2.1 Introduction

Transduction was discovered by Joshua Lederberg and Norton Zinder in 1951, while looking for a system of conjugation and recombination (chapter 4) in Salmonella typhimurium. When they grew together two different mutant strains, one of which was lysogenic for phage 22 (P22), they were able to recover rare prototrophs from the mixed culture. They were surprised to find that cell contact was not required since prototrophs were still recovered when the two strains were grown side by side but separated by a fine sintered glass filter through which the bacteria could not pass, and they concluded that this genetic exchange was promoted by a DNase-resistant filterable agent. Very soon afterwards Zinder demonstrated that the filterable agent was the temperate phage P22 and that the phage particles themselves were capable of transferring fragments of genetic material from a donor to a recipient strain, where they could be recombined into the recipient chromosome. They called this process transduction, literally 'leading across'.

2.2 Generalised transduction

Transduction, the transfer of a small piece of DNA from one bacterial cell to another by a phage particle, has been described in many different bacteria but it has been most extensively used to analyse the genetic fine structure of the S. typhimurium, E. coli and B. subtilis chromosomes; it is also extensively used as a tool in strain construction. We will primarily consider P1-mediated transduction in E. coli, discovered by E. S. Lennox in 1955; this, like PSS-mediated transduction in Salmonella, is a system of generalised transduction, so-called because almost any bacterial gene can be transferred from a donor to a recipient.
P1 has an icosahedral head enclosing a single linear molecule of DNA approximately 100 kb long and a complex tail made up of a rigid core tube, a contractile sheath, base plate and tail fibres. It is a temperate phage and so, when it infects an *E. coli* cell, it can either enter the lytic cycle and lyse the cell or it may lysogenise it. When P1 lysogenises a cell it does not, like many temperate phages (λ, for example) integrate into the chromosome of the host cell but the phage genome is maintained as a circular molecule of autonomously replicating plasmid DNA. However, in transduction experiments it is customary to use the virulent mutant P1**vir** which does not lysogenise; this has the advantage that the transductants are not lysogenised by the normal phage particles present in the transducing lysate and so remain phage-sensitive and can be used in further transduction experiments.

In the laboratory, transduction is carried out in two stages. First, a cell-free suspension of phage is prepared by growing P1 on a suitable donor strain of *E. coli* and, second, these phages are used to infect a genetically different recipient strain and genetic recombinants (called transductants) selected by plating the infected cells on a suitable selective medium.

P1-transducing phage is prepared by the lytic infection of 10^8* donor bacteria with about 10^6 P1 particles; after the phage has replicated and the donor cells have lysed, any bacterial debris is removed by centrifugation and the supernatant is shaken with chloroform to kill any surviving bacteria. The vast majority of the maturing phage will encapsidate a headful (about 100 kb) of P1 DNA and these will become normal P1 particles. However, during the later stages of the infective process a small proportion (3 x 10^-3) of the maturing phages encapsidate a segment of the host chromosome instead of packaging a phage genome; these segments, like the phage chromosome, are about 100 kb long, or about 1/40 of the bacterial chromosome. Although the fragments of *E. coli* DNA packaged by P1 are of constant size, the fragments including any particular donor gene are of variable composition; this is because the headful packaging mechanism does not always commence from the same site on the donor chromosome. This is in contrast to the fragments of *Salmonella* DNA packaged by P22 which are of both constant size and composition (see section 2.3.1); it appears that the P22 packaging mechanism always commences from one or more particular sites and then proceeds by packaging sequential headfuls.

These transducing phage particles contain no phage DNA at all and so can neither lyse nor lysogenise the host cells they infect. A good phage preparation may contain as many as 10^{11} particles per ml but only about 0.3 per cent of these contain bacterial DNA and are transducing particles; thus for any given gene the frequency of transducing particles will be about 1/40 x 3/1000 or 7.5 x 10^-5 (note, however, that some mutants of P1 produce a much higher frequency of transducing phage). Since over 1100 loci have been identified around the *E. coli* chromosome, the average fragment of transducing DNA contains 25–30 known loci.