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Recent Progress in the Molecular Regulation of Floral Shape and Structure in Orchids

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Abstract

Orchid flowers exhibit remarkable morphological diversity, arising from the interplay between a conserved MADS-box regulatory framework and lineage-specific developmental innovations. This review examines recent molecular advances in orchid floral organ identity, zygomorphy, labellum morphogenesis, and developmental plasticity. Functional perturbation and protein-protein interaction studies have refined classical floral identity models by providing experimental support for higher-order MADS-box protein complexes involving B-class, *AGL6*, and SEPALLATA proteins, while the roles of C- and D-class genes in reproductive organ development and canonical A-class genes in floral organ identity remain incompletely resolved. We distinguish whole-flower zygomorphy from labellum identity, highlighting MADS-box complexes as key determinants of perianth organ identity, particularly labellum specification, while the molecular basis of orchid floral symmetry remains less clearly understood. Additional regulatory factors, including TCP, MYB, WOX, and NAC family members, have been implicated in regional growth, cell differentiation, and floral organ morphogenesis, although their hierarchical relationships with MADS-box regulators remain incompletely understood. Hormonal, epigenetic, and small RNA-mediated regulation may provide additional layers of developmental control and contribute to floral morphological plasticity. Despite these advances, the molecular links between early floral organ identity specification and subsequent morphogenesis remain incompletely understood. A major challenge is to determine how early identity regulators establish spatially restricted patterns of cell proliferation, expansion, and differentiation that ultimately generate the complex three-dimensional architecture of orchid flowers.

Keywords

Orchidaceae; Floral Organ; Floral Zygomorphy; MADS-Box

1. Introduction

Orchidaceae exhibit exceptional floral diversity, typically comprising three outer and three inner tepals (the median differentiating into the labellum) and a fused gynostemium [1]. The classical ABCDE model established that floral organ identity is

specified by MIKC-type MADS-box transcription factors, with SEPALLATA proteins providing essential E-class activity [2][3]. Orchids retain this combinatorial logic but feature extensive duplication and diversification, giving rise to the 'Orchid Code' model [4], 'Homeotic Orchid Tepal' (HOT) model [5] and 'Perianth code' (P code) model[6]. In *Dendrobium*, some cell populations that lip-specialized cells, vascular cells and pigment cells could drive tepal morphology [7]. In *Cymbidium ensifolium*, *CeLFY* activates the promoters of *CeAP1s*, promoting sepal and petal proliferation [8]. Previous research indicated that the evolution of 3D flower shapes in orchids can be strongly influenced by phylogenetic constraint and conservatism while having no significant influence on species diversification [9]. This review addresses floral organ identity, zygomorphy and labellum morphogenesis, and floral shape plasticity.

2. Core Molecular Models of Floral Organ Identity Specification in Orchids

2.1. Class B MADS-Box Genes and Updates to the "Orchid Code"

B-class activity is central to the differentiation of the two lateral petals and the labellum from the outer tepals. Early studies in *Dendrobium* and *Oncidium* identified multiple *AP3/DEF*-like and *PI/GLO*-like genes with overlapping but distinct organ expression [10][11]. Phylogenetic and expression analyses subsequently showed that orchid *AP3/DEF*-like genes fall into duplicated clades with different expression strengths in sepals, petals, and the labellum. This pattern formed the basis of the Orchid Code, in which combinatorial expression and dosage of duplicated B-class paralogs contribute to organ-specific perianth identities [12] [13].

The P-code model added functional and biochemical resolution to this framework. In *Oncidium* and *Phalaenopsis*[6] defined the SP complex associated with sepal/petal identity and an L complex associated with labellum identity. Each complex contains a *PI*-like partner together with a distinct *AP3*-like and *AGL6*-like protein. In previous study, perturbing the relevant genes in orchids changed perianth identity, and reciprocal expression shifts in peloric or BigLip material supported the organ-specific assignments [14]. Single silencing of *PaSEP1* or *PaSEP3* produced weak effects, whereas combined silencing with *OAGL6-1* or *OAGL6-2* generated severe, additive transformations of sepals/petals or the labellum toward leaf-like organs [15]. Moreover, in *Cymbidium goeringii* and *Rhynchostylis retusa*, organ-specific expression and interaction patterns of B, *AGL6*, and *SEP* homologs are consistent with differentiated perianth complexes [16][17]. In *Cymbidium ensifolium*, comparisons among wild type, lip-like sepal, lip-like petal, and peloric material connected *CeAP3-3/CeAP3-4*, *CeAGL6-2*, and *CeSEP2* with labellum fate [18].

2.2. Class C/D Genes and Regulation of Reproductive Organ Development

C- and D-class genes regulate the reproductive region of orchid flowers, including

the gynostemium, ovules, and floral meristem. Early analyses of *Dendrobium crumenatum* and *Oncidium* homologs established organ-biased expression and showed that orchid C/D proteins can alter floral development when expressed in *Arabidopsis* [10][19]. In *Dendrobium 'Chao Praya Smile'*, *DOAG1* is a C-class *AGAMOUS*-like gene, whereas *DOAG2* is D-class. Artificial-microRNA knockdown in *Dendrobium* showed that both genes contribute to reproductive organ identity [20]. In a multi-tepal *C. ensifolium* variety, additional sepals and petals coincided with gynostemium loss. *CeLFY* activated *CeAP1* promoters, whereas structural variation in *CeAG* promoters weakened *CeLFY* binding and reporter activation; transgenic assays supported functions of the candidate genes in floral organ development [8].

2.3. Pan-Regulatory Functions of Class E Genes

SEPALLATA proteins provide E-class activity by participating in multiple floral homeotic complexes. In *Arabidopsis*, loss of *SEP* function compromises B- and C-dependent organ identities, and MADS complexes containing SEP proteins can reprogram vegetative tissue toward floral fates [2][3]. In Orchid, four *SEP*-like genes in *Phalaenopsis* show overlapping expression but distinct evolutionary histories and phenotypic effects; silencing *PeSEP2* or *PeSEP3* altered floral programs and reduced expression of several B-class genes[21]. Moreover, *AP1/AGL9*-like genes, including *SEP*- and *AGL6*-related members, produced different effects in *Arabidopsis* and displayed non-equivalent expression patterns [22]. More recently, four *C. sinense SEP* paralogs showed different expression, localization, interaction, and heterologous overexpression effects, supporting divergence while leaving their native requirements unresolved [23]. Furthermore, genome association linked promoter SNPs in *CsSEP4* to gynostemium variants in *C. sinense* [24].

2.4. Functional Evolution and Controversy of Class A Genes

Orchid *AP1/FUL*-lineage genes do not consistently show an outer-whorl expression domain, and orthology alone does not establish an *Arabidopsis*-like A function.[25]. *DOAP1* promoted flowering when expressed in *Arabidopsis* and was associated with reproductive development in *Dendrobium* [26]. In *C. sinense*, multi-omics, hormone treatments, *Arabidopsis* transformation, and transient protoplast expression connected *CsAP1* with floral bud activation and hormone-responsive gene expression [27]. Taken together, orchid *AP1/FUL*-lineage genes are best viewed as evolutionarily flexible regulators.

3. Molecular Regulatory Mechanisms of Floral Morphogenesis in Orchids

3.1. Regulation of Floral Zygomorphy (Floral Asymmetry)

The best-resolved genetic framework for floral zygomorphy comes from core eudicots. In *Antirrhinum*, dorsal CYCLOIDEA-family TCP factors establish dorsal

identity and activate RADIALIS, while DIVARICATA and DRIF-related MYB proteins participate in ventral and lateral differentiation through antagonistic interactions [28][29][30]. This network provides a comparative model, not a default mechanism for every bilateral flower.

Current orchid evidence does not yet justify calling a *CYC*-like gene the master regulator of the dorsoventral axis. In *D. nobile*, 23 TCP genes showed stage- and organ-specific expression; putative MADS-binding motifs were present in many promoters, and selected TCP proteins interacted with one another or with a MADS protein [31]. A predicted motif is not evidence of in vivo binding, and a protein interaction does not establish a dorsoventral function. Native loss-of-function or allele evidence linking an orchid CYC-like factor to peloria remains lacking. The orchid MYB components are better supported biochemically than developmentally. Orchid DIV-, RAD-, and DRIF-like proteins retain characteristic interaction capacities, suggesting that parts of the eudicot network are evolutionarily available [32]. Their spatial functions in orchid meristems, however, have not been demonstrated by native perturbation. Pan-orchid transcriptomics has nominated additional ALOG, bZIP, and HD-ZIP candidates associated with complex perianth traits[33].

Peloric Cymbidium provides a different perspective. Transcriptome-wide comparison of normal and peloric C. sinense linked altered perianth symmetry with shifts in B-class and *AGL6* gene expression, supporting a homeotic explanation for conversion between labellum and petal identities [34]. The P-code experiments similarly show that changing *AP3/AGL6* complex activity can generate petal-to-lip or lip-to-petal transformations [6][14]. The distinction is also illustrated by *PaWOX3* and *PaWOX3B*. Silencing either or both genes in otherwise normal Phalaenopsis did not transform floral symmetry. Their contribution became evident when *PaWOX3* or *PaWOX3B* was co-silenced with *OAGL6-2*: the resulting BigLip organs lost their local bilateral symmetry[35].

3.2. Regulation of Labellum Morphology

The labellum is both an organ identity and a three-dimensional structure. ATAC-seq and RNA-seq comparisons between a lip-like petal and the labellum in *Phalaenopsis* identified *PeNAC67*, *PeKAN2*, and *PeSCL23*. Protein-interaction and stability assays indicated that these factors interact with B-class proteins, particularly *PeMADS3*, and the authors proposed competitive assemblies that shift petal-like tissue toward petal or lip differentiation [36]. YABBY and DROOPING LEAF-like genes are plausible polarity and lamina-growth regulators, but the orchid evidence is mainly comparative. A genome-wide survey in three *Dendrobium* species identified YABBY paralogs and organ- or stage-biased expression in *D. chrysotoxum*; it did not demonstrate that a specific member controls labellum size or margins [37].

In some recent studies, the *D. devonianum* single-cell atlas identified epidermal

trajectories and candidate networks associated with fringed labellum margins, while the *Phalaenopsis* spatial atlas provides complementary organ-level coordinates [38][39]. Furthermore, three-dimensional shape requires regional rather than uniform growth. Comparative cytology and transcriptomics across *Dendrobium Section Spatulata* associated sepal curvature with differences in cell size, cell number, and candidate growth pathways, but did not test a causal regulator[40].

4. Regulation of Floral Shape in Orchids

Floral plasticity is the capacity of a genotype to produce different phenotypes across environments or developmental conditions. Hormones clearly regulate orchid reproductive development, but their stage-specific effects must be respected. In C. sinense, integrated transcriptomic, proteomic, and metabolomic analysis identified GA and ABA as opposing hubs during floral bud dormancy and activation. Exogenous GA accelerated bud elongation, whereas ABA prolonged dormancy; *CsAP1* responded to these treatments and showed flowering-related activity in heterologous and transient assays [27]. During *Phalaenopsis* opening, hormone profiles correlate with the transition to cell expansion, but causal contributions of individual hormones remain to be tested at matched stages [41].

Chromatin state may reinforce organ-specific transcription. In *Phalaenopsis*, *PeMADS4* showed labellum/column-enriched expression together with increased *H3K9K14* acetylation in a defined genomic region, and promoter constructs revealed sequence-dependent activity [42]. The association is consistent with coordinated cis-regulatory and chromatin control, but it does not identify the responsible acetyltransferase. By contrast, the *C. sinense CsSEP4* study resolved a fixed cis-regulatory mechanism: promoter *SNPs* disrupted *CsbZIP26* binding and activation [24].

Small RNAs provide another possible regulatory layer. Integrated mRNA-miRNA analysis of a multi-tepal C. goeringii mutant identified candidate miRNA-target pairs associated with floral patterning, including predicted links to TCP and GRF regulators[43]. Culture conditions can induce abnormal orchid flowers, yet differential expression should not be mistaken for an environmental mechanism. Comparison of normal and abnormal in vitro C. nanulum flowers revealed changes in hormone signaling and floral-development candidates, including MADS-box genes [44]. Genome and atlas resources can make these tests more precise. The C. ensifolium and C. sinense genomes support allele-aware analysis; the Phalaenopsis spatial atlas and Dendrobium single-cell trajectories identify the cell types in which a plastic response should be measured; and pan-orchid transcriptomics provides cross-lineage candidates[45][46][38][39][33]. These datasets are most informative when coupled to perturbation rather than used to infer direct edges from co-expression alone.

5. Conclusion and Open Questions

Research on orchid floral development has progressed from expression-based models to experimentally testable complex models, identifying key regulatory nodes, yet a continuous mechanistic pathway from meristems to mature three-dimensional form remains unresolved. Key open questions include how organ identity translates into regional growth programs, the upstream molecular basis of floral symmetry and phenotypic plasticity, and the allele-level resolution of horticultural variations. Furthermore, expanding taxonomic sampling and integrating multidimensional functional tools are essential. Strictly defining evidence levels will ultimately transform an expanding catalog of candidate genes into mechanistic explanations for orchid morphological diversity.

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