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Diploid studies: The preceding evidence points to a chromosomal localization of the Lp lysogenicity determinant closely linked to a series of Gal loci. Evidence for the segregation of a prophage linked to the $Gal_4$ locus ruled out the possibility of a random distribution of cytoplasmic particles in cells carrying $\lambda$(10). These observations have since been extended to $Gal_2$ and $Gal_4$ hybrids (all heterozygous $Lp^+/s$), and also $Gal_4^+Lp^+/Gal_4^-Lp^r$ diploids (table 10). A study of such diploids segregating out distinguishable $\lambda$ types is in preparation. Preliminary evidence also has been obtained elsewhere from crosses with lysogenic parents, one carrying a mutant $\lambda$ (or one "doubly lysogenic") the other doubly sensitive, which yielded Gal/Lp progeny in parental couplings (1).

The mutational independence of Gal and Lp was also examined in the doubly homozygous diploid. Comparable experiments with the closely-$Lac_1$ and $V_6$ loci have already been reported. $Lac^+$ reversions were selected in $Lac^-V_6^r/Lac^-V_6^s$ diploids. The resulting doubly heterozygous diploids were of two types: $Lac^+V_6^r/Lac^-V_6^s$ and $Lac^-V_6^r/Lac^+V_6^s$, and with equal frequency (11).

A double homozygote $Gal_2^+Lp^s/Gal_2^-Lp^s$, also segregating a few other markers, (and unfortunately also $Lp_2$) was prepared by stepwise exposure of

(177)

the double heterozygote to U-V (14) and the isolation of suitable "reorganized" diploids. The resulting diploid, H-331 was infected with $\lambda$. Several $Gal_2^-Lp^+/Gal_2^-Lps$ isolations, A to G, were then allowed to papillate on EMS galactose agar. Independently occurring $Gal^+$ were selected, and the segregation pattern of Lp and $Gal_2$ of the resulting double heterozygotes was tested. The incidence of mutation to $Gal^+$ on the $Lp^+$ chromosome (coupling phase, or cis configuration) was compared with that on the $Lp^s$ chromosome (repulsion phase, or trans-configuration). The analysis included a single $Gal^+$ and a single $Gal^-$ segregant from a large number of diploids, (pair analysis) and the examination of many segregants from a single mass diploid culture (random analysis). From diploid B, 5 cis configurations and 6 trans configurations were scored. The conclusion from this evidence (table 11) is that the condition of the Lp locus, whether lysogenic or sensitive, has no significant bearing on which one of the 2 $Gal^-$ alleles will mutate to $Gal^+$. (These preliminary data will be expanded, and also extended to a corresponding study of diploids first made heterozygous $Gal_2^-Lp^s/Gal_2^+Lp^s$, and then infected with $\lambda$.)

The above studies provide two kinds of $Lp^+/Lp^s$; $Gal^+/Gal^-$ diploids: $\lambda$ coupled on the one hand with $Gal^+$ (cis) and on the other, with $Gal_2^-$ (trans) If the activity of from "trans" bacteria is confined to non $Gal_2^-$ recipient cells, a chromosomal but not nuclear limitation to $\lambda$ specificity is indicated. All $Gal^-$ including $Gal_2^-$ is expected to respond to cis $\lambda$. A difference in $\lambda$ from these diploids which are phenotypically identical, and genetically identical except for the arrangement of component parts established a "position effect." So far, only $\lambda$ from the trans-type diploid has been prepared. Table shows that while $Gal_4^-$ ($Gal_2^+Gal_4^-$) cells are subject to transduction, only rare $Gal_2^+$ transductions were recovered. The development of an adequate diploid culture to satisfy the nutritional prerequisites for U-V induction in K-12 (3,5) and an intermediate growth period necessarily permits some selection for haploid segregants. The yield of $\lambda$ obtained very probably includes a limited portion derived from $Gal_2^-Lp^+$ and $Gal_2^+Lp^+$ haploids. The latter crossover types may account for those transductions which were found. The data so far allow the tentative conclusion of a position effect hypothesis and strengthen the concept of an intimate relationship of $\lambda$ and Gal at a specific action site on the chromosome. Transductions of the double homozygote H-331 and lysogenic

derivatives has apparently been obtained. The analysis is complicated by the fact that diploid-haploid instability can be confounded with transduction instability.

## COMPARATIVE GENETICS OF Lp AND Gal IN OTHER LINES

Among the independently isolated crossable strains of E. coli (12) the wild type of three lines (28,47, and 51) were sensitive to λ carried by line 1. A fourth, line 31, threw off rough variants which were all λ sensitive. These strains occurred in nature as $F^-$ but could be altered to $F^+$ by growth with K-12 or suitable derivatives. So far, at least one $Gal^-$ mutant is subject to transduction. Preliminary intra-line-47 crosses established an Lp locus like that of K-12, and a Gal-Lp linkage. Very little mapping work has been completed among these strain, and the emphasis so far in these studies has been the genetic behavior of λ in outcrosses with K-12.

Sensitives of each line are readily lysogenized by K-12 λ but these lysogenics show a reduction of eop on K-12 sensitive indicators. This system is entirely analagous to host modification demonstrated for T2 (19) and λ produced by strain C (2). The terminology established for these systems will be used to describe the properties of our strains.

Thus lines 28,31, and 47 can be designated as λ* lysogenic or λ* sensitive. Line 1 sensitives are more resistant to λ* than to type λ. λ* can be introduced at low rates into λ sensitive hosts, but normal rather than λ* is recovered. Similarly, normal λ is converted to λ* after a single passage in λ* sensitive hosts. The four phenotypes are readily distinguishable in cross-brush tests as follows:

| Example | Type | Reaction with: λ-sens. C bacteria | λ*-sens. B bacteria | λ | λ* |
|---|---|---|---|---|---|
| line 1 lysogenic | A | + | + | R | R |
| line 47 sensitive | B | - | - | S | S |
| line 1 sensitive | C | - | - | S | R |
| line 47 lysogenic | D | - | + | R | R |

+/- = lysogenic or not; R/S = resistant or sensitive

Two major hypotheses can be tested by intercrossing these types:

I Lp controls all reactions: the types A-D are determined at a single locus.

II Lp controls lysogenicity/ sensitivity; another locus, Mp, controls resistance or sensitivity to λ*.

(a) Both λ and λ* are fixed at Lp in phenotypes A and D.

(b) λ is fixed at Lp in type A; λ* is fixed at Mp in type D.

The consequences of these hypotheses are shown in table 12. The critical crosses for I and II are A x B and C x D. The only decisive cross for II a vs. II b is A x D. II b would be favored by the recovery of sensitive recombinants as well as a novel genotype whose phenotypic effects are unpredictable. Since there is a possibility that Lp and Mp are closely linked a large sample of progeny many be required. One must bear in mind, in reviewing these intercross data that the prototrophs represent recombination of as yet unmapped nutritional factors. In addition, chromosome and other irregularities correlated with interstrain hybrids have not been analysed.

Effective transductions have been achieved in these strains. Gal- in lines 47 and 31 have been used as recipients, for $\lambda$ produced by line 1, 28, 31, and 47. A reduction in the effectiveness of transduction to line 1 recipients is parallel with the reduced effectiveness of lysogenization. In general no important differences with the K-12 mechanism have been demonstrated. Hypothesis II b is doubtful so far. The differentiation of the $\lambda$* of different lines is still to be tested. A single intercross shows no genetic difference so far.

In preparing this report, it has been necessary to make numerous references to the unpublished work carried on in this laboratory by Professor J. Lederberg, Mr. M. L. Morse, and others, under other auspices. These are cited by number to the bibliography.

Table 1

Characteristics of F (compatibility factor) and λ (virus)

| Criterion | F status | λ (effects) |
|---|---|---|
| (1) Yield of recombinants | Decisive | None |
| (2) Type of recombinants | Decisive | None |
| (3) Transmission to recombinants | 100% | Segregated according to linkage with selected nutritional markers; behaves as a genetic locus. |
| (4) Transmission by infection | Rapid and fixed | Results in mixed clones (3). |
| (5) Cell-free preparations | Not yet accomplished | Easily filtered. |
| (6) Effect of antiserum | Slight if any | Blocks adsorption |
| (7) Role in $Gal^+$ transduction | None | Decisive |

Table 2

The Effect of λ on % $Gal^-$ Progeny

| $H^-Gal^-$ parent x | $T^-L^-Th^-Gal^+$ parent lysogenic | immune |
|---|---|---|
| lysogenic | 8.0 | 7.1 |
| immune | 6.3 | 6.3 |
| sensitive | 6.7 | 10.1 |

Table 3

Linkage of Gal, Lp, and Hfr

W-1895 x W-2308 (TLB)

BM Hfr  Xyl⁻ Gal⁺ Lac⁺ ara⁻ Mal⁺ Lp^s Lp^r V_1^R

Part A:

| Genotypes recovered[1] | | | Total |
|---|---|---|---|
| Gal | Lp | F | |
| + | + | + | 14 * |
| − | s | − | 29 * |
| + | s | + | 5 |
| − | + | − | 0 |
| + | s | − | 4 |
| − | + | + | 0 |

Part B: 2 x 2 contingencies

| | $Gal^+$ | $Gal^-$ | Total | $F^+$ | $F^-$ | Total |
|---|---|---|---|---|---|---|
| $F^+$ | 20* | 0 | 20 | | | |
| $F^-$ | 9 | 31* | 40 | | | |
| $Lp^+$ | 15* | 0 | 15 | 13* | 5 | 18 |
| $Lp^s$ | 11 | 29* | 40 | 6 | 33* | 39 |
| $Lac^+$ | 26* | 5 | 31 | 22* | 9 | 31 |
| $Lac^-$ | 4 | 26* | 30 | 7 | 27* | 34 |
| $V_1^r$ | 1* | 9 | 10 | 1* | 9 | 10 |
| $V_1^s$ | 28 | 21* | 49 | 23 | 20* | 43 |
| $Xyl_2^+$ | 9* | 1 | 10 | 7* | 2 | 9 |
| $Xyl_2^-$ | 20 | 30* | 50 | 16 | 7* | 23 |

* Parental combination

1 Selected as $Gal^+$ and $Gal^-$ prototrophs.

Table 4

Lysogenization in Transduced and Nontransduced $Lp^s$

Part A: $Gal^+$ and $Gal^-$ from single papillae

| $Gal^+/Gal^-$ Pair type | Number |
|---|---|
| $Lp^+/Lp^+$ | 13 |
| $Lp^+/Lp^s$ | 15 |
| $Lp^s/Lp^+$ | 3 |
| $Lp^s/Lp^s$ | 2 |
| $Lp^r/Lp^s$ | 2 |
| % $Gal^+$ sensitive | 15.2 |
| % Gal- sensitive | 47.2 |

| | $Gal^-$ $Lp^s$ | $Gal^-$ $Lp^+$ |
|---|---|---|
| $Gal^+$ $Lp^s$ | 2 | 3 |
| $Gal^+$ $Lp^+$ | 17 | 13 |

Part B: Lysogenization of transduced and inserted $Gal^+$

| $Lp^s$ strains | Av. No. $Gal^+$ recovered: Control | Treated* | Types in mixture | No. tested | % lysogenic |
|---|---|---|---|---|---|
| $Gal^+Lac^+$ | 109 | 92 | $Gal^+Lac^+$ (inserts) | 46 | 68.5 |
| $Gal^-Lac^-$ | 11** | 432 | $Gal^-Lac^-$ (original) | 40 | 72.5 |
| Mixture*** | 106.5 | 419 | $Gal^+Lac^-$ (transductions) | 103 | 100. |

* $10^9$

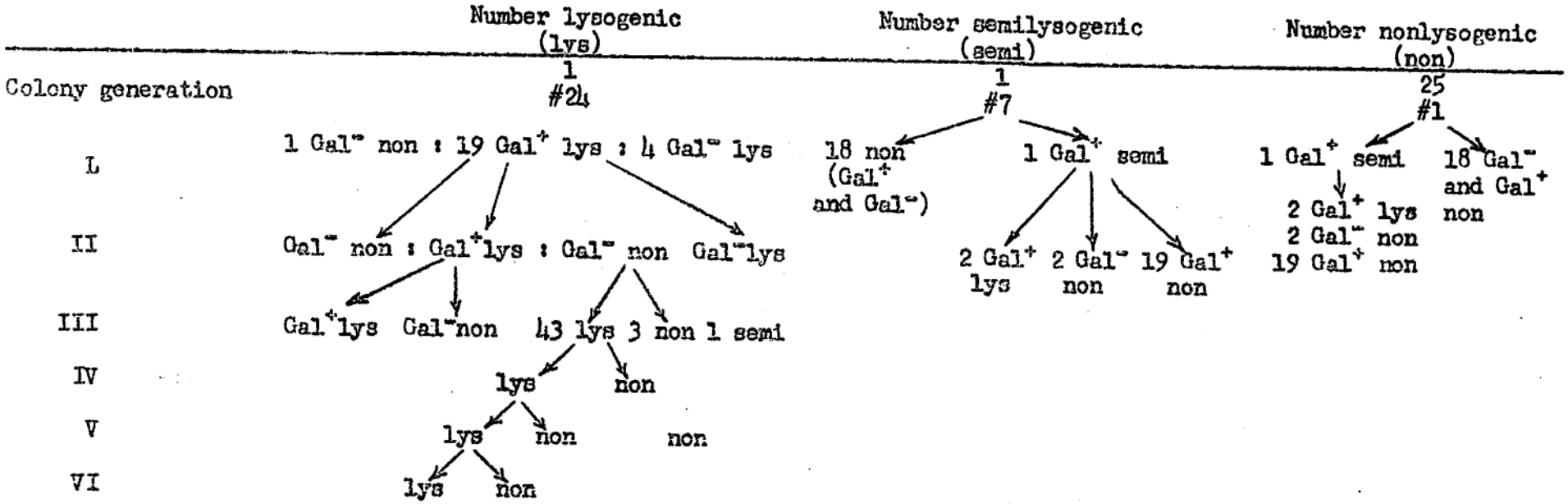
** Spontaneous reversions per $10^8$ inoculum

*** $10^8$ Gal-Lac- and 109 $Gal^+Lac^+$.

Table 5

Transductions to $Gal_4^-$ Immune-I: Segregation Patterns

Exp. 385: Strain 1924: 27 $Gal^+$




Exp. 431: Strain 2110: 38 $Gal^+$: 28 non, 1 semi (#23), and 9 lys

| | |
|---|---|
| Segregation patterns of lys | all $Gal^+$ lys, all $Gal^-$ non: 2 |
| | all $Gal^+$ lys, all $Gal^-$ lys: 5 |
| | all $Gal^+$ lys, $Gal^-$ lys and non 2 |
| | both $Gal^+$ and $Gal^-$ non: #23 |

Table 6

Survival and Transduction with Irradiated λ

| | No phage | Untreated phage | U-V[1] | X-ray[2] ( x $10^3$ r) 50 | 100 | 150 | 200 |
|---|---|---|---|---|---|---|---|
| Av. plaques/ml x $10^5$ | 0 | 127,000 | 16.9 | 41,667 | 3,975 | 377 | 100 |
| % survival | - | 100 | 0.013 | 32.8 | 3.13 | 0.297 | 0.008 |
| $Lp^S$ bacteria | | | | | | | |
| No. $Gal^+$ papillae | 20 | 1,000 | 170 | 250 | 85 | 30 | 30 |
| % " " | 0.5 | 100 | 34 | 25 | 17 | 6 | 6 |
| $Lp^r$ bacteria | | | | | | | |
| No. $Gal^+$ papillae | 39 | 60 | - | 135 | 115 | 31 | 20 |
| % " " | 65 | 100 | | 225 | 191.7 | 5.2 | 3.3 |

1 20 minutes, sterilamp

2 $10^3$ r/min. at 250 K.V., courtesy A. Novick, Radiobiology Inst., U. of Chicago.

Table 7

Segregation of Gal, Lp,... diploids

| A. H-324 Segregation of $Lp_2$, $B_1$, not tabulated. | | | | | | | B. H-325 Segregation of $V_6$, Mtl, $Lp_2$, $B_1$ not tabulated. | |
|---|---|---|---|---|---|---|---|---|
| $Gal_2^-$ | $Gal_2^+$ | Lp | Mal | Xyl | M | T,L | $Gal_1^-$ | $Gal_1^+$ |
| 1 | 47 | + | + | + | - | - | 1 | 49 |
| 0 | 1 | + | + | - | - | - | 0 | 0 |
| 0 | 1 | + | + | + | - | + | 2 | 0 |
| 0 | 0 | + | + | + | + | - | 0 | 1 |
| 1 | 0 | + | + | + | + | + | 0 | 0 |
| 2 | 0 | + | + | - | + | + | 0 | 0 |
| 25 | 0 | s | - | - | + | + | 13 | 0 |
| 9 | 1 | s | + | + | - | - | 13 | 1 |
| 3 | 0 | s | - | - | - | - | 0 | 0 |
| 6 | 0 | s | + | + | - | + | 7 | 0 |
| 1 | 0 | s | - | + | + | + | 0 | 0 |
| 2 | 0 | s | + | + | + | + | 3 | 0 |
| 0 | 0 | s | - | - | - | + | 12 | 0 |
| 50 | 50 | Total tested | | | | | 51 | 51 |

Table 8

Allelic Specificity of the Gal - λ Transduction at the Gal 1, Gal 2, and Gal 4 loci.

| λ- donor bacteria | | | Recipient cells | | |
|---|---|---|---|---|---|
| Gal 1 | Gal 2 | Gal 4 | 1-2+4+ | 1+2-4+ | 1+2+4- |
| + | + | + | + | + | + |
| - | + | + | - | + | + |
| + | - | + | + | - | + |
| + | + | - | + | + | - |
| diploids: | | | | | |
| + / + | - / + | + Lp$^+$ / + Lp$^s$ (trans) | No data | ± (21)* | + (300)* |
| + / + | + / - | + Lp$^+$ / + Lp$^s$ (cis) | | No data | |

* Gal + papillae per $10^9$ λ

Table 9

Summary of Current Allelism Tests

| Exp. No. | Gal$^-$ type | F$^-$ parent | F$^+$ parent | Total** progeny | No. Gal$^+$ | Maxim. % Gal+ |
|---|---|---|---|---|---|---|
| 535* | 1 x 4 | W-750 Lp$^+$ | W-2234 Lp$^S$ | 5000 | 17 | 0.3 |
| 563* | | | | 2000 | 15 | 0.75 |
| 534* | 2 x 4 | W-1210 Lp$^+$ | W-2234 Lp$^S$ | 6000 | 25 | 0.4 |
| 563* | | | | 1600 | 11 | 0.68 |
| 580* | | | | 2400 | 8 | 0.3 |
| 535 | 4 x 3 | W-518 Lp$^S$ | W-2315 Lp$^+$ | 807 | 6 | 0.74 |
| 582 | 4 x ?3 | W-518 Lp$^S$ | W-2315 Lp$^S$ | 5000 | 0 | 0 |
| | | | | 6700 | 5 | 0.06 |
| 583 | 1 x ? | W-2291 Lp$^S$ | W-583 Lp$^+$ | 7603 | 2 | 0.026 |

* All Gal$^+$ recombinants in these experiments are Lp$^S$.

**Estimated total.

Table 10

Behavior of Gal and Lp in Lac +/- Diploids

| Type of cross | | Parents F | (T L Th) | M | $Lac_1$ | $Lac_4$ | $Gal_1$ | $Gal_4$ | Lp | Diploid progeny Gal | Lp |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. Het diploids | (a)(Het) | + | - | + | + | + | + | + | + | +/- | +/∘ or -/∘ 1/ 5/ |
| | | + | + | - | - | + | + | - | s | | |
| | (b)(Het) | + | - | + | + | + | + | + | + | +/∘ or -/∘ | not segregating |
| | | + | + | - | - | + | - | + | + | | |
| 2. $Lac1^-$ x $Lac_4^-$ | (a) | - | - | + | + | - | + | + | + | Mostly +/∘ | Mostly +/∘ 2/ |
| | | + | + | - | - | + | + | - | s | | |
| | (b) | + | - | + | + | - | + | + | + | Mostly -/∘ | Mostly s/∘ 2/ |
| | | - | + | - | - | + | + | - | s | | |
| 3. Haploid x auxotrophic diploid | (a) | - 4/ | -/∘ | +/- | +/- | -/+ | + | +/∘ | +/∘ | $Gal^+$ $Lp^+$ / Gal-$Lp^s$ (linked) 3/ | |
| | | + | + | - | - | + | + | - | s | | |
| | (b) | same, except M- parent is $Lp^r$ | | | | | | | | $Gal^+$ $Lp^+$ / Gal-$Lp^r$ (linked) | |

1/ In Het crosses, Lp does not segregate. Gal 1 and Gal 4, two closely linked loci also differ: Gal 4 segregates, but Gal 1 does not.

2/ Diploids resulting from delayed disjunction revealed by heterozygotes of two Lac pseudoalleles show no segregation of Gal or Lp. Reversal of F status reverses the polarity of the Gal, Lp segregation.

3/ The only successful demonstration of heterozygosity of Gal and Lp.

4/ Aeration phenocopy.

5/ +/∘ indicates purity for +, whether hemizygous or homozygous.

Table 11

Segregation Patterns of $Gal^+$ Reversions in $Gal_2^-Lp^s/Gal_2^-Lp^+$ Diploids

| Diploid number | Total segregants | $Gal^+$ | | $Gal^-$ | | $Gal^+$ | | $Gal^-$ | | $Gal^+$ | | $Gal^-$ | | Inferred type of diploid |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | $Lp^+$ | $Lp^s$ | $Lp^+$ | $Lp^s$ | $Lp_2^r$ | $Lp_2^s$ | $Lp_2^r$ | $Lp_2^s$ | $Mal^+$ | $Mal^-$ | $Mal^+$ | $Mal^-$ | |
| A 1 | 161 | 76 | 6 | 3 | 76 | 45 | 0 | 39 | 0 | 1 | 53 | 17 | 36 | cis |
| B 1 | 121 | 2 | 58 | 60 | 1 | 52 | 8 | 60 | 1 | 38 | 22 | 61 | 0 | trans |
| B 2 | 73 | 0 | 40 | 41 | 0 | 32 | 7 | 31 | 0 | 33 | 7 | 33 | 0 | trans |
| B 3 | 76 | 61 | 4 | 1 | 10 | 65 | 0 | 57 | 5 | 65 | 0 | 44 | 18 | cis |
| C 1 | 48 | 1 | 23 | 24 | 0 | 23 | 1 | 24 | 0 | 9 | 15 | 24 | 0 | trans |
| E 1 | 60 | 30 | 0 | 3 | 27 | 26 | 4 | 24 | 6 | 30 | 0 | 16 | 14 | cis |
| E 2 | 24 | 0 | 12 | 12 | 0 | 12 | 0 | 12 | 0 | 6 | 6 | 12 | 0 | trans |
| E 3 | 23 | 12 | 0 | 0 | 11 | 12 | 0 | 11 | 0 | 12 | 0 | 3 | 8 | cis |
| F 1 | 66 | 32 | 1 | 2 | 31 | 31 | 2 | 30 | 3 | 32 | 1 | 21 | 12 | cis |
| F 2 | 40 | 20 | 0 | 1 | 19 | 20 | 0 | 20 | 0 | 20 | 0 | 7 | 13 | cis |
| F 3 | 23 | 12 | 0 | 0 | 11 | 12 | 0 | 10 | 1 | 12 | 0 | 3 | 8 | cis |
| F 4 | 18 | 11 | 0 | 1 | 6 | 10 | 1 | 0 | 7 | 11 | 0 | 7 | 0 | cis |

Table 12

Genetic Determination of Host Modification: line 1 lines 28, 31, 47

| | | Genotypes Under | | | | |
|---|---|---|---|---|---|---|
| | | Hypothesis I Lp locus with alleles | Hypothesis IIa fixed at Lp, modified by Mp | | Hypothesis IIb fixed at Lp in line 1, at Mp in other lines | |
| Phenotypes | Symbol | Lp | Lp | Mp | Lp | Mp |
| lysogenic | A | + | + | r | + | r |
| sensitive* | B | s* | s | s | s | s |
| sensitive | C | s | s | r | s | r |
| lysogenic* | D | ++ | + | s | s | + |
| A X B | | None | C, D | | C, D | |
| B X C | | None | None | | None | |
| C X D | | None | A, B | | A, B | |
| A X D | | None | None | | B and $Lp^+Mp^+$ | |

| EXPTL. RESULTS: | Lines crossed | Type | A | B | C | D | Gal char. |
|---|---|---|---|---|---|---|---|
| Expt. No. 419 | 1 x 28 | A $Gal^-$ x B | 0 | 46 | 1 | 0 | + |
| | | | 18 | 0 | 0 | 0 | - |
| | | C $Gal^-$ x D | 0 | 0 | 0 | 34 | + |
| | | | 2 | 8 | 18 | 3 | - |
| 418 | 1 x 31 | A $Gal^-$ x B | 3 | 43 | 26 | 1 | No record |
| 420 | | A $Gal^-$ x B | 4 | 22 | 28 | 12 | $Gal^+$ only |
| 423 | | A $Gal^-$ x B | 8 | 2 | 1 | 37 | + |
| | | | 0 | 1 | 0 | 0 | - |
| 423 | | C x D $Gal^-$ | 28 | 1 | 3 | 0 | (and 28 $Lp_2^r$) B or C |
| 444 | | C $Gal^-$ x D | 2 | 2 | 19 | 0 | mostly $Gal^-$ |
| 502 | | B $Gal^-$ x C | 0 | 15 | 13 | 0 | + |
| | | | 0 | 13 | 68 | 0 | - |
| 443 | 31 x 31 | B x A | 0 | 26 | 0 | 1 | |
| 468 | 1 x 47 | A x B $Gal^-$ | 51 | 0 | 0 | 6 | + |
| | | | 0 | 2 | 2 | 3 | - |
| 527 | | A $Gal^-$ x B | 4 | 7 | 1 | 9 | + |
| | | | 41 | 0 | 0 | 2 | - |
| 528 | | B x C $Gal^-$ | 0 | 13 | 17 | 0 | + |
| | | | 0 | 8 | 24 | 0 | - |
| 529 | | C $Gal^-$ x D | 3 | 2 | 2 | 21 | + |
| | | | 2 | 2 | 28 | 0 | - |
| 523 | | A $Gal^-$ x D | 8 | 0 | 0 | 52 | + |
| | | | 37 | 0 | 0 | 19 | - |

$F^-$ parent underlined.

Table 13

Genetic Control of the Semiresistant Phenotypes:

Nonlysogenic (W-2147) and Lysogenic (W-2172)

Part I

| Phenotype symbol | $Lp_1$ | $Lp_2$ | Example | Hypothesis I: A new allele at $Lp_2$: $Lp_1$ | $Lp_2$ | Hypothesis II: A 3rd locus, $Lp_3$, is involved: $Lp_3$ |
|---|---|---|---|---|---|---|
| A | + | s | Type lysogenic | + | s | s |
| B | + | r | Immune-2 lysogenic | + | r | s |
| C | + | p | W-2172 mutant | + | s | p |
| D | s | s | Type sensitive | s | s | s |
| E | s | r | Immune-2 | s | r | s |
| F | s | p | W-2147 mutant | s | s | p |

B x F, C x E Yields: B, F, E, C progeny — Yields B, F, E, C, A, D progeny

Results:

| | B x F No. of Progeny | | | | | | C x E No. of Progeny | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | A | B | C | D | E | F | A | B | C | D | E | F |
| $Mal^+$ | 55 | 1 | 1 | 1 | 0 | 1 | 22 | 2 | 1 | 26 | 0 | 1 |
| $Mal^-$ | 0 | 58 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 59 | 0 |

Part II Linkage of $Lp_3$ to $Lp_1$--Gal and $Lp_2$--Mal ?

| Parents | $Mal^+ Lp_1^s$ | $Mal^+ Lp_1^+$ | $Mal^- Lp_1^s$ | $Mal^- Lp_1^+$ |
|---|---|---|---|---|
| F $Mal^+$ x B $Mal^-$ | 4 | 56 | 1 | 58 |
| C $Mal^+$ x E $Mal^-$ | 27 | 25 | 59 | 0 |
| | $Mal^+ Lp_2^s$ | $Mal^+ Lp_2^r$ | $Mal^- Lp_2^s$ | $Mal^- Lp_2^a$ |
| F $Mal^+$ x B $Mal^-$ | 59 | 1 | 0 | 59 |
| C $Mal^+$ x E $Mal^-$ | 51 | 2 | 0 | 59 |
| | $Mal^+ Lp_3^s$ | $Mal^+ Lp_3^p$ | $Mal^- Lp_3^s$ | $Mal^- Lp_3^p$ |
| F $Mal^+$ x B $Mal^-$ | 57 | 3 | 59 | 0 |
| C $Mal^+$ x E $Mal^-$ | 50 | 2 | 50 | 0 |

| | | | | |
|---|---|---|---|---|
| C $Gal^+$ x D $Gal^-$ | $Gal^+ Lp1^+$ | $Gal^+ Lp1^s$ | $Gal^- Lp1^+$ | $Gal^- Lp^s$ |
| | 60 | 0 | 0 | 28 |
| | $Gal^+ Lp_3^s$ | $Gal^+ Lp_3^p$ | $Gal^- Lp_3^s$ | $Gal^- Lp_3^p$ |
| | 37 | 23 | 37 | 26 |

The above data are consistent with the hypothesis that an $Lp_3$ locus separable from $Lp_1$ and $Lp_2$ modifies the reaction to $\lambda$-1 and $\lambda$-2. This locus is not linked to $Lp_1$--Gal or $Lp_2$--Mal.

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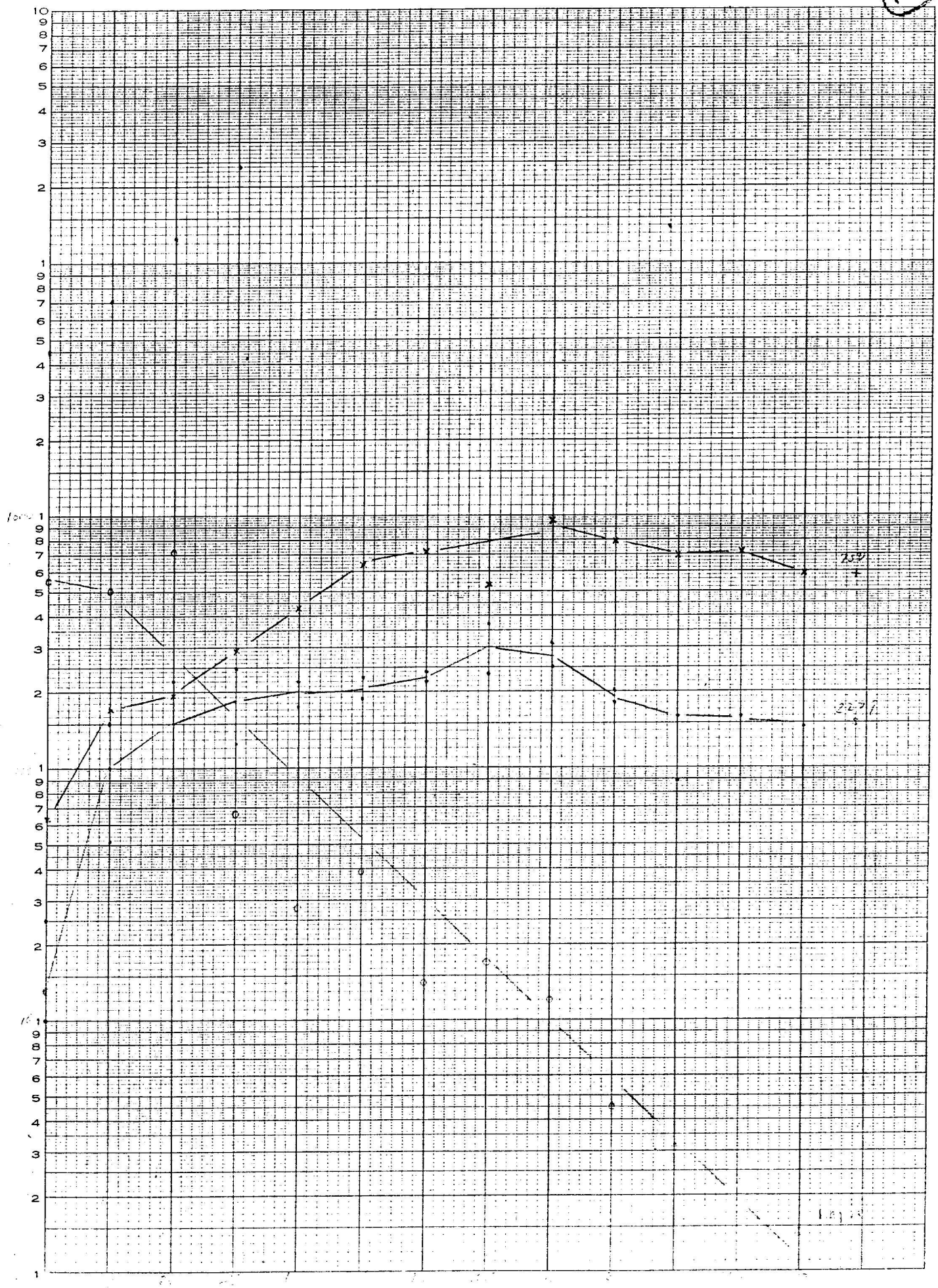

Keysort cards carry 68 bits. The following scheme is tentatively suggested for organizing the stockbook. Further suggestions urgently requested.

| | bits |
|---|---|
| Stock number and series (3 digits only) | 11 |
| Line: (1; 2-10; 11-20; 21-40; 41-..;) and E. coli not wg; Not E. coli; .....; | 3 |
| Event and agency: | 3 |

"Mutation" spontaneous, sporad.
spont; selected
UV
X-rays or other mutagen

Not "mutation": new isolate or receipt
segreg. orrecombinant (sex or --x)
Infection (F or lambda...)
"Cure" " " "

| | |
|---|---|
| Kind of locus changed: | 3 |

Not indicated
$Lp_1$ $or_x$
Gal (by transduction)
F
auxotroph
fermentation
Sm
Other resistance

20

Genotype: 1 bit each for:

| | | | |
|---|---|---|---|
| Gal 1, 2, 4, x | 4 | S (incl $S^d$) | 2 |
| Lac 1, x | 2 | Other resist. (lv fut) | 2 |
| Mal 1, x | 2 | Fla | |
| Xyl, Mtl, Stl, Ara, Stl, Glu, Suc, Cell, Rh, X M, (T, L) | 10 | | |
| Other aux: AA, Vit, Pur, etc. | 2 | misc. | 5 |
| Hfr; F | 3 | | 64 |
| Het | 2 | | |
| Heterogenote or heterozygote | 1 | lyophil | 1 |
| any suppressor | 1 | | |
| any temp.-sens. | 1 | who entered | 3 |
| Lp or other phage | 3 | | 68 |
| $V_1$ $V_6$ $V_x$ $Lp_2$ $Lp_x$ | 5 | | |
| | 35 | | |

# Incidence of Homozygotes

| Rye | Ends | Egs | No. Tested | | |
|---|---|---|---|---|---|
| 341 | 2- | 4- | 17 | (3 seg segs from each) | 2 HFT 2- / 3×17 = 52 ✓ |
| | 4- | 2- | 5 | (about 9 segs from each) | 0 HFT / 9×5 = 45 |
| 311 | 2- | 6- | 30 | (single seg) | 1 HFT 6- / 30 (no tests for 2-) ✓ |
| 309 | 7- | 2- | 5 | (6 segs from each) | 1 HFT 7 / 30 (no tests for 2-) |
| 295 | 2- | 1-4- | 152 | (single seg) only 1-4- tested | 1 HFT 1-4 / 14 (no tests for others) |
| 293 | 2- | 4- | 5 | (sep. segs) | 1 HFT 2- / 11 \| 2 HFT 2- / 11 \| 0/11 \| 1 HFT 2- / 11 \| 7 HFT 4- out / 12 \| 0/10 |
| 291 | 8- | 4- | 3 | (sep. segs) | 0/20 \| 0/22 \| 0/8 |
| 248 | 1- | + | 4 | single | 0/4 |
| 247B | 8 | 4 | 1 | single | 1/1 HFT 4- |
| 247A | 8 | + | 4 | single | 0/4 |
| 243 | 1 | 8 | 3 | single | 0/3 |
| 242 | 4 | 8 | 1 | single | 0/1 |
| 241 | 1- | 2 | 24 | single - done against 1-, 2- | 2 HFT 2- / 24 |
| 236c | 8 | 4 | 1 | single | 0/1 |
| 212 | 4 | + | 4 | single | 0/4 |
| 209 | 2 | 1 | 2 | " | 0/2 |
| 205 | 4 | + | 3 | " | 0/3 |
| 202 | 4 | 2 | 18 | " | 1 HFT 2- / 1 HFT 4- / 18 |
| 198 | 4 | 2 | 16 | " | 0/16 |
| 196 | 2 | + | 4 | " | 0/4 |
| 192B | 1 | 2 | 9 | " | 2 HFT 1- / 1 HFT 2- / 9 |
| 192A | 1 | + | 4 | " | 0/4 |

24/385

0/30

24/ca 200

# Corrected Estimations of Homogeneous Frequency

| range | 2⁻ | 1⁻ | 4⁻ | 6⁻ | 7⁻ | 8⁻ |
|---|---|---|---|---|---|---|
| 341 | 2/47 (I) | | 0/5 (A) | | | |
| | 0/4 (A) | | 0/41 (I) | | | |
| 311 | | | | 1/3 (A) | | |
| 309 | | | | | 1/27 (I) | |
| 293 | 1/10 (I) | | 0/1 (A) | | | |
| | 2/10 (I) | | 0/1 (A) | | | |
| | 0/10 (I) | | 0/1 (A) | | | |
| | 1/10 (I) | | 0/1 (A) | | | |
| | 0/9 (I) | | 0/1 (A) | | | |
| 291 | | | | | 0/46 (I) | |
| 277 | | 0/4 (I) | | | | |
| 247B | | | 1/1 (A) | | | |
| 247A | | | | | 0/4 (I) | |
| 243 | | | | | 0/3 (A) | |
| 242 | | | | | 0/1 (A) | |
| 241 | 2/2 (A) | 0/22 (I) | | | | |
| 236c | | | 0/1 (A) | | | |
| 212 | | | 0/4 (I) | | | |
| 209 | | 0/2 (A) | | | | |
| 205 | | | 0/3 (I) | | | |
| 202 | 1/3 (A) | | 1/14 (I) | | | |
| 192 | | | 0/16 (I) | | | |
| 196 | 0/4 (I) | | | | | |
| 1943 | 1/5 (A) | 2/4 (I) | | | | |
| 1941 | " | " (I) | | | | |

| | 2⁻ | 1⁻ | 4⁻ | 6⁻ | 7⁻ | 8⁻ |
|---|---|---|---|---|---|---|
| I | 4/14 | 2/34 | 1/18 | | | |
| A | 6/98 | 2/2 | 1/12 | | | |

General

| | 2⁻ | 1⁻ | 4⁻ | 6⁻ | 7⁻ | 8⁻ |
|---|---|---|---|---|---|---|
| | 10/114 | 2/36 | 2/94 | 1/3 | 1/37 | 0/54 |
| | 0.09 | 0.06 | 0.02 | 0.33 | 0.03 | 0.00 |

16

6/11 0.33

2⁻ 0.09

1⁻ 0.06

7⁻ 0.03

4⁻ 0.02

8⁻ 0.00

Obtained from

Exdigenda (0.04) 10/240

Etgenuti (0.19) 6/31

10 HFT/240

6/31

1⁻

-/+ 0/23

| | Page | | F+ | F− | (+) | Total | % + |
|---|---|---|---|---|---|---|---|
| 1X3 | 200 | | M⁻ $GaI_1^-$ $Hp^+$ (710) | $TLB_1^-$ $GaI_3^-$ $Hp^+$ (2238) | 2 | ca. 1600 | 0.13 ✓ |
| 1X2 | 214 | (1) | M⁻ $GaI_1^-$ $Hp^+$ (713) | $TLB_1 \equiv GaI_2^-$ $Hp^+$ (2251) | 4 | 1957 | 0.2 ✓ |
| 1X2 | | (2) | " | " | 4 | ca. 6517 | 0.06 ✓ |
| 1X2 | | | M⁻ $GaI_4^-$ $Hp^+$ (711) | $TLB_1 \equiv GaI_2^-$ $Hp^+$ (2251) | 0 | 1039 | 0 ✓ |
| 8X2 | | (1) | M⁻ $GaI_4^-$ $Hp^+$ (2254) | $TLB_1 \equiv GaI_2^-$ $Hp^+$ (2251) | 3 | ca 6840 | 0.04 ✓ |
| 8X2 | | (2) | " | " | 0 | ca 9640 | 0. ✓ |
| 8X2 | | | " | " | 0 | ca. 1872 | 0. ✓ |
| 1X2 | 199 | | M⁻ $GaI_1^-$ $Hp^+$ (750) | $TLB_1 \equiv GaI_2^-$ $Hp^+$ | 2 | ca 1500 | 0.13 ✓ |
| 1X4 | 210 | | M⁻ $GaI_1^-$ $Hp^+$ (750) | $TLB_1^-$ $GaI_4^-$ $Hp^+$ $F^+$ (1426) | 6 | 4588 | 0.13 ✓ |
| 1X2 | 240 | | M⁻ $GaI_1^-$ $Hp^+$ (750) | $TLB_1$ $GaI_4^-$ $Hp^+$ (2251) | 1 | 3606 | 0.03 ✓ |
| 4X4 | 171 | | M⁻ $GaI_4^-$ $Hp^+$ (570) | $TLB_1$ $GaI_2^-$ $Hp^+$ (962) | 5 | 1289 | 0.38 ✓ |
| 2X4 | 171a | | " $Hp^+$ (711) | " | 0 | 706 | 0.0 ✓ |
| 2X4 | 174 | | " | " | 0 | 200 | 0.0 ✓ |
| 2X4 | 175 | | " | " | 1 | 358 | 0.28 ✓ |
| Farnesol 2X4 | 337 | | M⁻ $GaI_4^-$ $Hp^+$ (1402) $F^-$ | $TLB_1^-$ $GaI_2^-$ $Hp^+$ $F^+$ | 7 | 3771 | 0.18 |

| | | (+) | Total | % + |
|---|---|---|---|---|
| 1X2 | (1) | 1 | 1957 | 0.2 |
| | (2) | 4 | ca 6517 | 0.06 |
| | (3) | 2 | ca 1500 | 0.13 |
| | (4) | 1 | 3606 | 0.03 |
| | | | Ave 5/13680 | 0.06 % |
| 1X3 | (1) | 2 | ca 1600 | 0.13 % |
| 1X4 | (1) | 6 | 4588 | 0.13 % |

| 2X4 | (+) | Total | % + |
|---|---|---|---|
| | 0 | 1039 | 0. |
| | 5 | 1289 | 0.38 |
| | 0 | 706 | 0. |
| | 0 | 200 | 0. |
| | 1 | 358 | 0.28 |
| | 6 / 3592 | | 0.17 |
| 4X2 | 7 | 3771 | 0.18 |

Ave F+ ↗

| | + | Total | % + |
|---|---|---|---|
| 8X2 (1) | 3 | ca 6840 | 0.04 |
| (2) | 0 | ca 9640 | 0 |
| (3) | 0 | ca 1872 | 0 |