

Ancient asymmetries in the evolution of flowers

Pilar Cubas^{*}, Enrico Coen[†] and José Miguel Martínez Zapater^{*}

Dorsoventral asymmetry in flowers is thought to have evolved many times independently as a specialized adaptation to animal pollinators [1, 2]. To understand how such a complex trait could have arisen repeatedly, we have compared the expression of a gene controlling dorsoventral asymmetry in *Antirrhinum* with its counterpart in *Arabidopsis*, a distantly related species with radially symmetrical flowers. We found that the *Arabidopsis* gene is expressed asymmetrically in floral meristems, even though they are destined to form symmetrical flowers. This suggests that, although the flowers of the common ancestor were probably radially symmetrical, they may have had an incipient asymmetry, evident at the level of early gene activity, which could have been recruited many times during evolution to generate asymmetric flowers.

Addresses: ^{*}Centro Nacional de Biotecnología/Instituto de Investigaciones Agrarias, Departamento de Biología Molecular de Plantas, Universidad Autónoma de Madrid, Cantoblanco, 28049, Madrid, Spain. [†]John Innes Centre, Colney Lane, Norwich, NR47UH, United Kingdom.

Correspondence: Pilar Cubas
E-mail: pcubas@cnb.uam.es

Phone: 34-915854688; Fax: 34-915854506

Received: 1 May 2001
Revised: 16 May 2001
Accepted: 16 May 2001

Published: 10 July 2001

Current Biology 2001, 11:1050–1052

0960-9822/01/\$ – see front matter
© 2001 Elsevier Science Ltd. All rights reserved.

There are many examples in which complex morphological traits have arisen repeatedly during evolution [3, 4, 5]. However, the molecular mechanisms underlying such events are unclear in most cases. One possibility is that entirely different mechanisms arose for each event. Alternatively, the ancestor could have been evolutionarily poised, such that slight modifications of the same mechanism allowed the trait to be generated repeatedly. We have tested these possibilities in the case of floral asymmetry evolution.

The *cycloidea* (*cyc*) gene plays a key role in establishing dorsoventral asymmetry in *Antirrhinum* (snapdragon) flowers (Figure 1a) [6]. The *cyc* gene is expressed at a very early stage in the dorsal (adaxial) region of floral meri-

stems, where it affects growth rate and primordium initiation [6]. Expression continues through to later stages in dorsal primordia to affect the asymmetry, size and shape, and cell types of petals and stamens. *CYC* is a member of the TCP family of DNA-binding proteins, many examples of which have now been identified in the genome of *Arabidopsis* [7]. Of these, *TCP1* is the most similar to *CYC* and represents a likely ortholog. We analyzed the expression of *TCP1* in *Arabidopsis* to determine how a *cyc* ortholog might be expressed in a species with radially symmetrical flowers. Like *cyc*, *TCP1* was expressed at very early stages of development, stages 1 and 2 [8], in the dorsal part of flower meristems (Figure 1c). However, in contrast to *cyc*, *TCP1* was not expressed from stage 3 onward (Figure 1c). The transience of *TCP1* expression may account, at least in part, for the lack of dorsoventral asymmetry detected at the morphological level in the adult *Arabidopsis* flowers. *TCP1* was also expressed in the dorsal (adaxial) region of all axillary shoot meristems (Figure 1d), in a similar pattern to that in floral meristems. This shows that common prepatterns are present in both types of axillary meristems and makes *TCP1* a molecular marker for axillary versus apical meristems. This also shows that, similar to lateral organs [9], axillary meristems have an underlying dorsoventral asymmetry. In contrast to the situation in flowers, *TCP1* expression in axillary shoot meristems was maintained during later stages of development (Figure 1e).

These results indicate that dorsoventral asymmetry in *cyc/TCP1* gene expression predates the divergence of *Antirrhinum* and *Arabidopsis*. Thus, the common ancestor of these species, which presumably had radially symmetrical flowers, would have had asymmetric expression of the ancestral *cyc/TCP1* gene in its axillary flower and/or shoot meristems. This incipient asymmetry could then have been recruited many times independently, by changes in timing of expression and interactions with target genes, so that it became manifest at the morphological level as the dorsoventral asymmetry of the flower.

Acknowledgements

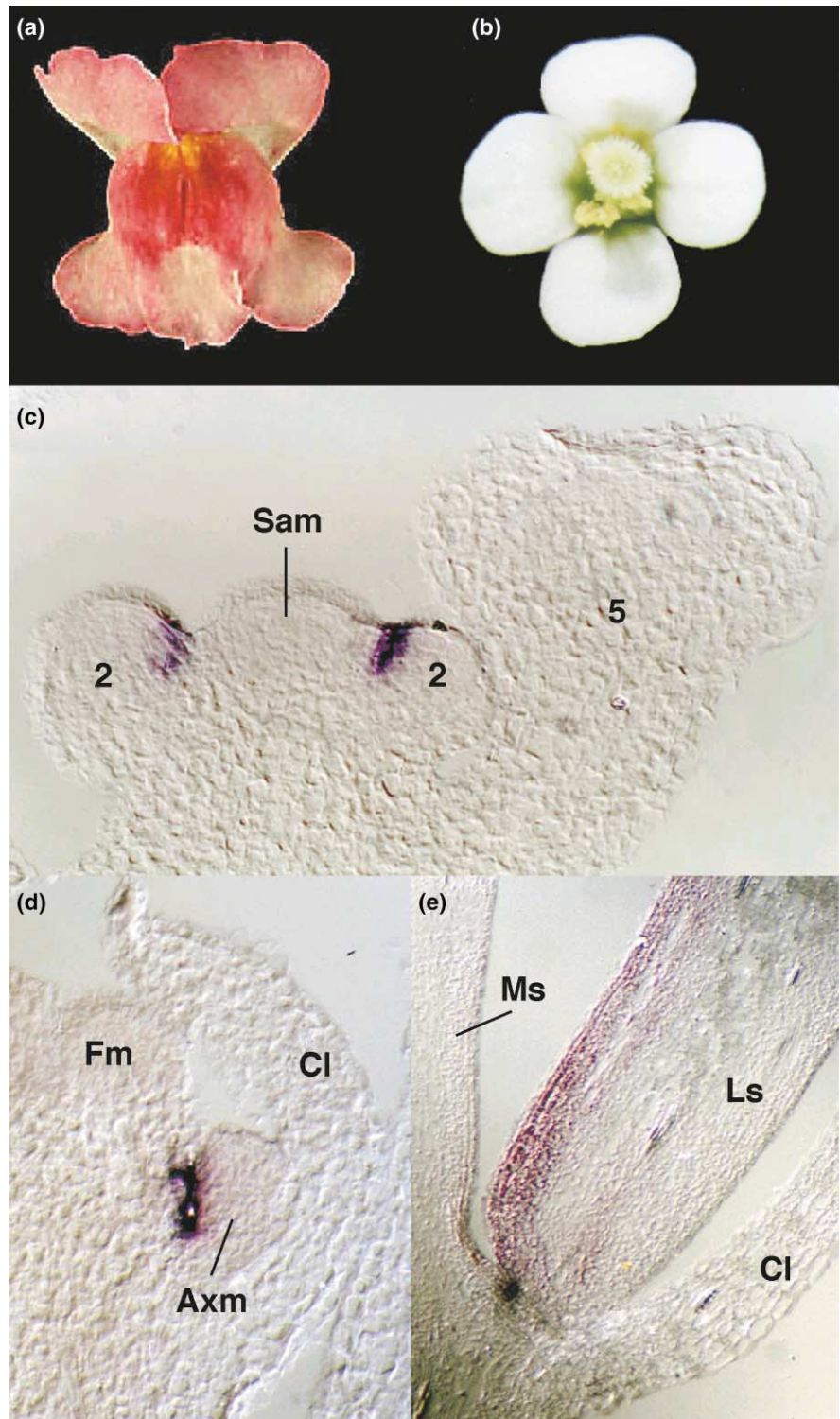
This work was supported by grant AGF98-0206 from Comision Interministerial de Ciencia y Tecnologia (CICYT) (Spain). Support to research activity at Centro Nacional de Biotecnología is provided through specific agreement with Consejo Superior de Investigaciones Científicas-Instituto Nacional de Investigaciones Agrarias (CSIC-INIA). P.C. was a recipient of a postdoctoral MEC contract (Spain).

References

1. Stebbins GL: Flowering Plants: Evolution Above the Species Level. Cambridge, MA: Harvard University Press; 1974.
2. Donoghue MJ, Ree R, Baum DA: **Phylogeny and the evolution of flower symmetry in Asteridae**. *Trends Plant Sci* 1998, **3**:311–317.
3. Funk DJ: **Isolating a role for neutral selection in speciation:**

Figure 1

Asymmetrical expression of *TCP1* during *Arabidopsis* development. **(a)** *Antirrhinum* flower. **(b)** *Arabidopsis* flower. **(c–e)** Sections of *Arabidopsis* tissue probed with digoxigenin-labeled *TCP1* antisense RNA according to the protocol described in [10]. **(c)** *TCP1* mRNA accumulates in the dorsal (adaxial) region of stage 2 floral meristems. This expression may be responsible for the delayed initiation of the dorsal sepal primordium. *TCP1* is not expressed in stage 5 flower buds, when sepals, petals, and stamens are being formed. **(d)** *TCP1* is transcribed in the dorsal part of shoot axillary meristems. Note that this early expression pattern is similar to that in **(c)**; **(e)** *TCP1* expression is maintained in the dorsal part of lateral shoots during their elongation. Numbers indicate stages according to Smyth [8]. Cl, cauline leaf; Sam, shoot apical meristem; Axm, shoot axillary meristem; Fm, flower meristem; Ms, main shoot; Ls, lateral shoot.



- host adaptation and sexual isolation in *Neochlamisus bebbianae* leaf beetles.** *Evolution* 1998, **52**:1744-1759.
4. Rundle HD, Nagel L, Wenrick Boughman J, Schluter D: **Natural selection and parallel speciation in sympatric sticklebacks.** *Science* 2000, **287**:306-308.
 5. Salvini-Plawen L, Mair E: **On the evolution of photoreceptors and eyes.** *Evol Biol* 1977, **10**:207-263.
 6. Luo D, Carpenter R, Vincent C, Copsey L, Coen E: **Origin of floral asymmetry.** *Nature* 1996, **383**:794-799.
 7. Cubas P, Lauter N, Doebley J, Coen E: **The TCP domain: a motif found in proteins regulating plant growth and development.** *Plant J* 1999, **18**:215-222.
 8. Smyth DR, Bowman JL, Meyerowitz EM: **Early flower development in *Arabidopsis*.** *Plant Cell* 1990, **2**:755-767.
 9. Bowman J: **Axial patterning in leaves and other lateral organs.** *Curr Opin Genet Dev* 2000, **10**:399-404.
 10. Coen ES, Romero JM, Doyle S, Elliott R, Murphy G, Carpenter R: **Floricaula: a homeotic gene required for flower development in *Antirrhinum majus*.** *Cell* 1990, **63**:1311-1322.