

# Flowers' wings, fruitflies' petals

Claude Desplan and Thomas Lecuit

The technique of clonal analysis allows dividing cells in a developing organ to be marked and tracked. The aim of such studies, in plants as well as animals, is to understand how tissues acquire their form and size.

Over the past decade, molecular genetics has started to deliver answers to the age-old question of how an organism acquires its final design. The work concerned has shown that morphogen molecules 'pattern' tissues<sup>1</sup>, and so has provided a clear view of how cell identity is spatially and temporally defined in a growing organism. But this patterning has remained an abstract concept, based simply on how different domains of gene expression are established immediately downstream of a particular morphogen. How these molecular events lead to the overall form of the tissue, often several days later, has remained a black box.

Writing on page 161 of this issue<sup>2</sup>, Rolland-Lagan, Bangham and Coen offer a fresh view of the problem. The authors analysed a simple plant tissue, the petal lobe of *Antirrhinum* (snapdragon), to describe how a tissue acquires its form. The petal is particularly amenable to this study because of its simple organization, and because cell movements, which are involved in the acquisition of form in animals, are clearly extremely limited in plants. Rolland-Lagan *et al.* provide a simple, quantitative, dynamic model in which just a few parameters are sufficient to explain the final shape of the tissue.

The authors used classical clonal analysis in their experiments. They generated and followed the fate of small patches of marked tissue distinguished, for instance, by colour, each being the progeny of an individual cell (Fig. 1a). By comparing average characteristics of clones induced at various times for each region of the petal, they could compute growth rate (that is, the time between two cell divisions), the extent of anisotropy of growth (how much the descendants of dividing cells accumulate preferentially along a given axis) and the main direction of growth.

Rolland-Lagan *et al.* measured the average values and spatiotemporal fluctuations of these parameters. They then assessed the significance of the experimental measurements using computer simulations. The first notable conclusion is that the estimated parameters (growth rate, anisotropy and direction of growth) are sufficient to generate the correct changes in petal shape. Remarkably, the observed localized differences in cell division rates, anisotropy or direction are not essential for generating petal asymmetry, as the simulation works well with fixed average values for these three

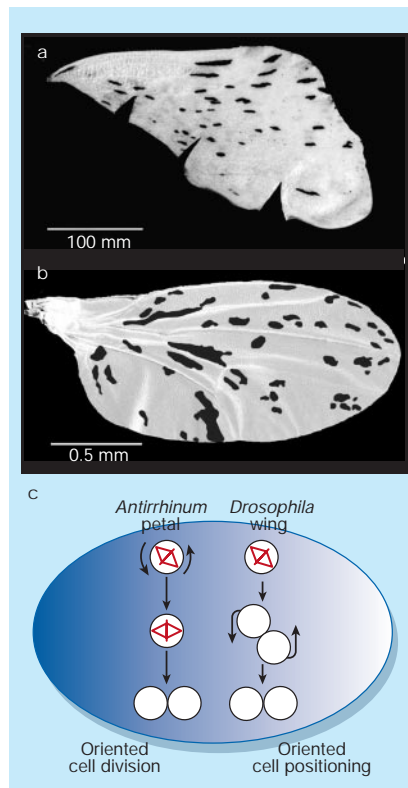


Figure 1 Clonal analysis and organ shape.

a. *Antirrhinum* petal, for which Rolland-Lagan *et al.*<sup>1</sup> inferred patterns of cell divisions from the shape of marked clones of cells. b. The *Drosophila* wing, which has been subject to similar analyses. Both petals and wings display a marked asymmetry in clone growth, possibly in response to unknown long-range signals. c. In the *Antirrhinum* petal, such long-range signals could orient cell division, whereas in the *Drosophila* wing the plane of division is random but cell positioning is oriented. In each case, the result is asymmetric clone growth along the main tissue axis. a is a light-microscope image and b is a scanning electron micrograph; courtesy of A.-G. Rolland-Lagan and K. Lee, respectively.

types of parameter. The authors also suggest that long-range signals orient cell divisions. Overall, these results appear to be amazingly simple and make it possible to identify the genetic components that control the three parameters. This could lead to a generalized model for other tissues, not only in plants but also in animals, even if more parameters are necessary.

Since the early 1970s, the wing of the fruitfly *Drosophila* has also been subjected to clonal analysis to address the problem of how tissue shape is controlled. Garcia-Bellido and co-workers, among others, have studied how the shape and size of the fly wing is created by cells dividing in the precursor of the developing wing, the imaginal disc. The comparison between this system and the flower petal is striking (Fig. 1a, b). Although they did not reach the same level of quantitative analysis, some of the conclusions of these earlier investigations<sup>3,4</sup> are evidently similar to those of the latest studies<sup>1</sup>, and some are different.

The main similarity is that cell divisions occur throughout the tissue rather than as a wave or in a growth zone. Clone proliferation is also anisotropic, although the direction of asymmetric growth changes at different stages in the developing fly wing. Clones generally grow along the main tissue axes (Fig. 1a, b), reflecting the overall tissue shape. Finally, both systems seem to rely on long-range signals (Fig. 1c). For the flower petal, the long-range signal could specify the main direction of cell growth and division. In the fly wing, morphogens such as the Decapentaplegic or Wingless proteins could also direct the ordered positioning of cells along the morphogenetic gradients, although they do not affect the plane of cell divisions, as their orientation seems to be random<sup>4,5</sup>. There are, however, variations on this theme and Garcia-Bellido's 'entelechia' model<sup>5</sup> calls for local monitoring of positional values that control cell division and cell positioning, independent of a long-range gradient. Here, an interesting parallel can be drawn with the establishment of tissue polarity<sup>6</sup>, in which long-range signals orient planar cell polarity acquired by self-propagating, local cell-cell interactions.

What else regulates tissue shape and size? In particular, what is the contribution of cell number and cell size? This question has been addressed in both plants and animals, where mutations in the *cdc2* gene limit cell division but organ size is maintained through a compensation mechanism that increases cell size<sup>4,7,8</sup>. Moreover, several mutations that severely distort the relative size of individual clones fail to alter the shape and size of the organ in the fly (for instance, mutations in *Minute*<sup>9</sup>). These findings suggest that global dimensions are also measured in an organ, or

even at the level of the whole organism. How this is done is a fundamental question that remains unanswered.

Plants and animals might have invented multicellularity independently. Yet despite the obvious differences at the molecular level, there are strong similarities in their strategies for controlling organ shape and size. At a higher level again, however, further controls exist that are fundamentally different between plants and animals — those that determine the relationship of organ size to organism size (allometry). As a plant grows larger, its mature flowers or leaves stay the same size. In animals, all organs grow proportionally. No doubt future quantitative studies on different systems, as offered by Rolland-Lagan *et al.* for the petal, will pave the way for a more complete understanding of this fascinating phenomenon. ■

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Astronomy

# Atmosphere out of that world

David Charbonneau

A planet orbiting very close to a Sun-like star is apparently enveloped by an extended atmosphere of hydrogen atoms, and may be losing mass because of the intense radiation from the parent star.

Of the one hundred or so planets known to orbit nearby Sun-like stars, one is unique. Its name is HD209458b, and the plane of its orbit is fortuitously tilted so that, once every revolution, observers on Earth see the planet in eclipse — in ‘transit’ — in front of its star. Although the planet is similar to Jupiter in mass and size, it is a hundred times closer to its star than Jupiter is to the Sun. As a result, the planet’s gravity must battle the intense heat and stellar radiation to retain its atmosphere.

On page 143 of this issue, Alfred Vidal-Madjar and colleagues<sup>1</sup> present evidence that the planet may be losing this fight. Based on observations by the Hubble Space Telescope, they infer that an extended envelope of hydrogen surrounds the planet and suggest that it is a ‘cometary tail’ of material being evaporated from the object. As a result, this planet may slowly be losing mass over time. The implication is that planets initially located even closer to their stars would not survive long, a conclusion that agrees with the observed paucity of extrasolar planets in such orbits.

Following the first detection<sup>2</sup> of a distant planet orbiting a Sun-like star in 1995, plans were soon made for the spectroscopic investigation of possible planetary atmospheres. These studies stemmed from the desire to obtain direct information on the composition and local conditions of such planets. Researchers realized that the data would yield insights into the formation and

dynamical evolution processes that had shaped these bodies, and might reveal whether such events had been similar to, or different from, those that had occurred in our own Solar System. But the direct approach — first isolating the light from a distant planet, and then performing spectroscopy on it — still remains beyond our technological reach. The stumbling-blocks are the very small angular separation of the

planet and parent star (as observed from Earth), coupled with the extremely high contrast ratio of the pair. For comparison, consider that although Jupiter is the brightest planet of the Solar System, it shines in reflected sunlight with an intensity that is only a few parts per billion that of the Sun.

With the discovery<sup>3–5</sup> of the first extra-solar planet to transit its parent star, several researchers<sup>6–8</sup> quickly identified a golden opportunity to sidestep the technological limitations described above. During transit, some of the light from the parent star filters through the outer reaches of the planetary atmosphere, and has impressed upon it the additional spectroscopic absorption features of the atmospheric constituents. By taking the ratio of stellar spectra observed in and out of eclipse, the stellar features are removed, and those of the planet are isolated. With this technique, the glare of the central star is no longer a hindrance, but rather a probe of the planetary atmosphere.

This method had its first success in 2001, when colleagues and I detected<sup>9</sup> sodium in the atmosphere of HD209458b. But although sodium is spectroscopically very active, it is only a trace component of the atmosphere. Hydrogen, on the other hand, is the majority constituent of this gas-giant planet, and thus has much greater diagnostic potential. With this in mind, Vidal-Madjar *et al.*<sup>1</sup> observed three separate passages of HD209458b in front of its parent star. During each event, they measured a 15% dimming in the starlight (Fig. 1) emitted at the wavelength corresponding to a fundamental transition of the hydrogen atom. The large amplitude of this signal is somewhat of a surprise. The planet’s radius is roughly 1.35 times that of Jupiter, so that the planet blocks only 1.5% of the area of the star — indeed,

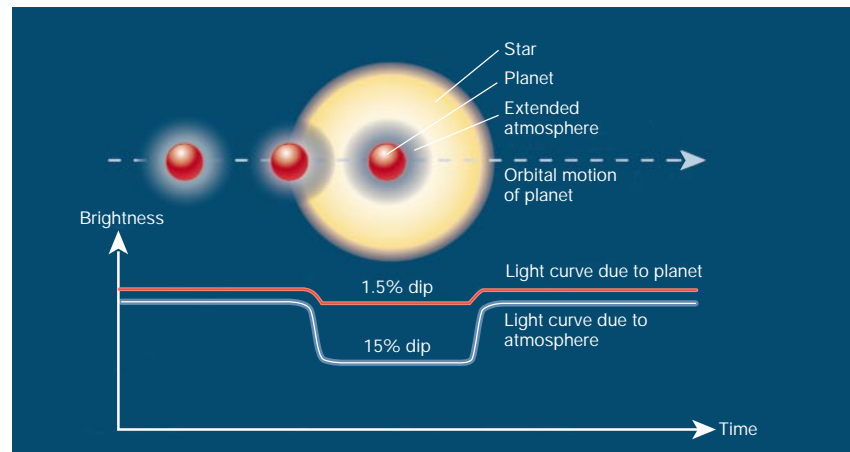


Figure 1 The observations from which Vidal-Madjar *et al.*<sup>1</sup> conclude that the planet HD209458b has an extended atmosphere. Passage of the planet in front of its parent star blocks 1.5% of the starlight when observed at most wavelengths, producing the small characteristic dip in the light curve (red line). Vidal-Madjar *et al.* observed a much deeper transit depth of 15% (blue line) at the wavelength of a transition of atomic hydrogen, from which they deduce that an atmosphere of hydrogen envelops the planet. It appears to extend beyond the gravitational reach of the planet, implying that some of the hydrogen atoms are escaping.