The relationships of vascular plants

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Recent phylogenetic research indicates that vascular plants evolved from bryophyte-like ancestors and that this involved extensive modifications to the life cycle. These conclusions are supported by a range of systematic data, including gene sequences, as well as evidence from comparative morphology and the fossil record. Within vascular plants, there is compelling evidence for two major clades, which have been termed lycophytes (clubmosses) and euphyllophytes (seed plants, ferns, horsetails). The implications of recent phylogenetic work are discussed with reference to life cycle evolution and the interpretation of stratigraphic inconsistencies in the early fossil record of land plants. Life cycles are shown to have passed through an isomorphic phase in the early stages of vascular plant evolution. Thus, the gametophyte generation of all living vascular plants is the product of massive morphological reduction. Phylogenetic research corroborates earlier suggestions of a major representational bias in the early fossil record. Mega-fossils document a sequence of appearance of groups that is at odds with that predicted by cladogram topology. It is argued here that the pattern of appearance and diversification of plant megafossils owes more to changing geological conditions than to rapid biological diversification.

Keywords: vascular plant; bryophyte; phylogeny; life cycle

1. INTRODUCTION

The development of a robust phylogenetic framework for vascular plants is widely perceived as crucial to addressing a raft of important issues concerning the origins of the terrestrial flora, life cycle evolution and morphogenesis in plants. Recent work has shown that the relationships of vascular plants must be evaluated within the broader context of land plants as a whole. Yet, deep phylogenetic questions such as these are difficult to resolve, not least because the early evolution of the land flora took place over 400 Myr ago (Late Silurian–Early Devonian). Numerous phylogenetic hypotheses have been proposed, giving rise to a bewildering diversity of ideas, some of which are reflected in current taxonomic practice (Kenrick & Crane 1997*a*). One of the legacies of this chequered systematic history is the broad acceptance of a classification that groups land plants into two categories, termed 'vascular plants' (tracheophytes) and 'bryophytes'. All land plants can be classified into one of these groups on the basis of their life cycles and the extent to which the diploid spore-bearing (sporophyte) and haploid gamete-bearing (gametophyte) phases develop. Bryophytes possess a small, parasitic sporophyte, which is little more than a simple sporangium, borne on a larger, thalloid or leafy gametophyte. The life cycle of vascular plants is the antithesis of that in bryophytes. Here the sporophyte is independent, morphologically complex and frequently a very large organism. These striking differences in life history create additional problems for phylogenetics by obscuring the crucial morphological comparisons necessary for constructing a robust phylogenetic tree. This difficulty is further exacerbated by the even larger disjunction between land plants and their closest relatives in the green algae (Charophyceae).

Remarkable developments in phylogenetics over the past 20 years are beginning to resolve some of these seemingly insoluble problems and have brought the remaining critical questions into much sharper focus. It is clear now that all land plants share a common terrestrial origin and that vascular plants probably are—in an important evolutionary sense—just 'bryophytes' with a highly modified life history.

This new perspective on the evolution of vascular plants and bryophytes has emerged from several decades of phylogenetic research. Key developments include the application of transmission electron microscopy (TEM) to the study of cell ultrastructure and cell division in green algae and land plants (Mattox & Stewart 1984; Pickett-Heaps & Marchant 1972; Stewart & Mattox 1975). These data cut across insuperable difficulties at the cellular level to give a truly comparable subcellular data set from green algae to gymnosperms. The application of cladistic methods has also had a major impact through the development of a rational and explicit way of choosing among competing phylogenies. Using a cladistic approach, Mishler & Churchill (1984, 1985) showed that the diverse data of comparative morphology are most simply explained by a hypothesis of land plant monophyly. Controversially, this analysis indicated that mosses are more closely related to vascular plants than they are to liverworts. In other words, bryophytes are a paraphyletic group. More recently, molecular data on gene sequences and genome structure have provided a wealth of new information from chloroplast, mitochondrion and nucleus (Crowe *et al.* 1997; Duff & Nickrent 1999; Hedderson *et al.* 1998; Kranz *et al.* 1995; Lewis *et al.* 1997; Malek *et al.* 1996; Mishler *et al.* 1994; Nishiyama & Kato 1999; Qiu *et al.* 1998). Results corroborate the paraphyly of bryophytes, but they are less clear about the relationships
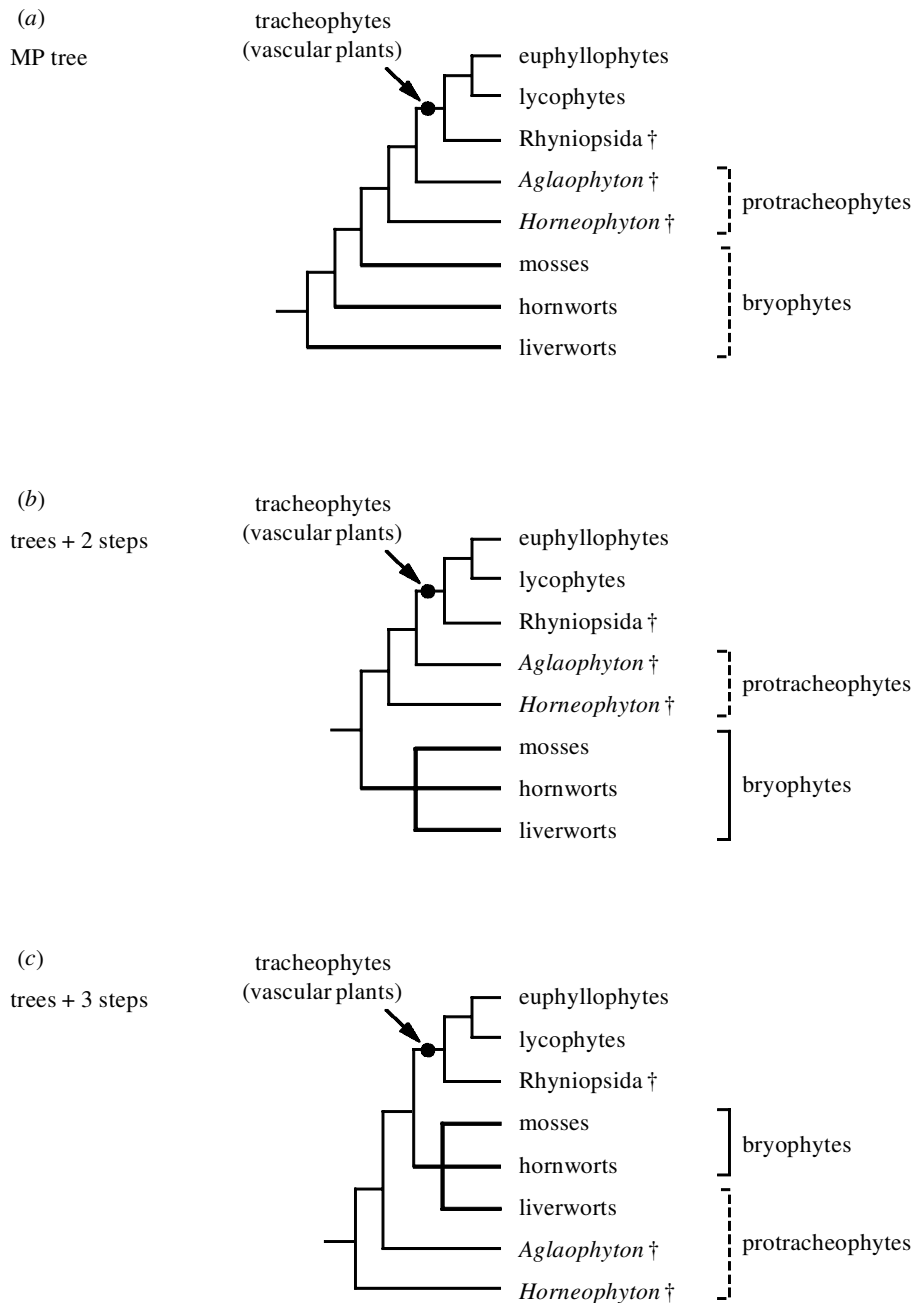
(*a*)

MP tree

tracheophytes
(vascular plants)

― euphyllophytes
― lycophytes
― Rhyniopsida †
― *Aglaophyton* †
― *Horneophyton* †
― mosses
― hornworts
― liverworts

protracheophytes

bryophytes

(*b*)

trees + 2 steps

tracheophytes
(vascular plants)

― euphyllophytes
― lycophytes
― Rhyniopsida †
― *Aglaophyton* †
― *Horneophyton* †
― mosses
― hornworts
― liverworts

protracheophytes

bryophytes

(*c*)

trees + 3 steps

tracheophytes
(vascular plants)

― euphyllophytes
― lycophytes
― Rhyniopsida †
― mosses
― hornworts
― liverworts
― *Aglaophyton* †
― *Horneophyton* †

bryophytes

protracheophytes

Figure 1. Summary cladograms of relationships among basal land plants from the phylogenetic study of living and fossil species by Kenrick & Crane (1997*a*). † = extinct taxon. (*a*) Most parsimonious (MP) tree showing bryophytes paraphyletic to vascular plants. Early megafossils fall into the vasular plant stem group. (*b*) Trees two steps longer than the most parsimonious tree resolved bryophytes as a monophyletic and sister group to vascular plants. (*c*) Trees three steps longer than the most parsimonious tree resolved protracheophytes as paraphyletic to bryophytes and vascular plants.

of various bryophyte groups to vascular plants. This paper reviews recent phylogenetic developments and examines some of their consequences for life cycle evolution and the interpretation of stratigraphic patterns in the early fossil record of land plants.

2. PHYLOGENETIC OVERVIEW

(a) *Vascular plants and bryophytes*

One of the key phylogenetic questions in plant systematics is the nature of the relationship between vascular plants and the other major living groups of land plants, collectively termed bryophytes (i.e. liverworts,

hornworts, mosses). The first detailed cladistic analysis of this problem was based on the comparative morphology of living species (Mishler & Churchill 1984, 1985). Results indicated that whereas these four groups are monophyletic, some bryophytes (i.e. mosses) are more closely related to vascular plants than they are to other bryophytes (Mishler & Churchill 1984, 1985; figure 1). Specifically, this controversial result implied that mosses and vascular plants share a common ancestor with a bryophyte-like life history and that there has been a major shift in life cycle from gametophyte-dominated to sporophyte-dominated in the lineage leading to vascular plants. Subsequent phylogenetic studies based on comparative morphology,

gene sequences and genomic structure continue to favour paraphyly of bryophytes, but there is as yet no consensus on the precise nature of the relationships among these four major plant groups.

A moss + vascular plant clade is supported by several morphological analyses of living and fossil plants (Kenrick & Crane 1997*a,b*; Mishler & Churchill 1984, 1985; figure 1) and studies that have integrated morphology with data on 18S and 26S rRNA sequences (Mishler *et al*. 1994). However, the chloroplast gene *rbcL* favours a hornwort + vascular plant clade (Lewis *et al*. 1997). Both hypotheses are consistent with the distribution of three mitochondrial group II introns sampled across a wide range of land plants (Qiu *et al*. 1998). These data support the hypothesis that liverworts are either a sister group to all other land plants or perhaps a basal paraphyletic assemblage. A third pattern resolves vascular plants as a sister group to a moss + liverwort clade. This hypothesis is consistent with evidence from male gamete development and ultrastructure (Garbary & Renzaglia 1998), as well as analyses based on gene sequences from the nucleus (18S rRNA; Hedderson *et al*. 1996) and the mitochondrion (19Sr DNA; Duff & Nickrent 1999). This pattern also receives support from a recent analysis based on several plastid genes (*rbcL*, *psaA*, *psaB*, *psbD*, *rpoC2*; Nishiyama & Kato 1999).

Support for these hypotheses, as measured by bootstrap and decay indices, is generally comparatively low, and alternative topologies are only marginally less parsimonious. Based on mitochondrial *cox3* sequences, Malek *et al*. (1996) resolved hornworts as basal in embryophytes, but the relationships of liverworts, mosses and vascular plants had very low support. Data on spermatogenesis and sperm ultrastructure indicate that bryophytes are monophyletic (Garbary *et al*. 1993; Maden *et al*. 1997), but sampling is comparatively sparse and there is concern about character independence in some data domains (e.g. the ultrastructure of the spermatozoid flagellum). Recoding of the Garbary *et al*. (1993) data by Mishler *et al*. (1994) and Garbary & Renzaglia (1998) produced a tree topology that is consistent with bryophyte paraphyly.

The absence of consensus among data sets and the generally low levels of support for alternative phylogenetic hypotheses are most likely a consequence of several problems that emerge at this phylogenetic level in plants. First, the cladogenic events that led to the evolution of these groups occurred between 470 and 400 Myr ago (Kenrick & Crane 1997*b*). The interval of time spanning group divergence is short in comparison with the length of time between these events and the present. In other words, phylogenetic methods are likely to perform poorly because of imbalance in branch length (i.e. short internal branches combined with long terminal branches, see Felsenstein 1978; Huelsenbeck 1995). Second, the great differences between comparable phases of the bryophyte and vascular plant life cycle create difficulties in identifying homologies for morphological analyses. The absence of a fossil record of stem group mosses, liverworts and hornworts exacerbates this problem (Kenrick & Crane 1997*a*). Third, in morphological analyses, rooting the tree and character polarity are problematic because of the comparatively large gap between land plants and their closest relatives in the green algae (Charophyceae). There are enormous differences between the gametophytes of land plants and those of the charophycean algae. Also, sporophytes are absent from charophycean algae, and there is no compelling fossil evidence for stem group land plants (Kenrick & Crane 1997*a*). A consequence of these life cycle differences is that sporophyte characteristics cannot be polarized in basal land plants. One approach to addressing these problems is to add aditional data (Poe & Swofford 1999), and there is evidence that combining data from different molecular studies will provide a more robust solution (Mishler *et al*. 1994; Nishiyama & Kato 1999). A second approach is to add additional taxa and to break up long branches (Swofford *et al*. 1996). This would be achieved most effectively through the better documentation of fossil bryophytes from the Palaeozoic.

(b) *Rhyniophytes and basal vascular plants*

There is almost universal support for monophyly of the vascular plants crown group (i.e. the clade containing all living species: euphyllophytes + lycophytes; figure 1). Moderate to high bootstrap support has been reported from the analysis of 18S rRNA (Hedderson *et al*. 1998; Kranz & Huss 1996), and the mitochondrial 19S rDNA (Duff & Nickrent 1999) and *cox3* (Malek *et al*. 1996) genes. Monophyly is supported by data on the ultrastructure and development of the male gamete (Garbary & Renzaglia 1998) and from general comparative morphology (Kenrick & Crane 1997*a*; Stevenson & Loconte 1996). Analyses based on the chloroplast gene *rbcL* do not resolve vascular plants as monophyletic (Manhart 1994). The *rbcL*-based analyses, however, provide highly incongruent results with little bootstrap support among basal groups. It seems likely that the noise-to-signal ratio for *rbcL* is extremely high at this level in land plants (Manhart 1994).

Inclusion of fossils indicates that the extinct Rhyniophytina (Banks 1992; Edwards & Edwards 1986) are a grade of organization comprising stem group vascular plants ('protracheophytes') as well as probable basal members of the crown group (Kenrick & Crane 1997*a*; figure 1). Monophyly of the stem-based group is supported in morphological cladistic analyses, indicating that structures such as the tracheid are homologous in vascular plants. Marginally less parsimonious topologies would be consistent with the rooting of certain bryophyte groups within the vascular plant stem-based group (figure 1). In other words, the evolution of mosses from protracheophytes through, among other things, loss of sporophyte branching is consistent with trees three steps longer than the most parsimonious tree. Note, however, that this type of relationship is also consistent with monophyly of the vascular plant crown group and is therefore detectable only in analyses that include fossils (Kenrick & Crane 1997*a*).

(c) *Lycophytes and euphyllophytes*

In vascular plants, the weight of evidence from comparative morphology, gene sequences and data on genome structure favours lycophytes as sister group to a clade comprising all other living vascular plants (euphyllophytes; figure 1). Lycophytes are consistently resolved as sister group to euphyllophytes based on nuclear (18S rRNA, Kranz & Huss 1996) and mitochondrial (19S

rDNA, Duff & Nickrent 1999; *cox3*, Malek *et al*. 1996) gene sequences. The euphyllophyte clade is also strongly corroborated by a 30 kb inversion in the chloroplast genome, which is absent from lycophytes and liverworts (Raubeson & Jansen 1992). Furthermore, there is strong support from comparative morphology for this topology, particularly from studies that include fossils (Kenrick & Crane 1997*a,b*; Stevenson & Loconte 1996).

Conflicting data from other gene sequences generally exhibit low bootstrap support on the critical basal branches and they are mutually contradictory. The *rbcL* gene resolves lycophytes as sister group to seed plants (Manhart 1994; Wikström & Kenrick 1997), but support for this relationship and consistency indices are very low. In an analysis of relationships among pteridophytes, the chloroplast *atpB* sequence resolved lycophytes as polyphyletic (Wolf 1997). This result is highly unparsimonious with respect to comparative morphology and is not supported by other molecular data. *Selaginella* was placed sister group to all other vascular plants, but *Huperzia* and *Isoetes* grouped within ferns. Combining *atpB* and *rbcL* for pteridophytes placed *Selaginella* within ferns, and a *Huperzia + Isoetes* clade as sister group to ferns (Wolf 1997). In view of the behaviour of lycophytes in *rbcL* data sets, inclusion of seed plant sequences in this combined analysis may well have had a significant affect on tree topology.

Relationships among basal living and fossil euphyllophytes are still rather poorly resolved. Living groups such as leptosporangiate ferns, Ophioglossales, Marattiales, *Equisetum* and seed plants are clearly monophyletic (Doyle 1998; Kenrick & Crane 1997*a*; Pryer *et al*. 1995; Rothwell & Serbet 1994; Vangerow *et al*. 1999), but the bootstrap support for relationships among these groups in sequence-based studies is generally low (Duff & Nickrent 1999; Hedderson *et al*. 1998; Kranz & Huss 1996; Malek *et al*. 1996; Pahnke *et al*. 1996; Pryer *et al*. 1995; Wolf 1997) and critical taxa are frequently missing. No consistent pattern has yet emerged. Duff & Nickrent (1999) resolved a well-supported fern + *Equisetum* clade as sister group to seed plants, in agreement with one fossil-based cladistic analysis (Kenrick & Crane 1997*a*). But the sample of leptosporangiate ferns was based on a single species of *Polypodium*, and Marattiales and *Psilotum* were absent from the analysis. The basal groups of living euphyllophytes are morphologically quite divergent, and phylogenetic studies based on the comparative morphology of living species show that there are comparatively few characteristics supporting tree topology (Stevenson & Loconte 1996). This study placed *Equisetum* sister group to a clade comprising leptosporangiate ferns, eusporangiate ferns and seed plants, a result that is consistent with at least one cladistic analysis that includes fossils (Rothwell 1996).

Consideration of fossil evidence from the Late Palaeozoic underlines further basic similarities among these diverse living groups. The seed plant stem group contains plants (progymnosperms) with some of the wood and branching characteristics of seed plants, but which retain the plesiomorphic free-sporing life cycle. Other key fossil groups include cladoxylopsids and zygopterids. These two groups are widely thought to be related to ferns and *Equisetum*, although the precise nature of this relationship remains unresolved (Stein *et al*. 1984). One fossil-based cladistic analysis has found support for this hypothesis

(Kenrick & Crane 1997*a*). Controversially, Rothwell (1996) found cladoxylopsids and zygopterids to be more closely related to seed plants than to either ferns or *Equisetum*. The prospects of resolving this issue are comparatively good, because of the excellent fossil record of these groups. Further detailed work on the morphology of Late Palaeozoic plants is required, in particular the reconstruction of whole plants.

(d) *The problematic* Psilotum *and* Tmesipteris

One group that figures prominently in higher-level phylogenetic studies of vascular plants is the Psilotaceae: a group comprising some 15 species of fern-like plants classified into two genera, *Psilotum* and *Tmesipteris*. Psilotaceae are problematic, and in the recent literature there have been two very different interpretations of the relationships and hence the evolution of the group. The problem revolves around how to interpret the simple sporophyte and gametophyte morphology. The simplicity of these plants has been interpreted as plesiomorphic and they have been compared with the simple sporophytes of early fossil vascular plants (e.g. *Rhynia*). Under this hypothesis, these relicts from the Devonian Period should emerge as sister group to all other vascular plants (Bremer 1985). However, Gensel (1977, 1992) has pointed out that there are few unequivocal characters linking Psilotaceae to rhyniophytes or trimerophytes. An alternative hypothesis views the morphological simplicity of Psilotaceae as a product of reduction, perhaps related to the epiphytic habit, which is typical of many species. Based on a detailed comparative study of gametophyte and sporophyte Bierhorst (1977) argued that Psilotaceae are closely related to leptosporangiate ferns, specifically *Stromatopteris* (Gleicheniaceae). Although aspects of this hypothesis have been criticized, in particular the formulation of homologies in the stem/leaf system (Kaplan 1977), there are similarities between Psilotaceae and several basal groups in ferns in general (Kenrick & Crane 1997*a*; Pryer *et al*. 1995; Stevenson & Loconte 1996). Molecular data provide compelling evidence that Psilotaceae are related to basal euphyllophytes. Psilotaceae share a 30 kb inversion in the chloroplast genome that is unique to the euphyllophyte clade (Raubeson & Jansen 1992). 18S rRNA sequences group *Psilotum* in basal euphyllophytes (Kranz & Huss 1996). More specifically, a close relationship between Psilotaceae and Ophioglossales is supported by data from three chloroplast gene sequences (*rbcL*, Manhart 1994; 16S rDNA, Manhart 1995; *atpB*, Wolf 1997) and the mitochondrial *cox3* (Malek *et al*. 1996) and *nad5* genes (Vangerow *et al*. 1999).

3. VASCULAR PLANTS AS BRYOPHYTES

Even though many details of land plant phylogeny remain unresolved, it is clear that bryophytes and vascular plants are very closely related indeed. The weight of evidence favours a single origin of land plants and implies that vascular plants *are* bryophytes with a highly modified life history. This result has far-reaching consequences for interpreting land plant morphology. It implies that the major features shared by most land plants (e.g. multicellular gametangia, diplobiontic life cycle, stomates, sporangium) originated from a common
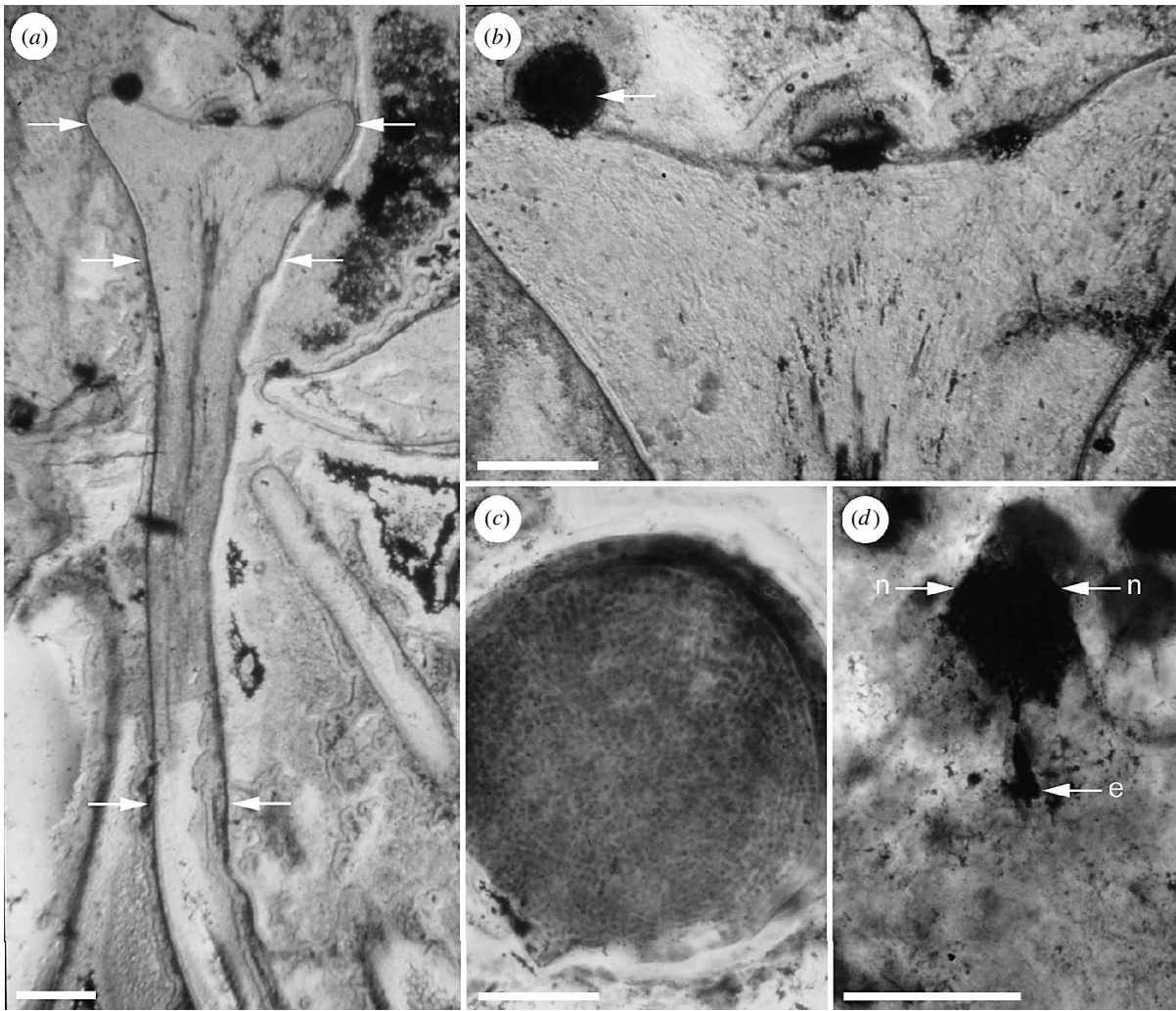
Figure 2. Exceptionally well-preserved silicified fossil gametophytes of stem group vascular plants from the 400 Myr old Rhynie chert, Scotland (courtesy W. Remy and H. Hass, Westfälische Wilhelms-Universität, Münster). (*a*) Terminal part of gametophytic axis of *Lyonophyton rhyniensis* comprising slender axis (lower pair arrows) terminating in expanded gametangiophore (upper pair arrows) (scale = 1 mm). (*b*) Details of upper surface of gametangiophore from (*a*) bearing spherical antheridium (arrow) (scale = 500 μm). (*c*) Transverse section of antheridium of *L. rhyniensis* showing details of spermatid mother cells (scale = 100 μm). (*d*) Archegonium of *Langiophyton mackiei* showing neck (arrows, n) and egg chamber (arrow, e) (scale = 100 μm).

ancestor and that any differences observed today are the result of divergent evolution. In other words, similarities among major groups are not the result of convergence on a similar set of adaptations to life on land, rather they result from a common ancestry. We should therefore expect substantial similarities at the molecular developmental level between organ systems in bryophytes and their homologues in vascular plants (Kenrick & Crane 1997*b*). This prediction is currently untested.

Among living plants, life cycles have been used as a basis for distinguishing vascular plants from bryophytes, but this clear distinction breaks down in the early fossil record. The diploid (sporophyte) phase of the vascular plant life cycle is much more highly differentiated and larger than the equivalent phase in liverworts and mosses. The origin of these differences can be traced through a series of extinct morphological intermediates (Kenrick 1994; Remy *et al.* 1993; Remy & Hass 1996). Palaeobotanical data show that the early vascular plant sporophytes resemble much more closely the bryophyte model (Edwards *et al.* 1995; Raven 1985, 1993, 1995). Protracheo-

phyte sporophytes are of a similar size and level of tissue differentiation to the larger mosses. Other similarities include the absence of leaves and the presence of simple terminal sporangia (Edwards 1993, 1996; Edwards *et al.* 1995; Fanning *et al.* 1992). With these data in mind, it is possible to recognize several key developments that were prerequisite to the divergence and subsequent diversification of the vascular plant sporophyte: (i) the development of apical growth leading inevitably to indeterminate growth, sporophytic branching and the multiplication of parts; (ii) escape from nutritional dependence on the gametophyte (loss of sporophytic parasitism); and (iii) differentiation of various tissue systems for biomechanical support (Kenrick & Crane 1997*a,b*; Niklas 1994, 1997; Speck & Vogellehner 1991, 1994).

In contrast to the sporophyte, the haploid (gametophyte) phase of the vascular plant life cycle is much smaller and generally less well-differentiated than the equivalent phase in bryophytes. In seed plants, the gametophyte is minute, and it is nutritionally dependent on the sporophyte. In some groups of ferns and fern allies, it is
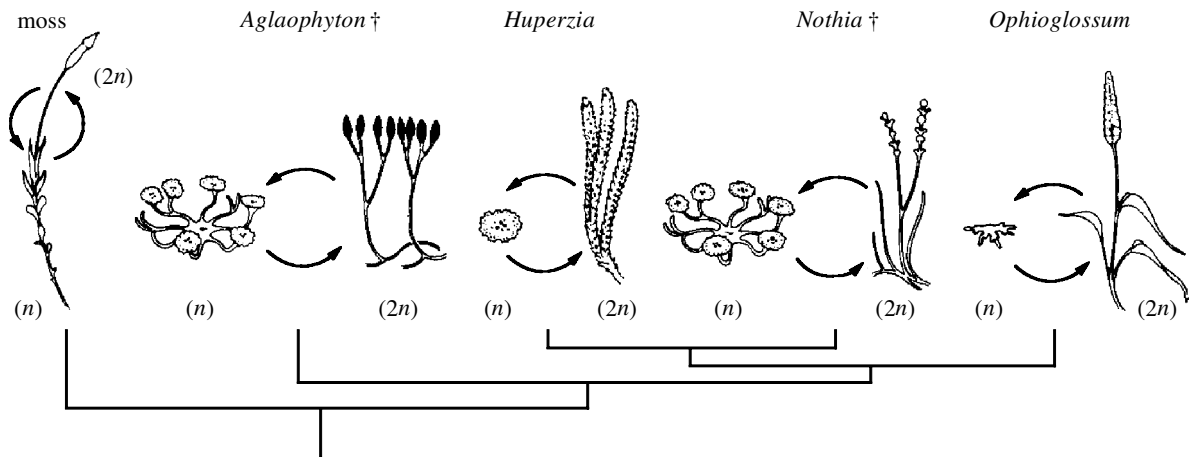
Figure 3. Hypothesis of life cycle evolution in basal vascular plants. † = extinct taxon. Evidence from phylogeny and the fossil record indicates that the vascular plant life cycle evolved from a bryophytic life cycle in which the sporophyte ($2n$) is parasitic on the gametophyte (n). There was a transitional phase (now extinct) in which the life cycle was more or less isomorphic (here represented by the extinct plants *Aglaophyton* and *Nothia*). The gametophytes of modern vascular plants are highly reduced, but groups such as Lycopodiaceae (*Huperzia*) and Ophioglossales (*Ophioglossum*) retain vestiges of this earlier morphological complexity (see Kenrick 1994).

subterranean and saprophytic; in others, it is photo-synthetic. In many ferns, the gametophyte is thalloid, whereas in some it resembles a branched axis, and in others it is more or less disc-shaped with a peculiar ring meristem. The origin of these differences has never been fully explained.

New evidence from the fossil record is beginning to shed light on the origin of the gametophyte phase of the vascular plant life cycle. Recent discoveries document comparatively large and highly differentiated gameto-phytes in early vascular plants and protracheophytes (Kenrick 1994; Remy *et al.* 1993; figure 2*a–d*). Although completely lacking leaves, perhaps the closest modern analogue for these plants would be the larger moss game-tophytes in the Polytrichales. This new fossil evidence implies that vascular tissues and stomates have been lost in the gametophytes of living vascular plants. Likewise, gametophyte branching and gametangiophore develop-ment has been much reduced or lost completely. In other words, the morphology of the gametophyte generation in living vascular plants is the product of extensive loss or reduction, which has probably occurred independently in several lineages. Most unexpectedly, the transition from gametophyte-dominated to sporophyte-dominated life cycles in land plants involved a now extinct isomorphic intermediate phase (figure 3), implying similar patterns of gene expression early on in both phases of the life cycle.

4. IMPLICATIONS FOR LAND PLANT ORIGINS

The hierarchical structure of a phylogenetic tree dictates a logical sequence to clade formation that can be compared with the actual pattern of appearance of groups in the fossil record (see Norell & Novacek 1992; Siddall 1998; Smith 1994). The phylogenetic and strati-graphic approaches provide essentially independent esti-mates of the sequence in which events occurred. Because congruence between the results of these two processes is expected, any deviation indicates that there is a problem

with the phylogenetic tree, the fossil record or perhaps both (Smith 1994). The paraphyletic relationship of bryo-phytes to vascular plants implies that the earliest land plants were bryophyte-like organisms. Therefore, the sequence of appearance of groups in the fossil record should show bryophytes preceding vascular plants. This pattern is consistent with microfossil evidence (dispersed spores) but it conflicts with the megafossils (Kenrick & Crane 1997*a*,*b*).

Fossil spores document a Mid-Ordovician origin of land plants (*ca*. 476 Myr) and a major diversification during the Late Ordovician and Silurian (Gray 1985, 1993; Wellman 1993, 1995, 1996; Wellman & Richardson 1993). Although the affinities of the early spore producers are controversial, there is mounting evidence from later spore/megafossil associations (Edwards *et al.* 1995; Fanning *et al.* 1991; Wellman *et al.* 1998), spore wall ultra-structure (Taylor 1996) and fossil cuticles (Kroken *et al.* 1996) that they were produced by plants at the bryophyte grade. The spore evidence is thus consistent with the results of phylogenetic analysis. Megafossils, on the other hand, show a completely different pattern. Their strati-graphic appearance is the reverse of that predicted by cladogram topology and it substantially postdates the microfossil (spore) evidence (Kenrick & Crane 1997*b*). In the megafossil record, vascular plants and protracheo-phytes appear before bryophytes, and the diversification of land plants apparently begins in the Mid-Silurian. Can these inconsistencies be reconciled?

One source of potential error is the phylogenetic analysis. Inverting relationships to place bryophytes within crown group vascular plants or deriving bryo-phytes independently from other later algal groups would be more consistent with the stratigraphic appearance of megafossils. But these solutions are highly unparsimo-nious. Furthermore, the inversion of relationships would leave the early fossil record of bryophyte-like spores un-explained. A second and more likely source of error is a systematic representational bias in the megafossil record favouring vascular plants over bryophytes. There are
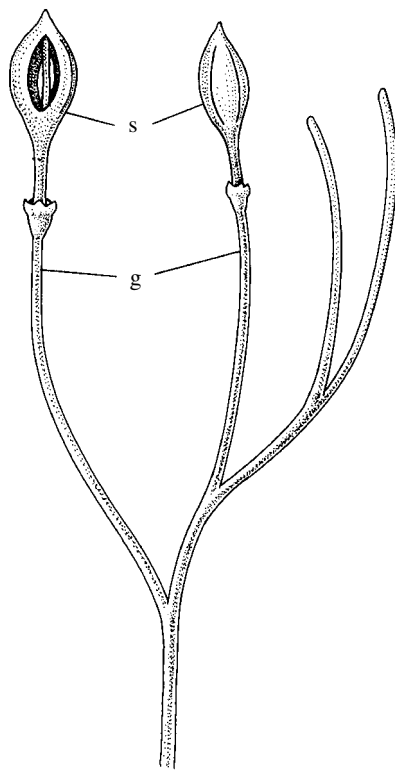
Figure 4. Hypothetical stem group moss before the evolution of gametophytic leaves. Small, unbranched, valvate sporophytes (s) with columella of *Andreaea* type attached terminally to naked, dichotomously branched gametophyte (g).

several observations that tend to favour representational bias as an explanation for these inconsistencies. First, bryophytes are generally rare in comparison with vascular plants throughout the pre-Quaternary fossil record. This fact is probably related to their comparatively small size, the absence of lignin and woody tissues (low fossilization potential), and collector bias favouring vascular plants. Second, a search image based on modern bryophytes is likely to be unproductive in the early fossil record. For example, leaves are a characteristic of modern moss gametophytes, but it is highly likely that stem group mosses were leafless (Mishler & Churchill 1984). Such leafless mosses would be difficult to recognize and to distinguish from stem group vascular plants (figure 4). Third, the rapid appearance of megafossils in the Early Devonian coincides with major facies changes driven by a widespread marine regression in northern Europe, one of the major sampling areas (Allen 1985; Gray & Boucot 1977). More generally, all Silurian land plant megafossils are from marine sediments, whereas Early Devonian plant localities are predominantly terrestrial (Edwards 1990). In contrast to megafossils, the spores of bryophytes and vascular plants are essentially equivalent in taphonomic terms. They are of similar size, composition and dispersal ability. Spores would therefore be expected to document more accurately the composition of the terrestrial flora at this time. Spores are also vastly more abundant and more widely dispersed into a broader range of facies (shallow marine, terrestrial) than are the megafossils. They are expected to give a more complete picture of

the timing of these events. Recent phylogenetic results therefore corroborate earlier suggestions that the pattern of appearance and early diversification of plants in the megafossil record owes more to changing geological conditions than to rapid biological diversification (Gray 1985; Gray & Boucot 1977).

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