



Horizontal gene transfer in microorganisms

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Horizontal gene transfer (HGT) is a major force in microbial evolution and a great source of genetic innovation in prokaryotes. The first evidence of HGT was reported in 1928 by Frederick Griffith, who noted that bacteria (pneumococci) are capable of transferring genetic information (virulence determinants) through a process known as transformation. Later, the identification of gene transfer mediated by plasmids (conjugation) and viruses (bacteriophages, transduction) and the recognition of transposable elements further improved our knowledge of gene flux and the importance of mobile genetic elements. The book *Horizontal gene transfer in microorganisms* provides state of the art information on this fascinating topic. The nine chapters are written by several experts in the field, including the book's editor M. Pilar Francino.

The flow of genes between different species is a form of genetic variation whose implications have yet to be fully appreciated. Strains of the same bacterial species frequently differ in up to 30–35% of their total genes in the genome, resulting in organisms with contrasting phenotypes and/or ecological strategies (e.g., highly invasive pathogens vs. commensal strains of *Escherichia coli*). Mobile genetic elements, such as transposons, phages and plasmids, account for most of the differences in gene content among closely related strains. This genomic flexibility contributes to the ability of bacteria to adapt to varying environmental challenges and thus ensure survival. The persistence of new genes depends on whether they are replicated as parts of integrated genomes. Genomes and genes evolve in response to natural selection at the organismal

level, as they regulate gene interactions and permanence (Chapter 1).

In prokaryotes, usually around 80% of the genome encodes proteins. Bacterial chromosomes also seem to be organized into regions with different gene expression levels. Functionally related genes are usually transcribed in operons or superoperons. Genomics and genome sequencing studies have confirmed that the position of genes in the chromosome is not random but the result of selection. However, despite these common organizing principles, prokaryotic genomes are extremely diverse. Bacterial genome sequencing has become so easy and accessible that the genomes of multiple strains of an increasing number of individual species have been and will be rapidly determined. These data sets provide for in-depth analysis of intra-species diversity.

The pan-genome is the sum of the core genome, i.e., those genes common to all strains, and the dispensable genome. The latter group of genes may confer adaptive advantages under certain environmental conditions, such as in the presence of antibiotics, xenobiotics, and other compounds. These genes also confer the important characteristics that allow the colonization of new ecological niches governed by biotic factors such as symbiotic and pathogenic relationships. Pan-genome analyses are aimed at interpreting the sequence data among widespread lateral gene flow. A comparison of 20 strains of *Escherichia coli* showed that the core genome consists of only 2000 genes, less than half the average genome size in a typical strain. Modifications of gene repertoires can strongly affect cellular

metabolism and morphology, and such changes can provide prokaryotes with the opportunities for adaptation to new ecological niches (Chapter 2). The mammalian-adapted bacterium *Bartonella* and plant-adapted rhizobia are discussed as examples in Chapter 3.

Horizontal gene transfer operates by a variety of mechanisms, relies on different ecological circumstances, and results in a wide range of fitness effects on the recipient organisms. Chapter 4 explores the barriers that limit HGT among microorganisms, such as DNA restriction. Exogenous DNA that survives restriction must be integrated into the bacterial host chromosome and then expressed in order to persist in the recipient cell. Transferred genes may continue evolving in different genomic and ecological environments. Chapter 5 analyzes the process of sequence divergence of transferred genes at different evolutionary time-scales in the Xanthomonadales, a group of plant pathogens belonging to Gammaproteobacteria. The genomes of the Xanthomonadales are the result of multiple HGT events from other Proteobacteria to the ancestral genome of the group. Chapter 6 discusses the environmental regulation of HGT, as opposed to genetic regulation at the cellular level as explained in Chapter 4. HGT has been studied in natural ecosystems, including soil, water, and the gut microbiota. Conditions in the gut are favorable for HGT because of the constant body temperature and inflow of nutrients, which support high population densities and vast diversity. Bacterial responses to host stress hormones can facilitate conjugative gene transfer between enteric bacteria. In in-vitro experiments, the physiological concentration of noradrenaline was shown to stimulate the transfer of a conjugative plasmid from a clinical strain of *Salmonella* sp. to an *E. coli* recipient. These mediators of host stress may affect HGT within the in vivo environment as well.

Plasmids, bacteriophage elements, transposons, and insertion sequences are mobile genetic elements because they can move between microbial cells. The total of all the mobile genetic elements in a cell is referred to as the mobilome. Despite the ability of plasmids to transfer across dif-

ferent taxonomic groups of bacteria, it is unclear which factors are responsible for plasmid continuance among bacterial populations. Chapter 7 describes the different hypotheses explaining the maintenance of plasmids.

Several approaches can be used to detect mobile genetic elements. In Chapter 8, four different experimental methodologies are described: sequencing studies, sequence-based screening, capture studies (hybridization with magnetic beads), and functional studies. The appearance and dissemination of antibiotic-resistance in bacterial pathogens have stimulated investigations of the genetic aspects of the different phenomena associated with resistance development, such as gene pickup, heterologous expression, HGT, and mutation. Chapter 9 focuses on HGT and recombination in the evolution of antibiotic resistance genes. Essentially any mobile genetic element found in bacteria can acquire resistance genes and promote their transmission; the type of element involved varies with the genus of the pathogen, but plasmid-mediated transmission is far and away the most common mechanism of HGT. Moreover, the existing processes of gene acquisition, transfer, modification, and expression are expanding and their presence in the modern biosphere is accelerating in response to anthropogenic influences.

Clearly, prokaryotes, are under different forms of selective pressures with respect to DNA exchange than most multicellular organisms. The theory of prokaryotic evolution needs further work as it must take into account the population genetics and molecular evolution of organisms that have no traditional species boundaries but share genes across considerable evolutionary distance. *Horizontal gene transfer in microorganisms* is an up-to-date and necessary review of the most topical aspects of HGT.

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