Review

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Trends in flower symmetry evolution revealed through phylogenetic and developmental genetic advances

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A striking aspect of flowering plant (angiosperm) diversity is variation in flower symmetry. From an ancestral form of radial symmetry (polysymmetry, actinomorphy), multiple evolutionary transitions have contributed to instances of non-radial forms, including bilateral symmetry (monosymmetry, zygomorphy) and asymmetry. Advances in flowering plant molecular phylogenetic research and studies of character evolution as well as detailed flower developmental genetic studies in a few model species (e.g. *Antirrhinum majus*, snapdragon) have provided a foundation for deep insights into flower symmetry evolution. From phylogenetic studies, we have a better understanding of where during flowering plant diversification transitions from radial to bilateral flower symmetry (and back to radial symmetry) have occurred. From developmental studies, we know that a genetic programme largely dependent on the functional action of the *CYCLOIDEA* gene is necessary for differentiation along the snapdragon dorsoventral flower axis. Bringing these two lines of inquiry together has provided surprising insights into both the parallel recruitment of a *CYC*-dependent developmental programme during independent transitions to bilateral flower symmetry, and the modifications to this programme in transitions back to radial flower symmetry, during flowering plant evolution.

1. Introduction

Variation in flower symmetry has attracted the attention of botanists for more than a century [1–4]. Research has centred on understanding the developmental mechanisms that establish patterns of symmetry, the ecological contexts in which alternative patterns of symmetry are favoured, and the evolutionary history of transitions between different forms. This research has provided key insights into how, when and why transitions in floral symmetry evolve.

During the diversification of flowering plants (angiosperms), there have been numerous evolutionary transitions between radial flower symmetry (polysymmetry, actinomorphy; figure 1*a*) and bilateral flower symmetry (monosymmetry, zygomorphy; figure 1*d*), or in more extreme cases, flower asymmetry (figure 1*c*) [5,6]. Bilateral symmetry is predominant in a number of species-rich lineages—for example, Lamiales (mints and allies) and Fabaceae (legumes) in eudicots, and Orchidaceae in the monocots. Bilateral symmetry in these lineages is not only common, but also highly elaborate. However, a survey of flowering plant lineages demonstrates that both elaborate and subtle forms of bilateral flower symmetry have evolved from radially symmetrical ancestors many times, and that reversals from bilateral to radial, or approximately radial symmetry are not uncommon (reviewed in [6]).

It is generally accepted that these transitions in flower symmetry are associated with pollination syndromes. For example, transitions from radial to bilateral flower symmetry appear to be linked to the evolution of specialized plant–pollinator interactions. Bilateral symmetry is most often evident in the petal and stamen whorls and may promote pollinator approach and legitimate (pollen transferring) landings, and may increase the specificity of pollen deposition during pollinator visits [7–9]. In part because of the relationship between
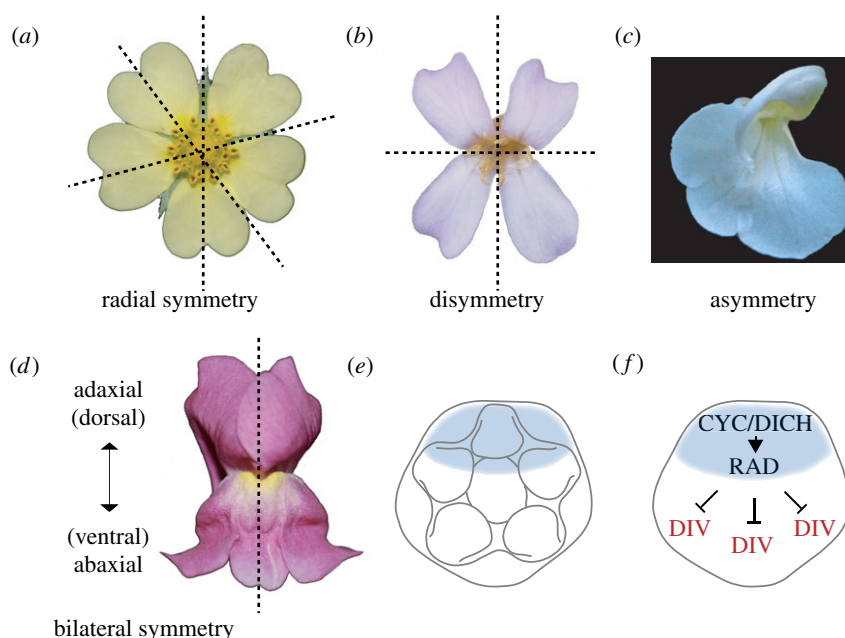
Figure 1. Flower symmetry diversity and bilateral flower symmetry developmental genetics. The range of floral symmetries include radial symmetry with multiple planes of mirror image symmetry (*a*, *Potentilla* sp.), disymmetry with two planes of mirror image symmetry (*b*, *Cardaminopsis arenosa*), asymmetry with zero planes of mirror image symmetry (*c*, *Pedicularis racemosa*) and bilateral symmetry with just a single plane of mirror image symmetry (*d*, *Antirrhinum majus*). At the developmental level, one or more genetic signals must differentiate the dorsal (adaxial) from the ventral (abaxial) domains of the developing flower, for example a genetic programme that distinguishes dorsal identity (*e*, dorsal shading in cartoon of early developing flower). In the model species *A. majus*, the genetic programme that establishes dorsoventral flower identity from early stages of development includes the dorsal identity genes and protein products CYCLOIDEA (CYC), DICHOTOMA (DICH) and RADIALIS (RAD) as well DIVARICATA (DIV) which specifies ventral flower development (*f*). DIV is excluded from the dorsal domain of the developing *A. majus* flower through post-translational negative regulation by RAD. *C. arenosa* flower is taken from image for which copyright is held by Meneerke bloem (http://commons.wikimedia.org/wiki/File:Cardaminopsis_arenosa_02.jpg). This image is used under a Creative Commons Attribution-Share Alike 3.0 Unported, 2.5 Generic, 2.0 Generic and 1.0 Generic licence. *P. racemosa* flower taken from image for which copyright is held by Jerry Friedman (http://commons.wikimedia.org/wiki/File:Pedicularis_racemosa1.jpg). This image is used under the Creative Commons Attribution-Share Alike 3.0 Unported licence. (Online version in colour.)

symmetry and specialized pollination biology, transitions to bilateral flower symmetry are hypothesized to represent key innovations associated with diversification of species-rich flowering plant lineages [10,11].

More recently, much attention has turned to the developmental programmes that specify bilateral flower symmetry. Now, many genes and genetic interactions necessary for the development of bilateral flowers are understood from the model species *Antirrhinum majus* (snapdragon, reviewed in [12]). Because of the historical interest in floral symmetry pollination ecology and evolution, these newer insights from *A. majus* provide the jumping board for comparative studies. The primary comparative question has been whether the developmental programme identified in *A. majus* contributes to the establishment of bilateral symmetry in other flowering plant lineages. Strikingly, current evidence suggests that a similar developmental programme, first identified in *A. majus*, has been recruited many times independently during the parallel evolution of bilateral flower symmetry (reviewed in [12–16]).

Linking model system findings (e.g. in *A. majus* flower development) to comparative developmental questions is not a new concept. Leslie Gottlieb (1936–2012) was an early and strong proponent of the idea that developmental genetic studies in model plant species can inform our understanding of natural variation in flower form [17,18]. For example, he furthered the hypothesis that induced mutations, identified early in the establishment of *A. majus* as a model species [19], may provide genetic information about floral traits that distinguish species or genera. With respect to floral symmetry, he recognized that *A. majus* mutants with increased petal and/or stamen number and radial flower symmetry may be significant for understanding *Verbascum* flower development. Likewise, he pointed out that *A. majus* mutants with a reduced corolla limb and tubular configuration show similarities to *Rhinanthus* flowers [18]. Similar to Gottlieb's early examples, many current comparative flower developmental genetic (evo-devo) studies aim to test how variation in genetic pathways, identified largely through loss or gain of function mutations in model plant species, may explain natural variation in flower form.

Extrapolating from model system studies of flower development to the genetic basis of interspecific variation in flower form is best approached in a phylogenetic framework. A well-resolved hypothesis of phylogenetic relationships among flowering plant species allows assessment of ancestral character states, and pinpoints evolutionary transitions towards or away from character states of interest. The past 40 plus years of molecular phylogenetic studies in flowering plants have provided and continue to provide this critical framework (reviewed in [20]). Early on, Gottlieb embraced molecular tools for plant phylogenetic and evolutionary studies [21–25]. His contributions made an impact that provided momentum to the field, and this momentum has not waned. We now have a clearer understanding of relationships among major lineages of flowering plants (figure 2*a* and see [26–28]); likewise, molecular phylogenetic studies have contributed to resolution of relationships within many key lineages (e.g. figure 2*b* and [29–32]). With respect to flower symmetry development and evolution, the products of molecular phylogenetic studies allow researchers to determine
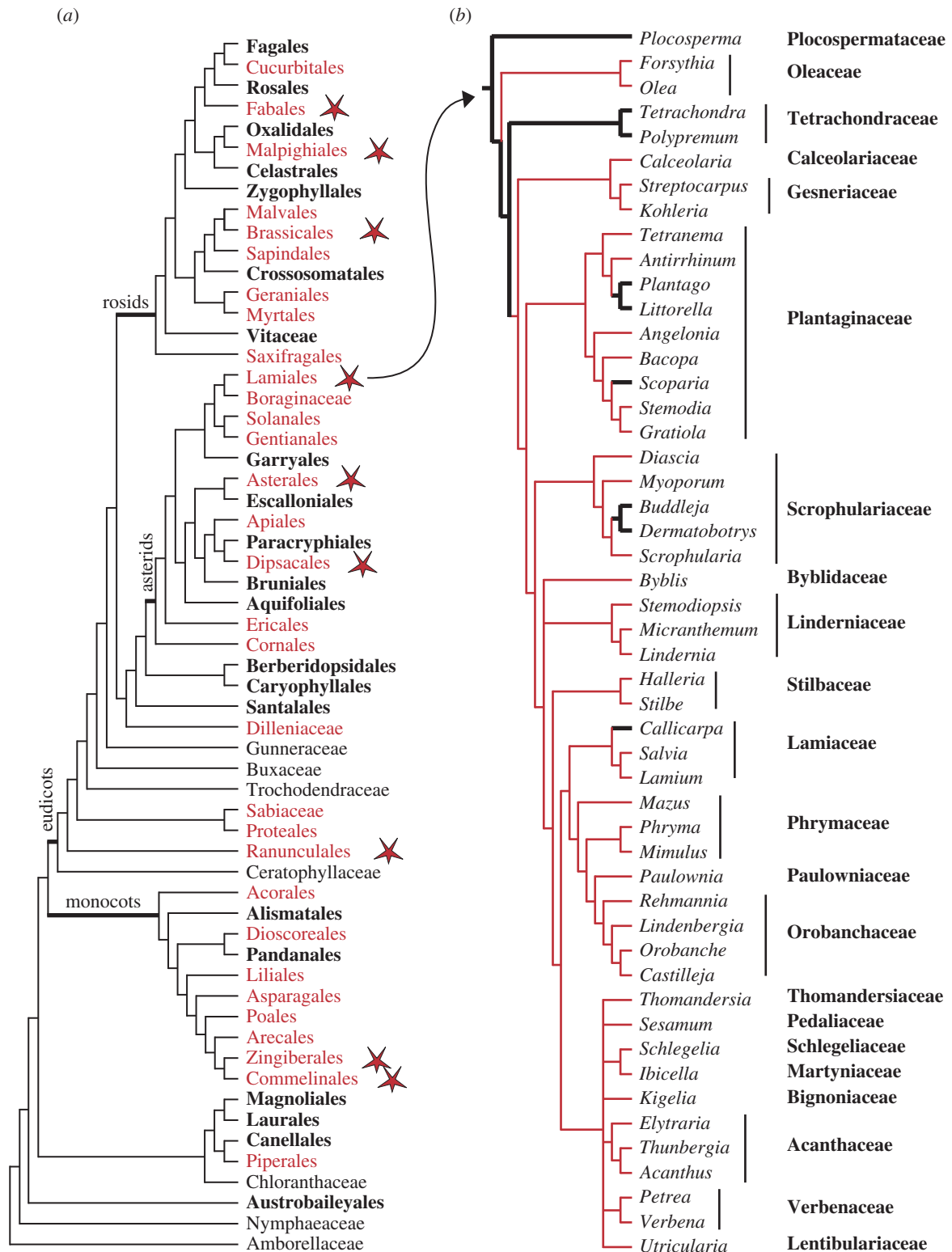
Figure 2. Evolutionary transitions in floral symmetry in a phylogenetic framework. (a) Phylogeny of major angiosperm lineages (from [26]). Lineages in which elaborate bilateral flower symmetry can be found (from [6]) are in red text (grey text in print version). Stars indicate lineages containing species for which *CYCLOI-DEA* homologues have been implicated in transitions to bilateral flower symmetry. (b) Phylogeny of representative Lamiales lineages (from [31]). One possible parsimonious history of floral symmetry evolution is shown suggesting multiple transitions from radial to bilateral flower symmetry early in Lamiales diversification, followed by multiple transitions from bilateral to radial (or approximately radial) flower symmetry. Lineages with radial flower symmetry are in black/bold; those with bilateral flower symmetry are in red or grey/not bold. Taxa were scored at the species level (see Schaferhoff *et al.* [31] for complete taxon list). Species exhibiting elaborate bilateral symmetry in the corolla and/or androecium were scored as having bilaterally symmetrical flowers. (Online version in colour.)

how often and in which lineages transition from radial flower symmetry to bilateral symmetry (and back to radial flower symmetry) have occurred [16,31,33–37], thus providing the framework for informed choice of species when addressing comparative developmental questions.

Here, I review some recent advances in understanding flower symmetry evolution. I address multiple important contributions of molecular phylogenies to the field. Additionally, I demonstrate how the past 10 years of linking model system findings to comparative developmental questions

has shed light on the extensive developmental parallelism in independent transitions between flower symmetry forms.

2. Diversity in floral symmetry

Although the focus of this review is evolutionary transitions between radial and bilateral flower symmetry (figure 1*a,d*), it is important to recognize that these two symmetry forms represent only part of the diversity in symmetry found across flowering plants. Flower symmetry is generally assessed via the face-on view of a flower at the time of anthesis, and is usually expressed most strongly in the petal and stamen whorls of the flower. Radially symmetrical flowers (figure 1*a*) display several planes of symmetry that bisect the flower into mirror images, and bilaterally symmetrical flowers (figure 1*d*) display just a single plane of mirror image symmetry. However, flowers may be disymmetrical (figure 1*b*), having just two planes of mirror image symmetry, or asymmetrical (figure 1*c*), lacking altogether a plane of symmetry that bisects the flower into mirror images. Interestingly, bilateral symmetry may often be an intermediate state between radial symmetry and asymmetry. For example, asymmetric *Pedicularis* (figure 1*c*) and asymmetric *Phaseolus* and *Lathyrus* are nested within Lamiales (figure 2*b*) and Faboideae, respectively, two flowering plant lineages in which bilateral flower symmetry is predominant. Likewise, multiple forms of bilateral flower symmetry are derived from disymmetry. For example, bilaterally symmetrical *Iberis* (Brassicaceae) and *Corydalis* (Papaveraceae) are derived from ancestors with disymmetrical flowers [38–41].

Bilateral flower symmetry itself can range from elaborate to subtle patterns of low complexity (reviewed in [6]). Most familiar forms of complex bilateral flower symmetry are the bilabiate (lipped and keeled) flower forms. In bilabiate flowers, reproductive organs (stamens and carpels) are found inside an elaborate corolla that is differentiated along the dorsal/ventral (adaxial/abaxial) floral axis. In lip flowers, the reproductive organs are held in the upper side of the corolla resulting in pollen transfer on the backs of visiting pollinators; in keel flowers, the reproductive organs are held in the lower (keel) side of the corolla resulting commonly in pollen transfer on the underside of pollinators. Bilaterally symmetrical flowers of the lip form are extremely prevalent in Lamiales (e.g. *A. majus*, figure 1*d*), but are found in other lineages, including Campanulales and Orchidaceae. Those of the keel form are well known from Fabaceae, but can also be found in Polygalaceae. Less elaborate forms of bilateral flower symmetry also result from organ differentiation primarily in the petal and/or stamen whorls, and may be due to displacement of organ initiation, size or shape variation in organs along the dorsoventral axis of the flower, or sigmoidal curvature of organs (reviewed in [6,16]).

3. A phylogenetic context for floral symmetry evolution

From assessments of taxonomic distribution of bilateral flower symmetry [1], and variation in the form of bilaterally symmetrical flower (e.g. lip versus keel bilabiate flowers), it has historically been quite clear that transitions from radial to bilateral flower symmetry were probably frequent during flowering plant diversification. However, it is only

in the context of robust phylogenetic hypotheses for the relationships among flowering plant lineages that we can determine along which lineages evolutionary transitions from radial to bilateral (and back to radial) flower symmetry have occurred [42]. And it is primarily advances in molecular phylogenetics that provide the context for studies of floral symmetry character evolution.

Studies that have used molecular phylogenies to reconstruct the ancestral flower conclude that it was radially symmetrical [43]. A clear understanding of the ancestral form of symmetry is an excellent starting point for determining where bilateral flower symmetry has been gained or lost in flowering plants. A number of recent molecular phylogenies that sample taxa at approximately the family level are now being used to assess patterns of floral character evolution, including symmetry [26–28]. Figure 2*a* shows the ordinal-level backbone phylogeny from Soltis *et al.* [26] on which orders containing species with more or less elaborate bilateral flower symmetry [6] are indicated. This is by no means a critical evaluation of floral symmetry evolution, but illustrates the widely dispersed nature of transitions to bilateral flower symmetry. Citerne *et al.* [16] undertook an excellent analysis of floral symmetry evolution on the estimate of flowering plant family relationships presented in Bremer *et al.* [27]. Using a parsimony approach, and scoring for flower symmetry at the family level (which is likely to underestimate the number of transitions to bilateral flower symmetry), they identified a single transition to bilateral flower symmetry among the basal angiosperms, 23 transitions in monocots, and 46 independent transitions in the eudicots. Therefore, using a well resolved and densely sampled (at the family level) estimate of flowering plant phylogeny, Citerne *et al.* [16] suggest at least 70 transitions to bilateral flower symmetry—twice as many as previously reported.

Studies of character evolution on large-scale phylogenies, such as the one undertaken by Citerne *et al.*, represent important advances in our understanding of floral evolution. Ideally, as advances are made in molecular phylogenetics, we will have at our disposal estimates of the flowering plant phylogeny that are densely sampled at the genus (or even species) level, and for which phylogenetic branch length estimates are available. It will be in this context that floral symmetry evolution will be most critically evaluated using statistical methods for ancestral state reconstruction [44]. That bilateral flower symmetry is a key innovation leading to increased diversification rates has been hypothesized, and to a limited extent tested [10,11]. As with studies of character state evolution, it will be in this context of densely sampled phylogenies that the relationships between shifts in flower symmetry and clade diversification will best be investigated [45]. Excitingly, researchers are anticipating these large datasets. For example, both the National Evolutionary Synthesis Center (NESCent)-supported working group 'Floral assembly: quantifying the composition of a complex adaptive structure' (http://www.nescent.org/science/awards_summary.php?id=90) and eFLOWER (http://eflower.myspecies.info/) are developing massive data matrices of floral traits, including floral symmetry, scored at the species level.

If we move our focus from the entire clade to specific lineages within flowering plants, then we find that more fully resolved assessments of floral symmetry evolution are possible. This more focused view will certainly suggest additional transitions to and from bilateral symmetry to those that

would be seen on an ordinal- or family-level sampled phylogeny of flowering plants. For example, Schaferhoff *et al.* [31] generated a densely sampled, well-resolved phylogeny of Lamiales. Scoring for corolla symmetry at just the family level of their backbone phylogeny, they recover one transition from radial to bilateral symmetry, and one transition back to radial symmetry. Using the same phylogeny, but scoring for corolla and stamen whorl symmetry at the species level, based on the species sampled in the Schaferhoff *et al.* [31] phylogeny, I recover possibly two transitions from radial to bilateral flower symmetry early in Lamiales diversification (considering the bilateral symmetry in the stamen whorl of many Oleaceae species), and multiple transitions from bilateral to radial flower symmetry (figure 2*b*). Others have undertaken similar analyses of floral symmetry evolution in large flowering plant lineages, scoring symmetry for genera or species. Some key findings are multiple transitions from radial to bilateral symmetry inferred during Solanaceae [29,35], Brassicaceae [38] and Ranunculales [46] diversification. By contrast, in Malpighiales, a single transition to bilateral flower symmetry is recovered, followed by multiple transitions from bilateral to radial symmetry [37,47].

4. Developmental genetics of floral symmetry

As described above, bilateral flower symmetry has evolved multiple times and its form varies in complexity. Research in the model species *A. majus*, with its elaborate bilabiate form (figure 1*d*), provided the first ground-breaking insights into the genetic control of bilateral flower symmetry. At the foundation of this control is a programme that differentiates dorsal (adaxial) and ventral (abaxial) flower identity from very early stages of floral organ initiation and differentiation (figure 1*e*).

Two recently duplicated TCP (Teosinte branched 1/Cycloidea/proliferating cell factors) family transcription factors [48–51], *CYCLOIDEA* (*CYC*) and *DICHOTOMA* (*DICH*), function partially redundantly to specify dorsal flower identity (figure 1*f*) [52,53]. These paralogues represent the upstream extent of our knowledge of dorsal flower specification. In other words, we do not yet know what gene products control the regulation of *CYC* and *DICH*. Expression of *CYC* and *DICH* corresponds with their function in specifying dorsal flower identity. Both are expressed in the dorsal region of the floral meristem from initiation, and their dorsal-restricted expression is maintained throughout petal and stamen development [52–54]. *CYC* and *DICH* expression and function in the dorsal flower domain are necessary for establishing the distinct shape of dorsal petals (figure 1*d*), abortion of the dorsal (medial) stamen, as well as petal and stamen merosity. In an *A. majus cyc;dich* double mutant background, flowers completely lack dorsal identity, are radially symmetrical and develop with ventral identity in the ventral, lateral and dorsal domains [52,53]. *CYC* and *DICH* appear to determine the distinct shape of dorsal petals and the formation of the dorsal staminode by affecting patterns of cell growth and proliferation. This is in line with the widely recognized function of TCP transcription factors in promoting and/or repressing tissue growth (reviewed in [12,51]).

While *CYC* and *DICH* are necessary to differentiate dorsal floral identity, a single MYB family transcription factor, *DIVARICATA* (*DIV*), functions to specify ventral identity (figure 1*f*) [54,55]. *DIV* expression and function in the ventral flower domain are necessary for establishing the shape of the

ventral (medial) petal, which distinctly contributes to the lower lip of the bilabiate *A. majus* flower (figure 1*d*). Interestingly, in early flower development, *DIV* is expressed in both the dorsal and ventral domains of the flower, but its expression becomes somewhat restricted to the developing ventral petal at later stages of development [54]. The effects of *CYC* and *DICH* on dorsal flower development and of *DIV* on ventral flower development are in part mediated through an additional MYB transcription factor, *RADIALIS* (*RAD*). *RAD* expression is positively regulated by *CYC* and *DICH*. Therefore, *RAD* expression and function are primarily restricted to the dorsal domain of developing flowers (figure 1*f*) [56,57]. It is RAD protein in the dorsal flower domain that post-translationally restricts DIV function to the ventral domain (figure 1*f*) [55,56,58,59].

5. Parallel recruitment of a *CYC*-dependent pathway in bilateral symmetry evolution

From extensive molecular phylogenetic work and studies of character evolution in flowering plants, we have a clearer understanding of the history of flower symmetry evolution. Additionally, from research on flower development in *A. majus*, we know at least one way by which flower symmetry can be established at the molecular level. Together, these provide a foundation for comparative developmental studies. Bilateral flower symmetry evolved early in the diversification of Lamiales (figure 2*b*); therefore, bilateral symmetry in *A. majus* is homologous to bilateral flower symmetry found in other Lamiid lineages (with the possible exception of Oleaceae; figure 2*b*). A reasonable, testable hypothesis is that the *A. majus CYC/RAD/DIV* developmental programme (figure 1*f*) evolved early in Lamiales and is conserved among relatives of *A. majus* with bilateral flower symmetry. In addition, either similar or divergent genetic programmes may have been recruited to specify independent origins of bilateral flower symmetry elsewhere in flowering plants (figure 2*a*). Possibilities include independent recruitment of a *CYC*-dependent programme to specify dorsal or ventral identity (figure 3*a,b*), or novel recruitment of a *CYC*-independent developmental programme to specify either dorsal or ventral flower identity (figure 3*c,d*). Results from many comparative studies now demonstrate that there is striking parallelism in the independent evolution of bilateral symmetry with a *CYC*-dependent programme frequently recruited to specify dorsal identity, and in some cases ventral identity (reviewed in [13,15,16]).

(a) Asterids

Limited data support the hypothesis that the *CYC/RAD/DIV* programme is conserved across Lamiales. In bilaterally symmetrical flowers of *Veronica* and *Gratiola* (belonging to the same family as *A. majus*, Plantaginaceae), *CYC* and *RAD* homologues are expressed in the dorsal regions of flowers and with nearly identical spatial distributions, suggesting conservation of positive regulation of the *RAD* gene by CYC protein [60]. This is also true in *Chirita* and *Bournea* from the early diverging Lamiales lineage Gesneriaceae [61,62]. Whether post-translational negative regulation of DIV by RAD protein is conserved in Lamiales is not clear and difficult to test, because analyses of *DIV* transcript localization will not reflect where in the flower DIV protein is present and
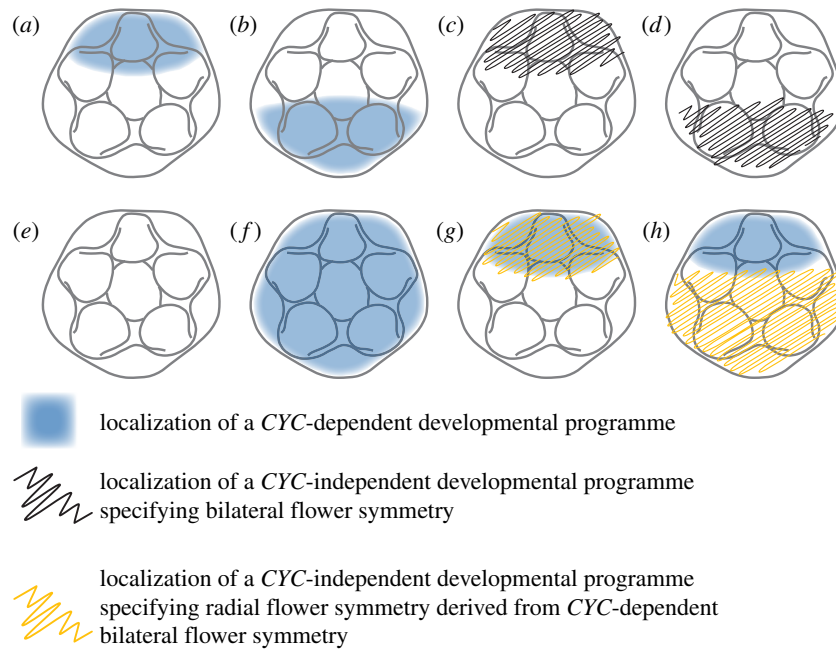
Figure 3. Hypothesized *CYC*-dependent and *CYC*-independent pathways for recurrent evolutionary transitions from radial to bilateral, and bilateral to radial flower symmetry. (*a,b*) A *CYC*-dependent programme is necessary for the development of bilateral flower symmetry through the specification of dorsal or ventral identity, respectively. (*c,d*) A *CYC*-independent programme is necessary for the development of bilateral flower symmetry through the specification of dorsal or ventral identity, respectively. (*e,f*) Radial flower symmetry is derived from *CYC*-dependent bilateral symmetry through loss of the dorsoventral restricted *CYC*-dependent programme. (*g,h*) Radial flower symmetry is derived from *CYC*-dependent bilateral symmetry through an independent programme that compensates for the effects of the *CYC*-dependent programme. (Online version in colour.)

functional (although see [62]). In addition to limited information on the conservation of the *CYC/RAD/DIV* programme within Lamiales, few studies have investigated the regulatory interactions among these genes/gene products in other asterid lineages (but see [63,64] summarized below), especially those most closely related to Lamiales (e.g. Boraginaceae, Solanales, Gentianales; figure 2*a*). In the distantly related model species *Arabidopsis thaliana* (rosid lineage), *CYC*- and *RAD*-like genes and gene products do not seem to be directly regulated by one another [57,65], but the phylogenetic distance makes it difficult to draw conclusions about when the *CYC/RAD* network interactions evolved.

Elsewhere within asterids, the role of *CYC*-like genes in independent transitions to bilateral flower symmetry has been investigated in Dipsacales and Asterales (figures 2*a* and 4). In the bilaterally symmetrical flower of *Lonicera* (Caprifoliaceae, Dipsicales), duplicate *CYC*-like genes are expressed in the dorsal or dorsal plus lateral petals (figure 4). This is in striking contrast to the radially symmetrical flowers of related *Viburnum* (Adoxaceae, Dipsacales) where these *CYC*-like orthologues show no pattern of differential expression across the floral axis. Interestingly, a *Lonicera RAD* orthologue is expressed similarly to one of the *Lonicera CYC* paralogues, providing some indication that the *CYC/RAD* regulatory interaction may have been established early in asterid evolution and retained in both Dipsacales and Lamiales, but this hypothesis requires extensive further testing.

Multiple lines of evidence demonstrate that *CYC*-like genes play a role in establishing the developmental differentiation of ray flowers (bilaterally symmetrical) from disc flowers (radially symmetrical) in Asteraceae inflorescences (capitula). *CYC* homologues in *Helianthus*, *Senecio* and *Gerbera* are preferentially expressed around the periphery of the capitulum where ray flowers are expected to develop, but either at low levels, or not at all in the region of disc flower development (figure 4) [66–68]. In *Helianthus* (sunflower), naturally occurring mutations transform disc flowers to ray flowers (double-flowered mutants), and ray flowers to disc-like tube flowers (tubular-rayed mutants). Double-flowered mutants are due to mutations that cause overexpression of a *CYC*-like gene in the region of disc flower development, thus causing their transformation to ray identity [66]. Similarly, transgenic overexpression of a *CYC* homologue in *Gerbera* leads to transformation of disc flowers to ray identity [68]. Tubular-rayed mutants are due to loss-of-function mutations in a *CYC*-like gene resulting in conversion of ray flowers to disc-like tubular flowers [66,69]. Interestingly, it appears to be different *CYC* paralogues in different Asteraceae lineages that are responsible for differentiation of ray flowers [66]. Although this is somewhat surprising, this is consistent with ray flowers having evolved multiple times in the family [70].

(b) Rosids

Similar to asterids, bilateral flower symmetry has evolved multiple times in rosids, and in at least three instances is associated with independent recruitment of a *CYC*-dependent developmental programme (Fabaceae, Brassicaceae and Malpighiaceae; figure 4). Developmental genetic studies of bilateral symmetry in *Lotus* and *Pisum* (Fabaceae) are extensive and second only to the work on floral symmetry in *A. majus*. In both *Lotus* and *Pisum*, there are three *CYC*-like paralogues. Through analysis of naturally occurring mutants, as well as gene silencing and overexpression transgenic studies, it is clear that two of these paralogues, *CYC1* and *CYC2* (LST in *Pisum*, and SQU1 in *Lotus*) function redundantly to establish dorsal petal identity [71–74]. Unlike in *A. majus* where the ground state for development seems to be lateral petal identity (*cyc;dich;div* mutant background [75]), in *Pisum* and *Lotus* the ground state appears to be ventral petal identity because in addition to dorsal identity controlled by *CYC1* and *CYC2*, the
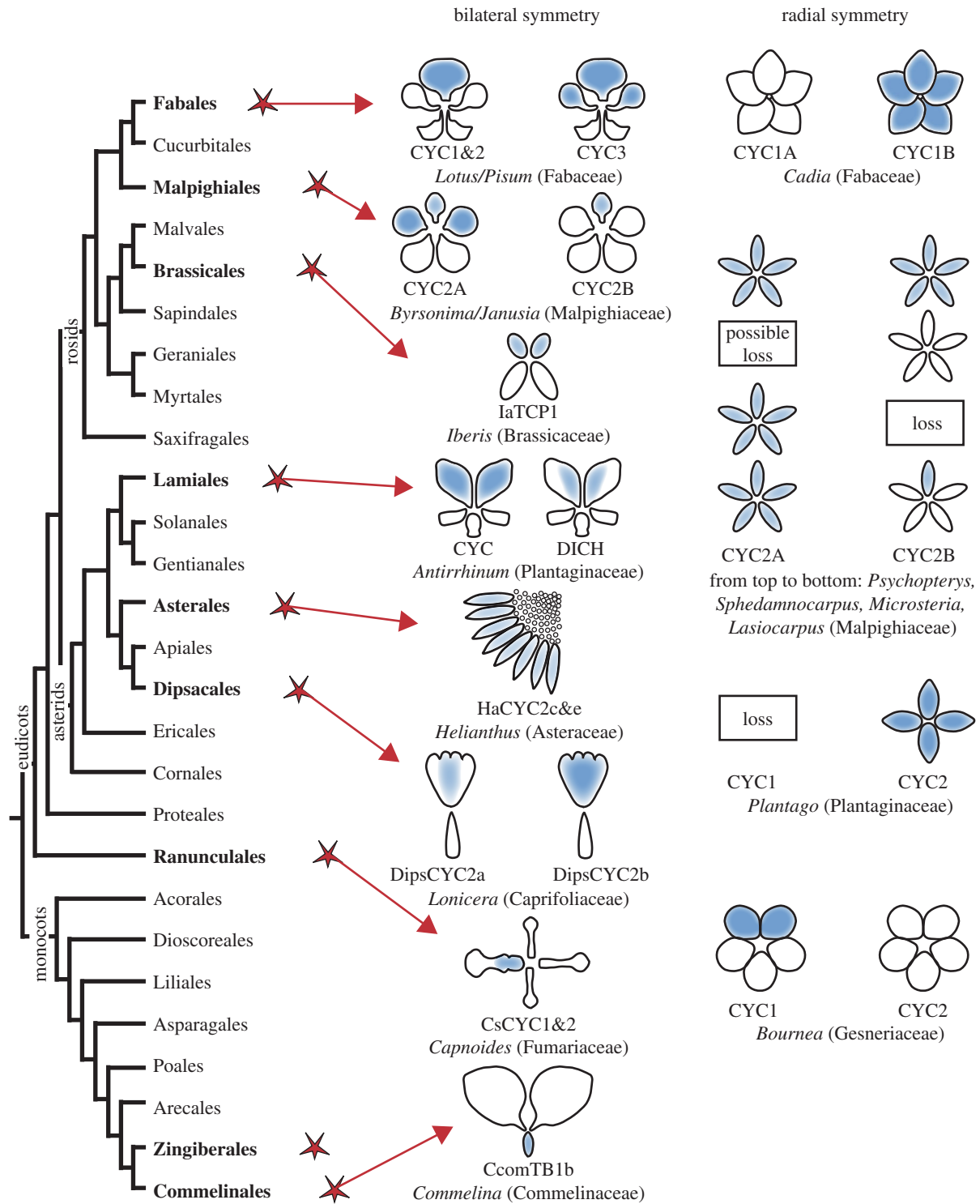
Figure 4. Summarized expression of *CYC*-like genes from comparative developmental genetic studies. Blue (grey in print version) shading indicates approximate pattern of *CYC*-like gene expression in the corolla of representative taxa. Phylogeny as in figure 2a, but for only the subset of orders with bilaterally symmetrical species. (Online version in colour.)

third paralogue, *CYC3* (K in *Pisum*, KEW in *Lotus*), directs the development of lateral petals (figure 4) [71–74].

In Brassicaceae, the role of *CYC*-like genes for directing development of bilateral flower symmetry has been investigated in *Iberis*, a close relative to the model species *Arabidopsis*. In *Iberis*, the two ventral petals are expanded relative to the two dorsal petals (figure 4). This difference is established late during *Iberis* flower development, and is associated with relatively late expression of *IaTCP1*, a *CYC* homologue, in the smaller dorsal petals (figure 4) [38,39]. Because *Iberis* is closely related to *Arabidopsis*, heterologous functional studies of *IaTCP1* in *Arabidopsis* provided meaningful assessment of *IaTCP1* function.

Overexpression of *IaTCP1* in *Arabidopsis* resulted in reduced cell proliferation in both vegetative organs and petals [39], consistent with reduced dorsal petal size where *IaTCP1* is expressed in *Iberis*. Lastly for the rosids, and similar to Fabaceae and Brassicaceae, *CYC*-like genes have been implicated in the evolution of bilateral symmetry in Malpighiaceae, with expression of *CYC*-like genes restricted to dorsal and dorsal/lateral petals (figure 4) [47].

(c) Early diverging eudicots and monocots

While most of the comparative work of flower symmetry developmental genetics has been undertaken in core eudicot lineages,

a handful of studies have tested whether the extensive parallel recruitment of a *CYC*-dependent programme for bilateral flower symmetry extends to non-core eudicot taxa. And again, we find evidence supporting a role for *CYC*-like genes in the development of bilaterally symmetrical flowers from early diverging eudicot and monocot lineages. Bilaterally symmetrical flowers of *Capnoides* in the Fumariodeae lineage of Papaveraceae (Ranunculales) are derived from disymmetric flowers [40,41]. The plane of bilateral symmetry in Fumariodeae flowers is transverse (figure 4), although partial resupination ultimately brings the transverse plane into dorsoventral orientation. In *Capnoides*, expression of two *CYC*-lineage paralogues [40,41] is asymmetric, with slightly stronger expression at the base of the outer petal that forms a nectary [76].

In monocots, transitions from radial to bilateral flower symmetry are pervasive [16], yet are quite under studied. In bilaterally symmetrical flowers of *Costus* and *Heliconia* (Zingerberales), as well as bilaterally symmetrical flowers of *Commelina* (Commelinales), expression of at least one *CYC*-like gene is asymmetric across the dorsoventral flower axis. In both monocot lineages studied, asymmetric *CYC*-like gene expression in the perianth is restricted to the ventral side of flowers (figure 4) [77,78]. This is in striking contrast to the general pattern of a *CYC*-dependent programme independently recruited to specify dorsal flower development across eudicots (figure 4). It is interesting to note, however, that a *CYC*-like gene from rice, *RETARDED PALEA1,* functions to specify palea development [79], an organ that develops on the dorsal side of grass florets. Whether the emerging pattern of dorsal flower expression in eudicots and ventral expression in monocots is a general pattern, perhaps reflecting developmental constraints, awaits further comparative work in monocots, as well as a clearer understanding of how *CYC* homologue expression is regulated during monocot and eudicot flower development.

6. Evolutionary transitions from bilateral to radial flower symmetry

Given the frequent association of bilateral symmetry with restricted expression of *CYC*-like genes to either the dorsal (most dicots), or ventral (most monocots) side of developing flowers, it is expected that reversals from *CYC*-dependent bilateral symmetry to radial symmetry will involve functional or regulatory changes to *CYC* homologues or their upstream regulators. There are, however, multiple hypothesized ways by which *CYC*-dependent bilateral flower symmetry might be lost in derived species with radial flower symmetry. One possibility is complete loss of *CYC*-like gene expression in flowers, through either regulatory evolution or gene loss (figure 3e). By contrast, regulatory evolution may result in expansion of *CYC*-like gene expression across the dorsoventral axis of developing flowers (figure 4f). Alternatively, the evolution of radial symmetry from *CYC*-dependent bilateral symmetry could arise through mechanisms independent of functional or regulatory evolution of *CYC*-like genes. For instance, compensatory changes might evolve in genes/genetic pathways downstream of *CYC*, or in developmental pathways non-overlapping with a *CYC*-like programme (figure 4g,h). Results from multiple comparative studies suggest that evolutionary changes at or upstream of *CYC*-like genes frequently underlie transitions from *CYC*-dependent bilateral to radial flower symmetry.

However, results from some studies are not inconsistent with a hypothesis of compensatory evolution.

Examples of derived radial symmetry (from *CYC*-dependent bilateral symmetry) for which the expression of *CYC* homologues has been studied include *Plantago* (Plantaginaceae, Lamiales), *Cadia* (Fabaceae, Fabales), two independent transitions to radial from bilateral symmetry in Gesneriaceae (Lamiales)—*Bournea* and *Tengia*, and four independent transitions to radial from bilateral symmetry in Malpighiaceae (Malpighiales)—*Psychopterys, Sphedamnocarpus, Microsteria* and *Lasiiocarpus* (figure 4) [62,80–83]. For each of these, two or more paralogous *CYC*-like genes are dorsally expressed in close relatives. Therefore, expression of all paralogues was investigated in these derived radially symmetrical lineages.

The most common pattern observed is a paralogue-specific combination of *CYC* loss of expression (figure 3e) with expanded *CYC* expression (figure 3f). In *Plantago, Tengia, Cadia* and *Microsteria*, one *CYC*-like paralogue (or set of closely related paralogues in the case of *Tengia*) is expressed across the dorsoventral flower axis, owing to regulatory evolution either at or upstream of that paralogue. The other *CYC*-like paralogue has been lost (*Plantago* and *Microsteria*), or is no longer expressed in flowers (*Cadia* and *Tengia*) [80–83]. Alternatively, both *CYC*-like paralogues are expressed across the dorsoventral flower axis (*Psychopterys*), or neither is expressed in flowers (*Sphedamnocarpus*) [82]. For two studied lineages with derived radially symmetrical flowers, one *CYC*-like paralogue has either expanded or lost floral expression, but the other paralogue retains dorsal-specific expression (*Lasiocarpus* and *Bournea*, respectively) [81,82]. In these cases, dorsal-specific *CYC*-like gene expression should be interpreted with caution. Dorsally restricted expression may be transient, or only occur early in development, and therefore may not specify a dorsal-specific developmental programme. Alternatively, there may indeed be functional consequences to retention of dorsal-specific expression, and these developmental consequences may be compensated by evolutionary changes in downstream or independent developmental programmes (figure 3g,h).

7. Prospects

Our current knowledge of the repeated recruitment of a *CYC*-dependent developmental programme during independent transitions to bilateral flower symmetry is staggering. These insights are possible through a combination of advances in flowering plant molecular phylogenetic research and studies of character evolution, as well as detailed flower developmental genetic studies in a few model species (namely *A. majus* and *L. japonica*). Likewise, it is daunting to imagine how little we would know about these evolutionary developmental processes had evolution not proceeded with such extensive parallelism. I believe we are now justified in stating that parallel recruitment of a *CYC*-dependent developmental programme for bilateral flower symmetry is extensive. However, we have yet to determine the depth of this parallelism: does independent recruitment occur through regulatory changes at *CYC*-like loci, or through evolutionary changes to one or multiple upstream regulators of *CYC*, or through a combination of these possibilities that is taxon specific? Additionally, paralogues belonging to different *CYC*-like gene lineages are implicated in the evolution of bilateral

flower symmetry in the core eudicots, early diverging eudicots and monocots. Also, *CYC*-like genes are generally regulators of cell proliferation [51]. Other than this broad recruitment from different *CYC* paralogue groups, and a possible general role in regulating cell proliferation, we know little about the specific function or regulation of *CYC*-dependent genetic pathways that might shed light on why they have so frequently been recruited to flower symmetry developmental programmes.

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