

absence of Pax5, maturation in the bone marrow proceeds to the next stage, pre-BI, during which D_H and J_H heavy-chain gene elements recombine⁶, initiating the process that creates a unique antigen-binding site for the antibody. E2A and EBP cannot be sufficient for B-cell commitment because both are still expressed in cells deficient in Pax5 protein⁶.

B-lymphoid maturation can be recapitulated *in vitro*⁷. Pre-BI cells from bone marrow can be cultured for prolonged periods on support cells in the presence of interleukin-7 (IL-7), but, once removed from IL-7, they complete rearrangement of their immunoglobulin genes and differentiate into B cells bearing antibody receptors. As expected, Nutt *et al.*¹ found that pre-BI cells from Pax5-deficient mice were completely unable to differentiate into B cells when depleted of IL-7, unless Pax5 expression was restored.

The big surprise came serendipitously, when cultures that were left unattended for too long ran out of IL-7. Whereas the wild-type cells differentiated into mature B cells and died, the Pax5^{-/-} cells survived and many changed form, looking suspiciously like myeloid cells. Intrigued by this metamorphosis, Nutt *et al.*¹ started adding known myeloid cytokines to the IL-7-starved cultures. They found that the cells now exhibited a remarkable range of potentialities, as shown in Fig. 1. The cytokine M-CSF (macrophage colony-stimulating factor) induced terminally differentiated macrophages; GM-CSF (granulocyte-macrophage CSF) produced dendritic cells capable of activating T cells; Trance produced multinucleated osteoclasts; and G-CSF treatment following application of a cytokine cocktail produced granulocytes. The cells could also be persuaded to become natural killer cells, if cultured on support cells in IL-2. Even more strikingly, Rolink *et al.*² found that Pax5-deficient clones could fully reconstitute T-cell development in immunodeficient mice, and the resulting thymocytes were hallmarked by clonal D_H - J_H rearrangements indicative of their B-lymphoid origin, as well as having rearranged T-cell-receptor genes.

Significantly, single-cell sorting confirmed that individual Pax5^{-/-} pre-BI cells were multipotential — multiple subclones developed into macrophages, osteoclasts, dendritic cells or T cells, although production of natural killer cells and granulocytes was more variable. Clearly, Pax5-deficient pre-BI cells are not merely thwarted B-lymphoid cells. These cells could not save lethally irradiated mice, so not all haematopoietic options appear to be open to them. Nevertheless, it will be important to determine their full potentiality, both *in vitro* and in various *in vivo* settings. In particular, can they also be persuaded to become erythroid cells or platelet-producing megakaryocytes? Spleen-colony assays in irradiated mice

should shed some light on this question.

These studies^{1,2} confirm and extend previous evidence for the differentiation plasticity of certain early B-lymphoid cells (see ref. 8) and suggest that alternative fates are preserved in stem and progenitor cells by simultaneous low expression of master genes for several lineages⁹. Consistent with this view, Pax5^{-/-} pre-BI cells express genes from several lineage-affiliated programmes.

In normal B-lymphocyte development, the function of Pax5 thus appears to be just as much to suppress promiscuous transcription of genes specific for other haematopoietic lineages as to promote the expression of B-cell-specific genes. Complete suppression of other fates and full commitment to a B-cell future probably require a threshold level of Pax5 protein because, intriguingly, although both Pax5 alleles are expressed in immature B cells, only one allele is used in the earlier progenitors¹⁰.

The search is now on for the relevant target genes controlled by Pax5. Comparative screens of Pax5 mutant complementary DNA against that of normal pre-BI cells have identified several genes activated or repressed by Pax5, although to date none of them can alone account for the early developmental block¹¹.

Optics

Liquid versus photonic crystals

Eli Yablonovitch

A new paradigm has emerged in the past decade, in which the band-structure concepts of solid-state physics are applied to radio, microwave and optical waves. This has led to the invention of new forms of photonic crystal structures for controlling electromagnetic waves in three dimensions^{1,2}. These new structures are inspired by the three-dimensional geometry of both natural crystals and those that arise only in the human imagination. The latest step in this saga appeared in a paper in *Physical Review Letters*, in which Busch and John³ propose the first marriage of liquid crystals and photonic crystals. To appreciate this fully we have to recall the epic struggle to find an artificial crystal structure that would do for electromagnetic waves what a semiconductor crystal does for electron waves — a three-dimensional photonic bandgap that excludes a chosen range of frequencies.

The first proposals for a photonic bandgap^{4,5} called for face-centred-cubic (fcc) artificial crystals, because that geometry appeared to have the most promising interactions with electromagnetic waves. But it was surprisingly difficult to make a photonic bandgap and it was two years

The Pax5-deficient pre-BI cell lines are relatively robust and amenable to retroviral transduction and therefore should help to illuminate many aspects of haematopoietic differentiation. They are ideal test-tubes for screening for lineage-committing transcription factors, as well as for identifying their target genes. With inducible vectors, even the earliest steps in the developmental programmes should be accessible. The scientific fate of these fascinating cells, which flirt with so many destinies, seems assured. ■

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before an apparent success was reported⁶. That triumph was to be short lived. After some serious computations^{7,8}, a number of theorists agreed that it was actually a pseudo-gap masquerading as a real gap. This led to considerable concern, hand wringing and editorializing⁹.

The anxiety did not last long. Ho, Chan and Soukoulis¹⁰ discovered that a special

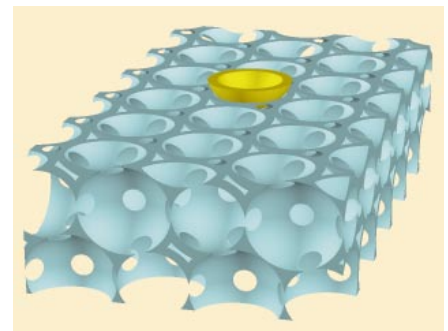


Figure 1 A marriage of liquid and photonic crystals. An inverse opal photonic crystal structure partially infiltrated with liquid crystal molecules, as proposed by Busch and John³. Electro-optic tuning can cause the photonic bandgap to wink in and out of existence

type of fcc packing, in which there are two atoms in each face-centred unit cell, possessed the long-sought photonic bandgaps. Those two atoms per cell are the famous diamond structure of engagement rings, hard industrial stone and silicon electronic chips — now reinvented for electromagnetic waves and Maxwell's equations. Diamond topologies quickly led to the first working photonic-bandgap crystal¹¹, albeit at inappropriately named 'microwave dimensions'. These structures are not microscopic at all. They are big and easy to make in a conventional machine shop, but their complex geometry is hard to fabricate at optical wavelengths^{12,13}.

Nature, of course, prefers to make simple fcc crystals. For example, SiO₂ spheres naturally self-assemble as fcc in opal, another jewel. As we saw, simple, easy-to-make fcc crystal structures had been proposed as photonic bandgaps^{4,5}, initially corroborated⁶, and finally rejected^{3,8,10}. But the tables were to turn again. The periodic structure of a crystal forces the frequencies to fit into a series of allowed bands. Everyone had been looking for a forbidden bandgap in fcc between the second and third bands. Gazing higher, between the eighth and ninth bands, Joe Haus and colleagues¹⁴ discovered a true forbidden gap in fcc; it was not a large one — only a few per cent of its central frequency — but it was a forbidden gap nonetheless.

The fcc geometry preferred by Maxwell's equations consists of spherical voids that are easily made by etching away spheres in a matrix of our choosing. Busch and John³ chose a silicon matrix, very appropriate to our times. They then added a new ingredient by calculating what would happen if the spherical voids of the photonic crystal were partially filled with liquid crystals (Fig. 1). We recognize liquid crystals as the electro-optic display molecules in portable computers. An electric field can rotate these molecules, thereby modulating the refractive index of the twisted nematic liquid crystal from $n = 1.4$ to $n = 1.6$, a fairly respectable change. Busch and John show that by applying an electric field to their hypothetical material a 2% photonic bandgap may be completely opened or closed. They give this new concept the rather glamorous name of a 'tunable electromagnetic vacuum'. Electromagnetic fluctuations are indeed being tuned in and out of existence, but they exist within tangible materials like silicon and liquid crystal molecules, rather than a vacuum.

In fact, as much as 40% of Busch and John's proposed photonic structure is a vacuum. To work correctly, the spherical voids must have their internal surfaces coated by the liquid-crystal molecules, so becoming half filled and leaving voids that may be difficult to achieve in practice. Nonetheless, Busch and John have linked forever the fields of liquid and photonic crystals. For example,

such materials could lead to light-emitting diode displays with pixels whose colours can be altered.

It is possible that the liquid/photonic crystal idea might bear fruit in structures even simpler than the three-dimensional fcc crystals. Two-dimensional photonic crystal semiconductor films have recently made the tiniest lasers, and probably the tiniest electromagnetic cavities, ever¹⁵. In conjunction with liquid crystals, they can be subject to extraordinarily delicate control, over lasing and other functions. Among possible applications, we may find photonic crystal lasers¹ in tiny optical integrated circuits, or we may see photonic crystals performing as simple white pigments or as radio wave structures in wireless information appliances, such as palmtop computers and sophisticated mobile phones².

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Photosynthesis

Stealing the limelight on the forest floor

By only opening their stomata — the pores in their leaves through which carbon dioxide enters and water leaves — at night, and thus achieving a temporary carbon dioxide fix using the enzyme phosphoenol pyruvate carboxylase, so-called CAM plants are able to minimize water loss. Not surprisingly, they are typically associated with arid environments. But a question mark hangs over certain bromeliads (members of the pineapple family) that grow in the deeply shaded understory of Central American rainforests. Such moist, low-light environments seem inappropriate for CAM plants, but the work of John Skillman *et al.* has shown that they occupy a niche in which high light tolerance and drought resistance have unexpected advantages (*Ecology* **80**, 1584–1593; 1999).

Most of the CAM plants in rainforests are epiphytes, growing perched on the branches of trees. Here, without access to groundwater, CAM metabolism helps them to survive occasional hot, dry spells. But there are also CAM plants growing in the shady understory. *Aechmea magdalenae*, pictured here, is a ground-dwelling bromeliad that grows in a range of habitats in



Central America, from well-drained, open locations to moist, shaded sites on the forest floor. Skillman and Winter previously found that *Aechmea* is capable of high photosynthetic rates under bright light (*Plant Physiol.* **113**, 441–450; 1997). But how can it compete in the shade — particularly as CAM plants are less efficient photosynthesizers than 'C₃' plants (the most widespread form of plant metabolism) where light levels are low?

One possible explanation is that *Aechmea* is particularly adept at exploiting the occasional patches of high-intensity sunlight ('sunflecks') that penetrate the dense canopy of the forest. Using chlorophyll fluorescence, which records the energy-trapping stage of photosynthesis, Skillman *et al.*

found that experimental artificial sunflecks produced a much stronger response in *Aechmea* than that found in C₃ plants from the same habitat, accompanied by a shorter lag phase for the plant to adjust to the new light conditions.

They also found that *Aechmea* allocates less energy to root formation, and grows more slowly, than associated C₃ plants. But it can gain an advantage over other plant species during the dry season. When soil water becomes scarce, the water conservation properties of the bromeliad, resulting from its tough leaves and its capacity to keep its stomata closed in the daytime, ensure survival and continued growth. *Aechmea* grows best during the dry season, whereas the C₃ plants grow best in the wet season. Although the forest floor is generally shady and moist, there is clearly a niche here for a plant that can take advantage of brief periods of high light and low water availability. Even among shade plants, there are some destined to grab the limelight.

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