BACTERIAL AND YEAST GENETICS: A HISTORICAL ACCOUNT

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Summary

Bacterial genetics has led to the establishment of the universal "central dogma" on the transfer of genetic information, and yeast genetics has resulted in a number of discoveries that provided essential clues to understanding complex phenomena in many fields of higher eukaryotes. It is no longer surprising to find that results obtained in yeast are applicable to higher eukaryotes in almost every field of molecular biology. Thus the direct outcome of molecular genetics of bacteria, bacteriophages, plasmids, and yeast furnished the basis for contemporary biotechnology, in which these organisms have been playing the most important roles instrumentally as well as ideologically. Thanks to this technonogy, nucleotide sequencing of the whole genome has been completed or initiated in a large variety of organisms from viruses to human in the last decade. Microbial genetics initially chose only a small number of genera or species as the model organisms for elucidating universal phenomena rather than for understanding the respective organisms for their own sake. In other words, microbial genetics has developed rapidly, because it has been intentionally ignoring the variety and diversity of biological subjects. Consequently, organisms in which no genetic analytical systems have been developed, such as many pathogenic bacteria or viruses, or industrially useful yeast, have remained poorly understood in many aspects despite being closely associated with human life. Completion of genome sequencing of such organisms has now been solving this dilemma of the twentieth century's molecular genetics to a great extent. The history of microbial genetics thus teaches us how basic science is important to human society despite the initial lack of demonstrable application.

1. Bacterial genetics

1.1. Introduction - Bacterial Genetics

One of the characteristics of biology is the diversity and variety of its subjects. A group of scientists in the early 1940s thought that there was a hierarchy in urgency among a vast variety of biological phenomena as research subjects, and that the urgency should

be assessed in terms of the universality of a phenomenon to be studied—the more universal the phenomenon, the more urgent the study. They then reached the conclusion that the most universal feature of living organisms is the "resembles make resembles" phenomenon, i.e. inheritance.

They believed that it was this phenomenon that should be elucidated first. They then chose certain bacteria as appropriate objects to study the inheritance for the following reasoning: (1) They have short generation times, which shorten the time necessary for experimentation. (2) They are easily handled without special skills. (3) They grow on simple culture media, which reduces necessary expense for supplies. (4) They pass most of, if not the entire, life cycle within a single cell, which facilitates collection of a large cell mass of one kind.

Also, the simple organization of the cell structure seemed to be advantageous in interpreting experimental results. These features of bacteria are quite appropriate for analysis of heredity through not only genetic but also biochemical approaches. This attitude of scientists yielded a new discipline of biological science, i.e. microbial genetics, which later developed to "molecular genetics". Since there have been a number of textbooks and reviews as cited in the Bibliography, this chapter may well be a reiteration of these materials.

Nevertheless, it should give a useful introduction to those who wish to quickly survey the history of this scientific discipline that emerged and developed at the end of the twentieth century.

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1.2. *Escherichia coli* and its related bacterial species

1.2.1. Cell structure, growth, and mutations

For the above reasoning, the pioneering workers picked up *Escherichia coli* (and its bacteriophages) as the first choice for genetic studies. This bacterial species is one of the enteric bacilli naturally inhabiting the intestinal tract, mainly in the colon, of vertebrates including humans.

The cell is rod-shaped, 2 to 3 μm in length and 0.4 to 0.6 μm in breadth. Bacterial cells have a protective coat, called a cell wall, beneath which a plasma membrane encloses cytoplasm. Unlike animal or plant cells, no nucleus is seen in bacterial cytoplasm. On account of this feature, bacteria are classified as "prokaryote" in contrast to the former, which are collectively called "eukaryote".

In a rich medium, called "nutrient broth", the wild type cells of *E. coli* divide once in 15 to 20 minutes by binary fission; apical extension and septum formation at the middle (see Figure 1). It similarly grows in a simple synthetic medium composed of ammonium sulfate, glucose, and salts, with a little longer division time than in nutrient broth.

These characteristics made this microorganism particularly easy to handle in the laboratory as well as suitable for genetic studies.

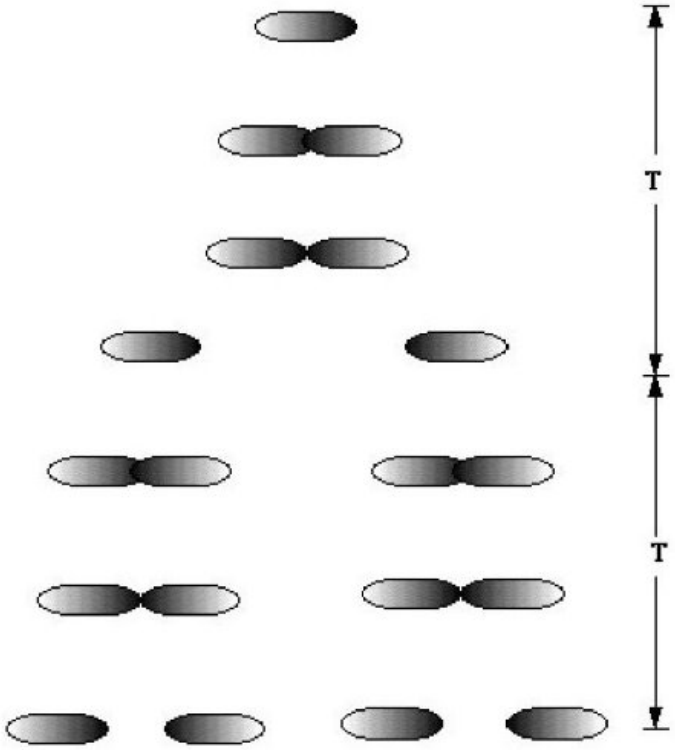

Figure 1. Schematic representation of bacterial cell division. Rod-shaped forms showing cells of *Escherichia coli* divide in binary fission. T to the right represents time required for one cycle of cell division.

Even if *E. coli* fulfills the requirements for the object of genetics, how could one identify genes in bacteria? In the early 1940s, people could not even imagine the existence of inheritable traits in such a tiny organism like *E. coli*. This question had been answered in the red bread mold *Neurospora crassa* by Beadle and Tatum as early as in1941 (see *Heredity and Environment; Light signal transduction in plants and fungi)*. Before the microorganism, the fruit fly, *Drosophila* was used as one of the most advanced objects in genetics. At that time the gene was a conceptual entity that determined certain phenotype, like color of eyes or length of legs. Beadle and Tatum who had previously collaborated in a biochemical analysis of eye pigment formation of *Drosophila* encountered the red bread mold *Neurospora crassa*.

They realized that this mold was not only amenable for genetic analysis like *Drosophila*, but also able to grow in a simple synthetic medium, provided that the vitamin biotin was added as the only complex organic supplement. In the light of a series of genetic as well as biochemical studies with *N. crassa*, they proposed the now so-called "**one gene/one enzyme hypothesis**" that every gene in the organism directs the activity of the corresponding enzyme. They succeeded in isolation of a set of genetically distinct mutants of *Neurospora crassa*, all of which required an amino acid. In parallel, they established that the amino acid was synthesized through a biochemical pathway comprising several steps, each of which is catalyzed by a distinct enzyme. They then found that the respective mutant was defective in the distinct enzyme in the

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synthetic pathway of that amino acid. That is to say that one gene corresponds to one enzyme.

Precursor	→	substance I	→	substance II	→	substance III	→	amino acid
Enzyme	A		B		C		D	
Gene	U		X		Y		Z	

Suppose in the above scheme, a precursor is converted to substance I by catalytic function of enzyme A, and successive conversions of substance I to an amino acid are catalyzed by enzymes B, C, and D, respectively. Beadle and Tatum proposed that synthesis of the respective enzyme is directed by gene U, X, Y, and Z.

In the early 1940s, Luria and Delbrück (1943) demonstrate that, when several 10^7 cells of *Escherichia coli* strain B were spread with a T1phage on an agar medium, most cells were killed but a few cells which survived gave rise to colonies. ["**Phage**" originally called "**bacteriophage**" is a virus propagating in bacterial cells (see 1.2.6. Bacteriophages)]. Such phage-resistant cells, when encountering that phage again, were no longer killed by the same phage. Thus it was concluded that phage-resistance could be used as a stable inheritable trait. At that time, however, many scientists still believed that the hypothesis of Lamark, regarding the inheritance of acquired traits, was true for bacteria, even though the hypothesis had already been disproved for higher organisms. The first task of Luria and Delbruck was then to examine whether the T1-resistance trait arose by spontaneous mutation of a gene or by adaptation to T1 phage. In other words, they had to determine whether T1-resistant cells existed before the encounter with T1 or emerged after the exposure to it. These two alternative models for the origin of T1 resistant bacteria led to different statistical predictions concerning the dynamics of their appearance. To this end, Luria and Delbruck exploited a statistic method called "**fluctuation test**", and proved that the acquisition of phage-resistance was due to spontaneous mutation rather than adaptation (see Figure 2). Thus twenty 0.2 ml cultures (individual cultures) and one 10 ml culture ("bulk culture") of nutrient medium were inoculated with about 1000 *E. coli* B cells per ml, and incubated until the bacteria in all cultures reached a cell density of 10^8 cells per ml. Each of twenty individual cultures was spread onto a plate that had been pre-spread with enough T1 phage. At the same time, the ten 0.2 ml-aliquots of the bulk culture were spread onto ten plates that had been similarly pre-spread with T1 phage. After incubating all these 30 plates, the number of colonies emerged were counted (see Table 1). As is seen in the Table, the mean number of T1-resistant (designated Ton^r) colonies per plate from the bulk culture was almost equal to the value of variance. By contrast, the mean number of Ton^r colonies per plate from individual cultures are subject to great variation. These results are reasonably explained only by assuming that the Ton^r mutation occurred by spontaneous mutation and that T1 phage played a role just to select pre-existing ton^r mutants (see Figure 2).

Individual cultures		Bulk culture	
Culture no.	Ton^r bacteria	Culture no.	Ton^r bacteria
1	1	1	14

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2	0	2	15
3	3	3	13
4	0	4	21
5	0	5	15
6	5	6	14
7	0	7	26
8	5	8	16
9	0	9	20
10	6	10	13
11	107		
12	0		
13	0		
14	0		
15	1		
16	0		
17	0		
18	64		
19	0		
20	35		
Mean (n)	11.3		16.7
$Variance_n$	694		15
$Variance_n/n$	61		0.9

From S. E. Luria and M. Delbruck (1943)

Table 1. The Fluctuation Test of the spontaneous origin of T1phage-resistant *E. coli* mutants

Later, a completely new technique was invented by Joshua Lederberg and Ester Lederberg in 1952, called "**replica-plating**" to support the Luria-Delbruck theory on the spontaneity of the origin of mutants. This technique enabled isolation of streptomycin-resistant mutant cells who had never been exposed to streptomycin before from streptomycin-sensitive K12 cells (see Figure 3). First, several 10^5 cells of *E. coli* K12 were spread on an agar plate without streptomycin. The plate was incubated overnight at 37^oC and cells were allowed to grow to confluent. Cells were then transferred to a new plate containing streptomycin by using a cylindrical block covered with sterile velveteen. The replica plate was incubated until streptomycin-resistant colonies appeared, while the original or master plate was kept in a refrigerator. Cells on the master plate that grew at the position corresponding to that streptomycin-resistant colonies appeared on the replica-plate were collected, resuspended in sterile water, and spread on antibiotics-free plate.

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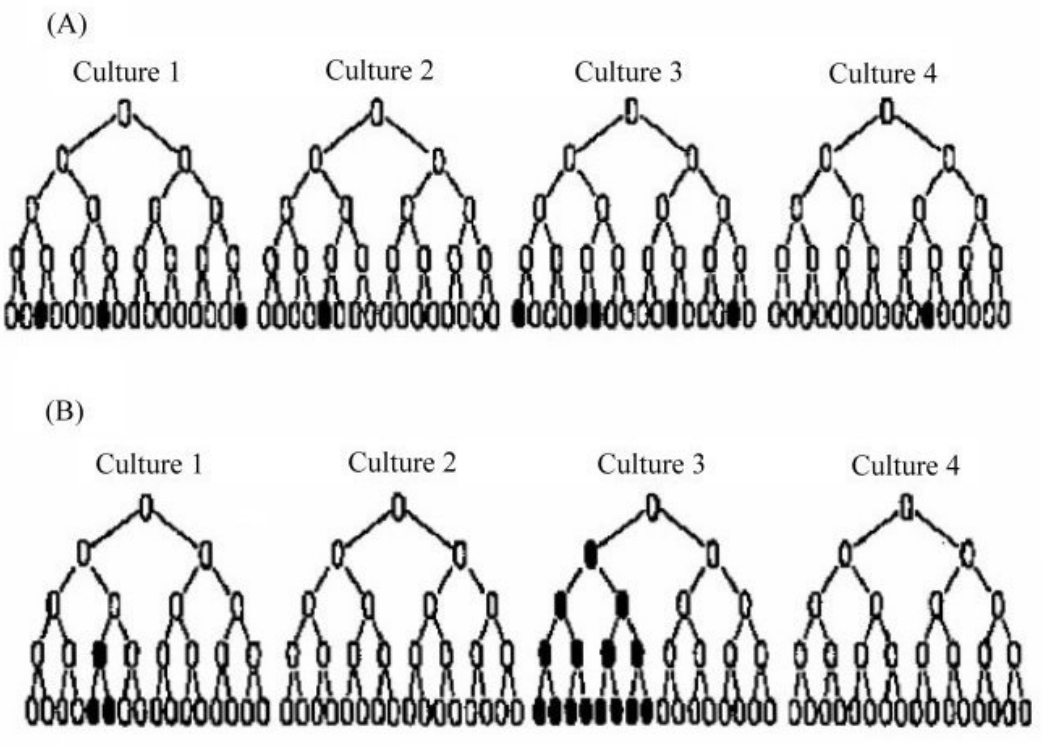

Figure 2. Fluctuation test. Schematic representation of the appearance of ten Ton^r mutant *E. coli* in four parallel cultures of wild type *E. coli*. A. Sample distribution to be expected if the Ton^r character were induced upon contact with T1 phage. B. Sample distribution to be expected if the Ton^r character appeared as a consequence of spontaneous mutation.
[Modified from G. Stent (1971) "Molecular Genetics" W. H. Freeman and Company]

The plate was incubated overnight to make the second master plate. Several cycles of replica-plating gave well-isolated colonies on a pair of master plate and replica plate, and thus colonies on the master plate comprised streptomycin-resistant mutants that had never been exposed to this antibiotic. This technique thus contributed a strong support to the notion that the streptomycin-resistant mutants were originated from selection of rare spontaneously arisen mutants in a large bacterial population. Besides, the technique has been used widely in microbial genetics to examine a large number of strains for various phenotypes at a time. For example, a single plate containing several hundreds of colonies or patches of bacteria can serve as the master plate for some twenty replica-plates. Only with this technique, one could examine several thousands of clones for twenty different traits within an hour.

Genetic Nomenclature; Various types of traits or phenotypes have been used as genetic markers in the *E. coli* chromosome, and generally, each phenotype corresponds to a distinct gene. The genetic nomenclature of bacterial genes is now standardized as follows: The symbol of a gene consists of three lower-case letters of the alphabet in italics, abbreviated from the corresponding phenotype. For example, the resistance to T1 phage or to streptomycin is designated *ton* or *str*, respectively. The corresponding

phenotypes are expressed as Ton^r or Str^r, respectively. In many cases, the gene symbol is followed by a capital letter of the alphabet, like *metA* or *leuB*, which represent certain types of methionine- or leucine-requiring phenotypes, respectively. Each of these genes encodes an enzyme involved in biosynthesis of methionine or leucine, respectively. Stable alterations in sugar utilization are also useful phenotypes in bacterial genetics, such as lactose- and galactose-non-fermentation, which are designated *lac* and *gal*, respectively. The *lac* genes include *lacZ, lacY, lacA, and lacI*, encoding ˜galactosidase, lactose-permease, tiogalactoside transacetylase, and repressor of the *lac* operon (see below). The *gal* genes include *galK, galT, galE, and galU*, encoding galactokinase, galactose-1-phosphate uridyl transferase, uridine diphosphogalactose-4-epimerase, and uridine diphosphoglucose pyrophosphorylase, respectively.

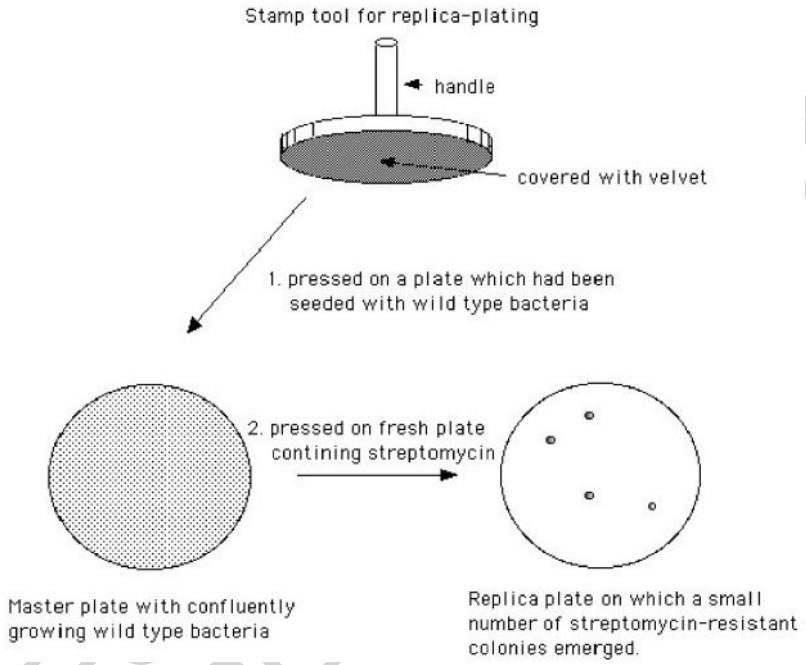

Figure 3. Replica plating method to isolate streptomycin-resistant mutants (see text for explanation)

Conditional lethal mutations; Cells constituting plants or animals have two sets of chromosomes per cell, the feature of which is called "**diploid**". By contrast, bacteria are "**haploid**" by nature containing a single chromosome or a single set of chromosomes, and therefore, mutants in genes whose functions are indispensable for growth at the physiological conditions were often non-viable. Such genes were thought to be almost impossible to handle until the discovery of "**conditional lethal mutation**". Every bacterium has its optimal temperature for growth, and *E. coli* and its related bacterial species will grow within a temperature range of some 30 ^oC to 37 ^oC. One could isolate a mutant that is able to grow at lower temperatures below 37 ^oC, like 30 ^oC or lower, but not at 37 ^oC or higher. These are called "temperature-sensitive mutations" and are abbreviated as *ts*. By contrast, "cold (-temperature)-sensitive mutants" can also be obtained, capable of growing only at lower-than normal temperatures. The reason for the temperature-dependence is that the protein encoded by a mutated gene is non-functional at that temperature.

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Jones, E. W., Pringle, J. R. and Broach, J. R. (Eds.) (1992): *The Molecular and Cellular Biology of the Yeast Saccharomyces, Vol. 2. Gene Expression*. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY, 810 pp. [The second volume of this three- volume set contains unique studies on the gene expression in the yeast *Saccharomyces cerevisiae* from biochemical as well as molecular biological points of views. It also contains a review on the mating type interconversion in *Schizosaccharomyces pombe*.]

Pringle, J. R., Broach, J. R. and Jones, E. W. (Eds.) (1997).: *The Molecular and Cellular Biology of the Yeast* Saccharomyces, *Vol. 3. Cell cycle and Cell Biology.* Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY, 1107 pp. [The third volume of this three-volume set contains excellent reviews on cell biology and cell cycle control of the yeast *Saccharomyces cerevisiae*, one of the fields to which yeast studies contributed to a great extent.]

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Biographical Sketch

Toshio Fukasawa graduated from Keio University School of Medicine in 1954. He trained as an Internship trainee at Keio University Hospital from 1954 to 1955. He was Instructor of the Department of Microbiology at Keio University School of Medicine from 1955 to 1962 (under Prof. Daizo Ushiba). He received the degree of Doctor of Medical Science (equivalent to Ph.D.) from Keio University, and was appointed as Instructor of the Institute for Protein Research at Osaka University from 1962 to 1965 (under Prof. Kiyoshi Kurahashi). Appointed as Visiting Lecturer of Department of Biology at Massachusetts Institute of Technology (under Prof. S.E. Luria) in 1963, and as Visiting Scientist of the National Institute of Arthritis and Metabolic Diseases at the National Institute of Health from 1963 to 1965 (under Dr. Bruce N. Ames). He was Associate Professor of the Institute for Protein Research at Osaka University from 1965 to 1974, and Professor of Research Unit of Molecular Genetics at Keio University School of Medicine from 1974 to 1995. Concurrently appointed as Professor of Department of Microbiology at Keio University School of Medicine from 1989 to 1995. He received the title of Professor Emeritus of Keio University. He was appointed as Special Guest Investigator of Kazusa DNA Research Institute from 1995 to 1998.

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