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THE EVOLUTION OF PLANT DEVELOPMENT[1]

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The last decade has witnessed a resurgence in the study of the evolution of plant development, combining investigations in systematics, developmental morphology, molecular developmental genetics, and molecular evolution. The integration of phylogenetic studies, structural analyses of fossil and extant taxa, and molecular developmental genetic information allows the formulation of explicit and testable hypotheses for the evolution of morphological characters. These comprehensive approaches provide opportunities to dissect the evolution of major developmental transitions among land plants, including those associated with apical meristems, the origins of the root/shoot dichotomy, diversification of leaves, and origin and subsequent modification of flower structure. The evolution of these major developmental innovations is discussed within both phylogenetic and molecular genetic contexts. We conclude that it is the combination of these approaches that will lead to the greatest understanding of the evolution of plant development.

Key words: apical meristem; flower; leaf; origin; plant systematics; root; shoot.

Evolutionary developmental biology, or the study of the underlying developmental basis for the origin and diversification of organismic structure, has matured into a vigorous discipline in the last 20 years. Beginning in the 1970s, with such seminal works as those by Eldredge and Gould (on punctuated equilibrium; 1972), Gould (*Ontogeny and Phylogeny*; 1977), Alberch et al. (on the formalization of heterochronic models of developmental evolution; 1979), and McKinney and McNamara (*Heterochrony: The Evolution of Ontogeny*; 1991, as well as earlier papers), attention was focused on the role of development during the evolutionary diversification of metazoan morphology. Within only a few years, modification of development with respect to timing (heterochrony), ontogenetic sequence (addition or deletion of specific developmental events), and positional status (heterotopy), as well as analysis of the rate of evolutionary change (i.e., gradual vs. saltational or punctuated), had become central themes in the search for explanation of the historical pattern of metazoan diversity.

At approximately the same time, the century-and-a-half-old discipline of animal embryology, which had been excluded from the evolutionary ''modern synthesis'' of the 1940s and 1950s (Gilbert et al., 1996), began to undergo a resurgence. Embryologists began to incorporate molecular and genetic techniques into their studies of early developmental events. Discovery of the homeobox genes in *Drosophila* (Scott and Weiner, 1984; McGinnis et al., 1984) and elucidation of the ubiquitous roles of homeobox-containing genes in the establishment of developmental pattern in phylogenetically diverse metazoans (*Caenorhabditis elegans*, *Drosophila*, *Xenopus*, and *Mus*; Wilkins, 2002; Arthur, 2002) led to a revival of interest in the mechanistic basis of evolutionary diversification. By the mid-1980s, molecular biologists, embryologists, comparative morphologists, and paleontologists shared a common vision and goal: the complete explanation of the evolutionary history of developmental modifications that have given rise to the diversity of extant (and extinct) metazoans.

The study of the evolution of development was initially driven by studies of animal systems. However, it remains unclear to what extent the results from animal systems can be generalized to plants. Plants and animals each evolved independently from unicellular ancestors. For this reason alone, it seems likely that many, if not most, of the specific molecular developmental mechanisms underlying the evolution of multicellularity and structural complexity in these two major groups of complex eukaryotes will differ in significant ways (Kaplan and Hagemann, 1991; Meyerowitz, 2002). Thus, the principles that have been elucidated in the study of animal evolutionary developmental biology may have limited explanatory powers in the realm of plant diversification.

The resurgence in the study of the evolution of plant development in recent years has been accelerated, in part, by recent successes in elucidating the molecular genetic basis of plant developmental processes, including the isolation and characterization of genes that underlie flower, leaf, and root development (see also reviews by Cronk, 2001; Shepard and Purugganan, 2002; Kellogg, 2004). For example, the identification of the role of MADS-box transcription factor genes in flower development in several model angiosperm species such as *Arabidopsis thaliana*, *Antirrhinum majus*, and *Zea mays* provided the basis for early studies on the molecular evolution of genes that control the development of floral structure as well as subsequent analyses of these genes in a number of other nonflowering plant taxa (Purugganan et al., 1995; Theissen, 2001; Lawton-Rauh et al., 2000).

There remain, however, major gaps in our understanding of the evolution of plant development and morphological homology. Progress in the field will have to be driven both by successes and opportunities provided by molecular developmental genetic studies, as well as a more robust understanding of plant phylogenetic relationships, and continued analysis of comparative plant morphologies of extant and (most importantly) extinct taxa. In this review, we will address basic questions associated with the broad evolutionary developmental history of the bauplan and organs of land plants. We will also

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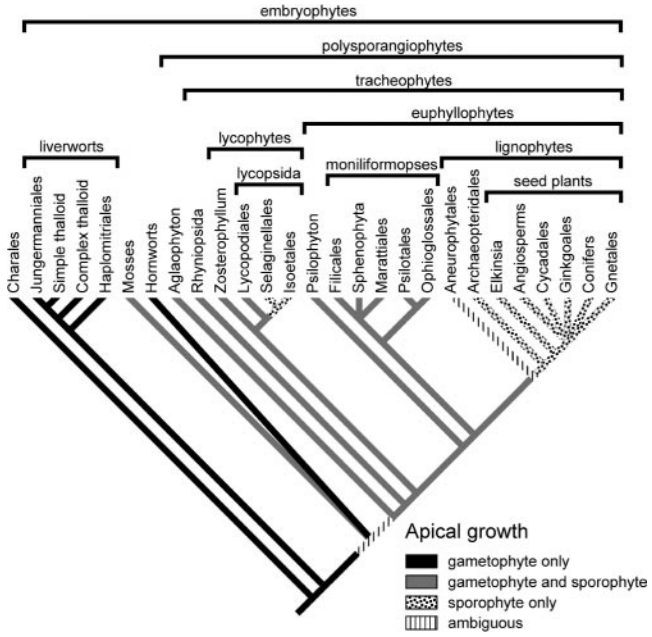

Fig. 1. Evolution of apical growth. The common ancestor of embryophytes and their closest relatives display apical growth in the gametophyte generation (Charales lack an alternation of generations; the only diploid phase is the zygote). Apical growth in the sporophytes of mosses and polysporangiophytes may or may not be homologous (in terms of a developmental process expressed in the sporophyte). Loss of apical growth in the gametophyte generation is associated with transitions to heterospory.

discuss the key roles that phylogenetic analyses and molecular developmental genetic studies play in developing a comprehensive understanding of how plant developmental processes evolve.

THE PHYLOGENETIC CONTEXT OF THE EVOLUTION OF PLANT DEVELOPMENT

Phylogenetic relationships of extant embryophytes—To understand the origin and early evolutionary history of land plants (embryophytes), a clear formulation of phylogenetic interrelationships is essential. Once robust phylogenetic hypotheses are established, comparative developmental analyses can be used to infer and reconstruct the evolutionary history of a broad range of biological characters. Thus, study of plant evolutionary developmental biology, like that of any group of organisms, relies on the interplay of phylogenetics and comparative biology.

In the last 20 years, much has been revealed about the interrelationships of land plants. Phylogenetic analyses have converged on the closest extant relatives of land plants, members of the charophycean grade of green algae, and almost certainly, either the Coleochaetales or the Charales (Fig. 1; Manhart and Palmer, 1990; Graham et al., 1991; McCourt, 1995; Karol et al., 2001). Analysis of the phylogenetic relationships of the earliest land plant lineages has proven more difficult. DNA sequence-based analyses and morphological cladistic analyses have yielded virtually every possible topological placement of liverworts, hornworts, and mosses at the base of the embryophyte phylogeny (Lewis et al., 1997; Crandall-Stotler and Stotler, 2000; Goffinet, 2000; Shaw and Renzaglia, 2004); typically, liverworts or hornworts are hypothesized to be sister to all other extant land plants (Shaw and Renzaglia, 2004). It is worth noting that rare genomic markers (in this case, intron content in the mitochondrial gene *nad1*) provide compelling evidence that liverworts may be sister to all other land plants (Qiu et al., 1998; Dombrovska and Qiu, 2004).

Evolutionary plant morphologists have long believed that extant tracheophytes are divided into two major lineages (Fig. 1): lycopsids and all other vascular plants (ferns, horsetails, and seed plants). Recent morphological cladistic analyses and molecular phylogenetic analyses have provided strong support for this hypothesis (Kenrick and Crane, 1997a, b; Pryer et al., 2001). In addition, molecular phylogenetic analyses (e.g., Pryer et al., 2001; Dombrovska and Qiu, 2004) have supported the concept that extant euphyllophytes (Fig. 1) are divided into two major clades: moniliformopses (= monilophytes; horsetails and ferns) and seed plants. Although the monophyly of seed plants has been well established in the last 20 years (Crane, 1985; Doyle and Donoghue, 1986), the nesting of sphenopsids (*Equisetum*) within a clade containing all extant ferns had not been fully anticipated (although see Skog and Banks, 1973; Stein et al., 1984; Doyle, 1998). Moreover, the long-enigmatic Psilotales (*Psilotum* and *Tmesipteris*) have now been shown to be sister to Ophioglossales (Fig. 1). Thus, the rootless condition of Psilotales must be the result of developmental loss of this organ system (because all close relatives produce roots; Fig. 2), and the leaves of *Psilotum* (*Psilotum* is often mistakenly thought to be ''leafless'') are highly reduced.

Seed plant interrelationships are currently unresolved (Burleigh and Mathews, 2004). Although the hypothesis that Gnetales are closely related to angiosperms was consistently supported in phylogenetic analyses of the 1980s and 1990s, almost every molecular phylogenetic analysis of extant seed plants since 1996 (Goremykin et al., 1996; Chaw et al., 1997; Hansen et al., 1999; Qiu et al., 1999; Samigullin et al., 1999; Bowe et al., 2000; Chaw et al., 2000; Frohlich and Parker, 2000; Sanderson et al., 2000; Soltis et al., 2002b) has failed to support an exclusive relationship between the Gnetales and angiosperms (although see Rydin et al., 2002, whose analysis could not rule out this relationship). Instead, recent molecular phylogenetic analyses typically have reported that Gnetales is most closely related to, or even nested within, conifers, or is sister to all other extant gymnosperms. An additional finding of many recent molecular phylogenetic studies is that extant gymnosperms (cycads, *Ginkgo*, conifers, Gnetales) may comprise a monophyletic group that is the sister lineage to flowering plants (but see Sanderson et al., 2000; Chaw et al., 2000; and Bowe et al., 2000 for analyses that yield paraphyletic gymnosperms). The most comprehensive recent molecular phylogentic analysis finds consistent but not exclusive support for a nesting of Gnetales within conifers (although Rydin et al., 2002 found high support for conifer monophyly), with *Gingko* sister to that clade and cycads sister to all other extant gymnosperms (Burleigh and Mathews, 2004). However, the conflicting results of recent molecular sequence analyses as well as issues of congruence between molecular phylogenetic hypotheses and interpretations of rare genomic markers (see citations in Burleigh and Mathews, 2004), the stratigraphic record, and comparative morphological analyses indicate it may yet be some time before the final chapter is written on the interrelationships of cycads, *Ginkgo*, conifers, Gnetales, and angiosperms (Crane et al., 2004).

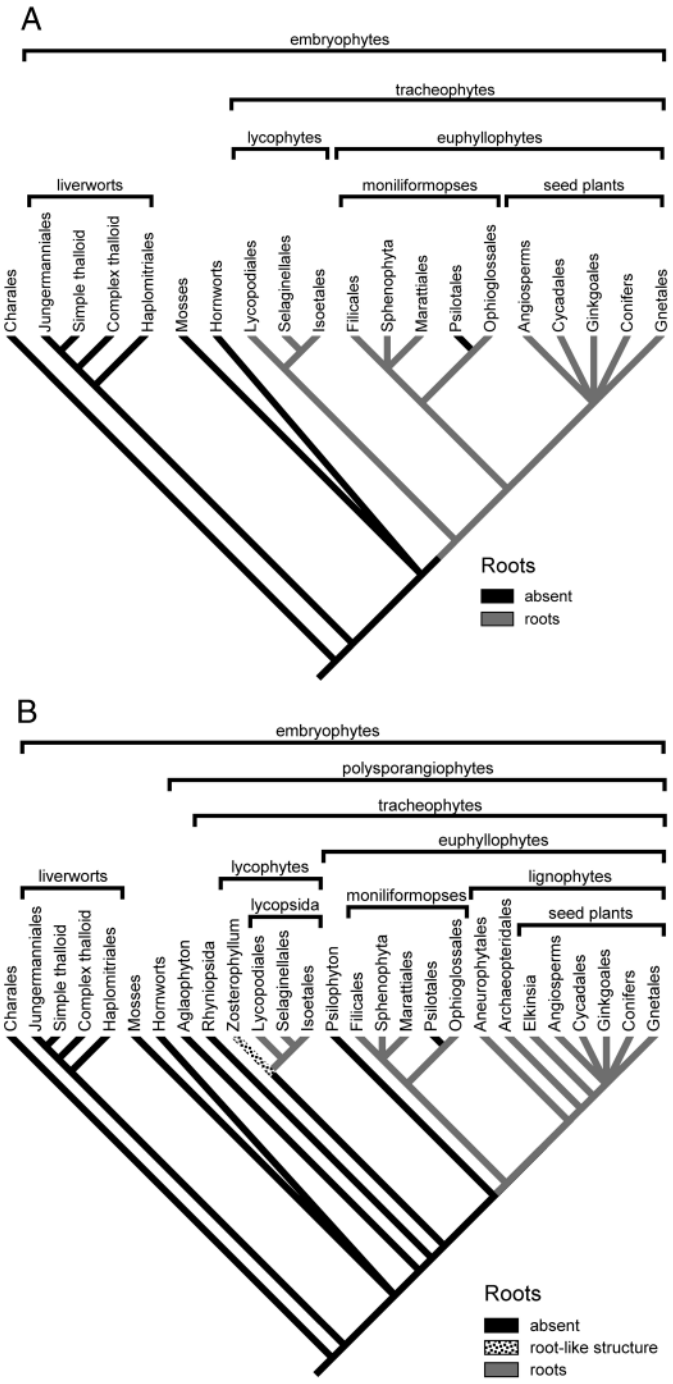

Fig. 2. Evolution of roots. (A) In the absence of integration of fossil taxa into a phylogeny, it might be concluded that the roots of all extant plants are homologous, but this is an artifact because key fossil taxa appear to lack roots. (B) When key fossil taxa are integrated into the phylogeny for analysis of root evolution, it is apparent that there have been two evolutionary origins of roots. One origin is in the Lycophyta, perhaps from telomic systems that grow into substrate, as found in *Zosterophyllum*. Another independent origin is observed in the common ancestor of extant euphyllophytes.

Where do fossil taxa fit into the molecular phylogenetic framework?—Deciphering the specific events associated with key evolutionary developmental transitions often requires a detailed knowledge of fossil species and clades and their phylogenetic placement. Thus, the inability of molecular phylogenetic analyses to place fossil taxa within the resulting topologies poses a major limitation to reconstructing the origin and early diversification of plant organs. In many cases, we simply do not know the phylogenetic position of important fossil taxa. Most Mesozoic seed plant lineages, although well understood from a morphological perspective, remain ambiguous within a phylogenetic context (Crane et al., 2004). The same can be said of many critical Devonian vascular plant taxa, including purported fern ancestral groups such as the cladoxylopsids (Bateman et al., 1992; Doyle, 1998). Nevertheless, hypotheses for phylogenetic placement of a number of fossil taxa critical to reconstructing major evolutionary development are improving.

The importance of placing fossil taxa into a phylogenetic framework to generate reasonable hypotheses of character evolution cannot be overstated (Kenrick and Crane, 1997a; Doyle, 1998). Attempts to reconstruct character evolution at relatively deep levels of embryophyte history using phylogenetic analyses of extant-only lineages can result in fundamentally flawed hypotheses. For example, all extant lycophytes and euphyllophytes (except Psilotales) have roots. Parsimonious interpretation of character evolution based on analyses of extant-*only* tracheophytes appears to support the hypothesis that the roots of lycopsids and euphyllophytes are homologous (as proposed by Schneider et al., 2002), having been inherited from a common ancestor (Fig. 2A). However, when key fossil taxa are integrated into the tree, support for this conclusion evaporates (Fig. 2B). Based on reconstructions of early fossil lycophytes and euphyllophytes (Kenrick and Crane, 1997b; Gensel et al., 2001; Raven and Edwards, 2001), the common ancestors of both lycophytes and euphyllophytes appear to lack roots, thereby supporting the hypothesis that the root structures of these two major extant lineages of plants are not homologous (Fig. 2B).

A similar contrast in evolutionary historical interpretation can be seen with respect to the origin of leaves in tracheophytes. All extant tracheophytes produce leaves. Mapping of leaf characters onto a tree of extant tracheophytes (all of which have leaves produced in phyllotactic patterns from the flanks of shoot apical meristems) has been taken by Schneider et al. (2000) to indicate (erroneously) that leaves of seed plants, moniliformopses, and lycopsids are homologous. However, phylogenetic placement of key fossil taxa (e.g., Devonian taxa such as *Psilophyton* and *Pertica* among euphyllophytes and aneurophytes among lignophytes) indicates that each of the common ancestors of both moniliformopses and lignophytes were leafless (assuming no character reversals from leafy shoots to telomic, leafless shoots) and that there was a separate evolutionary origin of leaves in each of these two lineages. Integration of fossil taxa into phylogenetic hypotheses in this case demonstrates that the leaves of extant moniliformopses and seed plants are not homologous.

THE MAJOR ISSUES IN THE EVOLUTION OF PLANT DEVELOPMENT

The diversification of land plants has been accompanied by key developmental innovations that led to major facets of morphology. The genetic bases for many of these morphological features and/or developmental processes are now being elucidated in model angiosperm species, as well as in a growing number of nonflowering and, from a technical standpoint, nonmodel plant taxa. For the first time, we are witnessing the

emergence of ever-broadening opportunities to integrate molecular genetic studies into investigations of the evolutionary diversification of land plants. Here we review four major features of land plant morphology and development, providing a phylogenetic, comparative morphological, and molecular genetic context for future work in the study of the evolution of plant development.

The evolution of apical growth—Indeterminate apical growth from either a single or group of pluripotent stem cell(s) (apical initials, or collectively promeristem sensu Clowes, 1961) is one of the developmental hallmarks of land plants and has played a significant role in the evolution of plant form and function. Based on developmental patterns found in ancient land plant lineages such as liverworts, hornworts, and mosses and on growth characteristics of land plant outgroups (Charales and Coleochaetales), the first land plants expressed a pattern of apical growth in the gametophyte generation (Fig. 1; Mishler and Churchill, 1985; Graham et al., 2000). The sporophytes of liverworts and hornworts lack an apical meristem (Cooke et al., 2003), and this is likely to be the plesiomorphic condition for the diploid phase of land plants (Fig. 1; Mishler and Churchill, 1984; Graham et al., 2000).

The sporophytes of many mosses appear to have a transitory expression of an apical cell during embryogenesis (Smith, 1955; Renzaglia et al., 2000; Cooke et al., 2003). Given the potential placement of hornworts as sister group to the tracheophytes (among extant lineages), the issue of whether the apical cell of moss sporophytes is homologous with that of the sporophytes of vascular plants remains an open question. In either case, it is clear that a common ancestor of polysporangiophytes was the first land plant to express a prolonged phase of apical growth in the sporophyte (Fig. 1).

The alternation of generations among land plants provides fertile ground to examine the origin of developmental innovations within a complex life cycle and the potential heterochronic and heterotopic transfer of these innovations to a temporally, genetically, and morphologically distinct phase of the life cycle. In the case of apical growth, it is simplest to assume that the underlying developmental mechanisms for apical growth (i.e., maintenance of a ''stem cell'' population at a growing tip) that were initially present in the gametophytes of land plants were eventually co-opted for expression (once or twice) in the sporophyte generation of the life cycle. If this is the case, it is reasonable to expect that the molecular developmental programs in extant land plants with apical growth in both the gametophyte and sporophyte generation (lycopods, ferns, horsetails) may reveal evidence of this shared or ''borrowed'' biology (Nishiyama et al., 2003).

What can molecular developmental genetics tell us about the evolution of apical growth in plants? The starting point for the study of molecular developmental programs for apical growth in land plants is the genetic analysis of the organization of the shoot apical meristem (SAM) in the model angiosperm, *Arabidopsis thaliana* (see reviews by Fletcher, 2002; Carles and Fletcher, 2003). The SAM of flowering plants is typically described as comprised of histologically distinct cell layers: the tunica, comprised of the outer anticlinally dividing cell files, and the corpus, found beneath the tunica (Steeves and Sussex, 1989). However, this organization is not a universal feature of SAM organization in land plants; indeed, it is not found outside the angiosperms and Gnetales. Kaplan and Cooke (1997) summarized the earlier views of Hagemann (1967), who described a general cytohistological zonation model that divides the SAM into an initial zone, comprised of slowly dividing stem cells surrounded by a peripheral morphogenetic zone of more rapidly dividing cells that are recruited for the differentiation of leaf and stem tissues. The power of this model of SAM organization derives from its ability to cover the entire phylogenetic breadth of land plants (it is general to SAMs, whereas the tunica–corpus concept is specific only to a subset of SAMs). Moreover, Hagemann's morphogenetic and initial zones find broad overlap with currently known patterns of gene expression in shoot apical meristems (for review of gene expression patterns, see Bowman and Eshed, 2000). Thus, recognition of cytohistological zonation is almost certainly a more biologically meaningful way of analyzing the activities of the SAM.

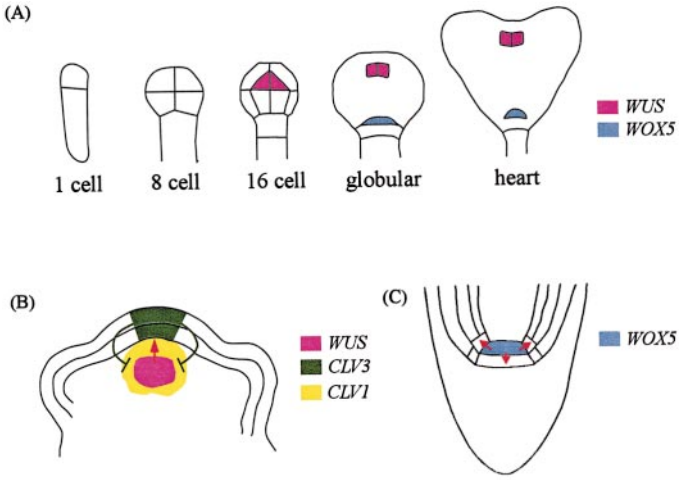

Fig. 3. Establishment and maintenance of stem cells in the shoot apical meristem (SAM) and root apical meristem (RAM) of the model dicot, *Arabidopsis thaliana*. (A) The root/shoot dichotomy is established early during embryogenesis as is evident from the expression of the stem cell maintenance gene *WUSCHEL* (*WUS*) at the presumptive organizing center (OC) in shoots, and its paralog, *WUSCHEL-related homeobox5* (*WOX5*), at the presumptive quiescent center (QC) in roots. (B) *WUS* expression is confined to the OC in the SAM, overlaps and is required for *CLAVATA1* (*CLV1*) expression, and promotes CLAVATA3 (CLV3) function in the cells above it. CLV3 acts nonautonomously via interactions with its receptor, CLV1, to repress *WUS* expression, thus establishing a feedback loop that maintains the stem cell population. (C) *WOX5* is expressed in the QC in roots and acts multidirectionally to maintain stem cell populations in the root apical meristem. (Adapted from Baurle and Laux, 2003; Byrne et al., 2003.)

Molecular expression analyses subdivide Hagemann's initial zone into two regions, a stem cell population found at the summit of the meristem that expresses the *CLAVATA3* (*CLV3*) gene subtended by the more centrally located organizing center (OC) that expresses the homeodomain transcription factor, *WUSCHEL* (*WUS*) (Bowman and Eshed, 2000). The OC is responsible for the production and maintenance of these apical initials. In the model eudicot, *A. thaliana*, a balanced population of stem cells is maintained by an autoregulatory feedback loop between *WUS* and a receptor-like kinase pathway comprised of two leucine-rich repeat (LRR) receptor kinases encoded by *CLAVATA1* (*CLV1*) and *CLAVATA2* (*CLV2*) and their putative ligand encoded by *CLV3* (Clark et al., 1997; Jeong et al., 1999; Brand et al., 2000; Schoof et al., 2000; Lenhard and Laux, 2003). *WUS* expression is confined to the OC early in embryogenesis and to the mature SAM (Fig. 3;

Mayer et al., 1998); it overlaps and is required for *CLV1* expression and promotes *CLV3* function in the cells above it (Fig. 3B). CLV3 acts non-autonomously via interactions with its receptor, CLV1, to repress *WUS* gene expression (Rojo et al., 2002; Lenhard and Laux, 2003). This feedback loop is essential for maintaining the proper balance of stem cells in the SAM; overexpression of *WUS* leads to uncontrolled proliferation of stem cells, whereas overexpression of *CLV3* leads to loss of meristem function (Brand et al., 2000; Schoof et al., 2000).

To maintain a functioning vegetative meristem, leaf organogenesis must be confined to the periphery of the SAM, and stem cell differentiation must be repressed. Key to this repression is the class I *KNOTTED-like HOMEOBOX* (*KNOX*) family of homeodomain transcription factors. *KNOX* genes, such as *SHOOT MERISTEMLESS* (*STM*) and *BREVIPEDICELLUS* (*BP*), and *knotted1-like from Arabidopsis thaliana2* (*KNAT2*) are expressed in the SAM but excluded from the leaf primordia (Kerstetter et al., 1994; Lincoln et al., 1994; Long et al., 1996). Overexpression of *KNOX* genes leads to altered, often compound, leaf morphology and, in some cases, the formation of ectopic meristems (Sinha et al., 1993; Chuck et al., 1996; Hareven et al., 1996; Janssen et al., 1998). This observation leads to the supposition that the evolution of shoot and leaf morphology was intimately tied to the functional diversification of the *KNOX*-gene family members.

In contrast to the wealth of knowledge we have concerning the molecular control of meristem organization in model angiosperms, we know relatively little about the genetics of meristem maintenance in other lineages of land plants. Studies of nonflowering plant homologs of angiosperm meristem function genes may provide insights into the history of the underlying genetic system(s) that govern apical growth in sporophytes and gametophytes. It would be important to determine, for example, when in the evolutionary history of the land plants the *CLV1/CLV3/WUS* interaction that controls SAM development in angiosperms originated and whether a similar and/or homologous genetic system is involved in apical cell maintenance in basal land plants.

There has been some limited success in isolating genes associated with apical meristem function in land plants other than angiosperms. Investigators, for example, have managed to isolate *KNOX* genes from the moss, *Physcomitrella patens* (this model system is described in Cove, 2000). Both class I and class II *KNOX* genes have been isolated from *Physcomitrella*, indicating these two classes of genes diverged before the separation of the moss lineage from its sister group (Champagne and Ashton, 2001). Furthermore, the two moss class I *KNOX* genes arose by a duplication event specific to this moss lineage (Champagne and Ashton, 2001), which may have led to lineage-specific functional diversification of the class I *KNOX* genes in mosses. The function of these regulatory genes in mosses remains to be seen; it is not known whether they function in the gametophyte and/or the sporophyte apical meristems. However, with the advent of targeted gene knockouts in *Physcomitrella*, such data are obtainable (Bezanilla et al., 2003).

The origin of roots—Three questions surrounding the origins and evolution of roots remain unresolved: (1) Are roots of different land plant lineages (lycophytes and euphyllophytes) homologous? (2) Are the developmental genetic programs that give rise to roots and shoots similar? (3) Do the shared features of histogenesis in shoots and roots arise from common developmental programs first expressed in land plant sporophytes prior to the origin(s) of roots?

Homology of roots between land plant groups—Phylogenetic mapping of the evolution of roots indicates that organs selected to penetrate the substrate (also anchor the plant body and absorb water and minerals) evolved at least twice: once each within the Lycophytina and the Euphyllophytina (Fig. 2B). This has been the conventional wisdom for many years (Bierhorst, 1971; Kenrick and Crane, 1997a, b; Dolan and Scheres, 1998; Doyle, 1998; Raven and Edwards, 2001; Boyce and Knoll, 2002). The current supposition is that the earliest polysporangiophytes did not possess morphologically distinct root and shoot systems, at least in the sense that extant vascular plants do. Rather, these sporophytes were comprised of telomes, axial systems that dichotomize at their apices. Many have equated early telomic systems with leafless stems (e.g., Gifford and Forster, 1989; Kenrick and Crane, 1997a; Kenrick, 2001) and suggested that roots evolved from these aboveground axial systems. If this is the case, then roots are in essence serially homologous with shoots (Gensel et al., 2001).

Although the precise interrelationships of zosterophylls and their relationship(s) to lycopsids remain ambiguous (Bateman et al., 1992; Gensel, 1992; Hueber, 1992; Kenrick and Crane, 1997b; Gensel and Berry, 2001), the sporophyte of the common ancestor of the encompassing clade that includes zosterophylls and lycopsids (Lycophytina) appears to have been a telomic (axial) plant with equal dichotomous branching. A number of early zosterophylls and lycopsids (e.g., *Zosterophyllum*, *Sawdonia*, *Bathurstia*, *Crenaticaulis*, *Hsua*, *Drepanophycus*, and *Asteroxylon*) have ''rootlike structures'' in which some telomic axes grew downwards, whereas others were erect and ''shootlike'' (Rayner, 1984; Li and Edwards, 1995; Doyle, 1998; Gensel et al., 2001; Gensel and Berry, 2001; Raven and Edwards, 2001). It is unknown whether these rootlike structures, which grew into adjacent substrates, had a root cap or an apical organization similar to the aboveground photosynthetic telomes (Raven and Edwards, 2001). Gensel et al. (2001) hypothesized that the roots of extant lycopsids arose from an original dichotomizing telomic system in which one of the dichotomizing axes became specialized for photosynthetic activity (shoot system) and the other became specialized for belowground development.

There is no fossil evidence of rooting systems in early euphyllophytes such as *Psilophyton* and *Pertica* (Raven and Edwards, 2001). The assumption is that the sporophyte of the common ancestor of euphyllophytes was a telomic plant that lacked root/shoot organization. If the common ancestors of lycophytes and euphyllophytes were both rootless, the roots of lycopsids and euphyllophytes must be homoplasious (Fig. 2B). If this is the case, the roots of both major groups of extant tracheophytes have converged upon highly similar patterns of development. The root apical meristems of euphyllophytes and lycophytes possess a root cap that derives from the root apical meristem and physically protects the delicate meristematic cells. There is at least one notable difference between the roots of lycopsids and those of euphyllophytes: lycopsid roots branch dichotomously from their apex, whereas euphyllophyte roots typically form lateral roots endogenously and subapically (Gifford and Foster, 1989).

The currently accepted evolutionary scenario for root origins depends on the assumption that the absence of roots in

early fossil polysporangiophytes is an accurate representation of historical reality. A critical examination of the paleobotanical literature demonstrates that the question of a single vs. multiple origins of the ''root'' may be more ambiguous than is typically assumed to be the case. Early polysporangiophytes often exhibit preferential preservation of aerial as opposed to subterranean structures (aboveground parts are often transported by water to a distant site prior to fossilization). Thus, it is difficult to be confident that all of the early polysporangiophytes lacked roots (with root apical organization) or other primordial rooting structures (Kenrick and Crane, 1997b; P. Gensel, University of North Carolina, personal communication). Indeed, Kenrick and Crane (1997a) decided to omit root characters from their phylogenetic analysis of early land plants, given this uncertainty. For the time being, it is reasonable to conclude that the question of the homology of roots in lycophytes and euphyllophytes is unresolved. Future comparative studies of the genes underlying development of roots in these two plant groups may prove useful to the resolution of questions regarding root organ(s) and homology in tracheophytes.

Homology of genetic programs that give rise to roots and shoots—Molecular developmental genetic analyses are congruent with the fact that, at least in the angiosperms, roots are similar to and may be evolutionarily derived from the developmental program associated with the SAM (Benfey, 1999). The cells responsible for the production and maintenance of stem cells in the shoot and root apical meristems (RAM) of flowering plants are found in regions that are referred to as the organizing center (OC) and quiescent center (QC), respectively. There are a few key differences in the OC and QC; the OC acts unidirectionally, maintaining a distal population of stem cells, and the QC is omnidirectional, maintaining both distal and proximal populations of stem cells. However, it is becoming clear from molecular genetic analyses that both the OC and QC have common molecular mechanisms that maintain stem cell populations (see reviews by Baurle and Laux, 2003; Byrne et al., 2003; Veit, 2004).

Although the same genes involved in stem cell maintenance in the SAM do not play a direct role in the RAM, similar classes of molecules have been co-opted for use in both meristems (Fig. 3). In *A. thaliana*, there is a reiteration of the receptor-like kinase pathway in the RAM, and ligands of the *CLV3/ESR*-related (*CLE*) gene family are involved. For example, when *CLE40* is overexpressed, both root and shoot growth is repressed, a result similar to that of *CLV3* overexpression (Hobe et al., 2003). In addition, another *CLV3*-like gene, *CLE19*, limits root growth when overexpressed (Chuck et al., 1996).

It is not clear that suppression of growth in the RAM is mediated by repression of *WUS*-like activity, although there is a *WUS*-like homeodomain gene identified in rice, *QUIESCENT CENTER HOMEOBOX* (*QHB*), expressed specifically in the cells comprising the QC (Kamiya et al., 2003). Overexpression of *QHB* causes proliferation of shoots, comparable to plants that overexpress *WUS*, indicating it may be acting on similar targets as *WUS* (Kamiya et al., 2003). A homologous *WUS*-like homeodomain gene, *WUSCHEL-related homeobox5* (*WOX5*), is similarly expressed in the QC of *A. thaliana* roots, indicating its function may be conserved across monocots and eudicots (Fig. 3; Haecker et al., 2004).

Homology of shared features of patterning and histogenesis in shoots and roots—Studies on the molecular mechanisms of radial patterning and histogenesis in angiosperm root and shoot development have supported a common molecular mechanism for development in these two systems. Two members of the GRAS-transcription factor family, *SCARECROW* (*SCR*) and *SHORTROOT* (*SHR*), are required for establishment of the endodermal layer in both roots and shoots (Pysh et al., 1999; Wysocka-Diller et al., 2000; Nakajima et al., 2001). *SCR* may also play a role in the control of cell division in the QC, where it is expressed. *SCR* is also expressed in the L1 layer of the SAM of flowering plants, although its function there has not been revealed by mutant analysis, possibly due to redundancy (Wysocka-Diller et al., 2000). The root and shoot also share a common genetic motif for determining epidermal cell fate (Dolan and Scheres, 1998; Schiefelbein, 2003). The *GLABRA2* (*GL2*) homeodomain-leucine zipper transcription factor, in conjunction with a host of other transcription regulators, including the *myb*-like transcription factors *WEREWOLF* (in roots) and its functionally redundant paralog *GL1* (in shoots), is required for the differentiation between trichoblasts (hair cells) and atrichoblasts in both the shoot and root (Oppenheimer et al., 1991; Rerie et al., 1994; Di Cristina et al., 1996; Masucci et al., 1996; Lee and Schiefelbein, 1999, 2001). *GL2* has contrasting roles in the root vs. the shoot; it suppresses the formation of trichoblasts in roots and promotes their formation in shoots (Rerie et al., 1994; Di Cristina et al., 1996; Masucci et al., 1996; Ohashi et al., 2002).

Molecular developmental genetic data indicate a duplication of the developmental module required for the maintenance of indeterminate growth. Although there is no direct overlap between some of the regulators involved in RAM and SAM maintenance, perhaps the same regulatory loci such as *WUS*-like genes were initially recruited for SAM and RAM formation; via subsequent gene duplication and subfunctionalization (Lynch and Force, 2000), these genes gained tissue-specific roles. Investigations into molecular genetics of apical meristems in basal land plants will address the question of homology between root and shoot and may help resolve the issue of single vs. multiple origins of the shoot/root dichotomy.

The evolution of leaves—Phylogenetic mapping of leaves among land plants indicates that leafy shoot systems have evolved at least five times over the course of embyrophyte history (Fig. 4). The phylogenetic and comparative morphological basis for this conclusion is robust, and it can be safely concluded that the leafy shoot systems of many different clades of land plants are homoplasious. Two large clades of land plants, liverworts and mosses, contain taxa with leafy shoots in the gametophyte generation (Fig. 4). Among extant vascular plants, leafy shoots are found in the sporophytes of lycophytes, moniliformopses, and seed plants and appear to have evolved separately in each of these groups (Fig. 4).

Leaves are hypothesized to have evolved once in the common ancestor of mosses (Mishler and Churchill, 1984; but see Renzaglia et al. [2000], who suggested that differences in the development of the shoot systems of *Takakia* and all other mosses are congruent with two separate origins of leafy shoots in mosses). Although the earliest land plants almost certainly had dorsiventrally flattened thalloid gametophytes, the common ancestor of mosses is hypothesized to have been a leafless radially symmetrical set of branching axes (Mishler and Churchill, 1984). For now, it is most parsimonious to assume that

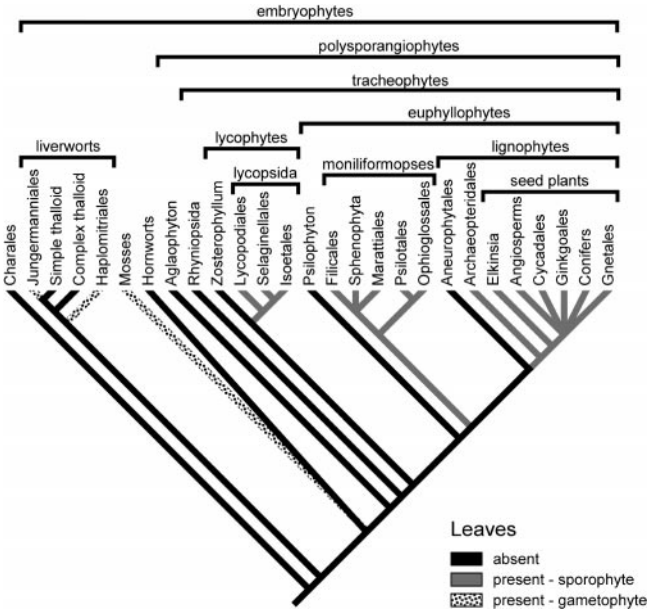

Fig. 4. Evolution of leaves. A minimum of three evolutionary origins of leaves are inferred in the gametophyte generation. One origin is among complex thalloid liverworts, another in simple thalloid liverworts, and a third in the common ancestor of extant mosses. Three evolutionary origins are also inferred in the sporophyte generation. One origin is in Lycopsida, another in the moniliformopses, and a third in the common ancestor of seed plants and Archaeopteridales.

the acquisition of a leafy shoot system in the gametophyte is a synapomorphy of mosses (Fig. 4).

Leafy liverworts may ultimately prove to be one of the most interesting clades in which to examine the evolution of leafy shoot architecture. Although the interrelationships of liverworts remain somewhat ambiguous, there is broad consensus that a simple thalloid morphology is plesiomorphic for the gametophyte generation (Shaw and Renzaglia, 2004). Many workers have speculated that leafy shoots evolved from an ancestral thalloid morphology at least twice in the gametophyte generation (Fig. 4; Schuster, 1966, 1979; Crandall-Stotler, 1981, 1984; Mishler and Churchill, 1985; Kenrick and Crane, 1997b; Shaw and Renzaglia, 2004). Renzaglia et al. (2000) speculated that there may have been as many as six separate origins of leafy shoots among liverwort gametophytes; Shaw and Renzaglia (2004) provide compelling evidence for the multiple origins of ''leaves'' in liverworts.

Most leafy liverworts are part of a large (species-rich) monophyletic group (essentially Jungermanniales) that is nested within a larger clade that includes simple thalloid liverworts (Lewis et al., 1997; Shaw and Renzaglia, 2004; B. Crandall-Stotler, University of Southern Illinois, personal communication; B. Mishler, University of California, Berkeley, personal communication; Y.-L. Qiu, University of Michigan, unpublished data). The phylogenetic placement of a small group of leafy liverworts in the genus *Haplomitrium* is uncertain, but the most recent studies have indicated that this clade may be sister to all other extant liverworts (Shaw and Renzaglia, 2004; B. Crandall-Stotler, University of Southern Illinois, personal communication; Y.-L. Qiu, University of Michigan, unpublished data). In either case, the phylogenetic distance of this clade from Jungermanniales indicates that *Haplomitrium* acquired a leafy shoot system in the gametophyte generation independently of the rest of the leafy liverworts. Thus, there appear to have been at least three separate origins of plants with leaf/stem organization of a shoot system in the gametophyte generation of the life cycle: two (and probably more) in liverworts and one in the common ancestor of all extant mosses.

It has long been hypothesized that the leaves of the sporophytes of lycopsids evolved separately from those of all other tracheophytes and that the common ancestor of lycophytes and euphyllophytes was leafless. Bower (1908) was among the first to present the ''enation'' concept for the origin of the typically simple and single-veined leaves of lycopsids. This classic evolutionary developmental theory posits that the leaves of lycophytes are elaborations of ''enations,'' small flaps (perhaps emergences or multicellular trichomes) of tissue that formed on the surfaces of telomes in zosterophylls (ancient lycophytes). The initial manifestation of enations was not vascularized; no leaf trace diverged from the vascular system of the telome. With time, leaf traces are hypothesized to have evolved to partially integrate these structures into the functional biology of a shoot system. *Asteroxylon* is usually identified as typifying this intermediate condition, with leaf traces that develop only to the base of the enations. The final step in the evolution of lycopsid leaves was the elaboration of a vascular trace into what is essentially a leaf. The enation theory for the origin of the lycopsid leaves is one of gradual elaboration of a simple, superficial, lateral structure.

Crane and Kenrick (1997) have proposed an entirely different hypothesis for the origin of lycopsid leaves involving the sterilization of a lateral sporangium-bearing axis. They posited that in early lycophytes a subset of sporangial structures that were already vascularized were reduced and sterilized to produce specialized photosynthetic organs, in essence, leaves. In support of their argument, Crane and Kenrick point out that there is no evidence of phyllotactic patterning of enations in zosterophylls (1997).

Phylogenetically based analysis of leafy shoot evolution among euphyllophytes indicates that the leaves of seed plants and moniliformopses are not homologous (Fig. 4). Both groups are believed to have megaphyllous leaves (derived from telomic axes), but as will be seen, the concept of a ''megaphyll'' may be misleading when assessing homologies among leaves. Megaphylls are hypothesized to have evolved from modification and congenital fusion of telomic systems through the processes of overtopping, planation, and webbing (Zimmerman, 1930, 1952; Stewart, 1964).

The starting point for the evolution of megaphylls is a simple telomic sporophyte with equal dichotomous branching. The phenomenon of overtopping results in unequal dichotomous branching in which one of the members of each dichotomy is dominant and grows upwards, while the other member gives rise to a lateral system of telomes that is determinate. The result is the formation of a main upright (and pseudomonopodial) axis that is associated with increased height. The standard example of such a plant is *Psilophyton*. In ancient lineages of plants with dichotomously branching telomes, each successive dichotomy is formed at right angles (90 degree angle of rotation) to the previous one. The developmental evolution of planation results in all of the dichotomies being formed in a single plane. Finally, the origin of megaphylls is thought to have involved the addition of photosynthetic tissue between the lateral planate dichotomous telomes (webbing). Unfortunately, the specific question of how webbing might

evolve has never been addressed satisfactorily from a developmental perspective.

The current consensus is that progymnosperms are paraphyletic, and the leaves of Archaeopteridales and seed plants are potentially homologous (although see Boyce and Knoll, 2002, who asserted that progymnosperms are monophyletic and acquired megaphyllous leaves independently from seed plants). Phylogenetic placement of telomic (leafless) Aneurophytales as the sister group of seed plants plus Archaeopteridales (both of which have leafy shoots; Doyle, 1998 and references therein) indicates that the common ancestor of lignophytes was leafless (telomic) and that leaves evolved in the common ancestor of seed plants plus their sister group, Archaeopteridales (Fig. 4). However, the leaves of heterosporous progymnosperms (Archaeopteridales) are relatively small simple ''megaphylls,'' whereas the leaves of early seed plants are almost exclusively large frondlike, compound structures. Doyle (1998) has hypothesized that megaphylls of Archaeopteridales are homologous with the leaflets of the compound leaves of early seed plants. If this assessment is correct, early seed plant megaphylls are not strictly homologous with the megaphylls of Archaeopteridales, but rather with an entire branch system bearing many simple megaphylls.

Although it is fairly certain that the ancestors of moniliformopses were leafless and telomic, there are currently sufficient ambiguities concerning the phylogenetic integration of fossil taxa (e.g., the various cladoxylopsids, *Ibyka*, *Rhacophyton*, and *Pseudosporochnus*) into the moniliformopses to question whether the leaves of horsetails, leptosporangiate ferns, and eusporangiate ferns are homologous. As with the case for homology among Archaeopteridales and seed plants, it is an open question whether all ''megaphylls'' in moniliformopses are morphologically equivalent. The compound leaves of leptosporangiate ferns, Marattiales, and Ophioglossales may have evolved from branch systems bearing simple leaves (Doyle, 1998). If this is the case, then the leaves of sphenopsids would be homologous with the leaflets of various extant fern clades. Alternatively, Rothwell (1999) has argued that the leaves of Filicales, Marattiales, Ophioglossales, and sphenopsids are homologous and derived from a single origin of megaphylls in their common ancestor.

Molecular developmental data may be able to address many questions regarding the origin of leaves. For example, molecular genetic analysis may help to assess the antecedent structure of leaves of lycopsids. If the microphyll is derived from (homologous with) a sterilized sporangium, it can be hypothesized that this kind of leaf will share gene expression patterns with the sporangia of the same organism (because they would be serial homologs). If the microphyll is derived from the gradual elaboration of an enation/emergence, this would potentially prove more difficult to evaluate because all enation-bearing taxa are extinct. Comparisons of molecular developmental data among the leaves of the major subgroups of moniliformopses may also prove useful in attacking this question of evolutionary history.

In general, it would also be interesting to determine if similar genetic systems in leaves were co-opted across diverse clades of land plants that have separate origins of leaflike structures. Unfortunately, we have limited knowledge of the molecular developmental genetics of leaves outside of angiosperm model species. There have thus far been no studies on the molecular basis of the evolution of leaf development over the course of land plant diversification. The recent analyses of

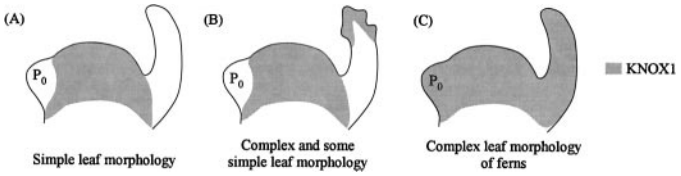

Fig. 5. Class I KNOTTED-like HOMEOBOX (KNOX1) protein expression domains in the shoot apical meristem and developing leaf primordia. (A) In some species with simple leaves, KNOX1 is excluded from developing leaf primordia. (B) In species with complex leaf morphology, KNOX1 is excluded from the initial leaf primordium (P_0), but is present in older leaf primordia in developing leaflets. KNOX1 is similarly expressed in some species with simple leaves, indicating other regulatory changes can influence leaf shape and that simple leaf morphology evolved multiple, independent times. (C) In the fern *Anogramma chaeophylla*, which also has complex leaf morphology, KNOX1 is not excluded from developing leaf primordia, indicating control of compound leaf morphogenesis evolved independently in this lineage. (Based on Bharathan et al., 2002.)

the molecular developmental genetics of leaf morphogenesis in these model systems, however, have provided an initial platform for further analyses across land plant taxa (see review by Kessler and Sinha, 2004).

In angiosperms such as *A. thaliana*, leaves are initiated at the shoot apex, and the developmental program of leaves is fundamentally different from that of stems. In contrast to an indeterminate, radially symmetric stem, leaf growth in angiosperms is determinate and usually exhibits adaxial/abaxial asymmetry. These opposing developmental programs coexist at the shoot apex, with leaves forming at the periphery of the SAM. Important to the loss of indeterminate growth in leaves is the downregulation of class I *KNOX* genes in the leaf primordia (Fig. 5A; Jackson et al., 1994). *KNOX* expression is repressed in incipient leaves by members of the *myb*-domain protein family including *ASYMMETRIC LEAVES1* (*AS1*) in *A. thaliana* and its orthologs *PHANTASTICA* (*PHAN*) from *Antirrhinum* and *ROUGHSHEATH2* (*RS2*) in maize (Waites et al., 1998; Timmermans et al., 1999; Tsiantis et al., 1999; Byrne et al., 2000). Analyses of homologs of these genes in other land plants may provide insights into the evolutionary origins of leaves and leaflike structures.

Although there has been little attention paid to investigating the molecular genetic basis for leaf/leaflike evolution across land plant taxa, there has been some interest in examining the genetic basis of leaf morphology within the angiosperms. The acquisition of abaxial/adaxial symmetry is a developmental innovation that typically distinguishes leaves from shoots. Leaf blade polarity is established by the coordinated expression of a number of different transcriptional regulators. Adaxializing factors include the *myb*-factors *PHAN* (in *Antirrhinum*) and *AS1*and *AS2* (in *Arabidopsis*), as well as the homeodomain-zipperIII (HD-ZIPIII) transcription factors *PHABULOSA* (*PHAB*), *PHAVOLUTA* (*PHAV*), and *REVOLUTA* (*REV*), also from *Arabidopsis* (Waites et al., 1998; Byrne et al., 2000; McConnell et al., 2001; Iwakawa et al., 2002; Xu et al., 2003). The *YABBY* and *KANADI* genes confer abaxial identity in *Arabidopsis* (Siegfried et al., 1999; Eshed et al., 2001; Kerstetter et al., 2001). In plants with simple leaves, such as *Arabidopsis*, loss of expression of either abaxial or adaxial genes causes radially symmetrical leaves expressing ad- or abaxial cell fates, respectively, to form (Siegfried et al., 1999; Kerstetter et al., 2001; McConnell et al., 2001; Iwakawa et al., 2002).

Repression of *PHAN* expression in compound tomato

leaves, however, transforms its pinnately compound leaf into a palmately compound one (Kim et al., 2003). This observation led Kim et al. (2003) to survey taxonomically diverse plant species with either pinnately or palmately compound leaves to see if this fundamental morphological distinction is correlated with altered *PHAN* expression. *PHAN* expression in pinnate leaves occurs across the whole adaxial face of the primordia, whereas *PHAN* is confined to the distal region of leaf primordia in palmately compound leaves (Kim et al., 2003). Thus, evolution of compound leaf morphology is further associated with alterations in the pattern of *PHAN* expression.

The study of the evolution of leaf development has heretofore focused on the molecular basis of simple vs. compound leaf development among species. In taxa with compound leaves, *KNOX* genes are expressed in leaf primordia, leading to maintenance of indeterminacy in the leaf (Hareven et al., 1996; Chen et al., 1997; Janssen et al., 1998; Bharathan et al., 2002). These observations, in conjunction with genetic analyses that show *KNOX* overexpression can increase the degree of dissection in compound leaves, have led to the hypothesis that compound leaves have arisen as a direct result of the altered expression of *KNOX* genes (Bharathan and Sinha, 2001). These studies have provided mechanistic support for the leaf–shoot continuum model, the hypothesis that leaves are, at least in euphyllophytes, derived from stemlike (axially indeterminate) organs (Bharathan and Sinha, 2001).

Compound leaves have evolved many times in angiosperms from the ancestral state of simple leaves. Bharathan and colleagues have examined molecular genetic differences that may underlie compound and simple leaves by analyzing *KNOX* expression in *Lepidium* (Brassicaceae), which contains a majority of species with compound leaves and a few species with reversions to simple leaves (Bharathan et al., 2002). *KNOX* gene expression is down-regulated in incipient leaf primordia (P_0) of all the surveyed species, regardless of final leaf morphology (Fig. 5). However, *KNOX* genes are expressed later in development in marginal outgrowths of both compound and simple leaves (Fig. 5B). In simple leaves, the development of these marginal outgrowths is secondarily constrained and manifests only as coarse teeth. This study stressed the importance of studying the evolution of morphology in a phylogenetic context. Although *KNOX* gene expression certainly plays a role in leaf morphogenesis, the manner in which *KNOX* expression has been co-opted to form either complex or simple leaves can differ among plant species.

It is clear from developmental genetic analyses that some key molecular players in leaf morphogenesis are being identified. However, given the multiple independent origins of leaves in land plant history, it is premature to assume that similar leaf morphologies are controlled by homologous molecular programs. Simple and compound leaves have evolved independently several times via alterations in different components of leaf molecular programs. For example, a noted exception to the role of *KNOX* genes in compound leaf morphogenesis can be found in pea, in which it is the expression of *PEAFLO*, the pea homolog to the meristem identity gene *LEAFY* in *Arabidopsis*, that is correlated with the development of compound leaves (Hofer et al., 1997, 2001; Gourlay et al., 2000).

There does appear to be a fundamental difference between *KNOX* gene expression in the compound leaves of ferns vs. seed plants. Whereas *KNOX* expression is repressed at the initial leaf primordium in extant seed plants, expression is not downregulated in the P_0 of the leptosporangiate fern, *Anogramma chaeophylla* (Fig. 5C; Kim et al., 2003). This single observation is congruent with the independent origin of leaves in ferns and seed plants.

More studies of this nature across other land plant taxa are necessary in order to examine the mechanisms by which different leaflike structures have evolved. Class I KNOX homologs have been isolated from *Welwitschia* (Pham and Sinha, 2003) and the conifer *Picea abies* (Sundas-Larsson et al., 1998). Also, a KNOX homolog that could be descended from the ancestral gene prior to the duplication of KNOX genes into two classes was found in the green alga *Acetabularia acetabulum* (Serikawa and Mandoli, 1999), an extremely distant relative of land plants (the most recent common ancestor is estimated at 956 million years ago [Hedges et al., 2004]). The KNOX expression patterns during leaf initiation in *Picea* and *Welwitschia* are consistent with those described for angiosperms. The role of *KNOX* in *Acetabularia* is unknown, although the expression pattern appears to be related to the transition to a reproductive stage (Serikawa and Mandoli, 1999). In addition to findings on the conservation of the *KNOX* genes in plant evolution, the molecular regulation of the adaxializing HD-ZIPIII genes, *PHAB*, *PHAV*, and *REV*, by microRNAs appears to have been conserved throughout 400 million years of embryophyte evolution, being present in all major lineages of land plants (Floyd and Bowman, 2004).

Origin and early evolution of the flower and basic floral organs—Along with the origins of vascular and seed plants, the origin of angiosperms represents one of the three most significant events in the 475-million-year evolutionary history of land plants (Friedman and Williams, in press). Although angiosperms are one of the most recent major groups of land plants to have evolved (the fossil record extends back to the Early Cretaceous; Crane et al., 1995; and discussed later), less is known about the origin and early evolutionary history of angiosperms than is the case for tracheophytes and seed plants.

There are currently two major obstacles to the reconstruction of historical events associated with the origin and early diversification of angiosperms. First, the macrofossil record of early flowering plants has shed little light on the question of which, if any, extant angiosperm floral morphology is the most ancient. The earliest floral macrofossils are all at least 10 million years younger than the first angiosperm microfossils (Friis et al., 2000). Fossils with affinities to diverse flowering plant lineages, including monocots (Crane et al., 1995, 2004), Platanaceae (Crane et al., 1993), Ceratophyllaceae (Herendeen, 1990), Nelumbonaceae (Upchurch et al., 1994), Nymphaeales (Friis et al., 2001), Laurales (Upchurch et al., 1994), Winteraceae (Walker et al., 1983), Chloranthaceae (Friis et al., 1986), Calycanthaceae (Friis et al., 1994), and with unknown affinity (e.g., Sun et al., 2002), are all found in Early Cretaceous floras (Friis et al., 2000). The fossil record provides excellent evidence of a rapid diversification in floral form during the earliest phases of recorded flowering plant history, but little clear evidence as to the morphology of the flowers of the first angiosperms.

An additional obstacle to the study of the origin of flowering plants derives from the complete uncertainty about the identity of the closest seed plant relatives of angiosperms (Doyle, 1998; Friedman and Floyd, 2001; Friedman and Williams, in press). Recent molecular phylogenetic studies (Goremykin et al., 1996; Chaw et al., 1997; Hansen et al., 1999; Qiu et al.,

1999; Samigullin et al., 1999; Bowe et al., 2000; Chaw et al., 2000; Frohlich and Parker, 2000; Sanderson et al., 2000; Zanis et al., 2002) have indicated that extant gymnosperms may be sister to the flowering plants, but there is considerable conflict among the topologies recovered from these analyses. Even if this recent molecular phylogenetic result for extant seed plants should stand the test of time there are a number of diverse Mesozoic extinct seed plant lineages (e.g., Bennettitales, Glossopteridales, and Pentoxylales) whose degree of relatedness to angiosperms remains uncertain. For the time being, establishing angiosperm outgroups will continue to be critical to assessing character state polarities and homologies of important flowering plant features, from the carpel to the second integument of the ovule.

Recent phylogenetic analyses of basal angiosperm interrelationships call into question longstanding assumptions about which lineages constitute the earliest divergent (and potentially plesiomorphic for many features) angiosperms. Although previous views focused on Magnoliaceae and close relatives (Takhtajan, 1969; Cronquist, 1981, 1988; Dahlgren, 1980, 1983; Walker et al., 1984; Donoghue and Doyle, 1989a, b; Thorne, 1992), recent analyses (Mathews and Donoghue, 1999; Parkinson et al., 1999; Qiu et al., 1999, 2000; Soltis et al., 1999; Graham et al., 2000; Zanis et al., 2002, 2003; Hilu et al., 2003; Borsch et al., 2003; Soltis and Soltis, 2004) have provided consensus on the basal extant lineages of angiosperms. These phylogenetic analyses have indicated that monotypic *Amborella* is probably sister to all other angiosperms; that Nymphaeales (Nymphaeaceae plus Cabombaceae) is sister to all angiosperms exclusive of *Amborella*; and that Illiciaceae, Schisandracea, Trimeniaceae, and Austrobaileyaceae comprise a clade (Austorobaileyales) that is sister to the remaining angiosperms.

Although carpels, stamens (microsporophylls with four sporangia), and bitegmic ovules are synapomorphies of angiosperms (Endress, 2001a), the basic homologies of these unique structures with those of nonflowering seed plants are entirely unknown. It is generally assumed that the carpel is a leaf homolog (megasporophyll), although there is an extensive 20th century literature on alternative hypotheses for the origin of the carpel (see Doyle and Donoghue, 1986). There is essentially no concrete evidence from the fossil record or extant nonflowering seed plant lineages to link the carpel structure to a morphological entity outside of angiosperms.

Reconstruction of the morphology of the earliest flower can be derived from comparisons among the most ancient extant lineages of flowering plants (e.g., Doyle and Endress, 2000; Zanis et al., 2003; Ronse De Craene et al., 2003). Although eudicot flowers such as those of *Arabidopsis* typically have four organ whorls (sepals, petals, stamens, and carpels), it is now evident that this type of organization did not characterize the first flowers (Endress, 2001b).

Although *Amborella* is dioecious, it is widely assumed that the first flowers were hermaphroditic (Endress and Igersheim, 1997) because the carpellate flowers of *Amborella* produce staminodes (Endress and Igersheim, 1997), thus demonstrating a fundamentally bisexual nature to its flower. Nevertheless, it is worth noting that unisexual flowers are common among the earliest angiosperm macrofossil assemblages (Friis et al., 2000).

Although some members of Nymphaeales produce flowers with distinct sepals and petals, *Amborella*, members of Austrobaileyales and other ancient clades of angiosperms do not demonstrate a sepal–petal dichotomy in the perianth. Rather, flowers in these taxa, often with helical phyllotaxy in the flower (as opposed to whorls of floral organs) produce a relatively uniform set of sterile floral organs referred to as tepals (Endress, 2001a, b; Soltis et al., 2002a; Ronse De Craene et al., 2003; Zanis et al., 2003). The general indication is that sepals, petals, and petaloid organs have had many separate origins (Kramer and Irish, 1999).

The study of the evolution of floral development has been the most active area of research in the study of the molecular basis for the evolution of plant development. Studies of the molecular developmental genetics of floral organogenesis, which has been extensively studied and described in great detail (see reviews by Jack, 2001; Lohmann and Weigel, 2002; Ferrario et al., 2004), have provided some clues to the diversification of floral morphology. Investigations into the molecular basis for the origin of this major evolutionary innovation invariably turn to the role of the homeotic transcription factors, MADS-box genes. MADS-box transcription factors are found in all eukaryotes, yet it is the extensive duplication and diversification of the class I, MIKC-lineage that is unique to plants (there are 39 members of this lineage in *Arabidopsis* alone) (Purugganan et al., 1995; Alvarez-Buylla et al., 2000b; Nam et al., 2003; Parenicova et al., 2003). As a family, the MIKC-type MADS-box genes are expressed in both vegetative and reproductive tissues (Rounsley et al., 1995; Alvarez-Buylla et al., 2000a). However, it is the floral organ identity genes that have received the most attention in both evolutionary and developmental studies (Ng and Yanofsky, 2001). This is understandable, because their gene functions are mainly conserved across a breadth of taxonomic groups and thus can be used to identify widely conserved organ identity programs. The temporal and spatial expression profiles of these genes, however, can vary between angiosperm taxa, and cannot necessarily be used to identify organ-level homology (e.g., stamen with stamen or petal with petal).

The canonical ABC model of floral development describes three classes of organ identity genes, and all but one of these homeotic genes are MADS-box genes (Bowman et al., 1991; Coen and Meyerowitz, 1991). Sepals are determined by A-class genes, petals by A- and B-class genes, stamens by B- and C-class genes, and carpels by C-class genes. This model has been updated to include the D-class, ovule-specific genes, and the E-class genes, which are expressed in the three inner floral whorls and form quaternary protein complexes with the other floral homeotic genes essential for correct organ formation (Fig. 6A; Jack, 2001; Theissen, 2001; Lohmann and Weigel, 2002).

The ABC model was first described in eudicots, including *Arabidopsis* and *Antirrhinum*; however, the extent of conservation of this patterning program has been questioned, especially with regards to the origin of perianth organs, which show great morphological diversity across angiosperms. In this regard, much attention has been placed on the role of B-class genes, orthologs of the *Arabidopsis PISTILLATA* (*PI*) and *APETALA3* (*AP3*) MADS genes. In rice, a monocot, B-class genes are expressed in the second and third floral whorls and specify the lodicules and stamens, indicating the conserved role of B-class genes in specifying petals and stamens in the common ancestor of monocots and eudicots (Kang et al., 1998; Ambrose et al., 2000; Lee et al., 2003; Xiao et al., 2003). However, in some species of lower eudicots, including Fumariaceae, Ranunculaceae, and Papaveraceae, B-class or-

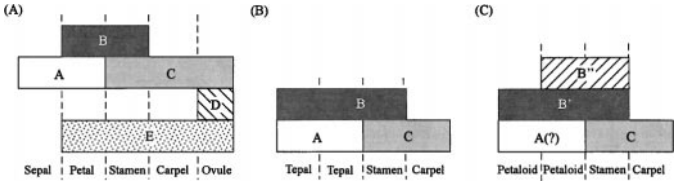

Fig. 6. Overlapping expression domains of MADS-box genes confers floral organ identity. (A) In the higher eudicot *Arabidopsis thaliana*, sepals are determined by A-class genes, petals by A- and B-class genes, stamens by B- and C-class genes, and carpels by C-class genes. D-class genes arose via an angiosperm-specific duplication of an ancestral C-class gene (Kramer et al., 2004), and specify ovule identity. E-class genes are required for organ specificity in the three inner whorls. (B) In the monocot *Tulipa gesneriana*, perianth organs are transformed to morphologically identical petaloid organs (tepals) and exhibit expanded expression of B-class genes into the first whorl, exemplifying the sliding boundary hypothesis (Kanno et al., 2003). (C) In the basal eudicot *Aquilegia alpina*, petaloid organ identity is conferred by the coexpression of B-class paralogs (B′ and B″) in the perianth whorls (Kramer et al., 2003).

thologs are not expressed uniformly or constantly in petals (Kramer and Irish, 1999). This observation may be consistent with multiple, independent origins of petals.

It is evident from genetic analyses of floral homeotic mutants that small changes in the expression patterns of floral MADS-box genes can lead to dramatic changes in floral structure. This observation has led to the hypothesis that the underlying cause of floral diversity is change in the expression domain of floral homeotic genes or the ''sliding boundary'' hypothesis (Bowman, 1997). For example, the phenotypically identical sepals and petals (tepals), of the monocot tulip both express B-class orthologs, indicating that they may have evolved via a shift in the expression of B-class genes to include the first whorl in addition to the second and third whorls (Fig. 6B; Kanno et al., 2003). However, analysis of B-class genes in the tepals of lily and asparagus, both monocots, does not support the sliding boundary hypothesis. Indeed, while the transcript of the lily *AP3*-homolog, *LMADS1*, is found in all four floral whorls, the LMADS1 protein is detected only in the second and third whorls (Tzeng and Yang, 2001). This observation indicates that *LMADS1* is posttranscriptionally regulated, a possibility which remains untested in tulip. Furthermore, asparagus B-class homolog transcripts are not detected in the outer tepal, being found only in the second and third floral whorls (Park et al., 2003, 2004). These results indicate that regulation of sepal and petal identity may differ in these monocots.

The sliding boundary hypothesis does not explain the phenotypically distinct petaloid organs in the two outer whorls of members of the ancient eudicot family Ranunculaceae. Morphological analyses have indicated independent origins of the second-whorl petaloid organs, which in some cases appear to be derived from stamens (Kosuge, 1994). Kramer and colleagues (2003) found evidence for multiple paralogs of the B-class genes, which apparently arose via gene duplication events occurring either before (*AP3*) or during (*PI*) the diversification of Ranunculacea. Whorl-specific expression differed between paralogs, indicating the petaloid organ developmental program is specified by the interactions between distinct B-class paralogs (Fig. 6C; Kramer et al., 2003).

It has been suggested that alterations in expression patterns of these and other floral developmental genes gave rise to the angiosperm flower. Studies of the floral transcription factor *LEAFY* and B-class MADS box genes in gymnosperms, for example, have led to the formulation of the mostly male theory of floral origin (Frohlich, 2003), which posits that the male and female reproductive units were combined in the angiosperm flower by the emergence of ectopic ovules on a subset of microsporophylls in originally unisexual cones of a gymnosperm ancestor (Frohlich, 2003). Another hypothesis for the origin of flowers has suggested a homeotic transformation of reproductive organs to either male or female from unisexual gymnosperm cones, leading to the evolution of an ancestral hermaphroditic flower (Theissen et al., 2002). In this hypothesis, changes in expression of the homologs to the B-class floral homeotic genes along the reproductive axis of the gymnosperm cone may result in the necessary developmental transformation to form a flower.

Functional studies of angiosperm floral genes and their gymnosperm homologs may help determine the extent to which these theories, or alternative molecular genetic mechanisms, can be invoked to explain how flowers originated. As more is known about the molecular genetic basis for the development of other floral organs, it may be possible to incorporate the new information into a better understanding of floral origins. For example, the genes for ovule and carpel development are now being elucidated in angiosperms (Gasser et al., 1998; Liu et al., 2000; Meister et al., 2002), and the functional orthologs in gymnosperms are just beginning to be described (Becker et al., 2002). Continued studies of these and other genes in both angiosperms and gymnosperms may help resolve some key questions regarding the origin of flowers.

Additional studies have also focused on other aspects of floral and inflorescence diversity, including the evolution of rosette flowering in Brassicaceae (Yoon and Baum, 2004) and actinomorphic vs. zygomorphic symmetry in flowers (Luo et al., 1996; Hileman et al., 2003). From these studies, it is evident that floral diversity can be generated by lineage-specific modifications of the ABC floral program, as well as other floral regulatory loci. The genomic analysis of expressed sequence tags (ESTs) in basal angiosperm flowers, as well as the development of model basal angiosperm species for genetic analysis, we hope will help answer the question of the origin of flowers by identifying genes that underlie the development of flowers in these taxa and by determining to what extent the floral genetic program is conserved across angiosperms (Baum et al., 2002; Soltis et al., 2002a; Buzgo et al., 2004).

SUMMARY

The integration of a detailed understanding of phylogenetic relationships among land plants, including fossil taxa, provides a framework for the study of the evolution of morphology and the underlying developmental processes that gave rise to plant form. When coupled with molecular genetic studies of the ontogeny of specific organs, this approach can provide an integrated and comprehensive picture of how developmental processes and morphologies have diversified in land plant evolution.

Investigations of the molecular basis for the evolution of plant development have focused largely on the evolution of flowers and the underlying genes that regulate floral morphogenesis. Other major features of land plant diversification, including the origins and diversification of apical growth patterns, leaves, and roots, have received far less attention and

provide opportunities for future investigations. Progress, however, will continue to rely on advances on several fronts. First, greater resolution of phylogenetic relationships will allow focused hypotheses to be generated and evaluated by comparative morphological data and molecular developmental genetics. Second, most studies of molecular developmental genetics have targeted a small handful of angiosperm species, particularly the eudicot *A. thaliana*. Detailed analyses on other major land plant groups, including liverworts, mosses, and the various clades of moniliformopses, lycophytes, and gymnosperms need to be undertaken to provide breadth in our comparative studies of molecular developmental genetics in plants. Molecular expression patterns derived from a broad phylogenetic sampling of metazoans have been the key to breaking some of the basic code that underlies animal evolutionary developmental biology. This will invariably require development of new model genetic systems that span all major land plant groups, which will permit functional dissection of developmental processes at the molecular genetic level. Finally, new technologies of plant genomics will allow rapid identification of genes in different land plant genomes that, coupled with more detailed functional analysis, may allow integration of functional developmental analyses and functional studies with comparative genomics.

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