Emerging Model Organisms

The Genus *Antirrhinum* (Snapdragon): A Flowering Plant Model for Evolution and Development

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INTRODUCTION

The *Antirrhinum* species group comprises approximately 20 morphologically diverse members that are able to form fertile hybrids. It includes the cultivated snapdragon *Antirrhinum majus*, which has been used as a model for biochemical and developmental genetics for more than 75 years. The research infrastructure for *A. majus*, together with the interfertility of the species group, allows *Antirrhinum* to be used to examine the genetic basis for plant diversity.

RELATED INFORMATION

For a review of the history of *Antirrhinum* genetics, see Schwarz-Sommer et al. (2003a). For a detailed presentation of the control of flower development in *Antirrhinum*, in comparison to that of other species, see Davies et al. (2006). The *A. majus* (snapdragon) genetic and genomic database is available at the DragonDB homepage, http://www.antirrhinum.net. The contents of this searchable database in AceDB schema include *Antirrhinum* sequences, mutants, maps, and publications. The *Antirrhinum* stock collection at The John Innes Centre can be viewed at http://www.jic.ac.uk/STAFF/enrico-coen/Rosemary/start.htm.

Protocols for **Cultivating *Antirrhinum*** (Hudson et al. 2008a) and **Propagating *Antirrhinum*** (Hudson et al. 2008b) are also available.

BACKGROUND INFORMATION

The garden snapdragon *A. majus* has several centuries' history of cultivation as a flowering ornamental. It emerged as a model organism during early studies of inheritance and mutation (e.g., the volume by Darwin [1868]) because of its diploid inheritance, ease of cultivation, and variation in morphology and flower color. Laboratory lines of *A. majus* were produced from cultivars, and a substantial collection of mutants had amassed during the course of the 20th century. This collection included lines with unstable mutations in pigment genes, which produced variegated flowers (Fig. 1a). (A wild-type *A. majus* flower is shown in Fig. 1b.) Transposons responsible for flower variegation were identified in the 1980s at the John Innes Centre in Norwich, United Kingdom, and the Max-Planck-Institut in Cologne, Germany, allowing genes involved in flower and leaf development and in pigmentation to be isolated by transposon tagging. *A. majus* subsequently provided the first insights into the regulation of many developmental processes that are conserved in flowering plants, including the specification of flower and floral organ identity, leaf and flower asymmetry, and the pollen component of gametophytic self-incompatibility. Because *A. majus* diverged from the more commonly used eudicot model *Arabidopsis thaliana* early in the history of flowering plants, it has proven to be useful in comparative developmental studies.

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The *Antirrhinum* species group also has a history of use in studies of natural variation. The close relatives of *A. majus* form a monophyletic group of approximately 20 species native to the Mediterranean region, particularly southwestern Europe and northern Africa. The species vary widely in morphology and ecology and are adapted to different—often extreme—habitats. However, all are able to form fertile hybrids with one another and with *A. majus*, allowing the identification of genes that underlie their differences (see, e.g., Langlade et al. 2005). Population genetic studies that have been applied to *Antirrhinum* species show different population sizes, geographic distributions, and breeding systems, from self-fertility to obligate out-crossing (see, e.g., Jiménez et al. 2002; Mateu-Andres and de Paco 2006).

SOURCES AND HUSBANDRY

Seeds from a large collection of *A. majus* mutants, their wild-type progenitors, and a limited number of other *Antirrhinum* species can be obtained from the Leibniz Institute of Plant Genetics and Crop Plant Research (IPK) in Gatersleben, Germany (http://gbis.ipk-gatersleben.de). Protocols for *Antirrhinum* husbandry can be found in most gardening books, and the necessary materials are readily available. Although tolerant of both frost and high temperatures, *Antirrhinum* species grow best at daytime temperatures of 17°C-25°C. In temperate regions, they are usually treated as half-hardy annuals and are transferred from a glasshouse to the open in the spring or grown entirely in a glasshouse. All species grow well from seeds, most flowering within 3-4 mo of sowing, and are readily propagated clonally from cuttings. Detailed methods for *Antirrhinum* culture and propagation are provided in **Cultivating *Antirrhinum*** (Hudson et al. 2008a) and **Propagating *Antirrhinum*** (Hudson et al. 2008b).

RELATIVES OF *A. MAJUS*

Antirrhinum is a member of the asterid clade of flowering plants. The more commonly used model species *Arabidopsis* is a member of the second major clade of broad-leaved plants—the rosids—from which asterids diverged an estimated 120 million yr ago. Within the asterids, *Antirrhinum* belongs to the order Lamiales, a close relative of the order Solanales, which includes other model species such as petunia and tomato. *Antirrhinum* was recently placed in the family Plantaginaceae (synonymous with Veronicaceae) following a revision of the classical family Scrophulariaceae based on DNA sequence variation (Olmstead et al. 2001).

Other aspects of *Antirrhinum* taxonomy remain controversial. The generic epithet "*Antirrhinum*" is now usually reserved for the monophyletic group of Old World perennials with a diploid chromosome number of 16. However, it is still applied to a broader monophyletic group that includes species with different chromosome numbers, such as the New World *Sairocarpus* and the annual *Misopates*, with which *Antirrhinum* species are unable to form fertile hybrids (see, e.g., Oyama and Baum 2004). Within *Antirrhinum sensu stricto*, a variable number of different species have been proposed, and relationships between taxa are currently unresolved. These taxonomic problems largely reflect the young age of the genus (<5 million yr) (Gübitz et al. 2003) and the effects of hybridization (see, e.g., Whibley et al. 2006); thus, attempts to reconstruct phylogenies based on nuclear or chloroplast DNA sequence variation have so far been unsuccessful (see, e.g., Jiménez et al. 2005). In the absence of a taxonomic revision based on a resolved phylogeny, the descriptions of approximately 20 species and their likely hybrids in *Flora Europaea* (Webb 1972) provide a realistic working guide.
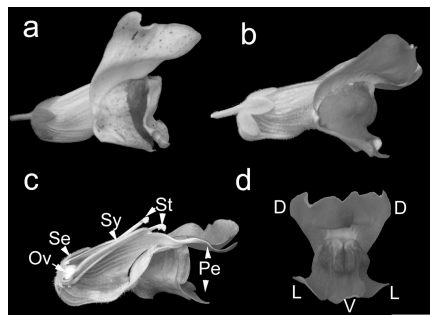

FIGURE 1. *Antirrhinum majus*. (a) The variegated flower caused by a transposon-induced mutation in a gene required for synthesis of anthocyanin pigments. Excision of the transposon can give rise to clones of wild-type cells able to produce magenta anthocyanins. (b) Wild-type *A. majus* flower. (c) Section of an *A. majus* flower, showing the four types of organs. (Ov) ovary; (Se) sepal; (Sy) style; (St) stamen; (Pe) petal. (d) Dorsoventral asymmetry of the *Antirrhinum* corolla. (D) Dorsal, (L) lateral, and (V) ventral petals, respectively. Bar, 10 mm.

The genus has traditionally been divided into three subsections or morphological groups (as in the volume by Rothmaler [1956]) that have received support from studies of isozyme and DNA variation. The subsection *Antirrhinum* includes the close relatives of *A. majus* and consists of species with similar upright growth, large organs, and pink or yellow flowers (Fig. 2a). These tend to be geographically widespread and grow in a variety of habitats. *A. majus* was probably domesticated in northeastern Spain or southwestern France from *Antirrhinum pseudomajus* (also known as *Antirrhinum majus* subspecies *pseudomajus*), from which it differs by having more darkly pigmented flowers, although traits such as flower color variation might have been introduced by introgression from other species. Members of subsection *Kickxiella*, in contrast, are usually restricted to rock faces and walls. They are also smaller, typically prostrate in habit, and have small white or pale pink flowers (Fig. 2b). They are geographically more restricted, and many are endemic to particular mountain regions. The two members of subsection *Streptosepalum* are pale- or yellow-flowered, of upright habit, and grow in hedges and rocky outcrops in northern Spain and Portugal (Fig. 2c). Distribution maps for all *Antirrhinum* species were produced by Rothmaler (1956) and can also be found in the volume by Stubbe (1966).

USES OF THE *A. MAJUS* MODEL SYSTEM

Biochemistry

Two aspects of *Antirrhinum* biochemistry relevant to their attraction of pollinating bees have been studied in detail. First, genes encoding the enzymes involved in the production of floral scents—phenylpropanoids and isoprenoids—have been identified from *A. majus* and used to study the regulation of scent production and the effects of variation in scent composition on pollinator attraction (see, e.g., Wright et al. 2005). Second, the basis for flower color variation in *Antirrhinum* has a long history of study, including the pioneering biochemical genetics of Muriel Wheldale in the early 20th century. Structural genes encoding most enzymes involved in the biosynthesis of magenta anthocyanins and the structurally related yellow aurones have been identified and isolated through a combination of genetics and biochemistry. Several regulatory genes encoding MYB or basic helix-loop-helix (bHLH) transcription factors are known to affect the intensity or pattern of pigmentation (Schwinn et al. 2006). In parallel, many of the genes underlying natural variation in *Antirrhinum* flower pigmentation were mapped or shown to be allelic to loci identified from mutations in *A. majus*. Three of the loci involved in natural variation have been isolated: Two encode the MYB transcription factors ROSEA and VENOSA, and the third is the structural gene *INCOLORATA*. Two additional genes—*SULFUREA* (*SULF*), which controls aurone pigmentation, and *ELUTA* (*EL*), which is
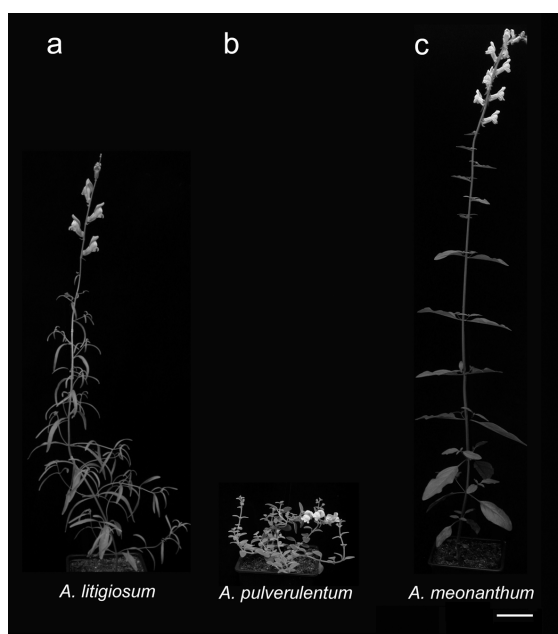

FIGURE 2. Representatives of the three traditional subsections of the genus *Antirrhinum*. (*a*) *Antirrhinum litigiosum* (also known as *Antirrhinum majus* subspecies *litigiosum*), a member of subsection *Antirrhinum*; (*b*) *Antirrhinum pulverulentum*, a member of subsection *Kickxiella*; (*c*) *Antirrhinum meonanthum*, a member of subsection *Streptosepalum*. Bar, 50 mm.

responsible for variation in the pigment pattern within the flower—have been mapped but not yet isolated. Flower color variation in *Antirrhinum* has been shown to affect pollinator behavior, and selection at loci including *SULF* and *EL* is likely to maintain the distinction between yellow-flowered *Antirrhinum striatum* and magenta-flowered *A. pseudomajus* in the face of hybridization (Whibley et al. 2006).

Development

The use of *A. majus* in parallel with other species, notably *Arabidopsis*, has led to an understanding of how the identity of flowers and floral organs is specified (for a recent review, see Davies et al. 2006). These processes are broadly conserved between the asterid *Antirrhinum* and the rosid *Arabidopsis*, which have similar inflorescence and floral structures (see Fig. 1c,d for the structure of the *Antirrhinum* flower). Both species, for example, contributed to the "ABC" model of floral organ specification, in which the combination of genes expressed in each of the whorls determines the identity of the floral organs (A genes specify sepals, A + B genes specify petals, B + C genes specify stamens, and C genes specify the carpel). However, the comparative use of *A. majus* further revealed subtle evolutionary differences in the way that the development of similar flowers can be regulated. *Antirrhinum* and *Arabidopsis*, for instance, use different genes to exclude the expression of C genes from the outermost parts of the developing flower—a role originally attributed to A-function genes—leading to a reevaluation of the A-function genes in both species (Keck et al. 2003; Davies et al. 2006). Similarly, the ancestral C function appears to have been transferred to different duplicated genes after the divergence of *Antirrhinum* from *Arabidopsis* (Causier et al. 2005). One notable aspect of the *Antirrhinum* flower that differs from *Arabidopsis* is its marked dorsoventral asymmetry (zygomorphy). Zygomorphy, considered to have coevolved with insect pollination, is apparent in the different morphologies of the dorsal, lateral, and ventral petals of *Antirrhinum* (Fig. 1d) and in stamen development. The dorsal and lateral petals are specified by the paralogous TCP transcription factor genes *CYCLOIDEA* (*CYC*) and *DICHOTOMA* (*DICH*), which act partly by activating dorsal expression of *RADIALIS* (*RAD*). RAD is a protein with a single MYB transcription factor repeat that is thought to compete with the two-repeat MYB protein encoded by the *DIVARICATA* (*DIV*) gene to antagonize its ventralizing effect (for review, see Almeida and Galego 2005). *CYC*-like genes have also been implicated in the evolution of floral asymmetry in other lineages. For example, ectopic *CYC* expression has been proposed to account for the evolution of the derived radially symmetrical flower of *Mohavea*, which is within the tribe Antirrhineae (Hileman et al. 2003). *CYC*-like genes are expressed asymmetrically in both rosids and asterids, including species that have radially symmetrical flowers (for review, see Cubas 2004). This indicates that ancestral, asymmetrically expressed *CYC*-like genes might have been recruited independently to produce zygomorphic flowers in different flowering plant lineages, a view recently supported by the effects of *cyc*-like mutants in the asterid legume *Lotus* (Feng et al. 2006).

Aided by a large collection of leaf-shape mutants, *A. majus* has also been useful in studies of leaf development. These studies have included the identification of genes involved in specifying leaf identity and promoting leaf growth (see, e.g., Golz et al. 2004) and in coordinating growth in the leaf blade to ensure the development of a flat organ (see, e.g., Nath et al. 2003).

Ecology and Population Genetics

Antirrhinum species have been the subject of population genetic studies, including those aimed at assessing genetic diversity in order to inform conservation strategies for rare endemic species (see, e.g., Mateu-Andres 2004). As with other taxa, genetic diversity has generally been found to be lower in smaller populations, and the distribution of genetic variants within and between populations has been correlated with their level of self-incompatibility. In addition, several genetically well-characterized aspects of *Antirrhinum* development and physiology are relevant to their reproductive ecology, including petal cell morphology, genetic self-incompatibility, flower color, and scent production.

Whereas cultivated *A. majus* and some wild species (e.g., *Antirrhinum valentinum*, *Antirrhinum subbaeticum*, and *Antirrhinum siculum*) are self-fertile, the majority of *Antirrhinum* species show gametophytic self-incompatibility that is determined by a single, complex *S* locus. Individuals of self-incompatible species reject pollen carrying an *S* allele that corresponds to one of their own alleles and are therefore obligate outbreeders. Through studies of relatives in the family Solanaceae, rejection of pollen was known to involve an *S*-encoded RNase that was expressed in the pistil (McClure et al. 1989), although the pollen-expressed component had remained elusive. Mapping and sequence

analysis of the active *S* locus of *Antirrhinum hispanicum*, followed by expression and functional studies, identified the likely pollen component to be an F-box protein involved in targeting the RNase for degradation (Lai et al. 2002).

Cells of the petal epidermis of *Antirrhinum*, like those of many flowering plants, have a conical shape that is dependent on activity of the MYB transcription factor encoded by *MIXTA*. These conical cells intensify flower color by reducing reflection, as revealed by *MIXTA* mutants with flat epidermal cells, and are important in attracting pollinating bees (Noda et al. 1994). In addition to having a role in the reproductive ecology of *Antirrhinum*, the misexpression of *MIXTA* or related genes can give rise to the formation of epidermal hairs (trichomes), indicating a common regulation of these two cell types and a role for other *MIXTA*-like genes in regulating multicellular trichome development in *Antirrhinum*. This latter function of *MIXTA*-like genes does not appear to be conserved in *Arabidopsis*, which has unicellular trichomes (for review, see Serna and Martin 2006).

GENETICS AND GENOMICS RESOURCES

A. majus is amenable to classical genetics. It has a relatively short generation time of ~4 mo, is diploid ($2n$ = 16), and is easily self- and cross-pollinated (see **Propagating *Antirrhinum*** [Hudson et al. 2008b]). A collection of classical mutants and corresponding wild-type lines originating from the work of Erwin Baur, Hans Stubbe, and their colleagues is maintained at the IPK. The phenotypes of most of the mutants in this collection have been described by Stubbe (1966) and cataloged by Hammer et al. (1990). Additional mutants and wild-type lines, generated at the John Innes Centre, are described at http://www.jic.ac.uk/STAFF/enrico-coen/Rosemary/start.htm.

A molecular recombination map, currently comprising more than 250 loci with an average distance between loci of ~2 cM, has been produced for *Antirrhinum* using hybrids between *A. majus* and wild species, and the map is maintained at www.antirrhinum.net. It has been aligned with a map of classical mutants and with the eight *Antirrhinum* chromosomes using fluorescence in situ hybridization (FISH) (Zhang et al. 2005). Maps constructed using hybrids between different *Antirrhinum* species are largely collinear, suggesting an absence of extensive chromosomal rearrangements, although distorted transmission of some genomic regions in interspecies hybrids can hinder genetic mapping (Schwarz-Sommer et al. 2003b). Recombinant inbred lines (RILs) and near-isogenic lines (NILs) have been produced from hybrids between different *Antirrhinum* species, allowing those genes that underlie differences between species to be identified.

Native *Antirrhinum* transposons have provided the basis for a number of genetic resources. Most spontaneous mutations in *A. majus* have been found to carry transposons belonging to one of two families: the *Tam3* family, which is similar to *Ac* in maize; and the *CACTA* family, which is homologous to *Spm/En* in maize. Mutagenic retroposons and miniature inverted repeat transposable elements (MITEs) have also been found. Transposition of the *CACTA* and *Tam3* families occurs by excision from the donor site and reintegration elsewhere in the genome and is promoted by low temperature. A number of *A. majus* lines were selected for high transposon activity based on flower variegation and have been used for forward genetic screens and for inactivating known genes to study their functions (see, e.g., Keck et al. 2003).

Transposon excision from pigment genes, which can be controlled with temperature, has been used to mark cells for fate and growth analysis (e.g., Rolland-Lagan et al. 2003), and excision from developmental genes has been used to examine cell autonomy of gene action (see, e.g., Golz et al. 2004). In many cases, it has been possible to establish stable periclinal chimeras in which layers of the shoot apical meristem comprise genetically different cells as the result of transposon excision (see, e.g., Carpenter and Coen 1995). Such chimeras can be maintained by vegetative propagation through cuttings.

Although stable transgenic *Antirrhinum* can be produced using *Agrobacterium tumefaciens* (Cui et al. 2003), transformation efficiency is low. Particle bombardment and *Agrobacterium* infiltration of developing petals have been used successfully to obtain transient expression of pigment genes and suppression by RNA interference (RNAi) (Schwinn et al. 2006; Shang et al. 2007).

Bacterial artificial chromosome (BAC) libraries have been produced from *A. majus* (Causier et al. 2005) and from an *A. majus* × *A. hispanicum* hybrid (Lai et al. 2002). Although the genome size of *A. majus* has been estimated at 430 Mb (Bennett and Leitch 1995), the recovery of clones from genomic libraries indicates that it might be at least twofold larger; therefore, the depth of coverage of existing BAC libraries is uncertain. Currently, only short BAC contigs have been assembled to allow positional

cloning in specific target regions (Cartolano et al. 2007). FISH has been used to locate BAC clones on *Antirrhinum* chromosomes (Zhang et al. 2005; Yang et al. 2007). An expressed sequence tag (EST) collection of approximately 12,000 unigenes from *A. majus* is available for searching at www.antirrhinum.net. Other DNA libraries include cDNA clones in yeast one-hybrid and two-hybrid vectors (see, e.g., Egea-Cortines et al. 1999).

TECHNICAL APPROACHES

Antirrhinum species are amenable to molecular genetic techniques. Most protocols that have been developed for *Arabidopsis*, including those for nucleic acid, protein, and organelle purification and for detection of RNA and proteins in situ, can be applied directly to *Antirrhinum* (see **Cultivating Antirrhinum** [Hudson et al. 2008a] and **Propagating *Antirrhinum*** [Hudson et al. 2008b]).

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