The use of a liquid electrolyte, as in the original cell design[4], may limit device stability because the liquid may evaporate when the cell is imperfectly sealed, and more generally diffusion and reaction of water or oxygen molecules may worsen cell performance. The liquid electrolyte also makes the manufacture of multi-cell modules difficult because cells must be connected electrically yet separated chemically, preferably on a single substrate. One way to remove some of these problems is to replace the liquid electrolyte with a solid conducting material. Researchers have tried polymer electrolytes that conduct ions[6] or inorganic materials such as CuI and CuSCN that conduct holes[7,8]. But so far, the devices produced have performed poorly.

The new approach of Bach *et al.*[1] is to use an amorphous conducting material. They have developed an organic hole-transport material (HTM), in which positive charges hop from one molecule to another. The material can be applied simply, by spin casting, and because the two halves of the molecule are perpendicular to each other (Fig. 1 on page 583), a three-dimensional structure is imposed that results in an amorphous solid state, without the grain boundaries that limit hole transport. Furthermore, the amorphous state is expected to form a better interface with the dye-covered TiO_2 electrode than would a crystalline state, ensuring efficient hole transport from the oxidized dye to the HTM. This has resulted in cells where up to 30% of incident photons are converted into a charge carrier. Although this value is still appreciably lower than the maximum conversion fraction of liquid electrolyte cells (up to 90%), it is very high for an organic solid device.

The open-circuit voltage of 342 mV, however, is much lower than the value that might be expected. That may indicate recombination losses, possibly owing to the partial doping of the HTM needed to obtain high enough conductivity. To achieve high-efficiency, solid-state, dye-sensitized solar cells, this is probably the biggest obstacle to be overcome. Furthermore, it remains to be seen whether the sensitivity of such solid-state devices to water or molecular oxygen is lower than that of liquid-based devices, and whether the ultraviolet stability is good enough.

Nevertheless, Bach *et al.* have taken the development of solid-state, dye-sensitized solar cells a stage further. These cells are still in their early infancy, particularly compared with inorganic thin-film devices, but the promise of very low production costs and reasonable to high efficiencies warrants intensive work in this area, even if it is many years before the resulting solar modules cover our roofs. □

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Floral patterning

A LEAFY link from outer space

Ben Scheres

The beautiful shape and colour patterns of flowers attract almost everybody, including developmental biologists. Studies of floral patterning have shown that the identity of floral organs is determined by a combinatorial code of homeotic genes, termed A, B and C, expressed in three separate regions of the flower[1]. This knowledge allows scientists (and biotech companies) to manipulate flowers to form organs at any position, yet the secret of how the three activities are put into the right place remains hidden. But on page 561 of this issue, Parcy *et al.*[2] bring new insights to this matter. They show that the LEAFY (LFY) protein is directly involved in activating the transcription of homeotic genes, together with at least one co-regulator, UNUSUAL FLORAL ORGANS (UFO). The genes that encode these proteins were originally isolated as *floricaula* and *fimbriata* in a flower that almost all of us have manipulated as children, the snapdragon[3,4].

Parcy and colleagues used *Arabidopsis thaliana* for their study. *Arabidopsis* flowers are formed on the flanks of inflorescence meristems — groups of stem cells that give rise to flower-carrying branches. Inflorescence meristems, in turn, derive from the shoot apical meristem. This is first laid down in the plant embryo, and it produces leaves in the vegetative phase before switching to the floral programme (Fig. 1). Within floral meristems, the sepals, petals, stamens and carpels are specified in concentric rings: A genes specify sepals; A and B genes, petals; B and C genes, stamens; and C genes alone, carpels. In *Arabidopsis*, A-gene function is carried out by the *APETALA1* (*AP1*) and *AP2* genes, B-gene function by *AP3* and *PISTILLATA*, and C-gene function by *AGAMOUS* (*AG*).

The *LFY* gene is a meristem-identity gene — it promotes the formation of floral meristems[3,5]. The gene product, LFY, is a DNA-binding nuclear protein that is expressed throughout the floral meristem[2]. Parcy *et al.* now show that LFY is also able to activate homeotic genes, and that this activity can be uncoupled from its meristem-identity function. These findings were primed by analysis of *lfy* mutants. Many *lfy* mutant flowers are transformed into inflorescence meristems, but some flowers eventually form, with abnormalities that suggest differential effects of LFY on the activity of homeotic genes. Parcy *et al.*[2] reasoned that the ability of LFY to activate homeotic genes

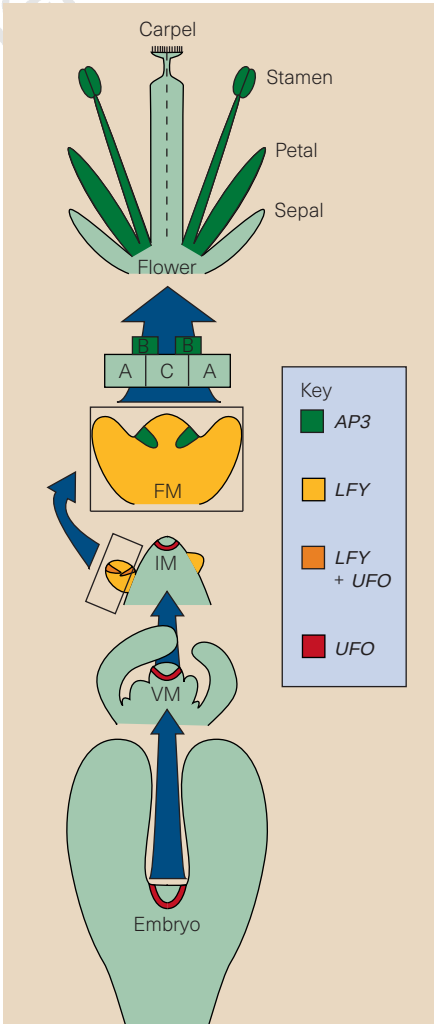

Figure 1 **Parcy and colleagues' model[2] for B-region patterning by a combination of spatial information from *UNUSUAL FLORAL ORGANS* (*UFO*) and flower-meristem specificity from *LEAFY* (*LFY*). There is patterned distribution of *UFO* RNA (red) from embryogenesis onward, then LFY protein (yellow) is expressed throughout stage-1–3 floral meristems, and the B-function gene *APETALA3* (*AP3*; green) is expressed in the region of overlap. VM, vegetative (shoot apical) meristem; IM, inflorescence meristem; FM, floral meristem.**

might be regulated differentially, to allow region-specific expression of these genes. Indeed, they concluded that LFY alone can initiate expression of *AP1* in the A region; that it requires an unknown cofactor to activate expression of *AG* in the C region; and that UFO acts together with LFY to activate *AP3* in the B region (Fig. 1).

To investigate whether LFY is directly involved in floral patterning, Parcy *et al.* made a constitutively active LFY variant by fusing a transcriptional-activator domain to the *LFY* gene. Transgenic plants carrying this construct formed floral meristems at the normal times and places, indicating that the early function of *LFY* was not altered. However, these transgenic plants expressed *AG* outside the flowers (ectopically), and early expression of *AP1* was increased. Whereas ectopic transcription of *AP1* could be induced by expression of LFY alone, induction of ectopic *AG* required expression of the activated form of LFY. This indicates that induction of *AG* — but not *AP1* — requires a flower-specific cofactor. Moreover, although neither LFY nor activated LFY could induce ectopic transcription of *AP3*, constitutive expression of the *UFO* gene with LFY could induce ubiquitous transcription of *AP3*. Promoter-binding and protein-interaction studies should now corroborate, at the molecular level, the regulatory interactions inferred from the *LFY* gene fusion.

Activation of *AG* leads to repression of *AP1*, thereby restricting *AP1* to the A region (that is, the petals and sepals)[6]. Because activation of *AG* in the C region leads to patterning of the A region, the postulated LFY co-regulators in the B and C regions form the minimal requirement to pattern flowers. As well as being involved in spatial control (along with the proposed co-regulators), LFY integrates temporal input from 'flowering time' genes, such as *CONSTANS*, which convey environmental information[7].

Additional thrilling news reported by Long and Barton[8] in *Development* is that UFO is expressed not only in a B-region pattern in floral meristems, but also in shoot meristems from embryogenesis onwards (Fig. 1). Furthermore, genes with shoot-meristem functions, such as *CLAVATA1*, are already expressed in a C-region-like pattern in the embryo[9]. These genes may provide, or respond to, cues from the C region. Thus, flowers can read out position from cues that are established in every shoot-derived meristem from embryogenesis onwards. In evolutionary terms, the floral pattern seems to hitchhike on spatial information that was in place in the more ancient shoot apical meristem.

Sceptics might raise their eyebrows at this point — we already know from animal development that new patterns can arise from pre-existing ones. However, the iterative initiation of patterning cues, which can serve different purposes under the control of environmental inputs, is a new situation. Moreover, a conceptual framework for plant patterning has not emerged in a single sweep, as it has in the fruitfly[10]. In plants, no fly equivalent is available, and genetic redundancy promises to be as omnipresent as in vertebrates. The repetitive nature of development further complicates analysis. All this makes one increasingly aware of the significance of this new link between flower and embryo. □

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Animal evolution

From deep time to late arrivals

Martin Brasier

In a paper published last week in *Science*[1], Adolf Seilacher and colleagues claim that they have found evidence of complex, multicellular animals in sediments generally thought to be more than 1,100 million years old. The sediments concerned are the Chorhat sandstones of the Vindhyan supergroup in central India. The authors report markings from the tops of bedding planes which, they suggest, are tunnels made by small worms burrowing just beneath the surface of bacterial mats. If these markings are accepted as evidence for the existence of animals more than a billion years ago, they would double the time span of the animal fossil record.

One context in which the report should be seen is what was thought to be a mismatch between the evidence provided by fossils and that provided by 'molecular clocks'. Hitherto, the oldest traces of complex-animal activity have been in the region of 550–600 million years old[2,3]. According to some researchers, however, this is much younger than evidence from analysis of the ribosomal RNA of living organisms would suggest. Assuming that gene sequences evolve with such regularity that differences can be used as 'molecular clocks', it can be argued that invertebrate lineages began to diverge about 1,200 million years ago[4]. This would mean that the earliest animals are missing from the fossil record because they left few, if any, remains. For example, they may have lived in the water column or as microscopic life in sediments. The so-called Cambrian 'explosion' 600 million years ago would then largely relate to the acquisition of skeletons.

Molecular clocks are notoriously difficult to calibrate, however, and these 'deep time' estimates for the divergence of the major groups of animals have been drastically

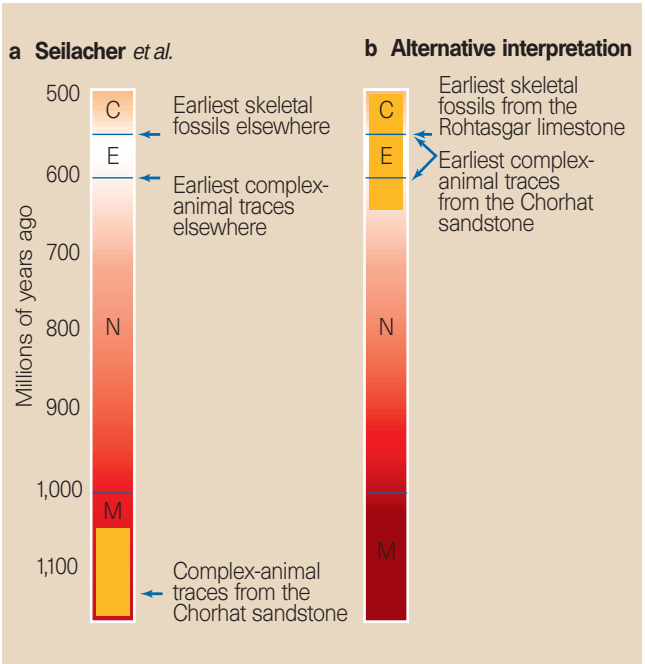

Figure 1 **Time and animal evolution.** a, **Seilacher and colleagues' view. Based on the authors' interpretation[1] of possible trace fossils in the Chorhat sandstone, the earliest evidence of complex animals appears about 1,100 million years ago, in the Mesoproterozoic (M) and well before the Neoproterozoic (N), Ediacaran (E) and Cambrian (C).** b, **An alternative interpretation, in which the trace fossils are only slightly older than newly discovered Cambrian skeletal fossils from the overlying Rohtasgar limestone[10]. The age span of the Vindhyan rocks is shown in yellow.**