of the transduction clone. The galactose positive reversions of these segregants are stable.

A charactersitic HFT culture has been obtained for each galactose negative as well as for wild type. These cultures were isolated initially by making lysates of random segregants from heterogenic transductions and assaying the lysates on the appropriate cells. This method is laborious and inefficient. To assist in the isolation a more rapid method was devised. Random segregant colonies were picked to small volumes of water or broth and samples of each suspension were then spotted on an EMB galactose plate spread with cells suitable for the detection of the HFT culture desired. The plate was given a small dose of UV (about 10-20 seconds at 50 cm from a Sterilamp) and incubated for 24 hours. At the end of this time HFT cultures were usually detected by the raised welt of galactose positive growth where lambda produced by the induction and lysis of the HFT culture had transformed bacteria of the background film of growth.

The incidence of HFT galactose negative cultures is not high. Of 67 segregants tested, 7 were found to be capable of HFT lysates. The true frequency might be higher than this, since purified segregants were examined and there was opportunity to pick HFT segregants from originally HFT clones.

Cultures giving HFT lysates that are pure for a particular galactose negative allele are suitable for allelism tests of unknown galactose negative cultures by the cross brush method.

Experiments with lysates giving a high frequency of transduction

Although the HFT lysates have not yet been obtained with phage titers comparable to LFT lysates the titers have been sufficient for transforming a large fraction of a cell population exposed to them. The largest fraction of transformation observed thus far has been 12.5 percent of exposed cells, but in most experiments the fraction has been between 1 and 5 percent.

The use of HFT lysates has permitted the study of several problems not attackable with LFT lysates. One of these is the relationship of transduction to lysogenization with the phage lambda. Another problem is that of the interaction of Gal_1 and Gal_4. Both of these problems will be dealt with in the next sections. With HFT lysates, transduction was experimentally feasible in X only when a galactose phenotype is generated that can be selected from a galactose negative background. HFT lysates, permit the detection of galactose negative segregants from transductions clones derived from galactose positive recipient cells. Transductions in this sense have facilitated further studies of the interaction of the galactose loci with the Lp locus.

The relationship of lysogenization to transduction

By exposing cultures of Lp^s cells to HFT lysates, diluting, and then plating on galactose medium to obtain isolated colonies it is possible to study the behavior of individual cells with regard to ~~their~~ transduction and lysogenization activities. Table 1~~4~~ shows the results of an experiment in which 1.1 percent of a cell population was transformed after exposure to a HFT lysate. The second portion of table 1~~4~~ gives the phage reactions of the galactose positive (transductions) and galactose negative colonies derived from cells exposed to the HFT lysate. All of the transductions were lysogenized or converted to the Lp^r state while the non-transformed colonies were either phage sensitive or contaminated with phage.

These results suggest that lambda carries the transducing activity. However, under the experimental conditions employed it could be argued that the transductions are the results of the action of two entities. The first, which would act upon the cells and makes them "potential" transductions, and the second, lambda, which in the process of lysogenizing the cells, would sometimes convert them to actual transductions. In order for so many phage contacts to result in transduction (1/3 of 3%) to be observed at all under this hypothesis, the "potentiating" agent would have to be present in about the order of ten-fold over excess of lambda. ~~(It might be argued that because (in this the experiment recorded in table 1~~4~~) only about one-third of the lambda-cell contacts became transductions that the ratio of the "potentiating" agent to lambda was not high. This would not necessarily be so, since this ratio (transductions/ total lambda contacts) could merely be an indication of the efficiency of lambda's conversion of potentiality to actuality.)~~ The observed linear proportionality of number of transductions to amount of HFT lysate at high dilutions (10^{-5}-10^{-6}) would simply make such an overwhelming excess of any accessory factor in addition to lambda as to make this hypothesis highly improbable.

unfeasible

At these ~~dilut~~ ~~dilut~~ dilutions the probability that a single cell would encounter both activities would be(approximately the square of the dilution (10^{10}-10^{12}). Lambda most certainly must be the vector of transductio~~n~~.

The interaction of Gal_1 and Gal_4 (Positive effect).

With the use of HFT lysates it has been possible to study the interaction of Gal_1-and Gal_4- cells with HFT Gal_4- and Gal_1- lysates respectively. The results from one set of interactions is shown in table 15. After a preliminary period for the adsorption of the transducing activities the cultures were centrifuged, the supernatant lysate discarded and the cells resuspended in broth. The cells were then diluted and plated on EMB ~~gluc~~ galactose medium. No galactose positive colonies were observed on the ~~control~~ ~~lysate~~ plates made from control unexposed cells or from lysate treated cells. After 24 hours incubation at 37C two raised, slightly orange pink colonies were observed in each experiment on the plates from cells exposed to lysate. These colonies were slightly larger than the other ~~galactose negative colonies~~ and after 24 hours developed

a roughened papillate surface. On streaking out they gave rise to positive colonies, negative colonies that remained negative, and to papillating galactose negative colonies.

In each experiment a number of galactose positive colonies derived from the papillating negative colonies were picked and streaked out twice for purification purposes. From the second streaking galactose negative segregants were obtained and classified with regard to negative allele. In each experiment idiotypic and allotypic segregants were observed and in one experiment amphitypic segregants were found. The amphitypic (Gal_1- Gal_4-) segregants were transformed to a wild type phenotype by lysates of wild type cells, and a lysate of the amphitype formed galactose positive transduction clones when applied to Gal_2- recipient cells.

The failure to realize a wild type phenotype when the positive alleles are in a trans-position, and its realization in the cis-position constitutes a positional effect for these loci.

The action of HFT lysates on lambda-2 resistant cultures

In the previous discussion (table 7) HFT lysates were stated not to transduce lambda-2 resistant recipient cells. HFT lysates, on the other hand, do transduce lambda-2 resistant cells, but at a low frequency (one per 16^6 transducing particles). This is presumably caused by the potency of HFT lysates, which helps to uncover any residual interaction of transducing phage and lambda-2 resistant bacteria, regardless of which element had varied. Such variation might then be either phenotypic (expressivity) or genotypic (mutation) either in virus or bacterium.

The interaction of HFT lysates with lambda-2 resistant cells is illustrated by the following observations. Some mutations to lambda-2 resistance are accompanied by a coincident change to inability to ferment maltose (E. Lederberg, unpublished). Reversions to ability to ferment maltose is accompanied by reversion to lambda-2 sensitivity and vice versa. These two phenotypic effects have never been separated in crosses and it is presumed that they are the result of a single mutation.

The transductions of a galactose negative, maltose negative lambda-2 resistant, lambda sensitive culture obtained by the action of an HFT lysate are of two types. Maltose positive and lambda-2 sensitive, and maltose negative and lambda-2 resistant. The first of these types represents the detection by the HFT lysate of reverse mutation of the locus in the recipient cells controlling lambda-2 resistance.

The second type of transduction in about 95 percent of the cases is stable for galactose fermentation. Study of the transformability of galactose negative segregants from the unstable transductions clones found showed them not to be susceptible

to a higher frequency of transduction than the parental maltose negative lambda-2 resistant culture. In these cases, at least, there has not been a mutational change in the recipient cell to a greater aptitude for transformation.

About 95 percent of the maltose negative lambda-2 resistant transductions have been found Lp^s, the remainder Lp^r. The Lp^r forms may be stable or segregating for galactose, but all segregating clones are Lp^r. Segregation for galactose fermentation is usually accompanied by segregation at Lp. Presumably in these cases there has been variation in the transducing particles, although it is possible that in the transductions ending in Lp^s clones that an agent distinct from lambda is opergting.

Crossing behavior of the transduction clones

In previous sections it was noted that transduction clones gave HFT lysates after UV induction. Since spontaneously produced phage is similar tp phage produced by the induction technic it might be expected that in crosses between transduction clones and galactose negative cultures, or between HFT galactose negative cultures and non-allelic galactose

There are several observations which suggest that transduction occur does not play an important part in such crosses. The first observation, ADD ination which minimizes the possibility, is that in a cross between an HFT allotypic segregant and an idiotypic tester, 11,200 prototrophs were examined before a galactose positive recombinant was encountered. A second observation is from the comparison of a cross between a lysogenic unstable transduction (capable of giving HFT lysates) with a Lp^s galactose negative culture, ADD with a cross between an Lp^r transduction (incapable of giving HFT lysates) with the same Lp^s galactose negative culture. A comparison of these crosses showed no significant increase in the number of galactose positive colonies in the cross between the lysogenic transduction and the sensitive culture. Apparently transduction does not confuse in any important way, the results of crosses.

The transmission of galactose heterogenicity in crosses is greatly influenced by the F polarity of the cross (table 1). When an unstable heterogenic F^+ culture is crossed with a non-allelic galactose negative Lp^s F^- culture, unstable galactose positive prototrophs are rare. When the unstable culture is F^-, and crossed with a non-allelic galactose negative Lp^s F^+ culture, most of the prototrophs are galactose positive and unstable. Some of the galactose negative prototrophs in these crosses can be explained by galactose negative segregants in the unstable galactose positive parent clone.

Galactose negative cultures that are not transformed by lysates.

Seventeen galactose negative mutants have been induced by means of ultraviolet light in auxotrpphic stocks suitable for crossing with the Gal_1-, Gal_2- and Gal_4- stocks used above. Of these 17, 14 were found to be transformed by lysates to wild type. Five of the 14 were recurrences of Gal_1- OR Gal_2-, four were apparently double mutations at Gal_1 and Gal_4, and the remaining five were new loci transduced by lysates. One of the three cultures not transformed by any lysate was examined further. Lysates of it (W23.12) transduced Gal_1^+, Gal_4^+, and Gal_6^+, but APPARENTLY NOT Gal_2^+. In recombination tests this culture has given galactose positive recombinants with both Gal_2- and Gal_4-. For explanation of these results it is necessary to postulate a double change, one OUTSIDE the SEGMENT THAT CAN BE TRANSDUCED loci, and one within the region, non-allelic to any of the known loci, which in addition gives an interaction with Gal_2- such that the heterozygous combination is not phenotypically galactose positive. AN unresolved technical difficulty seems a more likely explanation.

The study of the galactose negative cultures not transformed by lysates has been partly hindered by difficulty in discerning which cultures were truly "negative" and which cultures were merely "slow positive", so that galactose positive transductions are not readily selected.

DISCUSSION

The results presented above can be placed in an orderly fashion by the following scheme. When lysogenic cells are exposed to ultraviolet radiation and the prophage is induced to form mature phage, on rare occasions a fragment of the bacterial chromosome is included within a phage particle. When this particle injects its genetic material into another bacterial cell, the fragment is also injected and if the recipient bacterial cell has the proper genetic constitution the presence of this extra genic material is made obvious. ~~The fragment remains within the bacterial cells that survive, and its multiplication and distribution among the daughter cells closely but not completely parallels the multiplication and distribution of the other genetic material in the cell.~~

The allotypic fragment usually persists at cell division, so that segregating clones can be maintained indefinitely in mass culture. At least two additional events are inferred: (1) diploid crossing over leading to reorganized digenotes. Since these may be heterogenic or homogenic, a four strand (or more) stage is implied. (2) segregation occurs leading to stable haplogenotes, the state typical of E. coli. The fate of the fragment is unknown. Crossover haplogenotes (amphitypes) have also been isolated and may represent either a third process, or the first two in sequence (cf Pontecorvo, 1954). Since heterogenotes give HFT lysates, the fragment or a replica of it, is assumed to have a high probability of incorporation in the phage obtained by UV induction. The low yields suggest a burst of one phage particle, a reversal of transduction.

From this description it is evident that the genetic transfer is intimately associated with the process of lysogenization and lysogenicity. Concerning the process of lysogenization in K-12 little is known beyond the fact that cell and phage interact, there is a period of indecision, and the

infected bacterium either dies or generates a clone containing lysogenized cells. Once lysogenicity is established the capacity to produce phage behaves as a nulcear gene that is closely linked with a number of loci controlling galactose fermentation.

The first step in the scheme is the inclusion of a fragment of the within a phage particle. In Salmonella the fragment is a random section of the cell's genetic material, but in E. coli K-12, it is quite specific, for only a restricted group of loci are transduced by lambda. Again in contrast to Salmonella, "lytic" lambda is incompetent in transduction. This may reflect an inherent difference between lytic and UV induced phage.

In the establishment of lysogenicity the genetic material of lambda enters the cell and associates itself in some way with a specific region of the bacterial genome. In the induction process it is presumably emerges from its place and starts to multiply. Transduction could be accounted for by some latitude in the separation of the galactose loci from the prophage linked to them, and their common inclusion in some mature phage particles. The close genetic proximity of the galactose loci would suggest their increased liklihood of inclusion, but there is no necessity that closely linked genes be also spatially close to one another.

There are two types (HFT and NFT) of culture in which transducing particles are formed and it is legitimate to ask whether the two are different phenomena or merely quantitaively different aspects of a single phenomenon. The evidence for a unitary process is negative in nature. That is, no difference have been noted between HFT lysates and NFT lysates, except possibly the higher incidence of transductions that culminate in a phenotypic Lp^r reaction with the former. This exception, if it be one, could itself be explained on the basis of quantitative differences between the two lysates.

The study of the production of transducing particles in cultures giving HFT lysates has not passed beyond the preliminary stage. The evidence thus far suggests that most of the cells yield transducing particles and that the yield per cell is not large. With regard to the determination of the frequency of cells emitting transducing activity it should be noted that cultures started from a single colony with HFT property may contain as much as 30 percent of cells with NFT property by virtue of segregation.

The specific activity of the HFT lysates of segregating heterozygous galactose positive clones indicates that the fragment is preferentially included within the phage particles. Presumably exchange between fragment and intact chromosome can also occur so that instead of giving lysates predominately allotypic in character, idiotypic lysates are obtained. The exchange is sufficinetly rare, however, that observation remains objective in nature.

The nature of the association of the fragment with the infective phage particle is not known. Presumably the material is within the phage membrane since it is not attacked by desoxyribonuclease. The availability of lysates in which most of the phage particles have activity (HFT lysates) or have no activity (NFT lysates) suggests that morphological comparisons might possibly be made via electron micrsocopy of intact or disrupted phage particles.

The fragment enters the bacterial cell in company with the prophage, by analogy with T2, probably by the injection process (Hershey and Chase,1952).

The association of the fragment with the prophage in transduction to lysogenic cells cannot be stated in the absence of phage markers, since it is not possible to distinguish between the previously carried and the newly entered prophage. The carriage of more than a single prophage by cells of E. coli K-12 has been reported by Appleyard (1954) and it is likely that the transductions of lysogenic recipient cells are also carrying more than a single prophage.

In only one instance, from more than 250 segregations studied, has segregation from a transduction of lysogenic cell resulted in a change at Lp. In this case an idiotypic segregant became Lp^s, and this might have been a spontaneous "mutation".

In the transductions to Lp^s recipient cells the association between transducing prophage and the fragment is possibly better seen. These transductions are of two kinds, Lp^+ and Lp^r. All segregants from Lp^+ clones have been lysogenic. On the other hand, Lp^r transduction clones segregate Lp^r/Lp^s as well as Gal+/Gal-. The incidence of Lp^s Gal- idiotypes supports the notion that these loci are linked.

In considering the relationship of the fragment to the rest of the genome no specific statements can be made with regard to its perpetuity in the heterogenic clone. One would depend upon its possession of a functional centromere, so that it would behave as a small autonomous chromosome, or the fragment would be attached to the homologous chromosome segment, either intersitially or terminally. Either attachment position presents difficulties for crossing over, and the fragment as a separate chromosome seems more plausible.

In the above sections the results have been treated and discussed in a general way. It is obvious that the study of this transduction system has only begun and that many experiments and interesting observations will be made before the problem is completely understood. It is proposed to investigate lambda transduction further along the following lines.

1. Whether the production of transducing activity in HFT cultures is related to the interaction of radiation and cells, or is the result of a mutational like event in the cell population.

2. The production of transducing particles in HFT lysates.

3. The action of radiation on transducing particles and the possibility of inducing mutations.

6. Further studies on crossing over between fragment and idiotypic loci using additional markers.

7. The relationship between lysogenization and transduction, and between lysogenization and crossing over.

8. Estimation of the gene order of the transduced loci and their relationship to other mapped loci.

9. Study of the biochemical steps controlled by the various loci and the fermentation of galactose.

4. The detection of other loci within the transduced region.

5. The behavior of the fragment transduced during syngamy and meiosis.

SUMMARY

A cluster of loci in Escherichia coli K-12 was found previously to control the fermentation of galactose. Lysogenicity for the temperate bacteriophage, lambda, was also found to be closely linked to these loci in crosses. The phage lambda now has been found to transduce these loci, as can be readily demonstrated by mixing lysates of galactose positive cultures with galactose negative cells on a selective medium, EMB galactose agar. The transductions result in clones that are heterogenic, that is, they are diploid for a small region of chromosome. The small fragment of chromosome transduced appears to have a functional centromere, and is perpetuated within the clone even after many single colony isolations, but it may on some occasions be lost. While in the clone it has been found to crossover with its homologous region, on some occasions at least, at a four strand stage. Each of the new phage particles formed in lysates of heterogenotes has a high probability of containing ~~not only a fragment, but~~ the fragment carried in the heterogenic clone. A position effect on the expression of two of the transduced loci has been observed. Diheterogenotes of Gal_1 and Gal_4 are not phenotypically galactose positive in the *trans* positions, but are so in the *cis*.

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Table 16

The transmission of heterogenicity in crosses

Parental cells F^+	Parental cells F^-	Prototrophic recombinants Galactose (+)	Prototrophic recombinants Galactose (-)
$Gal_2^{\pm}$(1)	Gal_4- Lp^S	1*	about 6000
Gal_4- Lp^S	$Gal_2^{\pm}$(2)	541**	99

* unstable for galactose fermentation, 6 galactose negative segregants tested were Gal_2-

** 25 of 30 examined were unstable for galactose fermentation. One segregant from each of the 25 was tested, all were Gal_2-

(1) control platings showed the ratiom of (+)/(-) in this culture was 109/57

(2) control platings showed the ratio of (+)/(-) in this culture was 115/13

Gal_2- Lp^S	Gal+ Lp^+	329	25
Gal+ Lp^S	Gal_2- Lp^+	107 (approx.)	757 (approx.)

Table 1

Principal cultures

Wisconsin Stock Number	Genotype*
W518	F^+ M^- Lac_1- Gal_4- Lp^s
W750	F^+ M- Lac_1- Gal_1- Lp^+
W811	F^+ M- Lac_1- Gal_4- Lp^+
W902	F- T-L-B_1- Mal_1- Gal_2- Lp^+
W1210	F^+ M- Lac_1- Gal_2- Lp^+
W1436	F^+ T-L-B_1- Lac_1- Gal_4- Lp^s S^r
W1924	F^+ M- Lac_1- Gal_4- Lp^r
W2175	F^+ Gal_2- Lp^+
W2279	F^+ M-Lac_1- Gal_1- Lp^s
W2281	F^+ M- Lac_1- Gal_2- Lp^s

* Genotypic symbols refer to the following characters.

(1) Compatibility status, F

(2) Nutritional requirements; M, methionine; T, threonine; L, leucine; B_1, thiamin

(3) Fermentation reactions; Lac-, lactose negative; Gal-, galactose negative; Mal-, maltose negative

(4) Phage reaction; Lp^s, lambda sensitive; Lp^+, lambda lysogenic; Lp^r, lambda resistant, but not overtly lysogenic.

(5) Drug resistance; S, streptomycin

Table 2

Recombination between the various Galactose loci

Cross		Minimum Number of Prototrophic Recombinants	Percent Galactose Fermenting Recombinants
F_q^+ Gal_1-	X F⁻ Gal_2-	(1) 1500	0.13
		(2) 6517	0.06
		(3) 3603	0.03
		11620	0.06
F^+ Gal_4-	X F⁻ Gal_1-	4588	0.13
F^+ Gal_4-	X F⁻ Gal_2-	2654	0.23

F^+ Gal_1^- : W750

F- Gal_1- : W750 (aeration phenocopy)

F⁻ Gal_2- : W902

F^+ Gal_4^- : W811, W518, W1436

Table 3

Observations on lambda lysate transductions

Locus	Number of experiments	Cultures involved[1]
1. Loci not transduced		
Lac_1	1	W112
(serine or glycine)	1	W1678
Leucine	3	W1736, W1436[a]
Methionine	4	58-161, W811, W1821, W518[b]
Xylose	3	W1821[c]
Streptomycin	1	W518[d]
Proline	9	W1692, W1920, W2062[e]
	1 (lytic lambda)	W2062[f]
Mal_1	2	W2331, W2347[g]
Mal_x	1	W2071
Ara	1	W2307[h]
2. Loci transduced		
Gal_1	-	W750, W2279, W2280, W2373
Gal_2	-	W1210, W2175, W2281
Gal_3	-	W2297
Gal_4	-	W518, W811, W1821, W1436, W1924
Gal_6	-	W2070

(Footnotes table 3 continued)

f- lytic lambda grown on M- culture
g- lysate of prototrophic HFT Gal_2- culture
h- lysate of prototrophic HFT Gal_2- culture

Table 4

The interaction of lysates and cells of galactose negative cultures

Recipient Cells (Lp^+)		Plaque titer (x 10^{10})	No added lysate	Lysates Gal_1-	Gal_2-	Gal_4-	Wild type
			-	2.4	4.9	1.7	1.4
Gal_1-	(1)		2*	-	176	43	-
	(2)		2	2	-	-	405
Gal_2-	(1)		14	52	11	43	-
	(2)		20	-	10	-	356
Gal_4-	(1)		89	-	202	-	-
	(2)		50	85	-	-	417
	(3)		47	-	-	50	394

* The no added lysate plate which represents the number of spontaneous reversions occuring on the plate. The remaining figures are the numbers of papillae occuring on the plates per 0.1 ml of lysate added.

Table 5

Restoration by reverse mutation of the ability to transduce previously non-transducible loci

Recipient cells (Lp^+)	Reversion	Lysate: None	Lysate: Reversion
Gal_1-	Gal_1^+ (1)	0	648*
Gal_2-	Gal_2^+ (1)	10	96
	Gal_2^+ (2)	6	552
Gal_4-	Gal_4^+ (5)	39	204
	Gal_4^+ (8)	25	291

*number of papillae per plate, 0.1 ml of lysate plated.

The necessity of lambda adsorption for transduction

Table 6

The necessity of lambda adsorption for transduction#

Recipient Cells (Lp^+)	Lambda-2 phenotype** Lp Allele	Plate, Addition None	Wild type lysate
Gal_1-	s	1	426*
	r	1	2
Gal_2-	s	20	356
	r	14	14
Gal_4-	s	89	296
	r	50	57

*Number of papillae per plate, 0.1 ml of lysate plated

** s = lambda-2 sensitive, r = lambda-2 resistant. r forms do not adsorb either lambda or lambda-2

Table #7

The activity of lytically grown lambda

Experiment	Recipient cells	Lp Allele	Plate addition: None	Lytic lambda	Plaque titer
228	Gal_1-	+	3	2*	2.4×10^{10}
	Gal_2-	+	9	8	
	Gal_4-	s	9	8	
239	Gal_1-	+	2	0	2.4×10^{10}
	Gal_2-	+	6	2	
	Gal_4-	s	13	8	
254	Gal_1-	s	-	6**	2.4×10^{10}
	Gal_1-	+	-	3**	
	Gal_2-	s	-	9**	
	Gal_4-	s	-	6**	
	Gal_4-	+	-	39**	
280	Gal_1-	+	0	2**	8.6×10^{9}
	Gal_2-	+	1	2**	
	Gal_4-	+	14	10**	

*Papillae per plate, 0.1 ml lysate plated. Lysate prepared by growing Gal_4- lambda (UV induction) on a galactose fermenting culture.

**These papillae picked and streaked on EMB galactose medium and found stable for galactose fermentation.

Table 8

The specific activity of lysates of the transduction clones

Recipient Cell	Transducing lysate	Titers Plaques	Transductions on Lp^+ assay cells Gal_1-	Gal_2-	Gal_4-	P/T*
Gal_1-	wild type	5.8×10^8	2.4×10^6	1.8×10^7	1.3×10^7	32
Gal_1-	Gal_2-	7.2×10^9	1.2×10^8	1.0×10^6	-	60
Gal_1-	Gal_2- **	? $\times 10^6$	1.8×10^6	6.3×10^4	-	
Gal_2-	Gal_1-	6.2×10^8	4.3×10^7	1.5×10^8	-	4
Gal_4-	Gal_1-	1.5×10^8	5.0×10^7	7.5×10^7	7.4×10^7	2
Gal_4-	Gal_2-	7.3×10^8	2.5×10^7	2.8×10^5	-	29

* Ratio of plaques to transductions; the maximum transduction titer observed is used for this estimate. Usual ratio P/T is about 10^8.

** A second isolation.

Table 9

The occurrence of stable transductions

Recipient cells		Lysates											
		Wild type			Gal_1-			Gal_2-			Gal_4-		
		T/C*	C	T**	T/C	C	T	T/C	C	T	T/C	C	T
Gal_1-	Lp^s	38/1	1	14	-	-	-	11/1	1	11	30/1	1	29
	Lp^+	46/1	1	2	-	-	-	84/1	1	4	27/12	12	27
	Lp^+	143/1	1	42	-	-	-	92/1	1	0	-	-	-
Gal_2-	Lp^s	46/0	0	15	214/0	0	27	-	-	-	98/0	0	4
	Lp^+	248/17	17	21	83/14	14	61	-	-	-	79/14	14	52
	Lp^+	23/4	4	6	65/2	2	0	-	-	-	56/5	5	0
Gal_4-	Lp^s	835/19	19	383	72/29	29	72	472/11	11	20	-	-	-
	Lp^+	573/41	41	133	96/51	51	96	-	-	-	-	-	-
	Lp^r	320/31	31	127	-	-	-	238/31	31	50	-	-	-

* Papillae transduction plate/ papillae control plate. T = transduction plate, C = control plate

** Corrected for sample taken, $\frac{\text{stable obs.}}{\text{sample size}} \times \text{Papillae transd. plate}$

With the exception of the T/C column, numbers given are number of stable galactose fermenting papillae.