

region of the northern plains is a 3,300-km impact basin, a feature so large that it must date from the early heavy bombardment. That hypothesis was strengthened by the discovery of a broad depression, the outline of which coincides with that of the buried basin⁴, and by a large, positive, gravity anomaly having a magnitude consistent with the nearly complete infilling of an ancient impact depression by younger sedimentary and volcanic material⁵. But the work of Frey *et al.* extends the mapped area of ancient surface to nearly the entire northern lowlands and quantifies the density of impact features.

The crustal dichotomy, then, might be the most ancient structural feature preserved on the Martian surface. If so, there are several implications for our understanding of the geological and geophysical evolution of the planet. The northern lowlands must have exerted a primary influence on the flow direction of surface and subsurface water on Mars for the entire duration of preserved geological history⁶, and much of the material making up the veneer overlying the ancient northern surface probably consists of sediments. The high density of newly detected large impact structures within the Utopia basin — whose original depth might have been comparable to the nearly 10-km relief of Hellas, a partly filled basin of similar diameter in the south — implies that much of the resurfacing of the northern hemisphere occurred during the period of early impact bombardment. The incomplete burial of impact craters allows the thickness of the younger northern-plains units to be estimated at typically 1–2 km, but that figure could exceed 5 km in a few areas near major volcanic centres where no older craters can be seen². The difference in elevation between the north and the south requires a generally thinner crust in the north⁵. Because lateral flow of lower crust would tend to reduce such variations if the temperature at the base of the crust exceeded about half the local melting temperature^{5,7}, preservation of the dichotomy implies that the lower crust cooled rapidly after early crustal formation — perhaps as a result of deep hydrothermal circulation⁸.

A question, first raised when the crustal dichotomy was discovered, remains. What caused it? Suggestions have ranged from removal of crust in the northern hemisphere by one or more large impacts, to hemispherical differences in crustal addition or internal recycling by dynamical processes in the underlying mantle. None has proved fully persuasive⁹. At the least, however, the demonstration that the crust in both hemispheres formed very early in the history of Mars adds a fresh requirement for any successful explanation of this long-standing mystery. ■

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Embryology

Fluid flow and broken symmetry

Claudio D. Stern

The asymmetries between the right- and left-hand sides of the body are initiated at an early stage of development. Two groups provide welcome news of progress in revealing the mechanism concerned and its generality.

How an embryo first distinguishes its left from its right side has baffled embryologists for a long time. The rotational beating of cilia — hair-like structures attached to individual cells — is known to be essential for the process. But cilia have been seen only in mouse embryos, and it has remained unclear whether their movement could really generate the necessary molecular asymmetries. Papers by Essner *et al.*¹ and Nonaka *et al.*² (pages 37 and 96 of this issue) set our understanding on a much firmer footing in both respects.

Despite its superficial appearance of bilateral symmetry, the vertebrate body plan is asymmetric in several respects, most obviously in the position of internal organs such as the heart and parts of the gut. Left–right asymmetry first arises in the embryo at around the stage — the gastrula — when the three major cell layers of ectoderm, mesoderm and endoderm are first laid down. But until recently we knew virtually nothing about the molecular mechanisms responsible.

The turning point came in 1995 when four genes (*Sonic hedgehog*, *Nodal*, *HNF3 β* and the *Activin-receptor IIA*) were identified as being expressed on one or the other side of the chick embryo at the gastrula stage, and their activities were implicated in heart turning³. However, subsequent work revealed that only one of these, *Nodal*, is expressed asymmetrically in all vertebrates. Shortly afterwards it was discovered that a mouse mutant, called *iv* and characterized by random positioning of internal organs, carries a mutation that inactivates left–right dynein (LRD), a protein required for the beating of cilia⁴. Researchers then looked for cilia in the mouse gastrula and found that the ‘node’, a critical organizing structure in the midline of the early embryo, does indeed possess short cilia protruding from its cells, which beat in an anticlockwise circular motion and generate a leftwards flow of fluid that is strong enough to displace solid particles to the left^{5,6}. But again, the cilia could be found only in the mouse. Could different vertebrates

have evolved different ways of establishing asymmetry? And could the beating of cilia really be sufficient to generate molecular asymmetry by removing a ‘morphogen’ signal from one side of the embryo and enriching it on the other?

The papers by Essner *et al.*¹ and Nonaka *et al.*² answer both questions. Essner *et al.* reveal that cilia, as well as LRD, are indeed present in all the major vertebrate groups at appropriate stages and locations to generate left–right asymmetry. Nonaka *et al.* show that a flow of fluid in the reverse direction to that generated by cilia can randomize embryonic asymmetry — and that artificially induced fluid flow is enough to control the position of the internal organs in *iv* mutant mice.

The idea that the circular beating of tiny cilia could be enough to generate a biologically meaningful molecular gradient within a large, relatively open fluid space seemed rather unlikely when it was first proposed⁵. Nonaka and colleagues have designed an ingenious mechanical device to demonstrate that it is indeed possible to control the distribution of molecules by regulating the direction of fluid flow around embryonic cells. The experimental design was similar to one described nearly 20 years ago⁷. There, it was demonstrated that gentle flow applied to a wounded sheet of cells in culture restricted healing growth of the wound to the downstream side of the flow, as if it were controlled by the local distribution of a growth factor. The study by Nonaka *et al.* now reveals a likely role for this mechanism *in vivo*. It highlights the significance of bio-mechanical phenomena in generating biological pattern, an idea that has hitherto been broadly dismissed.

In contrast, the finding¹ that cilia and LRD are associated with the node or its equivalent structures in all major vertebrate groups is reassuring. Developmental biologists generally choose one ‘model’ organism or another according to the experimental advantages it offers, with the underlying assumption that the basic principles should

be much the same in different species. That this is generally true is evident in a huge body of data revealing that genes responsible for patterning the body of the fruitfly have similar functions in vertebrates.

Several questions remain open. What, for instance, are the critical molecules whose distribution is being controlled by ciliary beating? What mechanisms determine the direction of ciliary rotation within each ciliated cell? Why is *Nodal* the first asymmetrically expressed gene common to all vertebrates, whereas other factors are variable? And in the chick embryo, the earliest molecular asymmetry seems to be the right-sided localization of the *Activin-receptor IIA*³ just before the earliest expression of *LRD* and the appearance of nodal cilia¹, which raises the question of whether other symmetry-breaking mechanisms might exist at earlier stages of development. ■

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Materials science

Crystallization of silicon ideas

John Robertson

The more desirable form of silicon for use in display screens is also the more expensive to manufacture. Understanding how crystalline silicon forms could be a key to cheaper communications devices.

Amorphous silicon is the leading electronic material for large-area applications, used in solar cells and in the thin-film transistors that make up liquid-crystal displays. However, amorphous silicon suffers from an electrical instability that causes a gradual loss of conversion efficiency in solar cells. There is another form of silicon, nanocrystalline silicon, that is more stable and whose charge-carriers (electrons and holes) are more mobile, making it more attractive for use in these applications.

Amorphous silicon can be made easily by deposition from a silane (SiH₄) plasma, and nanocrystalline silicon can be made by the same process, under slightly modified conditions. But the exact means by which nanocrystalline silicon, rather than amorphous silicon, forms has been the subject of debate. Now Sriraman and colleagues¹ might have found the answer: on page 62 of this issue, they propose that hydrogen atoms from the silane plasma catalyse the

rearrangement of Si–Si bonds, triggering a solid-state transformation of the random amorphous-silicon network into the more ordered network of nanocrystalline silicon.

Nanocrystalline silicon can be deposited from a silane plasma that has been heavily diluted with hydrogen so that there is a high concentration of atomic hydrogen in the plasma. The most popular explanation of the deposition process has been that nanocrystalline silicon and amorphous silicon are deposited simultaneously, and then the atomic hydrogen etches away amorphous silicon more quickly, leaving mostly nanocrystalline silicon². Once formed, the two solid phases can then only interconvert via the gas phase.

An alternative explanation is that atomic hydrogen permeates the film of amorphous silicon, lowering the energy barriers to the rearrangement of the silicon network into a more stable, more ordered nanocrystalline lattice³. But, until now, the precise mecha-

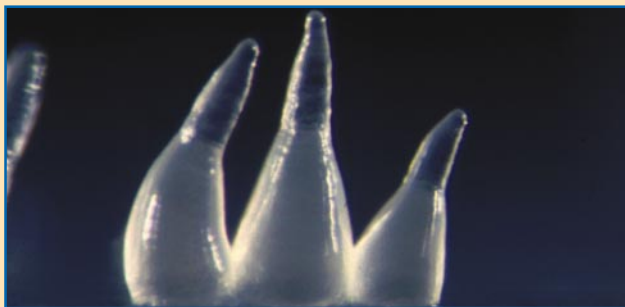
Genome sequencing

Stick it in the family album

You may feel that you have some relations that resemble the cellular slime mould *Dictyostelium discoideum*, shown here. If so, you would be right. For years there has been debate about where this organism sits on the tree of life, and whether it belongs with plants or animals. But a partial genomic sequence — that of chromosome 2, described by Gernot Glöckner *et al.* in this issue (*Nature* **418**, 79–85; 2002) — confirms its closer kinship with animals.

Dictyostelium — *Dicty* to its friends — is a soil amoeba but nonetheless a eukaryote: an organism with a membrane-bound nucleus. It has long been recognized as an excellent model organism. It shows much of the genetic flexibility of yeast, and has complex signalling pathways as well as chemical-sensing behaviours like those seen, for instance, in white blood cells.

A multinational team of sequencing centres (www.uni-koeln.de/dictyostelium/consortium.shtml) is sequencing the roughly 34 million bases of the *Dicty* genome and mining them for insights into eukaryotic life. But sequencing is dogged by the problem of high A–T base-pair content, and subsequent analysis is also challenging because of the high repetitive content (around 10%).



To surmount some of the hurdles in sequencing, the various groups constructed libraries from each chromosome separately and carried

out shotgun sequencing on each library. But the chromosomal libraries are only about 60% pure, so each group is also generating a whole-genome shotgun. By pooling the data from several libraries, Glöckner *et al.* could fish for the maximum number of pieces of chromosome 2 using known chromosome-2 genes as bait. Tying these pieces together and fitting them onto a backbone of clone-based sequences yielded a mostly complete chromosome sequence, which at 8.1 million bases

is about 25% of the genome.

Analysis of chromosome 2 indicates that there are 2,799 protein-coding genes and 73 transfer RNA. On this basis, the entire genome should contain 10,500 to 11,500 genes, with a density similar to that in budding and fission yeasts. Comparison with sequenced eukaryotic genomes revealed about 45% matches to protein-coding genes, and 55% unique to *Dicty*. Although this number seems high, it is in line with estimates for the available sequences of other eukaryotes.

At the same time, analysis of chromosome 2 has already uncovered more family resemblance, as it encodes proteins similar to several cytoskeleton-related and signalling proteins in animals.

With sequences of the remaining five chromosomes coming shortly, *Dicty* will soon need a page in the family photo album. **Chris Gunter**

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