PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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Phil. Trans. R. Soc. Lond. B 2000 **355**, 847-855
doi: 10.1098/rstb.2000.0619

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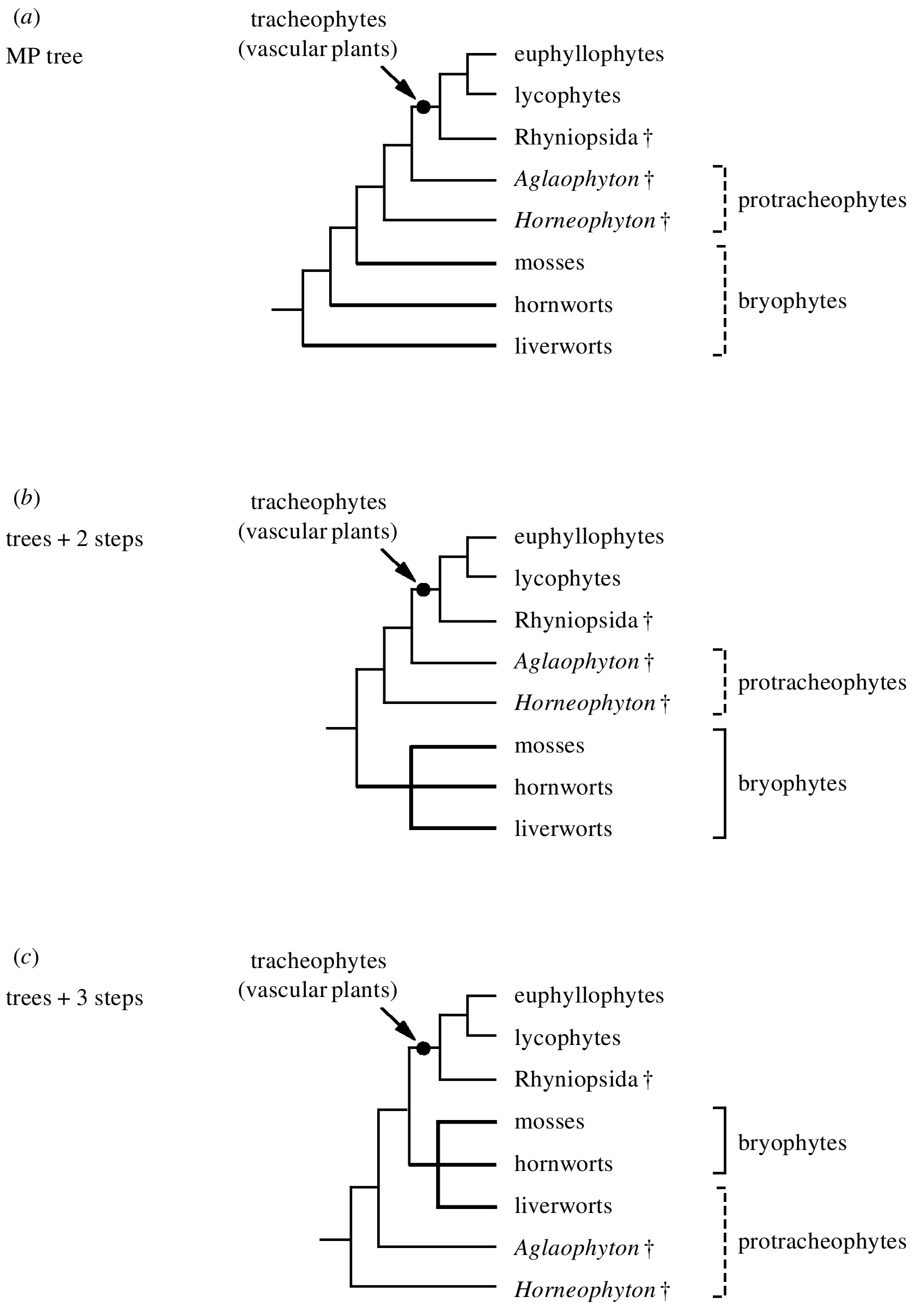
Recent phylogenetic research indicates that vascular plants evolved from bryophyte-like ancestors and that this involved extensive modifications to the life cycle. These conclusions are supported by a range of systematic data, including gene sequences, as well as evidence from comparative morphology 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. Megafossils 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

he development of a robust phylogenetic framework for ascular plants is widely perceived as crucial to addressng a raft of important issues concerning the origins of he terrestrial flora, life cycle evolution and morphoenesis in plants. Recent work has shown that the relationhips of vascular plants must be evaluated within the roader context of land plants as a whole. Yet, deep phyloenetic questions such as these are difficult to resolve, not east because the early evolution of the land flora took lace over 400 Myr ago (Late Silurian–Early Devonian). Numerous phylogenetic hypotheses have been proposed, iving 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 hequered systematic history is the broad acceptance of a lassification that groups land plants into two categories, ermed 'vascular plants' (tracheophytes) and 'bryophytes'. All land plants can be classified into one of these groups n the basis of their life cycles and the extent to which he diploid spore-bearing (sporophyte) and haploid amete-bearing (gametophyte) phases develop. Bryohytes possess a small, parasitic sporophyte, which is ttle more than a simple sporangium, borne on a larger, halloid or leafy gametophyte. The life cycle of vascular lants is the antithesis of that in bryophytes. Here the porophyte is independent, morphologically complex and requently a very large organism. These striking differnces in life history create additional problems for phyloenetics by obscuring the crucial morphological omparisons necessary for constructing a robust phylogenetic tree. This difficulty is further exacerbated by the ven larger disjunction between land plants and their losest 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



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

f various bryophyte groups to vascular plants. This aper reviews recent phylogenetic developments and xamines some of their consequences for life cycle evolu-ion and the interpretation of stratigraphic patterns in the arly fossil record of land plants.

2. PHYLOGENETIC OVERVIEW

(a) *Vascular plants and bryophytes*

One of the key phylogenetic questions in plant ystematics is the nature of the relationship between ascular plants and the other major living groups of land lants, 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, ene sequences and genomic structure continue to favour araphyly of bryophytes, but there is as yet no consensus n the precise nature of the relationships among these our major plant groups.

A moss + vascular plant clade is supported by several norphological analyses of living and fossil plants (Kenrick Crane 1997*a*,*b*; Mishler & Churchill 1984, 1985; gure 1) and studies that have integrated morphology vith data on 18S and 26S rRNA sequences (Mishler *et al.* 994). However, the chloroplast gene *rbcL* favours a hornvort + vascular plant clade (Lewis *et al.* 1997). Both ypotheses are consistent with the distribution of three nitochondrial group II introns sampled across a wide ange of land plants (Qiu *et al.* 1998). These data support he hypothesis that liverworts are either a sister group to ll other land plants or perhaps a basal paraphyletic ssemblage. A third pattern resolves vascular plants as a ster group to a moss + liverwort clade. This hypothesis consistent with evidence from male gamete development and ultrastructure (Garbary & Renzaglia 1998), as vell as analyses based on gene sequences from the nucleus 18S rRNA; Hedderson *et al.* 1996) and the mitochonrion (19Sr DNA; Duff & Nickrent 1999). This pattern lso receives support from a recent analysis based on everal plastid genes (*rbcL*, *psaA*, *psaB*, *psbD*, *rpoC2*; ishiyama & Kato 1999).

Support for these hypotheses, as measured by bootstrap nd decay indices, is generally comparatively low, and lternative topologies are only marginally less parsimoious. Based on mitochondrial *cox3* sequences, Malek *et al.* 1996) resolved hornworts as basal in embryophytes, but he relationships of liverworts, mosses and vascular plants ad very low support. Data on spermatogenesis and perm ultrastructure indicate that bryophytes are monohyletic (Garbary *et al.* 1993; Maden *et al.* 1997), but ampling is comparatively sparse and there is concern bout character independence in some data domains (e.g. he ultrastructure of the spermatozoid flagellum). ecoding of the Garbary *et al.* (1993) data by Mishler *al.* (1994) and Garbary & Renzaglia (1998) produced tree topology that is consistent with bryophyte araphyly.

The absence of consensus among data sets and the enerally low levels of support for alternative phylogenetic ypotheses are most likely a consequence of several roblems that emerge at this phylogenetic level in plants. irst, the cladogenic events that led to the evolution of hese groups occurred between 470 and 400 Myr ago Kenrick & Crane 1997*b*). The interval of time spanning roup divergence is short in comparison with the length f time between these events and the present. In other vords, phylogenetic methods are likely to perform poorly ecause of imbalance in branch length (i.e. short internal ranches combined with long terminal branches, see elsenstein 1978; Huelsenbeck 1995). Second, the great ifferences between comparable phases of the bryophyte nd vascular plant life cycle create difficulties in identifyng homologies for morphological analyses. The absence f a fossil record of stem group mosses, liverworts and ornworts exacerbates this problem (Kenrick & Crane 997*a*). Third, in morphological analyses, rooting the tree nd character polarity are problematic because of the omparatively 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 polorized 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

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

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

Relationships among basal living and fossil euphyllohytes are still rather poorly resolved. Living groups such s leptosporangiate ferns, Ophioglossales, Marattiales, *quisetum* 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 ootstrap support for relationships among these groups in equence-based studies is generally low (Duff & Nickrent 999; Hedderson *et al.* 1998; Kranz & Huss 1996; Malek *t al.* 1996; Pahnke *et al.* 1996; Pryer *et al.* 1995; Wolf 1997) nd critical taxa are frequently missing. No consistent attern has yet emerged. Duff & Nickrent (1999) resolved well-supported fern + *Equisetum* clade as sister group to eed plants, in agreement with one fossil-based cladistic nalysis (Kenrick & Crane 1997*a*). But the sample of eptosporangiate ferns was based on a single species of *olypodium*, and Marattiales and *Psilotum* were absent from he analysis. The basal groups of living euphyllophytes re morphologically quite divergent, and phylogenetic tudies based on the comparative morphology of living pecies show that there are comparatively few characterstics supporting tree topology (Stevenson & Loconte 996). This study placed *Equisetum* sister group to a clade omprising leptosporangiate ferns, eusporangiate ferns nd seed plants, a result that is consistent with at least ne cladistic analysis that includes fossils (Rothwell 1996).

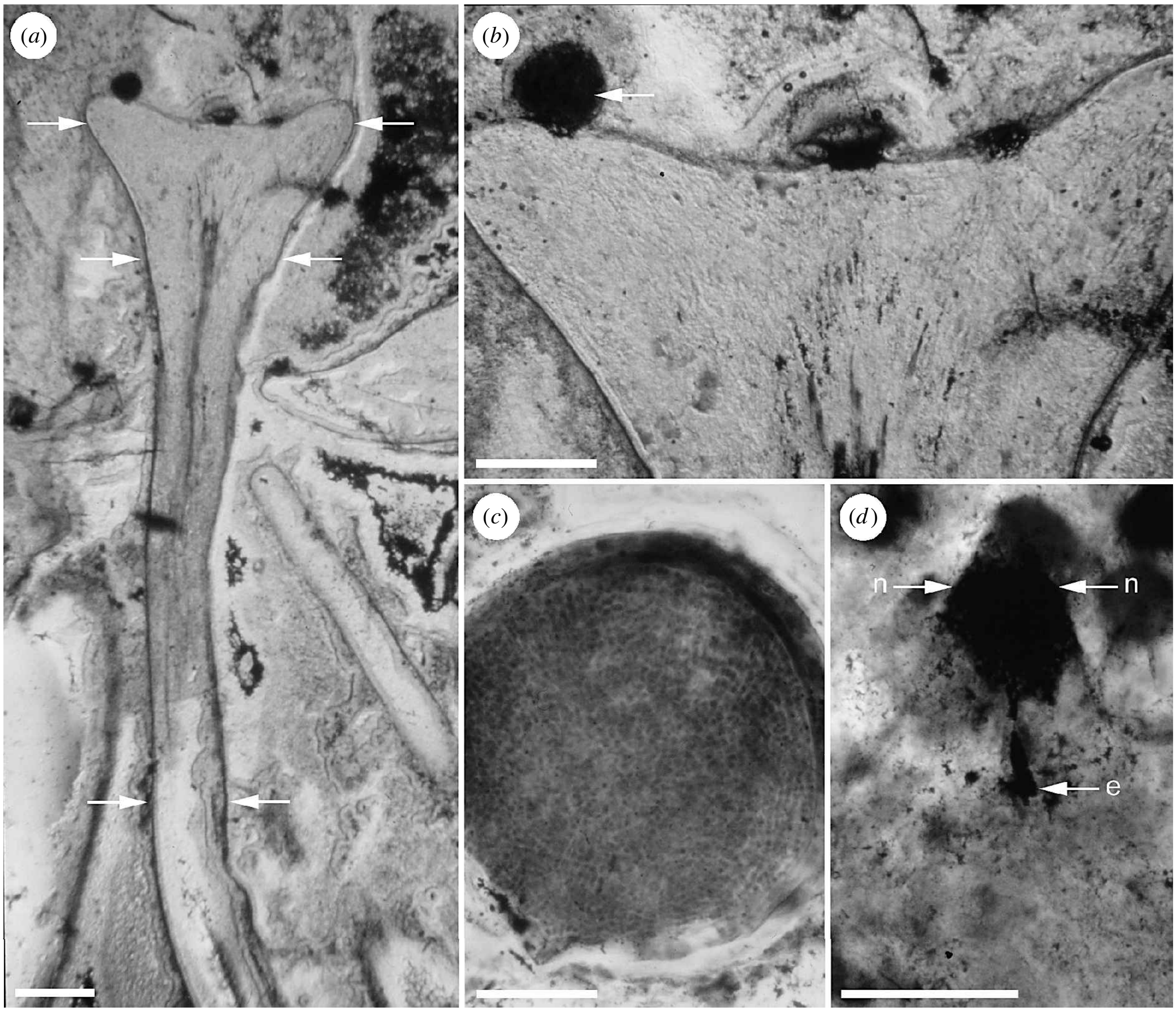
Consideration of fossil evidence from the Late Palaeooic underlines further basic similarities among these iverse living groups. The seed plant stem group contains lants (progymnosperms) with some of the wood and ranching characteristics of seed plants, but which retain he plesiomorphic free-sporing life cycle. Other key fossil roups include cladoxylopsids and zygopterids. These two roups are widely thought to be related to ferns and *Equietum*, although the precise nature of this relationship emains unresolved (Stein *et al.* 1984). One fossil-based ladistic 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

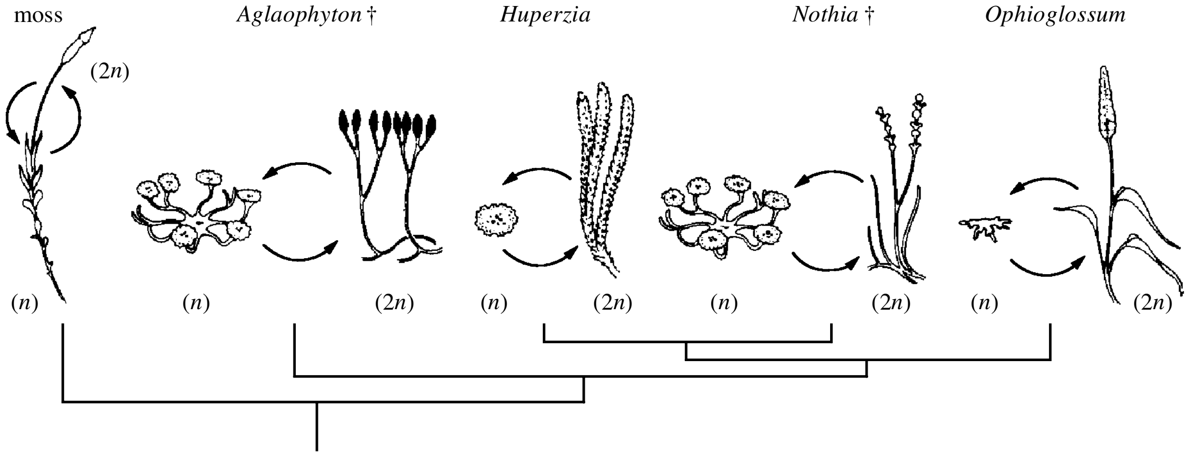


igure 2. Exceptionally well-preserved silicified fossil gametophytes of stem group vascular plants from the 400 Myr old Rhynie chert, Scotland (courtesy W. Remy and H. Hass, Westfälische Wilhelms–Universität, Münster). (*a*) Terminal part of ametophytic axis of *Lyonophyton rhyniensis* comprising slender 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).

ncestor and that any differences observed today are the esult of divergent evolution. In other words, similarities mong major groups are not the result of convergence on similar set of adaptations to life on land, rather they esult from a common ancestry. We should therefore xpect substantial similarities at the molecular developmental level between organ systems in bryophytes and heir homologues in vascular plants (Kenrick & Crane 997*b*). This prediction is currently untested.

Among living plants, life cycles have been used as a asis for distinguishing vascular plants from bryophytes, ut this clear distinction breaks down in the early fossil ecord. The diploid (sporophyte) phase of the vascular lant life cycle is much more highly differentiated and arger than the equivalent phase in liverworts and mosses. The origin of these differences can be traced through a eries of extinct morphological intermediates (Kenrick 994; Remy *et al.* 1993; Remy & Hass 1996). Palaeootanical data show that the early vascular plant sporohytes resemble much more closely the bryophyte model Edwards *et al.* 1995; Raven 1985, 1993, 1995). Protracheophyte 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



igure 3. Hypothesis of life cycle evolution in basal vascular plants. † = extinct taxon. Evidence from phylogeny and the fossil ecord indicates that the vascular plant life cycle evolved from a bryophytic life cycle in which the sporophyte (2*n*) is parasitic on he gametophyte (*n*). There was a transitional phase (now extinct) in which the life cycle was more or less isomorphic (here epresented by the extinct plants *Aglaophyton* and *Nothia*). The gametophytes of modern vascular plants are highly reduced, but roups such as Lycopodiaceae (*Huperzia*) and Ophioglossales (*Ophioglossum*) retain vestiges of this earlier morphological omplexity (see Kenrick 1994).

ubterranean and saprophytic; in others, it is photoynthetic. In many ferns, the gametophyte is thalloid, vhereas in some it resembles a branched axis, and in thers it is more or less disc-shaped with a peculiar ring neristem. The origin of these differences has never been ully explained.

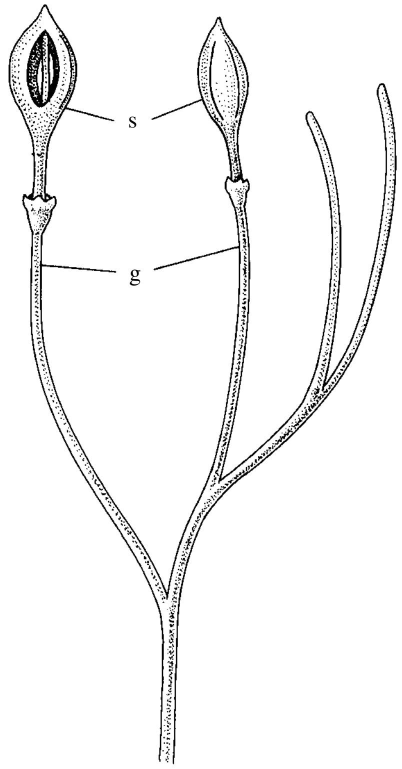
New evidence from the fossil record is beginning to hed light on the origin of the gametophyte phase of the ascular plant life cycle. Recent discoveries document omparatively large and highly differentiated gametohytes in early vascular plants and protracheophytes Kenrick 1994; Remy *et al.* 1993; figure 2*a*–*d*). Although ompletely lacking leaves, perhaps the closest modern nalogue for these plants would be the larger moss gameophytes in the Polytrichales. This new fossil evidence mplies that vascular tissues and stomates have been lost n the gametophytes of living vascular plants. Likewise, ametophyte branching and gametangiophore developnent has been much reduced or lost completely. In other vords, the morphology of the gametophyte generation in ving vascular plants is the product of extensive loss or eduction, which has probably occurred independently in everal lineages. Most unexpectedly, the transition from ametophyte-dominated to sporophyte-dominated life ycles in land plants involved a now extinct isomorphic ntermediate phase (figure 3), implying similar patterns f gene expression early on in both phases of the life ycle.

4. IMPLICATIONS FOR LAND PLANT ORIGINS

The hierarchical structure of a phylogenetic tree ictates a logical sequence to clade formation that can be ompared with the actual pattern of appearance of roups in the fossil record (see Norell & Novacek 1992; iddall 1998; Smith 1994). The phylogenetic and stratiraphic approaches provide essentially independent estinates of the sequence in which events occurred. Because ongruence between the results of these two processes is xpected, any deviation indicates that there is a problem with the phylogenetic tree, the fossil record or perhaps both (Smith 1994). The paraphyletic relationship of bryophytes 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 ultrastructure (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 stratigraphic 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 protracheophytes 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 bryophytes independently from other later algal groups would be more consistent with the stratigraphic appearance of megafossils. But these solutions are highly unparsimonious. Furthermore, the inversion of relationships would leave the early fossil record of bryophyte-like spores unexplained. A second and more likely source of error is a systematic representational bias in the megafossil record favouring vascular plants over bryophytes. There are



igure 4. Hypothetical stem group moss before the volution of gametophytic leaves. Small, unbranched, alvate sporophytes (s) with columella of *Andreaea* type ttached terminally to naked, dichotomously branched ametophyte (g).

everal observations that tend to favour representational ias as an explanation for these inconsistencies. First, ryophytes are generally rare in comparison with ascular plants throughout the pre-Quaternary fossil ecord. This fact is probably related to their compara-.vely small size, the absence of lignin and woody tissues low fossilization potential), and collector bias favouring ascular plants. Second, a search image based on modern ryophytes is likely to be unproductive in the early fossil ecord. For example, leaves are a characteristic of modern oss gametophytes, but it is highly likely that stem group osses were leafless (Mishler & Churchill 1984). Such eafless mosses would be difficult to recognize and to istinguish from stem group vascular plants (figure 4). hird, the rapid appearance of megafossils in the Early evonian coincides with major facies changes driven by a idespread marine regression in northern Europe, one of e major sampling areas (Allen 1985; Gray & Boucot 977). More generally, all Silurian land plant megafossils re from marine sediments, whereas Early Devonian lant localities are predominantly terrestrial (Edwards 990). In contrast to megafossils, the spores of bryophytes nd vascular plants are essentially equivalent in tapho-omic terms. They are of similar size, composition and ispersal ability. Spores would therefore be expected to ocument more accurately the composition of the terres-rial flora at this time. Spores are also vastly more abun-ant and more widely dispersed into a broader range of acies (shallow marine, terrestrial) than are the megafos-ls. 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).

I gratefully acknowledge a gift of transparencies from W. Remy and H. Hass (Abteilung Paläobotanik am Geologisch–Paläontologischen Institut, Westfälische Wilhelms–Universität, Münster, Germany), which form the basis of figure 2. Pollyanna Lidmark prepared figures 3 and 4.

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