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The Evolution of Plant Development: Past, Present and Future

PREFACE

Evo–Devo (evolutionary–developmental) studies aim to explain, at a molecular level, how developmental processes evolved. Such explanations may account for the big leaps that evolution has taken, often correlating with the origins of major new clades of organisms. In addition, evo–devo comparisons may explain present-day biodiversity, by characterizing the different routes that molecular evolution has followed in related lineages.

In recognition of the growing importance of plant evo–devo, a session devoted to this subject was included in the 15th Congress of the Federation of European Societies of Plant Biology (FESPB) held in Lyon, France in July 2006. The FESPB Evo–Devo Session was sponsored by Annals of Botany, as were two plenary lectures at the Congress that also focussed on the subjects of evo–devo and biodiversity. Accordingly, this ‘Highlight’ contains articles by authors who contributed to this FESPB Congress.

Plant evo–devo was initially made possible by advances in developmental genetics of model plants such as *Arabidopsis thaliana*, and in molecular phylogenetics. Our understanding of plant developmental genetics has been increasing at a steady rate since the early 1990s, while robust molecular phylogenies of the land plants have been available since around 2000, and are continually being refined to give improved taxonomic resolution (e.g. Stevens, 2001 onwards). The evo–devo approach to the study of macro-evolutionary events, such as the origin of major morphological novelties, usually begins with thoroughly investigated examples of developmental regulation in one or more model organisms. To study the origin of such developmental novelties, it is necessary to map their occurrence onto the phylogenetic tree of extant organisms, and to select species for study whose lineages diverged before and after the developmental changes of interest. Developmental innovations in land plants that can be studied in this way include the origins of and modifications to: vascular tissues, roots, microphylls, megaphylls, heterospores, pollen, ovules/seeds and the flower. This last novelty has perplexed evolutionary biologists ever since Charles Darwin, in a letter to Sir Joseph Hooker the then director of the Royal Botanic Gardens, Kew, described the origin of the flowering plants as an ‘Abominable Mystery’.

The origin of the flower is a particularly difficult question to address, mainly due to the lack of a close out-group to the flowering plants (angiosperms) and a poor fossil record. Molecular phylogenetic studies indicate that the extant gymnosperms, the closest living relatives of the angiosperms, form a monophyletic group that diverged from the angiosperm lineage some 300 million years ago (MYA), long before the probable origin of the flower, which is represented in the fossil record from around 130 MYA (Sun *et al.*, 2002). The question of flower origin is addressed in the present ‘Highlight’ by Theissen and Melzer (2007). They discuss the history of the genetic ABC and ABCDE Models for the specification of floral organs in model plants, and their extension to the more biochemically based Floral Quartet Model. They then describe the importance of these genetic and molecular models to evolutionary scenarios that seek to explain the origin of the flower. Theissen and Melzer point out a possible change in the biochemical behaviour of the floral MADS-box transcription factors involved in the Floral Quartet Model. These factors appear to act as quarternary complexes in model flowering plants, whereas orthologous proteins from gymnosperms seem capable only of forming binary complexes. Thus, a change in higher-level complex formation, possibly associated with the origin of E-function MADS-box transcription factors, may have been a key molecular event in the origin of the flower. Theissen and Melzer also review the literature on modifications to the whorl-specific expression of MADS-box floral transcription factors that may explain some of the diversification in floral development that has occurred since the origin of the angiosperms.

By contrast to the distant relationship between the living angiosperms and gymnosperms, molecular analyses within the flowering plant clade indicate a more even coverage of the phylogenetic tree by living groups. This is good news for evo–devo researchers who, as a consequence, can use the angiosperm tree to select species for study whose lineages diverged just before and after important evolutionary innovations. Perhaps one of the most significant modifications to flower architecture occurred at the base of the core eudicots: an enormous clade that contains the rosids, asterids and Caryophyllales, in addition to a number of smaller groups. At the base of the core eudicots, floral structure seems to have become stabilized in a whorled arrangement of organs. A clear differentiation in perianth organs is frequently present in core eudicots, in which first and second whorl organs show distinct sepal and petal morphologies, respectively. Ronse de Craene (2007) examines the evolutionary origin of petals in the core eudicots. By carefully surveying perianth structure throughout the eudicots, with particular emphasis on basal lineages of core eudicots, he concludes that core eudicot petals were originally derived from bract-like organs that invaded the flower. According to this view, stamen-derived petals, present in some core eudicots groups, would represent a secondarily derived feature, rather than the plesiomorphic state previously believed.

The flowers of some angiosperm species are monosymmetric (also termed zygomorphic, or bilaterally symmetric), possessing only one plane of symmetry, while others are polysymmetric (also termed actinomorphic). The evolution of monosymmetry from polysymmetry appears to have occurred many times independently within the flowering plants, in many cases as a result of co-evolution with specific pollination vectors. In this regard, Damerval and Nadot (2007) map floral symmetry and other floral traits onto the phylogenetic tree of the Ranunculales, which is sister to all other eudicots. These authors then use numerical techniques to examine the correlation between different character states in relation to floral symmetry. They conclude that none of several instances of restriction in floral symmetry that occurred independently in the Ranunculales depended on any particular pre-existing merism, or floral organ number. However, monosymmetry was only able to evolve in groups of Ranunculales in which the floral ground plan was already fixed, with defined numbers and positions of floral organs in each whorl. Mechanisms responsible for generating monosymmetric flowers are currently best understood in *Antirrhinum* and related taxa from the asterid clade of the core eudicots, in which TCP and MYB transcription factors are known to play important roles. Interestingly, homologues of TCP genes are involved in the control of floral symmetry in *Lotus*, from the distantly related rosid clade, while Damerval *et al.* (2007) have published evidence that similar genes are also involved in this process in the Ranunculales. Thus, homologous sets of genes seem to be responsible, in widely diverged taxa, for similar, though non-homologous, floral symmetry phenotypes.

For the moment, the implication of TCP genes in floral symmetry in Ranunculales relies mainly on comparisons of gene expression data with results obtained from model taxa such as *Antirrhinum*. However, this and other functional questions in non-model plants might soon be resolved directly by the use of virus-induced gene silencing (VIGS). This technique enables gene knockouts to be performed in numerous plant species for which no convenient genetic transformation protocol exists, and also has the advantage of yielding rapid results, typically requiring only a few days after viral infection for effects on target gene expression to become apparent. Both of these features are particularly important for evo–devo studies, as many groups of plants that occupy key phylogenetic positions have long life-cycles, or are not transformable by current methods. In this ‘Highlight’, Wege *et al.* (2007) demonstrate the effectiveness of a Tobacco Rattle Virus (TRV)-based VIGS vector system (Liu *et al.*, 2002) on *Eschscholzia californica* (Ranunculales), which may become a useful model basal eudicot for evo–devo studies. TRV seems to have a particularly broad host range, and the TRV–VIGS system has now been shown to be effective for gene knockouts in a number of non-model species, including *Papaver* (Hileman *et al.*, 2005) and *Aquilegia* (Gould and Kramer, 2007), also from the Ranunculales.

Another method for investigating the function of genes from non-model plants is the transformation of mutants of model plants with gene orthologues taken from the non-model species of interest. This technique has been used by Fourquin *et al.* (2007) to investigate conservation of protein function between orthologues of the transcription factor CRABS CLAW (CRC), which is involved in the development of the carpel, the female reproductive organ that encloses the ovules in angiosperms. Fourquin *et al.* conclude the *CRC* orthologues from *Arabidopsis* and *Amborella*, representing a very basal angiosperm lineage, to have partially conserved a common activity in the control of the establishment of abaxial–adaxial (outside–inside) polarity in the carpel since the radiation of the extant angiosperms, some 160 MYA. These authors further conclude that novel functions, adopted by *CRC* orthologues in the core eudicots to control nectary development, and by *CRC* orthologues in grasses to control carpel identity and leaf development, may have come about by evolutionary changes other than to the coding sequences of the genes concerned. The approach of swapping genes, or their coding sequences, between taxa is open to some criticism. The complementation of a mutation in one species using an orthologous gene from another may occur, even in cases where the functions of the two orthologues have diverged, while a lack of complementation in such experiments is not necessarily evidence of a change in the roles of orthologous genes, rather than just of genetic drift. Despite these interpretive challenges, however, such heterologous experiments can help to answer several precise questions in evolutionary and developmental biology.

Flowers, whose evolution has been investigated in the articles referred to above, develop during the reproductive phase of a plant’s life or growing season. The change from vegetative to reproductive phases causes the stem apical meristem to become an inflorescence meristem, and to generate floral meristems, rather than leaves. The structure of the inflorescence produced depends in part on the balance of developmental regulators that control the generation of floral meristems. Accordingly, the present ‘Highlight’ contains a review by Benlloch *et al.* (2007) that explains how subtle differences in the expression patterns or activities of three developmental regulators, LEAFY, TERMINAL FLOWER and APETALA1, can modify inflorescence structure to produce simple or double racemes, cymes, panicles and other forms. This case illustrates a very important point for evo–devo studies. Dramatic morphological differences can be generated by quite subtle developmental changes, which are in turn based on even more subtle modifications to regulatory relationships such as those between transcription factors and their target genes. To understand the evolution of developmental processes better, plant evo–devo research will have to go beyond the patterns of duplication and loss that have occurred in gene families encoding developmental regulators. This will involve characterizing and comparing the network of biochemical and biophysical interactions that control development in diverse plant groups.

The contents of this ‘Highlight’ illustrate many of the important issues for plant evo–devo, although there are others not covered here. Of particular importance to the future will be access to whole-genome sequence data from a wider taxonomic range of plants than is currently available, and the development of new molecular genetic models from across the land plants. For the moment, the moss *Physcomitrella patens* forms the only satisfactory non-flowering, developmental–genetic model plant. As the plant evo–devo field develops, its exponents will need to adapt new methods for the analysis of entire systems, coupled to mathematical modelling, rather than continue to rely on methods adapted only to the analysis of a few selected genes or interacting molecules.

Plant evo–devo should avoid becoming a self-serving discipline in which researchers erect a series of opposed and untestable hypotheses. Instead, testable evolutionary scenarios should be conceived that, where possible, take account of genetic, anatomical, biochemical, ecological and paleological data. Lastly, evo–devo should not concern itself only with the past, but should also engage with the present and indeed with the future. The study of micro-evolutionary changes, which were responsible for the domestication of the crop plants on which human nutrition depends, demonstrates just how important the evolutionary context is to both fundamental and applied research (see Doebley *et al.*, 2006). Thus, through the development of techniques to model transcriptional control interactions in diverse species, an offshoot of evo–devo research could actually lead to way to the rational design of new crop plants for the 21st Century (Theissen, 2000, 2001).

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