

NATIONAL ACADEMY OF SCIENCES

GEORGE WELLS BEADLE

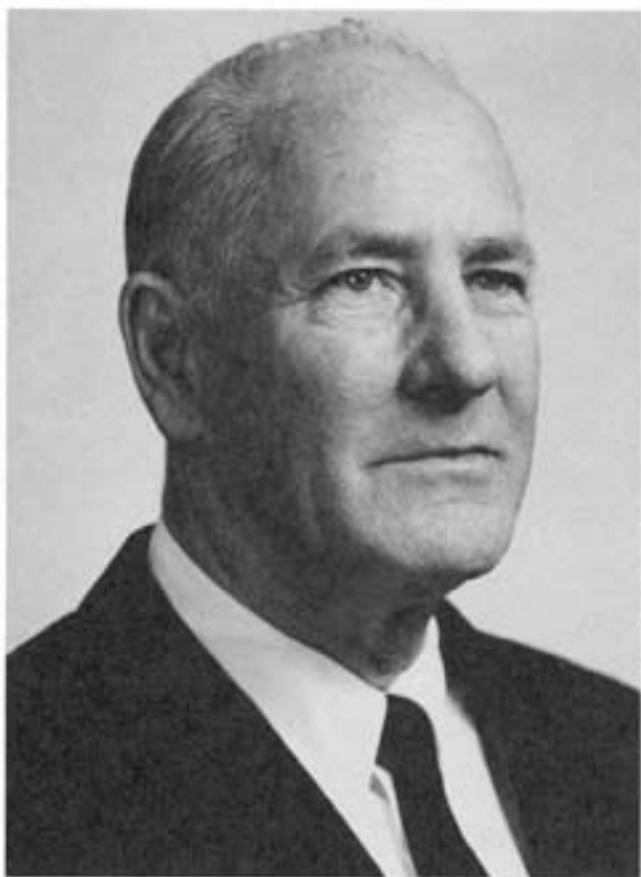
1903—1989

A Biographical Memoir by
NORMAN H. HOROWITZ

*Any opinions expressed in this memoir are those of the author(s)
and do not necessarily reflect the views of the
National Academy of Sciences.*

Biographical Memoir

COPYRIGHT 1990
NATIONAL ACADEMY OF SCIENCES
WASHINGTON D.C.



Courtesy, Institute for Biomedical Research, 1970

George Barden

GEORGE WELLS BEADLE

October 22, 1903–June 9, 1989

BY NORMAN H. HOROWITZ

GEORGE BEADLE WAS A GIANT in the field of modern genetics. He initiated the great series of advances made between 1941 and 1953 that brought the era of classical genetics to a close and launched the molecular age. For this achievement he received many honors, including the Nobel Prize. He was elected to the National Academy of Sciences in 1944 and served on its Council from 1969 to 1972.

Beadle also had a distinguished career as an academic administrator. When he retired in 1968, he was President of The University of Chicago. Long years in administration, however, did not dampen his love of experimental genetics, and after his retirement he resumed experimental work on a favorite subject—the origin of maize. In 1981, he gave up research altogether because of increasing disability from the Alzheimer's disease that eventually ended his life.

EDUCATION AND EARLY LIFE

Beadle—his oldest friends usually called him by his boyhood nickname, “Beets”—was born in Wahoo, Nebraska, to Hattie Albro and Chauncey Elmer Beadle, and he died in Pomona, California, at age eighty-five. He grew up on his father's forty-acre farm near Wahoo. The farm was a model for farms its size and was so designated by the U. S. Depart-

ment of Agriculture in 1908. Beets' mother died when he was four years old, and he and his brother and sister were raised by a succession of housekeepers.

As a boy he worked on the farm, and he retained the skills he learned as a gardener and beekeeper there, and his handiness with tools, for the rest of his life. Gardening remained one of his greatest pleasures, and the victory garden he grew around his home at Stanford during the War produced enough for two families. This garden included beehives, but Beets wouldn't eat the honey, saying he had been stung too many times as a boy. He loved corn, on the other hand, and raised several kinds, including a small Mexican variety that gave his garden the distinction of having the earliest sweet corn at Stanford. After his retirement to Pomona in 1982, he derived much pleasure from growing flowers, a hobby he pursued as long as his health permitted.

Beets did well in school and was inspired to go on to college by his high school science teacher, Bess MacDonald (the debt to whom he acknowledged more than once in later years). Despite his father's opinion that a farmer did not need all that education, he entered the University of Nebraska College of Agriculture in 1922. He graduated in 1926 with a B.S. degree and stayed on for another year to work for a master's degree with Franklin D. Keim.

His first scientific publication, with Keim, dealt with the ecology of grasses. At some point along the way under Keim's beneficent influence, Beets became interested in fundamental genetics and was persuaded to apply to the graduate school at Cornell University instead of going back to the farm. He entered Cornell in 1927 with a graduate assistantship and shortly afterward joined R. A. Emerson's research group on the cytogenetics of maize.

Corn genetics was new and exciting for Beets, and Emerson and his team—which included Barbara McClintock and

Marcus Rhoades—were inspiring. The result was that in the following five years, Beets published no fewer than fourteen papers dealing with investigations on maize, all begun while he was a graduate student at Cornell.

In 1928 he married Marion Hill, a graduate student in botany at Cornell, who assisted him with some of his early corn research. Their son, David, was born in 1931.

Beets received his Ph.D. in 1931 and was awarded a National Research Council Fellowship to do postdoctoral work in T. H. Morgan's Division of Biology at the California Institute of Technology. At Caltech, while finishing the work on maize cytogenetics he had started at Cornell—on genes for pollen sterility, sticky chromosomes, failure of cytokinesis, and chromosome behavior in maize-teosinte hybrids (a subject he would return to in his retirement)—Beadle also began doing research on *Drosophila*. Out of it would come one of the most interesting investigations of his career.

DROSOPHILA STUDIES: CROSSING OVER,
VERMILION AND CINNABAR

Beadle's *Drosophila* studies at Caltech were concerned with the results of crossing over within various chromosomal rearrangements. The important study of crossing over in attached-X chromosomes he conducted with Sterling Emerson showed that exchanges occur at random between any two non-sister chromatids. Another, reported jointly with A. H. Sturtevant (in a paper called "monumental" by E. B. Lewis), was the first systematic investigation of crossing over and disjunction in chromosomes bearing inversions.

In 1934, Boris Ephrussi arrived at Caltech from Paris to study *Drosophila* genetics with Morgan and Sturtevant. He was just two years older than Beadle and they became close friends. Ephrussi soon communicated to Beadle his own interest in the problem of gene action, and the two planned a

collaborative study on *Drosophila* that would use Ephrussi's skill in the techniques of tissue culture and transplantation.

In mid-1935, the two men went to Paris to carry out experiments in Ephrussi's laboratory at the Institut de Biologie. Though their attempts to grow imaginal discs in tissue culture failed, they succeeded in devising a method for transplanting discs from one larva to another that allowed the discs to continue to develop.

Before year's end, they had gone as far as they could with this methodology and had worked out a hypothesis to account for the interaction they observed between the vermilion and cinnabar genes in transplanted flies. The results, they showed, could be explained by the following assumptions: (1) the normal alleles of the two genes control the production of two specific substances, called the v^+ - and cn^+ -substances, both necessary for brown eye-pigment formation; (2) the v^+ -substance is a precursor of the cn^+ -substance; and (3) gene mutation blocks formation of the corresponding substance. It was not clear until much later that the two substances are actually precursors of the pigment, and Ephrussi and Beadle frequently referred to them as "hormones."

At the time, this small step was a great advance in the science of genetics, for it suggested that development could be broken down into series of gene-controlled chemical reactions—an idea that cried out for further investigation. It implanted in Beadle the germ of the one gene—one enzyme idea that he later brought to full flower. But first, the two eye-color substances had to be identified, a process that took five years. By that time, Beets was hunting bigger game.

Following his return from Paris, Beadle moved to Harvard University as an assistant professor. There, on a few brief occasions, he met a young woman who would later become my wife and who remembered him fondly afterwards as the only member of the Harvard faculty who spoke to Radcliffe undergraduates at Biology Departmental teas.

BEADLE AND TATUM

Beadle left Harvard the following year (1937) for Stanford University, where he had accepted an appointment as professor of biology. He was joined by biochemist Edward L. Tatum (1909–1975) as a research associate.¹

Over the next three years, Tatum contributed his skills to the work of isolating and identifying the two eye-color substances. With others, they established that the two substances were derivatives of tryptophan. By 1940, Tatum had obtained a crystalline preparation of the v^+ -substance, but he and Beadle were beaten to the identification by Butenandt, Weidel, and Becker, who had adopted the simple procedure of testing known metabolites of tryptophan for their biological activity. These researchers found that kynurenine is active as the v^+ -substance and that OH-kynurenine is active as the cn^+ -substance. Much later it was shown that condensation of two molecules of OH-kynurenine forms brown pigment.

Despite this setback in the laboratory, the years from 1937 to 1939 were not wasted for Beadle. During this period, he joined A. H. Sturtevant in writing a superlative textbook, *An Introduction to Genetics* (1939,5), praised by J. A. Moore as “the complete statement of classical genetics.”

NEUROSPORA CRASSA AND GENE ACTION

As a result of his *Drosophila* experience it became clear to Beadle that an entirely different method was needed to make headway with the problem of gene action. No other nonautonomous traits were known in *Drosophila*, and the autonomous ones—of which there were many—were of such towering complexity from the biochemical standpoint that it was hopeless to attempt to reduce them to their individual chemical steps.

Beets enjoyed telling how the solution to this problem came to him while he was listening to Tatum lecture in a

¹ See p. 356 for Joshua Lederberg's memoir of Tatum.

course on comparative biochemistry. Microbial species, Beets learned, differ in their nutritional requirements even though they share the same basic biochemistry. If these differences were genetic in origin, he thought to himself, it should be possible to induce gene mutations that would produce new nutritional requirements in the test organism. Such an approach, if successful, would allow the researchers to identify genes governing known biochemical compounds immediately, as opposed to the years needed to identify the unknown substances controlled by the usual kinds of genes, including most of those then known.

What was needed for such an undertaking was an organism that was genetically workable that could be grown on a chemically defined medium. Beadle knew just the organism. While still a graduate student at Cornell, he had heard about *Neurospora crassa*, the red bread mold. B. O. Dodge had come to the campus from the New York Botanical Garden to give a lecture on *Neurospora*. Beets remembered clearly that the lecture dealt with the genetics of the organism, including results on first- and second-division segregations of the mating-type and other loci. Even years later Beets was pleased to recall that he and a few other graduate students had been able to explain to the skeptical Dodge that his data could be explained by crossing over—or the lack of it—between the gene and its centromere.

Dodge had played an important role in the history of *Neurospora*. It was he who discovered that the ascospores could be germinated by heat, thus closing its life cycle and making the organism accessible for genetic study. He also did basic studies on its genetics and was enthusiastic about its possibilities for genetic research. He convinced T. H. Morgan, a close friend, to take some cultures with him to Pasadena when, in 1928, Morgan went out to found the Division of Biology at Caltech. Dodge, according to Beadle, told

Morgan that *Neurospora* would be “more important than *Drosophila* some day,” and, in Pasadena, Morgan assigned the cultures to graduate student Carl Lindegren, for his thesis in genetics. Lindegren studied the relation between first- and second-division segregations and crossing over. He completed his thesis in 1931, the year Beadle arrived at Caltech.

In 1940 the question of the nutritional requirements of *Neurospora* was still an open one. Previous workers had used nutrient agar as the growth medium, but this would not do for the experiment Beadle had in mind. Related fungi, however, were known to have simple requirements, and Tatum soon showed that *Neurospora* would grow on a synthetic medium containing sugar, salts, and a single growth factor—biotin—thenceforth referred to as “minimal medium.” Fortunately, purified concentrates of biotin had recently become available, and nothing now stood in the way of an experimental test of Beadle’s idea.

The final step was to clear the *Drosophila* cultures out of the Stanford lab and convert it into a laboratory for *Neurospora* genetics. The plan was to x-ray one parent of a cross and collect offspring (haploid ascospores isolated by hand) onto a medium designed to satisfy the maximum number of possible nutritional requirements (so-called “complete medium”). The resulting cultures would next be transferred to minimal medium. Growth on complete medium, combined with failure to grow on minimal medium, was to be taken as presumptive evidence of an induced nutritional requirement. The requirement would be identified, if possible, and the culture would be crossed to wild type to determine its heritability.

This scheme, in its time, was breathtakingly daring. Some nongeneticists still suspected that genes governed only trivial biological traits, such as eye color and bristle pattern, while important characters were determined in the cytoplasm by

an unknown mechanism. Many geneticists believed that gene action was far too complex to be resolved by any simple experiment. Indeed, the outcome of Beadle and Tatum's trial run was so uncertain that they agreed at the outset to test 5,000 ascospores before giving up the project and—to avoid early disappointment—isolated and stored over a thousand spores before testing any of them.

Success came with spore no. 299, which gave rise to a culture that grew on complete but not on minimal medium unless this was supplemented with pyridoxine. This mutant was followed by others showing requirements for thiamine and *p*-aminobenzoic acid, respectively. All three requirements were inherited as single-gene defects in crosses to wild type. These mutants were the subject of the first *Neurospora* paper by Beadle and Tatum (1941,2). Before long, mutants requiring amino acids, purines, and pyrimidines were also found, and the science of biochemical genetics had been born.

Beadle recognized that he and Tatum had discovered a new world of genetics and that more hands would be needed to explore it. Early in the fall of 1941 he came to Caltech to give a seminar on the new discoveries and to recruit a couple of research associates to join the enterprise. Since the first Beadle-Tatum paper on *Neurospora* had yet to be published, no one in the audience had an inkling of what was to come. The seminar was memorable. I recorded my recollection of it in an article written in honor of Beadle's seventieth birthday:

"The talk lasted only half an hour, and when it was suddenly over, the room was silent. The silence was a form of tribute. The audience was thinking: Nobody with such a discovery could stop talking about it after just thirty minutes—there must be more. Superimposed on this thought was the realization that something historic had happened. Each one of us, I suspect, was mentally surveying, as best he could, the consequences of the revolution that had just taken place. Finally, when it became clear that

Beadle had actually finished speaking, Prof. Frits Went—whose father had carried out the first nutritional studies on *Neurospora* in Java at the turn of the century—got to his feet and, with characteristic enthusiasm, addressed the graduate students in the room. This lecture proved, said Went, that biology is not a finished subject—there are still great discoveries to be made!” *Neurospora Newsletter* 20(1973):4–6

BEADLE AS LABORATORY HEAD

David Bonner and I accepted appointments with Beadle and joined his group at Stanford the following year. Later, H. K. Mitchell and Mary Houlahan (Mitchell) came. There were also graduate students (including A. H. Doermann and Adrian Srb) and a steady turnover of visitors in the lab.

The next four years were the most exciting of my life, and I imagine the same was true for everyone else in the lab. Before the *Neurospora* revolution, the idea of uniting genetics and biochemistry had been only a dream with a few scattered observations. Now, biochemical genetics was a real science, and it was all new. Incredibly, we privileged few had it all to ourselves. Every day brought unexpected new results, new mutants, new phenomena. It was a time when one went to work in the morning wondering what new excitement the day would bring.

Beadle presided over this scientific paradise with the enthusiasm, intelligence, and good humor that characterized everything he did. He was a popular and much admired boss. He worked in the lab with everyone else. He especially enjoyed working with his hands, and he had plenty of opportunity to indulge himself in this regard.

The laboratories were located in the basement (the “catcombs”) of Jordan Hall, a location that gave them a certain remoteness from the campus. There were a bench and lathe in the lab, and Beets used these to make small equipment and do minor repairs around the place; he called the campus shops only for major work and did as much as possible him-

self. I came to work early one morning and found him painting one of the rooms.

All this was in addition to his research and his teaching duties as a professor of biology. He always did more than anyone else. I recall going to a lab picnic at the beach one summer day, over the coast range of hills from the Stanford campus. We were bicycling to save gas, huffing and wheezing (we had no gears then); Beets differed from the rest of us only in that he was carrying a watermelon on his handlebars.

Beets knew his responsibilities and took them seriously. It was wartime, and he concerned himself with all that implied for the pursuit of fundamental research. He had to find financial support for the program while trying to keep his group together. He succeeded on both scores, obtaining support from both the Rockefeller and Nutrition foundations—support that continued throughout the war and even afterwards. The Committee on Medical Research of the Office of Scientific Research and Development classified the *Neurospora* program as essential to the war effort. As I recall, no senior researcher or graduate student was drafted, although some of us were called up for physical examinations.

Practical applications of *Neurospora* research were of potential utility to the war effort—in developing bioassays for vitamins and amino acids in preserved foods, and in searching for new vitamins and amino acids. Although the major thrust of the lab remained basic science, we worked on both these applications during the war years. Toward the end of World War II, Beadle was asked by the War Production Board to devote part of the effort of the lab to seeking mutants of *Penicillium* with increased yields of penicillin. He complied, of course, but we were not successful in this endeavor.

The biochemical and genetic studies carried out between 1941 and 1945 on *Neurospora* mutants in the Stanford laboratory showed that the biosynthesis of any given substance

of the organism is under the control of a set of nonallelic genes. Mutation of any one of these genes results in loss of the synthesis, due to blocking of a single step in the biosynthetic pathway.

Beadle summarized the whole field of biochemical genetics in an historic article in *Chemical Reviews* (1945,4). He proposed that the biochemical actions of genes could be explained by assuming that genes are responsible for enzyme specificity, the relation being that "a given enzyme will usually have its final specificity set by one and only one gene. The same is true of other unique proteins, for example, those functioning as antigens."

This statement became known as the "one gene—one enzyme" hypothesis of gene action and is Beadle's major legacy to fundamental genetics. Controversial at first (the controversy itself is an interesting reflection on the state of genetics at the time), it was eventually proved to be correct.

Yet, important though this summary statement of the *Neurospora* findings is in the history of science, there is little doubt that Beets' most inspired contribution to genetics was the method he devised with Tatum to produce the mutants from which the theory was derived. He showed how an important class of lethal mutations could be recovered by the use of a microorganism with known nutritional requirements. The same method, as Tatum later found, could be applied to bacteria. Tatum's student Joshua Lederberg, using the resulting mutants, demonstrated genetic recombination in *E. coli* and thereby founded modern bacterial genetics. Beadle, Tatum, and Lederberg shared the Nobel Prize in 1958.

CHAIRMAN OF THE DIVISION OF BIOLOGY,
CALIFORNIA INSTITUTE OF TECHNOLOGY

With the war drawing to a close in 1945, Tatum departed Stanford for Yale University and the team of Beadle and

Tatum dissolved. The following year Beadle returned to Caltech—this time to succeed T. H. Morgan as chairman of the Division of Biology.

Morgan had died, and there was a need to find as his successor a first-rate biologist who would continue the Morgan tradition: a strong emphasis on experimental, quantitative, and chemical biology. (Biochemistry had been included in Caltech's Biology Division since its inception.) It is interesting that the key figure in the negotiations on the Caltech side was the chemist Linus Pauling. Pauling had a lively interest in the new genetics, understood its importance, and later made important contributions to it. Beadle was the ideal choice, but it is doubtful if he would have made the move if it were not for Pauling's intercession.

For a time after returning to Caltech, Beets continued with laboratory research, but administrative matters began to absorb his attention and finally swallowed him up. He stopped working in the lab. His last research paper on Neurospora was published with David Bonner in 1946 (1946,1). After that, and for the next thirty years, his scientific writings consisted of reviews, lectures, historical essays, and a prize-winning book for young people, *The Language of Life: An Introduction to the Science of Genetics* (1966,1). The book was coauthored with his second wife, Muriel Barnett, a writer, whom he married in 1953 following his divorce. (Muriel's first husband having died, Beadle legally adopted her son, Redmond.)

In an autobiographical sketch published in 1974, Beets made the following revealing statement about his decision to give up laboratory research:

"In my own situation, I tried a quarter of a century ago what I thought of as an experiment in combining research in biochemical genetics with a substantial commitment to academic administration. I soon found that, unlike a number of my more versatile colleagues, I could not do justice to

both. Finding it increasingly difficult to reverse the decision I had made, I saw the commitment to administration through as best I could, often wondering if I could have come near keeping up with the ever increasing demands of research had I taken the other route. My doubts increased with time.”

He finally did in fact return to research, but only after his retirement.

As successor to the legendary Morgan, Beadle fulfilled all expectations. Faculty appointments made during his tenure as chairman included Max Delbrück, Renato Dulbecco, Ray Owen, Robert Sinsheimer, and Roger Sperry. These men were not only eminent, their appointment set the direction of the Biology Division’s post-war growth toward molecular, cellular, and behavioral biology—a direction the Division has followed ever since. In addition, the material wealth of the Division increased considerably during Beadle’s tenure. Not the least of the additions were two new laboratory buildings.

Informal, unaffected, and open, Beets was later described as a chairman who steered the Division without actually seeming to run it. He was at the same time hardheaded and witty, and his insights often took the form of memorable quips. My favorite of these—because it is both true and pure (unmistakable) Beadle—was: “It’s hard to make a good theory—a theory has to be reasonable, but a fact doesn’t.” I quoted this saying to great effect at a meeting on the origin of life held in Moscow in 1957, and I told Beets about it when I got back to Pasadena. He, as usual, could not remember saying it.

In 1961 Beadle left Caltech to become president of The University of Chicago. Why he took this job and what he did after he arrived in Chicago was for years a mystery to me and, I suspect, to most (if not all) of his old scientific friends. Everybody who visited The University at that time knew that it was in trouble because of urban decay in the surrounding

neighborhood. A little later, we heard about the spectacular student sit-ins, but none of this seemed to connect with the George Beadle we knew.

The mystery was cleared up in 1972—four years after Beadle's retirement—with the publication of a book by Muriel Beadle entitled *Where Has All The Ivy Gone?*, an honest and highly entertaining account of the Beadles' years at The University of Chicago. It explains why The University wanted Beets as its president (to restore its academic standing after difficult years that saw the loss of many first-class faculty members); why he took the job (it was put to him as a challenge by a persuasive Dean of the Law School, Edward Levi, who later succeeded Beadle as president); and what he did there (a great deal).

Friends of mine at The University have informed me that Beadle was much admired as president and that he did stanch the loss of faculty, particularly in the sciences and in medicine. He is also remembered by many for the garden he established on the campus near the president's house, where he could be observed working in the early morning. (Some were surprised to discover that this man was the president of the University, having thought him a hired gardener!)

In 1968 Beadle attained mandatory retirement age. He and Muriel decided to remain in Chicago and bought a home in Hyde Park, one of the neighborhoods saved by the urban renewal program they had both worked hard on.

Beets then returned to research, after twenty-three years in the wilderness. The problem he chose to investigate—the origin of maize—was one he was familiar with from his Cornell days. Maize is a cultivated plant that cannot survive in the wild. How did it arise?

R. A. Emerson and Beadle showed that it is closely related genetically and cytologically to teosinte, a plant that grows wild in Mexico and Guatemala. They considered teosinte the most plausible ancestor of maize. In 1939, Beadle found that

teosinte seeds—which are enclosed in a hard coat that makes them inedible—can be popped like ordinary popcorn, which would give prehistoric Americans an incentive to grow teosinte as a food plant. Once it was under cultivation, mutations could have been selected that, in time, would have transformed it into maize.

This theory was criticized by Paul Mangelsdorf, primarily because there was little archaeological evidence to support it. In its place he proposed that maize evolved from a hypothetical wild corn, now extinct. In his retirement Beadle decided to gather more evidence on the question. He displayed the same vigor and inventiveness in this undertaking that had distinguished the researches of his younger days.

In a lecture he delivered at Caltech in 1978 on the occasion of the fiftieth anniversary of the founding of the Biology Division, he summarized his findings. It was a brilliant tour de force, touching on every aspect of the subject: genetics, linguistics, palynology, archaeology, folklore, animal behavior. (What does a squirrel do when given seeds of maize and teosinte?) He described an experiment he had made on himself to decide whether teosinte meal was edible. He was informative, witty, and persuasive, his conclusion unambiguous: “Just when and where the American Indians transformed teosinte into corn we do not know, but it was surely the most remarkable single plant-breeding achievement of all time.”

This must have been one of Beets’s last public lectures. As a finale to a scientific life it could hardly have been better.

George Beadle has passed into history now. His papers are rarely read anymore; his lively presence is no longer felt. But the changes he brought about in biology are permanent. No scientist could ask for a grander memorial than that.

FOR THEIR COMMENTS on the manuscript, I am indebted to Muriel Beadle, Elizabeth Bertani, James Bonner, Edward and

Pamela Lewis, and Ray Owen. For answering my questions on a variety of matters, I thank Marion Beadle, Walton Galinat, Barbara McClintock, Oliver Nelson, Jane Overton, and Bernard Strauss. And I thank the personnel of the Caltech Archives for their un-failing courtesy.

HONORS AND DISTINCTIONS

HONORARY DEGREES

Doctor of Science

- 1947 Yale University
- 1949 University of Nebraska
- 1952 Northwestern University
- 1954 Rutgers University
- 1955 Kenyon College
- 1956 Wesleyan University
- 1959 Birmingham University
- 1959 Oxford University
- 1961 Pomona College
- 1962 Lake Forest College
- 1963 University of Rochester
- 1963 University of Illinois
- 1964 Brown University
- 1964 Kansas State University
- 1964 University of Pennsylvania
- 1966 Wabash College
- 1967 Syracuse University
- 1970 Loyola University, Chicago
- 1971 Hanover College
- 1972 Eureka College
- 1973 Butler University
- 1975 Gustavus Adolphus College
- 1976 Indiana State University

Legum Doctor (LL.D.)

- 1962 University of California, Los Angeles
- 1963 University of Miami
- 1963 Brandeis University
- 1966 Johns Hopkins University
- 1966 Beloit College
- 1969 University of Michigan

Litterarum Humaniorum Doctor (L.H.D.)

- 1966 Jewish Theological Seminary of America
- 1969 DePaul University
- 1969 University of Chicago
- 1969 Canisius College
- 1969 Knox College
- 1971 Roosevelt University
- 1971 Carroll College

Doctor of Public Service

- 1970 Ohio Northern University

AWARDS

- 1950 Lasker Award
- 1951 Dyer Award
- 1953 Emil Christian Hansen Prize (Denmark)
- 1958 Albert Einstein Commemorative Award in Science
- 1958 Nobel Prize in Physiology or Medicine (with E. L. Tatum and J. Lederberg)
- 1959 National Award, American Cancer Society
- 1960 Kimber Genetics Award
- 1967 Priestley Memorial Award
- 1967 Edison Prize, Best Science Book for Youth (with Muriel Beadle)
- 1972 Donald Forsha Jones Medal
- 1984 Thomas Hunt Morgan Medal

PROFESSIONAL AND HONORARY SOCIETIES

Genetics Society of America (president, 1945)
American Association for the Advancement of Science (president,
1955)
National Academy of Sciences (Council, 1969–1972)
American Philosophical Society
American Academy of Arts and Sciences
Royal Society
Danish Royal Academy of Sciences
Japan Academy
Istituto Lombardo di Scienze e Lettere (Milan)
Genetical Society of Great Britain
Indian Society of Genetics and Plant Breeding
Indian Natural Science Academy
Chicago Horticultural Society (president, 1968–1971)
Phi Beta Kappa
Sigma Xi

SELECTED BIBLIOGRAPHY

1927

With F. D. Keim. Relation of time of seeding to root development and winter survival of fall seeded grasses and legumes. *Ecology*, 8:251-64.

1928

With B. McClintock. A genic disturbance of meiosis in *Zea mays*. *Science*, 68:433.

1929

Yellow stripe—A factor for chlorophyll deficiency in maize located in the Pr pr chromosome. *Am. Nat.*, 68:189-192.
A gene for supernumerary mitoses during spore development in *Zea mays*. *Science*, 70:406-7.

1930

Heritable characters in maize. *J. Hered.*, 21:45-48.
Genetical and cytological studies of Mendelian asynapsis in *Zea mays*. *Cornell Univ. Memoir*, 129:3-23.
A fertile tetraploid hybrid between *Euchlaena perennis* and *Zea mays*. *Am. Nat.*, 69:190-92.

1931

A gene in *Zea mays* for failure of cytokinesis during meiosis. *Cytol.*, 3:142-55.
A gene in maize for supernumerary cell divisions following meiosis. *Cornell Univ. Memoir*, 135:3-12.

1932

A possible influence of the spindle fibre on crossing-over in *Drosophila*. *Proc. Natl. Acad. Sci. USA*, 18:160-65.
A gene in *Zea mays* for failure of cytokinesis during meiosis. *Cytol.*, 3:142-55.
Genes in maize for pollen sterility. *Genet.*, 17:413-31.
The relation of crossing over to chromosome association in *Zea-Euchlaena* hybrids. *Genet.*, 17:481-501.
Studies of *Euchlaena* and its hybrids with *Zea*. I. Chromosome be-

havior in *Euchlaena mexicana* and its hybrids with *Zea mays*. ZIAVA, 62:291-304.

With R. Emerson. Studies of *Euchlaena* and its hybrids with *Zea*. II. Crossing over between the chromosomes of *Euchlaena* and those of *Zea*. ZIAVA, 62:305-15.

A gene for sticky chromosomes in *Zea mays*. ZIAVA, 63:195-217.

1933

Studies of crossing-over in heterozygous translocations in *Drosophila melanogaster*. ZIAVA, 65:111-28.

With S. Emerson. Crossing-over near the spindle fiber in attached-X chromosomes of *Drosophila melanogaster*. ZIAVA, 65:129-40.

Further studies of asynaptic maize. Cytol., 4:269-287.

Polymitotic maize and the precocity hypothesis of chromosome conjugation. Cytol., 5:118-21.

1934

Crossing-over in attached-X triploids of *Drosophila melanogaster*. J. Genet., 29:277-309.

1935

Crossing over near the spindle attachment of the X chromosomes in attached-X triploids of *Drosophila melanogaster*. Genet., 20:179-91.

With S. Emerson. Further studies of crossing-over in attached-X chromosomes of *Drosophila melanogaster*. Genet., 20:192-206.

With R. A. Emerson and A. C. Fraser. A summary of linkage studies in maize. Cornell Univ. Memoir, 180:3-83.

With A. H. Sturtevant. X chromosome inversions and meiosis in *Drosophila melanogaster*. Proc. Natl. Acad. Sci. USA, 21:384-90.

With B. Ephrussi. La transplantation des disques imaginaux chez la Drosophile. C. R. Acad. Sci., 201:98.

With B. Ephrussi. Différenciation de la couleur de l'oeil cinnabar chez la Drosophile. C. R. Acad. Sci., 201:620.

With B. Ephrussi. La transplantation des ovaires chez la Drosophile. Bull. Biol. Belg., 69:492-502.

With B. Ephrussi. Sur les conditions de l'auto-différenciation des caractères mendéliens. C. R. Acad. Sci., 201:1148.

With B. Ephrussi. Transplantation in *Drosophila*. Proc. Natl. Acad. Sci. USA, 21:642-46.

1936

- With B. Ephrussi. A technique of transplantation for *Drosophila*. *Am. Nat.*, 70:218-25.
- With B. Ephrussi. The differentiation of eye pigments in *Drosophila* as studied by transplantation. *Genet.*, 21:225-47.
- With B. Ephrussi. Development of eye colors in *Drosophila*: Transplantation experiments with suppressor of vermilion. *Proc. Natl. Acad. Sci. USA*, 22:536-40.
- With B. Ephrussi and C. W. Clancy. Influence de la lymphe sur la couleur des yeux vermilion chez la *Drosophile*. *C. R. Acad. Sci.*, 203:545.
- With A. H. Sturtevant. The relation of inversions in the X chromosome of *Drosophila melanogaster* to crossing-over and disjunction. *Genet.*, 21:554-604.
- With Th. Dobzhansky. Studies on hybrid sterility IV. Transplanted testes in *Drosophila pseudoobscura*. *Genet.*, 21:832-40.
- With B. Ephrussi. Development of eye colors in *Drosophila*: Studies of the mutant claret. *J. Genet.*, 33:407-10.

1937

- With B. Ephrussi. Development of eye colors in *Drosophila*: Transplantation experiments on the interaction of vermilion with other eye colors. *Genet.*, 22:65-75.
- With B. Ephrussi. Development of eye colors in *Drosophila*: Diffusible substances and their interrelations. *Genet.*, 22:76-85.
- With B. Ephrussi. Développement des couleurs des yeux chez la *Drosophile*: Influence des implants sur la couleur des yeux de l'hôte. *Bull. Biol. Belg.*, 71:75-90.
- With B. Ephrussi. Développement des couleurs des yeux chez la *Drosophile*: Revue des expériences de transplantation. *Bull. Biol. Belg.*, 71:54-74.
- With C. W. Clancy. Ovary transplants in *Drosophila melanogaster*: Studies of the characters singed, fused, and female-sterile. *Biol. Bull.*, 72:47-56.
- With B. Ephrussi. Development of eye colors in *Drosophila*: The mutants bright and mahogany. *Am. Nat.*, 71:91-95.
- The development of eye colors in *Drosophila* as studied by transplantation. *Am. Nat.*, 71:120-26.
- With K. V. Thimann. Development of eye colors in *Drosophila*:

- Extraction of the diffusible substances concerned. Proc. Natl. Acad. Sci. USA, 23:143-46.
- Development of eye colors in *Drosophila*: Fat bodies and Malpighian tubes as sources of diffusible substances. Proc. Natl. Acad. Sci. USA, 23:146-52.
- With C. W. Clancy and B. Ephrussi. Development of eye colours in *Drosophila*: Pupal transplants and the influence of body fluid on vermilion. Proc. R. Soc. London, 122:98-105.
- The inheritance of the color of Malpighian tubes in *Drosophila melanogaster*. Am. Nat., 71:277-79.
- With B. Ephrussi. Ovary transplants in *Drosophila melanogaster*. Meiosis and crossing-over in superfemales. Proc. Natl. Acad. Sci. USA, 23:356-60.
- With B. Ephrussi. Development of eye colors in *Drosophila*: Production and release of cn^+ substance by the eyes of different eye color mutants. Genet., 22:479-83.
- Chromosome aberration and gene mutation in sticky chromosome plants of *Zea mays*. Cytol. Fujii Jubilee, pp. 43-56.
- Development of eye colors in *Drosophila*: Fat bodies and Malpighian tubes in relation to diffusible substances. Genet., 22:587-611.

1938

- With L. W. Law. Influence on eye color of feeding diffusible substances to *Drosophila melanogaster*. Proc. Soc. Exp. Biol. Med., 37:621-23.
- With R. Anderson and J. Maxwell. A comparison of the diffusible substances concerned with eye color development in *Drosophila*, *Ephestia* and *Habrobracon*. Proc. Natl. Acad. Sci. USA, 24:80-85.
- With E. L. Tatum. Development of eye colors in *Drosophila*: Some properties of the hormones concerned. J. Gen. Physiol., 22:239-53.
- With E. L. Tatum and C. W. Clancy. Food level in relation to rate of development and eye pigmentation in *Drosophila melanogaster*. Biol. Bull., 75:447-62.

1939

- Physiological aspects of genetics. Annu. Rev. Physiol., 1:41-62.
- Teosinte and the origin of maize. J. Hered., 30:245-47.

With E. L. Tatum and C. W. Clancy. Development of eye colors in *Drosophila*: Production of v^+ hormone by fat bodies. *Biol. Bull.*, 77:407-14.

With E. L. Tatum. Effect of diet on eye-color development in *Drosophila melanogaster*. *Biol. Bull.*, 77:415-22.

With A. H. Sturtevant. *An Introduction to Genetics*. Philadelphia: W. B. Saunders.

1940

With E. L. Tatum. Crystalline *Drosophila* eye-color hormone. *Science*, 91:458.

1941

With E. L. Tatum. Experimental control of development and differentiation. *Am. Nat.*, 75:107-16.

With E. L. Tatum. Genetic control of biochemical reactions in *Neurospora*. *Proc. Natl. Acad. Sci. USA*, 27:499-506.

1942

With E. L. Tatum. Genetic control of biochemical reactions in *Neurospora*: An "aminobenzoicless" mutant. *Proc. Natl. Acad. Sci. USA*, 28:234-43.

1943

With N. H. Horowitz. A microbiological method for the determination of choline by use of a mutant of *Neurospora*. *J. Biol. Chem.*, 150:325-33.

With D. Bonner and E. L. Tatum. The genetic control of biochemical reactions in *Neurospora*: A mutant strain requiring isoleucine and valine. *Arch. Biochem.*, 3:71-91.

With F. J. Ryan and E. L. Tatum. The tube method of measuring the growth rate of *Neurospora*. *Am. J. Bot.*, 30:784-99.

1944

With E. L. Tatum and D. Bonner. Anthranilic acid and the biosynthesis of indole and tryptophan by *Neurospora*. *Arch. Biochem.*, 3:477-78.

With V. L. Coonradt. Heterocaryosis in *Neurospora crassa*. *Genet.*, 29:291-308.

An inositolless mutant strain of *Neurospora* and its use in bioassays. *J. Biol. Chem.*, 156:683-89.

1945

With H. K. Mitchell and D. Bonner. Improvements in the cylinder-plate method for penicillin assay. *J. Bacteriol.*, 49:101-4.

With E. L. Tatum. Biochemical genetics of *Neurospora*. *Ann. Mo. Bot. Gard.*, 32:125-29.

With N. H. Horowitz, D. Bonner, H. K. Mitchell, and E. L. Tatum. Genic control of biochemical reactions in *Neurospora*. *Am. Nat.*, 79:304-17.

Biochemical genetics. *Chem. Rev.*, 37:15-96.

Genetics and metabolism in *Neurospora*. *Physiol. Rev.* 25:643-63.

With E. L. Tatum. *Neurospora*. II. Methods of producing and detecting mutations concerned with nutritional requirements. *Am. J. Bot.*, 32:678-86.

The genetic control of biochemical reactions. *Harvey Lect.*, 40:179-94.

Genes and the chemistry of the organism. *Am. Sci.*, 34:31-53, and 76.

1946

With D. Bonner. Mutant strains of *Neurospora* requiring nicotinamide or related compounds for growth. *Arch. Biochem.*, 11:319-28.

High-frequency radiation and the gene. *Science Life in the World*, New York: McGraw-Hill, Vol. 2, pp. 163-93.

1959

Genes and chemical reactions in *Neurospora*. In: *Les Prix Nobel*, pp. 147-59. Also in: *Science*, 129:1715-19.

1960

Evolution in microorganisms, with special reference to the fungi. *ANL*, 47:301-19.

1963

Genetics and modern biology. *Jayne Lectures for 1962*. *Am. Philos. Soc.*, 57:1-73.

1966

With Muriel B. Beadle. *The Language of Life: An Introduction to the Science of Genetics*. New York: Doubleday (Doubleday Anchor-book, 1967).

Biochemical genetics: Some recollections. In: *Phage and the Origins of Molecular Biology*, eds. J. Cairns, G. S. Stent, and J. D. Watson, Cold Spring Harbor Laboratory of Quantitative Biology, pp. 23–32.

1972

The mystery of maize. *Field Mus. Nat. Hist. Bull.*, 43:2–11.

1973

Thomas Hunt Morgan. In: *Dictionary of American Biography*, Supplement 3 (1941–1945), New York: Chas. Scribners Sons, pp. 538–41.

1974

Recollections. *Annu. Rev. Biochem.* 43:1–13.

1980

The origin of maize. In: *Genes, Cells, and Behavior*, eds. N. H. Horowitz and E. Hutchings, Jr., San Francisco: W. H. Freeman and Co., pp. 81–87.

Ancestry of corn. *Sci. Am.*, 242(1):112–19.

1981

Origin of corn: Pollen evidence. *Science*, 213:890–92.