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Current Opinion in Microbiology

# Embracing the enemy: the diversification of microbial gene repertoires by phage-mediated horizontal gene transfer

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Bacteriophages and archaeal viruses contribute, through lysogenic conversion or transduction, to the horizontal transfer of genetic material between microbial genomes. Recent genomics, metagenomics, and single cell studies have shown that lysogenic conversion is widespread and provides hosts with adaptive traits often associated with biotic interactions. The quantification of the evolutionary impact of transduction has lagged behind and requires further theoretical and experimental work. Nevertheless, recent studies suggested that generalized transduction plays a role in the transfer of antibiotic resistance genes and in the acquisition of novel genes during intra-specific bacterial competition. The characteristics of transduction and lysogenic conversion complement those of other mechanisms of transfer, and could play a key role in the spread of adaptive genes between communities.

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**Current Opinion in Microbiology** 2017, **38**:66–73

This review comes from a themed issue on **Mobile genetic elements and HGT in prokaryotes**

Edited by **Andrew Lang**, **J Thomas Beatty**, and **Phoebe Rice**

http://dx.doi.org/10.1016/j.mib.2017.04.010



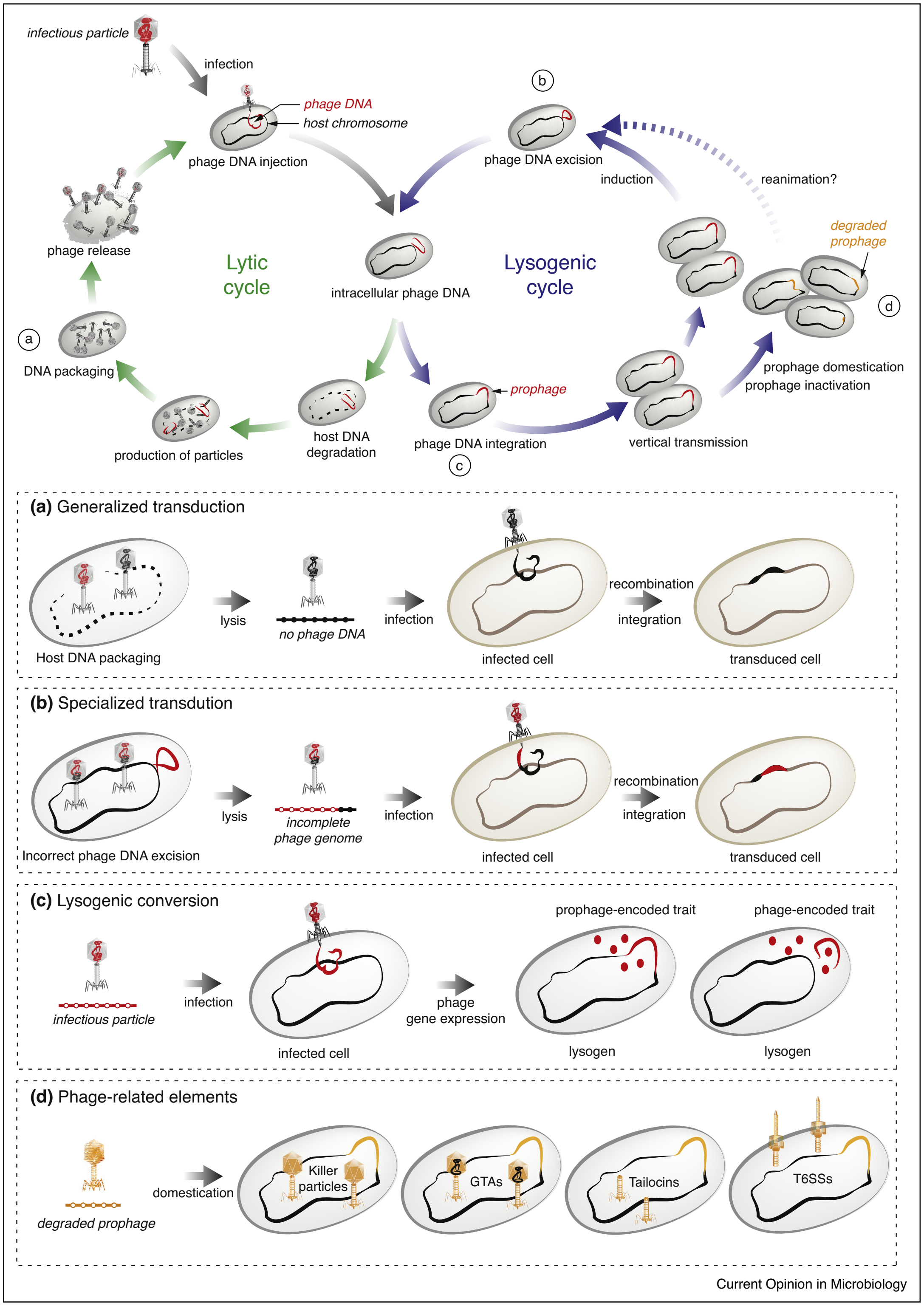
Horizontal gene transfer (HGT) drives the evolution of the genomes of Prokaryotes and includes three major mechanisms that involve bacteriophages and archaeal viruses (all called phages henceforth) (Figure 1). The outcomes of these processes depend on phages' lifestyles, packaging mechanisms, and a number of other molecular processes. Temperate phages may integrate temporarily the host genome, and the expression of their traits produces phenotypic changes that are not involved in the phage lifecycle and that are collectively known as *lysogenic conversion* [1]. The resulting prophages may excise erroneously and transfer a neighbouring piece of the host chromosome in a process called *specialized transduction*. Finally, host DNA may be erroneously packaged in the capsid and be transferred by *generalized transduction* to other hosts [2]. The amount of DNA transduced by phages is typically slightly superior to the size of its genome and depends on the internal volume of the capsid [3]. Other mechanisms of HGT implicate virion particles. They are reviewed in other articles of this issue and include transduction by gene transfer agents, the transfer of phages by vesicles, and the subversion of phage virions by genomic islands such as SaPI.

After several decades of less intense study, phages have come back to the spotlight due to increased interest in phage therapies to circumvent antibiotic resistance, to the discovery of numerous phage-encoded virulence factors, and because of phages' role in the regulation of microbial populations [4–6]. Transduction and lysogenic conversion, discovered many decades ago, are relevant for all these topics. They facilitate the spread of antibiotic resistance and virulence factors and, in the case of lysogenic conversion, may protect hosts from other phages. A combination of recent single-cell, genomics, metagenomics (viromes in particular), mathematical modelling, and other techniques has spurred a renewed interest in transduction as a force driving the diversification of microbial populations. This review focus on the most recent works on phage-mediated HGT. It also points to certain gaps in the current knowledge, many of which are caused by the immense diversity of the phage world [7], and the consequent difficulty in making generalizations from studies in specific model systems.

## Lysogenic conversion

Lysogeny often involves the integration of the temperate phage genome in the host chromosome, even if a growing number of prophages are found to replicate in cells as plasmids [8,9]. The expression of prophage genes leads to phenotypic changes in the host that may affect many different traits, including virulence, motility, and inter-bacterial competition (see Refs. [5,10] for reviews). The identification of the determinants of the decision between lysis and lysogeny can thus illuminate the role of lysogenic conversion in bacterial evolution.

**Figure 1**




Major phage-mediated HGT mechanisms.

Phages contribute to bacterial evolution by generating genetic diversity through horizontal gene transfer (HGT). Infection by temperate phages can lead to either the lytic cycle (represented in green) or the lysogenic cycle (represented in blue). Infection by virulent phages leads to the lytic cycle. *Transduction* occurs when newly forming phages acquire host genes and transfer them to other bacterial cells. (a) *Generalized transduction* can transfer random fragments of host or plasmid DNA into other phage sensitive cells. It occurs when phage packaging accidentally incorporates