souffreau et al. (2010, 2013)
Bangiophyceae	Multicellular				
Rhodophyta	Unicellular, colonial (filamentous)				
Florideophyceae					
Ochroista					
Bacillariophyceae					

(continued)

Table 3.1. (continued)

Taxon	Lifeform	Terrestrial	Desiccation tolerant	Oldest fossils	References
Ochrista Fucophyceae	Multicellular	No; <i>Pebetia</i> (high intertidal) drowns if continuously submerged (<i>Petrodroma</i> photobiont in high intertidal lichen <i>Verrucaria</i> spp.)	Yes	(570 Ma?)	Rugg and Norton (1987), Xu (2001), Sanders (2004), and Yuan et al. (2011)
Ochrista Tribophyceae	Unicellular, colonial multicellular, coenocytic (acellular)	<i>Botrydium</i> , <i>Vaucheria</i> (<i>Heterocapsa</i> photobiont in high intertidal lichen <i>Verrucaria</i> spp.)	?	600 Ma	Trschermak (1941), Javanau et al. (2003), and Butterfield (2004, 2007)

^aGeneral references: Hoffman (1989), Van den Hoek et al. (1995), Kenrick and Crane (1997), Gensel (2008), Lewis (2007), Graham and Wilcox (2009), Taylor et al. (2009), and Paffrey et al. (2011)

^bBased on the finding of Trebouxiophyceae in the Ordovician (Derenne et al. 1992), and branching order of the Chlorophyceae, Trebouxiophyceae and Ulvophyceae from molecular phylogenetics Lewis and McCourt (2004)

Table 3.2. The distribution of desiccation tolerance, desiccation intolerance, poikilohydry and homoiohydric among oxygenic photosynthetic organisms. The terms desiccation tolerance, desiccation intolerance, homoiohydric and poikilohydric are defined in ‘Definitions’ at the end of this Table.

	Desiccation tolerant	Desiccation intolerant
Poikilohydric	Terrestrial Cyanobacteria, free-living and lichenized. Terrestrial (and some aquatic) Charophyceae, Chlorophyceae (free-living and lichenized), Trebouxiophyceae (free-living and lichenized), Ulvophyceae, intertidal Trebouxiophyceae, Ulvophyceae, Bangiophyceae, Florideophyceae, Fucophyceae Many dispersed spores, pollen and seeds of embryophytes; vegetative stages of many terrestrial (and some aquatic) bryophytes	Most aquatic cyanobacteria and algae. Some aquatic bryophytes. Aquatic vascular plants
Homoiohydric	Vegetative stage of many heterosporous lycopods (Isoetales, Selaginellales), some ferns, a few flowering plants	Vegetative stage of terrestrial members of the lycopods, many ferns, gymnosperms, almost all angiosperms

It is important to realise that there is a continuum of the extent of desiccation tolerance from intolerance to long-term tolerance of equilibration with an atmosphere of low relative humidity, and between poikilohydry and homoiohydric. From Raven (1977, 1994a, b, 1995, 1996, 1997a, b, 1999a, b, 2002a, b, 2003), Woodward (1998), Raven and Edwards (2001, 2007), Raven and Andrews (2010), Edwards et al. (1996, 1997, 2003), Proctor et al. (1992, 2007), Alpert (2005), Oliver et al. (2005), Watkins et al. (2007b), Wang et al. (2009), and Table 3.1

Definitions

Desiccation Intolerance The inability of an organism, or phase in the life cycle of an organism, to recover from dehydration to some specified level, e.g. equilibration with an atmosphere of 50 % relative humidity.

Desiccation Tolerance The ability of an organism, or phase in the life cycle of an organism, to recover from dehydration to some specified level, e.g. equilibration with an atmosphere of 50 % relative humidity.

Homoiohydric The ability of an organism to regulate water loss, and hence remain hydrated, despite a lack of water supply equal to the potential rate of water loss to an unsaturated atmosphere. For plants homoiohydric involves a water uptake system (commonly a root system in the soil), an endohydric water transport system from the site of water uptake to the site of transpiratory water vapour loss, intercellular gas spaces, cuticle and stomata.

Poikilohydric The inability of an organism to regulate water loss, and hence remain hydrated, despite a lack of water supply equal to the potential rate of water loss to an unsaturated atmosphere. Poikilohydric plants may have one or more of the components of the homoiohydric apparatus (water uptake system (commonly a root system in the soil), an endohydric water transport system from the site of water uptake to the site of transpiratory water vapour loss, intercellular gas spaces, cuticle and stomata) but lack the full suite of components functioning in an integrated manner.

References Raven (1977), Csintalan et al. (2000), Alpert (2005), Turnbull and Robinson (2009).

(Csotonyi et al. 2010; Rubinstein et al. 2010; Wellman 2010; Brown and Lemmon 2011).

Most of these algal taxa with terrestrial species have at least some desiccation tolerant terrestrial representatives, both free-living and lichenized (Tables 3.1 and 3.2). Many algae which live in the marine intertidal and in small bodies of inland water are also desiccation tolerant, though some of them (Fucophyceae, Floridiophyceae) do not have terrestrial representatives. Furthermore, some terrestrial algae are known not to be desiccation tolerant (Bacillariophyceae (diatoms)

Soffreau et al. 2010), while others have apparently not been examined for desiccation tolerance (the unicellular bangiophycean *Porphyridium*). Terrestrial members of the cyanobacteria (free and lichenized), Chlorophyceae (free living and lichenized), Charophyceae, Trebouxiophyceae (free living and lichenized) and Ulvophyceae (free living and lichenized) have desiccation tolerant members (Tables 3.1 and 3.2).

The embryophytes seem to be ancestrally desiccation tolerant (Oliver et al. 2005) some in the vegetative state (sporophyte and

gametophyte) and more generally in dispersed spores (including pollen grains) and seeds (Brown and Lemmon 2011). Ancestral desiccation tolerance in embryophytes is of phylogenetic interest in relation to the desiccation tolerance (or otherwise) of extant representatives of the clades most likely to have given rise to the embryophytes (see Chap. 2). Among the embryophytes, most terrestrial bryophytes have desiccation tolerance in the vegetative phases as well as spores, and there is a greater fraction of organisms that are desiccation tolerant in the vegetative phase among plants at the pteridophyte grade of organization than among seed plants (Tables 3.1 and 3.2).

Most of the terrestrial algae and cyanobacteria are unicellular. Exceptions are the unbranched heterocystous filaments of the cyanobacterium *Nostoc*, the branched filamentous chlorophycean *Fritschiella*, the thalloid trebouxiophycean *Prasiola*, the branched filamentous ulvophycean *Trentepohlia* and the unbranched filamentous charophycean *Klebsormidium* (Table 3.1). The capacity for differentiation is clearly significant in the evolution and function of embryophytes, e.g. in the evolution of homoiohydric (see below). The red and brown algae, with no terrestrial representatives, have many genera with considerable structural complexity (Van den Hoek et al. 1995; Bell and Mooers 1997; Graham and Wilcox 2000).

All terrestrial algae and cyanobacteria, free-living and lichenized, are poikilohydric, as is the vegetative phase of bryophytes and of a few vascular plants, and many spores, pollen grains and seeds (Table 3.2). The photosynthetically competent sporophytes of some bryophytes have more homoiohydric features than do the gametophytes, but since the sporophyte depends on the poikilohydric gametophyte for water and soil-derived nutrients (matrotrophy) it is functionally poikilohydric. It is important to emphasize that there is a continuum of conditions between poikilohydric and homoiohydric (Proctor and Tuba 2002), just as there is a continuum for desiccation tolerance,

ranging from intolerance of even very limited water loss for a short period to tolerance of equilibration with an atmosphere of very low relative humidity over a long period. Homoiohydricity demands a certain minimum size and complexity (number of cell types), while poikilohydricity does not (Raven 1999a, b; Boyce 2008).

III. The Time of Origin of Photosynthetic Taxa with Emphasis on Those Which Occur on Land

Table 3.1 lists the earliest recorded fossils for major taxa of photosynthetic organisms. The dates come from body fossils (e.g. dasycladalean green algae from the Ulvophyceae and coralline red algae from the Florideophyceae in the Cambrian), from taxon-specific biomarkers (e.g. cyanobacteria from the Palaeoproterozoic, and Trebouxiophyceae from the Ordovician), and the accumulation of O₂ earlier in the Palaeoproterozoic (evidence of oxygenic photosynthesis, hence cyanobacteria) (Table 3.1). Recent evidence (Sánchez-Baracaldo et al. 2005; Blank and Sánchez-Baracaldo 2010) suggests that the earliest cyanobacteria were from freshwater habitats, and that global oxygenation could only occur after cyanobacteria had colonized the ocean. In two cases the occurrence of green algal clades (Charophyceae, Chlorophyceae (Fig. 3.1a, b)) before the earliest known fossil for that clade is inferred from the occurrence of other clades of green algae (Trebouxiophyceae, Ulvophyceae) and the branching order of the green algae and embryophytes indicated by molecular phylogenetic studies (Lewis and McCourt 2004; Turmel et al. 2008). For the Chlorophyceae and Ulvophyceae there are body fossil indications of their presence 700–800 Ga ago (Butterfield et al. 1988). Table 3.1 shows that cyanobacteria occurred before the origin of embryophytes, as did all four of the green algal clades (Charophyceae, Chlorophyceae, Trebouxiophyceae, Ulvophyceae) with terrestrial representatives, as well as the

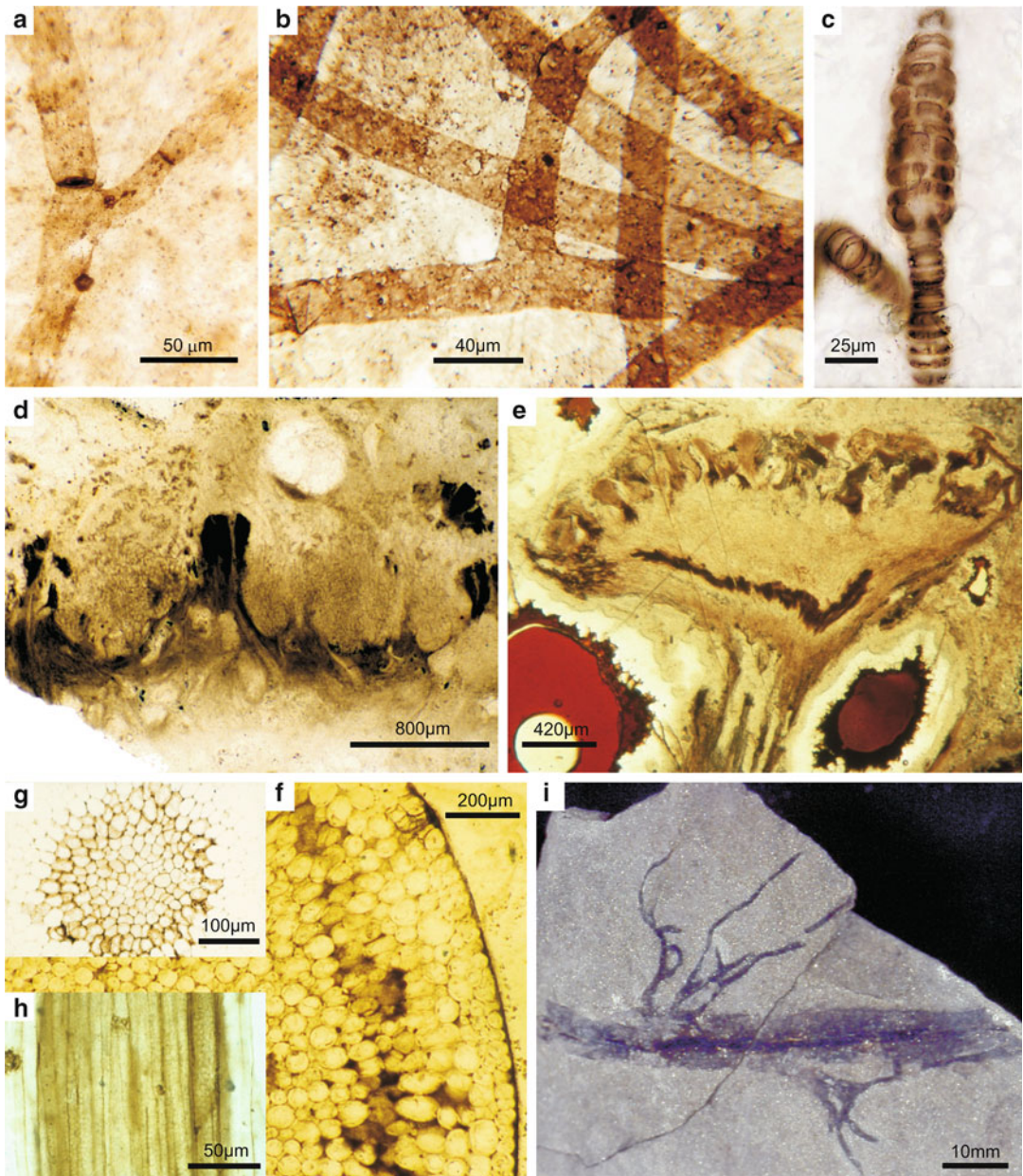


Fig. 3.1. (a) Proterocladus, a siphonocladalean green alga, Svanbergfjellet Formation, Spitsbergen, late Proterozoic (c. 750 myr). (**a-c** courtesy of Dr Nick Butterfield, Cambridge). (**b**) *Palaeovaucheria*, a vaucheriacean alga, Lakhanda Formation, Siberia, late Mesoproterozoic (c. 1000 myr). (**c**) *Bangiomorpha pubescens*, a red alga, Hunting Formation, Arctic Canada, Mesoproterozoic (c. 1200 myr). (**d**) *Winfrenatia reticulata*, an early lichen, showing a section of a thallus with hyphal pockets (arrows), with cyanobacteria inside. Rhynie Chert, Scotland, Pragian-Emsian (Lower Devonian, c. 404 myr). (Courtesy of Prof. Tom Taylor, Kansas). (**e**) *Kidstonophyton discoides*, longitudinal section through the distal regions of a male gametophyte with antheridia of ?*Nothia aphylla*, Rhynie Chert, Scotland, Pragian (Lower Devonian, c. 404 Myrs). (Courtesy of Prof. Hans Kerp, Münster). (**f-h**) *Aglaophyton major*, sections through upright stems of sporophyte; (**f**) transverse section of ground tissues with cuticle and zone of arbuscular mycorrhizae in cortex, (**g**) TS of central conducting cells, (**h**) LS of central conducting cells lacking conventional thickenings, Rhynie Chert, Scotland, Pragian – Emsian (Lower Devonian, c. 404 myr). (**i**) *Drepanophycus spinaeformis*, a lycophyte represented here by rhizome and lateral roots. Strathmore Group, Scotland, Emsian (Lower Devonian, c. 400 myr).

Prasinophyceae with no known terrestrial representatives. This provides a wide range of photosynthetic organisms that could have been on land before the embryophytes evolved. As is indicated in Table 3.1 and in the discussion above, all of these algae (including cyanobacteria) have desiccation tolerant members as well as representatives with some differentiation of their thalli. It would seem that there were other clades of chlorophyll b-containing organisms than the Charophyceae which had some of the attributes of the ancestor of the embryophytes, e.g. desiccation tolerance, terrestrial habit, presence of plasmodesmata, localized growing points (Raven 1977, 2005; Sarkar et al. 2009; Popper et al. 2011).

Other clades of algae are less likely to have been represented among terrestrial biota at or just before the time that the embryophytes evolved. For the Rhodophyta the two classes considered here (Bangiophyceae and Florideophyceae) have fossil records dating from pre-Ordovician times (Fig. 3.1c; Table 3.1); the acidophilic Cyanidiophyceae are not considered here. Extant unicellular bangiophycean red algae (e.g. *Porphyridium*) which can grow in terrestrial habitats are not known to be desiccation tolerant; the most complex member of the Bangiophyceae is less complex than the most complex member of the Florideophyceae, a class with no terrestrial members: some live in fresh waters but none on land.

Among the Ochrophyta (= Heterokontophyta) the oldest known fossils are of the Tribophyceae from the Neoproterozoic: the extant tribophytes that live on land are apparently not desiccation tolerant, and the lichenized (presumably) desiccation tolerant tribophyte is intertidal rather than terrestrial (Table 3.1). The diatoms are only known from much later in the fossil record, and fossil-calibrated phylogenies suggest that (unpreserved) ancestral diatoms probably arose less than 250 Ma ago (Table 3.1; see also Guillou 2011; Ichiniomiya et al. 2011). While fossils from as early as the Ediacaran have been assigned to the Fucophyceae these organisms could

have been members of the Rhodophyta (Table 3.1).

As for fossils of lichenized algae, no terrestrial lichens are known in the fossil record until *Winfrenatia* (Fig. 3.1d) from the 410 Ma Rhynie Chert (Taylor et al. 1995), although what seems to be a marine lichen was found in 600 Ma marine sediments (Yuan et al. 2005). *Winfrenatia* has no parallels among extant lichens since, although the inhabitant was a cyanobacterium as in many modern lichens, the exhabitant was a glomeromycote rather than an ascomycote or a basidiomycote (Karatygin et al. 2009). Whether the ascomycotes and basidiomycotes had evolved by 470 Ma, with the earliest fossil evidence of embryophytes, is not clear; although Raven and Andrews (2010) suggest that the basidiomycotes had not evolved by the Silurian. However Hueber (2001) had earlier placed Lower Devonian *Prototaxites* in the basidiomycotes and this genus is also recorded in the mid Silurian. Work in progress in Cardiff suggests the presence of terrestrial lichens before 410 Ma in the Welsh Borderland.

It should be noted that molecular clock extrapolations to the time of origin of clades (see Heckman et al. 2001) can be subject to considerable error (Graur and Martin 2003), and such extrapolations have been avoided in the preceding four paragraphs. Clarke et al. (2011) present a time-scale for plant evolution using fossil calibration and a critical use of molecular calibrations.

The possible taxa of terrestrial oxygenic photosynthetic organisms at the time leading up to earliest known embryophytes is of unicellular and filamentous (including heterocystous) cyanobacteria, with green alga from the four clades Charophyceae, Chlorophyceae, Trebouxiophyceae and Ulvophyceae. Some of the cyanobacteria and algae could have been lichenized. It must be emphasised that these suggestions are based on fossils from marine or lacustrine sediments, and include range extensions based on the use of dated fossils of a sister clade to infer the date of

origin of a clade which lacks a fossil record at the relevant time.

IV. Evidence of Primary Productivity on Land Before and Contemporary with the First Evidence of Embryophytes

We can appeal to geochemical evidence, i.e. the occurrence of biologically stimulated weathering, suggesting the occurrence of terrestrial primary productivity prior to 470 Ma ago. It might be expected that minerotrophic photosynthetic organisms, i.e. those obtaining nutrient elements other than carbon from weathered rocks, would have more effect on weathering than ombrotrophic photosynthetic organisms, i.e. those obtaining nutrient elements by dry (gaseous, e.g. ammonia, nitrogen dioxide, acquired in a similar manner to carbon dioxide) or wet (aqueous solution) deposition from the atmosphere. Examples of predominantly ombrotrophic organisms are terrestrial algae, many terrestrial bryophytes (Ayres et al. 2006; Jones et al. 2007a, b) and a few (e.g. epiphytic) vascular plants, while some bryophytes and almost all vascular plants are predominantly minerotrophic. Baars et al. (2008) show that the bryophytes grown on a peat/sand substrate do not have a significant effect on chemical weathering via provision of CO₂ to ground water, in contrast to vascular plants with their greater vertical extent of below-ground structures. Lenton et al. (2012) have explored the extent of weathering produced by the moss *Physcomitrella patens*. This limitation may also apply to the endohydric sporophytes of *Aglaophyton* (with an atypical form of water conducting tissues, Fig. 3.1f–h) which has more or less horizontal rhizomes with little vertical penetration. The vascular plant model is structurally exemplified by the lycophyte *Drepanophycus* (Fig. 3.1i) with rooting structures which penetrated at least several cm into the sediment, but in a depositional environment composed of material which had been previously weathered. To have a

major effect on weathering the plant must have underground structures penetrating at least several cm into the regolith or cracks in rock. Photosynthate produced in the above-ground structures using atmospheric CO₂ is conducted to underground structures where it is used in growth and maintenance, both of which generate CO₂. Herbivores, parasites and decomposers also produce CO₂ below ground. There is restricted diffusion of CO₂ back to the atmosphere, so CO₂ accumulates to a higher steady-state concentration than in the atmosphere, thus increasing the rate of chemical weathering. It would be expected that microalgae have even less effect on weathering than do bryophytes. Lichens, by contrast, can carry out significant weathering (Gadd and Raven 2010).

A number of lines of evidence have been brought forward which are consistent with biologically enhanced weathering on land before the first fossil evidence for embryophytes. Lenton and Watson (2004) have modelled phosphate weathering and have outcomes consistent with biotically enhanced weathering in the Neoproterozoic. Kennedy et al. (2006; see Derry 2006) have investigated the occurrence of pedogenic (soil-produced) clay minerals in mudstones from the Neoproterozoic and the Cambrian, and found a five-fold increase from 750 to 500 Ma, again consistent with biotically enhanced weathering on land. The more widely used technique of measuring the ⁸⁷Sr:⁸⁶Sr in marine carbonates (Lenton and Watson 2004; Derry 2006; Kennedy et al. 2006) as an indicator of terrestrial weathering has been refined to take into account seawater processes which alter the ⁸⁷Sr:⁸⁶Sr of carbonates (Shields 2007). While the data indicate increased terrestrial weathering in the Neoproterozoic and into the Cambrian, there is a long-term decrease from the late Cambrian onwards (Shields 2007). The decreasing weathering takes us into the Silurian and Devonian when there were terrestrial embryophytes in the form of vascular plants plus non-vascular polysporangiophytes (Raven and Edwards 2001) and uncharacterized organisms with substantial

underground structures, which are possible fungi (Hillier et al. 2008). An important point about biological effects on weathering is that the long-term (geological) variations in weathering are coupled to the volcanic production of CO₂ in the exogenic cycle (Shields 2007). The changes in atmospheric CO₂ content over geological time intervals reflect the difference between the inputs of CO₂ by volcanism and removal by weathering, with subsequent CaCO₃ precipitation and long-term incorporation into sediments in the ocean. It should be remembered that abiotic weathering is temperature dependent, and that trace gases could have had a larger forcing effect on global temperature in greenhouse worlds such as occurred in parts of the Early and Mid Palaeozoic than occurs today, so abiotic weathering could have been greater than expected for atmospheric CO₂ levels (Beerling et al. 2011). Overall, the evidence for pre-Ordovician photosynthetic life on land, based largely on weathering rates, is indirect and can be subject to other interpretations.

Consideration of the possible functioning of the organisms represented by early terrestrial fossils requires that their structure is understood. Fossils of macroscopic eukaryotes from the Proterozoic include a bangiophycean red alga (Butterfield et al. 1990; Butterfield 2000), possible chlorophycean and ulvophycean green algae (Butterfield et al. 1988), a vaucheriacean tribophycean (Chromista) alga (Butterfield 2004) and a number of probable red and/or brown seaweeds (Yuan et al. 2011), as well as a probable lichen (Yuan et al. 2005). However, this evidence for Proterozoic structural complexity of free-living and symbiotic algae relates almost entirely to fossils from marine sediments.

There are few continental fossils of photosynthetic organisms, other than the meiospores of embryophytes (cf. Wellman et al. 2003), of undisputed terrestrial rather than aquatic origin, before the Mid to Late Silurian. Strother et al. (2011) report fossils of multicellular eukaryotic organisms which are apparently photosynthetic and which

occurred in continental rocks just over a billion years old. These organisms probably lived in a lake, but could have been exposed to the atmosphere during seasonal or other drawdowns of the water level. Yang et al. (2004) report a bryophyte-like fossil, *Parafunaria sinensis*, from the Early-Middle Cambrian of China, although there is no evidence as to internal structure. Tomescu et al. (2006) report continental cyanobacterial macrophytes from the Early Silurian (Llandovery), although these seem as likely to be aquatic as terrestrial. Tomescu and Rothwell (2006; see also Strother 2010; Strother et al. 2011) discuss an Early Silurian wetland flora of thalloid organisms from less than 1 cm to greater than 10 cm long (see Bomfleur et al. 2010 for Triassic occurrence of thalloid organisms). These organisms were (presumably) photosynthetic and amphibious. Tomescu et al. (2009) used the closely similar values of the natural abundance of carbon isotopes in two of these thalloid organisms with that of the bulk carbon in the strata to suggest that these organisms were major primary producers in what, from the quantity of organic carbon, could have been a productive wetland (Tomescu et al. 2009). Tomescu et al. (2009) point out that carbon isotope ratios for the thalloid organisms are similar to those for ventilated (Meyer et al. 2008) liverworts such as *Lunularia* and *Marchantia* predicted by the BRYOCARB model (Fletcher et al. 2004). Of course, there could be other primary producers with closely similar carbon stable isotope ratios; since nothing is known of such producers, the conclusions of Tomescu et al. (2009) can be tentatively accepted. The non-marine status of the wetland flora was substantiated by Tomescu et al. (2009) on the basis of significant differences between the carbon isotope ratio of the thalloid organisms and the local bulk organic carbon on the one hand, and of organic carbon in marine sediments of the Early Silurian on the other. However, this averaged marine carbon isotope value presumably relates to phytoplankton, while the thalloid organisms would be more closely related, morphologically and

functionally if not necessarily phylogenetically, to benthic marine macroalgae. The present $\delta^{13}\text{C}$ for marine phytoplankton is about -23‰ for low and medium latitudes with lower (more negative) values at high latitudes. However, the range of $\delta^{13}\text{C}$ for extant marine macrophytes is from -3 to -35‰ (Raven et al. 2002a, b; Marconi et al. 2011), so it would be difficult today to distinguish these organisms from terrestrial or many freshwater organisms (see Fletcher et al. 2004). Wu et al. (2011) describe a Lower-Middle Cambrian fossil which they tentatively relate, in overall morphology, to the chlorophycean sub-aerial alga *Fritschella*, although the fossil was from a marine deposit, and the heterotrichous morphology is also found in several other clades of algae (Fritsch 1945). As with the marine macroalgae of Yuan et al. (2011) it is not possible to attribute the thalloid organisms of Tomescu and Rothwell (2006) and Tomescu et al. (2009) to higher taxa.

V. Terrestrial Photosynthetic Organisms in the Upper Silurian and Devonian

A. Upper Silurian

Upper Silurian strata have fossils which are clearly the sporophyte phase of embryophytes, e.g. *Baragwanathia* (Fig. 3.2a), *Bathurstia* and *Cooksonia* (Edwards 1996; Kotyk et al. 2002; Taylor et al. 2009). These organisms are polysporangiophytes and, where data are available, they have tracheophyte attributes. As for phylogenetic attribution, there are examples of lycophytes (*Baragwanathia*), rhyniophytes (*Cooksonia*, Fig. 3.2c–e) and zosterophyllophytes (*Bathurstia*). Edwards (1996, 2000) describes fossils of vegetative structures and sporangia (and are thus sporophytes) from Upper Silurian and Lower Devonian strata which are characterized by small size: these too all seem to be polysporangiophytes. Functionally the Upper Silurian sporophytes are widely considered to be homoiohydric:

however, Boyce (2008) points out that the smaller plants, including smaller specimens of *Cooksonia* (Fig. 3.2b, g), are unlikely to have been homoiohydric since there is a minimum size limit for homoiohydry (Raven 1999a, b). The Upper Silurian fossils give no obvious evidence as to the gametophyte phase of the plants (but see Gerrienne and Gonez 2011) nor of monosporangiophytic sporophytes, which characterize bryophytes.

The Upper Silurian tracheophytes do not help to resolve the order in which homoiohydric attributes arose, since this time interval had the first occurrence of xylem and of stomata (and, presumably, intercellular gas spaces). The molecular phylogenetic and other cladistic evidence generally favours ‘stomata first’ (Edwards et al. 1997; Kenrick and Crane 1997; Renzaglia et al. 2000; Shaw and Renzaglia 2004, 2011; Bowman 2011), and it is plausible that fitness increases can be attributed to the occurrence of stomata with functionality as in extant seed plant stomata on thalloid organisms without an endohydric conducting system (Raven 1984, 1993a, b, 1996, 2002a, b; see also Edwards et al. 1997; Woodward 1998; Berry et al. 2010; Beerling and Franks 2009; Hartung 2010; Khandelwal et al. 2010). The only extant analogues of this situation are in the gametophytes of marchantialean liverworts, where the anatomically complex pores show only a passive, reactive, response to thallus water status rather than the proactive, active response of extant seed plant stomata whose opening and closing responds to soil water availability, the desiccating properties of the atmosphere, and whether photosynthesis is possible at the plastid level. Using stomatal anatomy to suggest function in fossil stomata in non-seed plants is complicated by the present uncertainty on the extent to which moss, lycophyte and fern stomata show a proactive rather than a passive response to their environment (Doi and Shimazaki 2008; Doi et al. 2008; Brodribb et al. 2010; Bowman 2011; Brodribb and MacAdam 2011; Chater et al. 2011; McAllister and Bergman 2011; Ruzsala et al. 2011), and the extent to which stomatal density and index

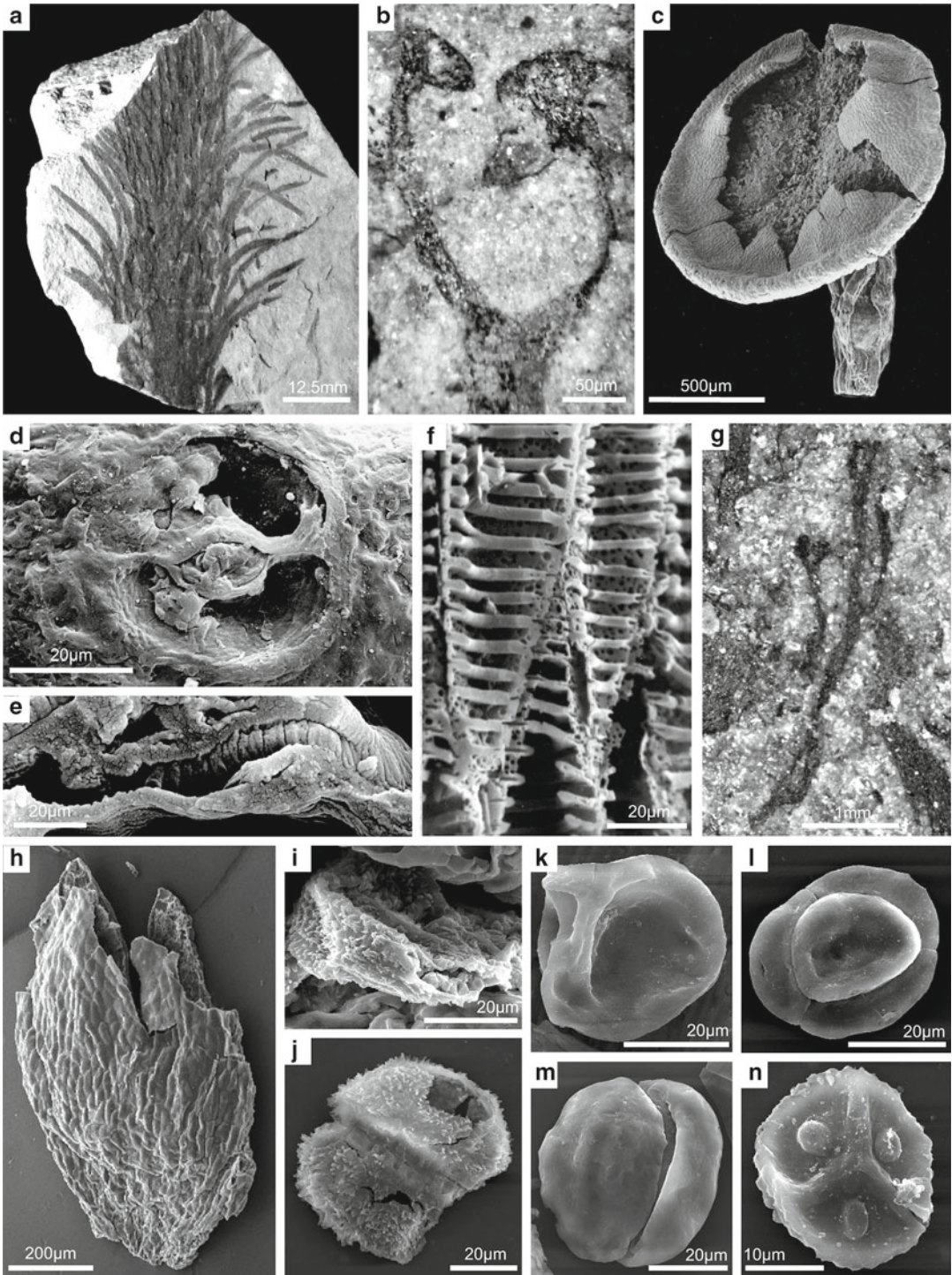


Fig. 3.2. (a) *Baragwanathia longifolia*, an herbaceous lycophyte, Wilson Creek Shale, Victoria, Australia, Pragian (Lower Devonian, c. 410 myr). (b) *Cooksonia* sp. its earliest record, Cloncannon Formation, Ireland, upper Wenlock (Silurian, c. 425 myr). (c–e) *Cooksonia pertoni*, SEM of charcoalified specimen, Ditton Group, Welsh Borderland, England, lower Lochkovian (Lower Devonian, c. 414 myr), (d) Surface view of

in non-seed plants is controlled by their environment (Baars and Edwards 2008; Ruzsala et al. 2011).

Endohydry, but not true xylem, occurred in several now-extinct polysporangiophytes; xylem seems to have had a single origin in the ancestor of tracheophytes (Kenrick and Crane 1997; see Raven 2003). Much recent attention has been focussed on the evolution of xylem at the functional level (Fig. 3.2f; Edwards 2003; Sperry 2003; Brodribb et al. 2007; Pitterman 2010; Wilson and Fischer 2011) and the origin of lignin (Ligrone et al. 2008; Weng and Chapple 2010; Espiñaire et al. 2011; Popper et al. 2011), including the possible role of horizontal gene transfer (Emiliani et al. 2009) and the occurrence of lignin in red algae (Martone et al. 2009).

The Upper Silurian plants also had cuticles. While essential for homoiohydric, cuticles have been found in earlier deposits, although it is not clear what organisms they belonged to, whether cuticularization is polyphyletic, and what were the function(s) of early cuticles (Edwards et al. 1996; Budke et al. 2011). There is no evidence as to the occurrence of below-ground structures of the sporophytes. To summarize, the order of acquisition of structures related to homoiohydric suggest that the cuticle was the first, followed by stomata and intercellular gas spaces, and finally by xylem. Roots, on fossil evidence, first appeared in the Lower Devonian in zosterophyllophytes and lycophytes and the Middle Devonian in the euphyllophytes. The Upper Silurian lycophyte *Baragwanathia* has microphylls, but there is no evidence in the Upper Silurian of any of the polyphyletic planar lateral struc-

tures ('megaphylls') found in euphyllophytes from the Lower Devonian onwards.

While much attention has been focussed on the Upper Silurian embryophytes, it must be remembered that there were also plant-like thalloid organisms (Taylor et al. 2009; Strother 2010). An example is the estimate by Strother (2010) of the fraction of pixels in scans of the Downtonian (Upper Silurian) slabs used by Lang (1937) which showed thalloid rather than axial fossils; the thalloid organisms compose 0.941–0.999 of the area occupied by plant fossils (Strother 2010). *Prototaxites*, a bulky axial organism recently attributed to the basidiomycetes which appeared in the Wenlock (Silurian) and extended into the Upper Devonian, is dealt with below.

B. Lower Devonian

The Lower Devonian has a number of sites with excellent preservation, e.g. the Rhynie and Windyfield cherts, although it has been pointed out that the preservation depends on geological factors relating to hot springs which could in turn mean that the preserved plants have specialized physiologies and so might not be representative of most terrestrial vegetation (Channing and Edwards 2009). In addition to the three genera mentioned for the Late Silurian, a number of other genera of polysporangiophytes in these and other clades have been found. As well as tracheophytes, i.e., rhyniophytes, zosterophyllophytes, lycophytes and trimerophytes, there were also polysporangiophytes lacking tracheids but with some other form of endohydric conducting system, e.g. *Aglaophyton* (Fig. 3.1f–h), and a range of dispersed

←
 Fig. 3.2. (continued) stoma and stem subtending sporangium in Fig. 3.2c, (e) fractured LS with tracheids from stem in Fig. 3.2c. (f) Longitudinally fractured tracheids of *Gosslingia breconensis*, a zosterophyll, Senni Beds, Brecon Beacons, Wales, Pragian (Lower Devonian, c. 410 myr). (g) Much branched coalified compression with terminal sporangia, St. Maughans Formation, Brecon Beacons, lower Lochkovian (Lower Devonian, c. 414 myr). (h–i) *Partitatheca splendida*, SEM of coalified sporangium with valvate dehiscence and stomata, Ditton Group, lower Lochkovian (Lower Devonian, c. 414 myr), (i) *Cymbohilates horridus* var. *splendida*, a permanent sculptured dyad from sporangium in Fig. 3.2h. (j–n) SEMs of dispersed spores, St. Maughans Formation, Brecon Beacons, lower Lochkovian (Lower Devonian, c. 414 myr). (j) *Cymbohilates horridus* var. A, a permanent sculptured dyad, (k) *Tetrahedraletes medinensis*, a permanent laevigate tetrad, (l) tetrad of laevigate trilete monads, ? *Ambitisporites*, (m) *Dyadospora murusdensa*, a separating laevigate dyad, (n) *Aneurospora* sp., a trilete monad.

embryophyte spores (Taylor et al. 2011). As well as sporophytes there are also the associated gametophytes for some of the organisms, identified by the possession of antheridia and archegonia (Fig. 3.1d). Although gametophytes defined in this way have only so far been found in the Rhynie Chert (Taylor et al. 2009), somewhat similar structures, a few with putative gametangia, have been found in other Lower Devonian deposits (Gerrienne and Gonez 2011). The sporophytes and the gametophytes both have homoiohydric characteristics. Other structures found in fossils from the Early Devonian are roots in zosterophyllophytes and lycophytes, and leaves (Raven and Edwards 2001; Taylor et al. 2009; Raven and Andrews 2010; Hao et al. 2010; see Grebe 2011; Ropello et al. 2011), as well as secondary xylem (Gerrienne et al. 2011) in euphylllophytes. The very small size of the earliest known leaves in a Lower Devonian euphylllophyte has been related to problems with heat dissipation from larger leaves when there is little loss of energy as the latent heat of evaporation in the prevailing high atmospheric CO₂ concentrations (Beerling 2005). While all the Rhynie Chert mycorrhizal fungi are glomeromycetes (Fig. 3.1f), i.e. as are extant arbuscular mycorrhizas (Smith and Read 2008), molecular phylogenetic studies show that *Endogone*-like mucoromycetes form symbioses with several earliest-branching land plants (Bidartondo et al. 2011; see also Bidartondo and Duckett 2010). However, there is no fossil evidence for associations between embryophytes and mucoromycetes. There are some Lower Devonian fossils which have been attributed to embryophytes at the bryophyte grade of organization. *Sporogonites* resembles a thalloid liverwort or hornwort, with several sporophytes associated with a thalloid putative gametophyte (Taylor et al. 2009).

Finally for the Lower Devonian embryophytes are the small much branched plants (Fig. 3.2g) from South Wales investigated by Morris et al. (2011). These plants are probably not large enough to be capable of homoiohydric (Boyce 2008). Many of these plants produced

the cryptospores (so named because the affinities of the producers were then unknown, when compared with the trilete spores produced by tracheophytes) (Fig. 3.2h–n) that provide evidence for land plants in the Ordovician and Silurian (Edwards et al. 2012).

While not dismissing the challenges that remain in understanding the functioning of the tracheophytes and, more generally, the other polysporangiophytes, it is also important to examine the functioning of Lower Devonian macroscopic organisms which are not necessarily embryophytes and which are believed to be photosynthetic. Examples are *Pachytheca*, *Parka* and *Spongiophyton* (Taylor et al. 2009), and tiny much branched plants of uncertain affinities (Morris et al. 2011).

Pachytheca (Fig. 3.3b) is found in Upper Silurian-Lower Devonian sediments as spheres 1–10 mm in diameter with a medulla of densely spaced intertwined tubes and a cortex of radial tubes with (possibly) a cuticle on the surface (Taylor et al. 2009). After early suggestions that *Pachytheca* was a green alga it has been variously suggested to be a stage in the life cycle of *Parka* or to be the propagules of *Prototaxites* (Taylor et al. 2009). Chemical analyses suggest affinities (aromatic hydrocarbons and alkylphenols) between *Pachytheca* and *Prototaxites* (Abbott et al. 1998). Such an association is consistent with the similar $\delta^{13}\text{C}$ values for *Pachytheca* ($-27.5 \pm 0.7\%$) and for *Prototaxites* from the same locality ($-28.0 \pm 1.0\%$) (Abbott et al. 1998). In view of the diversity of $\delta^{13}\text{C}$ values for *Prototaxites* (Boyce et al. 2007; Hobbie and Boyce 2010) it would be useful to have more paired $\delta^{13}\text{C}$ values of *Pachytheca* and *Prototaxites* for further testing the possible relationship. Paired analyses from potential underground root-like structures also would be helpful.

Parka decipiens (Fig. 3.3a) is common in the Old Red Sandstone (Upper Silurian-Lower Devonian) as disks some 70 mm in diameter, with pockets of spore-like structures (monads?) lacking any haplotypic feature but suggestive of a reproductive function (Hemsley 1989; Taylor et al. 2009).

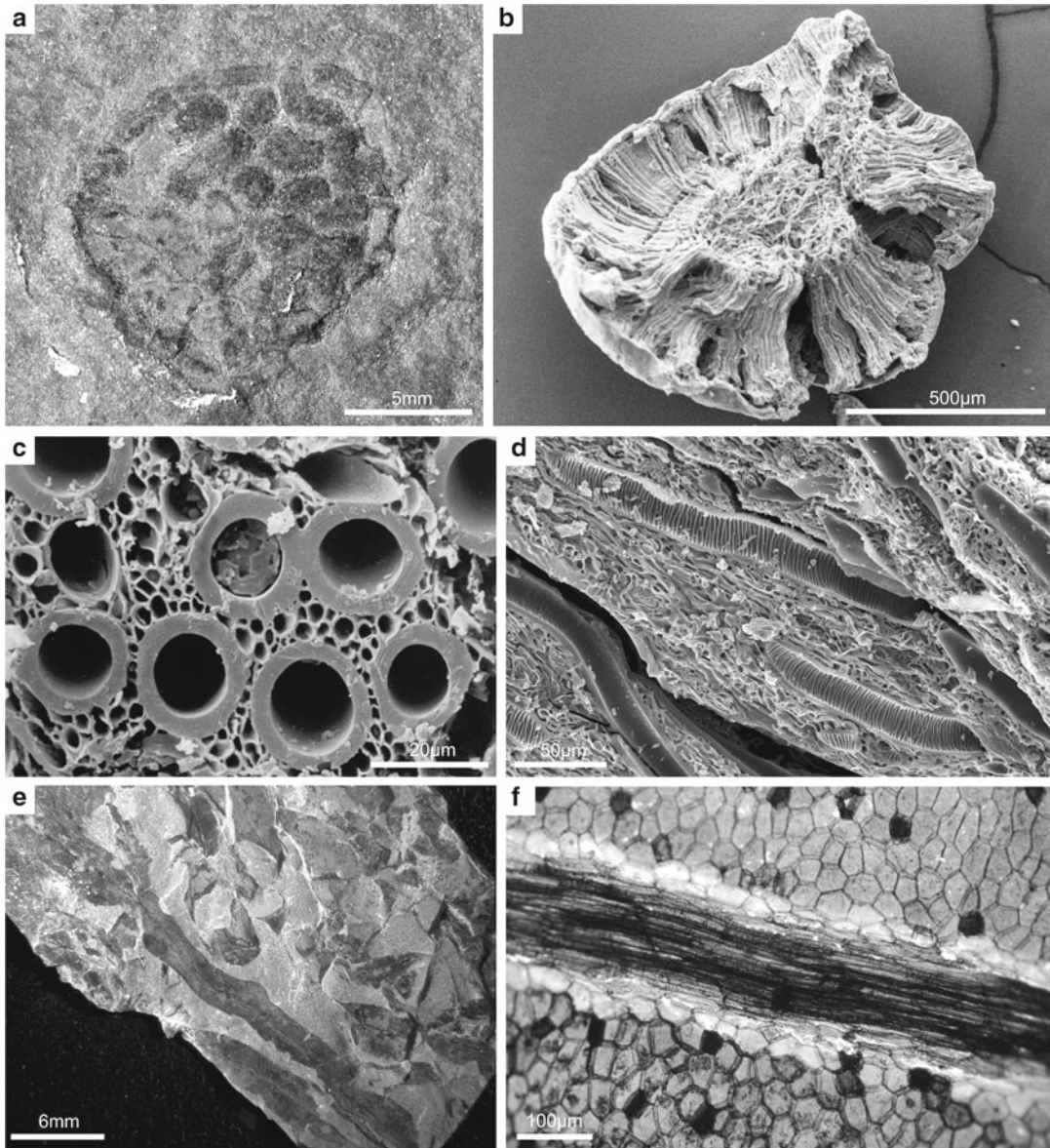


Fig. 3.3. (a) *Parka decipiens*, compression fossil of uncertain affinity. Dundee Formation, Myreton, Scotland, Lochkovian (Lower Devonian, c. 415 myr). (b) *Pachytheca* sp., SEM of fractured sphere showing cortex and medulla. Ditton Group, Welsh Borderland, England, lower Lochkovian (Lower Devonian, c. 414 myr). (c) *Prototaxites* sp., SEM of transverse fracture, Ditton Group, Welsh Borderland, England, lower Lochkovian (Lower Devonian, c. 414 myr). (d) *Nematasketum* sp., SEM of longitudinal fractured specimen, St. Maughans Formation, Brecon Beacons, lower Lochkovian (Lower Devonian, c. 414 myr). (e) *Metzgeriothallus sharonae*, coalified jungermanniopsid liverwort, Plattekill Formation, Cairo, N.Y. State, Givetian (upper Middle Devonian, c. 388 myr), (f) isolated thallus of liverwort in Fig. 3.3e, showing cells of central costa and thallus wings. (e–f courtesy of Linda Hernick, NY State).

The simplicity of their vegetative structure allows comparisons with the charophycean alga *Coleochaete* and the protonemal stage

of the gametophyte of the moss *Sphagnum*, though without definitive assignment to these or any other higher taxa. The purportedly

reproductive structures of *Parka* have no obvious extant analogues. These organisms could have lived in wetlands, in which case they would presumably function like the organisms described by Tomescu and Rothwell (2006) and Tomescu et al. (2009). There seem to be no carbon isotope measurements on *Parka*. The organic macromolecules of *Parka* are distinct from those of *Pachythea* and *Prototaxites* (Abbott et al. 1998).

The dichotomizing terrestrial *Spongiophyton* has been considered as an intermediate between algae and tracheophytes: it has tubular dichotomizing morphology, a thick cuticle and a scattered surface pores; specimens are some 25 by 25 mm (Gensel et al. 1991; Jarhren et al. 2003; Fletcher et al. 2004; Taylor et al. 2009). *Spongiophyton* has also been the subject of carbon isotope studies (Javaneau et al. 2003; Fletcher et al. 2004). Javaneau et al. (2003) claimed that the $\delta^{13}\text{C}$ values of *Spongiophyton* showed that their photosynthetic metabolism was similar to that of extant lichens. However, a more detailed analysis of the $\delta^{13}\text{C}$ values of *Spongiophyton* and comparison with extant hornworts, lichens, liverworts and mosses show that the *Spongiophyton* $\delta^{13}\text{C}$ values are statistically indistinguishable from the values from the four extant groups, although the range for *Spongiophyton* spp. is less than that for each of the four extant groups. It can be said that *Spongiophyton* does not exhibit the most positive $\delta^{13}\text{C}$ values seen for those lichens and hornworts with CCMs (Smith and Griffiths 1996a, b, 1998; Hanson et al. 2002), which might be expected granted the high atmospheric CO_2 levels in the Early Devonian. *Spongiophyton* spp. also do not show the most negative $\delta^{13}\text{C}$ values for extant lichens, liverworts and mosses. The most negative $\delta^{13}\text{C}$ values for extant organisms are a function of C_3 physiology with a high CO_2 conductance relative to biochemical conductance values related to the structure of the organism and also to the absence of an external water film decreasing CO_2 conductance. A further possible contributory factor is the enrichment of the local atmosphere in ^{13}C -depleted CO_2 from soil respiration of

organic carbon produced by taller plants, which is unlikely to be a major factor in the Early Devonian. The high CO_2 level in the Early Devonian atmosphere would, for a given ratio of CO_2 diffusive conductance to biochemical conductance in organisms lacking CO_2 concentrating mechanisms (CCMs), give lower $\delta^{13}\text{C}$ values for organic carbon than with the present CO_2 level.

C. Middle Devonian

The Middle Devonian shows further elaboration of vascular plants (euphyllphytes with roots, more widespread secondary thickening with forests of cladoxyloids (Stein et al. 2012), leaves, heterospory), and the loss of non-vascular polysporangiophytes such as *Aglaophyton* as well as several tracheophytes (Stein et al. 2007; Taylor et al. 2009; Raven and Andrews 2010; Gerrienne et al. 2011). The Middle Devonian also has the first unequivocal fossils of the vegetative structure of a bryophyte (Hernick et al. 2008; cf. Chang and Graham 2011). The organism, *Metzgeriothallus sharonae*, is a liverwort of the order Metzgeriales in the Jungermannopsida. As Hernick et al. (2008) point out, the discovery of *Metzgeriothallus sharonae* (Fig. 3.3e, f) puts the separation of the Metzgeriales and Jungermanniales, and hence of the Jungermannopsida and the Marchantiopsida, at no later than the Middle Devonian (cf. Chang and Graham 2011).

D. Upper Devonian

In the Upper Devonian there were gymnosperms among the euphyllphyte vascular plants (Taylor et al. 2009; Raven and Edwards 2004). Among non-tracheophytes there was the liverwort *Pallaviciniites* (= *Hepaticites*) *devonicus* (Hueber 1961). There is also the enigmatic *Protosalvinia* (= *Foerstia*) (Taylor et al. 2009), a thalloid, apparently terrestrial photosynthetic organism of unknown affinities (Romankiw et al. 2007). The thalli have an apical notch and conceptacles containing spores; it is not known if these are meiospores. *Protosalvinia* has been suggested to

be an alga, a bryophyte or a fern, but no firm conclusions have been drawn. There seem to have been no carbon stable isotope natural abundance studies of the possible photosynthetic pathway of *Protosalvinia*, although there have been ^{13}C -NMR studies of the chemistry of the organism which were interpreted as showing vascular plant affinities (Romankiw et al. 2007).

E. Prototaxites

Prototaxites (Fig. 3.3c) is found in Middle Silurian to Upper Devonian strata; it is made up of tubes which occur in cylindrical structures, apparently above ground, up to a metre in diameter and several metres long (Taylor et al. 2009). Some large Lower Devonian below-ground structures may be attributable to *Prototaxites*, but these are preserved as casts (Hillier et al. 2008). Suggestions as to the nature of *Prototaxites* include a fungus, an alga, a lichen or, most recently, rolled-up liverwort mats (Hueber 2001; Boyce and Hotton 2010; Graham et al. 2010a, b; Taylor et al. 2010; Edwards and Axe 2012). Carbon isotope values for *Prototaxites* have been interpreted in several ways (Boyce et al. 2007; Graham et al. 2010a, b; Hobbie and Boyce 2010; Taylor et al. 2010). There is a large diversity of $\delta^{13}\text{C}$ values among specimens (Boyce et al. 2007), and the interpretation of Hobbie and Boyce (2010) that this organism was a fungus obtaining organic carbon from a wide range of terrestrial and amphibious primary producers and, after floods, aquatic primary producers and that of Graham et al. (2010a, b) involving mixotrophic nutrition of the liverworts contributing to *Prototaxites* specimens are equally plausible. Edwards and Axe (2012) suggest fungal affinities for *Nematasketum*, an organism similar to *Prototaxites* (Fig. 3.3d). An alternative explanation for the variation in carbon isotope ratio among *Prototaxites* spp. can be found in the very significant developmentally or environmentally determined variations in $\delta^{13}\text{C}$ within a species showing facultative expression of Crassulacean Acid Metabolism (-14 to -28%) (Winter and

Smith 1996). However, there is no precedent for Crassulacean Acid Metabolism in the Palaeozoic or in lichens (Winter and Smith 1996).

VI. Photosynthetic Capacities

A. Extant Organisms

The discussion above shows that there is large range of morphologies and anatomies among Silurian and Devonian embryophytes and other terrestrial organisms thought to have been photosynthetic. Raven (1995; see also Raven 1992, 1993a, b) summarized photosynthetic rates on a ground area basis for extant terrestrial plants with a range of morphologies and mechanisms of CO_2 assimilation (Table 3.3). The values from Raven (1995) are supplemented in Table 3.3 with data on the rates of photosynthesis of a hornwort with a CCM (Smith and Griffiths 1996a, b) and emersed intertidal fucoid brown macroalgae (Surif 1989; Surif and Raven 1989, 1990) as indicators of the photosynthetic capacity of additional thalloid organisms at close to their optimal degree of hydration for photosynthesis, i.e. sufficiently hydrated to allow the maximum biochemical capacity for photosynthesis but without sufficient surface water to significantly restrict diffusive supply of CO_2 from the atmosphere to the surface of photosynthetic structures. There is also recognition of the amplification of surface area by the occurrence of vertical photosynthetic lamellae on the leaves of polytrichaceous mosses (Marschall and Proctor 2004; Proctor 2005; Waite and Sack 2010), the role of CCMs in hornworts (Smith and Griffiths 1996a, b; Hanson et al. 2002; Griffiths et al. 2006; Meyer et al. 2008), and additional information on the role of intercellular gas spaces in marchantiaceous liverworts (Griffiths et al. 2006; Proctor 2010). A final addition is the area-based photosynthetic rates of moss populations for comparison with the predictions based on the photosynthetic rate per unit leaf area and the leaf area index (Rice et al. 2008; Waite and Sack 2010).

There is only one rate of net photosynthesis on a ground area basis for organisms or associations without multiple layers and photosynthetic tissue separated by atmospheric gases, and also lacking both CCMs and developmentally produced intercellular gas spaces which can distribute external CO_2 to photosynthetic cells (i.e. are unventilated) (Table 3.3); the measured rate is less than $1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. All the rates for unventilated organisms with CCMs are higher (Table 3.3), with the exception of the hornwort with a CCM. However, rates of photosynthetic electron transport through photosystem II estimated from chlorophyll fluorescence (Hanson et al. 2002; Griffiths et al. 2006) shows substantially greater photosynthetic capacity in a hornwort with a CCM but with an unventilated thallus than in an unventilated hornwort lacking a CCM, with an intermediate photosynthetic capacity for a ventilated thalloid liverwort without a CCM.

Turning to organisms lacking CCMs and with two or more layers of unventilated photosynthetic tissue separated by atmospheric gases, the measured rates for mosses (other than the Polytrichaceae) are up to $6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ substrate area s}^{-1}$ (Table 3.3). This value is lower than that predicted from the photosynthetic rate of individual leaves and the occurrence of ten layers of leaves (Table 3.3), perhaps as a result of shading of lower leaves by upper leaves and/or of photo-inhibition of the upper leaves. The photosynthetic rate per unit leaf projected area is higher for the leaves of polytrichaceous mosses with vertical photosynthetic lamellae on the adaxial leaf surface than for other mosses lacking such lamellae, leading to the prediction of higher photosynthetic rates by a canopy of polytrichaceous mosses than of other mosses with the same leaf area index.

The final category involving bryophytes is that of organisms lacking CCMs with only a single layer of thalloid photosynthetic tissue, but with ventilation of the thallus involving non-stomatal pores linking the gas spaces and the atmosphere. Table 3.3 shows that the marchantiaceous liverworts have higher rates

of photosynthesis than do the thalli of unventilated liverworts; this conclusion is borne out by measurements of electron transport rate discussed above (Griffiths et al. 2006) as well as from estimates of a light saturation parameter (Marschall and Proctor 2004; Proctor 2010). Comparison of the marchantiaceous liverworts with ventilated crustose or foliose lichens is complicated by the variable presence of CCMs in lichens, but the rate is similar to that of the ventilated thalloid liverworts. The photosynthetic sporophytes of hornworts and most mosses are ventilated and have stomata but, since they are permanently dependent on the poikilohydric gametophyte to supply water and inorganic nutrients, they are not homoiohydric, and the quantitative importance of sporophyte photosynthesis is uncertain.

Organisms with ventilated photosynthetic tissues and a leaf (or thallus) area index in excess of 1 are the sporophytes of vascular plants, some of which (C_4 and Crassulacean Acid Metabolism (CAM) plants) have CCMs. There are also fruticose lichens, again some with photobionts expressing CCMs. Table 3.3 shows that the poikilohydric fruticose lichens have net photosynthetic rates on a substrate area basis higher than those measured for bryophytes, but less than that for C_3 and, especially, C_4 plants.

Water content is a very significant determinant of the photosynthetic rate for poikilohydric organisms on land. There is water content (water per unit dry matter) at which the maximum rate of photosynthesis using atmospheric CO_2 is achieved. As the water content increases above this optimum value the rates of photosynthesis are increasing, limited by diffusion of CO_2 from the air-water interface to the chloroplasts through an increasing thickness of water, while decreasing water contents below the optimum value leads to increasing restriction on photosynthesis by limitations within the intracellular photosynthetic machinery (e.g. Williams and Flanagan 1998). The effect of the water film in restricting CO_2 diffusion at supraoptimal water contents is possibly less significant for endohydric bryophytes with a

less wettable (cuticle with wax) surface (Raven 1977, 2002a, b).

In addition to the variations in the rates of photosynthesis on a substrate area basis among the extant organisms which can photosynthesize using atmospheric CO₂, there are also measurements and predictions of the extent to which the various organisms use resources in assimilating CO₂. Well characterized effects among homoiohydric plants are the small transpiratory water loss per unit CO₂ assimilated in CAM plants relative to that in C₃ plants, with C₄ plants intermediate, and the potential for a greater photosynthetic rate per unit nitrogen in the photosynthetic apparatus in C₄ and CAM plants than for C₃ plants. These increases in the photosynthesis per unit water lost, and in photosynthetic rate per unit nitrogen, in plants with CCMs are not limited to homoiohydric plants; the arguments also apply to poikilohydric plants (Surif and Raven 1989; Griffiths et al. 2006). A greater water use efficiency of CO₂ assimilation in poikilohydric photosynthetic organisms with CCMs would mean that the organism could assimilate more CO₂ in a hydration – desiccation cycle than would an otherwise similar organisms lacking a CCM, assuming that the organism with a CCM has the same sensitivity to desiccation as organisms lacking CCMs. Maberly and Madsen (1990) have shown that a quarter of the photosynthesis by the high intertidal fucoid brown alga *Fucus spiralis* occurs when the alga is immersed rather than submersed; the extent to which this depends on the occurrence of a CCM in this alga is not clear. This also applies to the variety of microscopic green algae from four classes which occur in desert crusts: some have CCMs, at least in so far as these can be expected to occur in organisms with pyrenoids (Table 3.1). All cyanobacteria, including those in desert crust, have CCMs.

B. Relevance to the Colonization of Land by Photosynthetic Organisms

In examining the implications for colonization of the land we must consider both the

structure of the fossils of (putatively) photosynthetic organisms, and the environmental conditions. Of the environmental conditions the most significant is probably the higher CO₂ partial pressure in the Ordovician, Silurian and at least the Early Devonian. Such higher CO₂ concentrations means that the Form IB Rubiscos of C₃ embryophytes would be operating at closer to saturation with CO₂, granted similar conductance to CO₂ to those in extant organism of similar structure. This provides the potential for more rapid photosynthesis per unit photosynthetic tissue and per unit nitrogen in the photosynthetic tissue. A proviso here is that many extant vascular plants downregulate expression of Rubisco when grown in high CO₂, although overall the response is usually an increase in photosynthetic rate in the higher CO₂ level. In addition, in extant vascular plants in high CO₂ there is a decreased diffusive conductance to CO₂; this decrease could permit a rate of photosynthesis which was still greater than is found in the present atmosphere but with a significantly smaller water vapour loss per unit of CO₂ assimilated, and a correspondingly higher temperature of the photosynthetic structures relative to that of the atmosphere. The temperature difference argument has been used in the context of the small size of the earliest euphyllophyte leaves in the relatively high temperatures of the Early Devonian: larger leaves would have a higher leaf temperature. Waite and Sack (2010) found that bryophytes have a lower photosynthetic nitrogen use efficiency than neighbouring C₃ vascular plants, although this could well be related to some extent to some other attributes of bryophytes. One of these is the greater general shade adaptation in the bryophytes than in vascular plants, although the data in Waite and Sack (2010) refer to bryophytes and neighbouring (in similar environments) habitats. Acclimation to low irradiance in *Tortula ruralis* involves, as in many other photosynthetic organisms, an increase in nitrogen in dry matter (Hamerlynk et al. 2002). A further possibility is greater nitrogen content (possibly storage, in evolutionary

terms the accumulation against some future deterministic or stochastic event) in desiccation-tolerant organisms, remembering that a greater fraction of bryophytes than vascular plants exhibit desiccation tolerance (Proctor et al. 2007; Tymms and Ganff 1979; Wilson et al. 2001; Oliver et al. 2011). A final consideration is a smaller possibilities for nitrogen retranslocation within bryophytes than within vascular plants (Raven 2003).

Turning to the photosynthetic significance of the range of morphologies in the early photosynthetic organisms on land, much attention has been paid to organisms whose structures most closely resemble those of extant plants. These are the sporophytes of fossil vascular plants such as lycophytes (including zosterophyllophytes) and rhyniophytes, and rhyniophytoid plants, whose mode of preservation allows quantitative estimates to be made of stomatal frequency, maximum stomatal conductance, and the conductance of the endohydric (xylem or xylem-like) conducting system (Raven 1977, 1984, 2003; Konrad et al. 2000; Roth-Nebelsick et al. 2000; Roth-Nebelsick 2001, 2005; Roth-Nebelsick and Konrad 2005; Wilson and Fischer 2011; Boyce 2010; Edwards 2004). Matching of the conductance of the endohydric conducting system and of the stomatal conductance (Raven 1977, 1984; Konrad et al. 2000; Roth-Nebelsick et al. 2000) has been suggested as at least a partial explanation of the low stomatal density and stomatal conductance in *Asteroxylon*: the low stomatal conductance restricts the likelihood of failure by cavitation or embolism of the low conductance xylem by restricting the potential for transpiration (Wilson and Fischer 2011). While maximum stomatal conductance can be computed for the earliest stomata-bearing plants, the effectiveness of stomata in decreasing the possibility of xylem failure is increased pre-emptive closure, i.e. the capacity to sense a large evaporative demand by the atmosphere and a limited water supply from the soil and to decrease stomatal opening. The occurrence of these pre-emptive responses was discovered in, and well char-

acterized from, seed plants (predominantly angiosperms); however, their occurrence in non-seed embryophytes is still controversial (Brodribb et al. 2010; Bowman 2011; Brodribb and MacAdam 2011; Chater et al. 2011; Ruszala et al. 2011). Until this question is resolved we must hesitate in attributing the full seed plant range of environmental responses of stomata to extant and fossil sporophytes of non-seed plants, with the possibility that their homoiohydric mechanisms show less precise responses to the environment. One way of addressing the question of the outcome of stomatal activity in regulating water loss per unit dry matter increase is to examine the natural abundance of carbon stable isotopes (Farquhar et al. 1989). Extant C₃ ferns and C₃ flowering plants from the same epiphytic habit have closely similar carbon isotope ratios (Hietz et al. 1999), with similar results from more spatially wide-ranging surveys (Smith and Epstein 1971; Watkins et al. 2007a).

As we have already seen, not all the Silurian and Lower Devonian plants can be readily assigned to an extant ecophysiological category. Staying initially with the sporophyte phase of embryophytes, some of the Devonian polysporangiophytes (e.g. cooksonioids) have axial diameters which are too small (Boyce 2008) to function in homoiohydric gas exchange (Raven 1999a, b). This led Boyce (2008) to suggest that these structures, with their pronounced peripheral stereome, were matrotrophic on the gametophytes phase. Boyce (2008) followed suggestions of Edwards (1996) and Edwards et al. (1996, 1998), that the rare stomata on these plants were involved in increasing solute flow to the sporangium in the transpiration stream, and then in drying out the sporangium prior to spore dispersal with continued support from the stereome (cf. Duckett et al. 2009, 2010).

The embryophyte gametophytes from the Rhynie Chert have somewhat different vegetative morphologies from those of the corresponding sporophytes (Taylor et al. 2009). However, the gametophytes resemble the sporophytes in having the suite of homoiohydric characteristics, i.e. endohydric conducting

system, cuticle, intercellular gas spaces and stomata. These anatomical findings are consistent with both the sporophyte and the gametophyte phase, a situation without parallel in other known extinct, or extant, plants. Among other things, the occurrence of homoiohydricity in both phases means that the initially matrotrophic sporophyte is nourished by a homoiohydric gametophyte, rather than a poikilohydric gametophyte as in all extant free-sporing embryophytes.

The more thalloid terrestrial or amphibious photosynthetic organisms were presumably poikilohydric. The optimum water content per unit dry matter for photosynthesis using atmospheric CO₂ would be expected to be lower, or the range of water contents at which photosynthesis was maximal would be larger, because of the decreased diffusive restriction on CO₂ supply to chloroplast for a given water film thickness with the higher atmospheric CO₂ concentration.

VII. Conclusion

In addition to the dominant vascular plants on land today there are ecologically and biogeochemically significant contributions to primary productivity on land from bryophytes, lichens and free-living cyanobacteria and algae. The limited primary productivity on land before fossil evidence of embryophyte spores (470 Ma ago) presumably involved free living, and possibly lichenized, cyanobacteria and green algae. The first fossils of the vegetative phase of bryophytes do not occur until the Middle Devonian (380 Ma ago), yet tracheophytes are known from 420 Ma ago, thalloid terrestrial or amphibious primary producers are known from even earlier, and molecular phylogenetic studies show that bryophytes preceded vascular plants. The absence of early fossils makes it difficult to comment on the photosynthetic capacities of early bryophytes, and we rely on extrapolations of photosynthetic rates of extant bryophytes of various life forms to indicate their possible contribution.

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