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Current Trends in Developmental Genetics and Phylogenetic Patterns of Flower Symmetry

Renu Puri and Anjana Rustagi

Abstract

Flower Symmetry is a key evolutionary innovation in some lineages of angiosperms. The flowers of the primitive angiosperm plants were radially symmetrical actinomorphic. Later bilaterally symmetrical zygomorphic flowers independently evolved in several clades of angiosperms. This transition of trait is associated with an adaptation to specialized methods of pollination. Zygomorphic flowers allow more specific plant insect interaction. So, the transition from radial symmetry to bilateral symmetry facilitates reproductive isolation which in turn might have led to diversification or rapid speciation of some lineages in angiosperms. Phylogenetic analyses in lineages of angiosperms revealed that few clades have shown that there have been reversals, that is, there is transition from bilateral symmetry to radial symmetry. When such studies are correlated with genetic studies, it is revealed that CYC (TCP family) transcription factors are responsible for the transition of this floral trait. Phylogenetic analyses, genetic studies and Evo-Devo analyses can answer important questions such as what other transition in floral symmetry is found in angiosperms? Is there a pattern of floral symmetry transition in different lineages? Do these transitions act as key innovation for the clades in which they have evolved?

Keywords: floral symmetry, zygomorphic, actinomorphic, phylogeny, asymmetry

1. Introduction

Flower is a significant novelty for evolutionary success in angiosperms. It primarily comprises four whorls—sepals, petals, stamens, and carpels. The shape of the flower changes because of change in the shape or morphology of any of these whorls. This gives rise to different shape and symmetry of flowers. The change in symmetry can occur in any of the whorl; however, it is widely studied in petals [1]. Floral symmetry is an important trait as it impacts the visual appearance of a flower. Hence, it's been a fascination for human eye. Pollinators are usually attracted to flowers due to its diverse forms of colors but also due to the symmetry it possesses, thereby contributing to the plant pollination syndrome [2–4]. Broadly there are the two types of floral symmetry, radial symmetry also known as polysymmetry or actinomorphy and bilateral symmetry also known as monosymmetry or zygomorphy. Flowers with radial symmetry have more than two planes of symmetry and are called as actinomorphic. Flowers with bilateral symmetry have single plane of symmetry and are called as zygomorphic [5–7]. There is another rare form of symmetry

Figure 1.

Different types of floral symmetry. A. Radial symmetry (more than one plane of symmetry, polysymmetry, actinomorphy). B. Bilateral symmetry (single plane of symmetry, monosymmetry, zygomorphy). C. asymmetry (no plane of symmetry). D. Flower of *Catharanthus roseus* showing radial symmetry, E. flower of *impatiens* sp. showing bilateral symmetry and F. flower of *canna* sp. showing asymmetry.

in flowers that is known as asymmetry [8]. This refers to morphologies where there is no pane of symmetry (**Figure 1**).

These categories have been studied at various different levels such as the molecular aspects of these transitions and how the pollinators perceive them [5, 6]. There have been transitions from actinomorphy to zygomorphy many times during the diversification of angiosperms, and these transitions are more common in species-rich lineages such as Fabaceae, Lamiales, and Orchidaceae. However, reversals from zygomorphy to actinomorphy are also reported [9–12].

We in this chapter focus on the different genetic studies, which have been conducted to understand the molecular basis of the variation in floral symmetry and what do we get to know when these studies are correlated with phylogenetic studies. These studies have provided insights into how and when these transitions in floral symmetry evolve.

2. Diversity of floral symmetry in angiosperm flowers

Apart from the flower symmetry categories mentioned above, there are many other forms of flower symmetry such partial zygomorphy and few others. There are different degrees of symmetry. In the year 1925, based on the aspects of symmetry as used in crystallography, new terms were introduced. Of those rotational symmetry, mirror symmetry and spiral symmetry are to name a few [13].

Later correlation studies between floral symmetry and pollination biology were conducted. These studies focused on how pollinators perceived flowers. With these studies, three-dimensional aspects were added to the floral symmetry terminology [10, 14, 15]. After around 75 years, an elaborated and modified classification was proposed, which was also based on visual perception of flowers by

the pollinators [2, 3]. These terminally only applied to very discreet flower forms and only in mature flowers [16].

However, there are variable degrees of floral symmetry at different developmental stages. This variation can also be seen in different lineages, or there might be convergent evolution of this state in two different and closely unrelated clades. Endress [5] considered these two aspects, that is, developmental changes and phylogenetic changes, and identified three forms of monosymmetry and three forms of asymmetry.

First form of monosymmetry is found in taxa with elaborated monosymmetric flowers, for example, Lamiales, Asterales, and Leguminosae. The second is taxa in which monosymmetry arises, but predominantly the group is polysymmetric, e.g., *Passiflora lobata* (Passifloraceae) and *Chiranthodendron pentadactylon* (Malvaceae). The third form is evolution of monosymmetry form by reduction, e.g., in case of *Hippuris* (Antirrhinaceae). First form of asymmetry is seen in taxa, which are predominantly monosymmetric, e.g., *Vigna* (Leguminosae). Second form is unordered asymmetry in flowers of basal angiosperms, e.g., *Zygogynum* (Winteraceae). Third form is asymmetry, which arises due to reduction, e.g., *Centranthus* (Valerianaceae) [5].

3. The genetic basis of flower symmetry

The genetics of a flower is regulated by specific transcription factors (TFs) [17]. TFs such as MADS (First alphabet of MCM1 in yeast, AGAMOUS in Arabidopsis, DEFICIENS in snapdragon, and SERUM RESPONSE FACTOR in human)-box are widely studied for various developmental pathways from root development to fruit development. One important role is determination of organ development in flower. ABCDE model and its modifications are based on the different functions of MADS-box TFs [18–25].

Floral development is also controlled by other set of TFs Known as MYB TFs. These TFs are found in all eukaryotic organisms and identified by the presence of MYB R Repeats. Each repeat is about 52 amino acids. Based on these repeats, the MYB TFs are classified into 4R, 3R, 2R, and 1R-MYB types. In plants, the most common are 2R-MYB TFs (R2R3) [26–29].

Recent studies show that MYB TFs, DIV-and-RAD-interacting-factors (DRIF), DIVARICATA (DIV) and, RADIALIS (RAD) play important role in floral symmetry [30, 31]. The studies revealed that these MYB TFs interact with TCP (TCP family name is derived from its first three characterized members, first alphabet of TB1, TEOSINTE BRANCHED 1; CYC, CYCLOIDEA and PCFs, proliferating cell factors) TFs. CYCLOIDEA (CYC) and DICHOTOMA (DICH) are two paralogs that belong to TCP family. They are expressed in the dorsal region of flowers, and they are vital to control floral symmetry [32]. The studies show that these TFs and their orthologs and paralogs have similar interactions in Dicots and monocots.

3.1 Developmental genetics of floral symmetry in dicots

The molecular basis of floral symmetry was first studied in *Antirrhinum majus*, which has zygomorphic flowers [33]. In the dorsal region, there is interaction of RAD and DRIF. CYC is expressed only in the dorsal region of flower. RAD promoter and intron have CYC target sequence. When CYC binds to RAD promoter, it causes synthesis of RAD protein. The DIV protein Interacts with DRIF but when RAD binds to DRIF, DIV/DRIF complex is not formed and thus not able to activate downstream ventral gene. In the ventral region, CYC is not expressed and likewise RAD is not activated. DRIF is free to bind to its target sequence present on the DIV

promoter region [34, 35]. This heterodimer complex, *DIV/DRIFT* complex activates the ventral genes. This differential expression of *CYC* in dorsal and ventral region of snapdragon flower causes dorsoventral symmetry (**Figure 2**) [36–38].

Flower of *A. majus* is an example from Lamiales where there is elaborated zygomorphy. Within Lamiaceae in family Gesneriaceae, the clade has zygomorphic flowers. However, *Conandron ramondiioides* have actinomorphic flowers [39]. This is the case of reversal from zygomorphy to actinomorphy. In this species, there is change in the expression of the homologs of above TFs. In case of petals and stamen, there is loss of expression of *CrCYC* and *CrRAD* so the *DIV* is active and ventral genes are activated (**Figure 3**) [40–42].

Another member of clade lamiales *Plantago lanceolata* shows actinomorphic flowers [43]. Interestingly here *CYC* A clade gene is absent, but *PlCYC-B* clade gene is expressed. *PlCYC-B* at early stages is present in ground tissue, and later it expresses in stamens till the upper portion of filament. *PlCYC* is absent in petals. Homolog of *RAD* gene is absent, and *PlDIV*, ortholog of *DIV* is expressed in lateral petals and in the ovary. Absence of *CYC-A* clade and *RAD* gene in the dorsal part of flower might have been responsible for radial symmetry (**Figure 4**) [44, 45].

More complex mechanism takes place in Asteraceae. Here the inflorescence is complex and is known as capitulum. For example, in *Senecio vulgaris*, the disc florets have radial symmetry and ray florets have bilateral symmetry [46]. Here there are *CYC*-like genes *RAY1*, *RAY2*, and *Ray3*. Unlike as in *A. majus*, *RAY1* and *RAY2* are expressed in entire ray floret, and *RAY3* expresses only in ventral region. *MYB* genes *SvDIV1B* and *SvRAD* are expressed only in the ray florets at early stages. *SvRAD* expresses in ventral region. At later stages, *SvDIV1B* expresses in disc florets too (**Figure 5**) [47].

Figure 2.
Molecular genetic control of floral symmetry in *Antirrhinum majus*.

Figure 3.
Molecular genetic control of floral symmetry in *Conandron sp.*

Figure 4.
Molecular genetic control of floral symmetry in *Plantago sp.*

Figure 5.
Molecular genetic control of floral symmetry in *Senecio vulgaris*.

3.2 Developmental genetics of floral symmetry in monocots

Little is known about floral symmetry in monocots. Orchidaceae family supports the DDR (DDR stands for *DIV*, *RAD*, and *DIV*-and-*RAD*-Interacting Factor *DRIF*)

Figure 6.
Molecular genetic control of floral symmetry in Orchidaceae.

regulatory module [48]. Recent study revealed that *DIV*, *DRIFT*, and *RAD* interact with each other and work as regulatory unit. DDR module is more conserved in monocots than in dicots. Orchids show resupination before anthesis and dorsally placed structure becomes ventral in position. *DIV* and *DRIFT* express in ventral structures and after resupination take dorsal position. In the lip high level of *RAD* expression prevents activation of *DIV*. *RAD* is responsible for lip determination in orchids (**Figure 6**) [49].

4. Other putative genes

Apart from *MYB* and *TCP* family, other putative genes need to be identified. Few genes are identified in model plant *Arabidopsis*. One such is *RABBIT EARS* (*RBE*). It belongs to C2H2 Zinc finger TFs family. Its expression is regulated by Auxin. When this gene is muted, then two of the petals do not elongate and give rise to bilateral flower. *RBE* further regulates *TCP4* negatively by binding directly to its target sequence to the *TCP4* promoter [41]. The role of *CYC* and *CYC*-like genes, which belong to *TCP* family, is already known. Other putative *TCP* members could be analyzed to reveal other pathways responsible for flower symmetry.

Other putative genes are such as *AINTEGUMENTA-LIKE 6* (*AIL6*), *AUXIN-REGULATED GENE INVOLVED IN ORGAN GROWTH* (*ARGOS*), *AINTEGUMENTA* (*ANT*), *BIGPETALp* (*BPEp*), and *JAGGED* (*JAG*). The differential expression of these genes plays important role in floral organ development. Further analyses on non-model species that have different floral symmetries can reveal their role in floral symmetry [41]. The identification of these genes will not only help to identify the QTL for floral traits but also for phylogenetic studies. The homologs of these genes can further help us to understand the evolution of these genes and the gene families.

5. Phylogenetic pattern in floral symmetry

Floral symmetry patterns are best understood in phylogeny context. These studies help in understanding how often the transition from radial symmetry to bilateral symmetry has occurred and vice versa. It also gives insight on what lineages these transitions have taken place and when those transitions occurred on geological timescale.

We now have clear understanding about the major lineages of angiosperms. Recent studies focus on mapping various morphological traits on these robust phylogenetic analyses. In relation to floral symmetry, recent studies have constructed it as a character and different forms (radial symmetry, bilateral symmetry, asymmetry, etc.) on phylogenies [50]. Such robust studies have answered the abovementioned questions.

Studies revealed that the ancestral flower of angiosperms was radially symmetrical [8]. Floral symmetry character reconstruction on ordinal phylogeny also revealed the same scenario and showed that the transition to bilateral symmetry is widespread on angiosperm phylogeny. Parsimony reconstruction on family phylogeny revealed that there are at least 70 such transitions from radial to bilateral symmetry in angiosperms including 23 in monocots and 46 in eudicots [50].

Later studies focused on detailed phylogeny of smaller clades. Character reconstruction of floral symmetry in Lamiales at family level revealed one transition from radial to bilateral symmetry and one vice versa [51]. Multiple transitions from radial to bilateral symmetry were observed in Brassicaceae, Ranunculaceae, and Solanaceae [52–54].

S.no	Clade names
Group 1	Amborrellales, Pandanales, Arecales, Dasypogonaceae, ceratophyllales, Trochodendrales, Buxales, Gunnerales, Dileniales, Vitales, Celastrales, Oxalidales, Fagales, Crossosomatales, Picramniales, Heurteales, Malvales, Berberidopssidales, Cornales, Nymphaellales, Austrabaileyales, Chalaranthales, Canellales, Magnoliales, Petrosaviales, Aquifoliales, Escalloniales, Bruniales, Paracryphiales, Garryales, Icacinaceae, Metteniusaceae, Oncothecaceae, Vahliaceae

Table 1.
List of clades in which radial symmetry is conserved in all or most of its descendents.

S.no	Clade names
Group 2	Piperales, Laurales, Acorales, Alismatales, Dioscoreales, Liliales, Asparagales, Poales, Commelinales, ranunculales, Proteales, Sabiales, Saxifragales, Zygophyllales, Malpighiales, Fabales, Rosales, Cucurbitales, Geraniales, Myrtales, Sapindales, Brassicales, Santalales, Caryophyllales, Ericales. Apiales, Dipsacales, Asterals, Boraginaceae, Gentianales, Solanales

Table 2.
List of clades in which bilateral symmetry evolved independently.

S.no	Clade names
Group 3	Zingiberales, Lalmiales Acorales, Fabales, Dispacales

Table 3.
List of clades in which bilateral symmetry evolved early as a single event.

S.no	Clade names
Group 2	Orchidaceae, Fabaceae, Malpighiaceae, Capparaceae, Cleomaceae, Brassicaceae, Caprifoliaceae and Aster-aceae

Table 4.
List of clades in which there was reversal from bilateral symmetry to radial symmetry.

Bilateral symmetry has evolved at least 130 times independently in different clades, and there were at least 70 reversals [55]. Based upon these transitions, four basic groups have been observed. These are: first, there are clades where radial symmetry is conserved (**Table 1**). Second, clades wherein bilateral symmetry has evolved independently (**Table 2**). Third, clades wherein bilateral symmetry arises as single early event (**Table 3**), and fourth group includes clades that show reversal to radial symmetry (**Table 4**). Basal angiosperms have radial symmetry with exceptions such as in *Glossocalyx*. Radial symmetry is also conserved in ancestral monocots and Eudicots. More robust phylogenetic studies in future can further reveal detailed transitions.

6. Floral symmetry on geological timescale

First fossil remains of flowers with inserted flower parts are found to be from early Cretaceous period (Barremian-Aptian period) around 125 million years ago (Ma.). This fossil represents the flowers of the ancestors of early Nympheales [56, 57]. The first fossil of a flower, which is pentamerous, was reported from late Cretaceous period (Cenomanian period) around 100 Ma. This fossil remains has both petals and sepals. It is considered as a representative of ancient ancestor of Eudicots [58].

Clearly, the above fossil records show that there was a transition from closed floral structure to an open floral structure. The flower evolved from closed noncyclic structures to more open and cyclic forms. This transition took place in Mid-Cretaceous period. It is during this period that many floral traits evolve. Many of these traits are key innovations. This floral trait evolution coincides with the major diversification period of angiosperms [59, 60].

The first transition from radial symmetry to bilateral symmetry can be traced to the first radiation in angiosperms. These flower remains are reported from Turonian fossils from late Cretaceous, which is around 100 Ma. These flower fossils have staminodal nectaries making the radial flower partially bilateral. These flowers fossils are the first report of zygomorphic flower form, although these forms were not exactly bilaterally symmetrical. These fossils represented the precursors or ancestors of zygomorphic flowers [59, 61].

First complete zygomorphic flowers are recorded from Paleogene (Paleocene-Eocene period) around 55 Ma [59]. This is the time period where a second major diversification of angiosperms took place. So, we have seen that both the radiation events of angiosperms diversification coincide with the evolution of floral traits including floral symmetry [61]. Thus, floral symmetry transition is clearly the key innovation, which might have played crucial role in radiation of angiosperms. Of course, there might be other factors too that played their part. One such factor is evolution of pollinators.

Interestingly, the evolution of those floral traits that lead to diversification of angiosperms in the above-said events coincides with the advent of specialized pollinators. Also, the evolution of bilateral symmetry in some plant lineages cooccurs

with the time period when there was a rise of some bee families. Thus, in some lineages the Coevolution of insect pollinators with the floral symmetry holds true [2, 5]. Although there are other abiotic and biotic factors that are needed to be taking into account such as climatic conditions and various architectural components of flower.

7. Conclusion

Great deal of progress is being made on study of floral symmetry evolution in dicots. The *MYB* TFs and *TCPs* play an important role in understanding the molecular genetic basis of floral symmetry. However, there is a scope to identify other putative genes that might be having evolutionary significance. Robust studies should be taken up, especially among monocots to unravel modulators of floral symmetry patterns.

Most of the species-rich lineages have bilateral symmetry. Based on this observation, many hypothesize that bilateral symmetry is related to increased specificity to pollinators, thereby increasing the chances of reproductive isolation. This holds true for many taxa, but not all lineages of angiosperms follow the same pattern.

Evolution is a highly complex phenomenon, and diversification of species is dependent on various factors and not just one single trait. Therefore, it is necessary to take holistic approach and to combine other factors such as developmental stages, floral mechanics, etc., with the phylogenetic framework to get a detailed answers about floral symmetry.

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Author details

Renu Puri and Anjana Rustagi*

Department of Botany, Gargi College, University of Delhi, Delhi, India

*Address all correspondence to: anjana.rustagi@gargi.du.ac.in

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