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Evolution of floral symmetry: a state of the art

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Abstract

The genetic determinants of the organisation and variation of the flower, a striking feature of the angiosperms, are only beginning to be deciphered. Floral symmetry has recurrently evolved among angiosperms, zygomorphy (monosymmetry) being a key innovation due to its role in the plant-pollination interaction. As such, it represents a case study for evo-devo. Phylogenetic comparative studies conducted in two eudicot clades, the Ranunculales and the Asteridae *sensu* APGII, have shown that the evolution of this trait is dependent upon the architectural context of the flower. Genetic and developmental bases of zygomorphy have been investigated in several unrelated model species. In all these species, zygomorphy appears to be controlled, at least partially, by genes belonging to the TCP gene family of transcription factors and named *CYC*-like genes. Exploring the molecular bases of zygomorphy in non-model species spanning the diversity of angiosperms, but also the developmental processes involved, are now essential to understand the evolution of floral symmetry. ***To cite this article: F. Jabbour et al., C. R. Biologies 332 (2009).***

Résumé

Évolution de la symétrie florale : une esquisse des connaissances actuelles. La symétrie de la fleur a subi des modifications au cours de l'évolution des angiospermes, et la zygomorphie (ou symétrie bilatérale) est considérée comme une innovation clé. Du fait de l'importance des processus de développement pour son élaboration et des questions soulevées par son homoplasie, la symétrie florale est devenue un modèle en evo-devo. Des analyses phylogénétiques comparatives menées dans deux clades d'eudicotylédones, les Ranunculales et les Asteridae *sensu* APGII, ont montré que l'évolution de ce trait était dépendante du plan d'organisation de la fleur. Chez différentes espèces modèles, le contrôle génétique de la zygomorphie ainsi que sa mise en place durant le développement sont en partie contrôlés par des gènes appartenant à la famille des gènes *CYC*-like, codant pour des facteurs de transcription. Décrypter les bases moléculaires de la zygomorphie chez des espèces non modèles, représentatives de la diversité des angiospermes, mais aussi les processus ontogéniques impliqués dans sa mise en place, sont deux aspects complémentaires essentiels pour la compréhension de l'évolution de la symétrie florale. ***Pour citer cet article : F. Jabbour et al., C. R. Biologies 332 (2009).***

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1. Introduction

The origin of phenotypic novelties is a central question for evolutionary biologists. For understanding how genomic changes can give rise to innovations at more integrative levels, it is mandatory to decipher the mechanisms underlying embryonic development. Evolutionary developmental biology or evo-devo addresses this question by using the knowledge about genes controlling development in model organisms, and comparing developmental processes and their molecular bases in different organisms in a phylogenetic framework [1]. Homology can be assessed and distinguished from homoplasy (parallel or convergent evolution) only by comparing characters in a phylogenetic context. The possibility to investigate the developmental and molecular bases of morphological structures led to redefine homology as a hierarchical concept dependent upon a phylogenetic framework [2], of which consistency at various levels (activator genes, target genes, regulatory networks, developmental processes, morphological structures) can be investigated. Consistency, or lack of consistency, of homology at different scales of complexity may help deciphering the relative part of selection and constraints in the evolution of morphological structures.

In animals, the concept of body plan has contributed to evolutionary analyses of morphological innovations like for instance, analyses of molecular evolution of *Hox* genes as related with segment formation in Arthropods [3]. It has pinpointed the role of the developmental genetic toolkit in determining the identity, number and pattern of body parts in animals. Most of the toolkit genes consist of transcription factor genes and genes involved in signalling pathways, *i.e.*, genes modifying the expression of other genes. Their functional consequences and further phenotypic impact are highly correlated with their spatial and temporal pattern of expression. In plants, the concept of body plan has been largely ignored until the late 1990s, even if the vascular plants have long been hypothesized to have evolved from a simple body plan that has diversified into the large array of architectures seen today. The study of the molecular and developmental bases of specific traits has long been restricted to a few model species (*e.g. Arabidopsis thaliana*, Brassicaceae, *Antirrhinum majus* or snapdragon, Plantaginaceae *sensu* [4], *Oryza sativa* or rice, Poaceae), most of which being derived angiosperms. With the increasing influence of evo-devo as an integrative discipline, there is now a trend towards extending the analyses to a broader taxonomic sampling and larger array of traits [5,6].

Seminal evo-devo studies in plants have been dedicated to one of the most remarkable innovation of angiosperms, the flower that may have played a major role in their evolutionary success (more than 235,000 extant species [7]). Considerable work has been devoted to unravelling determinants of the identity of floral pieces, namely sepals, petals, stamens and carpels. Based on mutant studies in the model species *An. majus* and *Ar. thaliana*, the ABC model was elaborated [8–10]. The A function determines sepal identity, A + B function, petal identity, B + C function, stamen identity and C function, carpel identity. This model was recently complexified by the discovery of the D function involved in ovule development, and the E function that interacts with the A, B and C functions [11]. Interestingly, all but one of the genes specifying the organ identity belong to a single family of transcription factors, the MADS box genes of MIKC type [12].

Although the genetic determinants of the basic floral ground-plan are now well established [13–15], the molecular bases underlying the large variation in flower architecture (shape, number, colour and synorganization of floral parts) (see Fig. 1) are far from being deciphered. Floral symmetry participates in the attractiveness and beauty of the flowers to the human eye. It is also an integrative architectural trait that account for the astonishing diversity of flower form. Two main types of symmetry are recognized, actinomorphy (polysymmetry, *i.e.*, radial symmetry) and zygomorphy (monosymmetry, *i.e.*, bilateral symmetry). Zygomorphic flowers appear relatively late in the fossil record (late Cretaceous, *ca*. 70 mya) compared to the accepted period for angiosperm origin (early Cretaceous, *ca*. 150 mya) [16–18]. Actinomorphy is considered as the ancestral state for angiosperms, and basal angiosperms mainly have actinomorphic flowers [19]. Zygomorphy evolved several times independently from actinomorphy throughout the angiosperms with multiple reversals towards actinomorphy [20,21]. Changes in floral symmetry may result in changes in efficient pollinator range, which in turn can set up sexual barriers leading to speciation [17]. Accordingly, as a derived architectural trait generally associated with lineage di-