Minireview

Variations on a theme: flower development and evolution

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Abstract

A recent study, comparing the maize *SILKY1* gene to its well-characterized homolog *APETALA3* from *Arabidopsis*, has provided some of the first evidence pointing to conservation of homeotic gene function between monocots and dicots.

The genomics era has heralded the accumulation of an unprecedented amount of sequence information from a vast array of species. With this wealth of information, the issue at hand is to determine to what extent homologous genes from different species function in a similar manner, as well as the extent to which their roles have diversified. Gene expression and loss-of-function studies are now paving the way for comparative functional studies in several model species, and may soon provide us with mechanistic explanations for how different morphologies have evolved.

The angiosperms (the flowering plants) arose about 130 million years ago and gave rise to over 250,000 extant species that contain a remarkable diversity of floral forms. Although flowers have dramatically different forms in different species, there are some basic structural similarities. Flowers contain stamens (male reproductive organs) and carpels (female reproductive organs) surrounded by sterile perianth organs. In many species, the perianth is composed of distinct petals and sepals, while in other species the petals and sepals are indistinguishable and are referred to as tepals.

How did the vast array of different floral morphologies arise? Recent evidence is converging to support the idea that the primitive angiosperm flower consisted of reproductive organs, with few or no perianth organs. Several recent phylogenetic analyses have independently provided support for placing *Amborella*, with its diminutive flowers containing reproductive organs and just a few tepals, at the base of the angiosperm tree [1-4]. This evidence suggests that the primitive angiosperm flower was small and few-parted, in contrast to the more traditional view that the earliest angiosperms had large, multiparted flowers similar to present day magnolias [5,6]. In addition, the fossil evidence, although fragmentary, also supports the idea that the primitive angiosperm flower lacked perianth organs [7-9]. If the earliest angiosperm flower indeed consisted of just stamens and carpels, then perianth organs must have arisen during the course of angiosperm evolution. Within the angiosperms, two monophyletic groups have been identified, the monocots and the eudicots, and these are contained within a basal assemblage of magnoliid dicots (Figure 1). Petals are thought to have arisen multiple times in different angiosperm lineages and, in particular, monocot and core eudicot petals are thought to have arisen independently [10]. This would imply that all petals are not homologous organs and has important implications for comparing the roles of the floral homeotic genes in different species.

Extensive experimental studies on the roles of the floral homeotic genes in *Arabidopsis* and other core eudicot species have led to the formulation of the ABC model of floral development [11,12]. This model posits that three classes of floral homeotic genes, termed A, B and C, function in overlapping domains to give rise to the different floral organs: the sepals, petals, stamens, and carpels (Figure 2). In *Arabidopsis*, the B-group genes, *APETALA3* (*AP3*) and *PISTILLATA* (*PI*), act together to specify petal and stamen identities. These two genes encode MADS-box-containing DNA-binding proteins and presumably act by regulating the transcription of downstream genes responsible

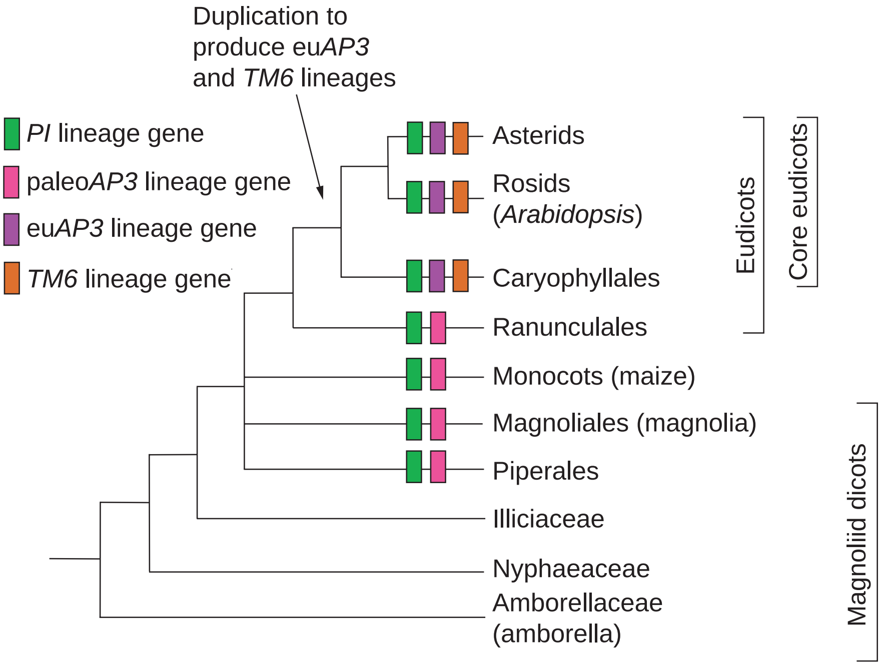


Figure 1
Simplified tree of the angiosperms, based on [2]. Common names of representatives of selected lineages in parentheses. A duplication event in the *AP3* lineage gave rise to the eu*AP3* and *TM6* lineages in core eudicots [22]. Clades in which one or more examples of a particular gene lineage have been found are marked with a colored box.

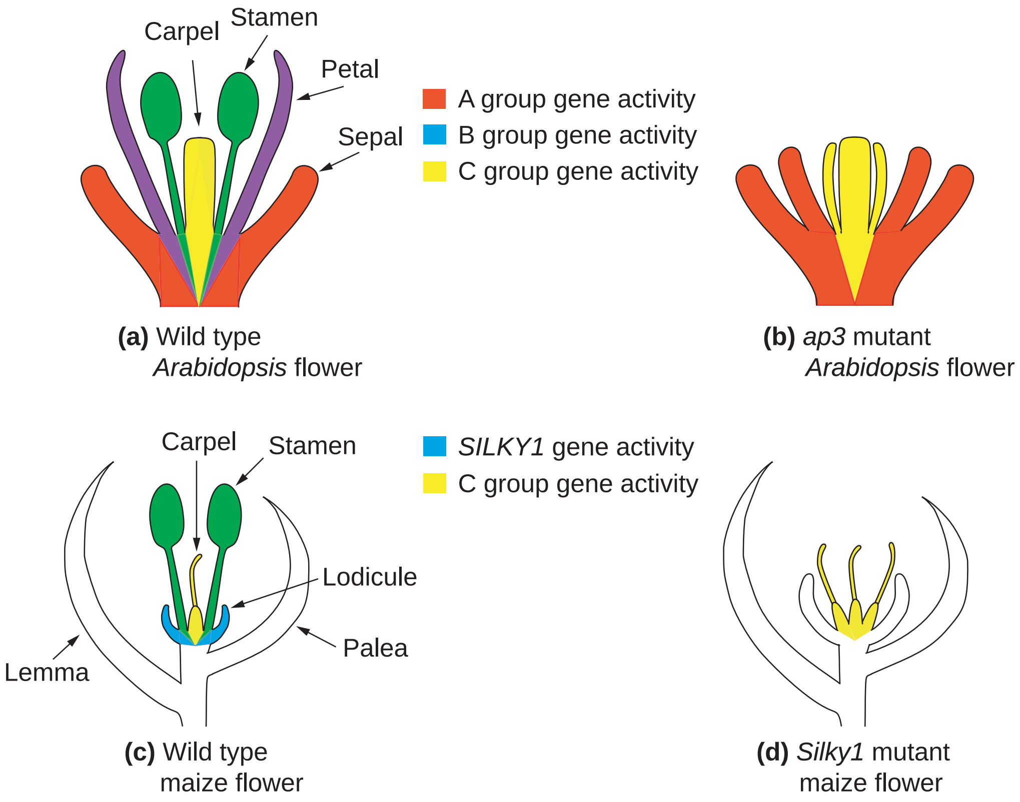
for petal and stamen morphogenesis and cell-type specific differentiation [13,14].

Cloning and characterization of B group genes from a wide array of other species has indicated that the *AP3* and *PI* gene lineages arose prior to the diversification of the angiosperms, suggesting that ancestral *AP3*- and *PI*-like genes were present before flowers evolved [15-18]. A few gymnosperm *AP3*- and *PI*-like genes have been identified and shown to be expressed in male reproductive organs [15,17,19,20]. Since gymnosperms do not have perianths, this supports the contention that the ancestral role of the B-group genes was in specifying male reproductive organ development.

When the angiosperms arose and diversified, how did the role(s) of the B-group genes change? How, and in which lineages, did the B-group genes acquire an additional role in specifying petal development? One way in which B-group genes may have acquired new functions is through gene duplication. An ancient duplication event occurred in the *AP3* lineage at the base of the core eudicots (Figure 1) and may be associated with the independent origin of petals in this group [21]. The evolution of the 'eu*AP3*' lineage with new sequence characteristics may reflect the acquisition of new functions that include the specification of core eudicot petal identity. The monocots, on the other hand, contain *AP3*-like genes that are more similar in sequence to the ancestral 'paleo*AP3*' lineage genes [22].

Characterization of the maize *Silky1* gene, a member of the paleo*AP3* lineage, has begun to shed light on the similarities and differences in the roles of the eudicot eu*AP3* lineage genes and the monocot paleo*AP3* lineage genes. Maize, like other grasses, has flowers which are highly derived and contain stamens and carpels surrounded by sterile organs known as paleas, lemmas and lodicules. *Silky1* is expressed in lodicules and stamens [23]. Mutations in *Silky1* result in a transformation of the stamens to carpel-like structures complete with the characteristic long silk, but also result in lodicules being replaced by organs with characteristics of lemmas and paleas [23]. In comparison, mutations in the *Arabidopsis AP3* gene result in homeotic transformations of stamens into carpel-like structures and petals into sepal-like structures (Figure 2) [24].

How do the roles of the *Arabidopsis AP3* gene and the maize *Silky1* gene compare? Since all stamens are homologous (that is to say, they have a common evolutionary origin), it is perhaps not surprising that these *Arabidopsis* 'eu*AP3*' and the maize 'paleo*AP3*' lineage genes are both required for stamen identity. It is unclear though if *AP3* and *Silky1* have similar roles in perianth development. Petals are thought to



(a) Wild type *Arabidopsis* flower

(b) *ap3* mutant *Arabidopsis* flower

(c) Wild type maize flower

(d) *Silky1* mutant maize flower

Figure 2
(a) *Arabidopsis*, like other core eudicots, has flowers that contain four whorls of floral organs: sepals, petals, stamens and carpels. A combination of A, B and C group floral homeotic gene activities results in specification of different organ identities [11]. Petals result from a combination of A+B activities, and stamens result from a combination of B+C activities. **(b)** Mutation of the B group gene *AP3* results in a loss of B group gene activity, resulting in a transformation of petals to sepals and of stamens to carpels. **(c)** The maize flower is composed of a lemma, a palea, lodicules and the reproductive organs. During maize flower differentiation, abortion of the carpels results in functionally male flowers, while abortion of the stamens results in functionally female flowers. **(d)** Mutations in the *SILKY1* gene result in a transformation of stamens to carpels and the replacement of lodicules with structures that resemble paleas or lemmas [23].

have evolved independently in the core eudicots and in the monocots; and furthermore, in the grasses, it is unclear as to whether lodicules are perianth organs or represent modified sterile stamens [25-27]. The fact that *Silky1* mutations cause a transformation of the lodicule has been used to support the idea that lodicules are homologous to petals, but this does not take into account the fact that homology implies common descent [23,28]. An alternative possibility is that the lodicule represents another organ type that has no counterpart in the eudicot flower [25].

The roles of the *Arabidopsis AP3* gene in petal development and the maize *Silky1* gene in lodicule development could result from parallel evolution [29]. In other words, similar developmental modifications may have occurred independently in the eudicots and in the monocots. In the case of the eudicots, the eu*AP3* gene lineage appears to have been recruited to specifying petal identity in addition to stamen identity. In the monocots, a similar scenario may have taken place independently, such that the paleo*AP3* lineage genes may have been recruited to a new role in lodicule development.

The question of how *AP3*-like genes are involved in specifying non-reproductive structures may have as many solutions as there have been independent origins of perianth parts. Critically comparing the roles of homologous homeotic genes in different species will require an understanding of their evolutionary relationships, as well as genetic tests of function. The tools needed are already in place: sequence information is providing the basis for developing robust angiosperm phylogenies, and the potential exists to genetically manipulate a wide array of plant species using *Agrobacterium*-mediated transformation. By analyzing the roles of the homeotic genes in a wide range of angiosperm species, we should soon be able to understand how the evolution of developmental mechanisms is causally linked to changes in floral morphology.

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