

## Plant paleoecology and evolutionary inference: two examples from the Paleozoic

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Received 5 September 1994; revised and accepted 20 December 1994

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### Abstract

Paleobotany can contribute much to evolutionary scenario-building. Here, we use two case studies — the Devonian-Carboniferous vascular plant radiation and the largely coeval evolution of heterosporous from homosporous life histories — to examine the interface between phylogeny and ecology. Our observations challenge some tenets of the neo-Darwinian orthodoxy, notably the assumed role of competition mediated selection as an active driving force, rather than a passive filter, of evolution.

The Devonian-Carboniferous class-level radiation of vascular plants was prompted by attainment of a complexity threshold and delimited the morphological envelope that enclosed an apparently fractal pattern of subsequent, lower level radiations. The contrast of low speciation rates with exceptionally high rates of phenotypic divergence in the Devonian suggests a non-adaptive “novelty” radiation, perhaps reflecting saltational evolution via “hopeful monsters”. Successive lower level radiations were more constrained by the ecological hierarchy that resulted from progressive niche differentiation and saturation. This in turn reflected increased speciation rates, thereby completing a well defined negative feedback loop in the coevolution of phenotypic and ecological differentiation.

Heterosporous life histories evolved independently in at least ten lineages. Heterospory allows the sporophyte to impose, via differential development, a single fixed gender on each gametophyte prior to spore release. Although the resulting life history is less flexible than homosporous, which on recent evidence includes a range of subtle and sophisticated strategies, it promotes the sporophyte as the primary target for selection. Gametophytes effectively perform the role of gametes and are released into the environment prior to fertilization, thus favoring aquatic-amphibious habitats resistant to occupation by homosporous pteridophytes; terrestrial heterospory requires apomixis. Although the profound iteration of heterospory implies a strong adaptive advantage, repeated gradual evolution via inferior intermediates exhibiting exosporous heterospory seems unlikely.

Seed-plant success reflects economic efficiency and the subsequent evolution of effective pollination syndromes, rather than integumentation of the ovule. Major radiations of heterosporous lineages and subsequently of seed-plants required perturbation of pre-existing communities by extrinsic environmental changes rather than genuinely competitive displacement. This typical manifestation of “home-field advantage” further emphasizes the intimate relationship between phylogeny and ecology, and allows us to make predictions that can be tested by further paleobotanical research.

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## 1. Introduction

### 1.1. Neo-Darwinism in paleobiology

Fossils of vascular land plants reveal a record of vast morphological change and enormous taxic diversification following humble beginnings in the Silurian. Historically, paleobotanists have applied and extrapolated the tenets of neo-Darwinian gradualism to explain the increase in plant structural complexity. The focus has been on morphological transformation, considered in isolation from the environment and often described in terms of individual organs rather than in a whole-plant context. Most theorizing has been limited to application of the axioms of gradual change to cases of presumed ancestor–descendant relationship, often in progressive linear sequences of several taxa (e.g. Mägdefrau, 1956). With a few notable exceptions (e.g. Stidd, 1980), the phylogenies themselves are usually determined intuitively from the very same expectations of gradual descent with modification. As a consequence, the literature is filled with numerous examples of hypothetical intermediates, inferred “mechanisms” such as phyletic slide and recurvation, and, perhaps most seriously, the misuse of the population-level concept of selection pressure, treating it as a creative force rather than as a short-hand term describing the process of sorting **existing** alleles by natural selection. In fact, the plant fossil record has rarely been used to enlarge our understanding of evolution as a bona fide process.

With the rise of cladistics and other explicit means of objectively assessing relationships (Stein et al., 1984; Stein, 1987; Crane, 1990; Bateman et al., 1992; Doyle and Donoghue, 1992; Gensel, 1992; Nixon et al., 1994) the potential circularity between phylogeny reconstruction and evolutionary inference has been broken. In theory, modern phylogenetic methods permit a pattern to be determined without specific mechanistic assumptions; explanatory hypotheses compete post hoc for the best phylogenetic fit. Admittedly, analysis of pattern rarely specifies a single evolutionary process; rather it constrains the range of possibilities by falsifying some potential processes (e.g. Frumhoff and Reeve, 1994; Leroi et al., 1994). At

the same time the breadth of morphological hypotheses has been enriched by modern concepts imported from developmental biology (Rothwell, 1987; Trivett and Rothwell, 1988; Mosbrugger, 1990; Stein, 1993; Bateman, 1994; Bateman and DiMichele, 1994a). Results include greater emphasis on macroevolution (Wight, 1987; DiMichele et al., 1989; Bateman, 1994; Bateman and DiMichele, 1994b), challenges to the concept of competition as the all-pervasive driving mechanism in plant evolution (Scott and Galtier, 1985; DiMichele et al., 1987; Valentine et al., 1991), and the recognition that selection may act more often as a passive filter than as an active vector of evolution (Rothwell, 1987).

These great strides have been made in a relatively few years, yet one major aspect of a complete picture remains poorly understood ecology (more specifically, the particular habitat preferences and limited ecological amplitudes of each species). Commonly, ecology is assumed to influence evolution through competition (e.g. Knoll, 1986), though assertions about competition rely on the usually untested assumption that species share one or more common limiting resources. Of course, inferring the ecological preferences of long-extinct plants can be an obtuse exercise, but it is possible (e.g. Scott, 1978; Bateman, 1991; Phillips and DiMichele, 1992). Certainly, such inference is essential if paleobotany is to develop credible explanations for the evolution of plant form. Ecology is even more central in attempts to use fossil plant data to test or elaborate evolutionary theories. To use the classic analogy of Hutchinson (1965), organisms are the actors in a great evolutionary play, and ecology is the (ever-changing) stage.

In this essay we adopt an unashamedly critical and polarized position on the issue of evolutionary dynamics, stressing broad macroevolutionary patterns over examples of intra-generic speciation. Our objective is not to deny gradual microevolution. Rather, we wish to emphasize the role of ecology in dictating new and sometimes alternative explanations for significant events in plant evolution. Sadly, paleobotany barely participated in the great punctuated equilibrium debate of the 1970s and 1980s. Now that ecology has come of age in

paleontology, paleobotanists again are presented with an opportunity to integrate the plant fossil record with basic studies of evolutionary processes. This can be done only by escaping the constraints of theoretical orthodoxy, notably the uncritical acceptance of insensibly gradual, competitively driven evolutionary change without serious consideration of the important ecological component.

### 1.2. *Scope and objectives*

The goal of this essay is to examine the role of paleoecology in constructing evolutionary explanations for taxic–phylogenetic, morphological, and biogeographic patterns. We will advocate greater awareness of the vast amount of accessible ecological data and incorporation of “ecological thinking” into paleobotanical scenario-building.

Typical use of the term “ecology” is undesirably general; it can refer to the autecologies of individual species, the central environmental tendencies of an entire clade of organisms, or the dynamic interactions of species at the community, landscape, or biome levels. Excluded, however, are speculations about environmental “selection pressures” as creative forces. Ecological considerations, when inferred independently of the organisms in question, can constrain evolutionary scenarios in many ways, some obvious but others more cryptic. Our chosen examples focus on two areas.

First, in reconstructing the controls on major morphological transformations, environmental information may modify the interpretation of the timing and causes of morphological differences between presumed ancestor and descendant(s). The evolution of heterosporous plants from homosporous ancestors and the ultimate evolution of seed plants serve to test the idea of a progression of biologically superior (or better adapted) life histories.

Second, the fossil record contains important examples of major evolutionary radiations in which both the stem lineages and the limits of a morphological envelope are established early, followed by relatively routine filling of the morphological space via less profound speciation events. The Devonian–Mississippian radiation of vascular

plants, arguably the most profound evolutionary diversification in land-plant history, demonstrates that radiations can be self-limiting, constrained by the interaction of ecospace and morphological complexity.

## 2. **Case study I: Ecological constraints on adaptive scenarios — evolution of heterospory and the seed habit**

### 2.1. *Background: the nature of heterospory*

With the exception of the tree ferns, nearly all numerically abundant and taxonomically diverse lineages of trees have been heterosporous. This observation demonstrates irrefutably that heterothallic heterospory, in which male and female sex organs are produced on separate gametophytes derived from small and large sized spores, respectively (for detailed terminology see Bateman and DiMichele, 1994b), confers significant ecological advantages. Phylogenetic patterns suggest that heterospory evolved independently at least ten times among vascular plants (Bateman and DiMichele, 1994b; Bateman, 1995), including the zosterophylls, selaginellalean plus rhizomorphic lycopsids, equisetaleans, several filicalean ferns, and several progymnosperms plus their descendants, the seed plants (Fig. 1). Thus, there was no single case of directional selection generating a highly adapted heterosporous lineage from which all subsequent heterosporous lineages diverged. The strongly iterative nature of the life history lends credence to the view that it is an inevitable outgrowth of homosporous ancestors and that it confers a significant adaptive advantage (e.g. Chaloner and Pettitt, 1987).

Inspection of the fossil record leads to three generally accepted conclusions: heterospory is an evolutionarily successful life history, free-sporing heterospory is clearly derived relative to homosporous (as is the seed habit relative to heterospory, however these terms are defined), and the homosporous–heterosporous–seed habit transition sequence represents a progressive increase in reproductive sophistication (Table 1). The evolution of the seed has been the focal point of a series of intermittently

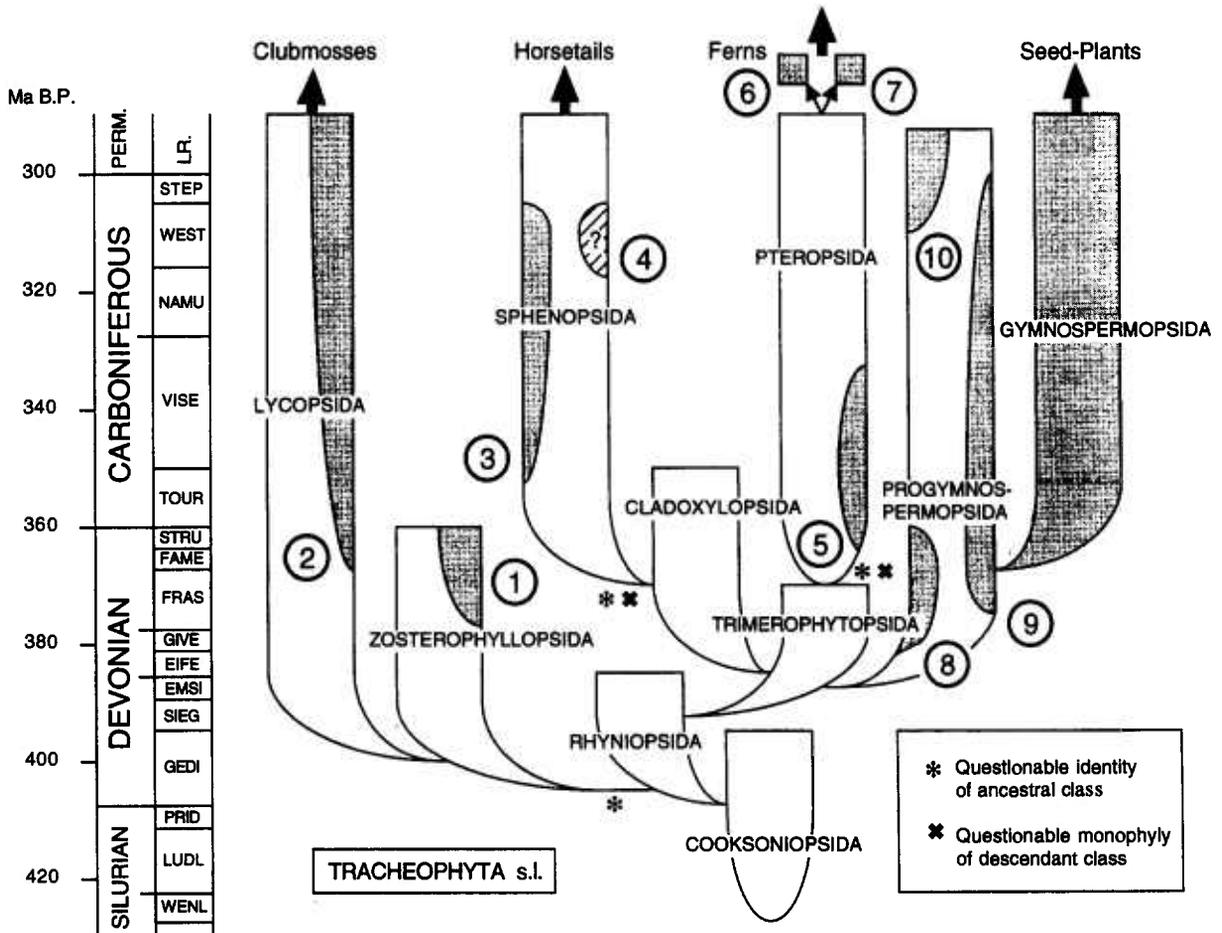


Fig. 1. Tentative non-numerical phylogeny of all tracheophyte classes, showing putative ancestor–descendant relationships plus divergence dates, and occurrence of heterospory. Note that (1) the entire post-cooksonioid radiation occurred within the Devonian, and (2) a minimum of ten independent origins of heterospory is indicated by the stippling, taking into account recent assertions of monophyly for the Salviniales plus Marsileales based on morphological (Rothwell and Stockey, 1994) and molecular (e.g. Hasebe et al., 1994) data. (1) Some Barinophytales; (2) all Sellaginellales plus all rhizomorph-bearing lycopsids (*Isoetes* s.l.); (3) some Equisetales; (4) some Sphenophyllales (doubtful); (5) some Stauropteridales; (6) all Hydropteridales (Salviniales plus Marsileales); (7) some Filicales (e.g. *Platyzoma*); (8) some Aneurophytales; (9) some Archaeopteridales, ?all Protopytales, all Cecropsidales; (10) some Neogerathiales. (Modified after Bateman and DiMichele, 1994b, fig. 11.)

contentious debates (Thomson, 1934; Andrews, 1963; Pettitt and Beck, 1968; Pettitt, 1970; Steeves, 1983; Chaloner and Pettitt, 1987; DiMichele et al., 1989; Chaloner and Hemsley, 1991). Recently, the increasing rigor of phylogenetic reconstructions has sharpened the debate on ancestry (Meyen, 1984; Beck, 1985; Stein and Beck, 1987; Donoghue, 1989; Donoghue and Doyle, 1989; Galtier and Rowe, 1989; Crane, 1990; Doyle and Donoghue, 1992; Bateman and DiMichele, 1994b; Rothwell

and Serbet, 1994). Heterospory has received less conceptual attention (Willson, 1981; Haig and Westoby, 1988b; DiMichele et al., 1989; Bateman and DiMichele, 1994b), and most paleobotanical scenarios have treated it merely as an intermediate stage in the evolution of the seed.

Nearly all studies of the evolution of heterospory have focused on structure alone. Little attention has been paid to the ecological preferences of the taxa or life histories in question, or even to the

breadth of variation in the ancestral, supposedly primitive homosporous condition. This problem has been compounded by an insistent desire to place all known morphological forms (or classes of forms) into continuous progressions, despite the lack of formal phylogenetic support for such schemes (Andrews, 1963; Tiffney, 1981; Chaloner and Pettitt, 1987; Chaloner and Hemsley, 1991). These scenarios are rooted in an acceptance of gradual transformation of form, driven by “selective pressures” for functionally superior morphologies. The foremost assumption of this form of gradualism is competition. Successive, increasingly complex morphologies must be competitively superior to the ancestral forms, and increase in complexity must be associated with increase in fitness.

However, for competition to favor the rise of the advanced architectures at the expense of the primitive ancestral forms, there must be little or no ecological differentiation between ancestor and descendant. Unfortunately, the details needed to fit this view to even the most rudimentary evolutionary models are rarely given. Are such transformations allopatric, or is mass selection across entire species involved? What are the environmental conditions under which the transformation occurred, and what kinds of advantages are conferred by the derived morphologies under those circumstances?

## 2.2. Ecological constraints and the homosporous–heterosporous transition

Heterosporous plants evolved from ancestors that possessed a remarkably flexible and advanced reproductive strategy, namely homosporous (Table 1). A survey of recent literature on extant pteridophytes (Willson, 1981; Haig and Westoby,

1988a; Sheffield, 1994; Bateman and DiMichele, 1994b) indicates a wide range of variation within the basic homosporous pattern of alternation of free-living generations. For example, in many fern species the gametophytes rely on chemical signals (antheridiogens) to mediate population-level sex ratios and control the timing of gametogenesis and syngamy, and in most species at least some gametophytes retain their potential for self-fertilization. Thus, the gametophyte generation is closely attuned to local environmental conditions and can effectively regulate its reproductive functions. The main disadvantage of homosporous seems to be the need for ecological coordination between the gametophyte and sporophyte generations. In particular, the sporophyte must grow at or near the point of syngamy, a location dictated by the gametophyte. Thus, evolution away from the norm of mesic, moist environments is unusual. The evolution of aquatic–amphibious habit on the part of both sporophyte and gametophyte seems to have been particularly demanding once a fully terrestriated, homosporous life history was established. “Return” to the water requires numerous changes in morphology and physiology of both sporophyte and gametophyte. However, as free-living, independent life history phases, regulation of development and phenotype, and the selective factors acting on that phenotype are partially (largely?) independent, even though the two phases share a common genome. Increased terrestriation, in contrast, is limited mainly by syngamy, which can be accommodated in many ways, including through apomixis. Overall, therefore, homosporous is an effective life history in terra firma habitats. Limits on homosporous ferns, lycopsids, and sphenopsids in modern habitats may reflect the limitations of vegetative architecture and “house-

Table 1  
Characteristics of four categories of vascular plant life histories

	Gametophyte	Dominant phase	Sex ratio	♂/♀ control: timing of gametogenesis	Functional dependence of ♂/♀ on ⊕;
Homosporous	Free living	Codominance	Labile	Labile, ♂/♀ controlled	Independent
Anisospory	Free living	Codominance	Fixed	Labile, ♂/♀ controlled	Independent
Heterosporous	Endosporic	Sporophyte	Fixed	Mainly ⊕ controlled	Independent
Seed habit	Endosporic	Sporophyte	Fixed	Wholly ⊕ controlled	Dependent

keeping” physiology more than reproductive biology. The common view of homospority as an inferior life history waiting to be displaced is difficult to justify, particularly in mesic habitats.

In contrast with homospority, the gametophytes of heterosporous plants are strictly unisexual (Fig. 2). Sex ratios are determined by the sporophyte epigenetically (developmentally rather than through sex chromosomes) during sporangial maturation. In effect, microspores and megaspores function as gametes. The way gametophytes

respond to environmental variability, including conditions unfavorable for gametogenesis, is to enter diapause (suspended development) immediately after release and before “germination” (note that this ability was probably available in their homosporous ancestors – spores of most extant ferns accumulate in the soil as spore banks; Dyer and Lindsay, 1992). This is a remarkably inflexible life-history strategy, given that spores are released directly into the environment without the potential to form a photosynthetic, free-living, indepen-

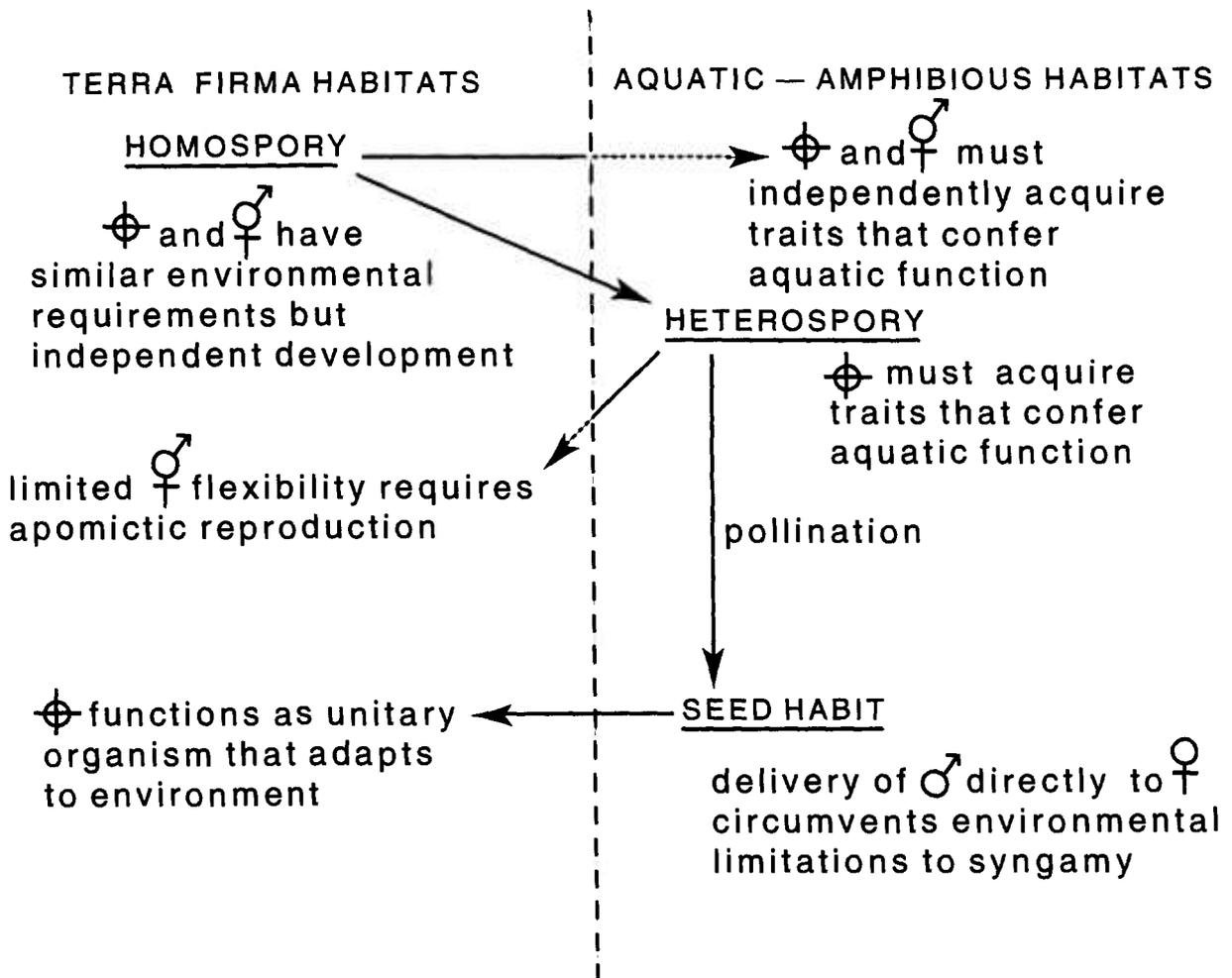


Fig. 2. Constraints on life history evolution in terra firma and aquatic-amphibious habitats, as the sporophyte gradually co-opts the gender control previously exercised by the gametophyte. Note especially the ineffectiveness of (1) homospority in aquatic-amphibious environments and (2) heterospority in terra firma habitats without apomixis or reliable pollination. Dotted lines indicate transitions that have been rare in plant history due to ecological constraints. Solid lines suggest the morphological-ecological history leading from homosporous plants to seed plants.

dently self-supporting individual. How then did free-sporing heterosporous plants become successful ecologically? Current evidence suggests that heterosporous plants have been ecologically dominant only in environments with ample free moisture, notably aquatic and amphibious habitats. In such environments spores-as-gametes are most likely to encounter conditions favorable for fulfilling their function, though even here the extant Salviniaceae and Marsileaceae possess sophisticated sporocarps that allow a resting phase following sporogenesis. Admittedly, some species of extant heterosporous plants grow in mesic to xeric habitats, but in these environments apogamy predominates (DiMichele et al., 1989; Bateman and DiMichele, 1994b).

What advantage is conferred by a free-sporing heterosporous mode of reproduction? The most obvious characteristic is unity of form. The sporophyte is the dominant phase of the life cycle and becomes the focus of selection on vegetative function and environmental tolerance (Table 1, Fig. 2). However, because the gametophytes and gametes must be released into the environment, the gametophyte generation continues to constrain the conditions under which the system can function effectively. In gaining the advantages of a compressed life cycle, the potential to colonize terra firma habitats is severely curtailed by the sporophytically fixed sex ratio, the inability of gametophytes to adjust to most environmental vagaries, and the strict requirement for moisture during spore germination and syngamy.

Although many reviewers have appealed to an “intermediate” evolutionary stage between homosporous and heterosporous (of the heterothallic, endosporic variety), we regard heterosporous with free-living gametophytes as one of the great paleobotanical fantasies. These are imagined intermediate forms between homosporous ancestors and each of the independent origins of heterosporous. In most interpretations of neo-Darwinism, first principles dictate gradual transformation of form and hence an insensible series of intermediates. A supposed vindication of that expectation was the discovery of a rare filicalean fern *Platyzoma* (Tryon, 1964) that possesses such a life history. Although Sussex (1966) soon warned against treating *Platyzoma* as

anything more than an evolutionary curiosity, it nonetheless has risen to cult status. However, survey of the modern flora reveals no other examples of this life history. Examination of the ecological implications of the platyzomoid life history indicates that heterosporous with free-living gametophytes bears all the disadvantages of both homosporous and heterosporous with the advantages of neither: the ecological–evolutionary tension between the sporophyte and gametophyte remains, and the gametophytes are unable to adjust the sex ratio and timing of reproduction in response to environmental cues. If other such “intermediates” existed they are likely to have occurred as small, ephemeral populations and, therefore, on statistical principles alone were unlikely to survive for long periods. Allopatric isolates may be common products of the dynamics of the evolutionary process, but few appear to survive to establish long-lived clades; the ecological handicaps of the platyzomoid life history thus combine with the chance elements of evolution to make it doubly unlikely that such derived lineages would found new clades.

Homosporous in modern lower vascular plants encompasses a complex array of functional morphologies, some quite sophisticated in their control of sexual reproduction. Most of the biochemical adaptations found in extant ferns could not be recognized in the fossil record. However, there is no reason to caricature Devonian homosporous plants. By today’s filicalean standards, the life history represented by *Platyzoma* is functionally inferior to the complex life histories typical of many homosporous species. If complex homosporous life cycles evolved during the Devonian, free-living heterosporous is an unlikely intermediate form in the evolution of heterosporous, simply on ecological grounds.

### 2.3. An ecological perspective

Heterosporous is ecologically successful in a different set of environments than homosporous. The heterosporous life history is advantageous in aquatic and amphibious habitats where gametophytes are assured of favorable conditions; heterosporous plants in drier habitats generally are

apomictic (Fig. 2). In contrast, homospority is rare in aquatic habitats (the semi-aquatic fern *Ceratopteris* is an interesting exception that can complete its life cycle rapidly under aquatic conditions; Tryon and Tryon, 1982; Eberle et al., 1994). The extended gametophytic life-span of almost all homosporous plants permits a wider range of response in terra firma habitats. Nevertheless, the great differences in sporophytic and gametophytic form, and the continued requirement for surface moisture to effect fertilization, restrict the ability of homosporous species to radiate into aquatic habitats. As with heterosporous lineages, homosporous plants have been able to expand to the drier end of the environmental spectrum.

The transition to the aquatic–amphibious habitat is especially demanding. The need to modify evolutionarily both the sporophyte and gametophyte appears to have been a major factor that prevented homosporous plants from exploiting such environments. Thus, endospory is the single most important breakthrough that permits the invasion of aquatic habitats (Bateman and DiMichele, 1994b). Endospory leaves the sporophyte to face the vagaries of the environment. Only during reproduction must the gametophytes be released, and then only for a brief period. But it is this reproductive phase, despite the compression of the developmental stages between meiosis and syngamy, that restricts the choice of habitats, just as it opens the aquatic habitat to invasion.

We see no need to advance intermediate forms between homospority and endosporic heterospority, and have argued elsewhere (DiMichele et al., 1989; Bateman and DiMichele, 1994a,b) that the morphological transformation is developmentally controlled and thus can yield a “hopeful monster” in a single generation (see also Van Steenis, 1969; Arthur, 1984; Levin, 1993). Ecologically, early heterosporous forms probably entered and exploited an environment virtually unoccupied by other vascular plants. They were capable of passing through a selective filter almost impenetrable to homosporous plants. Consequently, there is no reason to invoke competitive superiority to explain the evolution of heterospority from homospority. Rather, it can be viewed as a happenstance that

permitted **escape** from competition (or, in other terms, exploitation of a new resource).

#### 2.4. Evolution of the seed

The earliest known seeds occur in Late Devonian swamp habitats (Gillespie et al., 1981), providing evidence that early seed plants preferentially occupied the same kinds of environments that were exploited by their heterosporous ancestors. However, the great diversity of early seed plants and seed morphologies occurs in terra firma habitats (Andrews, 1963; Long, 1975; Scott, 1980; Retallack and Dilcher, 1988; Rothwell and Scheckler, 1988), suggesting that seed plants radiated primarily in drier habitats. As with the homospority–heterospority transition, competitive superiority has often been invoked in the heterospority–seed habit transition. In both cases, rudimentary ecological analysis offers little support to the a priori hypothesis of competition.

Perhaps the most serious issue in considering the evolution of seed habit is its definition. Almost universally, seed habit is defined as a heterosporous condition in which the number of functional megaspores per megasporangium has been reduced to one. The one viable spore develops completely within the megasporangium, which is surrounded by additional tissue that is generally considered to be of sporophytic origin. As a consequence of this morphology, the male gametophyte, also endosporic in development, must be delivered to the seed, a process termed pollination. Most studies of seed evolution have focused on the elaboration of the integuments (Andrews, 1963), on the relative efficiency with which various early forms capture pollen (Niklas, 1981), or on likely ancestry (Beck, 1985; Crane, 1990; Rothwell and Serbet, 1994). The evolution of the seed habit itself has been addressed only tangentially, via conceptual gradualist arguments in which the seed is assembled step-wise through a now familiar series of morphological intermediates. Such scenarios constitute an evolutionary argument only if gradualism is again considered axiomatic, and if the final configuration of the seed is regarded as an optimal, stable morphology that is more likely to resist further evolutionary modifications than any of the

so-called “intermediate” forms. Once more, however, most of the critical intermediates are missing from the fossil record; either they have not yet been detected or they never existed.

From an ecological perspective only one “step” in this transformation is critical to the life history we view as the seed habit, namely delivery of the male gametophyte directly to the female. Thus, pollination is the key innovation, less from a morphological perspective than an ecological one. Plants with routine pollination have come as close to unifying the sporophyte and gametophyte into a single individual as can be achieved by sessile organisms (Bateman and DiMichele, 1994a,b). The gametophytes no longer place environmental restrictions on the sporophyte, which becomes limited largely by vegetative environmental tolerances rather than constraints on reproduction. It would be impossible to distinguish this breakthrough in the fossil record, due to the difficulty of distinguishing free-sporing “heterosporous” plants from structurally similar plants experiencing routine pollination.

It is likely that the first plants with pollination evolved within the aquatic–amphibious habitats occupied by their heterosporous predecessors (Fig. 2). The fossil record documents that seed plants did not achieve dominance in these environments until late in the Paleozoic. Rather, the most rapid increase in seed-plant diversity in terra firma habitats occurred through the Late Devonian and Early Carboniferous, where it rapidly became the dominant life history. Heterosporous plants continued to dominate wetland habitats until removed by **extrinsically** induced extinction (Phillips and Peppers, 1984; DiMichele and Aronson, 1992). Environmental place holding on ecological time-scales was termed “home-field advantage” by Pimm (1991). It seems that the pattern can be extrapolated to geological time intervals, especially at the level of higher taxa. As we will discuss in our second case study, the seed plant radiation may have been suppressed in aquatic–amphibious habitats by the already well established occupancy of earlier heterosporous plants (Knoll and Niklas, 1987). Certainly, the earliest seed plants probably had similar vegetative tolerances to their heterosporous precursors (Bateman and DiMichele,

1994b). It was their ability to reproduce under a wide range of conditions that enabled them to exploit parts of terra firma environments exploited by few homosporous plants. In addition, the bifacial cambium of seed plants, permitting massive wood production while retaining effective photosynthate transport, may have allowed them to partition terra firma habitats in ways not previously possible. Their reproductive methods allowed them to pass the filter between aquatic–amphibious and terra firma settings, but it was primarily vegetative specialization (“economic factors” *sensu* Eldredge, 1989) that facilitated their exploitation of drier habitats.

When ecological factors are considered it appears that seed plants may have come into competition with heterosporous plants—and lost! The first seed plants grew in environments already heavily saturated with heterosporous species (particularly lycopsids and progymnosperms) as place holders. Although some species may have become established, the fossil record demonstrates that seed plant species failed to dominate aquatic–amphibious environments until the latest Paleozoic. In contrast to their origin, the early radiation of seed plants may have occurred under conditions of relatively little competitively mediated selection (note that this also applies to several earlier radiations of heterosporous species). Pollination was a “pre-adaptation” that permitted a major switch in the ecological amplitude of an entire clade, a *bona fide* key innovation (a morphological or physiological innovation that permits a clade to switch resources and escape competitive constraints). It was not until abiotically driven extinctions eliminated heterosporous tree forms that seed plants were able to colonize aquatic–amphibious habitats.

It could be argued that the radiation of several distinct heterosporous clades in wetlands during the Paleozoic (Fig. 1) contradicts the argument that home-field advantage should dissuade multiple radiations of similar life history strategies in similar habitats (B.H. Tiffney, *pers. commun.*, 1994). However, the radiations in aquatic–amphibious environments are an edaphic complex of habitats, and thus offer a number of niches for exploitation; they effectively constitute a biome.

Freshwater aquatic–amphibious habitats also are isolated relative to most drier terrestrial habitats, offering more opportunity for local establishment of derived clades. Although several, mainly lower-vascular plant groups radiated within wetlands during the Paleozoic, most of these radiations produced limited numbers of taxa. The seed plants were no exception to this rule; the radiation of this group in aquatic–amphibious settings produced few taxa. It was not until they entered drier habitats that a major radiation took place. The aquatic–amphibious environment of the Paleozoic offered limited opportunity for radiation due both to physical restriction and the presence of numerous occupants.

Unlike the heterospory–homospory transition, no catastrophic structural changes are required in the heterospory–seed habit transition. Rather, the structural modifications that are so well documented in the fossil record are mere postscripts to seed plant origins. Certainly, integumentation affects pollination efficiency and enhances gametophyte protection, and various micropylar and cupule modifications were instrumental in the **radiation** of seed plants. But an understanding of the patterns of change through time in these accessory structures does not lead to a greater understanding of the **origin** of this subsequently dominant life history.

### 3. Case study II: The radiation of vascular land plants and the emergence of the ecological hierarchy

#### 3.1. Major land-plant radiations

By the end of the Early Carboniferous, terrestrial vascular plants had undergone two of the three major radiations evident in the fossil record (Fig. 1). The first occurred during the Siluro-Devonian and gave rise to the cooksonioids, zosterophylls, lycopsids, rhyniophytes, and trimerophytes (Banks, 1975; Gensel and Andrews, 1984; Knoll et al., 1984; Niklas et al., 1985). The second spanned the Late Devonian–Early Carboniferous and generated the selaginellalean and rhizomorphic lycopsids, sphenopsids, progymnosperms, seed plants, and several “fern” groups, including

the “zygopterid” and filicalean lineages (Chaloner and Sheerin, 1979; Scott, 1980; Stein et al., 1984; Galtier and Scott, 1985; Meyen, 1987; Crane, 1990). Within-clade radiations lagged behind by about one geological stage but conformed to the basic architectural themes established in the earlier major diversification (but note that this lag may be explained partly by sampling of species in the fossil record: on average, a class will be more readily detected than an order; D.H. Erwin, pers. commun., 1984). The radiation of the angiosperms is the final (and ongoing) diversification of vascular plants; it has resulted in several architectural forms not represented in the earlier radiations, such as monocotyledonous vegetative organization and the herbaceous habit, though we regard these as relatively minor modifications of the earlier seed-plant bauplan.

Figs. 1 and 3 show that the Devono-Carboniferous radiation established what traditional Linnean taxonomy has regarded as classes of vascular plants: Lycopsida, Sphenopsida, Pteropsida, Progymnospermopsida, Spermatoopsida (we here follow the taxonomic system of Knoll and Rothwell, 1981). The phylogenetic studies of Crane and colleagues (Crane, 1990; Kenrick and Crane, 1991) have provided informal names that capture more accurately the phylogenetic structure of the relationships, and conform broadly to the traditional Linnean taxa. In effect, Linnean higher taxa are short-hand for the distinctive vegetative and reproductive architectural characteristics that separate the major clades.

The degree of phylogenetic resolution is highly variable both within and between major clades. The pattern attending the origin of the sphenopsids is the best studied. Stein et al. (1984) showed that the sphenopsids originated from an as yet incompletely resolved pool of potentially ancestral forms. Although the broad patterns of descent are clear for groups other than the sphenopsids, transitional morphologies have not been found that clearly link specific sublineages. In particular, ancestral homosporous lycopsids or trimerophytes are not well connected to the derived clades, such as the rhizomorphic lycopsids, the various fern lineages, or the progymnosperms. Relationships between the wholly extinct progymnosperms and the puta-

tively descendant seed plants remain contentious. The many morphological and phylogenetic studies have all been handicapped by the paucity of fully reconstructed progymnosperms. As indicated by the sphenopsids, the Late Devonian was a time of wide-ranging morphological innovation. The “morphological envelope” was largely circumscribed during this time; it was filled during subsequent lower level radiations, which played on the major structural themes that had already evolved (Bateman, 1991). This potentially fractal taxonomic pattern is evident in the early class level radiation and subsequent order level radiations summarized in Fig. 3, though a more rigorous analysis extended to lower taxonomic levels is desirable (cf. Erwin et al., 1987).

Surprisingly little ecological attention has been devoted to this fundamental class-level radiation. Most discussion has centered on the evolution of particular morphological features, such as the tree habit, vascular morphology, or seeds. This focus overlooks their more profound context as part of the evolution of nearly all major architectural plans in vascular plants, an event that occurred during a remarkably short period relative to the total history of the tracheophytes. The literature on this interval and its evolutionary history is broad; key papers are summarized below. Many taxonomically restricted features did not occur

randomly across physical habitats; rather, the radiation was characterized by strong clade–environment interactions. Chaloner and Sheerin (1979) documented the preceding accumulation of morphological innovations during the Devonian, and Banks (1980) provided a biostratigraphic context for the major taxa. Knoll et al. (1984) described patterns of diversification during the Devonian and, most significantly, quantified the degree of morphological differentiation among the major groups. Knoll and Niklas (1987) argued for a quantitative adaptationist approach to evaluating evolutionary scenarios that encompassed biomechanical attributes of organisms but lacked a detailed paleoecological component. More explicitly ecological studies, focusing mainly on floristics, include those of Scheckler (1986a,b), Bateman (1991), and Scott and coworkers (for summary see Scott, 1990). Retallack and Dilcher (1988) examined the ecological implications of inferred Early Carboniferous seed-plant biologies, and Raymond (1987) evaluated the paleobiogeographic distribution of major morphological traits. Several studies used a range of approaches to evaluate phylogenetic relationships (e.g. Chaloner and Sheerin, 1979; Knoll and Rothwell, 1981; Meyen, 1984; Stein et al., 1984; Crane, 1988). It is from the totality of approaches that a picture of the radiation emerges.

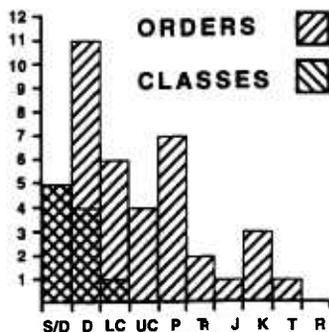


Fig. 3. Timing of origination of class and order level taxa indicated by the fossil record. Ordinal level originations peak later and are far more extended. Classes are Cooksoniopsida, Rhyniopsida, Trimerophytopsida, Zosterophyllopsida, Lycopsidea, Progymnospermopsida, Cladoxylopsida, Spermatoopsida, Sphenopsida, Pteropsida (see Fig. 1). Orders from Knoll and Rothwell (1981); angiosperms are treated as an order.

### 3.2. Questions of scale

We will briefly review the literature relevant to the ecological implications of the Devonian–Carboniferous radiation. Invertebrate and vertebrate paleontology have developed many concepts that are broadly applicable to interpretation of patterns in the plant fossil record. Suggestions that plant and animal evolution were guided by different suites of mechanisms should be scrutinized in light of existing theory. The basic shapes of basal radiations, the nature of morphological discontinuity among lineages, and the basic tenets of speciation are the same for plants and animals. The literature review that follows is intended to emphasize existing explanatory models that apply as well to plants as to the animals on which they were formulated. Crucial questions about the class-

level vascular plant radiation are, what caused it to begin and what caused it to end? We will argue that upward causation is the key, especially the degree to which processes operating at the scale of local populations within communities can account for the phylogenetic shape and ecological consequences of a major phenotypic radiation. It appears likely that the ecological spatio-temporal hierarchy with which we are familiar (community > landscape > biome) did not exist in the Late Devonian, but evolved in concert with the morphological radiation. As it developed, the hierarchy began to constrain (or perhaps contain) the spatial and temporal ranges over which population-level processes could act, and thus increasingly channelled the vascular plant radiation.

Valentine (1980) suggested that during the early Paleozoic radiation in marine ecosystems speciation was limited by the availability and size of “empty” niche space. Organisms exhibiting minor functional modifications needed only small low-competition ecospace in which to establish themselves, whereas carriers of major structural or functional deviations needed larger volumes of

space because they were likely to have very low fitness and little competitive ability. Valentine’s model predicted that ecospace existed independently of the occupying organisms. It was most widely available at the onset of a radiation and rapidly filled as it became colonized via major phenotypic jumps (Fig. 4). Subsequent speciation tended to deviate progressively less from the initially established architectural themes because there were no low-competition ecological voids that could accommodate major phenotypic change.

This type of radiation was classified by Erwin (1992) as a “novelty” event: one that takes place under low selection and involves organisms with weak genetic and architectural constraints. The novelty radiation is followed by more typically “adaptive” radiations within the limits of the ecological space occupied by the founding lineage(s). Erwin (1992) noted that in the fossil record of marine invertebrates events of this type tended to occur in the Paleozoic, presumably because empty ecological space was more common then, and because genomic and developmental

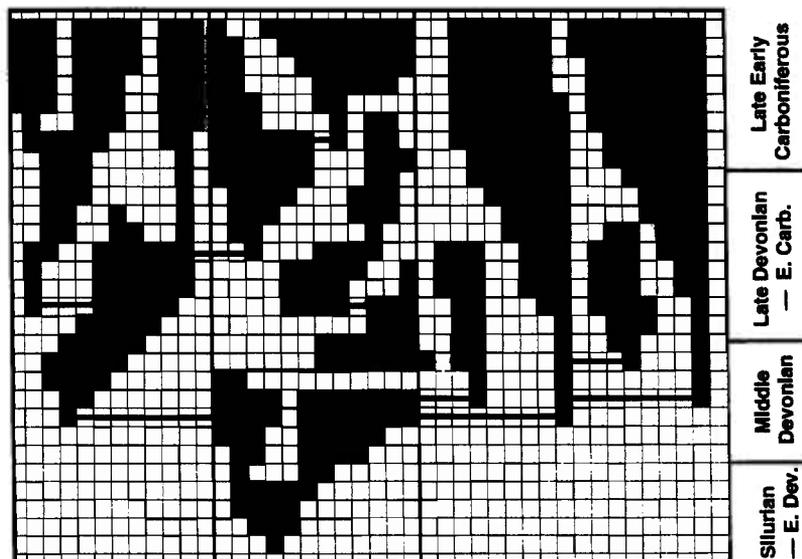


Fig. 4. Hypothetical pattern of rapid occupation of the available ecospace following class-level originations in the Siluro-Devonian. Squares represent “adaptive” space (tesserae in the model of Valentine, 1980). Founders of a major clade require more adaptive space than subsequent speciation events that are smaller scale modifications of that same basic theme. Space filling combines with progressive canalization of development and architectural constraint to limit both the opportunity for survival of highly divergent forms and the likelihood of their occurrence.

constraints were less entrenched, permitting more phenotypic variation. In Valentine's scenario there is a progressive interaction between morphological change (the engine of which is not of immediate concern; it is assumed that a spectrum of variation, from tiny differences to large discontinuities, is present at all times) and ecological space, even though the ecological space is regarded as largely predefined. Fundamentally, the ecological factors of standard neo-Darwinian evolution (principally, the chance location of a suitably low competition site by a population bearing a derived phenotype, generally via an allopatric event) are those controlling speciation, irrespective of the degree of phenotypic deviation from the ancestor.

Significant parts of Stanley's (1975, 1979, 1990) "species selection" paradigm also focus on the interaction of extinction and origination rates in evolving lineages and thus treat ecological factors as at least partially dependent on biotic factors. Stanley demonstrated that high rates of speciation (as opposed to origination, which was assumed to be stochastically constant) within clades must be accompanied by high rates of extinction, and that large population sizes tend to reduce the likelihood of speciation. Both factors reflect the interactions of speciation and adaptive (niche) space. Origination may provide a wide range of variation for selection but there also must be sufficient adaptive space to allow the establishment of small derived populations. Without extinction, phenotypically derived forms tend to encounter ecologically similar ancestors; generalists with large population sizes are on average more resistant to extinction, so these groups tend to occupy extensive ecospace for relatively long periods and have relatively low speciation rates.

Damuth (1985) argued for a more clearly population-centered, and hence more ecologically centered, formulation of species selection; selection among species takes place through the interactions of "avatars": local community-specific populations of larger species ("ecotopodemes" *sensu* Gilmour and Heslop-Harrison, 1954). In Damuth's formulation avatars are to species as individuals are to populations. They provide the basis for an ecological analysis of selection among species, a model broadly consistent with that of Stanley but more

explicit with regard to the all-important level in the organismal hierarchy at which constraints operate.

The interaction of ecological and evolutionary dynamics on long time scales also has been addressed by other workers. As detailed by Vermeij (1987), the concept of escalation explicitly requires environmentally forced ecological disruption to break up co-evolved species complexes. Such complexes effectively exert home-field advantage and exclude "invaders" from access to resources. Extinctions open up resources and permit comparatively brief bursts of competitively driven evolution. Brett and Baird (1995) provided perhaps the most explicit link between landscape- and biome-level changes in marine faunas and synchronous, macroevolutionary changes in many of the component lineages. They argued that early Paleozoic faunas persisted taxonomically and structurally for several million years. Periods of persistence were terminated by brief intervals of rapid turnover, accompanied by the emergence of new ecological structures. Major evolutionary divergences were concentrated in several lineages during these intervals of ecological disequilibrium; these were "ecologically induced" radiations *sensu* Erwin (1992). Simpson (1944) viewed major phenotypic changes as rapid shifts from one adaptive peak to another (this is consistent with the pattern outlined in Fig. 4). Calling such changes "quantum evolution", Simpson visualized a causal combination of happenstance attainment of a threshold level of "pre-adaptation" coinciding with unusually great ecological opportunity. Simpson (1953) later brought these concepts more in line with standard neo-Darwinian models of allopatric speciation, which implicitly require an ecologically uniformitarian viewpoint.

In contrast to models in which ecology is implicitly or explicitly central, most macroevolutionary models have focused on the origin of variation, or on the "internal" morphological constraints to phenotypic change, in which ecology plays a role only as a final, passive selective filter (*sensu* Rothwell, 1987). Several authors (e.g. Bateson, 1894; Goldschmidt, 1940; Schindewolf, 1950; and later Eldredge and Gould, 1972; Gould and Eldredge, 1977; Gould and Lewontin, 1979; Stidd,

1980; Arthur, 1984, 1987; Levinton, 1988; Gould, 1991; Stebbins, 1992) looked for developmental factors to explain the alternation of short-term phenotypic change and long-term phenotypic stasis. Such models view evolution within lineages as constrained principally by “historical” events, i.e. architectures created in the past that persist into the present (Gould and Lewontin, 1979; Gould and Vrba, 1982). Early, morphologically wide-ranging radiations are argued to be a consequence of poorly canalized developmental pathways and limited interactions among the architectural components of organisms. The fixation of lineages and architectures early in a radiation is thus strictly a consequence of ever-mounting constructional “burden” (sensu Riedl, 1979) and ever more complex developmental interactions (Gould, 1977).

Erwin and coworkers (Erwin and Valentine, 1984; Erwin et al., 1987; Erwin, 1993) argued that Valentine’s model needed to be modified by including such morphological and genetic constraints as those considered in more traditional formulations of macroevolution. Such constraints would reduce the likelihood of major phenotypic changes through time as developmental and genomic contingencies evolved (“canalization” sensu Waddington, 1942; see also Arthur, 1984).

The Devonian-Carboniferous origin of major vascular-plant architectures appears to be an Erwin-style “novelty” radiation. Early in such a radiation, highly derived forms may be able to survive even if they have ecological tolerances vastly different from their ancestors (equivalent to biome-scale differences). High extinction rates (Stanley, 1990) are not required at this stage because of low utilization of the full spectrum of resources. As resources become increasingly saturated, derived phenotypes begin to encounter “occupied” adaptive space more frequently, thus selecting against the more divergent forms. Smaller-scale evolutionary events, which were happening all along, begin to fill in the broad types of ecological space (e.g. “tropical wetlands”, “regularly disturbed stream-sides”). At this point, landscapes with multiple communities may emerge. Again, Valentine assumed that a full spectrum of phenotypic variations are always likely to occur; hopeful monsters

are always appearing, but their probability of long-term survival decreases rapidly as ecospace occupation increases; consideration of constraints enforced by increasing developmental complexity alters this expectation, reducing the expected breadth of divergences. A consequence of this model, which we discuss below, is that the ecological hierarchy evolves in complexity and connectivity as a major radiation proceeds. In doing so, it begins progressively to constrain that radiation in a negative feedback loop.

All of these macroevolutionary scenarios, whether or not they include an ecological component, contrast with the gradualism taken as the default in most paleobotanical forays into evolutionary biology, the most obvious example being Zimmermann’s (1959) unduly influential Telome Theory. Gradualist models are perhaps more “Darwinian” than “neo-Darwinian”. They rely on the assumption that the environment provides a uniform landscape across which blow prevailing winds, the “selective pressures” for whatever morphological feature is under study. Guided by competition, organisms are assumed to create an invariable background of minor phenotypic variation that is subject to constant gentle selection pressures. The result is a stately, continuous unfolding, not the discontinuous, fractally patterned process envisioned by most macroevolutionary models (Fig. 4). The “ecological” component in these gradualist models is often in practice merely the “selective pressures” themselves.

### 3.3. Major plant groups: initiation of the class-level radiation

“Why at that particular time?” is a question that can be asked about any phenotypic radiation at any taxonomic scale. Although the paleobotanical record clearly documents an architectural radiation of major proportions during the Late Devonian and Early Carboniferous (Fig. 1), the vascular plant radiation has been viewed either from the perspective of phylogenetic pattern or almost completely in terms of individual attributes, often considered pivotal in the evolution of plants (for example, the evolution of tree habit, seeds, and laminar megaphyllous leaves). Competitive

interaction among plants is taken to be the driving force (Chaloner and Sheerin, 1979; Tiffney, 1981; Knoll, 1984, 1986; Knoll et al., 1984; Knoll and Niklas, 1987; Traverse, 1988; Selden and Edwards, 1989), and this unique Late Devonian origin of widely divergent, complex architectures becomes obscured by an undesirably narrow focus on individual structural components of the major plant groups.

We suggest that phenotypic complexity played the most important role in the onset of the radiation, though detailed documentation of the assertion is outside the scope of this paper. Knoll et al. (1984) made the most credible attempt to date to document the increase in complexity that occurred during the Devonian (Fig. 5). For both the zosterophyll and trimerophyte lineages, they detected a rapid increase in morphological complexity during the Middle Devonian, reaching a plateau in the Late Devonian (and increasing again for lycopsids in the Early Carboniferous). This implies the existence of a phenotypic (and hence developmental) threshold of complexity that, once crossed, permitted rapid diversification—essentially complexity begetting complexity. This threshold was reached by the gradual accumulation of **potentially** adaptive morphological structures during the early phases of vascular land plant evolution (Chaloner

and Sheerin, 1979). Although simple early plants possessed most of the cell types found in modern angiosperms, diversity within particular categories of cell type (e.g. meristems, vascular tissues) was much lower. More importantly, early land plants possessed few organ systems. Together, these factors limited their ability to produce highly divergent derivative forms (and, by implication, offered an increasing probability of producing convergent derivative forms). However, once a critical mass of heritable phenotypic variability and complex developmental regulation were attained, large steps could be made in the degree of divergence between ancestor and descendant. In other words, the possibility for generating “hopeful monsters” was limited in the earliest phases of land plant evolution, but became increasingly likely as phenotypes and their regulation became more complex. This relationship between elaboration of complex morphology and its developmental control underpinned Zimmermann’s (1959) Telome Theory, which unfortunately has yet to be satisfactorily integrated with plant developmental mechanisms as they are understood today (e.g. Stidd, 1987).

This explanation does not rule out competition as an important selective filter, though competition among vascular plants is indirect and is not necessarily involved in the establishment of a novel lineage (Bateman and DiMichele, 1994a) (Fig. 6). Diffuse competition, perhaps landscape-scale escalation as envisioned to occur periodically by Vermeij (1987), could have driven the entire system once complex morphologies began to appear. However, competition and specific selective pressures alone are unlikely to account for the relatively short-term structural diversification of vascular plants belonging to widely divergent clades, unless the organisms were ecologically undifferentiated.

In this context, early land plants (Late Silurian and Early Devonian) appear to have undergone minimal ecological differentiation. “Communities” commonly consisted of patchworks of monotypic stands (e.g. Andrews et al., 1977), with many of the species using common resources and competing for the same space within streamside and wet floodplain habitats (Knoll et al., 1979; Tiffney, 1981; Tiffney and Niklas, 1985; Bateman, 1991;

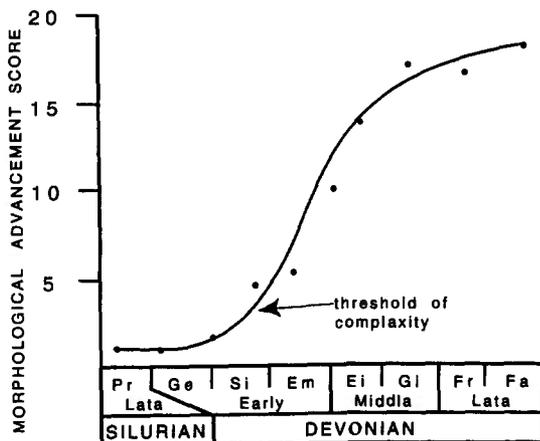


Fig. 5. Rapid increase in “morphological” advancement following attainment of a “threshold of complexity” in the Siegenian. [Modified from Knoll et al. (1984) who listed the criteria for calculation of the morphological advancement score.]

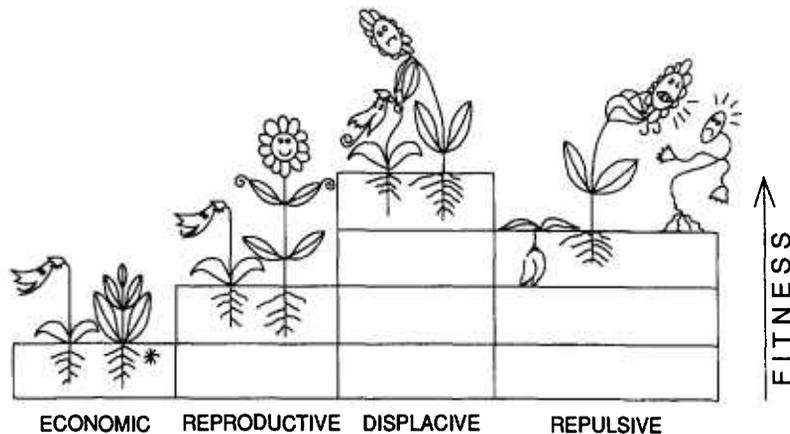


Fig. 6. Four phases of establishment of a new lineage. Once the genetically novel propagule (asterisked) germinates, its individual survival requires only economic establishment. However, lineage establishment necessitates reproduction and population expansion. Any current occupants of the preferred niche must be displaced, and the novel lineage must then resist attempted invasions from other prospective occupants of the niche. Note that (1) botanical “competition” can only be indirect and mediated via differential utilization of the same resources, and (2) the displacive phase of establishment requires a higher level of fitness than the repulsive phase (“home-field advantage” *sensu* Pimm, 1984, 1991). Establishment of low-fitness “hopeful monsters” therefore requires a vacant niche. (See also Bateman and DiMichele, 1994a.)

DiMichele et al., 1992). The dominant dynamics in these kinds of ecosystems would have been location and occupation of space. This was essentially an *r*-selected world. At this stage, the system should have been highly invadable from both ecological and evolutionary perspectives, due to the lack of integrated, multispecies communities on Early Devonian landscapes. Competition for space rather than light or nutrients should have permitted new species to invade and establish on undersaturated landscapes with few mutualistic interactions among species (cf. Fig. 6). In current “ecojargon”, the Early Devonian was a time of low connectance (plants had few coevolved interactions and interdependencies), high resilience (following disturbances, ecosystems were able to return to rapidly to the starting condition), and low resistance (ecosystems were easily invaded by species new to the area or newly evolved) (see Pimm, 1984). The long lag times in the development of ecological structure reflect natural lags in the evolutionary process; unlike today, in the Early Devonian there simply were no structurally complex species to invade the low resistance landscapes of the day.

The distinct ecological strategies of the major clades apparently evolved in concert with increas-

ing structural variability during the Early and Middle Devonian, when swamp and periswamp floras were already ecologically distinct (e.g. Tasch, 1957; Edwards, 1980; Gensel, 1987; Bateman, 1991; DiMichele et al., 1992). Thus, at this early stage in land plant history, ecology is less a constraint than a reflection of the progress of phenotypic evolution. When organisms began to evolve structural and physiological attributes that permitted them to escape the wetter landscapes, or to exploit those landscapes more fully, they encountered little counter-selection from existing occupants (cf. Fig. 6). In such a scenario, physical tolerance predominates over biotic interaction in dictating evolutionary pattern. This is fully consistent with the evolutionary model developed by Valentine (1980) and elaborated by Erwin et al. (1987).

#### 3.4. Ecological limits to the radiation

Why did the radiation of vascular plants stop with the three major lineages of lycopsids (homosporous forms, selaginellaleans, and rhizomorphic forms) and three or four major trimerophyte-derived lines (sphenopsids, progymnosperms—seed plants, and one or more distinct types of ferns)?

Certainly, these groups do not exhibit the full spectrum of possible ways to build a vascular plant. The answer is probably two-fold. Phenotypic and genotypic constraints, at some level, impose limits on subsequent morphological change. Thus, the maximum extent of phenotypic divergence per clade must have declined sharply once developmentally complex body plans evolved. A morphological argument of this type is difficult to test directly due to the antiquity of the event and our inability to sample the full spectrum of variability produced by any extinct species (as opposed to the full extent of variability that survived). Nonetheless, attempts have been made to use phylogenetics to gauge phenotypic disparity among Paleozoic marine invertebrates (Briggs et al., 1992; Foote, 1994), and similar paleobotanical studies would undoubtedly yield interesting results.

The second factor, again stated explicitly by Valentine (1980), is the progressive saturation of ecological resource space (Fig. 4). Most authors have treated ecological space as a relatively uniform background. Valentine's (1980) preferred analogy was pre-existing tesserae on a checkerboard (see also DiMichele et al., 1992; Hanski, 1994). Basal, highly divergent lineages are envisioned as needing disproportionately large amounts of ecospace, due largely to weakly canalized development and their consequent inability to withstand serious competition for resources. Later-evolving offshoots would need progressively smaller ecospace, within the larger initial space, as their competitive abilities became less hindered by weak developmental controls. Under this model, ecospace is pre-existing, predefined, and merely waiting for progressive occupation. Although heuristically useful, this convention is not particularly realistic, especially for the early phases of a novelty radiation into ecospace that has no prior biotic definition. In other words, the resources available to newly evolved species are not limited by the resource use patterns of pre-existing species.

Examination of the Late Devonian–Early Carboniferous vascular plant radiation suggests that terrestrial landscapes were transformed from poorly defined with little hierarchical structure to

increasingly well defined with distinct hierarchical structure. As major class-level lineages evolved and became established they began to partition the land surface and define the biotic characteristics of particular physical environments. These patterns then began to constrain the likelihood of establishment of subsequent highly divergent forms. Thus, clades and ecological space co-evolved; the morphological envelope and ecological envelope were established simultaneously (Fig. 4). As discussed earlier, an ecologically undersaturated environment favors a “novelty” radiation (*sensu* Erwin, 1992), particularly in the Paleozoic where complex morphologies and strong taxonomic preferences for particular ecological settings had not yet evolved. The combination of available ecological resource space and relatively simple organisms with weak developmental canalization enhances the survival of highly derived morphologies, which are generally classified as the stem lineages of higher taxa. Such radiations begin to slow as ecological–adaptive space is filled, which selects proportionately more against progressively more derived forms. As the survival of the more deviant phenotypes declines, ecospace is filled by the constantly present background of less profoundly modified derivatives, which we recognize as species within the major taxonomic groups.

Wetlands and terra firma landscapes formed the first major ecological dichotomy within what could be considered the lowland tropical biome. Early wetlands were primarily the province of heterosporous rhizomorphic lycopsids and possibly some heterosporous progymnosperms (Scheckler, 1986a,b; Rex and Scott, 1987; Scott, 1988). Although elements of other major lineages occurred in such environments, the former groups appear to have been ecologically centered there. In contrast, terra firma habitats, those with well drained to occasionally dry soils, became the province of a major seed-plant radiation during the Early Carboniferous (Bridge et al., 1980; Rex and Scott, 1987; Scott, 1988, 1990; Bateman and Scott, 1990; Galtier and Scott, 1990). Retallack and Dilcher (1988) argued that during the Early Carboniferous seed plants established the full spectrum of *r* to *K* seral strategists, with habits ranging from small shrubs to large trees, in habitats

ranging from wet streamsides to dry soils in disturbed environments. By noting this ecological dichotomy we do not mean to imply that the evolutionary events that gave rise to the earliest species in a particular clade necessarily occurred in the environment(s) in which the group ultimately radiated. In some instances, such as that of the seed plants discussed in the first case study, the habitats of origin and those of ultimate ecological success appear to be significantly different. Certainly, it has been suggested that “marginal”, “disturbed”, or “stressful” environments, marine and terrestrial, may be crucibles for major phenotypic divergences that later establish and radiate in more favorable settings (e.g. Axelrod, 1967; Hickey and Doyle, 1977; Bottjer and Jablonski, 1988; DiMichele and Aronson, 1992).

Sphenopsids, especially the larger calamitean species, were centered in aggradational environments such as stream- and lake-sides, later occupying parts of peat- and clastic swamps (Scheckler, 1986b). This is a narrow subset of the broader environmental spectrum. Calamitean sphenopsids were the only major woody tree group in the Devonian–Carboniferous with clonal, rhizomatous reproduction (Tiffney and Niklas, 1985). Examples of calamite burial and recovery growth are common in Late Carboniferous clastic sequences (Gastaldo, 1992); this ability may have been the key to their success in aggradational habitats, where equisetaleans (albeit herbaceous) remain common today.

The ferns appear to have been a diverse (and probably polyphyletic) group that occupied a wide range of environments, from wet swampy settings (*Rhacophyton*, zygopterids; Scott and Galtier, 1985; Scheckler, 1986a; Scott and Rex, 1987) to fire and flood disturbed environments (Scott and Galtier, 1985; Scott and Rex, 1987; Scott, 1988). Monodominant stands were common in the Early Carboniferous, both in wet and dry sites, and fusinization (charcoal preservation) is common. This suggests that ferns radiated in disturbed environments where habitat disruption favored plants that could colonize and reproduce rapidly, and spread to new disturbed sites before suffering extirpation (Scott et al., 1984; Scott and Galtier, 1985; Rex and Scott, 1987; Bateman and Scott,

1990). Small stature, homosporous habit, high reproductive output, and rhizomatous growth may have permitted them to exploit such environments, where the potential for establishment of new species would have been high.

These floristic patterns, recognizable in the Late Devonian–Early Carboniferous, continued into the Late Carboniferous (e.g. Scott, 1978; Pfefferkorn and Thomson, 1982; Phillips et al., 1985; Collinson and Scott, 1987; DiMichele and Phillips, 1994), where such ecological differentiation has been well documented both quantitatively and qualitatively. The Late Carboniferous also demonstrates the development of biomic differentiation within the tropical lowlands, where xeromorphic floras, consisting primarily of seed plants in general and conifers in particular, existed contemporaneously with the classic mesic–hydric biome that has long typified the “coal age” in paleobotany texts (Scott and Chaloner, 1983; Lyons and Darrah, 1989). Conifer-rich xeromorphic floras appeared first in subtropical latitudes during the early Late Carboniferous, subsequently migrating southward into the tropics (e.g. Zhou, 1994). This observation gives credence to the suggestion of Knoll and Niklas (1987) that vascular plants colonized most of the physiographic regions of the land surface early in their radiation.

The radiation of major groups was not accompanied by a significant increase in alpha-diversity (diversity within individual habitats). Bateman (1991) critically re-examined the primary literature on Late Paleozoic floras, focusing on the Early Carboniferous of northern England and southern Scotland. By attempting to hold facies constant to avoid pooling richness measurements from different kinds of habitats, and by emphasizing potential whole-plant species, he inferred that species richness remained relatively low through the class-level radiation, averaging eight species per assemblage and perhaps as few as four per strictly delimited uniform habitat. However, species in each habitat differed greatly, both phylogenetically and ecologically. This interpretation is consistent with Erwin's (1992) characterization of a novelty radiation, in which speciation rates are low but phenotypic divergence rates are high. Local habitats evidently remained relatively species

poor, but major lineages occupied ecologically distinct parts of the landscape.

#### 4. Conclusions

The Devonian-Carboniferous radiation of vascular plants reveals patterns and processes operating at different levels in the evolutionary and ecological hierarchy. Our chosen examples — the evolution of heterospory and the seed habit, and the larger phylogenetic pattern and timing of the radiation — reveal linkages between events happening at the populational and clade levels, at scales ranging from habitats to biomes. This radiation had several immediate and important consequences:

(1) The terrestrial land surface was partitioned into subenvironments that conformed strongly to the ecological centroids of the major class-level taxa. Each of the major class-level taxa dominated some portion of the land surface in the Carboniferous, generating a taxonomically egalitarian dominance–diversity spectrum unlike that of any subsequent time period. Today, for example, the world is largely dominated by seed plants, irrespective of whether one considers terra firma, aggradational, disturbed, or wetland habitats. Moreover, in most of these habitats a single phylogenetically trivial but ecologically preeminent group, the angiosperms, is dominant.

(2) Alpha-diversity remained low in nearly all Devonian-Carboniferous assemblages. However, subsequent radiations in all groups elevated diversities. These radiations began in the mid-Early Carboniferous and were largely complete by the mid-Late Carboniferous in the humid lowlands, though in the drier uplands they appear to have continued into the Mesozoic.

(3) Radiations at lower taxonomic levels remained confined, for the most part, to subcompartments of the landscape. In the case of heterospory, for example, the earliest plants with this life history successfully occupied wetlands and remained the dominant elements in these habitats until major extrinsically induced extinctions eventually permitted seed plants to occupy the vacated resource space. In this way, the early radiations of plants confined and directed later

evolutionary events. “Home-field advantage” appears to operate at the level of population dynamics, but its effects are manifested most strongly at the levels of community organization and landscape partitioning by major clades.

(4) Resource partitioning within communities increased, following the increase in the diversity of life habits and life histories. All landscapes included species specialized for the full spectrum of life histories, from short-lived, opportunistic to long-lived, site-occupying strategies.

(5) We believe that the vascular-plant architectural radiation is a manifestation of “home-field advantage” (sensu Pimm, 1991) on a scale much greater than that observed in modern ecosystems. The initial radiation appears to have occurred under low competition into a landscape that was unoccupied or undersaturated (probably by primitive homosporous plants, possibly vascular s.l.) (Scott, 1980, 1990; Kenrick and Crane, 1991). Initial occupation interacted both with natural selection and developmental canalization. As organisms became more complex morphologically the likelihood of further major increases in complexity declined, reducing the average phenotypic distance between ancestor and descendant species (though this increases the potential for profound evolutionary **decreases** in complexity, breaking canalization and resetting the evolutionary clock; Bateman, 1994, 1995). As ecological resource space became increasingly saturated the likelihood of survival of major phenotypic deviants declined, due to progressive increase in the average intensity of selection. Also, the initial long-phase radiation occurred in a near-vacuum; the potential niches had never been occupied (primary vacancy). However, as increasingly inhospitable habitats were colonized, the only opportunities lay in the secondarily vacant niches that resulted from extrinsic environmental perturbations. Thus, large evolutionary jumps simultaneously became increasingly less likely to occur and much less likely to survive if they did occur (Valentine, 1980; Erwin et al., 1987; Bateman and DiMichele, 1994a).

(6) It is always tempting to find causation at the ecological level that confines a particular problem. Our chosen examples — the origin of heterospory and the seed habit — may indeed have been

mediated by strong proximate causes operating within local ecosystems. However, study of the hierarchy of ecological organization under which these patterns originated cautions us to consider the larger context. Biotic structure and interactions at levels above populations and communities may exert profound constraints on evolutionary patterns.

(7) All of the key aspects of the above evolutionary–ecological theory are at least testable indirectly via the plant fossil record. Three distinct types of paleontological data are required.

First, reconstructed fossil plant species should be integrated with extant species in well founded phylogenetic analyses (e.g. Crane, 1988; Donoghue, 1989; Doyle and Donoghue, 1992; Bateman and DiMichele, 1994a; Bateman, 1994, 1995). Including the most complete range of relevant coded taxa is unimportant for determining sister-group relationships and thereby classifying taxa on the basis of monophyly, but it is essential for the interpretation of underlying evolutionary mechanisms. On average, maximizing the number of coded taxa included in an analysis minimizes the number of character-state transitions on each branch of the most parsimonious cladogram. This, in turn, maximizes the probability of determining the **sequence** of acquisition of character states within a lineage by distributing them on successive branches of the tree (the null hypothesis must be that all of the character states on a single branch of a cladogram were acquired together as a single evolutionary event: Bateman and DiMichele, 1994a).

Such sequences are especially important in cases like heterospory, where an apparently simple life-history change affects, either directly or indirectly, an extensive range of phenotypic characters (Bateman and DiMichele, 1994b). It is the highly iterative nature of heterospory, and the apparently broadly similar sequence of character-state acquisition in each independently evolving lineage, that most strongly implicates an underlying adaptive drive (Bateman, 1995). An additional benefit of integrated phylogenies is the ability to quantify morphological disparity via branch lengths, and thus to compare the relative magnitudes of succes-

sive radiations (e.g. Briggs et al., 1992; Foote, 1994).

The relative timing of the origin and radiation of a clade is crucial to many of the arguments advanced in this paper. Thus, the second important line of evidence is the date of first appearance of a taxon (or character) in the fossil record. Given that any species will inevitably have existed prior to its earliest detected appearance, the fossil record offers only a minimum estimate of the absolute age of that species. Moreover, there are often severe contradictions between the relative timing of appearance of taxa (1) observed in the fossil record, and (2) predicted by the relative positions of nodes (branch points) in a cladogram (e.g. Fisher, 1992; Norell and Novacek, 1992; Huelsenbeck, 1994). Despite these difficulties, relative timing of events can help to limit the range of possible interpretations of causes and constraints, specifically those of the origin of a key innovation and the subsequent evolutionary radiation. For example, the first five origins of heterospory occurred during a relatively brief period of 20 Myr in the Mid-Late Devonian (Fig. 1). This suggests that several lineages that diverged during the earliest (Siluro-Devonian) vascular plant radiation crossed a vegetative complexity threshold that allowed them to occupy aquatic–amphibious habitats, but the origins are insufficiently closely spaced to suggest forcing by an extrinsic factor such as a catastrophic extinction event that freed niches for recolonization.

The third line of evidence necessary is the environment of growth of fossil species, as inferred during paleoecological studies. Given *in situ* fossils (e.g. DiMichele and Nelson, 1989; Wing et al., 1992) or adequate reconstruction of transported fossils, much information can be gathered about the preferred habitat(s) in which particular evolutionary radiations took place (admittedly this should not be equated with the habitat in which a key innovation first originated, which is far more difficult to determine due to the low probability of detection). In particular, we have argued repeatedly for the importance of home-field advantage in determining the ecological dominants of particular habitats. Home-field advantage assumes that the species occupying a particular niche in a partic-

ular habitat will resist invasion by similar phenotypes (even of high fitness); this can be tested in the fossil record if the plants are sufficiently well known and their preferred habitats have been established.

### Acknowledgements

We thank Thomas N. Taylor and Ruben Cuneo for the invitation and support to participate in the symposium from which this paper is an outgrowth. Dan S. Chaney and Mary Parrish kindly prepared final drafts of the figures. We especially thank Bruce H. Tiffney and Douglas H. Erwin for detailed, thoughtful reviews. This is publication No. 25 from the Evolution of Terrestrial Ecosystems Consortium, which provided partial support.

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