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stresses in the upper crust and triggering earthquakes remains unclear, yet these two very different tectonic regimes share a common feature:  $^3\text{He}/^4\text{He}$  ratios much higher than expected for regions virtually devoid of mantle melting (8, 9). Looking more closely at the helium isotope characteristics of such regions—spatially and temporally—may provide evidence coupling the leaking mantle

to one of our greatest natural hazards.

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## GENETICS

# Paradigm for Life

James O. McInerney and Davide Pisani

It has been known for more than 60 years that prokaryotes can swap their DNA through the processes of conjugation, transformation, and transduction (1). This acquisition of foreign genes is generally referred to as horizontal gene transfer (as opposed to vertical inheritance, in which an organism receives DNA from an ancestor).

The consequence is that each prokaryotic chromosome is a mosaic of vertically inherited and horizontally acquired genes (2). On page 1449 of this issue, Sorek *et al.* (3) report the first large-scale empirical analysis of the transferability of genes by analyzing the introduction of almost a quarter of a million genes from other eubacterial and archaeobacterial species into the eubacterium

*Escherichia coli*. The findings provide insight into the likely evolutionary history of prokaryotes and indicate that interspecies gene transfer is not restricted to special categories of genes, nor are there categories of genes that cannot be transferred.

The role of horizontal gene transfer in evolution has raised fierce debate about the relevance of the Tree of Life, a long-accepted representation of the interrelatedness of living things through evolutionary time, based primarily on the sequence of the genes that encode the small subunit of ribosomal RNA (4). The question is whether this depiction should be replaced with a network, or Web of

Life (5) (see the figure). Whereas a tree reflects evolution as a process in which new species arise, or branch, from specific ancestors, a web may more accurately portray microbial evolution based on the rise of variation (and new species) through the lateral transfer of genetic information between distantly related species.

Using phylogenetic methods, it has been proposed under the complexity hypothesis that not all genes are equally affected by horizontal gene transfer (6). Two classes of genes have been identified.

**Tree or Web?** There is an ongoing debate about whether the genetic relationship of life on the planet should be depicted as a Tree or Web of Life.

Informational genes—those involved in DNA replication, transcription, and translation—are part of more complex protein-interaction networks and are thus less likely to be involved in horizontal gene transfer. So-called operational genes—those involved in day-to-day processes of cell maintenance, such as genes that control energy metabolism and the biosynthesis of nucleotides and amino acids—may be more prone to transfer (6). This has led to the notion that a core of nontransferred or rarely transferred genes might have kept track of the clonal history of prokaryotes. If this prediction were true, the Tree of Life hypothesis would hold, even in the presence of rampant horizontal gene transfer (5).

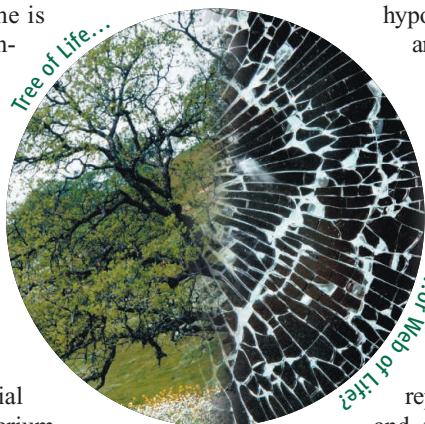
Up to now, a major obstacle to understanding the role of horizontal gene transfer in evolution was the lack of large-scale experimental evidence that might corroborate or reject the existence of a core set of genes. Sorek *et al.*

Lateral gene transfer may have spurred microbial evolution, producing a pattern of evolution that resembles a network, rather than a tree.

have gone a considerable way in providing data to test this idea. The authors found that among 246,045 genes from 79 different species of prokaryotes, there was no single gene that, along with all its prokaryotic homologs, resisted transfer by way of a plasmid (thus, gene transfer by transduction) into *E. coli*. However, whereas all gene families could be cloned into *E. coli*, some genes were not easily transferred. Members of informational gene families represent a substantial fraction of those resilient to cloning, lending more weight to the complexity hypothesis (6). And even though 1402 genes were impossible to transfer, favoring the existence of core genes, transferable orthologs of these genes were found, thus opposing the core hypothesis.

There are currently almost 6000 accepted prokaryotic species, but the analysis by Sorek *et al.* could only deal with *E. coli*, because adequate data are currently available only for this species. It is possible that if a different host was used, a different set of untransferable genes might have been identified.

Sorek *et al.* also report that genes from prokaryotic genomes enriched in the nucleotide bases guanine (G) and cytosine (C) are more transferable, consistent with the observation that the synonymous usage pattern of codons (triplets of nucleotide bases that encode amino acids) in recently acquired genes in *E. coli* is different from that of native genes (2). The explanation might be that promoter regions (DNA sequences that control the transcription of a gene) in the *E. coli* genome are GC-poor; hence, GC-rich promoters might not work well and would result in nontranscription. It is thought that one of the most important ways to introduce foreign DNA into an organism is by stealth: repressing the expression of the introduced gene until



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it is widely distributed in the host species and then allowing expression (7). The stealth model of successful horizontal gene transfer implies that it may be easier to introduce DNA from a distant relative with different nucleotide base composition and different promoter characteristics than from a closer relative. For example, Sorek *et al.* show that  $\gamma$ -proteobacterial genes are more difficult to transfer into *E. coli*, which is itself a  $\gamma$ -proteobacterium. This is consistent with the observation that a well-supported tree seems to exist only toward the tips of the Tree of Life (within bacterial phyla, there is a strong phylogenetic signal associated with vertically inherited genes) (8, 9).

The question now is whether experimentally forced horizontal gene transfer is a fair comparison to that in nature. In the laboratory, cloned genes carried on a plasmid remain in an *E. coli* cell under strong selection conditions for the plasmid (such as antibiotic resistance). In such conditions, only highly deleterious genes would be

absent from the set of cloned genes. The non-transferred genes must therefore be a subset of those that would never successfully propagate in *E. coli* in a natural setting.

Many of the forced horizontally transferred genes would never remain in *E. coli* outside the laboratory because they would not be associated with the selection genes used in experimental analyses, such as those that confer antibiotic resistance. Evolutionary biologist W. Ford Doolittle stated that if horizontal gene transfer was not limited to special categories of genes, then no system of classification could be considered natural (5). The results of Sorek *et al.* show that even if some barriers to horizontal gene transfer into *E. coli* exist (they seem to be associated with dosage-toxicity effects), they are rather low. Data on more than one host would answer whether the results are peculiar to *E. coli*.

For now, we know the profile of gene resistance to lateral transfer in one organism, but the existence of a prokaryotic Tree of Life remains an open question. Sorek *et al.*

do not address the issue of horizontal transfer and genomic fusions in eukaryotes. However, recent analyses show that eukaryotes have a chimeric nature (9, 10). When eukaryotes are included in our considerations of evolution, the phylogeny of life seems better represented by a network than a tree, making any core genes-based argument in favor of the Tree of Life essentially irrelevant.

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## CHEMISTRY

# Surface-Conducting Diamond

Christoph E. Nebel

On page 1424 of this issue, Chakrapani *et al.* (1) prove experimentally that an insulator—diamond—can become a metal by charge transfer from the solid to the liquid (2). A similar type of charge transfer has long been known to occur in solid/solid junctions used in ultrafast transistors (3). The effect should find application, for example, in chemical and biological sensors.

In solid/solid junctions, electrons migrate from the semiconductor with the larger band gap (a band of “forbidden” energies that cannot be occupied by electrons) into the semiconductor with the lower band gap, thereby losing energy and becoming trapped because they cannot climb back over the interfacial barrier. This motion separates the negatively charged electrons from their positively charged donors and is one of the reasons for the ultrahigh mobility of electrons in this two-dimensional system.

Chakrapani *et al.* now prove that a similar phenomenon takes place at the solid/liquid

interface, based on the migration of carriers from the solid (diamond) into the liquid (electrolyte). The authors show unambiguously that electrons from diamond transfer into redox electronic states of the electrolyte. This transfer generates a highly conductive surface layer in diamond, which originates from missing electrons (termed “holes”).

In 1989, Landstrass and Ravi showed that diamond can be reversibly transformed from insulating to metallic (3). The work attracted much attention and controversy. Two groups developed electrochemical models to explain the observations (4, 5), but both teams focused on water layers adsorbed in the diamond surface. These layers are ill-defined and their electrochemical properties are thus difficult to pin down. Therefore, the electrochemical basis for the observed effect has not been understood until the present work.

The migration (or tunneling) of electrons from diamond into the electrolyte requires that empty electronic states exist in the liquid and that they can be reached without having to cross a substantial energy barrier. In semiconductors, the valence band is filled with electrons and therefore can be considered the main electron source in this process. However, most

Experiments reveal the mechanism by which diamond surfaces can become conducting.

semiconductors have a valence-band maximum lower in energy than corresponding electrochemical levels (5). To reverse this scenario, a strong electronic surface-dipole layer is required. In the case of diamond, the properties of this dipole layer—and hence the electron affinity of the diamond surface—can be tuned by using hydrogen and oxygen atoms to terminate carbon bonds at the surface (6).

With changing termination from oxygen to hydrogen, the valence-band maximum shifts continuously to higher energies (see the figure). This continuous variation of the surface energy can be used to tune the energetic levels of diamond with respect to redox molecular levels at the solid/liquid interface. It is comparable to the band-gap engineering at the solid/solid interface of semiconductors and will be important for the optimization of bioelectronic devices; diamond is a highly promising material for such devices, because it provides strong bonding to biomolecules like DNA and proteins (7).

The surface conductivity properties generated by this “transfer doping” are interesting, because the holes in diamond are confined to a fairly deep yet very narrow energy well (8, 9). Theoretically, holes can propagate in this

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