26. Evolution of conjugative transfer systems

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The definition of conjugation as genetic transfer requiring contact between donor and recipient bacteria encompasses a variety of systems. Discussion will focus on conjugation of gram-negative bacteria and, in particular, on the systems encoded by plasmids of the F, B, I, N, and P incompatibility groups. The genetic diversity of these systems, common organisational features, and the evolutionary relationship between conjugative system and incompatibility group will be reviewed.

Each system includes genes affecting cellular interactions (pilus and exclusion determinants) and genes for the processing of the plasmid DNA. Pili can be separated into different morphological classes that promote conjugation in preferred environments. Exclusion genes have evolved to inhibit DNA transfer between cells harbouring closely related plasmids. DNA processing involves nicking at the origin of transfer site, DNA unwinding and transfer of a specific strand to the recipient cell where the complementary strand is synthesised. Multifunctional polypeptides have evolved to promote some of these stages. These polypeptides act analogously to certain bacterial and phage DNA replication proteins and are transmitted selectively to the recipient cell.

27. Plasmid evolution and the release of genetically engineered microbes

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28. The role of transposable elements in the evolution of plasmids

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Transposable elements are discrete DNA sequences that, in general, encode functions that allow them to recombine into other sites on the same or on a different DNA molecule. They can mediate plasmid evolution in several ways. The most obvious change for which these elements are responsible and the primary result of their activity is the addition to DNA molecules of new nucleotide sequences *i.e.*, those that define the element, including genes unconnected with transposition. Secondary consequences, such as deletion or sequence inversion may then follow, as a direct result of further transposition activity or as the result of the host cell's recombination system acting on regions of intra-molecular nucleotide homology. Transposable elements can also mediate fusions between two DNA molecules, either directly, as a consequence of transposition, or indirectly, by providing regions of nucleotide homology on different DNA molecules that can serve as substrates for the host cell's recombination system.

These various activities rearrange DNA sequences, more or less at random; the success of a particular rearrangement is likely to depend on several factors, including the identity of the particular sequences rearranged, functions newly acquired and the utility of the new plasmid to its host. These points will be developed and illustrated.

29. The maintainence of the transposons in bacterial populations: theoretical predictions and experimental observations

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We have developed mathematical models of the population dynamics of transposons in populations of bacteria carrying conjugative plasmids. The results of our analysis of the properties of these models indicate that there are conditions under which replicative (but not conservative) transposons can become established and maintained in bacterial populations by hitchhiking on conjugative plasmids. This can obtain even when these movable elements confer a fitness disadvantage on their host bacterium. The conditions for maintaining these purely "parasitic" trans-

posons are, however, restrictive: (1) the cost of carriage of the transposons has to be low, on the order of the transposition rate; (2) the rate of plasmid turnover (transfer to new recipients) has to be high, in excess of that anticipated for natural populations. Even when these conditions are met, the rate of ascent of a parasitic transposon is of the same order as the transposition rate 10^{-4} or lower per generation.

In an effort to examine the reality of this model and validity this prediction, we studied the population dynamics Tn3 and Tn5 in chemostat and serial transfer populations of *E. coli* K-12 and the plasmid R100-1. We estimated the parameters of this model and followed the fate of Tn3 and Tn5 when low frequencies of *E. coli* carrying these transposons on R100-1 were introduced into populations of *E. coli* carrying this plasmid without the transposon. We interpreted the results of the invasion-when-rare experiments as being consistent with the prediction made from our theoretical analysis, that transposition would contribute little to the ascent of transposons and their maintenance in bacterial populations.

We discuss the implications of these theoretical and experimental results to hypotheses about the evolution and maintenance of bacterial transposons.

30. A theoretical point of view on plasmid evolution

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Many properties of plasmids, like conjugation and surface exclusion, directly affect the dynamics of plasmids in a bacterial population. In which direction such properties will evolve in a plasmid population can be calculated using some of the methods developed in Eukaryote population genetics. For instance, the Evolutionary Stable Strategy (ESS) concept: It is the combination of properties of a certain plasmid stable against invasion by a mutant of that plasmid with a (slightly) other strategy.

Using such methods I have investigated whether a population of plasmids can be invaded by a mutant inducing Surface Exclusion (SE). In this calculation it is assumed that the membrane adaptations, causing SE, decrease the growth rate of the bacterial host. It appears that SE against plasmids of the same incompatibility group is advantageous if the transfer rate is high and the copy number low. Against compatible plasmids it will not be profitable if the excluded plasmid increases the growth rate of the host and the transfer rate is not affected by the presence of the other plasmid.

31. The evolution of catabolic plasmids

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Since 1972 the existence of plasmids encoding the catabolic pathways for a wide range of carbon compounds including aromatic and aliphatic hydrocarbons, xenobiotic pesticides, halogenated compounds and naturally occurring terpenes have been reported. Most of these have been found in members of the genus *Pseudomonas* and the two best studied are involved in toluene/xylene and in naphthalene catabolism (TOL and NAH plasmids respectively).

The evolution of these plasmids will be considered from the point of view of (a) their structural plasticity under changing biochemical selection pressures (b) the relationship between the DNA encoding similar biochemical sequences on different plasmids and (c) the existence on some of relatively stable diverge gene duplications. The hypothesis will be proposed that some of the more complex pathways, as found on the TOL and NAH plasmids, may have evolved from the acquisition of metabolic "modules".

32. Evolutionary relationships among antibiotic resistance determinants

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Antibiotic resistance genes are found, predominantly, in two classes of micro-organisms: antibiotic producers and clinical isolates from humans or animals. The roles of the resistance determinants in the two sources are essentially identical, in that they are required to protect the host organisms from the inhibitory action of exogenous or endogenous antibiotic substances.