

TCP transcription factors in action: shaping floral traits and inflorescence architectures

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Abstract

TCP transcription factors are plant-specific regulatory proteins known to play major roles in controlling floral traits and inflorescence architecture. This review highlights the recent advancements in understanding the multifaceted roles of TCP genes in floral symmetry establishment, pseudanthia development, and regulation of floral pigmentation. The review examines the interplay between the TCP proteins and other gene families, such as MADS-box and MYB transcription factors, to shape floral morphology. Specifically, we explore how TCP transcription factors influence downstream genes associated with pigment biosynthesis and affect floral orientation. The current understanding of TCP genes serves as a basis for designing molecular breeding strategies to create desired floral features that enhance both fitness and aesthetic value.

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Introduction

Extensive diversity in flower morphology not only contributes to the aesthetic appeal of plants but is also significant for ecological adaptation and agricultural productivity. Multiple factors affect the intricate overall appearance of flowers, including the arrangement, number, type, shape, size, and color of floral organs, all of which are governed by sophisticated molecular mechanisms (Fig. 1)^[1].

In this review, we focus on TCP transcription factors, a family of plant-specific proteins, and their critical roles in defining flower morphology and inflorescence architecture. Building on previous studies that have shed light on TCP functions in flower development^[2–4], we explore the spatial-temporal regulatory activities of TCP proteins. We also highlight recent research that has discovered their interactions with other gene families, such as those encoding MADS-box and MYB transcription factors, to understand their impact on floral traits, including symmetry, organ development, and pigmentation. We aim to provide an updated synthesis of the current knowledge on TCP transcription factors, emphasizing their potential applications in ornamental plant breeding to enhance both aesthetic value and fitness.

An overview of TCP transcription factors

TCP transcription factors are plant-specific proteins defined by a conserved TCP domain, named after TEOSINTE BRANCHED1 (TB1) from maize (*Zea mays*), CYCLOIDEA (CYC) from snapdragon (*Antirrhinum majus*), and PROLIFERATING CELL FACTOR (PCF) from rice (*Oryza sativa*)^[5]. Based on their domain variations, TCP genes are divided into two subfamilies: class I (TCP-P, related to PCF genes) and class II (TCP-C, comprising CINCINNATA-like (CIN) and CYC/TB1-like genes) (Fig. 2a)^[6]. PCF and CIN-like genes are more ancient, and found in basal land plants, while CYC/TB1-like genes are unique to angiosperms^[6]. In core eudicots, major duplications have led to CYC1, CYC2, and CYC3 clades, while additional, independent

lineage-specific duplications have produced species-specific genes^[7–9]. This gene expansion, driven by dispersed duplications that promote gene family diversification by allowing duplicate genes to evolve independently, as well as whole-genome or segmental duplications that lead to polyploidy or structural variations in the genome has facilitated the emergence of new gene functions and contributed to plant diversity and the emergence of evolutionary innovations^[10,11]. Besides the TCP domain necessary for DNA binding and protein interactions, class II proteins often feature additional conserved motifs, contributing to the specification of different TCP subclades (Fig. 2b)^[5,9,12]. For example, the 18–20 residue arginine-rich R domain is missing in all class I proteins but is present in class II proteins; the glutamic acid-cysteine-glutamic acid (ECE) motif is highly conserved in CYC/TB1 clade proteins; the microRNA miR319 target site is found only in a subset of CIN-like genes^[5,9,12].

Over the years, numerous studies have revealed that TCP proteins regulate vital developmental processes in plants, including leaf development (Supplementary Table S1), shoot branching (Supplementary Table S2), and flowering time (Supplementary Table S3), as well as flower (Supplementary Table S4), and inflorescence (Supplementary Table S5) development^[4,12,13]. Their primary function is to control cell proliferation and expansion, acting as activators or repressors depending on the presence of specific regulatory domains or interacting protein partners^[12]. The following sections focus on TCP gene functions in flower and inflorescence development, and particularly on their roles in petal morphology, pigmentation, as well as the regulatory networks they are involved in.

Spatial and temporal expression of TCP genes in the regulation of flower development

Floral symmetry is categorized into bilateral (zygomorphy), radial (actinomorphy), and asymmetric forms. The emergence of zygomorphy has evolved repeatedly in angiosperms, and at least 199

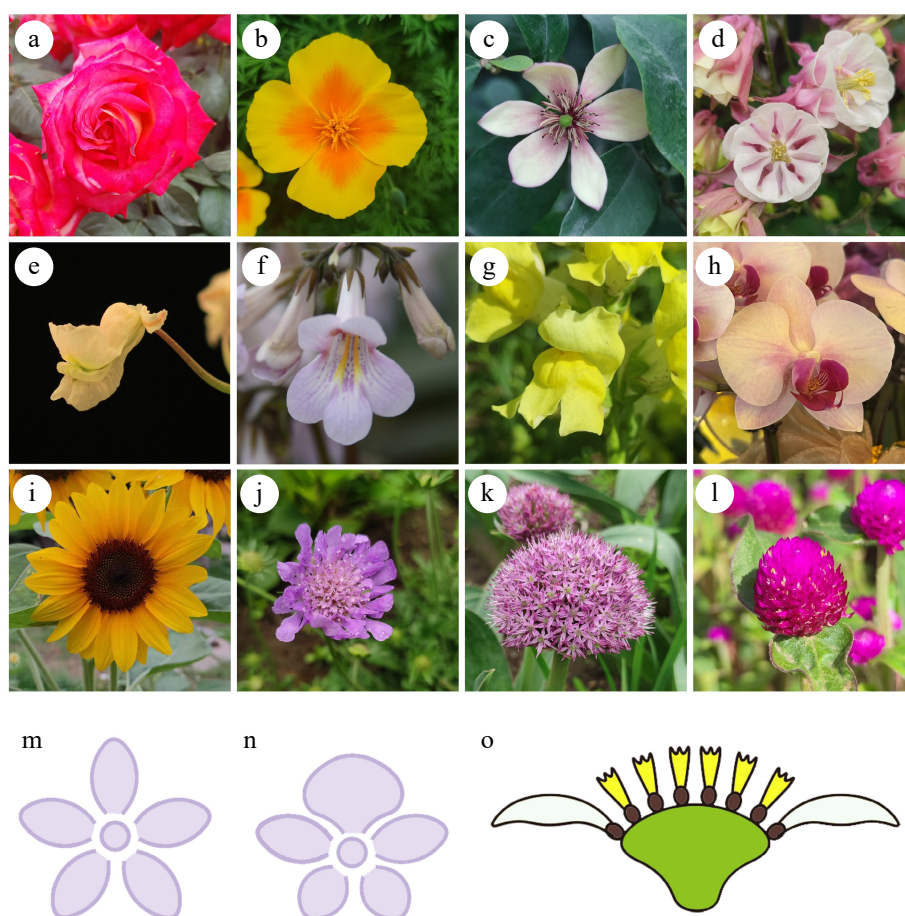


Fig. 1 Floral symmetry and inflorescence patterns in ornamental plants. Actinomorphic (radially symmetrical) flowers: (a) *Rosa hybrida*; (b) *Eschscholzia californica*; (c) *Michelia figo*; (d) *Aquilegia viridiflora*. Zygomorphic (bilaterally symmetrical) flowers: (e) *Cysticapnos vesicaria*; (f) *Primulina* 'Flying Wings' (*P. fimbriopala* × *P. linearifolia*); (g) *Antirrhinum majus*; (h) *Phalaenopsis aphrodite*. Pseudanthia (false flowers): (i) *Helianthus annuus*; (j) *Scabiosa comosa*; (k) *Allium giganteum*; (l) *Gomphrena globosa*. Schematic diagrams of (m) actinomorphic flower, (n) zygomorphic flower, and (o) pseudanthia.

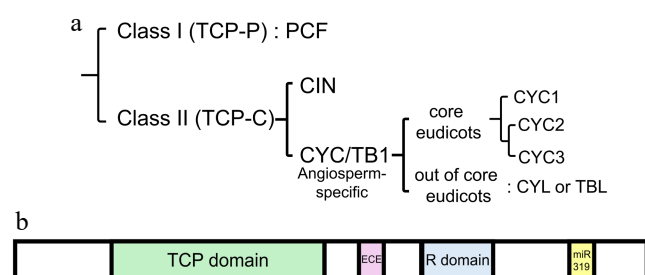


Fig. 2 Classification and structural domains of TCP transcription factors. (a) Phylogenetic classification of TCP transcription factors into two major classes: Class I (TCP-P), represented by the PCF subfamily, and Class II (TCP-C), which is further divided into CIN-like and *CYC/TB1* subclades. The *CYC/TB1* subclade is angiosperm-specific and further differentiates into distinct lineages in core and non-core eudicots. In core eudicots, three paralogous groups (*CYC1*, *CYC2*, and *CYC3*) are typically present, while in non-core eudicots, homologs are referred to as *CYC*-like (*CYL*) or *TB1*-like (*TBL*). (b) Schematic representation of the conserved domains in Class II TCP proteins: the TCP domain (green), the ECE motif (pink), the R domain (blue) and the miR319 target site (yellow). They contribute to the specification of different TCP subclades.

transitions between zygomorphy and actinomorphy has been documented^[14]. These shifts are influenced by the spatial arrangement and differentiation of perianth parts (first and second whorls of flowers) and variations in the third whorl (stamen or staminode)

(Fig. 1). Zygomorphy, in particular, is often linked to specialized plant-pollinator interactions and adaptive radiation^[15]. Genetic evidence indicates that TCP transcription factors, especially *CYC*-like genes, are central to the repeated evolution of zygomorphy in angiosperms (Fig. 3 & Supplementary Fig. S1).

Peloria: bridging historical observations with genetic insights

The term 'Peloria' (Greek for 'monster'), first introduced by Carl Linnaeus, describes the actinomorphic mutants in typically zygomorphic flowers, such as *Linaria* and snapdragon, where all floral organs adopt a ventral identity^[16]. The dysfunction of the originally dorsal-specific *CYC2*-clade gene underlies the peloric phenotype, through methylation and transcriptional silencing of *Lcyc* in *Linaria* and transposon disruption of *cyc* in snapdragon, respectively^[17,18]. This term not only identifies a specific morphological anomaly but also provides insights into the genetic and evolutionary dynamics of floral structure.

Dorsal-specific expression pattern of *CYC* genes

Across a wide range of angiosperms, *CYC2* genes exhibit a conserved dorsal-specific expression pattern that correlates with dorso-ventral asymmetry. Snapdragon serves as a key model for studying floral symmetry, with two critical *CYC2* clade genes, *CYC* and *DICHOTOMA* (*DICH*), orchestrating the development of dorsal petal and staminode identity (Fig. 3a)^[17,19]. Interestingly, in *Arabidopsis*, a distantly related species with actinomorphic flowers, the *CYC*

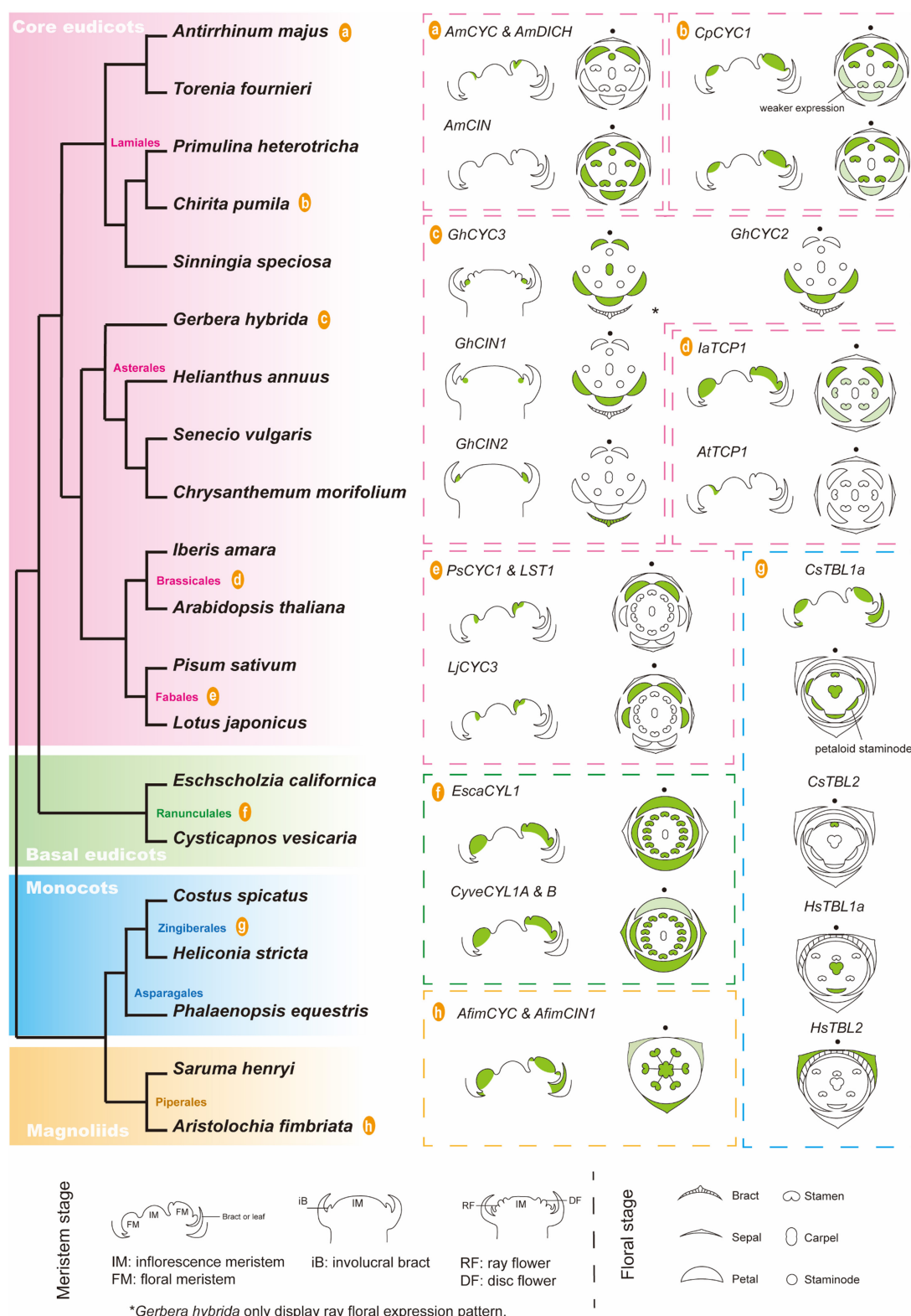


Fig. 3 Phylogenetic distribution and floral expression patterns of CYC/TB1 homologs across angiosperms. The left panel depicts a simplified phylogeny of angiosperm lineages, including core eudicots (pink), basal eudicots (green), monocots (blue), and magnoliids (yellow). Representative species from different clades are shown. The right panel illustrates the spatial and temporal expression patterns of CYC/TB1 homologs in floral primordia and floral organs at different development stages. Genes with documented roles in floral symmetry regulation are displayed, with expression domains highlighted in green and undetected expression in white. Expression is mapped onto floral diagrams, with petals, sepals, stamens, and carpels indicated according to the key at the bottom. Legend symbols indicate meristem and floral stages: IM, inflorescence meristem; FM, floral meristem; iB, involucral bract; RF, ray flower; DF, disc flower. * denote species with ray flower-specific expression (*Gerbera hybrida*). The black dot represents the stem indicating dorsal position. Dashed lines separate different angiosperm groups for comparative analysis.

ortholog *TCP1* also exhibits a restricted dorsal expression pattern in incipient floral meristems (FMs); however, this pattern is transient in FMs until stage 5 (Fig. 3d)^[20]. In contrast, *Iberis amara*, also a member of the Brassicaceae family as *Arabidopsis*, develops a zygomorphic corolla, owing to the time difference of *laTCP1* expression^[21]. *laTCP1* lacks an asymmetric early expression but displays an asymmetric late expression in the dorsal domain resulting in unequal petal growth (Fig. 3d)^[21]. Ectopic expression studies of three orthologous *CYC* genes in *Arabidopsis* reveal that *AmCYC* promotes petal expansion, whereas *TCP1* and *laTCP1* inhibit growth, though all share roles in cell cycle regulation^[21]. Despite their divergent influence on growth, orthologous *CYC* genes share a conserved role in cell cycle regulation. In snapdragon, *AmCYC* was shown to repress *CYCLIN D3b* and another cell cycle gene in the dorsal stamen, either directly or indirectly^[22]. More recently, research in *Chrysanthemum lavandulifolium* (Asteraceae) confirmed that *CYC2b* directly activates *CYC2A2;1* expression to modulate cell division during petal growth^[23]. These findings highlight conservation of *CYC* genes in the regulation of cell cycle dynamics, while also revealing their functional divergence in modulating petal growth across different species.

Expression pattern expansion of *CYC* genes

CYC2 gene expression sometimes extends beyond the dorsal domain of flowers, influencing the final floral forms. In Gesneriaceae (*Primula heterotricha* and *Chirita pumila*), *CYC2* orthologs (*PhCYC1C*, *PhCYC1D*, and *CpCYC2*) exhibit a transition from uniformly early expression to a restricted expression in the late dorsal petal and dorsal and lateral staminodes (Fig. 3b)^[24,25]. *CpCYC2* transcripts continue to be expressed in the ventral functional stamen (Fig. 3b)^[25]. In Fabaceae, *CYC2*-like paralogs (named *CYC1*, *CYC2*, and *CYC3*) determine petal identity in both dorsal and lateral positions in *Lotus* and *Pisum*, with divergent functional roles: *CYC1* and *CYC2* define the dorsal petal identity, whereas *CYC3* contribute to the development of lateral petals (Fig. 3e)^[26–28]. These findings emphasize the role of *CYC2* gene expression in defining petal identity and highlight the diversification of these genes across distinct floral regions.

Ventral-specific expression patterns of *CYC* genes

The transition from dorsal to ventral expression patterns of *CYC*-like (*CYL*) genes is commonly observed in basal eudicots and monocots. Rather than being involved in the initial establishment of zygomorphy, *CYL* genes often show increased ventral expression during the later stages of perianth development^[8]. In the basal eudicot family Papaveraceae, *CYL* genes display uniform expression at young FMs (Fig. 3f)^[29]. Later, in actinomorphic *Eschscholzia californica*, *CYL* genes uniformly promote stamen and petal development, while in the zygomorphic *Cysticapnos vesicaria*, *CyveCYLs* are predominantly expressed in ventral petals and sepals, with reduced expression in dorsal petals (Fig. 3f). Silencing *CyveCYLs* results in the dorsalization of ventral petals, converting zygomorphic flowers into dissymmetric or even actinomorphic forms^[29].

In monocots, *TB1*-like (*TBL*) duplicates exhibit divergent expression patterns in floral organs, influencing floral symmetry. In the Commelinaceae family, *TB1a* expression is stronger in ventral tepals and stamens of bilaterally symmetrical *Commelina* but is absent in radially symmetrical *Tradescantia*^[30]. In Zingiberales, *ZinTBL1a* accumulates in the dorsal staminode of *Heliconia stricta* and various ventral floral parts of *Costus spicatus*, whereas *ZinTBL2* is enriched in the ventral sepals of *H. stricta* and in the dorsal fertile stamens of *C. spicatus* (Fig. 3g)^[31]. Although ventral-specific *CYC2* expression is uncommon in core eudicots, it has been observed in the ventral petal primordia of ray flowers in gerbera (*Gerbera hybrida*)^[32] and chrysanthemum (*Chrysanthemum morifolium*)^[33]. Additionally, the

resupinated flowers of Lobelioideae (Campanulaceae), which undergo a 180° twist upon opening, exhibit high expression of *CamCYC2A* and *CamCYC2B* in the ventrally oriented petal lobes that correspond to the dorsal domain of the initial floral meristem^[34]. These patterns reflect that *CYC*-like genes are also adapted to regulate the ventral domains of the flowers, contributing to the intricate modulation of floral symmetry.

The role of *CIN*- and *PCF*-like *TCP* factors in flower development

Beyond *CYC*-like genes, also *PCF* and *CIN*-like *TCP* genes play significant roles in flower development, particularly in regulating cell growth across angiosperms. In core eudicots, *Arabidopsis* *PCF*-like *TCP15/14* and *CIN*-like *TCPs* share regulatory pathways to modulate cell growth and differentiation^[35], with *CIN*-like *TCP5*, *TCP13*, and *TCP17* promoting petal maturation through cell cycle control^[36,37]. In chrysanthemum, *TCP20*, a member of the *PCF* clade, enhances petal elongation via cell expansion^[38].

In monocots and early diverging angiosperms, *CIN* and *PCF* genes have diversified, often compensating for limited *CYC*-like gene copies in establishing bilateral symmetry^[39,40]. In *Aristolochia* (Aristolochiaceae), *CIN* and *CYC* genes promote cell division, thus sustaining differential perianth expansion in the ventral portion of the limb during middle and late flower developmental stages (Fig. 3h)^[39]. In *Phalaenopsis* orchids, *PCF6*-like gene upregulation is associated with *peloric* mutants, while *CYC*-like genes remain unaffected^[41]; *CIN8* may modulate cell proliferation in developing petals^[42] and interacts with *PCF10* to regulate ovule development by modulating cell division^[43]. These data indicate the critical and diverse roles of *TCP* transcription factors in shaping floral symmetry and organ development across angiosperms.

CYC-like genes in inflorescence development

CYC2 genes in flower type differentiation in Asteraceae

Among various inflorescence architectures, pseudanthia, or 'false flowers' are multiflowered structures that resemble single flowers. The central region of the pseudanthia functions as a reproductive center while the colorful periphery attracts pollinators and protects the reproductive organs^[44]. Among various pseudanthia in flowering plants, the flower head (capitulum) of the Asteraceae (sunflower) family is the most unambiguous example. Characteristically, the radiate capitulum consists of numerous morphologically distinct flowers attached to an enlarged receptacle, with zygomorphic ray flowers forming the showy outer ring and nearly actinomorphic disc flowers occupying the center (Fig. 3a). How the capitulum evolved and how the flower types differentiated have fascinated botanists for centuries^[45]. Coincidentally in the year 2008, studies in the Asteraceae family, including *Gerbera hybrida* (Mutisieae)^[32], *Helianthus annuus* (Heliantheae)^[46], and *Senecio vulgaris* (Senecioneae)^[47] revealed that the *CYC2* clade *TCP* genes play a pivotal role in flower type differentiation. Subsequent research across various Asteraceae species, such as chrysanthemum^[33,48–52], *Anacyclus*^[53], marigold (*Tagetes erecta*)^[54], and the Asteraceae species mentioned above^[55–58], has confirmed the conserved function of *CYC2* paralogs in regulating flower type differentiation.

To date, Asteraceae possesses the highest copy numbers of *CYC2*-like members, up to six copies, originating from duplications of a single ancestral gene^[48]. These *CYC2* homologs typically express at the capitulum margin, where the ray flowers emerge, and their expression is reduced or absent in central disc flowers (Figs 3c & 4a). Within the ray flower primordia, genes such as *GhCYC2*, *RAY3*, and

CmCYC2c are ventrally expressed, correlating with the elongation of the ventral ligule (Figs 3c & 4a)^[32,33,58]. Notably, the chrysanthemum *CYC2c* influences diverse shapes of the ray flowers (flat, spoon, and tubular ray petal types) through extra expression in the dorsal domain of tubular ray flowers^[52]. *CYC2* genes have also been associated with the so-called double cultivars, where all flowers in the capitulum are ray-like. In the double or crested gerbera variety, the ray specific *GhCYC3* was notably upregulated in central flower primordia compared to the wild type indicating that it plays a major role in regulating ray identity^[55]. Similarly, the inner ray flowers in the semi-double ray chrysanthemum also show upregulation of *CYC2c* and *CYC2d*^[48].

Functional diversification of *CYC2* homologs during flower type differentiation in Asteraceae capitulum is complicated^[45,59,60]. So far, none of the transgenic lines with overexpression or RNAi of *CYC2*-like genes in Asteraceae species show full conversion of ray-to-disc or disc-to-ray^[32,48,49,55,61]. The only exception is the sunflower *cyc2c* natural mutant whose ray flowers convert to disc flowers^[62,63] or lose initiation completely^[64]. Therefore, the precise functional roles

of the *CYC2* homologs and how they diversify are worth further illustration.

CYC2 genes in different Asteraceae capitulum types

The *CYC2*-type TCP genes directly influence the presence and morphology of the ray florets, thereby contributing to the formation of different types of capitulum in the Asteraceae family. A range of capitular forms has been described in Asteraceae, including radiate (marginal ray and central disc flowers), disciform (modified marginal ray and central disc flowers), discoid (full of disc flowers), and ligulate (full of bisexual ray flowers) capitula^[45]. Dominant *CYC2* genes are crucial for ray flower development and influence the variation of capitulum types within the Asteraceae family. For instance, the radiate capitula in *Chrysanthemum sensu lato* feature large and colorful ray flowers surrounding the yellow disc flowers. In contrast, the *Ajania* lineage, characterized by disciform capitula with slightly asymmetric marginal flowers, has evolved through dysfunction in *CYC2g*—a gene analogous to *CYC2c*—due to a promoter region deletion^[61,65,66]. Specifically, a 20-nt deletion in the promoter

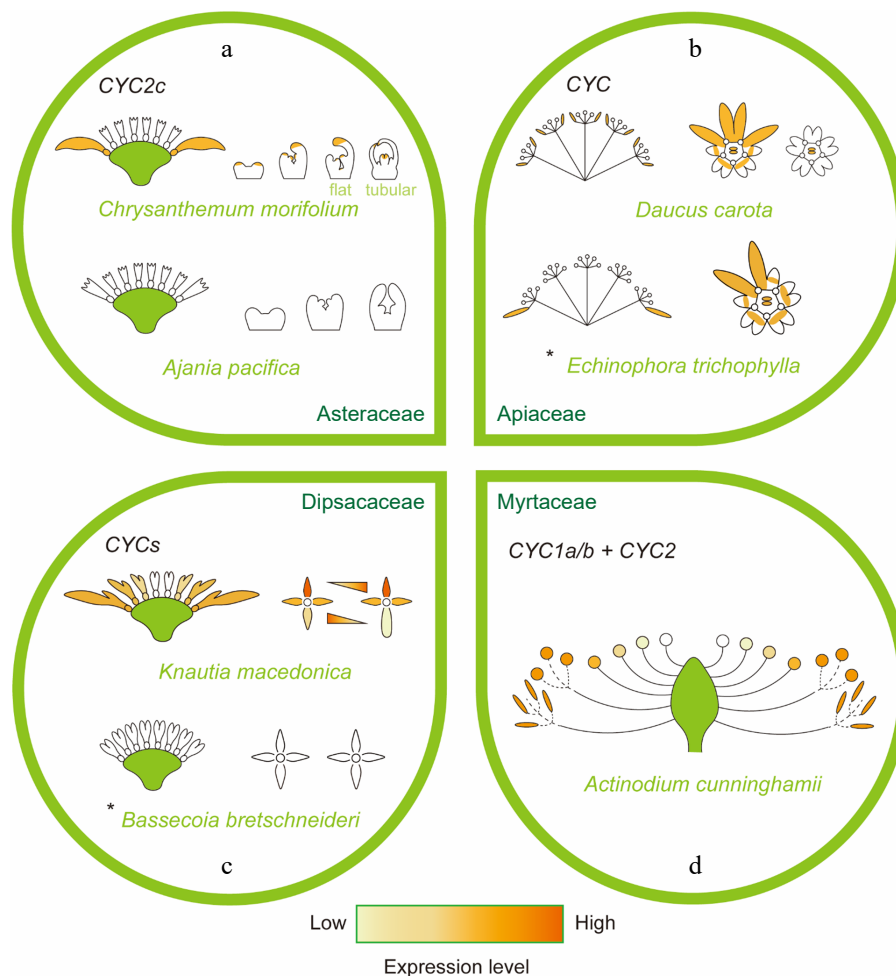


Fig. 4 Expression levels and spatial patterns of *CYC* genes in various pseudanthia structures across four plant families. (a) In Asteraceae, the expression of *CYC2c* (analogous to *CYC2g*) is associated with floral zygomorphy in *Chrysanthemum morifolium*, with stronger expression in ray flowers, while absent expression in disc flowers and the flowers of *Ajania pacifica*; meanwhile, tubular and flat ray flowers show different expression pattern of *CYC2c* in ventral petal primordia. (b) In Apiaceae, *CYC* expression contributes to floral asymmetry in *Daucus carota* and *Echinophora trichophylla**, where marginal flowers show higher expression levels at their elongated petals. (c) In Dipsacaceae, multiple *CYC* homologs regulate zygomorphy in *Knautia macedonica*, and their expression gradient level contributes to floral symmetry variation, while *Bassecoia bretscheideri* exhibits actinomorphic flowers with low *CYC2c* copies and absent *CYC* expression. (d) In Myrtaceae, the *CYC1* genes show a gradient expression from outer ray-like branches to inner flowers and are likely to control branch suppression in *Actinodium cunninghamii*. Expression intensity is in a gradient from low (white) to high (orange). * Indicates insufficient data and hypothetical interpretations.

region of the *Ajania*-type *CYC2g* gene likely suppresses its expression, resulting in disc-like marginal flowers (Fig. 4a)^[61]. Moreover, *CYC2g*, *CYC2d*, and *CYC2e*, located in tandem on the same chromosome, may act collectively to alter capitulum forms, and loss of function of *CYC2d* and *CYC2e* would shift radiate capitulum to discoid one that consists only of disc flowers in radially symmetrical and bisexual pattern^[67]. In ligulate capitulum such as dandelions (*Taraxacum mongolicum*), *CYC2g* and *CYC2c* are expressed in outer ray flowers, while *CYC2b* and *CYC2e* expression gradually decreases inward, shaping ligulate capitula with bisexual ray flowers^[48]. Therefore, *CYC2* clade genes, not all but several dominant ones, may play important roles in the formation of ray flowers and exhibit diverse expression patterns, contributing to the transition among different capitulum types within Asteraceae.

CYC/TB1-like genes in pseudanthia patterning beyond Asteraceae

Beyond the functional studies of *CYC2* clade genes in the Asteraceae family, expression analyses of *CYC/TB1*-like genes have revealed their involvement in the patterning of pseudanthia inflorescence architectures in other families, such as Apiaceae^[68], Dipsacaceae^[69,70], and Myrtaceae^[71] (Fig. 4). The Apiaceae subfamily Apioideae forms unique complex umbels that produce small umbels known as umbellets. The pseudocorolla, in diverse forms, surrounding the entire umbel or each umbellet, gives rise to either a single pseudanthium (*Echinophora trichophylla*), or multiple pseudanthia (*Daucus carota*) (Fig. 4b). *CYC2*-like genes express predominantly in peripheral flowers of the entire umbel or individual umbellet, and their expression is reduced in inner radial flowers (Fig. 4b)^[68]. In Dipsacaceae, the radiate species like *Knautia macedonica* exhibit weakly zygomorphic internal flowers that gradually transition to enhanced zygomorphic external flowers (Fig. 4c). More *CYC*-like gene copies were detected in *K. macedonica* than the discoid species like *Bassecoia bretschneideri*, hinting at a potential role of these genes in the evolution of disc- and ray-like flowers^[69]. Expression analysis reveals that *CYC* genes dynamically influence dorsoventral petal development, with certain *CYC3* paralogs contributing to floral symmetry^[70]. In Myrtaceae, *Actinodium* inflorescences display a distinct type of pseudanthium where the proximal branches mimic ray-like flowers (Fig. 4d). The *CYC1* genes show a gradient in their expression from outer ray-like branches to inner flowers and are likely to control branch suppression^[71]. The diversity of these expression patterns illustrates the convergent evolution of pseudanthia across families, driven by the recruitment of *CYC/TB1*-like genes for novel developmental roles.

Co-option of petal morphology with pigmentation and floral orientation

Floral diversity encompasses a wide range of morphological features, including floral symmetry and pigmentation patterns. Recently, an increasing number of examples indicate that *CYC*- and *CIN*-like genes have been co-opted to regulate flower color through regulatory and biosynthetic genes of the pigmentation pathways and meanwhile affecting floral orientation.

CYC2-MYB in pigmentation

Torenia fournieri (Linderniaceae) exhibits zygomorphic flowers with distinct pigmentation patterns: two white dorsal petals, two violet lateral petals, and a ventral petal with yellow spots. Su et al. found that the *CYC*-*RAD* module that is primarily exemplified in snapdragon where *AmCYC* directly activates *RADIALIS* (*RAD*) to control floral symmetry, orchestrates both petal shape and corolla pigmentation in *Torenia*^[72]. In dorsal floral primordia, the regulatory

loop of *TfCYC2* and *TfRAD1* establishes corolla asymmetry and white pigmentation. Overexpression of these genes produces white lateral and ventral petals with dorsal lobe characteristics, while *TfCYC2* downregulation or *tfrad1* mutation results in violet dorsal petals. This phenotype resembles the 'Piccolo Mix' cultivar, which lacks *TfCYC2* expression due to retrotransposon integration^[72,73]. *TfCYC2* represses the expression of a *R2R3*-MYB gene *TfMYB1*, that controls anthocyanin biosynthesis and violet pigmentation on lateral and ventral petals, resulting in the distinctive asymmetric pigmentation pattern (Fig. 5a)^[72]. However, the mechanism for yellow spot formation remains unclear.

CYC2 in nectar guide and floral orientation

In *Chirita pumila* (Gesneriaceae), *CYC2* genes regulate both the yellow nectar guide pigmentation in ventral petals and the horizontal orientation of flowers, beyond their conserved role in controlling floral symmetry^[25]. Overexpression of *CpCYC1* and *CpCYC2* produces upward-facing, dorsalized flowers without nectar guides, while double mutants show ventralized flowers with uniform yellow guides. *CpCYC1* and *CpCYC2* regulate asymmetry and inhibit flavonoid synthesis by repressing the flavonoid synthesis-related gene *CpF3'5'H* (Fig. 5a)^[25]. Similarly, in gloxinia (*Sinningia speciosa*; Gesneriaceae), a 10 bp deletion in the *CYC2* gene *SsCYC* alters floral orientation and symmetry, resulting in Darwin's *peloric* gloxinia^[74]. These findings highlight the role of *CYC2* genes in exemplifying how horizontal flower positioning enhances pollinator specificity and pollination efficiency through flower zygomorphy^[15]. Thus, the repeated emergence of zygomorphic flowers and their integrated traits, including asymmetric nectar guides and floral horizontal orientation, are driven by the recruitment of *CYC2* genes as pleiotropic regulators in angiosperms.

CYC2-CCD4a in capitulum pigmentation

CYC2-mediated floral trait integration also extends to capitulum-type inflorescences. Zhang et al. described how capitulum pigmentation patterns are affected by co-option of the carotenoid cleavage dioxygenase gene *CCD4a* into the *CYC2*-regulated flower type differentiation network^[65]. Specifically: 1) for white/pink radiate capitula, intact *CYC2g* and *CCD4a* enable ray-specific *CYC2g* to activate *CCD4a*, degrading carotenoids and leading to white ray flowers; 2) in yellow radiate capitula, *CYC2g* is ray-specific but *CCD4a* is absent from the genome, causing carotenoids accumulation in the ray flowers; 3) in yellow disciform capitula, *CYC2g* is not expressed in the margin flowers and *CCD4a* is absent or mutated in the genome, or not activated due to the dysfunctional *CYC2g*, causing minor asymmetric yellow flowers at the margin (Fig. 5a)^[65]. Thus, *CYC2* genes are integrated with pigmentation pathways to achieve morphological and color variations also at the inflorescence level.

CIN in petal pigmentation

Beyond the *CYC*-pigmentation modules, *CIN*-like TCP proteins also play key roles in regulating petal pigmentation. In *Arabidopsis*, mutants for multiple *CIN*-like TCP genes produce green petals, whereas the expression of TCP4 complements this phenotype by directly repressing chlorophyll biosynthetic genes in the distal petal regions (Fig. 5a)^[75]. A similar phenomenon was seen in different plant species, including lilies, *Kalanchoe blossfeldiana*, and *Orychophragmus violaceus*^[75]. In chrysanthemum, disruption of TCP functions leads to shorter ray ligules and the conversion of white petals into green ones, while TCP3-disrupted transgenic torenia plants exhibit fringed petal margins, altered color patterns, and reduced anthocyanin accumulation^[76]. Although green petals are less attractive to pollinators, they hold potential for ornamental breeding.

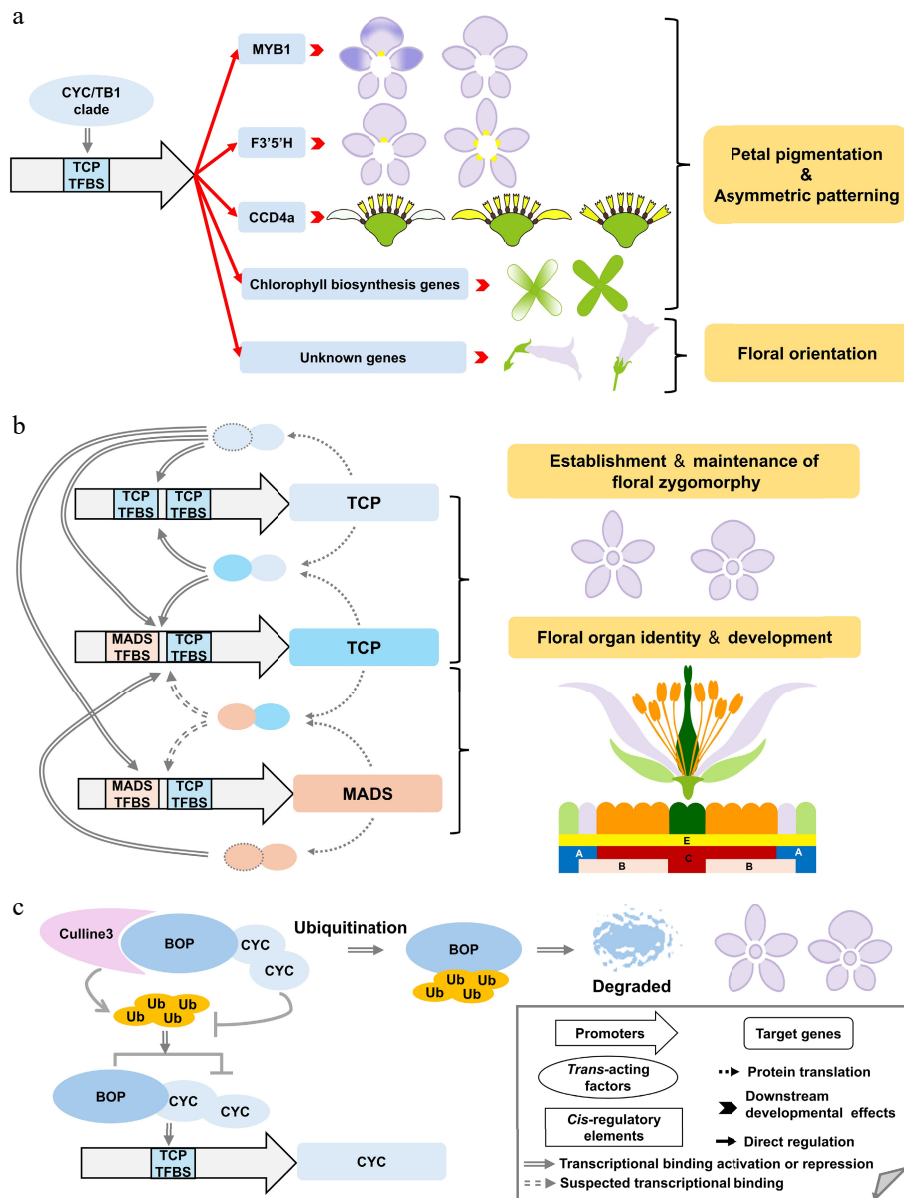


Fig. 5 Regulatory network of TCP transcription factors in flower and inflorescence development. (a) Co-option of petal morphology with pigmentation and floral orientation. The *CYC/TB1* clade regulates petal pigmentation, asymmetric patterning, and floral orientation through TCP transcription factor binding sites (TFBS). Downstream targets include *MYB1*, *F3'5'H*, *CCD4a*, and chlorophyll biosynthesis genes, which modulate floral symmetry and pigmentation patterning, as well as additional unknown factors that contribute to floral orientation. (b) Auto- and cross-regulation among TCP and MADS-box genes. TCP transcription factors regulate each other through auto- and cross-regulatory feedback loops to establish and maintain floral zygomorphy. TCPs regulate and interact with MADS-box genes contribute to floral organ identity establishment and development. (c) BOP-CYC interaction module. MIBOP self-ubiquitinates and suppresses MICYC2A self-activation, while MICYC2A impedes MIBOP ubiquitination, creating a molecular tug-of-war that fine-tunes flower symmetry. This module ensures precise spatial and temporal control of CYC expression in floral symmetry patterning.

Regulatory network of TCP transcription factors

Flower development is orchestrated by a sophisticated interplay among transcription factors. The interaction partners and regulatory networks of TCP proteins, including TCP, MADS, and MYB, as well as other factors, are essential for establishing floral dorsoventral asymmetry and regulating cell proliferation and differentiation, collectively shaping floral architecture.

Auto- and cross-regulation among TCP members

The maintenance of asymmetric expression of the *CYC2* genes is mediated through intricate auto- and cross-regulatory mechanisms

among TCP members (Fig. 5b). Evidence to direct regulatory interactions has been obtained in Gesneriaceae^[24,25] and Scrophulariaceae^[77]. For instance, in *Primulina heterotricha*, *CYC1C* and *CYC1D* form a double positive feedback loop critical for maintaining zygomorphic flowers^[24]. *Chirita pumila* exhibits a regulatory system where CpCYC1 self-activates and represses CpCYC2, ensuring stable dorsoventral asymmetry^[25]. Similarly, in monkeyflower (*Mimulus lewisii*), self-activation of *MICYC2A* is fundamental for flower symmetry^[77]. This auto- and cross-regulatory mechanism among *CYC2* genes ensures the persistent asymmetric expression needed for maintaining zygomorphy, a key innovation in angiosperm evolution.

Furthermore, CIN clade genes are also involved in the regulatory network with CYC2 genes in floral symmetry patterning. Distinct regulatory changes have been observed in *Petrocosmea* species (Gesneriaceae), where *cis*- and *trans*-regulatory variations underlie the differential expression of *CYC1C*, *CYC1D*, and *CIN1*, driving petal morphological diversity: expression level differences at the dorsal petals are driven by *cis*-regulatory modifications to *CYC1C* and *trans*-acting variations to *CYC1D*, while both regulatory types affect *CIN1* expression in all petals^[78]. In gerbera, CIN-like TCP transcription factors, GhCIN1 and GhCIN2, act as upstream regulators of *GhCYC3*, impacting the development of ray primordia ontogeny^[79]. Hence, the interplay between CYC- and CIN-like TCPs illustrates their coordinated roles in shaping flower symmetry to various degrees.

TCP proteins form homodimers and heterodimers, enhancing functional specificity. Studies in *Arabidopsis*, chrysanthemum, gerbera, and sunflower show that CYC/TB1-like proteins function in complexes with conserved interaction capacities, thus enhancing functional specificity and displaying distinct recognition affinity^[56,80]. Furthermore, genome-wide analysis for 47 terrestrial plants revealed the tendency of protein complexes formation among 535 TCP candidates, suggesting their conserved interaction networks during evolution^[81]. Altogether, these interconnected regulatory networks and TCP interaction complexes exemplify how coordinated gene expression and protein interactions drive the development and diversification of floral forms in angiosperms.

Cross-regulation with MADS-box transcription factors

MADS-box transcription factors are key candidates for functioning alongside TCP proteins to control flower morphology. These interactions form complex regulatory networks and protein assemblies essential for establishing diverse floral architectures in angiosperms (Fig. 5b). The dominant role of MADS-box B-class genes in petal identity has been linked to TCP regulation in shaping floral structures. For example, in snapdragon, *AmCYC* expression in dorsal petals (whorls 2 and 3) depends on the presence of floral organ identity B genes; in B gene mutants, *CYC* expression is restricted to whorl 3, demonstrating the reliance of *CYC* on B-class gene function for proper expression^[82]. In *C. vesicaria*, silencing *CyveCYLs* leads to petaloid sepal formation and upregulation of B-class MADS-box genes, highlighting the role of the TCP-MADS network in sepal-petal differentiation^[29]. On the other hand, the regulation of CYC2 clade genes by C and E class MADS-box genes has been widely reported in Asteraceae species. In gerbera, the E-class *GRCD5* and the C-class *GAGA1* MADS-box transcription factors regulate *GhCYC3*, with E-class genes influencing ray flower petal development and C-class genes modulating stamen formation^[79]. In sunflower, the conversion of disc to ray-like flowers in the *long petal mutant (lpm)* is associated with increased C-class *HaMADS3* expression and decreased E-class *HaMADS7/HaMADS8* levels, and *cis*-regulatory elements analyses suggesting these MADS-box genes may control *HaCYC2c* expression^[83]. Besides, in chrysanthemum, protein complex formation between ABCE-class and CYC2-like proteins has been observed, underscoring their joint role in the development of reproductive organs and petals of ray flowers^[80].

CYC/TB1-like genes and MADS-box genes share duplication patterns, which may be associated with major floral morphological transitions during the evolution of core eudicots^[9]. These duplications suggest a potential co-evolution of regulatory pathways. Parallel studies in Commelinaceae have demonstrated a coordinated involvement of TCP and MADS-box genes in the independent evolution of bilateral symmetry in angiosperms^[30]. In orchids (*Dendrobium nobile*), protein interactions between TCP and MADS-box genes have been observed, and MADS-specific binding sites were

detected in TCP gene promoters, indicating a complex regulatory mechanism underlying perianth development in monocots^[84]. The complex interplay between TCP and MADS-box genes highlights their importance in floral development and evolution.

Regulatory network with MYB factors

CYC2-like TCP transcription factors are also known to cooperate with MYB family members to determine floral dorsoventral asymmetry. In snapdragon, two CYC2 paralogs *CYC* and *DICHOTOMA (DICH)* specify dorsal identity partially through the activation of the MYB transcription factor *RAD*^[85,86]. *RAD*, in turn, suppresses the ventral identity factor *DIVARICATA (DIV)* by competing for the *DRIF (DIV-and-RAD-Interacting-Factor)* protein, ensuring precise dorsoventral asymmetry^[87]. This regulatory framework extends to the Asteraceae family. In *Senecio vulgaris*, the homologous genes *RAY3*, *SvRAD*, and *SvDIV1B* regulate floral symmetry in the capitulum^[58]. *RAY3* and *SvRAD* promote ventral petal growth, while *SvDIV1B* represses it, demonstrating evolutionary divergence that results in distinct floral architectures compared to the dorsal petal elongation observed in snapdragon^[58], highlighting spatial pattern modifications that result in diverse floral architectures across plant species.

Building on the role of TCP and MYB transcription factors in regulating floral asymmetry, their influence extends beyond symmetry determination to pathways that govern petal morphology and pigmentation, highlighting their broader impact on floral traits critical for pollination. CIN homologs in snapdragon (*CIN*) and petunia (*LANCEOLATE (LA)*) modulate cell morphogenesis in the petal epidermis. These homologs share functional similarities with R2R3 MYB factor *MIXTA*, collectively shaping petal cell structure and enhancing color intensity and visual signals that are crucial for pollinator attraction^[88–90]. These data underscore the multifaceted roles of CYC2-like TCP and MYB transcription factors, from orchestrating floral dorsoventral asymmetry to influencing petal cellular morphology and pigmentation, collectively driving the evolution of diverse floral traits for reproductive success.

BOP-CYC module: post-translational regulation

The CYC-regulated symmetry network has recently been shown to be integrated with ubiquitin-mediated post-translational mechanism. In monkeyflowers (*Mimulus*), three allelic mutants showed upregulated *MICYC2A* and *MICYC2B* expression and altered floral symmetry from zygomorphy to actinomorphy, and three independent mutations in the ortholog of *Arabidopsis BLADE-ONE-PETIOLE (BOP)* were detected in these mutants^[77]. The overlapping spatio-temporal expression pattern of *MIBOP* and *MICYC2A* at the dorsal region of the floral meristem suggests their potential direct regulation. Specifically, BOP functions as an E3 ligase adaptor, undergoing self-ubiquitination while concurrently suppressing the self-activation of *CYC2A*; conversely, *CYC2A* interferes with BOP's ubiquitination, establishing a post-translational regulatory feedback loop (Fig. 5c). The highly conserved BOP-CYC interaction module is suggested to have a widespread evolutionary influence on floral symmetry across angiosperms^[77]. This discovery highlights the pivotal role of ubiquitin-mediated post-translational regulation in the evolution and maintenance of floral symmetry, highlighting the complexity and evolutionary significance of these mechanisms in shaping floral diversity.

In summary, the regulatory network of TCP transcription factors plays a pivotal role in orchestrating flower development by integrating both transcriptional and post-translational mechanisms, as well as protein complex networks. Their coordinated action ensures the differentiation of cells into appropriate types and controls organ growth. Further investigation of these regulatory layers will provide us with an understanding of the molecular mechanisms underlying

the repeated co-option of TCP-dependent pathways in flower and inflorescence development. Such studies will advance our knowledge of floral morphogenesis and could have significant implications for horticultural and evolutionary biology.

TCP in ornamental plants

Ornamental plants, with a wide array of species, are cultivated for their aesthetic attributes, including morphology, color, and fragrance. Their beauty has captivated human senses for millennia, inspiring cultural practices and significant investments in the horticultural industry. Nowadays, ornamental plants hold substantial economic value, being integral to gardening, landscape design, and floriculture as cut flowers, which constitute a multibillion-dollar global market. The domestication, breeding, and commercial cultivation of these plants reflect an aesthetics-driven dimension of human sociocultural evolution, which has coevolved with socioeconomic shifts and the integration of scientific advances^[91].

Recent molecular studies, powered by high-throughput sequencing, have enabled genome-wide identification of TCP transcription factors across ornamental species (Supplementary Table S6). These studies have revealed their divergent expression patterns in different tissues and focus on certain developmental pathways, such as shoot branching, terpenoid indole alkaloid biosynthesis, stress responses, leaf morphology, and flower development (Supplementary Tables S1–S5). Notably, beyond CYC genes, several CIN genes exhibit functional potential in shaping flower morphology. In an orchid species *Erycina pusilla*, two CIN clade genes *EpTCP11* and *EpTCP26* are flower-development related and show relatively high expression in the dorsal labellum or tepals^[92]. In *Prunus mume* (plum blossom), CIN genes may influence double petal formation^[93], while in petunia (*P. axillaris*), PaCIN genes are linked to petal size differences between large- and small-flowered lines^[94]. Despite the availability of extensive genomic data, comprehensive functional studies of TCP genes in ornamental plants remain insufficient. Ongoing research in this area holds promise for innovations in ornamental plant breeding, enabling the combination of beauty with desirable functional traits.

Concluding remarks and future research

Flowers function as 'sensory billboards', using morphology, color, and fragrance to attract pollinators and captivate human interest^[95,96]. TCP transcription factors are integral to these visual signals, regulating floral symmetry and organ development as well as pigment biosynthesis. Floral fragrance, primarily emitted from petals and other floral tissues, may also intersect with TCP-regulated pathways, presenting a compelling area for further research^[97]. Flower development processes exhibit domino effects, where alternations in one process can lead to changes in another. Therefore, it is intriguing to explore how distinct flower traits are integrated, and possibility interlinked into the TCP network.

The evolution of floral zygomorphy is tightly linked to CYC-like TCP genes and their interplay with MADS, MYB, and other factors. They work collectively to orchestrate perianth identity, size, and shape, as well as staminode formation, contributing to morphological adaptations that enhance pollination efficiency, such as ventral petals acting as landing platforms for pollinators^[14]. The timing and regulation of organ primordia initiation by CYC genes are crucial, with CYC-expressing organs often initiating later but eventually reaching comparable sizes. Disruption of CYC function results in uniform development timing or increased primordia numbers, a phenomenon observed in Plantaginaceae, Fabaceae, Linderniaceae,

and Asteraceae species^[17,18,28,72,79,98]. Consequently, the precise mechanism of how CYC genes regulate organ primordia initiation, not only the initiation time but also the numbers of primordia, remains to be demonstrated.

Flower morphology changes involve shifts in organ arrangement, size, or pigmentation, all modulated by TCP factors in a coordinated manner. Gene duplication has driven TCP diversification, enhancing adaptability and evolutionary complexity, though it also introduces functional redundancy that complicates genetic analysis^[11]. Future research employing multi-target CRISPR approaches could unravel these redundancies, advancing our understanding of TCP functions^[99]. Ultimately, TCP transcription factors hold promise for molecular breeding, enabling the development of ornamental plants with optimized aesthetics and fitness.

Author contributions

The authors confirm contribution to the paper as follows: study design: Zhao Y; figures preparation: Hu X, Wang Y; draft manuscript writing: Hu X; writing and finalizing manuscript: Hu X, Wang Y, Zhao Y. All authors reviewed the results and approved the final version of the manuscript.

Data availability

The data supporting the findings of this study are available within the supplementary materials.

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Conflict of interest

The authors declare that they have no conflict of interest.

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