The origin and early evolution of plants on land

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The origin and early evolution of land plants in the mid-Palaeozoic era, between about 480 and 360 million years ago, was an important event in the history of life, with far-reaching consequences for the evolution of terrestrial organisms and global environments. A recent surge of interest, catalysed by palaeobotanical discoveries and advances in the systematics of living plants, provides a revised perspective on the evolution of early land plants and suggests new directions for future research.

The origin and early diversification of land plants marks an interval of unparalleled innovation in the history of plant life. From a simple plant body consisting of only a few cells, land plants (liverworts, hornworts, mosses and vascular plants) evolved an elaborate two-phase life cycle and an extraordinary array of complex organs and tissue systems. Specialized sexual organs (gametangia), stems with an intricate fluid transport mechanism (vascular tissue), structural tissues (such as wood), epidermal structures for respiratory gas exchange (stomates), leaves and roots of various kinds, diverse spore-bearing organs (sporangia), seeds and the tree habit had all evolved by the end of the Devonian period. These and other innovations led to the initial assembly of plant-dominated terrestrial ecosystems, and had a great effect on the global environment.

Early ideas on the origin of land plants were based on living groups, but since the discovery of exceptionally well-preserved fossil plants in the Early Devonian Rhynie Chert, research has focused almost exclusively on the fossil record of vascular plants[1,2]. During the 1970s, syntheses of palaeobotanical and stratigraphic data emphasized the Late Silurian and Devonian periods as the critical interval during which the initial diversification of vascular plants occurred[1,2], and identified a group of simple fossils (rhyniophytes, such as *Cooksonia* and *Rhynia*) as the likely ancestral forms[2]. They also supported earlier hypotheses of two main lines of evolution: one comprising clubmosses (Fig. 1f) and extinct relatives, the other including all other living vascular plants (ferns, horsetails and seed plants; Fig. 1g–j) and related fossils[1,2]. During the past two decades, the discovery of fossil spores from as far back as the mid-Ordovician period[3], improved knowledge of living green algae[4,5], renewed interest in the phylogenetic position of other relevant groups such as mosses and liverworts[5], and advances in molecular systematics[5–14], together with unexpected new data on the structure and biology of Silurian and Devonian fossils[15–25], have provided a broader perspective on the origin of a land flora[26]. These new data indicate that the early diversification of land plants substantially pre-dates the Late Silurian to Early Devonian, and suggest that the main basal lineages originated over a period of more than 100 million years (Myr).

Patterns in the early fossil record

Evidence on the origin and diversification of land plants has come mainly from dispersed spores and megafossils. Gray recognized three new plant-based epochs (Eoembryophytic, Eotracheophytic and Eutracheophytic) spanning the origin and early establishment of land plants: each is characterized by the relative abundance of spore types and megafossils[3]. This synthesis highlights diversification and floral change in the Ordovician and Silurian[3,27,28], and emphasizes a major discrepancy between evidence from spores and megafossils: unequivocal land plant megafossils are first recognized in the fossil record roughly 50 Myr after the appearance of land plant spores.

Eoembryophytic (mid-Ordovician [early Llanvirn: ~476 Myr] to Early Silurian [late Llandovery: ~432 Myr])[3]. Spore tetrads (comprising four membrane-bound spores; Fig. 2d) appear over a broad geographic area in the mid-Ordovician and provide the first good evidence of land plants[3,26,29]. The combination of a decay-resistant wall (implying the presence of sporopollenin) and tetrahedral configuration (implying haploid meiotic products) is diagnostic of land plants. The precise relationships of the spore producers within land plants are controversial, but evidence of tetrads and other spore types (such as dyads) in Late Silurian and Devonian megafossils[16,30], as well as data on spore wall ultrastructure[25] and the structure of fossil cuticles[31], support previous suggestions of a land flora of liverwort-like plants (Fig. 1c)[3]. Some early spores and cuticles may also represent extinct transitional lineages between charophycean algae (Fig. 1a, b) and liverworts (Box 1), but precise understanding of their affinities is hindered by the dearth of associated megafossils.

Eotracheophytic (Early Silurian [latest Llandovery: ~432 Myr] to Early Devonian [mid Lochkovian: ~402 Myr])[3]. The early Silurian (latest Llandovery) marks the beginning of a decline in diversity of tetrads and a rise to dominance of individually dispersed, simple spores, which are found in several basal land plant groups (such as hornworts, some mosses, and early vascular plants)[3]. Although tetrads remain dominant in some Early Devonian localities from northwestern Europe[32], the elaboration of simple spores and turnover of spore 'species'[3] provide evidence of increasing land plant diversity and vegetational change. Although spores have been observed in Silurian megafossils, the affinities of most dispersed forms remain unknown, indicating that substantial land plant diversity is currently undetected in the megafossil record[30].

The earliest unequivocal land plant megafossils are from the mid-Silurian of northern Europe[33], and lowermost Upper Silurian of Bolivia[34] and Australia[35], and the uppermost Silurian of northwestern China[36]. Early assemblages include clubmosses (such as *Baragwanathia*) and related early fossils (such as zosterophylls, some species of *Cooksonia*), and various other plants of uncertain affinity (such as *Salopella* and *Hedeia*; Fig. 3). These data document an influx into land plant communities of diverse but generally small (usually less than 10 cm tall) organisms related to vascular plants (Fig. 3). Exceptions to the generally small size include the clubmoss *Baragwanathia*[37] and the large and much-branched *Pinnatiramosus* from the early Silurian of China[38]. The habit and branching of *Pinnatiramosus* is similar to that of green algae in the Caulerpales, but the presence of tracheid-like tubes is inconsistent with this interpretation[39]. Additional details, including conclusive data on reproductive structures, are needed to clarify the relationships of this enigmatic plant.

Data from northern Europe, Siberia, Podolia (southwestern Ukraine), Libya, Vietnam, Bolivia, Australia and Xinjiang and Yunnan (China) document increasing land plant diversity into

the base of the Devonian[33–36,40]. These fossils, together with the relative chronology implicit in current hypotheses of relationship, imply a minimum mid-Silurian origin for several important vascular plant groups (Box 1; Fig. 4).

Eutracheophytic (Early Devonian [late Lochkovian: ~398 Myr] to mid-Permian [~256 Myr])[3]. In the Early Devonian (late Lochkovian) the diversity of spores and megafossils increased dramatically[29,40–42]. Early assemblages include the classic floras from the Rhynie Chert[20,43,44], the Gaspé Peninsula of eastern Canada[43,44], New York State[43,44], the Rhine Valley of Germany[45], Belgium[46], Australia[35] and Yunnan Province (China)[33], which document a substantial increase in vascular plant diversity, including the appearance and early diversification of many important living groups.

Building a land plant

Phylogenetic studies favour a single origin of land plants from charophycean green algae (Box 1). Based on the ecology of living species, a freshwater origin of land plants seems likely, but direct evidence from the fossil record is inconclusive as mid-Palaeozoic charophytes are found in both freshwater and, more commonly, marine facies[47]. Living charophycean algae (Fig. 1a, b) possess several biosynthetic attributes that are expressed more fully among land plants, including the capacity to produce sporopollenin, cutin, phenolic compounds and the glycolate oxidase pathway[4,48]. However, the absence of well-developed sporophytes, gametophytes with sexual organs of land plant type, cuticle and non-motile, airborne, sporopollenin-walled spores suggests that these innovations evolved during the transition to the land[4,18]. In contrast to animal groups, the entire multicellular diploid phase of the plant life cycle probably evolved in a terrestrial setting.

The transition from an aqueous to a gaseous medium exposed plants to new physical conditions that resulted in key physiological and structural changes. Important metabolic pathways leading to lignins, flavenoids, cutins and plant hormones in vascular plants probably arose from pre-existing elements of primary metabolism in charophycean algae and bryophytes[4]. Although the evolution of these pathways is poorly understood, possible phenolic precursors have been detected in charophycean algae[4,31], and elements of auxin metabolism have been recognized in mosses and hornworts[49].

Phylogenetic studies predict that early land plants were small and morphologically simple, and this hypothesis is borne out by fossil evidence (Fig. 3). Early fossils bear a strong resemblance to the simple spore-producing phase of living mosses and liverworts (Fig. 1d, e and 5)[16,26,50,51], and these similarities extend to the anatomical details of the spore-bearing organs and the vascular system[19]. The
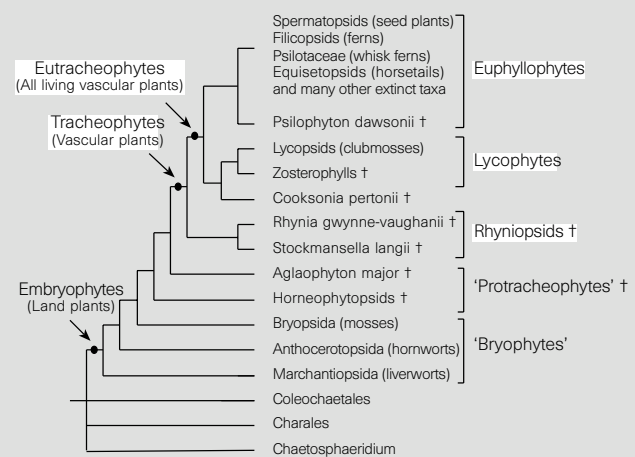

Box 1 Relationships among land plants

Land plants (embryophytes) are most closely related to the Charophyceae, a small group of predominantly freshwater green algae, within which either Coleochaetales (~15 living species; Fig. 1a) or Charales (~400 living species; Fig. 1b), or a group containing both, is sister group to land plants[4,5,10,12,74].

Land-plant monophyly is supported by comparative morphology[4,5,26,75] and gene sequences (18S rRNA, mitochondrial DNA: *cox III*)[12,14]. Relationships among the major basal living groups are uncertain[4,5,26,76,77], but the best-supported hypothesis resolves liverworts (Fig. 1c) as basal and either mosses (Fig. 1e) or hornworts (Fig. 1d) as the living sister group to vascular plants (tracheophytes)[4,5,13,14,26,75]. Less parsimonious hypotheses recognize bryophyte monophyly and either a sister-group relationship with vascular plants[26] or an origin from within basal vascular plants[14,76,78].

Among vascular plants, living ferns (Fig. 1g), horsetails (Fig. 1i) and seed plants (Fig. 1j) (euphyllophytes) are the sister group to clubmosses (Fig. 1f)[13,14,26,75,79]. Euphyllophyte monophyly is strongly supported by comparative morphology[26] and a unique 30-kb inversion in the chloroplast genome[8], as well as sequence data from 18S rRNA[13] and mitochondrial DNA (*cox III*)[14]. These data also provide evidence that the enigmatic Psilotaceae (Fig. 1h) (a group of simple plants once thought to be living relicts of the earliest vascular plants) are more closely related to the fern–seed plant lineage than to basal vascular plants (clubmosses or the extinct rhyniophytes). Within vascular plants, molecular and morphological assessments of phylogeny at the level of orders and below give similar results[11], but at deeper levels (for example, the divergence of major groups of ferns, horsetails and seed plants) phylogenetic resolution is poor. These difficulties highlight the problems of approaches based solely on living species[7,80]. Combined analyses of molecular sequences from multiple loci, and large-scale structural characteristics of the genome (such as introns and inversions), may be more useful in assessing deep phylogenetic patterns.

Megafossils fill some of the substantial morphological 'gaps' among living groups. Phylogenetic analyses[19,26] interpolate two Early Devonian Rhynie Chert plants, *Aglaophyton* and *Horneophyton*, between bryophytes and basal vascular plants as they possess some features unique to vascular plants (a branched, nutritionally independent sporophyte) but also retain bryophyte-like characteristics (terminal sporangia, columella in *Horneophyton*, and the absence of leaves, roots and tracheids with well-defined thickenings). The discovery of previously unrecognized diversity in

(cladogram diagram)

Spermatopsids (seed plants)
Filicopsids (ferns)
Psilotaceae (whisk ferns)
Equisetopsids (horsetails)
and many other extinct taxa
— Euphyllophytes

Eutracheophytes (All living vascular plants)

Psilophyton dawsonii †

Tracheophytes (Vascular plants)

Lycopsids (clubmosses)
Zosterophylls †
— Lycophytes
Cooksonia pertonii †

Rhynia gwynne-vaughanii †
Stockmansella langii †
— Rhyniopsids †

Aglaophyton major †
Horneophytopsids †
— 'Protracheophytes' †

Embryophytes (Land plants)

Bryopsida (mosses)
Anthocerotopsida (hornworts)
Marchantiopsida (liverworts)
— 'Bryophytes'

Coleochaetales
Charales
Chaetosphaeridium

extinct *Cooksonia* and similar early fossils (such as *Tortilicaulis*, *Uskiella*, *Caia*[15–17,81]) (Fig. 3) suggests that simple early land plants (once grouped as rhyniophytes[1]) are an unnatural assemblage[26]. Some *Cooksonia* species may be among the precursors to vascular plants (protracheophytes), whereas others are vascular plants apparently allied to the clubmoss lineage[26].

Clubmosses emerge from a poorly resolved grade of extinct *Zosterophyllum*-like plants (Fig. 4), although most zosterophylls form a monophyletic group[26]. Within clubmosses, early leafy herbaceous fossils such as *Baragwanathia* and *Asteroxylon* are basal[26,82], and living Lycopodiaceae are resolved as sister group to a calde that comprises the extinct herbaceous Protolepidodendrales, living *Selaginella* and the predominantly arborescent carboniferous lepidodendrids, including living *Isoetes*[26,82] (Fig. 4).

Euphyliophytes make up more than 99% of living vascular plants and exhibit much greater diversity than lycophytes. Relationships among basal euphyllophytes are still poorly understood[26]. Further progress requires a better understanding of the relationships of several fossil groups of uncertain status (such as Trimerophytina, Cladoxylales and Zygopteridales)[26,79].
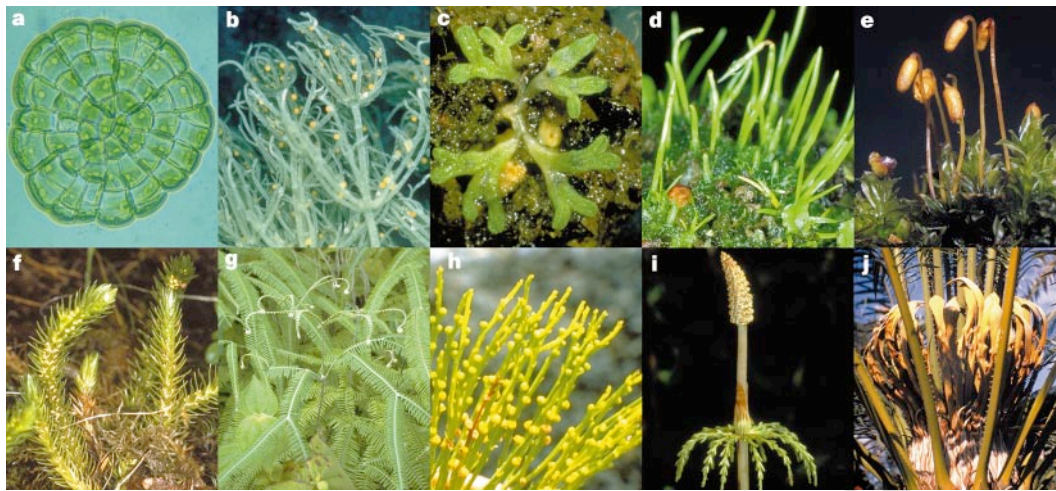
Figure 1 Morphological diversity among basal living land plants and potential land-plant sister groups. **a**, *Coleochaete orbicularis* (Charophyceae) gametophyte; magnification ×75 (photograph courtesy of L. E. Graham). **b**, *Chara* (Charophyoceae) gametophyte; magnification ×1.5 (photograph courtesy of M. Feist). **c**, *Riccia* (liverwort) gametophyte showing sporangia (black) embedded in the thallus; magnification ×5 (photograph courtesy of A. N. Drinnan). **d**, *Anthoceros* (hornwort) gametophyte showing unbranched sporophytes; magnification ×2.5 (photograph courtesy of A. N. Drinnan). **e**, *Mnium* (moss) gametophyte showing unbranched sporophytes with terminal sporangia (cap- sule); magnification ×4.5 courtesy of W. Burger). **f**, *Huperzia* (clubmoss) sporophyte with leaves showing sessile yellow sporangia; magnification ×0.8. **g**, *Dicranopteris* (fern) sporophyte showing leaves with circinate vernation; magnification ×0.08. **h**, *Psilotum* (whisk fern) sporophyte with reduced leaves and spherical synangia (three fused sporangia); magnification ×0.4. **i**, *Equisetum* (horsetail) sporophyte with whorled branches, reduced leaves, and a terminal cone; magnification ×0.4. **j**, *Cycas* (seed plant) sporophyte showing leaves and terminal cone with seeds; magnification ×0.05 (photograph courtesy of W. Burger).
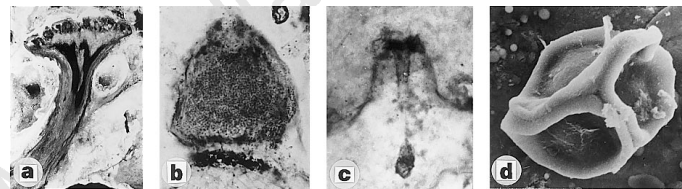
Figure 2 a, Longitudinal section of part of a silicified early fossil gametophyte (*Kidstonophyton discoides* from the Rhynie Chert). Antheridia (male sexual organs) are located on the upper surface of the branch; magnification ×3.4. **b**, Longitudinal section of antheridium of *Lyonophyton rhyniensis* from the Rhynie Chert; magnification ×40. **c**, Longitudinal section of archegonium (female sexual organ) of *Langiophyton mackiei* from the Rhynie Chert; magnification ×80. **a**–**c** are from the Remy Collection (slides 200, 90 and 330), Abteilung Paläobotanik, Westfälische Wilhelms-Universität, Münster, Germany (photographs courtesy of H. Hass and H. Kerp). **d**, Scanning electron micrograph of *Tetrahedraletes medinensis* showing a spore tetrad of possible liverwort affinity from the Late Ordovician (photograph courtesy of W. A. Taylor); magnification ×670.
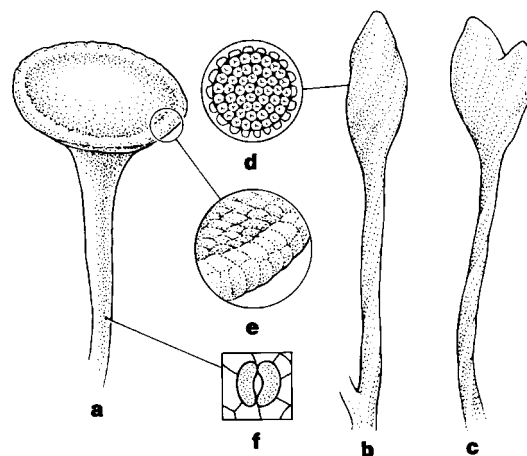
Figure 3 Sporophyte diversity in Early Devonian rhyniophyte fossils. **a**, *Cooksonia pertonii apiculispora*: sporophyte (incomplete proximally) with terminal sporangium[15]; magnification ×15. **b**, *Tortilicaulis offaeus*: sporophyte (incomplete proximally) with terminal sporangium[81]; magnification ×40. **c**. *Tortilicaulis offaeus*: sporophyte (incomplete proximally) with terminal bifurcating sporangium[81]; mag- nification ×30. **d**, Transverse section of sporangium showing thick wall and central spore mass; magnification ×70. **e**, Details of epidermis at rim of spor- angium; magnification ×45. **f**, Stomate with two reniform guard cells (stippled); magnification ×120.

Land-plant life cycles are characterized by alternating multicellular sexual (haploid gametophyte, *n*) and asexual phases (diploid sporophyte, 2*n*). Phylogenetic studies indicate that land plants inherited a multicellular gametophyte from their algal ancestors but that the sporophyte evolved during the transition to the land. Most megafossils are sporophytes, and until recently there was no direct early fossil evidence for the gametophyte phase. Recent discoveries of gametophytes in the Rhynie Chert (Early Devonian, 380–408 Myr) have shed new light on the evolution of land–plant life cycles[18,20].

Early gametophytes (**a** in figure) are more complex than in living plants and have branched stems bearing sexual organs on terminal cup- or shield-shaped structures (Fig. 2a). Archegonia (female gametangia) are flask-shaped with a neck canal and egg chamber, and are sunken as in hornworts and most vascular plants (Fig. 2c). Antheridia (male gametangia) are roughly spherical, sessile or with a poorly-defined stalk, and superficial (Fig. 2b). Gametophytes are very similar to associated sporophytes, and shared anatomical features (water-conducting tissues, epidermal patterns, and stomates) have been used to link corresponding elements of the life cycle[18,20]. Our provisional reconstruction of the life cycle of an early vascular plant is based on information from anatomically preserved plants and contemporaneous compression fossils.

The similarities between gametophyte and sporophyte in early fossil vascular plants contrast strongly with the marked dissimilarities typical of living land plants (**b** in figure). The phylogenetic position of fossils suggests that, after the development of a simple, unbranched, 'parasitic' sporophyte among early land colonizers at the bryophyte grade (such as mosses) there was elaboration of both gametophyte and sporophyte in vascular plants. The implications for interpreting life cycles in living vascular plants[18,26] are shown. The small, simple, often subterranean and saprophytic gametophytes of living clubmosses (such as Lycopodiaceae) and ferns (such as Psiloataceae, Stromatopteridaceae, Ophioglossaceae) result from morphological loss. Phylogenetic evidence indicates that gametophyte reduction was independent in clubmosses and the fern–seed plant lineage. These data provide a new interpretation of the gametophyte morphology of living clubmosses (Lycopodiaceae)[18].
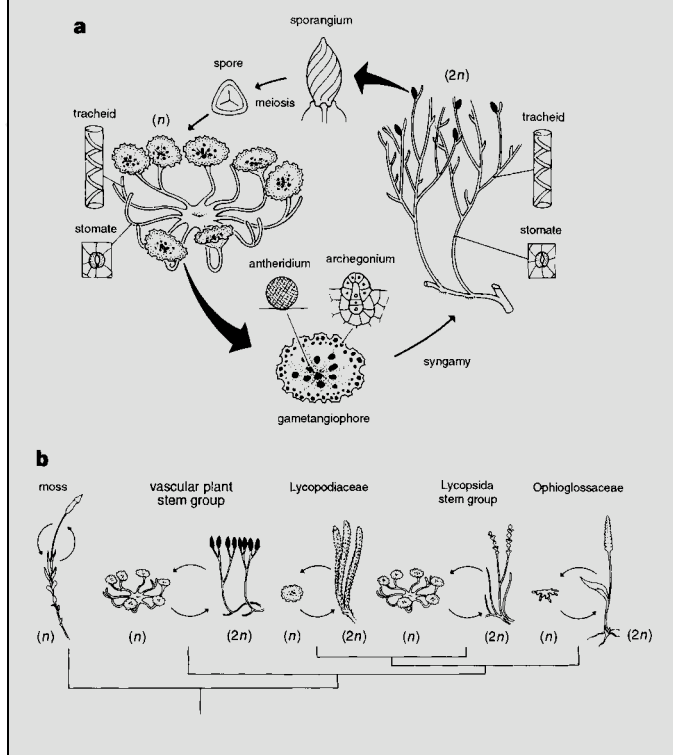
fossil record also documents significant differences from living groups, particularly in life cycles and the early evolution of the sexual phase (Box 2).

In common with some animal groups, internalization of vital functions and organs (such as gas exchange surfaces and sexual organs), combined with the development of impermeable exterior surfaces, seem to have been primary responses to life on land. Together, these changes resulted in more highly differentiated plants with stomates, multicellular sexual and spore-bearing organs, water-conducting and other tissue systems[52–54]. Morphological differentiation occurred in both phases of the life cycle (gametophyte and sporophyte), but there was subsequently a dramatic reduction in the gametophyte and a great increase in sporophyte complexity among vascular plants (Box 2). Apical growth and branching coupled with delayed initiation of spore-bearing organs were important innovations of vascular plants that led to a more complex architectural framework on which subsequent morphological diversification was based. The fossil record clearly shows that many vascular-plant organs can be interpreted in terms of modification (especially duplication and sterilization) of basic structural units such as the spore-bearing tissues and the stem[26,54]. In ferns and seed plants, much morphological diversity is clearly attributable to modifications of branching systems into a variety of leaf-like organs, whereas the relatively conservative clubmoss bauplan has a dearth of organ systems that can be interpreted as modified branches. In both lineages, however, meristem dormancy and abortion were early innovations, providing evidence of hormonal control and substantial phenotypic flexibility[21,26].

Early terrestrial ecosystems

The advent of land plants had important consequences for energy and nutrient fluxes among terrestrial and freshwater ecosystems[29,55] and hence for the evolution of animal groups that live in these habitats. The vegetational changes of the Silurian and Devonian also had a major impact on the atmosphere and other aspects of the global environment. The evolution of roots is thought to have been an important factor in the reduction of atmospheric CO_2 concentrations through increased weathering of Ca–Mg silicate minerals brought about by mechanical disruption and soil acidification[56,57]. Accelerated weathering has also been linked to the formation of Devonian and Early Carboniferous marine black shales[58], but this requires further investigation in view of similar deposits earlier and later in the geological record. Root-like impressions have been recognized in Late Silurian palaeosols[59], but the earliest unequivocal evidence comes from Early Devonian vascular plants[26], which have modified prostrate stems bearing rhizoids resembling those of living bryophytes. More substantial roots capable of anchoring large trees evolved independently in several groups during the Middle to Late Devonian.

A further series of innovations in vascular plants, including the biosynthesis of lignin and the origin of lateral meristems (cambium), were critical to the development of large plants, and these developments may have been stimulated by competition for light. Trees evolved independently in several major groups, resulting in stratified forest communities by the end of the Middle Devonian and the production of large amounts of highly decay-resistant organic material (in the form of lignified wood). The early evolution of lignin-decomposing fungi (some Ascomycetes, and Basidiomycetes) is still poorly understood[24], but these groups would have been essential for recycling much of the organic carbon.

The earliest land plants probably encountered terrestrial ecosystems that had been occupied by bacteria and protists[60,61], algae[4], lichens[23,62] and fungi[24] since the Late Proterozoic. A variety of enigmatic plants (such as *Protosalvinia*[44,63]) were also present, and some of the largest elements (*Prototaxites* 'trunks' >69 cm in diameter) may have been fungi[64]. Such organisms, or perhaps some rhyniophytes[16], may be the source of the microscopic tubular
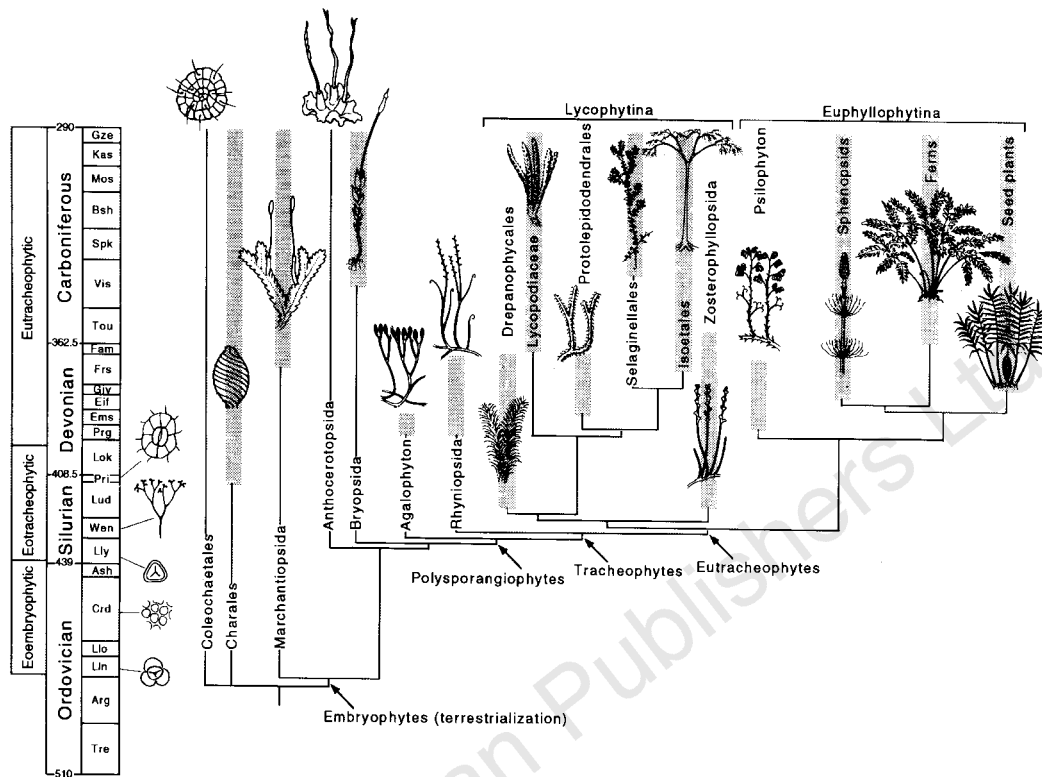
Figure 4 Simplified phylogenetic tree showing the minimum stratigraphic ranges of selected groups based on megafossils (thick bars) and their minimum implied range extensions (thin lines). Also illustrated alongside time scale are minimum age estimates for the appearance of certain important land-plant features (from the bottom: spore tetrads, cuticles, single trilete spores, megafossils and stomates). The first unequivocal record of charophycean algae is based on calcified charalean oogonia (female sexual organs) from the Late Silurian (Pridoli, ~410 Myr)[83] and distinctive gametophytes from the Early Devonian Rhynie Chert[44]. Proposed similarities between living *Coleochaete* and Early Devonian *Parka* remain to be confirmed[44]. Note that megafossil evidence for vascular plants precedes megafossil evidence of bryophytes and charophycean algae. Confirmation that the Early Devonian *Sporogonites* is a plant at the bryophyte grade could help to reduce this discrepancy. Tre, Tremadoc; Arg, Arenig; Lln, Llanvirn; Llo, Llandeilo; Crd, Caradoc; Ash, Ashgill; Lly, Llandovery; Wen, Wenlock; Lud, Ludlow; Pri, Pridoli; Lok, Lochkovian (Gedinnian); Prg, Pragian (Siegenian); Ems, Emsian; Eif, Eifelian; Giv, Givetian; Frs, Frasnian; Fam, Famennian; Tou, Tournaisian; Vis, Visean; Spk, Serpukhovian; Bsh, Bashkirian; Mos, Moscovian; Kas, Kasimovian; Gze, Gzelian.
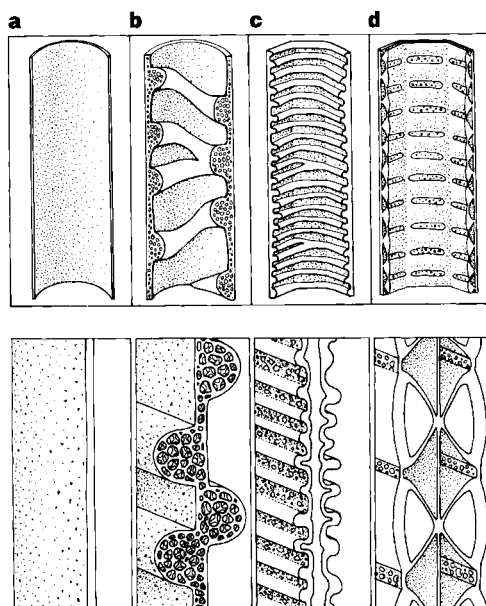
Figure 5 Diversity of water-conducting cells (tracheids) in early land plants (median longitudinal section through cells, basal and proximal end walls not shown; cells are ~20–40 μm diameter). **a**, Top, bryophyte hydroid; bottom, details of hydroid wall showing distribution of plasmodesmata-derived micropores (10–50 nm diameter; stipple)[84]. **b**, Top, S-type tracheid (fossil) of Rhyniopsida; bottom, details of S-type cell wall showing distribution of plasmodesmata-derived micropores (stipple) and 'spongy' interior to thickenings[19]. **c**, Top, G-type tracheid (fossil) of basal extinct eutracheophytes, which closely resemble the tracheids of some living vascular plants; bottom, details of G-type cell wall showing pores distributed between thickenings[19]. **d**, Top, scalariform pitted P-type tracheid (fossil) typical of trimerophyte grade plants (euphyllophytes); bottom, details of P-type cell wall showing pit chambers and sheet with pores that extends over pit apertures[26].

fragments commonly extracted from Silurian and Early Devonian sediments[28]. These tubes are often associated with cellular cuticular fragments (*Nematothallus* and *Cosmochlaina*) that may represent fragmented cuticular material from bryophyte-like plants[31]. The discovery of fungal arbusculae in Early Devonian megafossils[22] confirms earlier suggestions that endomycorrhizal associations were an important innovation in the colonization of the land[65].

In contrast to megascopic plants, which appear to have colonized the land only once, many animal groups made the transition to terrestrial existence independently and overcame the problems of water relations in different ways[52,66,67]. Early evidence for terrestrial animals is sparse[29,67–69], but by the Early Devonian exquisitely preserved arthropod faunas are known from several localities in North America, Germany and the United Kingdom[29,66,67]. These faunas document the appearance of diverse arthropod communities including centipedes, millipedes, trigonotarbids and their living relatives spiders, pseudoscorpions, mites (orbatids and endeostigmatids), arthropleurids (extinct arthropods), archaeognathans (primitive wingless insects), collembolans and possibly bristletails. Available evidence indicates that these animals were mainly predators and detritivores and, until the appearance of vertebrate herbivores in the latest Palaeozoic, most energy flow into animal components of early terrestrial ecosystems was probably through the decomposer pathway rather than direct herbivory[29]. Indirect evidence for herbivory comes from wound responses in the tissues of some fossil plants[70,71], and perhaps also from fossil faecal pellets containing abundant spores[70,72].

Future directions

The fossil record of spores, combined with phylogenetic studies, indicates that groups related to living bryophytes were early colonisers of the land, and suggests that several major lineages of vascular plant had already evolved by the mid-Silurian. Megafossils of land plants, however, appear much later, and in these assemblages there is a conspicuous bias toward the recognition and perhaps representation of vascular plants. The most important source of data on early megafossils has been the northern European (Laurussian) region, but the appearance of megafossils in this area coincides with facies changes driven by a widespread marine regression[28,73], and all Silurian land-plant megafossils are from marine sediments[33]. It seems likely that the onset of continental conditions in the Devonian of northern Europe allowed megafossils to be preserved at a time when vascular plants were well established but still diversifying. The rapid appearance of vascular plants in this region[40–42] owes as much to changing geological conditions as to rapid biological diversification[27,28]. Intensified sampling in areas that are remote from these regional events is therefore a high priority.

Palaeobotanical evidence shows that the major groups of living land plants are relicts, even though much modern species diversity *within* these groups may have evolved more recently. Data from the fossil record are therefore especially important for clarifying homologies among major organ systems which may otherwise be difficult to detect as a result of morphological divergence and extinction. Such combined studies of living and fossil plants provide an improved basis for comparative studies of plant development. They indicate, for example, that the ontogeny of leaves and spore-bearing organs in clubmosses are likely to share substantial similarities, but are unlikely to exhibit common features with leaves in seed plants, ferns and horsetails. They also suggest that fundamental features of land plants, such as the spore-bearing organs, stems, stomates and sexual organs, are each under the same kind of developmental control in all main groups. To explore these issues further, data are needed on the molecular basis of plant development from a broader selection of land plants than are currently under study. In the context of a more complete understanding of plant diversity than that provided by living plants alone, such data should be expected to confirm the underlying unity and relative simplicity of developmental processes in land plants. □

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1. Banks, H. P. Reclassification of Psilophyta. *Taxon* **24**, 401–413 (1975).
2. Chaloner, W. G. & Sheerin, A. in *The Devonian System* (eds House, M. R., Scrutton, C. T. & Bassett, M. G.) 145–161 (The Palaeontological Association, London, 1979).
3. Gray, J. Major Paleozoic land plant evolutionary bio-events. *Palaeogeog. Palaeoclimatol. Palaeocol.* **104**, 153–169 (1993).
4. Graham, L. E. *Origin of Land Plants* (Wiley, New York, 1993).
5. Mishler, B. D. *et al.* Phylogenetic relationships of the "green algae" and "bryophytes". *Ann. MO Bot. Gard.* **81**, 451–483 (1994).
6. Manhart, J. R. & Palmer, J. G. The gain of two chloroplast tRNA introns marks the green algal ancestors of land plants. *Nature* **345**, 268–270 (1990).
7. Manhart, J. R. Phylogenetic analysis of green plant *rbc*L sequences. *Mol. Phylogenet. Evol.* **3**, 114–127 (1994).
8. Raubeson, L. A. & Jansen, R. K. Chloroplast DNA evidence on the ancient evolutionary split in vascular land plants. *Science* **255**, 1697–1699 (1992).
9. Chapman, R. L. & Buchheim, M. A. Ribosomal RNA gene sequences: analysis and significance in the phylogeny and taxonomy of green algae. *Crit. Rev. Plant Sci.* **10**, 343–368 (1991).
10. McCourt, R. M., Karol, K. G., Guerlesquin, M. & Feist, M. Phylogeny of extant genera in the family Characeae (Charales, Charophyceae) based on *rbc*L sequences and morphology. *Am. J. Bot.* **83**, 125–131 (1996).
11. Pryer, K. M., Smith, A. R. & Skog, J. E. Phylogenetic relationships of extant ferns based on evidence from morphology and *rbc*L sequences. *Am. Fern J.* **85**, 205–282 (1995).
12. Kranz, H. D. *et al.* The origin of land plants: phylogenetic relationships among charophytes, bryophytes, and vascular plants inferred from complete small-subunit ribosomal RNA gene sequences. *J. Mol. Evol.* **41**, 74–84 (1995).
13. Kranz, H. D. & Huss, V. A. R. Molecular evolution of pteridophytes and their relationships to seed plants: evidence from complete 18S rRNA gene sequences. *Plant Syst. Evol.* **202**, 1–11 (1996).
14. Hiesel, R., von Haeseler, A. & Brennicke, A. Plant mitochondrial nucleic acid sequences as a tool for phylogenetic analysis. *Proc. Natl Acad. Sci. USA* **91**, 634–638 (1994).
15. Edwards, D., Davies, K. L. & Axe, L. A vascular conducting strand in the early land plant *Cooksonia*. *Nature* **357**, 683–685 (1992).
16. Edwards, D., Duckett, J. G. & Richardson, J. B. Hepatic characters in the earliest land plants. *Nature* **374**, 635–636 (1995).
17. Fanning, U., Edwards, D. & Richardson, J. B. A diverse assemblage of early land plants from the Lower Devonian of the Welsh Borderland. *Bot. J. Linn. Soc.* **109**, 161–188 (1992).
18. Kenrick, P. Alternation of generations in land plants: new phylogenetic and morphological evidence. *Biol. Rev.* **69**, 293–330 (1994).
19. Kenrick, P. & Crane, P. R. Water-conducting cells in early fossil land plants: implications for the early evolution of tracheophytes. *Bot. Gaz.* **152**, 335–356 (1991).
20. Remy, W. Gensel, P. G. & Hass, H. The gametophyte generation of some early Devonian land plants. *Int. J. Plant Sci.* **154**, 35–58 (1993).
21. Remy, W. & Hass, H. New information on gametophytes and sporophytes of *Aglaophyton major* and inferences about possible environmental adaptations. *Rev. Palaeobot. Palynol.* **90**, 175–194 (1996).
22. Remy, W., Taylor, T. N., Hass, H. & Kerp, H. Four hundred-million-year-old vesicular arbuscular mycorrhizae. *Proc. Nat Acad. Sci. USA* **91**, 11841–11843 (1994).
23. Stein, W. E., Harmon, G. D. & Hueber, F. M. in *International Workshop on the Biology and Evolutionary Implications on Early Devonian Plants* (Westfälische Wilhelms-Universität Münster, Germany, 1994).
24. Taylor, T. N. & Osborne, J. M. The importance of fungi in shaping the paleoecosystem. *Rev. Palaeobot. Palynol.* **90**, 249–262 (1996).
25. Taylor, W. A. Ultrastructure of lower Paleozoic dyads from southern Ohio. *Rev. Palaeobot. Palynol.* **92**, 269–280 (1996).
26. Kenrick, P. & Crane, P. R. *The Origin and Early Diversification of Land Plants: A Cladistic Study* (Smithsonian Institution Press, Washington DC, 1997).
27. Gray, J. The microfossil record of early land plants: advances in understanding of early terrestrialization, 1970–1984 *Phil. Trans. R. Soc. Lond. B* **309**, 167–195 (1985).
28. Gray, J. & Boucot, A. J. Early vascular land plants: proof and conjecture. *Lethaia* **10**, 145–174 (1977).
29. DiMichele, W. A. *et al.* in *Terrestrial Ecosystems Through Time: Evolutionary Paleoecology of Terrestrial Plants and Animals* (ed. Behrensmeyer, A. K.) 205–325 (Univ. Chicago Press, 1992).
30. Fanning, U., Richardson, J. B. & Edwards, D. in *Pollen and Spores* (eds Blackmore, S. & Barnes, S. H.) 25–47 (Clarendon, Oxford, 1991).
31. Kroken, S. B., Graham, L. E. & Cook, M. E. Occurrence and evolutionary significance of resistant cell walls in charophytes and bryophytes. *Am. J. Bot.* **83**, 1241–1254 (1996).
32. Wellman, C. H. & Richardson, J. B. Sporomorph assemblages from the 'Lower Old Red Sandstone' of Lorne, Scotland. *Special Papers Palaeontol.* **55**, 41–101 (1996).
33. Edwards, D. in *Palaeozoic Palaeogeography and Biogeography* (eds McKerrow, W. S. & Scotese, C. R.) 233–242 (Geological Society, London, 1990).
34. Morel, E., Edwards, D. & Iñiquez Rodriguez, M. The first record of *Cooksonia* from South America in the Silurian rocks of Bolivia. *Geol. Mag.* **132**, 449–452 (1995).
35. Tims, J. D. & Chambers, T. C. Rhyniophytina and Trimerophytina from the early land flora of Victoria, Australia. *Palaeontology* **27**, 265–279 (1984).
36. Cai, C.-Y., Dou, Y.-W. & Edwards, D. New observations on a Pridoli plant assemblage from north Xinjiang, northwest China, with comments on its evolutionary and palaeographical significance. *Geol. Mag.* **130**, 155–170 (1993).
37. Hueber, F. M. Thoughts on the early lycopsids and zosterophylls. *Ann. MO Bot. Gard.* **79**, 474–499 (1992).
38. Cai, C. *et al.* An early Silurian vascular plant. *Nature* **379**, 592 (1996).
39. Geng, B.-Y. Anatomy and morphology of *Pinnatiramosus*, a new plant from the Middle Silurian (Wenlockian) of China. *Acta Bot. Sin.* **28**, 664–670 (1986).
40. Raymond, A. & Metz, C. Laurussian land-plant diversity during the Silurian and Devonian: mass extinction, sampling bias, or both? *Paleobiology* **21**, 74–91 (1995).
41. Edwards, D. & Davies, M. S. in *Major evolutionary radiations* (eds Taylor, P. D. & Larwood, G. P.) 351–376 (Clarendon, Oxford, 1990).
42. Knoll, A. H., Niklas, K. J., Gensel, P. G. & Tiffney, B. H. Character diversification and patterns of evolution in early vascular plants. *Paleobiology* **10**, 34–47 (1984).
43. Gensel, P. G. & Andrews, H. N. *Plant Life in the Devonian* (Praeger, New York, 1984).

44. Taylor, T. N. & Taylor, E. L. *The Biology and Evolution of Fossil Plants* (Prentice Hall, New Jersey, 1993).
45. Schweitzer, H.-J. Die Unterdevonflora des Rheinlandes. *Palaeontographica B* **189,** 1–138 (1983).
46. Gerrienne, P. Inventaire des végétaux éodévoniens de Belgique. *Ann. Soc. Géol. Belg.* **116,** 105–117 (1993).
47. Tappan, H. N. *The Paleobiology of Plant Protists* (Freeman, San Francisco, 1980).
48. Raven, J. Plant responses to high O_2 concentrations: relevance to previous high O_2 episodes. *Palaeogeogr. Palaeoclimatol. Palaeocol.* **97,** 19–38 (1991).
49. Sztein, A. E., Cohen, J. D., Slovin, J. P. & Cooke, T. J. Auxin metabolism in representative land plants. *Am. J. Bot.* **82,** 1514–1521 (1995).
50. Edwards, D. New insights into early land ecosystems: a glimpse of a Lilliputian world. *Rev. Palaeobot. Palynol.* **90,** 159–174 (1996).
51. Edwards, D., Fanning, U. & Richardson, J. B. Stomata and sterome in early land plants. *Nature* **323,** 438–440 (1986).
52. Raven, J. A. Comparative physiology of plant and arthropod land adaptation. *Phil. Trans. R. Soc. Lond. B* **309,** 273–288 (1985).
53. Raven, J. A. The evolution of vascular plants in relation to quantitative functioning of dead water-conducting cells and stomata. *Biol. Rev.* **68,** 337–363 (1993).
54. Niklas, K. J. *Plant Allometry: The Scaling of Form and Process.* (Univ. Chicago Press, 1994).
55. Beerbower, R. in *Geological Factors and the Evolution of Plants* (ed. Tiffney, B. H.) 47–92 (Yale Univ. Press, New Haven, CT, 1985).
56. Berner, R. A. GEOCARB II: a revised model of atmospheric CO_2 over Phanerozoic time. *Am. J. Sci.* **294,** 56–91 (1994).
57. Mora, C. I., Driese, S. G. & Colarusso, L. A. Middle to Late Paleozoic atmospheric CO_2 levels from soil carbonate and organic matter. *Science* **271,** 1105–1107 (1996).
58. Algeo, T. J., Berner, R., Maynard, J. B. & Scheckler, S. E. Late Devonian oceanic anoxic events and biotic crises: "rooted" in the evolution of vascular land plants? *GSA Today* **5,** 45, 64–66 (1995).
59. Retallack, G. J. in *Paleosols: their Recognition and Interpretation* (ed. Wright, V. P.) (Blackwell, Oxford, 1986).
60. Knoll, A. H. The early evolution of eukaryotes: a geological perspective. *Science* **256,** 622–627 (1992).
61. Bengtson, S. (ed) *Early life on Earth.* (Columbia Univ. Press, New York, 1994).
62. Taylor, T. N., Hass, H., Remy, W. & Kerp, H. The oldest fossil lichen. *Nature* **378,** 244 (1995).
63. Hemsley, A. R. in *Ultrastructure of Fossil Spores and Pollen* (eds Kurmann, M. H. & Doyle, J. A.) 1–21 (Royal Botanic Gardens, Kew, 1994).
64. Hueber, F. M. in *International Workshop on the Biology and Evolutionary Implications of Early Devonian Plants* (Westfälische Wilhelms-Universität, Münster, 1994).
65. Simon, L., Bousquet, J., Léveque, C. & Lalonde, M. Origin and diversification of endomycorrhizal fungi with vascular plants. *Nature* **363,** 67–69 (1993).
66. Selden, P. A. & Edwards, D. in *Evolution and the Fossil Record* (eds Allen, K. C. & Briggs, D. E. G.) 122–152 (Belhaven, London, 1989).
67. Gray, J. & Shear, W. Early life on land. *Am. Sci.* **80,** 444–456 (1992).
68. Gray, J. & Boucot, A. J. Early Silurian nonmarine animal remains and the nature of the early continental ecosystem. *Acta Palaeontol. Pol.* **38,** 303–328 (1994).
69. Retallack, G. J. & Feakes, C. R. Trace fossil evidence for Late Ordovician animals on land. *Science* **235,** 61–63 (1987).
70. Scott, A. C., Stephenson, J. & Chaloner, W. G. Interaction and coevolution of plants and arthropods during the Palaeozoic and Mesozoic. *Phil. Trans. R. Soc. Lond. B* **336,** 129–165 (1992).
71. Banks, H. P. & Colthart, B. J. Plant-animal-fungal interactions in early Devonian trimerophytes from Gaspé, Canada. *Am. J. Bot.* **80,** 992–1001 (1993).
72. Edwards, D., Seldon, P. A., Richardson, J. B. & Axe, L. Coprolites as evidence for plant-animal interaction in Siluro-Devonian terrestrial ecosystems. *Nature* **377,** 329–331 (1995).
73. Allen, J. R. L. Marine to fresh water: the sedimentology of the interrupted environmental transition (Ludlow-Siegenian) in the Anglo-Welsh region. *Phil. Trans. R. Soc. Lond. B* **309,** 85–104 (1985).
74. Melkonian, M. & Surek, B. Phylogeny of the Chlorophyta: congruence between ultrastructural and molecular evidence. *Bull. Soc. Zool. Fr.* **120,** 191–208 (1995).
75. Bremer, K., Humphries, C. J., Mishler, B. D. & Churchill, S. P. On cladistic relationships in green plants. *Taxon* **36,** 339–349 (1987).
76. Garbary, D. J., Renzaglia, K. S. & Duckett, J. G. The phylogeny of land plants: a cladistic analysis based on male gametogenesis. *Plant Syst. Evol.* **188,** 237–269 (1993).
77. Capesius, I. A molecular phylogeny of bryophytes based on the nuclear encoded 18S rRNA genes. *J. Plant Physiol.* **146,** 59–63 (1995).
78. Taylor, T. N. The origin of land plants: some answers, more questions. *Taxon* **37,** 805–833 (1988).
79. Rothwell, G. W. in *Pteridiology in Perspective* (eds Camus, J. M., Gibby, M. & Johns, R. J.) (Royal Botanic Gardens, Kew) (in the press).
80. Albert, V. A. *et al.* Functional constraints and *rbc*L evidence for land plant phylogeny. *Ann. MO Bot. Gard.* **81,** 534–567 (1994).
81. Edwards, D., Fanning, U. & Richardson, J. B. Lower Devonian coalified sporangia from Shropshire: *Salopella* Edwards & Richardson and *Tortilicaulis* Edwards. *Bot. J. Linn. Soc.* **116,** 89–110 (1994).
82. Bateman, R. M., DiMichele, W. A. & Willard, D. A. Experimental cladistic analysis of anatomically preserved lycopsids from the Carboniferous of Euramerica: an essay on paleobotanical phylogenetics. *Ann. MO Bot. Gard.* **79,** 500–559 (1992).
83. Feist, M. & Grambast-Fessard, N. in *Calcareous Algae and Stromatolites* (ed. Riding, R.) 189–203 (Springer, Berlin, 1991).
84. Hébant, C. in *Bryophyte Systematics* (eds Clarke, G. C. S. & Duckett, J. G.) 365–383 (Academic, London, 1984).