

CHAPTER 1

Plant diversity has evolved and is evolving on the earth today according to the processes of natural selection. All basic "body plans" of vascular plants were in existence by the Early Carboniferous, approximately 340 million years ago, and each major radiation occupied a particular habitat type, for example, wetland versus terra firma, pristine versus disturbed environments. Today the great species diversity we see on the planet is dominated by just a few of these basic plant types. This chapter sets the stage to understanding the origin and radiation of plant diversity on the earth before the significant influence of humans. The implication is that plants may become more diverse in the number of species level over time, but less diverse in overall form. The history of life tells us that plants that are dominant and diverse today will certainly be inconspicuous or even extinct in the distant future.

EVOLUTION OF LAND PLANT DIVERSITY: MAJOR INNOVATIONS AND LINEAGES THROUGH TIME

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PLANT DIVERSITY VIEWED through the lens of deep time takes on a considerably different aspect than when examined in the present. Although the fossil record captures only fragments of the terrestrial world of the past 450 million years, it does indicate clearly that the world of today is simply a passing phase, the latest permutation in a string of spasmodic changes in the ecological organization of the terrestrial biosphere. The pace of change in species diversity and that of ecosystem structure and composition have followed broadly parallel paths, unquestionably related but not always changing in unison. Extending back to the Silurian and possibly the Ordovician, the landscapes of the emergent surface experienced vast changes. Accompanying these changes were increases in species diversity within an ever-narrowing phylogenetic spectrum of the total evolutionary tree of vascular plants. Compared with the Carboniferous, today's world has vastly more species but fewer major clades encompassing the ecologically dominant elements. Flowering plants hold sway in most nonboreal biomes (large-scale, climatically limited, ecological units). The totality and reliability of this pattern suggest that future

events will see a continued narrowing of the phylogenetic spectrum from which dominant groups are drawn.

THE EARLIEST RADIATIONS

The lineages of plants we recognize today trace their roots to the Late Silurian and Early Devonian. During that time, early embryophytes (bryophytes and vascular land plants) appeared, and the ancestral groups of subsequent radiations began to establish themselves in terrestrial ecosystems. The principal vascular-plant groups in this early monophyletic radiation encompassed three distinct body plans: rhyniophyte, lycophyte, and euphyllophyte (Kenrick and Crane 1997). The rhyniophytes were likely the basal-most group from which the others were descended (Banks 1975; Raubeson and Jansen 1992), and hence were markedly paraphyletic. Rhyniophyte morphology was extremely simple (plate 1.1A), consisting of rhizomes bearing small upright dichotomizing axes with some branch tips terminated in sporangia; the presence of roots is equivocal, and leaves were absent. The lycophytes included two lineages, the Zosterophylloids (plate 1.1C) and Lycopsiids; all lycopsids probably are descendants of a single zosterophyll ancestor. Similar in many aspects of morphology, the lycopsids survive until today and bear the leaves and roots that are so conspicuously lacking in the zosterophylls (Gensel 1992; Hueber 1992). The euphyllophytes were a complex group that encompassed enormous structural diversity. Early euphyllophytes included what have been called trimorphophytes, a paraphyletic group possessing anisotomous branching, terminal sporangia, isospores, complex stelar morphology, and often enations of various sorts, but lacking true leaves (plate 1.1B). From this plexus the remainder of the vascular plants arose during the Devonian (Gensel and Andrews 1984; Kenrick and Crane 1997).

The phylogenetic distinctiveness of the basal lineages of vascular plants has certainly been clarified by subsequent evolutionary divergence among their descendants. Had human taxonomists existed during the Late Silurian and Early Devonian, they would have faced a significantly greater challenge than we do in recognizing those aspects of body plan that differentiate these early plant lineages, lacking knowledge of subsequent evolutionary divergence among the plant lineages. Nonetheless, the often-asserted extinction of a spectrum of intermediate forms formerly linking these groups is not supported by the fossil record. No doubt there is a considerable body of plants of which we have no record and no knowledge, but the vast majority of these would likely have been minor variants of existing body plans. Missing "intermediates," however, are merely an unsubstantiated expectation derived from uncritical acceptance of evolution as a gradual unfolding of morphological form rather than the discontinuous process apparent in the vast wealth of fossil data (Gould 2002; Bateman and DiMichele 2003).

The species diversity encapsulated by this early radiation has proven difficult to assess. The most comprehensive compilations (Niklas et al. 1980; Knoll et al. 1984) suggest a sigmoidal increase in number of taxa, reaching a plateau in the Middle

Devonian. The reality of this pattern was challenged by Raymond and Metz (1995), who re-evaluated the effects of sampling intensity and taphonomy on this estimate. They concluded that, although diversity increased through time, the shape of the pattern of increase could not be reconstructed reliably due to the spatio-temporal unevenness of sampling.

Biogeography of the early radiation is similarly subject to interpretation as a consequence of sampling inequalities. Raymond (1987) and Edwards (1990) analyzed the available data and concluded that three major phytogeographic regions existed: the northern latitudes, the southern latitudes, and the equatorial tropics, the latter divisible into subprovinces. Kenrick and Crane (1997) concluded, however, that the data supporting even this basic tripartite pattern are weak and should be approached with caution. Thus, at this time, the loci of origin of vascular plants *per se* and of the major sublineages, and the pattern of their global spread, cannot be identified with confidence.

ACCRUAL OF MORPHOLOGICAL COMPLEXITY

Throughout the Devonian, plants accrued morphological complexity, which can be benchmarked by the first appearances of particular structural features. Chaloner and Sheerin (1979) made one of the earliest attempts to measure this phenotypic diversity by compiling the first occurrence of features such as laminate leaves, stomata, and sporangial characteristics, but without regard to the evolutionary lineages in which the attributes appeared, making this a crude but nonetheless interesting measure of the slow accretion of morphological innovations. Knoll et al. (1984) examined the patterns with greater consideration of phylogenetic relationships, developing a measure of morphological advancement and plotting the average scores for intervals of the Late Silurian and Devonian in both the euphyllophyte and lycophyte lineages. They recovered a sigmoidal pattern of increasing complexity in each group, reaching a plateau in the Middle through Late Devonian before beginning to rise again in the Carboniferous.

DiMichele and Bateman (1996) ascribed this rapid rise to the attainment of a threshold level of morphological-developmental complexity. Recognizing that morphology is an expression of degrees of developmental regulation (Stein 1993; Cronk et al. 2002), they speculated that certain levels of canalized (inherently constrained) morphology and developmental control were needed before major changes in body plan could be attained. Prior to reaching this threshold, any single lineage would have given rise only to minor phenotypic innovations as structure and its regulatory control accrued. In other words, there may have been an interval when differences between ancestral and descendant species were relatively minor; this is not to say that evolution was “gradual,” characterized by insensibly graded steps. We would argue that the size of the discrete steps was, *perforce*, smaller than later only due to the relative simplicity of body plans. Once at the threshold, major changes in body plan became possible between ancestor and descendant due to the greater opportunities for heterotopy (change in the relative position of expression

of canalized morphological modules) and heterochrony (change in the relative timing of expression of canalized morphological modules). This is especially the case in organisms with minimal developmental interdependencies among organ systems ("epigenetics": morphology created by developmental interaction, not specifically coded by the genome). The subsequent progressive increase in developmental constraints limiting contingency (the "epigenetic ratchet" of Levinton 1988) may have played a major role in later limitations on the origin of novelties. The diversification of lineages that accompanied this global increase in morphological complexity was considered to be a "novelty radiation" (Erwin 1992) by Bateman et al. (1998) because major increases in complexity were accompanied by relatively low rates of appearance of new species. This occurred in an ecologically undersaturated terrestrial landscape in which competition was minimal, permitting an unusually high probability for survival of derived forms (DiMichele et al. 1992; Bateman et al. 1998).

APPEARANCE OF MODERN BODY PLANS

Modern vascular-plant body plans began to make their appearance in the Middle Devonian, and all were present by the Early Carboniferous (DiMichele and Bateman 1996). The most difficult part of this pattern to explain is the similar timing of the radiation in the two major branches of vascular-plant diversity: the lycopsids and the euphyllophytes. Long separated evolutionarily, these major clades essentially simultaneously gave rise to a variety of distinctive body plans. In the lycopsids (Lycopsidea) there appeared the lycopodioids (Lycopodiales), selaginelloids (Selaginellales; plate 1.1D), and isoetoids (Isoetales; plate 1.1E). From the euphyllophyte lineage arose the sphenopsids (Sphenopsida; plate 1.1F), ferns (Filicopsida; plate 1.1G), progymnosperms (Progymnospermopsida), seed plants (Spermatopsida; plate 1.1H), and several enigmatic pteridophytic groups (e.g., Cladoxylales, Iridopteridales). The parallel patterns of these phenotypic radiations suggests that morphological evolution may have had a "clocklike" component as complexity accrued within such simple morphological backgrounds, the threshold being reached approximately contemporaneously in lycopsids and euphyllophytes (Bateman 1999).

The origin of vascular-plant body plans is the terrestrial equivalent of the metazoan radiation in the Cambrian. The Late Silurian–Early Devonian origination of the euphyllophyte and lycophyte clades, although profound, was not as important a step in restricting the pathways of evolutionary change as was the later diversification, reflecting what Gould (1991) termed contingency. The body plans that appear during this radiation differ radically from one another in design and mode of reproduction, and represent the fundamental architectural groups of vascular plants extant from that time onward. Subsequent evolution was nested within these body plans; as noted by Bateman et al. (1998), each subsequent radiation generated more species but fewer major morphological divergences than the last, the average

degree of phenotypic divergence between putative ancestor and descendant decreasing over time.

ECOLOGICAL SORTING

The Devonian-Carboniferous radiation was accompanied by clade-level ecological partitioning in which each of the major architectural groups was centered in a different part of the terrestrial landscape or had a distinct ecological role (DiMichele et al. 2001b). The principal division was between seed plants and isoetalean lycopsids. Seed plants apparently originated in wetland habitats in the Late Devonian but invaded and then radiated in terra firma environments during the Carboniferous (Gillespie et al. 1981; DiMichele and Bateman 1996). The terra firma landscape, vast in extent and environmentally heterogeneous, was an unexploited resource space permissive of radiations and survival of highly derived forms. Consequently, numerous variations on the seed-plant body plan evolved and survived, recognized taxonomically as orders, including the Carboniferous Lyginopteridales, Medullosales, and Callistophytales; the Permian Coniferales, Cycadales, and Peltaspermales; and the Mesozoic Caytoniales, Bennettitales, Cortsospermales, Gnetales, and "Angiospermales." The Isoetales, particularly the rhizomorphic lycopsids, also originated in wetlands (Scheckler 1986) but radiated there and became the dominant elements in wetlands during the Carboniferous, extending into the Permian in eastern parts of the Old World tropics. Although wetlands were extensive during much of the Paleozoic, the physical heterogeneity of these habitats was (and is) considerably less than that of terra firma, resulting in fewer evolutionary opportunities, which is reflected in much lower diversity in isoetalean body plans when compared to seed plants. The main dichotomy in isoetaleans *sensu lato* separates the paraphyletic "lepidodendrids" from the isoetaleans *sensu strictu* (Bateman et al. 1992). The lepidodendrids had complex aerial branching systems, elaborated "stigmarian" root systems, and often huge size. The isoetaleans *sensu strictu* were much smaller forms with cormose bases and mostly unbranched shoot systems. Forms with cormose bases first appear in the Late Devonian (Chitale and McGregor 1988), followed by the lepidodendrids in the Early Carboniferous.

Of the other major clades, the sphenopsids were primarily plants of physically stressful, aggradational habitats, such as streamsides or lake margins. As the only group to evolve tree size while retaining a rhizomatous habit, the arboreal sphenopsids demonstrated remarkable ability to recover from burial by sediment (Gastaldo 1992). This is a subset of the environment of exceptionally narrow breadth, providing little opportunity for the survival of new forms in the face of competition from incumbents. As a consequence, sphenopsids always have been of low diversity, both in species numbers and in variations on their body plan. The ferns appear monophyletic on the basis of molecular evidence (Pryer et al. 2001), but less clearly so on morphological evidence (Rothwell 1996). Early ferns radiated

in environments of disturbance as opportunists (Scott and Galtier 1985). Although later becoming dominant elements in some kinds of habitats, the opportunistic strategy persisted throughout the evolutionary history of ferns.

This pattern of ecological partitioning characterized the Carboniferous into the Early Permian, a period of more than 50 million years. It began to break down at higher latitudes in the early Late Carboniferous (Meyen 1982; Knoll 1984). In the tropics the pattern of disassembly was complex. Vegetation typical of the Late Carboniferous persisted in tropical rain forest areas of what is now China until the Late Permian. Elsewhere in the tropics, climatic changes disrupted the dominance-diversity patterns, leading first to ecological reorganization within the wetland species pool (DiMichele and Phillips 1996), and then to major changes in floras, plants from xeric paratropical areas replacing the ancestral wetland vegetation (Mapes and Gastaldo 1987; Broutin et al. 1990; DiMichele and Aronson 1992).

EVOLUTIONARY DYNAMICS: THE SPATIAL COMPONENT OF EVOLUTIONARY INNOVATION

Data from the fossil and modern records suggest that speciation occurs everywhere on the landscape where organisms exist. Areas of high diversity have been considered "hot spots," where the establishment and longevity (but perhaps not rate of origin) of new species are elevated; such areas may be found both in continental and island settings. "Background" speciation, however, seems to occur widely in space and approximately uniformly across the landscape, setting aside major environmental perturbations of heterogeneous effect such as glaciations.

The terrestrial fossil record also indicates a bias in the landscape position of major phenotypic divergence. All speciation does not entail the same ancestor-descendant distances. The vast majority of descendants differ from their immediate ancestor in minor ways. A very few differ in more significant ways, including fundamental differences in body plan and/or reproductive morphology. Such forms will be expected to possess developmental irregularities or structural abnormalities that initially may compromise fitness (Valentine 1980; Bateman and DiMichele 1994, 2002), requiring establishment in environments of little or no competition for resources.

For example, conifers first appear as fragments of charcoal in depositional basins that formed proximal to contemporaneous rising upland regions (Lyons and Darrah 1989). Typical macrofossil remains occur only later in lowland basins in association with other xeromorphic plants and with physical indicators of dry climates (Broutin et al. 1990; DiMichele and Aronson 1992). Similarly, evidence of many plants that came to dominate Mesozoic lowlands appears first as fragmentary remains in dry-climate deposits of late Paleozoic basinal lowlands, intercalated within more typical wetland deposits. Included are cycads (Mamay 1976), osmundaceous ferns (Miller 1971), and various conifer groups (Schweitzer 1986; DiMichele et al. 2001a). The angiosperms also evidently evolved in remote areas and moved into lowlands along river margins as weeds (Hickey and Doyle 1977;

Crane 1989). These data suggest that major clades originated in environmentally marginal areas, especially those where moisture limitation was significant. Such areas had the lowest levels of resource competition. Through time, such loci became ever more remote from the basinal lowlands as more proximal areas filled with species, increasing resource competition and the exclusionary effects of incumbency (occupation of a particular niche at a particular location, often termed "incumbent advantage": reviewed by DiMichele and Bateman 1996).

ECOLOGICAL REPLACEMENT DYNAMICS

At some point in history, lineages that had evolved in remote, environmentally marginal areas moved into basinal lowlands, and thus into the preservational window of the fossil record. Most such movements appear to have been examples of environmental tracking rather than competitive displacement of lineages already established in the lowlands. The Paleozoic tropical wetland flora, for example, remained compositionally distinct from the xeric flora. Where fossil deposits of these two floras are found intercalated in lowland basins, they have different environmental signatures and have few species in common (DiMichele and Aronson 1992). It appears that the xeric flora was moving into the basins during times of climatic drying. The ultimate replacement of the wetland flora by the xeric flora occurred as the Paleozoic tropics became severely dry during the Permian (Ziegler 1990), eliminating the wetland flora. When wet conditions returned, the elements of the prior flora were gone, resulting in the evolution of new wetland lineages from the surrounding xeric lineages. Thus, the evolution of major innovations in marginal habitats, becoming progressively more remote from ancient lowland regions, was complemented by the movement of these lineages back into the lowlands following major climatic changes and consequent ecological disruption.

EXPANSION OF THE ANGIOSPERMS

The angiosperms are the most species-rich group of vascular plants. As a consequence, they merit special attention in any consideration of diversity. The modern diversity of this group is accompanied by ecological dominance of most of the world's terrestrial ecosystems. The complexity and character of those ecosystems is a reflection of the great diversity of form that has evolved within the flowering plants.

Evidence from the fossil record strongly suggests that angiosperms originated in the tropics during the Early Cretaceous. These early angiosperms were likely small, opportunistic, dominantly woody plants that exploited disturbed habitats (Hickey and Doyle 1977). Multigene molecular phylogenies based entirely on extant species (e.g., Chaw et al. 2000) have recently undermined the paleobotanically favored "anthophyte hypothesis" (e.g., Doyle and Donoghue 1986; Donoghue and Doyle 2000). This theory interpolated gymnosperms that possess some angiosperm-like reproductive features (the extant Gnetales, together with the extinct Bennettiales

and Pentoxylales) between modern angiosperms and the paraphyletic pteridosperms of the Late Paleozoic and Mesozoic. The recent molecular phylogenies once more allow the possibility of origination of the angiosperm clade from one of the more derived pteridosperms (cf. Harris 1964; Long 1977). This lower phylogenetic placement should not be viewed as indicating that the modern angiosperms are relatively primitive, as they have accumulated many molecular and morphological apomorphies over the long period since they diverged from their gymnospermous ancestor.

The most significant characteristic of the flowering plants, relative to other seed plants, is their species diversity. The angiosperms elaborated the basic body plan into a wide range of phenotypic variation, encompassing a broader spectrum of differences than in the rest of the seed-plant clade. They have undergone an almost unbroken increase in species numbers throughout the late Mesozoic and Cenozoic (Lidgard and Crane 1990). The increase in species numbers was accompanied, initially, by the origin of many of the extant arborescent families by the end of the Late Cretaceous, a novelty radiation in its combination of high rates of innovation within a background of initially relatively low numbers of species; this mimics, but encompasses less morphological disparity than, other radiations at higher taxonomic rank that took place in the Devonian and Carboniferous. In the course of this dynamic, the angiosperms may have evolved greater genetic novelty than ever before, though perhaps largely through more diverse combinations of genes than those characterizing other, earlier groups. At the same time, the probability of successful establishment of profound phenotypic novelties, such as those that characterized the Middle and Late Devonian architectural novelty radiation, has never been lower (Bateman and DiMichele 2002, 2003).

Just as the angiosperms expanded at the expense of other Cretaceous plant clades, narrowing the phylogenetic spectrum of dominance, so too the early angiosperm clades have been replaced by the expansion of later-appearing clades within the angiosperms. This is particularly true of grasses and composites, which have become important to dominant elements in many ecosystems. We speculate that there may be an underlying fractal process in operation within the terrestrial vascular plants (Bateman and DiMichele 2003). The changes in dominant angiosperm groups through time may be driven by the same underlying process that controlled the larger-scale replacement of lower vascular plants by seed plants during the late Paleozoic, and the replacement of early seed-plant clades by newer seed-plant groups in the Mesozoic.

CONCLUSIONS

The history of plant diversity, resolved at the level of major evolutionary lineages, is a record of ever-shrinking phylogenetic dispersion of ecological dominance. In the Paleozoic, the land was divided among four (arguably, more than four) classes of plants and many orders, the latter especially among the seed plants. By latest Paleozoic and early Mesozoic, most of the lower vascular-plant clades had either gone

extinct (particularly those involved in the initial terrestrial radiation) or at least had retreated into the ecological shadows, largely the victims of climatic changes (Knoll 1984). A plethora of seed plants replaced these pteridophytes, bringing a great diversity of form, but primarily experimenting with only one broad reproductive theme, the seed habit.

With the rise of flowering plants, species-level diversity sky-rocketed, and with it a wide range of subtle variations on both vegetative and reproductive themes. Angiosperms explored more aspects of architecture than all other groups of seed plants combined. In a Linnean sense, however, they are an ordinal-level group (a fact masked by neobotanically focused classifications that routinely inflate the ranks of taxonomic groups within the angiosperms). In the Cenozoic, the same process began to occur within the angiosperms; the most recently originating groups, such as grasses and composites, are often dominantly herbaceous and began to expand at the expense of older lineages.

In this sense, the history of diversity reveals an ever-attenuating spectrum of dominant major clades. The pattern appears to be broadly "fractal," beginning with all vascular plants, replaced by seed plants and a variety of ferns, then angiosperms and polypodiaceous ferns, and most recently subgroups within the angiosperms. Extrapolation from the paleobotanical record suggests that this taxonomic attenuation is likely to continue, even if it is associated with further gentle increases in overall species diversity in those lineages that rise to dominance. Its natural projection, however, does not take into account the very recent depredations of human civilization.

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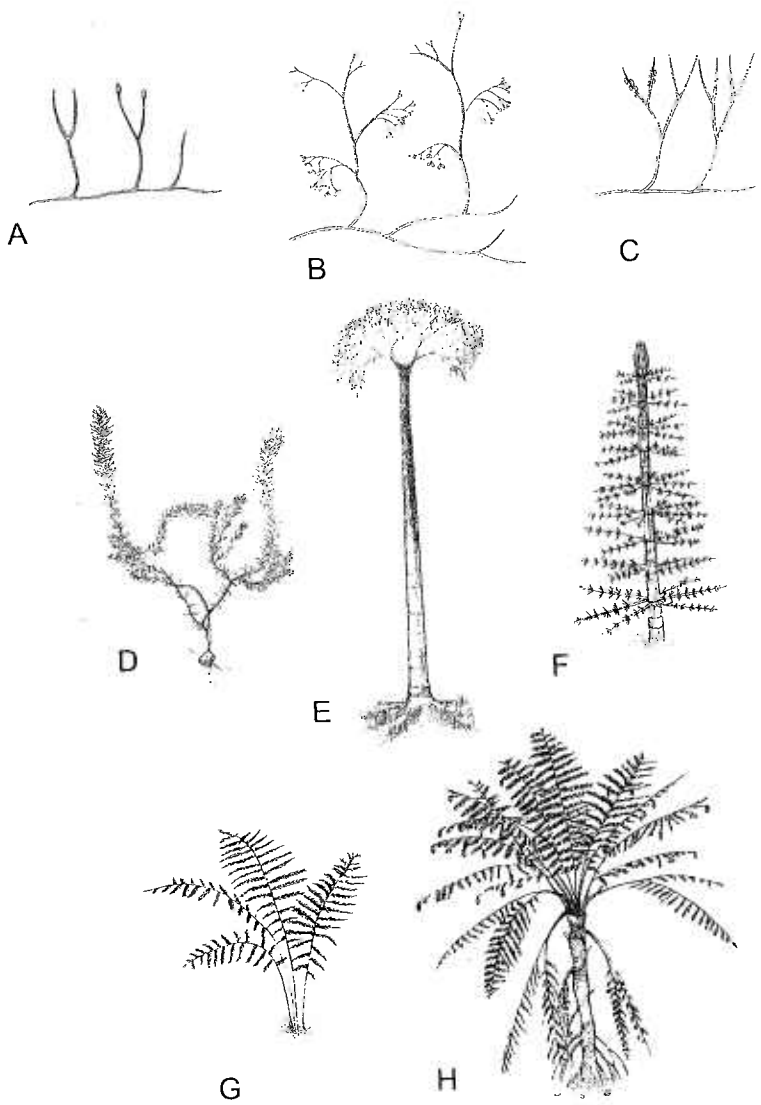


Plate 1.1 Reconstructions of vascular plants representative of major body-plan groups. A, Rhyniophyte, with naked, dichotomizing aerial axes, some terminated in sporangia. B, Trimerophyte, with unequally forked main upright axes, and paired sporangia terminating subordinate branches. C, Zosterophyll, with naked, dichotomizing aerial axes and laterally borne sporangia. D, Extant lycopsid, *Selaginella*. E, Extinct isoetalean lycopsid, *Lepidophloios*. F, Extinct sphenopsid, *Calamites*. G, Generalized small fern body plan, with fronds as the major organs of the plant. H, Extinct seed plant, *Medullosa*. Illustration by Mary E. Parrish.