Molecular evolution of flower development

Amy L. Lawton-Rauh, Elena R. Alvarez-Buylla and Michael D. Purugganan

Flowers, as reproductive structures of the most successful group of land plants, have been a central focus of study for both evolutionists and ecologists. Recent advances in unravelling the genetics of flower development have provided insight into the evolution of floral structures among angiosperms. The study of the evolution of genes that control floral morphogenesis permits us to draw inferences on the diversification of developmental systems, the origin of floral organs and the selective forces that drive evolutionary change among these plant reproductive structures.

Amy Lawton-Rauh and Michael D. Purugganan are at the Dept of Genetics, Box 7614, North Carolina State University, Raleigh, NC 27695, USA (allawton@unity.ncsu.edu;michaelp@unity.ncsu.edu); Elena R. Alvarez-Buylla is at the Instituto de Ecologia, Laboratorio Genetica Molecular y Evolucion, Universidad Nacional Autonoma de Mexico, AP-Postal 70-275, Mexico D.F. 04510, Mexico (abuylla@servidor.unam.mx).

Flowers are among the most visible and spectacular products of evolution. Floral structures first appeared in the fossil record among the seed plants, as determinate, sporophyll-bearing shoots, sometime during the early Cretaceous ~130 million years ago (Mya) (Refs 1,2); since then they have undergone considerable diversification in both form and function. These specialized reproductive structures display a stunning array of morphologies in extant flowering plant species, driven, in part, by selection associated with varied pollination and dispersion strategies. In recent years, studies of floral morphology in an evolutionary context have been buoyed by genetic analysis of developmental pathways underlying inflorescence and flower morphogenesis[3,4]. Isolation and characterization of loci known to participate in the genetic control of floral development have led to the formulation of models describing how floral regulatory genes interact with each other to pattern development in the angiosperm flower, including the classic ABC genetic model of floral organ identity[4] (Box 1). The genetic control of flower development is controlled by relatively few regulatory genes, which has provided evolutionary biologists with new opportunities to dissect the molecular basis of evolutionary change in plant reproductive morphology[5,6].

Evolution of MADS-box genes

Most floral regulatory genes that have been identified encode various sequence-specific DNA-binding transcriptional activators, including homeodomain (*BEL1*) (Ref. 7), zinc-finger (*SUPERMAN*) (Ref. 8) and novel regulatory proteins (*APETALA2* and *LEAFY*) (Refs 9,10). However, many of these loci belong to the eukaryotic MADS-box gene family whose products are characterized by the presence of the highly conserved 57-amino acid DNA-binding MADS domain[11]. In *Arabidopsis thaliana* (thale cress), at least 47 MADS-box sequences are known (E.R. Alvarez-Buylla *et al*., unpublished), including floral homeotic genes such as *AGAMOUS* (*AG*), *APETALA3* (*AP3*), *PISTILLATA* (*PI*) and several *AGAMOUS-LIKE* genes[12,13]. Given the large number of MADS-box genes involved in floral development, most studies on the molecular basis of floral developmental evolution have focused on these regulatory loci.

The first plant MADS-box genes identified encoded proteins that shared a common structure consisting of four separate domains. These included: the highly conserved DNA-binding MADS domain at the amino-terminus; a moderately conserved K domain, which probably forms a coiled-coil structure and participates in protein–protein interactions; a weakly conserved intervening region linking the MADS and K domains; and a poorly conserved carboxy-terminal domain that might function as a transactivation domain. The K domain is absent in all non-plant MADS-box genes and was thought to be a specific feature of these proteins only in plants. However, a recent study suggests that several plant MADS-box genes found at the base of the gene phylogeny do not share this stereotypical structure, and that the K domain appears to have evolved at or around the time of the major diversification of the gene family (E.R. Alvarez-Buylla *et al*., unpublished).

Early phylogenetic studies of MADS-box genes isolated from more than 19 plant species provided preliminary glimpses into patterns of diversification and evolution of developmental function in this important regulatory gene family[14–16]. Molecular evolutionary analyses indicate that major duplication events within the plant MADS-box gene family resulted in the establishment of at least four monophyletic floral homeotic gene groups: *AGAMOUS* (*AG*), *APETALA3* (*AP3*), *PISTILLATA* (*PI*) and *APETALA1/AGAMOUS-LIKE9* (*AP1/AGL9*) (Refs 14–16) (Fig. 1). Genetic and expression analyses indicate that members of a floral homeotic gene group tend to share similar developmental functions in flower and inflorescence morphogenesis[14–16], thus reflecting high conservation among evolutionarily related regulatory genes.

Members of the AGAMOUS (AG) group include the *Arabidopsis AGAMOUS* (*AG*), *Antirrhinum* (snapdragon) *PLENA*, and *Zea mays* (maize) *zag1* and *zmm2* loci; all are C-function genes involved in stamen and carpel development (Box 1). The *Arabidopsis AG* gene and its orthologs in other angiosperm species are expressed specifically in the floral reproductive organs[14], while gymnosperm orthologs, such as the *Gnetum GMM3* locus, are expressed in the pollen- and ovule-producing structures of the strobili[17]. The expression patterns of AG group members at different taxonomic levels suggest that these MADS-box genes diversified from their ancestral function to control reproductive organ differentiation. This diversification led to present-day C-function genes, which compartmentalize reproductive structures from sterile, nonreproductive tissues in the developing

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sporophyll. Interestingly, several genes in the AG clade (including *AGL1* and *AGL5*) are expressed in derived angiosperm-specific structures, such as carpels and fruits.

Conservation of function among evolutionarily related MADS-box genes is observed in the AP3 and PI group genes, which share B-class floral homeotic functions in petal and stamen differentiation[18]. These two gene groups appear to be sister to one another and arose via duplication from a single ancestral gene[14–16] (Fig. 1). In extant higher eudicots, such as *Antirrhinum* and *Arabidopsis*, petal and stamen differentiation requires loci from both the AP3 and PI gene groups[18]. The ancestral seed plant B-function locus might have served as a sex differentiation gene distinguishing male versus female reproductive organs in sporophylls[6]. For example, angiosperm B-function genes specify stamen, but not carpel, identity in flowering plants[18], and gymnosperm loci related to *AP3* and *PI* [*Gnetum GMM2* (Ref. 17) and *Picea abies* (Norway spruce) *DAL11–DAL13* (Ref. 19)] also are expressed in male, but not female, reproductive organs.

Although members of the AP3, PI and AG gene groups exhibit general conservation of developmental function, the AP1/AGL9 group is more diverse and contains genes expressed in a wider range of plant tissues. The AP1/AGL9 clade contains more members than the AP3, PI and AG floral homeotic gene groups and the basal (earliest diverging) loci in the AP1/AGL9 clade are expressed in both leaves and reproductive structures[12,13]. In addition to floral meristem identity, *APETALA1* is an A-class floral homeotic gene, which specifies sepal and petal development. However, the expression of other genes in the AP1/AGL9 group is not restricted to reproductive structures; *AGL3* is expressed in vegetative structures of the inflorescence shoot[12], and *AGL8* (*FRUITFULL*) coordinates tissue growth during fruit morphogenesis and is expressed in leaves[20].

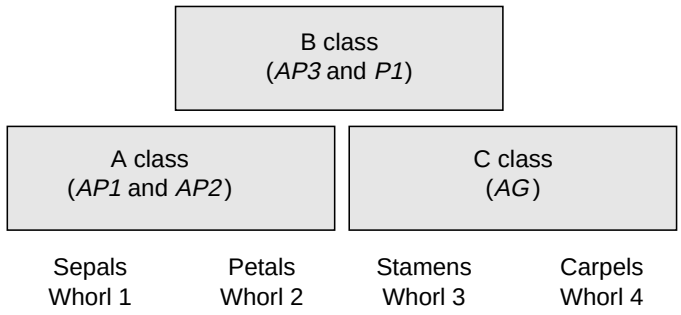
Other plant MADS-box loci with diverse expression patterns do not belong to these floral homeotic gene groups[13] (Fig. 1). Phylogenetic analyses indicate that these non-floral homeotic group loci represent the most basal members of the plant MADS-box gene family[16]. Several of these loci are expressed in inflorescences, although others are expressed in vegetative and/or embryonic structures of plants. For example, the *Arabidopsis AGL15* gene is expressed in embryos[13] and members of two other distinct, monophyletic MADS-box gene groups are expressed specifically in roots (E.R. Alvarez-Buylla *et al*., unpublished). The basal position of many of these loci suggests that plant MADS-box genes might originally have served to regulate vegetative and/or embryonic development, and subsequent duplications resulted in the derivation of new genes that control reproductive development in land plants[6].

Duplications within the MADS-box regulatory gene family, which gave rise to the major floral homeotic gene groups, appear to have occurred >285 Mya; however, floral homeotic functions continue to diversify at more recent timescales. For example, the ABC model of flower development predicts that C-class mutations lead to loss of both stamen and carpel identity in the inner floral whorls. Studies of the duplicate maize loci *zag1* and *zmm2* suggest that C-class floral homeotic function in this grass species results from nonoverlapping expression of these two loci in the maize flower[21]. *zag1* and *zmm2* are expressed specifically in carpels and stamens, respectively, suggesting that these two genes have partitioned the floral homeotic C function since they last shared a common ancestor within the grass family <60 Mya. The recent partitioning of C-class floral homeotic functions within some grass groups illustrates the evolutionary lability of the genetic mechanisms governing fundamental developmental programming among flowering plant taxa.

Box 1. The genetics of flower development

Development in plants relies on groups of undifferentiated embryonic cells called meristems, whose activities determine plant architecture and morphology. In *Arabidopsis thaliana* (Brassicaceae; thale cress) the reproductive phase begins when the shoot apical meristem transforms from being a vegetative meristem to an inflorescence meristem, in response to internal signals or external environmental cues. This reproductive, inflorescence meristem is indeterminate in *Arabidopsis* and primordia at the flanks of the growing meristem can either form secondary inflorescence shoots or become floral meristems that will develop into flowers.

Based on extensive molecular expression and genetic data, floral homeotic genes can be divided into two categories according to developmental fate: floral meristem identity genes, which regulate the identity of reproductive meristems; and organ identity genes, which control the identities of floral organs that form in developing flowers[3,4]. Expression of floral meristem identity genes, such as *LEAFY* (*LFY*), *APETALA1* (*AP1*) and *CAULIFLOWER* (*CAL*), leads to the formation of floral meristematic regions flanking the inflorescence meristem. Conversely, the expression of *TERMINAL FLOWER* (*TFL*), which maintains inflorescence meristem identity, downregulates the expression of the floral meristem gene *LFY*.



(Online: Fig. I)

Trends in Ecology & Evolution

The floral meristem is partitioned into three overlapping fields of gene activity leading to the definition of four concentric rings or whorls of floral organs. There are four floral organ whorls in *Arabidopsis*: whorl one (four sepals), whorl two (four petals), whorl three (six stamens) and whorl four (two fused carpels). The figure shows the ABC model of floral organ identity. The A-, B- and C-class floral organ identity genes are expressed in two adjacent whorls of the flower. At least one of the A-class genes (*APETALA2*) negatively regulates expression of the C-class *AGAMOUS* gene in the first two whorls. Conversely, *AG* expression in whorls 3 and 4 negatively regulates both *AP2* and *AP1* expression. Analysis of similar floral homeotic mutants between *Arabidopsis* and *Antirrhinum majus* (Scrophulariaceae) indicate that floral organ identity loci fall into one of three general classes: A-, B- and C-class homeotic genes. Genes of each class regulate floral organ development in two adjacent whorls and can interact in combination to determine the fate of organ primordia (Fig. I). In general, A-class genes (including *APETALA1* and *APETALA2*) affect development in whorls 1 and 2 (sepals and petals), B-class genes (including *APETALA3* and *PISTILLATA*) affect development in whorls 2 and 3 (petals and stamens) and C-class genes (*AGAMOUS*) affect development in whorls 3 and 4 (stamens and carpels). The ABC model further suggests that some A- and C-class genes are mutually antagonistic, such that mutations in the A-class gene *AP2* lead to the expansion of C-class gene expression to all four floral whorls. Conversely, mutations in the C-class *AG* locus lead to expression of both *AP1* and *AP2* in the third and fourth whorls.

Timing of floral homeotic gene origins

The timing of duplication events that led to the floral homeotic genes is of great evolutionary interest: are these floral developmental genes specific to flowering plants or did they pre-date the origin of flowers? Many MADS-box genes isolated from the gymnosperms *P. abies* (Norway spruce)[19,22], *P. mariana* (black spruce)[23] and *Gnetum gnemon* (melindjo)[17] are orthologous to known angiosperm floral homeotic loci and are members of previously identified floral homeotic groups[15,17,23]. Phylogenetic analyses

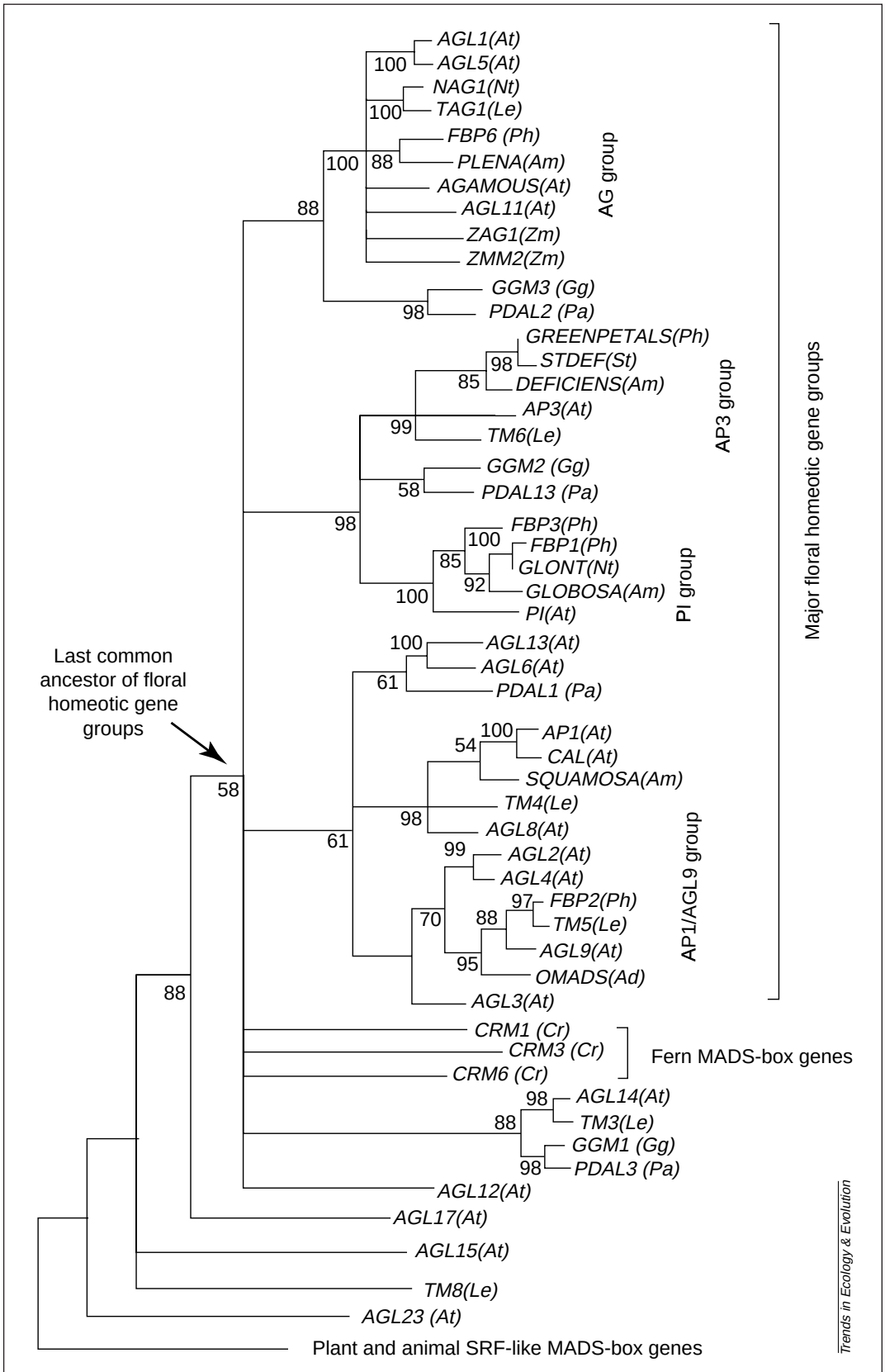


Fig. 1. Major relationships within the plant MADS-box regulatory gene family. This composite supertree is derived from several different analyses[14–17]. Not all major genes are shown, and the phylogeny from Theissen *et al.*[16] provides the backbone of the composite tree. The bootstrap support at nodes is taken from the individual studies, and only relationships consistent across the published phylogenies are shown. The major floral homeotic gene groups are indicated, as well as the fern MADS-box genes. Phylogenetic analyses also indicate a major split among eukaryotic MADS-box genes before the divergence of the plant and animal lineages, resulting in a separate plant SRF-like MADS-box gene group (E.R. Alvarez-Buylla *et al.*, unpublished). The species designations listed below are shown in brackets in the figure. Eudicots: *At, Arabidopsis thaliana*; *Nt, Nicotiana tabacum*; *Le, Lycopersicon esculentum*; *Ph, Petunia hybrida*; *Am, Antirrhinum majus*; *St, Solanum tuberosum*. Monocots: *Zm, Zea mays*; *Ad, Arandah x Deborah* orchid hybrid. Gymnosperms: *Gg, Gnetum gnemon*; *Pa, Picea abies*. Ferns: *Cr, Ceratopteris richardii*.

demonstrate that floral homeotic gene groups observed in angiosperms pre-date the divergence of flowering plants and gymnosperms ~285 Mya (Refs 14,15) (Fig. 1). Indeed, molecular clock studies suggest that the divergence of the four major floral homeotic gene groups might have occurred as early as 486 ± 45 Mya, during the Ordovician, and that the establishment of these genes coincided with the rise of land plants[15]. However, these molecular clock estimates assume evolutionary rate homogeneity among MADS-box loci; any significant, undetected temporal differences in substitution rates could distort estimates. If correct, however, these early estimates of MADS-box gene group divergences suggest that the major diversification of floral regulatory loci might be associated with the evolution of more elaborate and specialized reproductive morphologies during the early evolution of land plants[15,16].

More recent molecular analyses, which include MADS-box genes from two pteridophyte (fern) genera (*Ceratopteris* and *Ophioglossum*)[24,25], suggest that the establishment of the floral homeotic gene groups occurred more recently than the dates derived from molecular clock estimates. These studies also indicate that although floral homeotic gene groups predate seed plants, the gene groups arose after the separation of seed plants and ferns. However, the isolated pteridophyte loci might simply represent orthologs to more basal, nonfloral homeotic gene group lineages and indicate that pteridophyte orthologs to angiosperm floral genes have yet to be isolated. Alternatively, orthologs to the angiosperm floral homeotic loci might have been lost in pteridophytes after the divergence of ferns and seed plants. However,

to date, all studies agree that distinct floral regulatory gene groups were present in ancestral seed plant taxa before the evolution of flowers, probably to control reproductive organ differentiation, and that these developmental loci were co-opted to control floral morphogenesis when flowering plants evolved. Detailed genetic studies in other basal land plant taxa, including bryophytes (mosses, liverworts and hornworts) and lycophytes, could shed light on the functions of these regulatory loci in species whose reproductive structures are distantly related to angiosperm flowers.

Evolution of floral gene expression

Comparative gene expression studies between the families Brassicaceae (*Arabidopsis*), Scrophulariaceae (*Antirrhinum*) and Solanaceae (*Petunia*) indicate strong conservation of floral developmental gene functions across broad taxonomic levels. This functional conservation can be used to determine reproductive morphological homologies between distantly related angiosperm taxa, including organs representing unusual floral innovations. If we assume that the expression of a particular regulatory gene is both necessary and sufficient to control development of a particular organ in one or more model plant species, then expression patterns of the gene might identify homologous structures in diverse taxa. Thus, expression of orthologous MADS-box genes between distant species might allow us to identify structural homologies among derived floral organs and to examine the extent of developmental gene function conservation across angiosperm taxa. However, the use of such molecular expression markers should be used with caution because evolution (including co-option) of gene functions across distant lineages might lead to erroneous conclusions in assigning morphological homologies[26]. Nevertheless, initial use of floral homeotic genes to examine homologies indicates that this approach might offer additional evidence supporting the identification of morphological homologies among derived flower organs.

One example comes from Asteraceae species, where flowers display an array of bristles (pappus), which surround the corolla and serve as a seed dispersal aid. A long-standing debate is whether the pappus, which is positionally homologous to the calyx, is indeed a true calyx. A recent study of floral homeotic gene orthologs from *Gerbera hybrida* supports the argument that a pappus is, in fact, a true calyx[27]. Transgenic studies with *Gerbera* indicate that reduction of expression of either the *AG* ortholog *gaga2* or the *AP3* ortholog *gglo1* is accompanied by the transformation of carpels and petals, respectively, to pappus-like structures. Additionally, ectopic expression of *gglo1* leads to the replacement of a pappus with petaloid structures in the first whorl. These results are consistent with the hypothesis that pappus bristles are modified sepal structures.

Expression and genetic analyses of MADS-box genes also have been used to address questions regarding the evolution of floral organs in monocots[28]. For instance, the lodicules are enigmatic floral structures in grasses that have been described alternatively as modified petals or reduced staminodes. Another persistent question is whether the palea and lemma, inner bract-like organs in grass flowers, are homologous to eudicot sepals. In both cases, studies in maize[28] and *Oryza sativa* (rice)[29] have begun to provide molecular genetic clues to morphological homologies. Mutants in the maize *AP3* ortholog (*silky1*) (Ref. 28) and in the rice *PI* ortholog (*OSMADS4*) (Ref. 29) exhibit phenotypes remarkably similar to B-class homeotic mutations in eudicots, thus resulting in the development of carpelloid structures in whorl 3 and the replacement of lodicules with palea-like organs. Together, these investigations provide strong evidence that lodicules are homologous to eudicot petals and that paleae are homologous to eudicot sepals.

Recent molecular studies also have provided evidence supporting previous morphological investigations indicating that petals evolved independently several times during angiosperm evolution[30,31]. Morphological studies of flowers suggest that angiosperm petals are derived from either stamens (andropetals) or sepals and other sterile subtending organs (bracteopetals). Bracteopetals are distributed within the Magnoliid dicot orders Magnoliales, Piperales and Aristolochiales, but andropetals have evolved many times within lower eudicots, and at least once at the base of higher eudicots and monocots[32]. The independent origins of petals are supported by studies of *AP3* and *PI* homologs from several lower eudicot species whose petals are derived from bracts and, therefore, are not homologous to andropetals in *Arabidopsis* and *Antirrhinum*[31]. Among *Arabidopsis*, *Antirrhinum* and other higher eudicots, the B-function genes *AP3* and *PI* are expressed in petals throughout organ development. By contrast, orthologs to these loci in Ranunculids (lower eudicots) are expressed only weakly in petal primordia and progressively decrease in expression upon further differentiation of petals[31]. The dramatic differences in expression patterns of these loci suggest that petal identity in higher and lower eudicots is controlled by different loci, and provides strong molecular evidence supporting multiple independent origins of perianth organs among angiosperms.

The microevolution of flower development

The diversification of floral developmental patterns at the macroevolutionary level must originate from molecular variation present within species. A comprehensive understanding of the evolutionary dynamics of flower development thus requires investigation of the evolution of developmental loci at the population level or between closely related species. One approach has involved examining domesticated plant species, such as maize[33] and *Brassica oleracea* (the cole crops)[34], which both display clear divergence in within-species floral developmental programs arising from artificial selection by early farmers. For example, the evolution of the domesticated cauliflower (*B. oleracea* spp. *botrytis*) appears to be associated with mutations in the MADS-box floral meristem identity genes *CAULIFLOWER* and *APETALA1* (Refs 34,35). The dramatic inflorescence architectural differences between domesticated maize and its teosinte relatives also appear to arise, in part, from selection on the *teosinte-branched1 (tb1)* gene, a maize locus that belongs to the same regulatory gene family (the TCP gene family) as the *Antirrhinum* floral symmetry gene *CYCLOIDEA* (Ref. 33). Molecular population genetic analysis of *tb1* demonstrates that the evolution of the unique inflorescence architecture found in maize is associated with positive selection and adaptive divergence on the promoter of this developmental regulatory locus.

Although studies using domesticated species are instructive, the availability of sufficient genetic variation in developmental regulatory loci for adaptive diversification within natural populations remains unclear. At least one species, *Clarkia concinna* (pink ribbons), has been shown to exhibit a high frequency of natural floral homeotic conversion of petals to sepals in a wild population, as a result of the segregation of a single floral homeotic gene,

BICALYX (Ref. 36). Low-frequency natural variation in floral symmetry within *Linaria vulgaris* (common toadflax) also has been documented since the time of Linnaeus. In this case, the occurrence of radially symmetric flowers among the bilaterally symmetric (zygomorphic) flowers of this species has been attributed to epigenetic methylation changes in the *CYCLOIDEA* locus[37].

Population genetic studies of floral homeotic genes in the wild weed *A. thaliana* indicate that the *CAL* (Ref. 38), *AP3* and *PI* (Ref. 39) genes harbor considerable within-species diversity at the molecular level. These three loci display elevated levels of intra-specific amino acid diversity in protein sequence, as well as evidence of non-neutral evolution. However, the levels and distribution of allelic variation at these loci do not appear to be controlled by recent episodes of adaptive selection, but are shaped largely by demographic forces operating on this selfing species[39]. Nevertheless, there is evidence that molecular variation at some of these loci can result in differences in floral developmental functions. For example, naturally occurring alleles at the *CAL* locus can be distinguished by their differential capacities to direct floral meristem development[34,38]. The significant within-species molecular diversity in floral developmental genes, some of which might result in functionally distinguishable wild alleles, provides genetic material for selective forces to operate and potentially leads to macroevolutionary diversity in floral developmental programs.

Prospects

The recent wealth of data on the developmental genetics of flower and inflorescence morphogenesis have provided the impetus for new studies on the underlying molecular mechanisms of floral evolution. However, major gaps in our understanding still remain; for example, we still have little information on the function and evolution of orthologs of the eudicot floral homeotic genes in many basal land plant taxa, including the bryophytes, other pteridophyte and gymnosperm groups, and basal angiosperms. Data from a wider sampling of land plant groups can help address numerous issues, including the history of the diversification of genes involved in reproductive development, the role that duplication and diversification of genes play in plant diversity, and the potential identification of homologous structures among distantly related taxa. Moreover, studies on the evolution and function of MADS-box genes that function in other, nonfloral aspects of plant development should yield general insights into the mechanisms behind functional diversification of developmental gene families. Previous efforts to dissect the evolution of flower development also largely have ignored floral regulatory genes outside of the MADS-box loci. To fully understand the genetic interactions that result in floral innovations, a parallel effort must explore the evolution of non-MADS-box genes among both flowering and nonflowering plants. Finally, we need to understand the microevolutionary forces that shape the diversification of floral regulatory loci, which requires an analysis of the evolution of floral developmental genes in the context of both population genetics and ecology.

One of the more exciting aspects of current research in this area is the close collaboration of evolutionary, developmental and molecular geneticists. The result is a continued forging of links between classical plant evolutionary biology and molecular genetics. In the next few years, progress in this area will depend largely on the continuing interaction of molecular and organismal evolutionists. As is evident from the nascent work in this field, bridging the gap between evolutionary and developmental geneticists provides a fruitful source of new ideas, and a synthetic approach to general questions on the evolution of floral and plant development.

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Why are female birds ornamented?

Trond Amundsen

Sexual selection is now widely accepted as the main evolutionary explanation of extravagant male ornaments. By contrast, ornaments occurring in females have received little attention and often have been considered as nonadaptive, correlated effects of selection on males. However, recent comparative evidence suggests that female ornaments have evolved quite independently of male showiness. Also, new theoretical models predict that both male mate choice and female contest competition will occur under certain circumstances. This is supported by recent experimental studies. Thus, selection acting on females might be a widespread cause of female ornaments.

Trond Amundsen is at the Dept of Zoology, Norwegian University of Science and Technology, N-7491 Trondheim, Norway (trond.amundsen@chembio.ntnu.no).

Recently, sexual selection theory[1] has proved extremely successful in explaining extravagant male traits, such as colourful plumage and elaborate vocal and visual displays[2]. However, few attempts have been made to address whether sexual selection also acts to produce similar traits in females. This lack of interest has theoretical, as well as empirical, roots. Theoretically, it has been acknowledged that male reproductive success often is limited by access to females; thus, sexual competition selects for secondary sexual characters in males. When sexual selection acts on males, traditionally it has been assumed that it does not act on females. Empirically, the view that sexual selection is mainly about males has been corroborated by observations that females are often much less showy than males. There is no reason to challenge these theoretical and empirical statements as broad generalizations.

However, the fact that sexual selection acts on males does not preclude selection on females. Indeed, female showiness is far from uncommon. Having established a relatively detailed understanding of male visual extravaganza, it is now time to ask why females of many species are also beautifully decorated. For instance, among birds, conspicuous crests or beaks often occur in both sexes (e.g. auks and cormorants) and showy female colours are found in a variety of taxa (e.g. toucans, parrots, hummingbirds and tanagers). Likewise, many ungulate mammals have horns or antlers in both sexes, and many fish display identical colours in the two sexes (e.g. butterflyfishes) or showy colours specific to females (e.g. many wrasses). Among invertebrates, there are several taxa where females, not only males, display ornamental structures or colours. As stated by Johnstone and colleagues, 'nature abounds with biparental care species in which both sexes are ostentatiously plumed or brightly colored'[3].

Recently, studies focusing on female traits have enhanced our understanding of mate choice and sexual selection[4–6]. In spite of decorative female traits being taxonomically widespread, it is only since the late 1970s that evolutionary biologists have started to approach questions related to female ornamentation from a functional perspective[7]. During the past decade, theoretical[3,8] and empirical[9–13] research have provided intriguing results indicating that female showiness might be related to male mate choice and female competition. Clarifying the role of these two processes, and their selective consequences on female appearance, is essential for a complete and realistic understanding of animal mating dynamics.

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