

Return of the snapdragon

The belated arrival of the *Antirrhinum* genome sequence brings this classic model plant into the genomic age and opens up increased avenues for plant biology research.

Discoveries made in experimental models provide insight into the mechanisms working in other organisms. The models developed by the plant communities include *Arabidopsis*, *Physcomitrella patens*, *Antirrhinum* and petunia. The release of the *Arabidopsis* genome in 2000 granted this, already popular, experimental model a further advantage over other equally important species. In this issue of *Nature Plants*, Li et al. report the genome of the, much overlooked, *Antirrhinum majus* (snapdragon), removing its previous weaknesses and reinforcing its status as a research model.

The *Antirrhinum* genus used to be a classic model for flowering plants before the epoch of *Arabidopsis*. In fact, its history of being a research workhorse is very long, tracing back to the earliest inheritance studies of Darwin and Mendel in the nineteenth century. In the twentieth century, Erwin Baur established *Antirrhinum* as a model because it had specific advantages that made it a tractable experimental subject¹.

Native to the western Mediterranean, *Antirrhinum* has a very high level of natural phenotypic diversity, as recognized by the earliest geneticists. For example, the 18 species that make up the *Antirrhinum* genus exhibit a very wide range of interspecific variations in flower colour and pattern, fragrance, flowering time, and much else. Genetic instability widely exists in the *Antirrhinum* genus, constantly generating new variations; an intriguing phenomenon in itself. Their relatively small size and hardiness make it easy to cultivate and keep *Antirrhinum* on a large scale. These advantages, together with a small genome (only four times that of *Arabidopsis*), a short generation time of about three months, and the ease of performing self- and cross-pollination, made it particularly attractive for early experimental geneticists.

Two main collections of *Antirrhinum* mutants were established early on. One consists of more than 450 mutants, originally generated and collected by Baur, now available from the IPK-Gatersleben in Germany. The other is comprised of more than 300 mutants, generated by Rosemary Carpenter and colleagues at the John Innes

Center in the UK. Besides these research materials, standard molecular biological tools, such as genomic libraries and yeast two-hybrid libraries, as well as genetic tools such as linkage maps, have also been developed. However, genetic manipulations of *Antirrhinum* proved more difficult than in *Arabidopsis*.

The pioneering use of *Antirrhinum* by Baur and colleagues in the first several decades of the twentieth century led to a series of discoveries in plant genetics, such as the first confirmation of genetic linkage, cytoplasmic inheritance and genes responsible for flower colour and morphology². In the middle of the twentieth century, work on unstable mutations of *Antirrhinum* isolated the first autonomous transposon from a plant, Tam1³. Subsequently, more transposons were found and used to facilitate gene isolation through transposon-tagging systems.

The most important contribution of *Antirrhinum* research was in the area of developmental genetics. The first plant MADS-box gene, *DEFICIENS* (the orthologue of the *Arabidopsis* *APETALA3*), was cloned in *Antirrhinum*⁴, as well as the floral-organ identity gene *GLOBOSA*, and floral-meristem identity genes *LEAFY* and *APETALA1*. These homeotic mutants (together with related mutations in *Arabidopsis*), laid the foundations for the ABC model of flower patterning⁵. Also, zygomorphy has been intensively examined using *Antirrhinum*, and transcription factors such as *CYCLOIDEA* and *RADIALIS* were found to control its asymmetric growth⁶. The founding member of the *S-LOCUS F-BOX* genes controlling self-incompatibility was also found in *Antirrhinum*⁷. Moreover, *Antirrhinum* research has shed light on leaf development, anthocyanin biosynthesis, pigmentation and scent emission, and how these factors affect pollinator attraction, speciation and adaptive evolution.

Antirrhinum continues to attract researchers today, especially for investigations that are not possible with other model systems, such as perennial habit and flower colour evolution. It can be expected that the new, near-complete chromosome-scale genome of *A. majus* presented by Li et al. will make experiments with this model plant far more convenient.

For example, a recent work reported in *Science* using this reference genome identified a selection target underlying the evolution of flower colour pattern⁸.

No single species can represent all plant diversity. Recent developments in sequencing technologies, particularly long-read sequencing, provide opportunities to generate highly accurate and continuous reference genomes for many species at low costs, reducing the demand for simple genetics in experimental systems. Many species will become tractable for genetic and genomic studies and we will be better equipped to study lineage- or species-specific biological phenomena using new models. Investigations of previously overlooked experimental plants will thrive again, thanks to the new sequence resource. For functional studies, ease of transformation will always be a limitation, but breakthroughs can be expected.

However, it is far too soon to announce the end of model system research and trumpet the rise of non-model plants. If nothing else, research on model species promotes scientific cooperation and communication, tying communities together by promoting conversations and exchanges of experimental materials and ideas. Overlooked models — which *Antirrhinum* has some justification to consider itself — will provide stepping stones to the investigation of a more diverse range of species and questions. A clear picture of plant biology will only be secured by exploring a larger diversity of the plant kingdom: model, non-model and neglected-model plants alike. □

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