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Short Communication **Open Access**

The Non-Mobile Plasmid DNA Transfer in *E. Coli*

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Plasmid transfer, normally mediated by a mobile element on the conjugative plasmid or conserved DNA uptake machinery at the bacterial membrane, often promotes bacterial resistances to antibiotics and other adverse stresses. For example, the transfer of the recently emerging NDM-1 plasmid transforms a normal bacterium to a superbug which is able to inactivate all beta-lactam antibiotics. Plasmid transfer through conjugation has long been established in *Escherichia coli*. It has traditionally thought that this bacterium is not naturally transformable, although it has competence gene homologs potentially encoding a complete set of DNA uptake components. Our work established that a non-conjugative plasmid spontaneously enters *E. coli* on the surface of agar plates independent of the conserved DNA uptake machinery. We also showed that the transfer of plasmid on plates is regulated by a general stress response regulator RpoS and that the mutation of its lysine 173 significantly decreases the transformation rate. The abundant surface protein OmpA had previous been shown as a receptor for conjugation and bacteriophage infection. Our recent work demonstrated that OmpA blocks the transfer of plasmid on agar plates but promotes DNA transfer in Ca2+ solution, indicating that OmpA plays opposite roles in natural and artificial transformation. Together, our work has established a model for investigating the spread of non-conjugative plasmid transfer and provided two targets for controlling bacterial resistance caused by the transfer of the 'non-mobile' plasmid.

Plasmids are, along with phages and integrative conjugative elements, the key vectors of horizontal gene transfer and essential tools in genetic engineering. They often code for genes involved in detoxication, virulence, ecological interactions, and antibiotic resistance. Hence, an understanding of plasmid mobility is essential to an understanding of the evolution of these important bacterial traits, often involved in human health or well-being. However, while the last decades have seen a remarkable enlightenment of plasmid mobility mechanisms in model systems, the identification and characterization of plasmid mobility on a global scale remain unexplored. There is a need to devise such a tool for several reasons. First, if we want to give a systems biology answer to the problems of plasmid dissemination, e.g., the dissemination of multiple-drug-resistant bacteria in hospital or farm environments or the evolution of catabolic plasmids in contaminated environments, we must understand plasmid mobility. A global understanding of plasmid mobility can help us control the dissemination of these fastidious genes and thus help curve the recent increase in human mortality produced by infectious diseases in advanced countries. By the same token, it can help the efficiency of bioremediation efforts or the biological fight against other types of

damaging bacteria. Second, microbial ecology is undergoing a revolution caused by the availability of metagenomic approaches that allow the sampling of the genetic diversity of microbial communities. Knowing how information flows in such communities is essential to interpreting how communities respond to changes. Third, the ability of plasmids to move between different hosts is of technical and industrial importance. The identification of the diversity of mobility mechanisms might allow the development of new, more-efficient, and better-adapted vectors for genetic engineering and the release of genetically modified microorganisms for bioremediation and pest control, etc. Most prokaryotes remain genetically intractable, and an understanding of the natural mechanisms of gene mobility is bound to allow the creation of new tools. Finally, conjugation is a secretion system that must adapt to cell physiology. An understanding of its diversity might enlighten how existing variants of this secretion mechanism are adapted to peculiar cellular envelopes or environments.

In this review we make use of the abundant available genomic data to extract a few general concepts that, we hope, will help our understanding of plasmid mobility. To carry out such an analysis, we first established a computational protocol to identify conjugation and mobilization genetic modules in 1,730 plasmids and used these data to establish a plasmid classification system. This allowed an accurate classification of proteobacterial conjugative or mobilizable systems in a combination of four mating pair formation (MPF) and six mobilization families (the term family is used here as it refers to protein families, that is, a set of proteins that are related in sequence and share a biological function). Few genes, e.g., those coding for conjugative coupling proteins, relaxases, and VirB4 proteins, are at the core of plasmid conjugation. Together with several auxiliary genes, they have evolved into systems with specific adaptations to the cell physiology and to ecological strategies. Second, we used this inventory of plasmid mobility and family-specific genes to characterize systems in other prokaryotic clades. We found that, globally, one-fourth of the plasmids are conjugative, and as many are mobilizable. Half of all plasmids are classed as being nonmobilizable. Third, evolutionary analysis allowed us to trace the evolution of conjugation elements and showed an ancient divergence between mobility systems, with relaxases and type IV coupling proteins (T4CPs) often following separate paths from type IV secretion systems (T4SSs). Phylogenetic patterns of mobility proteins are consistent with the phylogeny of the host prokaryotes, suggesting that plasmid mobility is in general circumscribed within large clades. Surprisingly, most very large plasmids are nonmobilizable. We have made no attempt to change the naming of GenBank replicons. Therefore, we used all replicons named “plasmid” and none named “chromosome.” There is no consensual distinction between plasmids and chromosomes. We therefore review the claims that many very large plasmids are becoming secondary chromosomes. Indeed, we find that these plasmids tend to be nonmobilizable and contain appreciable amounts of essential genes. The last section of this article discusses outstanding issues in comparative genomics of plasmids in relation to the understating of their mobility.

The integration of foreign DNA into algal and plant plastid genomes is a rare event, with only a few known examples of horizontal gene transfer (HGT). Plasmids, which are well-studied drivers of HGT in prokaryotes, have been reported previously in red algae (Rhodophyta). However, the distribution of these mobile DNA elements and their sites of integration into the plastid (ptDNA), mitochondrial (mtDNA), and nuclear genomes of Rhodophyta remain unknown. Here we reconstructed the complex evolutionary history of plasmid-derived DNAs in red algae. Comparative analysis of 21 rhodophyte ptDNAs, including new genome data for 5 species, turned up 22 plasmid-derived open reading frames (ORFs) that showed syntenic and copy number variation among species, but were conserved within different individuals in three lineages. Several plasmid-derived homologs were found not only in ptDNA but also in mtDNA and in the nuclear genome of green plants, stramenopiles, and rhizarians. Phylogenetic and plasmid-derived ORF analyses showed that the majority of plasmid DNAs originated within red algae, whereas others were derived from cyanobacteria, other bacteria, and viruses. Our results elucidate the evolution of plasmid DNAs in red algae and suggest that they spread as parasitic genetic elements. This hypothesis is consistent with their sporadic distribution within Rhodophyta.