EARLY EVOLUTION OF LAND PLANTS: Phylogeny, Physiology, and Ecology of the Primary Terrestrial Radiation

Richard M. Bateman,[1] *Peter R. Crane,*[2] *William A. DiMichele,*[3] *Paul R. Kenrick,*[4] *Nick P. Rowe,*[5] *Thomas Speck,*[6] *and William E. Stein*[7]

[1]Royal Botanic Garden, 20A Inverleith Row, Edinburgh EH3 5LR, United Kingdom; e-mail: r.bateman@rbge.org.uk; [2]Department of Geology, The Field Museum, Chicago, Illinois 60605-2496; [3]Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560; [4]Department of Palaeontology, The Natural History Museum, London SW7 5BD, United Kingdom; [5]Laboratoire de Paléobotanique, Institut des Sciences de l'Evolution (UMR 5554 CNRS), Université de Montpellier II, 34095 Montpellier cedex 05, France; [6]Botanischer Garten der Albert-Ludwigs-Universität, D79104 Freiburg, Germany; [7]Department of Biological Sciences, Binghamton University, Binghamton, New York 13902-6000

KEY WORDS: biomechanics, cladistics, evolutionary radiation, novelty radiation, paleobotany, systematics

ABSTRACT

The Siluro-Devonian primary radiation of land biotas is the terrestrial equivalent of the much-debated Cambrian "explosion" of marine faunas. Both show the hallmarks of novelty radiations (phenotypic diversity increases much more rapidly than species diversity across an ecologically undersaturated and thus low-competition landscape), and both ended with the formation of evolutionary and ecological frameworks analogous to those of modern ecosystems. Profound improvements in understanding early land plant evolution reflect recent liberations from several research constraints: Cladistic techniques plus DNA sequence data from extant relatives have prompted revolutionary reinterpretations of land plant phylogeny, and thus of systematics and character-state acquisition patterns. Biomechanical and physiological experimental techniques developed for extant

263

plants have been extrapolated to fossil species, with interpretations both aided and complicated by the recent knowledge that global landmass positions, currents, climates, and atmospheric compositions have been profoundly variable (and thus nonuniformitarian) through the Phanerozoic. Combining phylogenetic and paleoecological data offers potential insights into the identity and function of key innovations, though current evidence suggests the importance of accumulating within lineages a critical mass of phenotypic character. Challenges to further progress include the lack of sequence data and paucity of phenotypic features among the early land plant clades, and a fossil record still inadequate to date accurately certain crucial evolutionary and ecological events.

INTRODUCTION

Within paleobotany, there are few more popular review topics than the origin and initial radiation of vascular land plants in the Silurian (438–410 mya) and Devonian (410–355 mya) periods (20, 21, 23, 25, 34, 37, 39, 40, 51, 56, 57, 66, 67, 70, 95, 97, 132). Fortunately, each crop of reviews is separated by remarkable empirical and conceptual advances in a wide range of fields that amply justify frequent reappraisals.

Recent Advances

Any uniformitarian views of the Earth's environment that have survived the paradigm shift of plate tectonics and continental drift have since been undermined by evidence of dramatic changes in global climate and atmospheric composition through the Phanerozoic. Thus, paleoecologists must now deal with profound changes in the environmental theater as well as the evolutionary play. During the Siluro-Devonian there was a strong concentration of land masses in the Southern Hemisphere, with only North America, northern Europe, and parts of China straddling the equator (115). Consequently, both atmospheric and oceanic currents contrasted starkly with modern patterns. Atmospheric CO_2 levels were falling precipitously and O_2 levels rising rapidly; both phenomena, driven at least in part by the "greening"of the continents, had profound implications for the physiological competence of land plants (3, 13, 14, 44, 80, 85, 97).

Building on earlier intuitive advances (5), the systematics of early land plants has been revolutionized by the integration of morphological data from living and fossil species to generate cladistic phylogenies (50, 64–66). These not only define putative monophyletic (and thus natural) groups of species but also elucidate the sequence of acquisition of features and functions within specific lineages (9, 75). Molecular phylogenies of extant species have further clarified evolutionary relationships and tested the supposed primitive nature of some "living fossils" (9, 139).

Reexamination of exceptionally preserved biotas, notably the Rhynie Chert (64, 98, 99), has elucidated the novel life histories of several early land plants as well as revealed abundant interspecific interactions within their communities. Biomechanical and physiological models erected around extant plant species have been extrapolated onto fossils, often with surprising results (12, 87, 96, 97, 122).

Advances in understanding the genetic underpinnings of major phenotypic changes of extant plants (2, 22) offer deeper understanding of the nature of speciation in general and radiations in particular (54). Plants are viewed increasingly as evolutionary models in their own right, rather than religiously shoe-horned into pre-existing theories built around higher animals (11). The resulting insights permit fresh comparisons between radiations on land and those in marine environments (cf. 25, 55).

Radiations in general are being defined more precisely and categorized usefully according to pattern of diversification and inferred causal mechanisms (10, 45, 138). More specifically, attempts are being made to tease apart the supposedly explosive Siluro-Devonian terrestrial radiation into a better-defined nested set of evolutionary bursts (40, 66, 67).

Four Phases of Plant Evolution

Bateman (7) attempted to simultaneously categorize and interpret ca. 1800 million years of plant evolution as four successive phases.

1. The Biochemical Phase characterized the extensive history of life prior to the Ordovician (510–438 mya; 97, 113). During this period, fundamental biochemical pathways such as those facilitating respiration and photosynthesis were established in anatomically simple cyanobacteria and algae that primarily occupied aqueous environments. Also, more sophisticated life histories followed the advent of meiosis.

2. The Anatomical Phase spanned the Ordovician and Silurian. Erstwhile pioneering land plants struggled with the physical and physiological problems posed by a terrestrial existence, challenged more by the hostile environment than by competition with one another. Most of the tissue types that characterize modern land plants evolved, together with the alternation between independent sporophytic and gametophytic generations that defines the pteridophytic life history.

   Focusing more directly on the fossil evidence, Edwards & Selden (40) recognized phases corresponding largely to those of Bateman, but they effectively subdivided his anatomical phase into an Upper Ordovician-Silurian (quasi)bryophytic phase (Phase 2a) and a later Silurian rhyniophytic phase

(Phase 2b). These broadly correspond to the liverwort-dominated "eoembryophytic" and explosive "eotracheophytic" phases, respectively, of Gray (57; see also 67).

3. The Morphological Phase of Bateman ("eutracheophytic" phase sensu 57) reached an acme in the Devonian. Fully terrestrialized land plants experimented with various arrangements of tissue types, apparently engendering morphological and architectural escalation. This greatly increased the range and maximum complexity of gross morphological form as well as maximum body sizes; species of several clades adapted to exploit the third dimension far more effectively.

4. The Behavioral Phase increased exponentially through the Carboniferous and Permian, building on the previous evolutionary phases and establishing the ecosystem dynamics that continue to control modern vegetation. In particular, interactions between individual plants and their abiotic environment were increasingly supplemented with biotic interactions among individuals, which facilitated coevolution with mycorrhizal and pathogenic fungi, and with animal pollinators, dispersers, and herbivores.

This review concerns primarily the intermediate anatomical and morphological phases, which conveniently present the strongest evidence in the fossil record. Phase 1—the presumed earlier transition to land of prokaryotic and simple eukaryotic oxygen producers and fungi—is taken as an essential precursor to the embryophytic life history and subsequent vascularization (40, 66, 97). The well-integrated, mainly seed plant–dominated communities of Phase 4 (25) are deemed too modern in aspect to merit discussion here; their phylogeny is reviewed elsewhere in this volume (28).

In this chapter we examine the anatomical and morphological phases of terrestrialization by reviewing recent advances in land plant phylogeny, physiology–biomechanics, and ecology. We then attempt to draw together the patterns evident in these disparate sources of data to infer potential processes underlying this most profound of all terrestrial radiations.

LAND PLANT PHYLOGENY

First we summarize present evidence for land plant phylogeny, beginning with the presumed Mid-Ordovician colonization of the land and ending with the Late Devonian origin of the seed plants; examples of these taxa are described in greater detail in recent paleobotany texts (131, 136). This section focuses on the relationships of higher taxa (primarily classes and orders) and uses a novel informal nomenclature to describe some recently delimited monophyletic

groups (66). Selected character-state transitions between potentially pivotal groups are elucidated in subsequent sections.

Phylogenetic studies based on comparative morphology (32, 56, 84) and molecular genetics (73, 78, 79, 81) provide compelling evidence for a close relationship between land plants and green algae, specifically the Charophyceae. Living Charophyceae are a small group of predominantly freshwater plants comprising simple unicellular and filamentous species (e.g. Klebsormidiales and Zygnematales), as well as highly differentiated forms (e.g. Charales) that include some of the most complex green algae (56). Charophyceae are a paraphyletic group, but the identity of the living land plant sister group remains unresolved. The most likely sister taxa to land plants are Coleochaetales (ca. 15 living species), Charales (ca. 400 living species), or a clade containing both.

The fossil record of charophycean algae is relatively poor, and the earliest evidence post-dates that of land plants (67). Fossils are limited mostly to decay-resistant or calcified parts of the life cycle, and only two groups (Charales, Zygnematales) are well represented. The earliest and most abundant charophycean algae are Charales (46), which first appear in the fossil record in the Late Silurian but probably had a considerably earlier origin, given that early fossils have well-developed and highly distinctive gametangia that resemble those of modern forms. The appearance of Charales in the fossil record may be linked to the evolution of calcification in the more derived members of this group. Zygnematales occur more rarely in the fossil record (58), and the group is first recognized in the Middle Devonian. The phylogenetically important Coleochaetales have not been recognized unequivocally in the fossil record. Some cuticular compressions in the Lower Devonian (notably *Parka*) resemble the delicate, filamentous thalli of living *Coleochaete orbicularis*, though other aspects of their morphology are inconsistent with this interpretation (cf. 61, 86).

Land Plants

Monophyly of land plants is strongly supported by comparative morphology (16, 32, 56, 66, 84) and nucleic acid sequences (62, 72, 73). Although relationships among the major basal living groups remain uncertain (4, 9, 32, 48, 56, 59, 66, 84), the hypothesis currently supported by the broadest range of data resolves "bryophytes" as paraphyletic, with liverworts basal in land plants and either mosses or hornworts as the living sister group to vascular plants. Liverworts themselves may be paraphyletic to other land plants, with marchantialeans basal and jungermannialeans more closely related to hornworts, mosses, or vascular plants (4, 15).

An alternative hypothesis, suggested by 18S rRNA sequences, places hornworts as basal and a liverwort-moss clade as sister group to vascular plants (59). Less parsimonious hypotheses recognize bryophyte monophyly and either a

sister group relationship with vascular plants (66) or an origin from within basal vascular plants (32, 48, 62, 132). Phylogenetic evidence suggests that "bryophytes"[1] in general, and liverwort-like plants in particular, should have been important components of early terrestrial floras (67).

Evidence from fossil spores indicates that land plants originated in the mid-Ordovician and that the divergence of the four major living clades (liverworts, hornworts, mosses, vascular plants) may have occurred during the Late Ordovician and Silurian (52, 57); this hypothesis is consistent with phylogenetic data that resolve "bryophytes" as a basal grade within land plants. In contrast, the megafossil record documents a Late Silurian origin and Early Devonian diversification of vascular plants and a much later origin of "bryophytes." Kenrick & Crane (66, 67) argued that the spore record provides a more accurate picture of the time of origin and pattern of early diversification of land plants than the megafossil record because spores are more numerous and less influenced by taphonomic biases. They suggested that the late appearance of "bryophytic" megafossils probably reflects the combined effects of under-representation of this group in the fossil record and also the difficulties of recognizing early plants at the "bryophyte" grade that may have lacked the distinctive features of living groups.

However, the late appearance also offers comfort to a minority of phylo-geneticists who view as credible scenarios of "bryophyte" origins via sporo-phytic reduction from isomorphic "pretracheophytes" (9), particularly if the Ordovician supposed bryophytic spores, cuticular sheets of cells, and tubes of nematophytes were in fact derived from free-living or lichenized fungi (128).

Liverworts

The most inclusive phylogenetic studies of liverworts resolve a jungermanni-alean (Metzgeriales, Jungermanniales, Calobryales) clade (4, 15, 83), a pattern consistent with traditional systematic treatments (114). Morphological studies indicate that Metzgeriales are paraphyletic to Jungermanniales (83), and this hypothesis has some support from 18S rRNA sequences (19). Recent mole-cular and morphological analyses also support monophyly of marchantialean liverworts (Sphaerocarpales, Marchantiales, Monocleales; 15). Within mar-chantialeans, the enigmatic Monocleales (two species) are nested within Mar-chantiales, and Sphaerocarpales are probably sister group to a Marchantiales–Monocleales clade.

Despite widespread support for an early origin of liverworts from phyloge-netic studies, the group has a poor fossil record. Some of the earliest land plant spores possess features that are consistent with a sphaerocarpalean affinity

---

[1]This use of quotes is a convention in phylogenetics for identifying taxa as paraphyletic grades rather than monophyletic clades.

(57, 137), but there are insufficient characters to substantiate an unequivocal affiliation with liverworts. Many early spores could also belong to extinct taxa in the stem groups of land plants or major basal land plant clades. Most Paleozoic megafossils are related to Metzgeriales, including the earliest unequivocal liverwort (Upper Devonian). The precise relationships of earlier liverwort-like megafossils (38, 49) require further clarification. Jungermanniales first appear in the Mesozoic, and there are only a handful of well-substantiated Jurassic and Cretaceous records. Sphaerocarpales are first documented in the Triassic, and Marchantiales are clearly present in the Mid–Late Triassic.

Hornworts

Hornworts are a small, divergent group of land plants comprising ca. 400 living species. Monophyly of hornworts is well supported and uncontroversial (32, 83, 84), though generic limits and relationships among genera are poorly resolved. *Notothylas* may be sister group to an *Anthoceros–Dendroceros–Megaceros–Phaeoceros* clade (83), though a marginally less parsimonious alternative solution interprets the small, simple sporophytes of *Notothylas* as derived, and taxa with larger sporophytes such as *Dendroceros* and *Megaceros* as basal in the group. The fossil record of hornworts is poor and has not yet contributed important information to cladistic studies of this group.

Mosses

Monophyly of mosses has broad support in recent phylogenetic studies (15, 59, 60, 82). Within mosses, Sphagnales and Andreaeales are consistently resolved as basal groups. Molecular data support two major clades of peristomate mosses: (*a*) a nematodontous clade comprising Buxbaumiales, Tetraphidales, Polytrichales, and perhaps Andreaeales and (*b*) an arthrodontous clade containing Bryales (59, 60). New morphological data on sporophytes and gametogenesis in *Takakia* provide compelling evidence for an affinity with basal mosses (Andreaeales, Sphagnales), rather than with liverworts (Calobryales), as previously hypothesized (32, 48, 101); this relationship is also supported by similarities in 18S rRNA sequences (59).

Mosses have a poor Paleozoic and Mesozoic megafossil record. Arthrodontous groups such as Dicranales, Pottiales, Funariales, Leucodontales, and Hypnales have been documented in the Late Permian and Early Triassic (118). Sphagnales are also known from the Late Permian (*Protosphagnum*). Putative Polytrichales have been reported from the Carboniferous, but the first unequivocal record is from the Late Cretaceous (71). The earliest megafossils of possible moss affinity include *Sporogonites* (Lower Devonian) and *Muscites* (Lower Carboniferous), though the latter is more likely to be a lycopsid (NP Rowe, unpublished data).

Vascular Plants

Monophyly of vascular plants is supported by comparative morphology (66, 130) and by data from 18S rRNA (72) and 16S rDNA sequences (77). The inclusion of fossils results in the recognition of several additional clades that cannot be discriminated among living taxa alone. Phylogenetic analyses (65, 66) interpolate two Early Devonian Rhynie Chert plants, *Aglaophyton* and *Horneophyton*, as paraphyletic between "bryophytes" and basal vascular plants because they possess some features unique to vascular plants sensu lato (e.g. branched, nutritionally independent sporophyte) but also retain several plesiomorphic, bryophyte-like characteristics (e.g. terminal sporangia, columella in *Horneophyton*, and the absence of leaves, roots, and tracheids with well-defined thickenings).

The discovery of previously unrecognized diversity in extinct *Cooksonia* and similar early fossils (e.g. *Tortilicaulis*, *Uskiella*, *Caia*; 38) also suggests that simple early land plants—once grouped as rhyniophytes (5)—are not a monophyletic assemblage (66). *Rhynia* and a few related fossils (*Taeniocrada*, *Stockmansella*) form a small but distinctive clade in the vascular plant stem group (rhyniopsids; 65, 66). Some *Cooksonia* species may be among the paraphyletic precursors of vascular plants ("protracheophytes"), whereas others are true vascular plants apparently allied to the clubmoss lineage. The eutracheophyte clade (vascular plant crown group) contains all living and most fossil vascular plants.

Lycophytes

The Lycophytina constitutes a distinctive basal clade within eutracheophytes (16, 62, 66, 72, 107). Monophyly of lycophytes has broad support from comparative morphology (66, 130) and molecular studies (72, 76, 139). Within lycophytes, the extinct, leafless zosterophylls are resolved as a basal grade. Derived zosterophylls with marked bilateral symmetry of their axes form the clade Zosterophyllopsida (66). Within the sister group of leafy lycopsids, there is strong support for monophyly of the ligulate and heterosporous clades (66, 76, 139). Also, Isoetaceae constitutes clearly the most closely related living group to the far more diverse arborescent lycopsids of the Late Paleozoic.

Small herbaceous lycophytes (Zosterophyllopsida, Drepanophycaceae) are among the earliest recognizable land plant megafossils, and the group was a prominent component of Early Devonian floras. Several major clades evolved during the Devonian, including the three living groups: Lycopodiaceae, Selaginellaceae, and Isoetaceae. All living lycopsids are herbaceous or pseudo-herbaceous, but substantial trees evolved within Isoetales sensu lato during the Late Devonian (8). These arboreous species dominated tropical lowland coastal swamps during the Carboniferous.

Euphyllophytes

In eutracheophytes, monophyly of a euphyllophyte clade comprising living horsetails, ferns, and seed plants has broad support (28, 29, 62, 66, 72, 94, 107, 130), whereas the widely recognized "trimerophytes" are viewed as paraphyletic or polyphyletic. Some conflicting molecular data sets place elements of lycopsids within euphyllophytes (77) or resolve lycopsids as sister group to seed plants (76), but internal consistency of the data is low and neither hypothesis is supported by comparative morphology. The euphyllophyte stem group contains early fossils such as the "trimerophytes" *Psilophyton* and *Pertica* (66).

Within euphyllophytes there is strong support for monophyly of leptosporangiate ferns (93), lignophytes (paraphyletic "progymnosperms" plus monophyletic seed plants), and seed plants (72, 76, 109, 130), as well as for a horsetail clade comprising living *Equisetum* plus extinct *Calamites* and *Archaeocalamites* (129). Relationships among these groups and other smaller living taxa (Ophioglossales, Marattiales, Psilotales) and extinct taxa (Cladoxylales, Zygopteridales, Iridopteridales, Stauropteridales) remain highly ambiguous. For morphological data, one hypothesis views ferns sensu lato as monophyletic. The basal dichotomy in ferns is between a clade containing living eusporangiate ferns plus Filicales (fern crown-group) and a clade comprising Upper Devonian–Lower Carboniferous fernlike fossils of the Cladoxylales, Zygopteridales, and Stauropteridales (106). An alternative hypothesis shows ferns as paraphyletic to seed plants. Certain fernlike fossils, and possibly also living eusporangiate ferns, are depicted as more closely related to seed plants than to leptosporangiate ferns (107, 130).

PHYSIOLOGY AND BIOMECHANICS

Bryophytes

Mechanical constraints on early land plants were probably negligible, given their small body size, limited height, and presumed prostrate (thalloid) organization. Biophysical constraints were governed primarily by direct exposure to the atmosphere, prompting the acquisition of outer envelopes to restrict dehydration of the plant body (cuticle) and spores (sporopollenin) (87, 90, 95–97, 124). If the earliest terrestrial embryophytes morphologically resembled extant liverworts and hornworts, growth forms probably included relatively thin, dorsiventrally organized thalloid structures lacking specialized conducting or supportive tissues. Despite several reports of thalloid organisms in pre-Devonian sediments (36, 136), their status as embryophytes remains equivocal as a result of limited preservation.

Possibly the earliest upright cylindrical structures among embryophytes were erect gametophores embedded in thalloid structures. Because the cylindrical structures lacked specialized vascular tissues or hypodermal steromes, the diameter and height of such columns would have been severely restricted by potential conductance (105) and relied on turgor pressure to maintain an upright stance. The height of female sporophyte-bearing gametophores may have conferred greater dispersal potential than that possessed by forms sporulating directly from the thallus surface, allowing spores to reach uncolonized areas beyond the dense, extensive clonal mat.

Extant mosses reflect a transition from a thalloid to an axial growth form bearing leaflike appendages. Although some gametophyte axes show tissue differentiation into conducting cells (hydroids and leptoids), small axial diameters conferred considerable mechanical constraints. Nevertheless, such forms would have exceeded the height and vertical complexity of thalloid communities, in addition to developing photosynthetic leaflike appendages that were in some species connected to the water-conducting strand. In many extant moss species, dispersal of spores is effected by an elongate sporophyte seta that releases the spores slightly above the gametophyte layer. If such morphologies existed among "bryophytic" early land plants, the tiny columns constituting gametophyte axes and sporophytic setae represent mechanical innovations for trapping light and elevating the height of release of spores into the air (87, 90). The largely cylindrical design of such structures shows the earliest evidence of plant organs adapted to resisting bending forces in all lateral directions.

"Protracheophytes" and Rhyniopsids

Anatomically preserved early vascular plants, notably from the Rhynie Chert, provide sufficient anatomical information (cf. 35, 100) to construct accurate models of the biomechanical properties and growth forms of fossil plant stems (121–123). Prerequisites for such studies are reliable data on the distribution of contrasting tissues in axial transverse sections and well-preserved cell walls for comparison with those few living plant tissues already subjected to detailed biomechanical investigation (for methods see 120–123).

In the "protracheophytes" *Aglaophyton major* and *Horneophyton lignieri*, the flexural stiffness of upright axes and rhizomes was achieved by the maintenance of turgor pressure. The central conducting strands of such stems gave insignificant support, whereas the combined inner and outer cortex provided 98% of stem flexural stiffness in *Aglaophyton*. Quantitative estimates (12, 13) indicate that *Aglaophyton* could have reached a height of 19–33 cm before failing mechanically, compared with previous estimates of ca. 20 cm (42) and 50–60 cm (68). In *Horneophyton*, the parenchymatous cortex would have provided 98% of the flexural stiffness in stems possessing extrapolated maximum heights of 12–20 cm.

Both plants relied on the maintenance of turgor to retain an upright posture. Sculptured and banded cylindrical elements comprising the central conducting strand probably emulated true xylem tissue in facilitating water transport and thus maintaining the turgor pressure of the entire axis. However, these elements were positioned too centrally in the axis to be of direct mechanical significance, and the thickened and banded walls of the elements were more mechanically suited to withstanding collapse by internal negative pressures of the lumen than increasing the stiffness of the tissue.

Among rhyniopsids, biomechanical models of *Rhynia gwynne-vaughanii* indicate that the stele of derived, S-type tracheids (65) similarly offers little direct contribution to flexural stiffness. The stem could have reached a maximum height of 13–22 cm without mechanical failure, supported largely by the parenchymatous cortex [99% of the stem flexural stiffness (123)]. In none of the rhyniopsids tested does the stele contribute significantly to flexural stiffness of the stem. The phylogenetically heterogeneous fossils assigned to *Cooksonia* (e.g. *Cooksonia pertonii*) are also turgor systems, although those showing differentiation of an outer hypodermal sterome may be predominantly supported by this tissue. The banded tracheid elements that characterize the earliest tracheophytes, like those of "protracheophytes," would not have been suitable for mechanical support against bending forces, though they were better designed for resisting internal negative pressures and facilitating maintenance of turgor pressure.

In summary, the earliest land plant axes tested indicate that upright axes of protracheophytes and rhyniopsids were dependent on a maintained turgor pressure to remain upright and to prevent wilting. This must have represented an important constraint on stem height and on the ability to support both terminal and lateral appendages (i.e. end-loads and branches). The appearance of conducting tissues represented a marked physiological and mechanical innovation for maintaining turgor pressure. It made possible a self-supporting axial growth habit that could far exceed in height the light-trapping and spore dispersal capabilities observed among thalloid gametophores and smaller-bodied bryophytic gametophytes and sporophytes. Despite these innovations, early terrestrial plants with turgor-stabilized axes would have been confined to habitats with a continuous and sufficient water supply that provided relatively high humidity (100).

Eutracheophytes

Mechanical investigations of "zosterophylls" sensu lato and basal lycopsids reveal few further innovations for improving axial mechanical stability. The turgescent cortex represented the predominant tissue contributing to the flexural stiffness of the stem in the lycopsids *Asteroxylon mackiei* (>95%) and *Drepanophycus spinaeformis* (84–98%), and a similar figure is calculated for

those primitive species of *Zosterophyllum* that lack hypodermal steromes (121, 123). In both lycopsid species, the lobed steles probably exerted little influence in direct mechanical support with likely values of 2–5%, and in *Drepanophycus*, maximum calculated values of up to only 16% toward flexural stiffness of the whole stem (87, 88, 105, 123).

During early terrestrialization, columnar growth forms reliant on maintenance of turgor pressure probably saturated habitats with unlimited water availability. The potential complexity of growth forms and communities would have been severely constrained to sparsely branched forms no higher than 1 m. Further morphological innovations would have been necessary to colonize water-limited habitats. We hypothesize that this next step in terrestrial colonization also involved lineages possessing turgor-stabilized upright stems. The high selective pressures needed to maintain high turgor pressures under even temporary water stress eventually drove the evolution of more complex and effective root systems for water uptake as well as an increase in cutinization of the epidermis and cell wall thickening of subepidermal tissues for reducing water loss via transpiration. The evolution of subepidermal layers in response to selective pressure for colonizing areas with temporary water stress was also a fortuitous preaptation for mechanical stability.

The appearance of a hypodermal sterome in zosterophylls probably marks the first mechanical innovation away from support based mostly on maintenance of turgor pressure. The production, and modulation during growth, of a ring of cortical fibers in an otherwise parenchymatous cortex would have permitted a wider range of mechanically viable structures and generated diverse small-bodied growth habits analogous to those of extant herbaceous lycopsids (110).

In the primitive "trimerophyte" *Psilophyton dawsonii*, the hypodermal sterome of collenchymatous-sclerenchymatous elements contributes significantly to the flexural stiffness of the entire stem (values of 96–99% result from calculations inputting either collenchyma or sclerenchyma as the outer tissue of the biomechanical model) (123). The predicted maximum height for a stem of *P. dawsonii* of basal stem diameter 6 mm is 75–200 cm, with the central steles contributing little to the flexural stiffness of the stems (<5%). Stems of the derived (sawdonialean) zosterophyll *Gosslingia breconensis* (basal diameter 4 mm) yield critical buckling lengths of 51–140 cm, depending on the tissue type employed in the model to represent the newly acquired hypodermal sterome (over 96% when modeled as collenchyma and over 99% when modeled as sclerenchyma) (123). Similar values characterize derived *Zosterophyllum* species possessing hypodermal steromes (123).

Among the Devonian plants analyzed, perhaps the earliest empirical evidence of a significant contribution to flexural stiffness from xylem tissue is observed in the protolepidodendralean lycopsid *Leclercqia complexa*. Modeling the outer sterome as collenchymatous tissue yielded a critical buckling height of 85–142

cm (basal diameter 7 mm) (123). However, the contribution toward flexural stiffness of the xylem was still only 42%, compared with 56% from the collenchymatous hypodermal sterome.

Thus, prior to the appearance of extensive woody cylinders and periderm, mechanical stability among early land plants shifted from organizations relying on turgor systems to those employing hypodermal steromes. As well as affording the possibility of greater height, cylinders of collenchymatous or sclerenchymatous tissues were almost certainly important for supporting increasingly complex branch systems. Larger evapotranspiration surfaces would have required yet more efficient water conductance than was supplied by the primary steles in small-bodied early land plants. This may partially explain the relatively larger and mechanically more significant steles observed in *Leclercqia* and similar taxa.

Lignophytes

The appearance of secondary growth in the Middle Devonian, following the initial phase of land plant evolution, influenced water conductance, canopy formation, and mechanical support, and also prompted diversification in growth forms. The appearance of secondary xylem in eutracheophytes was probably linked to the water supply of megaphylls and selection for enlarging canopy surfaces, mechanically supported by hypodermal steromes. Biomechanical analyses indicate that secondary xylem in some early seed plants (and probably many early lignophytes) did not provide significant mechanical support; for example, the outer sparganum cortex in *Calamopitys* contributed over 85% to flexural stiffness of the stem and was essential for supporting the large megaphyllous leaves (111). Secondary xylem was confined within the primary body of the stem in many aneurophyte "progymnosperms" and basal seed plants, offering little mechanical strength but probably enhancing water conduction. Significant mechanical contributions from secondary xylem, such as that observed among archaeopteridalean "progymnosperms," were possible only following additional developmental innovations; the most notable was periderm formation, which permitted the wood cylinder to exceed the limits of the primary body of the stem (119).

PALEOECOLOGY

The evolution of ecological patterns during the Devonian parallels the appearance of morphological and phylogenetic structure and diversity. The Devonian record suggests a steady increase in ecological complexity at all spatial scales, from an alien simplicity at the beginning to nearly modern organization by the onset of the Carboniferous (25). Early Devonian ecosystems were composed of structurally simple plants with dynamically simple interactions (39). The

differences in dynamics at local and landscape scales were slight and difficult to differentiate. By the end of the Devonian, landscapes were varied and local assemblages of plants were structurally complex, with much greater diversity of body plans, life histories, and survival strategies (112).

Early and Middle Devonian

Studies of Early Devonian landscapes (34, 39, 63) indicate that supposed communities consisted of patches of opportunistic clonal plants. Given that typical coeval plants were characterized by rhizoids or rudimentary true roots, were supported by turgor pressure, and showed homosporous life histories, most vascular plants were probably constrained to wetter parts of the landscape. Within these humid habitats there may have been more niche partitioning than generally supposed. Recent work on paleosols (63) implies that vascular plants had gained the capacity to colonize some habitats with seasonal moisture availability, pointing to the evolution of physiological drought tolerance. Furthermore, the recognition of probable roots in weakly developed paleosols of streamside environments (44) indicates that some groups of Early Devonian plants may have been more complex morphologically than previously believed, having the ability to tap into deeper sources of groundwater.

The Rhynie Chert flora, now one of the best-understood floras of the entire Paleozoic, offers a remarkable window into an Early Devonian ecosystem. Although sporophyte architecture was simple, many sporophyte ecological strategies clearly coexisted, such as the ability of *Rhynia gwynne-vaughanii* to spread rapidly over a substrate via deciduous lateral branches (41). Sporophyte diversification was matched by a wide array of gametophyte morphologies that record many variations on aids to syngamy (64, 98), and fungi played a "modern" spectrum of roles in the ecosystem (133, 135). Unfortunately, the supposedly archetypal Rhynie Chert flora appears to be an unusual assemblage specialized for life in a low-pH, periodically flooded habitat (9); the flora may have included species secondarily reduced for aquatic life habits. The Chert thus allows only a small and potentially relictual perspective on the ecology of this crucial time. Recent paleosol studies revealed evidence for prototype "forests" as early as the Middle Devonian from waterlogged soils of New York State (31) and even in well-drained habitats from Antarctica (103). Lowland wetland macrofossil assemblages also demonstrate increasing plant-animal interactions; the evolution of terrestrial arthropods was proceeding rapidly and may have included herbivory (74, 117).

Late Devonian

The evolution of community and landscape complexity escalated dramatically during the Late Devonian. Empirical studies of the relationship between

megafloras and environments of deposition (17, 112) have revealed the initial phases of landscape partitioning by the major plant clades. Floras typical of swamps that were dominated by the fernlike plant *Rhacophyton*, and periswamp areas that included lycopsids, were distinct from floras of interfluves and drier parts of flood plains, dominated by the arboreous "progymnosperm" *Archaeopteris*. Seed-bearing "pteridosperms" appear to have originated in wetter parts of the landscape but then spread as opportunists into areas of disturbance and physical stress, including relatively arid habitats (108).

Pioneering studies using paleosols to resolve vegetational patterns across Late Devonian landscapes (17, 102) revealed a range of conditions on vegetated floodplains, from fully saturated to well drained and apparently dry. More recent investigations of in situ tree stumps and root casts in Late Devonian paleosols (31) indicated growth of *Archaeopteris* trees in seasonally wet but well-drained habitats. They further suggested that limited evidence of tree growth in the drier parts of floodplains may reflect both biological and physical processes that remove critical paleosol evidence rather than the absence of open forests. The development of rooting, and the evolution of forests and complex landscapes, apparently played a major role in determining global climatic and geochemical balances (3, 13, 44, 97).

Clearly, ecological and evolutionary changes were strongly linked and included both positive and negative feedback systems. The simple systems that characterized the Early and Middle Devonian apparently offered low resistance to invasion by species possessing major evolutionary innovations (25). Chaloner & Sheerin (21) documented the origin of nearly all major tissue and organ types during the Devonian, yet studies of Devono-Carboniferous plant biomechanics (87, 90, 119, 121, 122) indicate that the early plants were far from the biomechanical optima permitted by their tissues and organs (69). Studies of the developmental controls on Devonian plants (127) similarly suggest to some of us that initial increases in the complexity of development created many opportunities for morphological diversification with relatively few constraints. Maximum plant stature increased in many clades, along with the average diversity of organ types borne by any single species and the frequency of compound reproductive structures (70). Yet DiMichele et al (26) argued that the rate of increase in diversity of body plans slowed during the Late Devonian, as those architectures that characterize modern taxonomic classes and orders became clearly recognizable.

The Late Devonian encapsulated all the major body plans of vascular plants, each characterizing one of the major "modern" clades: seed plants, ferns, sphenopsids, and several groups of lycopsids (the lack of high-level innovation subsequent to the Early Carboniferous, with the arguable exception of the rise of the angiosperms, presumably reflects intensifying morphological and

ecological constraints). Available (albeit limited) evidence indicates that each major lineage of plants had established a distinct ecological centroid by the Early Carboniferous (24, 26) and that together they had occupied a wide range of terrestrial habitats (31, 103). The result was the development of strong incumbency effects, or "home-field advantage" (see 53, 92, 104), whereby ecological resource occupation suppresses the likelihood of survival of new variants (138).

CHARACTERS AND PHYLOGENY RECONSTRUCTION

Strengths of the Phylogenetic Framework

Cladogram topology determines the relationships of higher taxa (and hence their delimitation into monophyletic groups) and the relative (but not absolute) timings of the speciation events that correspond to the lineage divergences. But more importantly, a rooted cladogram also provides an explicit evolutionary hypothesis that describes not only sister-group relationships but also character-state transitions. The relative position of character-state transitions determines branch lengths—effectively, the amount of evolution between the speciation events encompassed by the cladogram. This allows measurement of the phylogenetic distance among analyzed taxa as disparity (the number of characters separating taxa through their most recent shared divergence point) rather than as raw similarity (10, 18, 47).

The enhanced ability to understand character evolution is at least as valuable as recognizing clades, particularly where the analysis includes morphological data (9–11). Advantages include the replacement of statistical correlations by phylogenetic correlations among characters, so that the active origination of a character state can be distinguished from mere passive inheritance from a shared ancestor. Also, the co-occurrence of transitions in two or more characters on the same branches can be interpreted in terms of the underlying evolutionary mechanism. Given a cladistic branch of several character-state transitions, two extremes of interpretation are possible. The saltation model (9–11) argues for a null hypothesis that the co-transitional characters are developmentally linked (pleiotropic) and reflect a single speciation event. In contrast, the adaptive model (27, 75) assumes that the accumulation of developmentally independent character states in response to selection pressures is gradual, and probably involves phylogenetically intermediate species absent from the sampled terminal taxa (either deliberately excluded or not yet known to science).

More recently, morphological phylogenies have been supplemented (or, in many cases, supplanted) by molecular phylogenies based on nucleic acid base sequences. These have proved especially valuable for comparing taxa that are

highly morphologically divergent, plesiomorphically simple, or secondarily simplified by reduction (and hence have insufficient clearly homologous structures) and for elucidating cases of parallel evolution (9). Often, nonmolecular characters are "mapped" across molecular phylogenies rather than included in the parsimony analysis (54); this approach is preferable for ecological and continuously variable phenotypic characters but is a suboptimal way of analyzing discrete phenotypic characters (10).

Constraints on Molecular Phylogenies

The insights gained by applying phylogenetic techniques to the Siluro-Devonian radiation are remarkable given the many severe handicaps. First, extinct Paleozoic plants do not yield DNA, and large swathes of pioneering land plants have left no close extant relatives—half of the Paleozoic plant groups traditionally regarded as taxonomic classes (albeit most paraphyletic) are "extinct." Thus, molecular attempts to understand the evolutionary origins of bryophytes would be greatly assisted by sequencing extinct rhyniophytes (9). Similarly, studies of fern origins need DNA from extinct cladoxylaleans, stauropteridaleans, and zygopteridaleans; studies of equisetaleans need DNA from extinct iridopteridaleans; and studies of gymnosperms need DNA from extinct "trimerophytes" and "progymnosperms."

Second, the untestability of such groups extends to experimental approaches that (*a*) separate ecophenotypic from genetically controlled variation, (*b*) directly observe ontogeny, and (*c*) test for pleiotropic and epigenetic behavior in key developmental genes.

Third, the Siluro-Devonian radiation occurred either quickly (≤ 100 million years; see 66) or very quickly (35–50 million years; see 11) relative to the much longer period separating the radiation from present-day floras testable by sequencing. Such deep, rapid radiations are difficult to capture using clocklike molecules; those changing fast enough to capture the relationships of the classes and orders emerging during the radiation are now oversaturated with mutations, and slower molecules not oversaturated changed too slowly to capture key events (10).

Within vascular plants, molecular and morphological assessments of phylogeny at the level of orders and below give similar results (93), 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 weakness of analyses based solely on living species (cf. 1, 76). Rather, future progress hinges on solving the relationships of several fossil groups of uncertain status (e.g., "trimerophytes," Cladoxylales, Zygopteridales) with respect to the living ferns, horsetails, and seed plants (66, 107). Also, combined analyses of molecular sequences from multiple loci, and large-scale structural

characteristics of the genome (e.g. introns, inversions; 94), may prove more informative than oversaturated base mutations when assessing deep phylogenetic patterns in land plants.

Thus, molecular data have been less helpful that might be supposed in unravelling the Siluro-Devonian radiation, though they have usefully revealed the fallacy of viewing certain pteridophytes as "living fossils" unchanged since the radiation. The most notable examples are the phenotypically simple Psilotaceae and Ophioglossaceae, which are actually secondarily reduced "pseudoplesiomorphs" rather than truly primitive relicts (9, 93). Sequencing has also revealed that among truly primitive lineages, such as the homosporous lycopsid *Huperzia*, most of the extant species may nonetheless be of recent origin and trivially distinct (139); longevity of clades does not necessarily equate with longevity of their constituent species.

Constraints on Morphological Phylogenies

Drawbacks to molecular analyses place unusually strong emphasis on morphological studies, particularly those that successfully integrate extant "living fossils" and decidedly dead fossils. If the plant fossil record is taken at face value, a punctuational pattern is evident—long periods of stasis are separated by much shorter periods of rapid change (43). Although this model has found favor with few neo-Darwinians, it is nonetheless congruent with the neo-Darwinian tenet that the dominant mode of selection is stabilizing selection, which precludes morphological change. The periods of change can be viewed either as (*a*) the result of strong directional selection or as (*b*) drift or saltation in the absence of directional selection. Whatever the underlying cause, the key point is that there is no "morphological clock," and as morphology is the direct manifestation of evolution, it is best placed to resolve rapid, deep radiations (10).

Unfortunately, two factors seriously limit our ability to resolve radiations morphologically. The first is the patchy fossil record. This can be exaggerated—the best of the conceptual whole plants, painstakingly reconstructed during over a century of paleobotanical research, are remarkably well understood (for example, see the near-complete evidence of morphology and reproductive morphology in presumed primitive taxa such as *Aglaophyton* in References 66, 67, 99). However, for less readily preserved groups such as the "bryophytes," and preservationally challenging periods such as the all-important Late Silurian–Earliest Devonian, the plants and the resulting data are fragmentary. Consequently, discussions of the Siluro-Devonian frequently focus on the overall assemblage of phenotypic characters available to land plants during particular time slices (6, 21, 40, 70). Although this approach can encompass a much greater proportion of the fossil record, only suites of characters packaged in a single plant (and thus the expression of a single genome) offer meaningful evolutionary

interpretations. The pivotal role played by fossils in many plant phylogenies (29, 65–67, 91, 109) is often due to unique combinations of characters in a single species (9, 126). Doyle (30) famously compared and contrasted species trees with gene trees, but we could equally well contrast species trees with "organ trees" based on very limited data. Given the propensity of plants for mosaic evolution, such trees have poor probabilities of accuracy (12).

The second limiting factor is the relative paucity, simplicity, and high variability of features observed in the early land plants. This constraint reduces the number of potential synapomorphic characters. Also, the combination of morphological–anatomical simplicity and the impossibility of direct experimentation on extinct species renders primary homology more difficult to test before phylogeny reconstruction, and the small number of characters renders secondary homology difficult to test after phylogeny reconstruction by the congruence test of parsimony. These problems weaken key phylogenetic assertions. For example, the now widely accepted separation of the lycophytes from the remaining eutracheophytes (5, 6) leaves a group—the euphyllophytes of Kenrick & Crane (66)—diagnosed primarily by homologues to megaphyllous leaves, yet these are questionably present in the basal members of the clade (the paraphyletic "trimerophytes." Similarly, the synapomorphies of the ferns appear disconcertingly "retrospective" (125) when sought in basal fernlike taxa such as Iridopteridales, Cladoxylopsida, Stenokoleales, Stauropteridales, and Zygopteridaceae sensu lato, wherein characters such as branching patterns and stelar anatomy are ill defined and highly homoplastic (107).

Not surprisingly, homoplasy levels appear high in cladistic studies of Devonian plants; they may in part reflect genuine evolutionary processes rather than erroneous prior assertions of homology, given the presumed relatively poor developmental canalization (9, 26, 127). Stein (127) recently advocated a "strong-inference" approach, modeled on cladistics, for identifying homology at the level of developmental processes. Expanding on the "telome theory" of Zimmermann (140), units of developmental dynamic defining a relationship between external and/or internal environmental cues and developmental outcomes are termed evolutionary developmental gates (EDGs). Each hypothesized EDG employs a "logical conditional" (by analogy with logic gates in programming theory) and is assembled into networks specifying a causal relationship between developmental processes and resultant morphological structures. EDG networks can be tested by comparison with evidence of known developmental processes, computer modeling, and evolutionary-phylogenetic comparisons between hypothesized ancestor-descendant pairs (or, potentially, among sister groups as three-item statements).

To illustrate this approach, Stein proposed four developmental modules underlying the morphology of a primitive Devonian shoot system (telome): (*a*)

establishment of self-recognition and auxin activity at the shoot apex; (b) normal cell division, modeled as an iterative and recursive process; (c) developmental switches and cascades leading to normal tissue of epidermis, cortex, and vascular tissues; and (d) establishment of new shoot apices by reassignment of self-recognition of the apex, during either bifurcation or de novo apex formation. Although more detail is required to enable important evolutionary comparisons with more derived taxa, conceptualizing homology as a developmental dynamic (as opposed to static, end-result morphology) may significantly improve our understanding of both phylogenetic relationships and underlying developmental/evolutionary causal agents during the primary land plant radiation (127). The resulting phylogenetic characters would be truly transformational and their degrees of dependency truly tested (8, 9).

INTERPRETING THE SILURO-DEVONIAN RADIATION(S)

Defining and Categorizing Radiations

Evolutionary radiations pose three primary challenges: (a) satisfactorily defining a radiation; (b) distinguishing among the "unholy trinity" of clade origination, radiation, and migration; and (c) identifying the underlying cause(s) of the radiation. There are many definitions of radiations, despite the fact that most authors use no explicit definition. Bateman (10) argued that a radiation could be defined most effectively using one or both of two properties: species diversity and phenotypic character diversity (the latter being strongly positively correlated with higher taxonomic diversity). Using either criterion, the best measure is the net surfeit of rate of gain over rate of loss in a specified clade during a specified time interval. And using either criterion, the fossil record clearly suggests that the first major radiation of vascular land plants peaked during the Early Devonian (66, 70).

Timing originations is more problematic; the major Devonian clades emerge, apparently fully formed at ca. 400 mya, from a putative period of preservationally discouraging worldwide marine regression in the Late Silurian (66). Extrapolation from their cladogram suggests that all of the major clades between liverworts and euphyllophytes evolved during that period, offering a maximum window of 35 my for a multiclass level radiation from a single putative terrestrialized ancestor (11). However, Kenrick & Crane (66, Figure 7.15; 67, Figure 4) controversially depicted the liverworts as evolving at the beginning of the preservational hiatus, but the remaining embryophytes diverging close to the end. Middle Devonian origins for the primitive, arguably fernlike clade of cladoxylopsids and relatives, and of the "progymnosperms," were followed

by Late Devonian origins of the "pteridosperms," sphenopsids, and bona fide derived ferns, together spanning at least a further 35 my. Other workers also support a more prolonged radiation (40, 57; WE Stein, personal communication, 1998).

Proportionally, the increase in species number during the Early Devonian radiation is great, but the total numbers involved are small relative to the radical increase in phenotypic diversity. Rapid, highly divergent increases in complexity accompanied by relatively low speciation rates (and thus many vacant niches) constitute a novelty radiation sensu Erwin (45; see also 24, 26). This contrasts strongly with a niche-filling adaptive radiation, which also occurs within a single clade but involves slower and less profound phenotypic diversification and much greater species diversification. Given that this contrast relies on decoupling of phylogenetic disparity and species diversity (the latter correlating more closely with niche differentiation), it is theoretically possible that an adaptive radiation could be mistaken for a novelty radiation—but only in the unlikely event of massive extinction of phenotypically intermediate species that left no fossil record (11).

Environmental Conquests and Ecological Constraints

In retrospect (and in comparison with the Cambrian radiation of metazoan animals in the marine realm; 33), a novelty radiation should have been expected for the initial diversification of vascular plants; competition (and thus selection) has little role to play in habitats profoundly undersaturated in species. The very high rate of generation of profound phenotypic mutants evident in the modern flora is almost wholly filtered out by competition in saturated ecosystems (11). However, in the early Devonian ecosystems, saltational mutants would have been produced even more frequently, given their weaker developmental canalization and, in the case of "bryophytes" and "protracheophytes" with long-lived haploid phases, their lack of buffering by second alleles of specific genes. Also, mere economic establishment (preferably but not essentially accompanied by reproductive success; 24) would have been accomplished relatively easily in the undersaturated habitats.

Theory would then require subsequent radiations within the land plants at lower taxonomic levels to increasingly approach the adaptive mode, as developmental canalization strengthened and ecospace became increasingly crowded, encouraging competition and thus discouraging the establishment of radically novel phenotypes; ecological constraints generate a negative feedback loop (11, 24, 26, 45, 138). At this threshold of phenotypic and ecological complexity, other evolutionary processes come into play. Decreases in phenotypic complexity, such as those generating many "living fossils," can drive evolution by resetting the phenotypic clock, allowing the lineage to exploit a different

(relatively uncompetitive) niche (9). In a fully occupied landscape, incumbent advantage can exclude theoretically fitter organisms, denied a foothold through the happenstance of prior occupation by other species (24, 53, 92, 104).

Once primary vacancy of niches in a habitat has been eliminated (saturation), opportunities for further evolution within that habitat focus on subdivision of existing niches or the occupation of secondary vacancies created by extrinsic environmental perturbations (ecological radiations). Preaptation (specifically, exaptation) becomes increasingly evolutionarily credible, as the repertoire of phenotypic characters increases and extrinsically driven niche vacancies allow potential functional switching (if we transfer focus from the physical landscape to the theoretical adaptive landscape of gene frequency variation, the latter temporarily becomes a "seascape," changing too rapidly to be tracked by changes in gene frequencies through populations; 10). Alternatively, new habitats must be invaded, a challenge generally requiring additional key innovations.

Overall, this model predicts a nested and fractal pattern of radiations, each generating more species and fewer higher taxa than the last as the average degree of phenotypic divergence between ancestor and descendant decreases. It also implies that attempts to explain the Early Devonian increases in diversity using adaptive landscapes (69, 89) may be misplaced; competition among plants was restricted by their tenuous hold on the abiotic landscape, which acted as a passive environmental filter for any viable novel phenotypes.

When compared with the above model, observed patterns of diversity suggest that Early and Middle Devonian ecology offered weak constraints to evolution relative to the Late Devonian, given that much of the land surface was either uncolonized or minimally occupied by vascular plants. Potential for positive feedbacks was also strong in areas such as nutrient cycling, creation of new resource spaces by morphological innovation, and the development of mutualistic interactions with the concomitantly expanding faunas and mycotas. The constriction of such opportunities was probably scale-dependent, beginning within certain resource pools while greater flexibility persisted in others. Landscape-scale opportunities for evolutionary innovation may have remained permissive, even when more local opportunies were becoming increasingly constrained.

Elusive Key Innovations

Erwin's (45) caution against uncritical acceptance of assertions of key innovations could have been written specifically for the Siluro-Devonian terrestrial radiation; most authors (e.g. 6, 21, 40, 57, 69, 70, 90, 95, 117, 124, 132) have either explicitly or implicitly identified one or more key innovations as crucial to the success of a particular taxonomic group. A bona fide key innovation should be a synapomorphy that was acquired immediately prior to an equally bona fide evolutionary radiation and can be shown to have been a far greater

stimulus to that radiation than any other synapomorphies acquired on the same phylogenetic branch.

Following the preferred phylogeny of Kenrick & Crane (66), embryophyte synapomorphies include multicellular sporophytes and the desiccation resistance conferred by both cuticles and sporopollenin-walled spores. The functional values of these characters for terrestrialization are clear, yet there is no evidence that any or all of these characters prompted an immediate radiation. This conclusion also applies to the stomates that are present in most stomatophytes (tracheophytes plus "bryophytes" excluding liverworts), and the pronounced axial gametophyte, terminal gametangia, and well-developed sporangiophore of the mosses plus tracheophytes clade. The basal members of the Polysporangiomorpha clade are "protracheophyte"-grade genera such as *Horneophyton* and *Aglaophyton*. They exhibit branched, independent sporophytes isomorphic with gametophytes that possess sunken archegonia. Similarly, the rhyniopsids, basal to the tracheophytes sensu lato, provide the first evidence of vascular tissue more sophisticated than bryophytic leptomes and of diversification in sporangial morphology and function, together with stronger sporophytic dominance in the life history. The unique combinations of characters in these extinct taxa provide us with key information about the sequence of character acquisition within the land plant clade, but again they did not clearly engender a profound increase in the diversity of either phenotypic characters or species.

Even the subsequent dichotomy into the Lycophytina and Euphyllophytina, and within the Lycophytina into the Lycopsida and more derived zosterophylls of the Sawdoniales, did not immediately add greatly to the overall diversity of characters. The relative indistinctness of these groups is well illustrated by the paraphyletic or even polyphyletic nature of genera such as *Cooksonia* ("protracheophyte" grade) and *Zosterophyllum* ("zosterophyll" grade sensu lato) and by the ambiguous placements of the basal members of the "trimerophyte" grade within the euphyllophytes (66).

Rather, overall character diversity and complexity increased more rapidly when the more derived members of these first-formed vascular plant lineages became sufficiently distinct to show parallel evolution. Examples include the transition from unipolar (rhizomatous) to bipolar (upright) growth and the associated development of vascularized roots; the acquisition of leaves sensu lato by lineages as phylogenetically disparate as mosses, lycopsids, and various euphyllophyte groups; increasingly contrasting maturation patterns and cross-sectional complexity in vascular strands, and their consequences for biomechanical properties; and the much greater diversity and complexity of meristems that allowed the emergence of distinct orders of branching and a wider variety of (often disposable) organs.

Later in the Devonian, these characters were supplemented with the development of at least the early stages of secondary growth in perhaps five lineages (66) and with at least the early stages of heterospory in perhaps ten lineages (9, 24). Secondary thickening conferred the ability to exploit the vertical dimension, which in turn allowed a switch from a patchwork of monotypic "lawns" to more diverse nonclonal communities. Heterospory was a key precursor for more effective resourcing of propagules, facilitating more K-selective strategies. Both are tempting as key innovations, but neither has been tested effectively in this role.

Summarizing the biomechanical data, developmental processes leading to improvement of mechanical properties were driven primarily by selection for sustaining water supply, following the colonization of new biotopes or after reaching a critical height or sustainable level of branch complexity. Examples of such innovations include physiologically inactive water-conducting elements, the hypodermal sterome, and secondary xylem. These features served as important preaptations for improving mechanical properties, permitting greater sustainable height and more complex branched architectures. Among early land plants, biomechanical analyses indicate that structures evolved primarily for improving water relations were repeatedly co-opted for mechanical support. This resulted in relatively simple but multifunctional tissues, which significantly improved the potential for successfully colonizing new habitats and occupying an increasing variety of niches.

The appearance of secondary growth (arborescence sensu 8) did not only have significance for increasing stability of upright stems and the possibility of producing truly large-bodied (arboreous) growth forms; it also allowed a far wider spectrum of growth architectures, the basis for niche-filling habits that ranged from fully self-supporting plants to lianas. Secondary growth also conferred the ability to adjust conductance and mechanical properties of the axial system in accordance with local environmental conditions. For this reason, many of the early land plants probably faced severe constraints in exploiting new areas and niches compared with later phases of the primary land plant radiation.

CONCLUSIONS

No one character can be accused of having engendered the Siluro-Devonian radiation. Even if attempts are made to tease apart the radiation into a nested sequence of smaller-scale radiations, key innovations are still not readily identified. It seems more likely that a critical mass of phenotypic characters accumulated in several clades, eventually offering sufficient flexibility to define and divide many niches. This process eventually generated the threshold number of

niches necessary to form communities that exhibited broadly modern ecological dynamics (if not modern species diversity; 25, 26).

There can be little doubt that, as this threshold approached, the physiological adaptations that enabled the putative (if very poorly preserved) original terrestrialization event into ever-wet soils continued to evolve, aiding the invasion of habitats of increasing degrees of abiotic hostility. This process may well have been aided by profound changes in the environment, viewed increasingly as fundamentally nonuniformitarian in character. In particular, the precipitous decrease in atmospheric CO_2 and concomitant (if slightly delayed) increase in O_2 (toward its Late Carboniferous maximum; 13, 85) should have greatly increased the effective balance between photosynthesis and respiration. Thus, the didactic distinction made by Bateman (7) between the physiological, anatomical, and morphological phases of plant evolution is revealed as simplistic.

Moreover, Bateman's (7) attribution of the ecologically driven "behavioral phase" of plant evolution to the post-Devonian is being progressively undermined as it becomes increasingly clear that paleobiologists have underestimated the role of interkingdom coevolution in early terrestrial ecosystems. For example, many enigmatic fossil taxa such as the Nematophytales (putative liverworts of the all-important Late Silurian preservation gap) and *Prototaxites* are increasingly perceived as fungal, and *Spongiophyton* (from the Early Devonian of Gaspé; 128) has a fungal architecture strongly comparable with modern lecanoralean lichens. Also, the recognition of both mycorrhizal (135) and saprophytic (133) fungi in the Rhynie Chert strongly supports arguments that fungi played an important mediating role allowing plants to accommodate to the rigors of terrestrial life (97, 116). When its diverse carnivorous and phytophagous arthropods (74) and representatives of the embryophyte sister group, the aquatic charophytes (134), are also considered, the Chert graphically illustrates that understanding the origin and early diversification of the land flora requires consideration of relationships among kingdoms, as well as relationships among classes and orders within Plantae.

Despite recent successes, additional reconstructions of fossil species, and genuinely worldwide floristic treatments of Siluro-Devonian plant communities and habitats, are badly needed. Nonetheless, even the available data are considerably better than those underpinning the much-vaunted studies of the marine Cambrian "explosion" of animal life, and at the level of exceptionally preserved Lagerstätten, the terrestrial Rhynie Chert undoubtedly ranks alongside the marine Burgess Shale (11, 18, 33, 55). Devonian ecosystems evidently constitute an excellent working laboratory for studying the relationships between the form and function of organisms during profound evolutionary radiations—especially primary radiations that occur across an ecologically undersaturated landscape and in a strongly nonuniformitarian environment.

Literature Cited

1. Albert VA, Backlund A, Bremer K, Chase MW, Manhart JR, et al. 1994. Functional constraints and *rbc*L evidence for land plant phylogeny. *Ann. Mo. Bot. Gard.* 81:534–67
2. Albert VA, Gustafsson MHG, Di Laurenzio L. 1998. Ontogenetic systematics, molecular developmental genetics, and the angiosperm petal. In *Molecular Systematics of Plants 2*, ed. D Soltis, P Soltis, JJ Doyle. London: Chapman & Hall. In press
3. Algeo TJ, Berner RA, Maynard JB, Scheckler SE. 1995. Late Devonian oceanic anoxic events and biotic crises: "rooted" in the evolution of vascular plants? *GSA Today* 5:45, 64–66
4. Arrington JM, Mishler BD, Lewis LA, Vilgalys RJ, Manos PS. 1997. A molecular phylogeny of the bryophytes and their relationships to the tracheophytes based on chloroplast 16S and 23S ribosomal-coding genes. *Am. J. Bot.* 84:12 (Abstr.)
5. Banks HP. 1975. Reclassification of Psilophyta. *Taxon* 24:401–13
6. Banks HP. 1981. Time of appearance of some plant biocharacters during Siluro-Devonian time. *Can. J. Bot.* 59:1292–96
7. Bateman RM. 1991. Palaeoecology. In *Plant Fossils in Geological Investigation: The Palaeozoic*, ed. CJ Cleal, pp. 34–116. Chichester UK: Horwood
8. Bateman RM. 1994. Evolutionary–developmental change in the growth architecture of fossil rhizomorphic lycopsids: scenarios constructed on cladistic foundations. *Biol. Rev.* 69:527–97
9. Bateman RM. 1996. Nonfloral homoplasy and evolutionary scenarios in living and fossil land plants. In *Homoplasy: The Recurrence of Similarity in Evolution*, ed. MJ Sanderson, L Hufford, pp. 91–130. London: Academic
10. Bateman RM. 1998. Integrating molecular and morphological evidence for evolutionary radiations. In *Advances in Plant Molecular Systematics*, ed. PM Hollingsworth, RM Bateman, RJ Gornall. London: Chapman & Hall. In press
11. Bateman RM, DiMichele WA. 1994. Saltational evolution of form in vascular plants: a neoGoldschmidtian synthesis. In *Shape and Form in Plants and Fungi*, ed. DS Ingram, A Hudson, pp. 63–102. Linnean Society Symposium Series 16. London: Academic
12. Bateman RM, Simpson NJ. 1998. Comparing phylogenetic signals from reproductive and vegetative organs. In *Advances in Plant Reproductive Biology*, ed. S Owens, P Rudall. London: Royal Botanic Gardens Kew. In press
13. Berner RA. 1993. Palaeozoic atmosphere CO_2: importance of solar radiation and plant evolution. *Science* 261:68–70
14. Berner RA, Canfield DE. 1989. A new model for atmospheric oxygen over Phanerozoic time. *Am. J. Sci.* 289:333–61
15. Bopp M, Capesius I. 1996. New aspects of bryophyte taxonomy provided by a molecular approach. *Bot. Acta* 109:1–5
16. Bremer K, Humphries CJ, Mishler BD, Churchill SP. 1987. On cladistic relationships in green plants. *Taxon* 36:339–49
17. Bridge JS, van Veen PM, Matten LC. 1980. Aspects of sedimentology, palynology and palaeobotany of the Upper Devonian of southern Kerry Head, Co. Kerry, Ireland. *Geol. J.* 15:143–70
18. Briggs DEG, Fortey RA, Wills MA. 1992. Morphological disparity in the Cambrian. *Science* 256:1670–73
19. Capesius I, Bopp M. 1997. New classification of liverworts based on molecular and morphological data. *Plant Syst. Evol.* 207:87–97
20. Chaloner WG. 1988. Early land plants: the saga of a great conquest. In *Proc. 14th Int. Bot. Congr.*, ed. W Greuter, B Zimmer, pp. 301–6. Königstein, Germany: Koeltz
21. Chaloner WG, Sheerin A. 1979. Devonian macrofloras. *Spec. Pap. Palaeont.* 23:145–61
22. Coen E, Meyerowitz EM. 1991. The war of the whorls: genetic interactions controlling flower development. *Nature* 353:31–37
23. Collinson ME, Scott AC. 1987. Factors controlling the organisation and evolution of ancient plant communities. In *Organisation of Communities Past and Present*, ed. GHR Gee, PS Giller, pp. 399–420. Oxford: Blackwell
24. DiMichele WA, Bateman RM. 1996. Plant paleoecology and evolutionary

inference: two examples from the Paleo-zoic. *Rev. Palaeobot. Palynol.* 90:223–47

25. DiMichele WA, Hook RW, et al. 1992. Paleozoic terrestrial ecosystems. In *Terrestrial Ecosystems Through Time*, ed. AK Behrensmeyer, JD Damuth, WA DiMichele, et al, pp. 205–325. Chicago: Univ. Chicago Press

26. DiMichele WA, Stein WE Jr, Bateman RM. 1998. Evolution of primordial patterns of resource partitioning among vascular land plant classes during the Late Paleozoic. In *Anatomy of Major Radiations*, ed. W Allmon. New York: Columbia Univ. Press. In press

27. Donoghue MJ. 1989. Phylogeny and the analysis of evolutionary sequences, with examples from seed plants. *Evolution* 43:1137–56

28. Doyle JA. 1998. Evolutionary radiation of the earliest seed plants. *Annu. Rev. Ecol. Syst.* 29:

29. Doyle JA, Donoghue MJ. 1986. Seed plant phylogeny and the origin of angiosperms: an experimental cladistic approach. *Bot. Rev.* 52:321–431

30. Doyle JJ. 1992. Gene trees and species trees: molecular systematics as one-character taxonomy. *Syst. Bot.* 17:144–63

31. Driese SG, Mora CI, Ellick JM. 1997. Morphology and taphonomy of root and stump casts of the earliest trees (Middle to Late Devonian), Pennsylvania and New York, U.S.A. *Palaios* 12:524–37

32. Duncan TM, Renzaglia KS, Garbary DJ. 1997. Ultrastructure and phylogeny of the spermatozoids of *Chara vulgaris* (Charophyceae). *Plant Syst. Evol.* 204:125–40

33. Eble GJ. 1998. The role of development in evolutionary radiations. In *Biodiversity Dynamics: Turnover of Populations, Taxa, and Communities*, ed. ML McKinney. New York: Columbia Univ. Press. In press

34. Edwards D. 1980. Early land floras. In *The Terrestrial Environment and the Origin of Land Vertebrates*, ed. AL Panchen, pp. 55–85. New York: Academic

35. Edwards D. 1993. Cells and tissues in the vegetative sporophytes of early land plants. *New Phytol.* 125:225–47

36. Edwards D. 1996. New insights into early land ecosystems: a glimpse of a Lilliputian world. *Rev. Palaeobot. Palynol.* 90:159–74

37. Edwards D, Davies KL. 1990. Interpretations of early land plant radiations: 'facile adaptationist guesswork' or reasoned speculation? In *Major Evolution-*

ary Radiations, ed. PD Taylor, GP Larwood, pp. 351–76. Oxford: Oxford Univ. Press

38. Edwards D, Duckett JG, Richardson JB. 1995. Hepatic characters in the earliest land plants. *Nature* 374:635–36

39. Edwards D, Fanning U. 1985. Evolution and environment in the Late Silurian–Early Devonian: the rise of the pteridophytes. *Philos. Trans. R. Soc. London Ser. B* 309:147–65

40. Edwards D, Selden P. 1992. The development of early terrestrial ecosystems. *Bot. J. Scotl.* 46:337–66

41. Edwards DS. 1980. Evidence for the sporophyte status of the Lower Devonian plant *Rhynia gwynne-vaughnii* Kidston and Lang. *Rev. Palaeobot. Palynol.* 29:177–88

42. Edwards DS. 1986. *Aglaophyton major*, a non-vascular land-plant from the Devonian Rhynie Chert. *Bot. J. Linn. Soc.* 93:173–204

43. Eldredge N, Gould SJ. 1972. Punctuated equilibria: an alternative to phyletic gradualism. In *Models in Paleobiology*, ed. TJM Schopf, pp. 82–115. San Francisco: Freeman

44. Ellick J, Driese SG, Mora CI. 1998. Very large plant and root traces from the Early to Middle Devonian: implications for early terrestrial ecosystems and atmospheric p(CO_2). *Geology* 26:143–46

45. Erwin D. 1992. A preliminary classification of evolutionary radiations. *Hist. Biol.* 6:133–47

46. Feist M, Feist R. 1997. Oldest record of a bisexual plant. *Nature* 385:401

47. Foote M. 1994. Morphological disparity in Ordovician–Silurian crinoids and the early saturation of morphological space. *Paleobiology* 20:320–44

48. Garbary DJ, Renzaglia KS, Duckett JG. 1993. The phylogeny of land plants: a cladistic analysis based on male gametogenesis. *Plant Syst. Evol.* 188:237–69

49. Geng B-Y. 1992. Studies on Early Devonian flora of Sichuan. *Acta Phytotax. Sinica* 30:197–211

50. Gensel PG. 1992. Phylogenetic relationships of the zosterophylls and lycopsids: evidence from morphology, paleoecology, and cladistic methods of inference. *Ann. Mo. Bot. Gard.* 79:450–73

51. Gensel PG, Andrews HN. 1984. *Plant Life in the Devonian*. New York: Praeger

52. Gensel PG, Johnson NG, Strother PK. 1991. Early land plant debris: Hooker's "waifs and strays"? *Palaios* 5:520–47

53. Gilinsky NL, Bambach RK. 1987. Asymmetrical patterns of origination and

extinction in higher taxa. *Paleobiology* 13:427–45

54. Givnish TJ, Sytsma KJ, ed. 1997. *Molecular Evolution and Adaptive Radiation.* Cambridge: Cambridge Univ. Press

55. Gould SJ. 1989. *Wonderful Life: The Burgess Shale and the Nature of History.* New York: Norton

56. Graham LE. 1993. *Origin of Land Plants.* New York: Wiley

57. Gray J. 1993. Major Paleozoic land plant evolutionary bio-events. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 104:153–69

58. Grenfell HR. 1995. Probable fossil zygnematacean algal spore genera. *Rev. Palaeobot. Palynol.* 84:201–20

59. Hedderson TA, Chapman RL, Rootes WL. 1996. Phylogenetic relationships of bryophytes inferred from nuclear encoded rRNA gene sequences. *Plant Syst. Evol.* 200:213–24

60. Hedderson TA, Cox CJ, Goffinett B, Chapman RL. 1997. Phylogenetic relationships among the main moss lineages inferred from 18S rRNA gene sequences. *Am. J. Bot.* 84:17 (Abstr.)

61. Hemsley AR. 1994. The origin of the land plant sporophyte: an interpolational scenario. *Biol. Rev.* 69:263–74

62. Hiesel R, von Haeseler A, Brennicke A. 1994. Plant mitochondrial nucleic acid sequences as a tool for phylogenetic analysis. *Proc. Natl. Acad. Sci. USA* 91:634–38

63. Hotton CL, Hueber FM, Griffing DH, Bridge JS. 1998. Early terrestrial plant paleoenvironments: an example from the Emsian of Gaspé, Canada. In *Early Land Plants and Their Environments,* ed. PG Gensel, D Edwards. New York: Columbia Univ. Press. In press

64. Kenrick P. 1994. Alternation of generations in land plants: new phylogenetic and palaeobotanical evidence. *Biol. Rev.* 69:293–330

65. Kenrick P, Crane PR. 1991. Water-conducting cells in early fossil land plants: implications for the early evolution of tracheophytes. *Bot. Gaz.* 152:335–56

66. Kenrick P, Crane PR. 1997a. *The Origin and Early Diversification of Land Plants: A Cladistic Study.* Smithsonian Series in Comparative Evolutionary Biology. Washington, DC: Smithsonian Inst. Press

67. Kenrick P, Crane PR. 1997b. The origin and early evolution of plants on land. *Nature* 389:33–39

68. Kidston R, Lang WH. 1921. On Old Red Sandstone plants showing structure, from the Rhynie chert bed, Aberdeenshire. Part IV. Restorations of the vascular cryptogams, and discussion of their bearing on the general morphology of the Pteridophyta and the origin of the organisation of land-plants. *Trans. R. Soc. Edinburgh* 52:831–54

69. Knoll AH, Niklas KJ. 1987. Adaptation, plant evolution, and the fossil record. *Rev. Palaeobot. Palynol.* 50:127–49

70. Knoll AH, Niklas KJ, Gensel PG, Tiffney BH. 1984. Character diversification and patterns of evolution in early vascular plants. *Paleobiology* 10:34–47

71. Konopka AS, Herendeen PS, Smith Merrill GL, Crane PR. 1997. Sporophytes and gametophytes of Polytrichaceae from the Campanian (Late Cretaceous) of Georgia, U.S.A. *Int. J. Plant Sci.* 158:489–99

72. Kranz HD, Huss VAR. 1996. Molecular evolution of pteridophytes and their relationships to seed plants: evidence from complete 18S rRNA gene sequences. *Plant Syst. Evol.* 202:1–11

73. Kranz HD, Miks D, Siegler M-L, Capesius I, Sensen W, Huss VAR. 1995. 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

74. Labandeira CC, Phillips TL. 1996. Insect fluid-feeding on Upper Pennsylvanian tree ferns (Palaeodictyoptera, Marattiales) and the early history of the piercing-and-sucking functional feeding group. *Ann. Entomol. Soc. Am.* 89:157–83

75. Lauder GV. 1996. The argument from design. In *Adaptation,* ed. MR Ruse, GV Lauder, pp. 55–91. New York: Academic

76. Manhart JR. 1994. Phylogenetic analysis of green plant *rbc*L sequences. *Molec. Phylogeny Evol.* 3:114–27

77. Manhart JR. 1995. Chloroplast 16S rDNA sequences and phylogenetic relationships of fern allies and ferns. *Am. Fern J.* 85:182–92

78. Manhart JR, Palmer JD. 1990. The gain of two chloroplast tRNA introns marks the green algal ancestors of land plants. *Nature* 345:268–70

79. McCourt RM, Karol KG, Guerlesquin M, Feist M. 1996. Phylogeny of extant genera in the family Characeae (Charales, Charophyceae) based on *rbc*L sequences and morphology. *Am. J. Bot.* 83:125–31

80. McElwain JC, Chaloner WG. 1995. Stomatal index and density of fossil plants track atmospheric CO_2 in the Palaeozoic. *Ann. Bot.* 76:389–95

81. Melkonian M, Surek B. 1995. Phylogeny of the Chlorophyta: congruence between ultrastructural and molecular evidence. *Bull. Soc. Zool. France* 120:191–208

82. Mishler BD, Churchill SP. 1984. A cladistic approach to the phylogeny of the "bryophytes." *Brittonia* 36:406–24

83. Mishler BD, Churchill SP. 1985. Transition to a land flora: phylogenetic relationships of the green algae and bryophytes. *Cladistics* 1:305–28

84. Mishler BD, Lewis LA, Buchheim MA, Renzaglia KS, Garbary DJ, et al. 1994. Phylogenetic relationships of the "green algae" and "bryophytes." *Ann. Mo. Bot. Gard.* 81:451–83

85. Mora CI, Driese SG, Colarusso LA. 1996. Middle to Late Paleozoic atmospheric CO_2 levels from soil carbonate and organic matter. *Science* 271:1105–7

86. Niklas KJ. 1976. Morphological and ontogenetic reconstruction of *Parka decipiens* Fleming and *Pachytheca* Hooker from the Lower Old Red Sandstone, Scotland. *Trans. R. Soc. Edinburgh* B69:483–99

87. Niklas KJ. 1992. *Plant Biomechanics: An Engineering Approach to Plant Form and Function.* Chicago: Chicago Univ. Press

88. Niklas KJ. 1994a. *Plant Allometry: The Scaling of Form and Process.* Chicago: Chicago Univ. Press

89. Niklas KJ. 1994b. Morphological evolution through complex domains of fitness. *Proc. Natl. Acad. Sci. USA* 91:6772–79

90. Niklas KJ. 1997. *The Evolutionary Biology of Plants.* Chicago: Chicago Univ. Press

91. Nixon KC, Crepet WL, Stevenson D, Friis E-M. 1994. A reevaluation of seed plant phylogeny. *Ann. Mo. Bot. Gard.* 81:484–533

92. Pimm SL. 1991. *The Balance of Nature?* Chicago: Chicago Univ. Press

93. Pryer KM, Smith AR, Skog JE. 1995. Phylogenetic relationships of extant ferns based on evidence from morphology and *rbc*L sequences. *Am. Fern J.* 85:205–82

94. Raubeson LA, Jansen RK. 1992. Chloroplast DNA evidence on the ancient evolutionary split in vascular land plants. *Science* 255:1697–99

95. Raven JA. 1984. Physical correlates of the morphology of early vascular plants. *Bot. J. Linn. Soc.* 88:105–26

96. Raven JA. 1994. Physiological analyses of aspects of the functioning of vascular tissue in early land plants. *Bot. J. Scotl.* 47:49–64

97. Raven JA. 1995. The early evolution of land plants: aquatic ancestors and atmospheric interactions. *Bot. J. Scotl.* 47:151–75

98. Remy W, Gensel PG, Hass H. 1993. The gametophyte generation of some early Devonian land plants. *Int. J. Plant Sci.* 154:35–58

99. Remy W, Hass H. 1996. New information on gametophytes and sporophytes of *Aglaophyton major* and inferences about possible environmental adaptations. *Rev. Palaeobot. Palynol.* 90:175–93

100. Remy W, Remy D, Hass H. 1997. Organisation, Wuchsform und Lebensstrategien früher Landpflanzen der Unterdevons. *Bot. Jahrb. Syst.* 119:509–62

101. Renzaglia KS, McFarland KD, Smith DK. 1997. Anatomy and ultrastructure of the sporophyte of *Takakia ceratophylla* (Bryophyta). *Am. J. Bot.* 84:1337–50

102. Retallack GJ. 1985. Fossil soils as grounds for interpreting the advent of large plants and animals on land. *Philos. Trans. R. Soc. London Ser. B* 309:105–42

103. Retallack GJ. 1997. Early forest soils and their role in Devonian global change. *Science* 276:583–85

104. Rosenzweig M, McCord R. 1991. Incumbent replacements: evidence for long-term evolutionary progress. *Paleobiology* 17:202–13

105. Roth A, Mosbrugger V, Neugebauer J. 1994. Efficiency and evolution of water transport systems in higher plants—a modelling approach. *Philos. Trans. R. Soc. London Ser. B* 345:137–62

106. Rothwell GW. 1994. Phylogenetic relationships among ferns and gymnosperms: an overview. *J. Plant Res.* 107:411–16

107. Rothwell GW. 1996. Phylogenetic relationships of ferns: a paleobotanical perspective. In *Pteridology in Perspective*, ed. JM Camus, M Gibby, RJ Johns, pp. 395–404. London: Royal Botanic Gardens Kew

108. Rothwell GW, Scheckler SE. 1988. Biology of ancestral gymnosperms. In *Origin and Evolution of Gymnosperms*, ed. CB Beck, pp. 85–134. New York: Columbia Univ. Press

109. Rothwell GW, Serbet R. 1994. Lignophyte phylogeny and the evolution of spermatophytes: a numerical cladistic analysis. *Syst. Bot.* 19:443–82

110. Rowe NP, Speck T. 1997. Biomechanics of *Lycopodiella cernua* and *Huperzia squarrosa*: implications for inferring growth habits of fossil small-bodied lycopsids. *Med. Nederlands Inst. Toegep. Geowetensch. TNO* 58:293–302

111. Rowe NP, Speck T, Galtier J. 1993. Biomechanical analysis of a Palaeozoic

gymnosperm stem. *Proc. R. Soc. London (B)* 252:19–28

112. Scheckler SE. 1986. Geology, floristics and paleoecology of Late Devonian coal swamps from Appalachian Laurentia (USA). *Ann. Soc. Geol. Belg.* 109:209–22

113. Schopf JW. 1994. Disparate rates, differing fates: tempo and mode of evolution changed from the Precambrian to the Phanerozoic. *Proc. Natl. Acad. Sci. USA* 91:6735–42

114. Schuster RM. 1984. Evolution, phylogeny and classification of the Hepaticae. In *New Manual of Bryology*, ed. RM Schuster, pp. 892–1070. Japan: Hattori Botanical Laboratory

115. Scotese CR, McKerrow WS. 1990. Revised world maps and introduction. In *Palaeozoic Palaeogeography and Biogeography*, ed. WS McKerrow, CR Scotese, pp. 1–12. Geol. Soc. Lond. Mem. 12

116. Selosse M-A, Le Tacon F. 1998. The land flora: a phototroph-fungus partnership? *Trends Ecol. Evol.* 13:15–20

117. Shear W. 1991. The early development of terrestrial ecosystems. *Nature* 351:283–89

118. Smoot EL, Taylor TN. 1986. Structurally preserved fossil plants from Antarctica: II. A Permian moss from the Transantarctic Mountains. *Am. J. Bot.* 73:1683–91

119. Speck T, Rowe NP. 1994. Biomechanical analysis of *Pitus dayi*: early seed plant vegetative morphology and its implications on growth habit. *J. Plant Res.* 107:443–60

120. Speck T, Rowe NP. 1998. Biomechanical analysis. In *Fossil Plants and Spores: Modern Techniques*, ed. TP Jones, NP Rowe. London: Geol. Soc. Lond. Spec. Vol. In press

121. Speck T, Vogellehner D. 1988. Biophysical examinations of the bending stability of various stele types and the upright axes of early 'vascular' land plants. *Botanica Acta* 101:262–68

122. Speck T, Vogellehner D. 1992. Biomechanics and maximum height of some Devonian land plants. In *Palaeovegetational Development in Europe*, ed. J Kovar-Eder, pp. 413–22. Vienna: Museum of Natural History

123. Speck T, Vogellehner D. 1994. Devonische Landpflanzen mit und ohne hypodermales Sterom—eine biomechanische Analyse mit Überlegungen zur Frühevolution des Leit- und Festigungssystems. *Palaeontographica* B233:157–227

124. Spicer RA. 1989. Physiological characteristics of land plants in relation to environment through time. *Trans. R. Soc. Edinburgh* B80:321–29

125. Stein WE. 1983. *Iridopteris eriensis* from the Middle Devonian of North America, with sytematics of apparently related taxa. *Bot. Gaz.* 143:401–16

126. Stein WE. 1987. Phylogenetic analysis and fossil plants. *Rev. Palaeobot. Palynol.* 50:31–61

127. Stein WE. 1998. Developmental logic: establishing a relationship between developmental process and phylogenetic pattern in primitive vascular plants. Submitted

128. Stein WE, Harmon GD, Hueber FM. 1993. Lichens in the Lower Devonian of North America. *Geol. Soc. Amer. Abstr.* 25:82

129. Stein WE, Wight DC, Beck CB. 1984. Possible alternatives for the origin of Sphenopsida. *Syst. Bot.* 9:102–18

130. Stevenson DW, Loconte H. 1996. Ordinal and familial relationships of pteridophyte genera. In *Pteridology in Perspective*, ed. JM Camus, M Gibby, RJ Johns, pp. 435–67. London: Royal Botanic Gardens Kew

131. Stewart WN, Rothwell GW. 1993. *Paleobotany and the Evolution of Plants*. Cambridge: Cambridge Univ. Press. 2nd ed.

132. Taylor TN. 1988. The origin of land plants: some answers, more questions. *Taxon* 37:805–33

133. Taylor TN. 1990. Fungal associations in the terrestrial palaeoecosystem. *Trends Ecol. Evol.* 5:21–25

134. Tayor TN, Remy W, Hass H. 1992. Fungi from the Lower Devonian Rhynie Chert: Chytridiomycetes. *Am. J. Bot.* 79:1233–41

135. Taylor TN, Remy W, Hass H, Kerp H. 1995. Fossil arbuscular mycorrhizae from the early Devonian. *Mycologia* 87:560–73

136. Taylor TN, Taylor EL. 1993. *The Biology and Evolution of Fossil Plants*. Englewood Cliffs, NJ: Prentice-Hall

137. Taylor WA. 1996. Ultrastructure of Lower Paleozoic dyads from southern Ohio. *Rev. Palaeobot. Palynol.* 92:269–80

138. Valentine JW. 1980. Determinants of diversity in higher taxonomic categories. *Paleobiology* 6:444–50

139. Wikström N, Kenrick P. 1997. Phylogeny of Lycopodiaceae (Lycopsida) and the relationships of *Phylloglossum drummondii* Kunze based on *rbc*L sequences. *Int. J. Plant Sci.* 158:862–71

140. Zimmermann W. 1965. *Die Telomtheorie*. Stuttgart: Fischer