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DOMAIN 7 GENETICS AND GENETIC TOOLS

The Legacy of Genetic Analysis Advances Contemporary Research with *Escherichia coli* K-12 and *Salmonella enterica* serovar Typhimurium LT2

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ABSTRACT *Escherichia coli* K-12 and *Salmonella enterica* serovar Typhimurium LT2 became standard organisms for genetic analysis during the Truman administration. Half a century later, genetic analysis with these strains had become an art form, interpreted through 23 articles in the ambitious two-volume masterpiece edited by the late Fred Neidhardt and colleagues. These legacy articles now are available through *EcoSal Plus*, so as to inform and inspire contemporary genetic analyses in these standard organisms and their relatives.

> A standard organism suitable for genetic studies … must be designed so that the biochemistry, physiology, and even the genotype can be manipulated at will. Once the organism has been redesigned so that crosses, complementation, recombination and transformation can be carried out with facility, the modified organism can be used by all biologists … none of these standard organisms exists in nature; all have been painstakingly altered to perform the scientist's bidding.
>
> — Gerald R. Fink (1).

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We are accustomed to thinking that virtually any cultivable microbe can be a subject for genetic analysis. Broadly efficient methods for whole-genome sequencing, chromosome engineering, and transposon mutagenesis enable gene identification and analysis of null phenotypes in diverse species. But what next? Can one isolate and locate mutational alterations that confer phenotypes other than null? Are methods for complementation analysis rigorous and reliable? Can one build strains that carry multiple genetic alterations, and reliably authenticate their genotypes? Answers can vary greatly depending on the organism and even strain being evaluated, but, for a standard organism, the answers uniformly are positive.

The standard organisms *Escherichia coli* K-12 and *Salmonella enterica* serovar Typhimurium LT2 were adopted in early years as models for understanding bacterial molecular genetics, and therefore also for biochemistry and physiology. The resulting focus, by thousands of accomplished scientists working collectively over several decades, has left us a treasure of sophisticated—yet accessible—time-tested approaches.

Twenty years ago was a pivotal time in bacterial genetics. With the art of sequence-independent genetic analysis nearing its apotheosis, the first whole-genome sequences illuminated a stunning new way for routine investigations of gene structure and function in diverse species. Genome sequence information is indispensable today, but it cannot replace the basic operations of genetic analysis: mutation, segregation, recombination, and complementation. Happily, the second volume of Escherichia coli *and* Salmonella: *Cellular and Molecular Biology*, included nearly two dozen authoritative reviews detailing the approaches to these operations. These legacy articles now are available online through *EcoSal Plus*, with this short article as a guide. The reference section includes direct links to the original 1996 reviews referenced herein.

THE CHROMOSOME AND ITS PRODUCTS

One goal of genetic analysis is to determine linkage between loci. The resulting maps facilitate gene discovery, enable identification of linked selectable markers, and have many other uses. The detailed maps for *E. coli* K-12 (2) and *Salmonella* LT2 (3) culminated efforts over thirty years to compile and integrate mapping data from thousands of publications (one further update for *E. coli* K-12 appeared two years later [4]). Audaciously, both maps integrate genetic linkage with the locations of restriction endonuclease cleavage sites across the entire genome (5). Maps are annotated comprehensively with volumes of well-organized literature citations describing identification, mapping, and mutant phenotypes for each gene. These are knowledgeable guides into the primary literature when tracking down genetic selections, mutant phenotypes, or specific alleles.

Genomes contain not only structural genes, but also insertion sequences (6), repeated sequences (7), and cryptic prophages (8). These articles summarize the structures and chromosomal locations of these elements and provide excellent resources for understanding their variety and their relationships to one another.

Accurate genome annotation demands knowledge of encoded signals for transcription, translation, subcellular localization, and regulation, as well as consideration of codon usage and other parameters (9). A proteomics database documents the growth-dependent changes in synthesis rates for proteins resolved by two-dimensional gel electrophoresis (10). Once likely genes have been identified, the functions of protein products can be inferred from the nucleotide sequence (11). Finally, the system for categorizing protein products, ubiquitous in present-day genome analyses, was developed initially for *E. coli* K-12 and is elaborated here in detail (12). This information-rich article collects and organizes gene-by-gene annotation in a way that blends well (dare one say, *synergistically*?) with that presented in the linkage map annotation (2). These articles remain valuable for those who use DNA sequence information to infer gene structure and function.

ALTERATIONS IN THE GENOME

The bacterial genome is dynamic, experiencing a range of stable and transient alterations that can be encountered and even exploited by bacterial geneticists. These include not only mutagenesis (13) and homologous recombination (14), but also spontaneous rearrangements such as tandem duplications (15). This chromosomal dynamism is constrained in part by DNA repair mechanisms (16) and further impacted by plasmid maintenance (17), bacteriophages (18), transposition (19), and site-specific recombination (20). Experimental approaches in all these areas were highly developed, and these richly detailed articles contain much valuable information.

GENE TRANSFER: CONJUGATION

Lateral genetic exchange is the only way to form new gene combinations in bacteria. Discovery of F, the first known agent of gene transfer (21), led to the immediate, widespread adoption of *E. coli* K-12 as a standard organism for genetic analysis. This well-studied conjugable plasmid (22) can integrate into the chromosome, creating Hfr strains used for large-distance genetic mapping with both *E. coli* K-12 (23) and *Salmonella* LT2 (24). Hfr strains also generate F′ plasmids, containing chromosome segments of up to 100 kb or more, which are ideal for complementation analysis (25).

GENE TRANSFER: TRANSDUCTION AND TRANSFORMATION

The search for conjugation in *Salmonella*, with then-obvious medical importance, led instead to discovery of generalized transduction (26). This enabled genetic crosses at fine scale for mapping and strain construction and established *Salmonella* LT2 as a standard organism.

The ease of generalized transduction mediated by bacteriophages P22 (for *Salmonella*) and P1 (for *E. coli* K-12) made this the default approach for mapping, backcrosses, and strain construction (27), and finalized these strains as standard organisms. The utility of this technique in a variety of daily genetic operations cannot be overstated, and many have searched for generalized transducing phage active on other strains and species.

Meanwhile, specialized transduction of *E. coli* K-12 by bacteriophage λ enables construction of strains unambiguously diploid for a particular locus (28), facilitating complementation analyses and construction of dual-reporter strains. Finally, *E. coli* and *Salmonella* can be made competent for transformation (29).

STRAIN DERIVATIONS AND MAPPING

The standard organisms *E. coli* K-12 and *Salmonella* LT2 derive their utility not only from the well-validated genetic tools described above, but also from curated collections of strains with known pedigrees and genotypes (30, 31). The complex, lovingly detailed pedigrees for numerous *E. coli* K-12 mutant derivatives illustrate the importance of strain choice for a particular project. Indeed, it often is useful to pursue "mutants by mail," not only to save time, but also to build on work already done to validate particular alleles and their phenotypes (32, 33).

Genetic linkage mapping is valuable for assigning the lesions in newly isolated mutants to specific loci; it is rapid, accurate, and inexpensive (34). Of course, with genetic toolbox at hand, one still must design selections or screens that return informative mutants. Here, the impressive compilation by LaRossa (35) provides numerous examples of imaginative and specialized selections. These successful approaches provide inspiration for finding new ways to isolate new mutants. Transposable elements are integral to most genetic programs, not only as insertion mutagens, but also as linked markers, portable regions of homology, and more (36, 37).

CONCLUSION

The impressive two-volume compilations of all things *E. coli* and *Salmonella* has for good reason been an indispensable resource, found on laboratory bookshelves worldwide. Although technology such as DNA sequencing continually changes, the core intellectual approaches to genetic analysis are timeless. This collection of legacy articles can inform and enhance our approach to bacterial genetics now and in the years to come.

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