

GENOME WATCH

Microbial genomes as cheat sheets

Hayley M. Bennett



This month's Genome Watch describes how horizontal gene transfer from bacteria and archaea has allowed an alga to live in extreme environments.

Horizontal gene transfer (HGT) is the transfer of genes between organisms by a means other than direct inheritance from a parental cell. Within bacterial and archaeal domains, HGT is extensive and propagates fitness traits. However, so far only few studies have found evidence for HGT that contributed to eukaryotic evolution.

The red alga *Galdieria sulphuraria* lives in one of the most extreme eukaryotic habitats. It can be found in geothermal sulphuric springs and other hostile environments characterized by acidity, heat, darkness, and high concentrations of salts, arsenic and toxic metals. Genomic analysis¹ now suggests that *G. sulphuraria* has adapted to these extreme conditions by acquiring specialized enzymes and membrane proteins through HGT from a wide range of bacteria and archaea. After sequencing and assembly of the 14 Mb *G. sulphuraria* genome using plasmid, fosmid and BAC libraries, the algal genes were investigated phylogenetically for an evolutionary signature that would indicate inter-domain HGT. More than 75 genes or gene families were found to encode proteins with orthologues in only bacteria and archaea.

Many of these genes contribute to the metabolic versatility of *G. sulphuraria*, which can survive heterotrophically (without light) on more than 50 different carbon sources. Acetate permease genes in the algal genome are of bacterial origin, whereas some of the amino acid–polyamine–organocation transporter genes were acquired from archaea. Interestingly, two separate HGT events seem to have contributed to the ability of *G. sulphuraria* to survive on glycerol as the sole carbon source: gain of a glycerol dehydrogenase

gene from the order Bacillales and gain of a glycerol uptake facilitator gene from the order Xanthomonadales.

Soluble ATPases, which had not previously been observed in eukaryotes, make up two large protein families in *G. sulphuraria*. The correlation of ATPase gene copy numbers and heat tolerance in archaea suggests that soluble ATPases have a role in extreme temperature adaptation. The genomic arrangement of the ATPase genes in the alga indicates that they underwent a series of duplication and diversification events after transfer from archaea. This might have facilitated fine-tuning of the proteins to the requirements of the new host cell machinery and could also have given rise to new functional roles in the alga.

Arsenite methyltransferases, which bio-transform arsenic into less toxic forms, had previously been reported in *G. sulphuraria*². In the genomic analysis, an algal orthologue of ArsB, a bacterial arsenic efflux pump that provides resistance to the toxic element, was also identified¹. No similar protein has been found in other eukaryotes, and the two genes that encode algal ArsB lack introns (a typical feature of bacterial genes), providing further support for the HGT hypothesis. *G. sulphuraria* mercuric reductase, which detoxifies mercury, was also found to be of proteobacterial origin.

Although it seems that *G. sulphuraria* owes a considerable amount of its ability to survive in its specific niche to extremophilic neighbours,

not all of the success of this organism can be attributed to the procurement of genes from other species. The genome also revealed that *G. sulphuraria* has a single voltage-gated ion channel, as opposed to the 16 or more that can be found in other algal species. Instead, *G. sulphuraria* favours chloride channels, which do not conduct protons. This reduces the permeability of the alga to acid, enabling it to keep a neutral cytosol in low-pH environments, such as run-off water from the man-made mines and geothermal outflows in which the alga thrives.

G. sulphuraria is probably not the only eukaryote that evolved to survive in inhospitable environments with the help of genes from other organisms. Algal species found in polar sea ice possess intronless genes encoding unique ice-binding proteins originating from ice-associated bacteria³.

How the genes have been horizontally transferred from bacteria or archaea to algae remains an intriguing mystery. The sheer range and variety of donor species reported for *G. sulphuraria* is certainly surprising given that, previously, HGT was considered to be primarily a bacterial or archaeal trait. Whether cross-domain contributions to eukaryotic evolution are exceptional or commonplace remains to be seen as more genomic information becomes available.

Hayley M. Bennett is at the Sanger Institute, Wellcome Trust Genome Campus, Hinxton, Cambridge CB10 1SA, UK.
e-mail: microbes@sanger.ac.uk

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Competing interests statement

The author declares no competing financial interests.

