

EARLY HISTORY OF GENETICS
AT THE
UNIVERSITY OF WISCONSIN - MADISON¹

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Introduction

Some of the material I shall present has been drawn from a larger document prepared for the Oral History Project sponsored by the University Archives Division. Emeritus faculty members are invited to record on tape such academic experiences as they deem significant for development of the University. The record is intended primarily for future use by historians.

I have just completed assembling the material I have to contribute to the Project, and it is now being typed. A taped interview with a representative of the Archives presumably will follow.

I assume that Bill Stone got wind of what I was doing on the Project, and then invited me to share the account with you. I have consistently declined invitations to present seminars on and off campus since my formal retirement six years ago, but I was willing to make an exception in the present case. The reasons are:

(1) There are six of us in the department who are now on the Emeritus faculty - Wright, Irwin, W.K. Smith, Neal, Casida, and myself. In so far as we are continuing our local professional activities we are dependent to a significant degree on the department's charity. If we are asked, on occasion, to sing for our supper, as the saying goes, we can not, in good grace, decline. I would be less than honest, however, if I didn't state that my decision to comply with Bill Stone's request was based more on a sense of duty than on a preference for the task. One of my reactions to advancing age has been an increasing reluctance to sacrifice a diminishing future by becoming preoccupied with the past.

(2) Secondly, an emeritus staff member should have something unique to contribute to an account of the earlier history of the department. He can recount the past from first hand experience with some of the events that characterized it.

(3) The third reason I am talking to you today is that I sensed a real interest, indeed an eagerness, on the part of graduate students, to learn more about the background of the Laboratory of Genetics at Wisconsin. They would like to know out of what kinds of beginnings did the present complex organization evolve? What were the paths that led us to where we are? I am not capable of answering these questions in detail, and obviously not in the short time available at this meeting. From a long association with the department, however, I probably can relate enough about what happened in the past to provide some perspective to those of you who may be interested in digging further in one direction or another, on your own initiative.

(4) I wish, however, to issue a warning about the account I shall present. First, as mentioned earlier, much of the material I shall discuss has been drawn from the Oral History document. It is expected by the Archives Committee that the Oral History account will relate to my own professional activities. What I have prepared

¹Presented at a Laboratory of Genetics colloquium November 6, 1974.

for the Project, therefore, is not a history of genetics at Wisconsin but rather my account of my part in it. This greatly restricts, of course, the area covered. Inevitably also, the account will reflect my biases. I trust that eventually there will be countervailing factors that will offset the latter. The Oral History Project is also open to other retired staff members whose contributions can balance mine. I am concerned, however, that what I put into the permanent record be both factual and fair. I shall be grateful, therefore, if my colleagues here will call to my attention to anything I say today that appears to them to be in error or is misleading.

The Particular Topics Chosen

One must necessarily be selective in composing a report of this kind. I wish to indicate to you briefly, at the outset, the kinds of things I shall emphasize, and also some of the things in the history of the department on which I do not intend to dwell.

One thing on which we should be clear at the start. The period with which I shall be concerned dealt mostly with the "old" genetics. By old genetics I mean pre-molecular genetics. The old genetics, as a scientific discipline, was essentially an elaboration of Mendel's finding that the hereditary material was organized in an elaborate fashion. It assumed that the gene was the ultimate unit of the hereditary material by which particular phenotypes were determined. The gene also was the ultimate unit of mutation, and was considered not to be subdivisible by recombination. The principal experimental materials used during this period were peas, sweet peas, maize, snapdragons, fruit flies, mice, rats, guinea pigs and rabbits, in contrast to fungi, bacteria, and viruses which have been the objects of choice in molecular or the "new" genetics. Pedigree analysis, based on the scoring of gross phenotypes, after controlled matings, was the most commonly used experimental procedure. The most sophisticated equipment in the cytogeneticist's laboratory during the period under consideration was the light microscope.

An Exclusion

One thing I shall not do in this report is eulogize the scholarly accomplishments of my departmental colleagues, significant as they are. There are two reasons for this:

(1) First, the basic research accomplishments of the staff comprise the best documented and most accessible part of the department's records. They are reflected in the articles published in scientific journals. These research reports have been bound into 22 volumes, containing 1299 papers, as of 1970. The collected works are readily at hand on the shelves of the department library. (The number of departmental papers has since grown to 1806.)

(2) A second reason for not parading the scholarly achievements of my colleagues for further acclaim is that the "gold braid", so to speak, that has been distributed among us is best thought of in a social context as a stimulus to scientific effort in general, and not merely as recognition of the achievements of the particular individuals to whom it has been awarded.

I shall only say that among my colleagues, past and present, there are six who have been presidents of the Genetics Society of America, several who are members of the leading scholarly organizations of the United States, one Nobel laureate (Josh Lederberg), one foreign member of the Royal Society of London, who is also a past president of an International Genetics Congress, and the recipient of eight honorary doctorate degrees. This is Sewall Wright. (I recall that once when Sewall was being

complimented on his eight honorary degrees, he observed, with his acute numerical sense, "That's nothing special, Herbert Hoover had 84".)

Outline of the Talk

The particular items I have chosen to discuss are designed, not to provide completeness and comprehensiveness, which is impossible in any case in a talk of this kind, but to illustrate what I consider to be significant turning points in the early history of the department. The topics to which reference will be made in explaining these turning points may be listed as follows:

- 1) Staff roster and chronology, 1910-55.
- 2) W.D. Hoard, as the prime mover in starting the department.
- 3) Dean H.L. Russell, as an effective supporter of basic research in agriculture.
- 4) L.J. Cole, as the departmental founder.
- 5) The state of the genetic art in 1910 and for the 20 years following.
- 6) The department as an early center for graduate study in genetics, animal breeding, and plant breeding.
- 7) The problem of gaining a favorably recognized place in the Agricultural Experiment Station.
- 8) Continuation of growth, even in the depression years of the 30's.
- 9) Joining with the Zoology Department in offering a single introductory course in Genetics for the entire University.
- 10) Some direct contributions genetics made to agriculture.
- 11) The shift toward greater emphasis on basic research with the appointment of Lederberg.
- 12) The division of genetics into two administrative units, one in Agriculture, the other in the Medical School.
- 13) The reunion of the Departments of Genetics and Medical Genetics into the Laboratory of Genetics, as a single operating unit.

Founding of the Department

The Department of Genetics was established in the College of Agriculture here in 1910, the first of its kind in the U.S.. The man who initiated the move that led to founding the Department was W.D. Hoard whose bronze statue executed by Gutzon Borglum² stands on a marble pedestal at the head of Henry Quadrangle just outside our door.

W.D. Hoard

Hoard was the founder of Hoard's Dairymen, a leading dairy farming magazine published at Fort Atkinson, Wisconsin. He was a person in whom were united extraordinary native ability and an unwavering dedication to the task of improving public education at all levels. He was concerned with the dairy farmer's welfare in particular.

Hoard had only a minimum of formal education himself. He was born in New York State, and the only systematic instruction he received was in a little log school-house there. He attended this school until he was 14 years old. This was in pioneer times, 115 years ago. Hoard moved from New York to Watertown, Wisconsin in 1857, at 21 years of age.

Hoard, however, in spite of his limited schooling had an impelling desire for knowledge. Books became a prime source, and he read widely. Hoard had an extensive public life and the numerous professionally educated men with whom he came in contact became his teachers also. With W.D. Hoard, to live was an invitation and opportunity to learn. He was a student and a teacher all his life, a successfully self-educated man.

Hoard was especially interested in the welfare of rural people. Over a long life (he lived to be 82) he directed a continuing effort to securing for the farmer a representation in our educational system that would place him on a par, as a trained man, with every other profession.

Hoard himself became highly talented as an educator in the broad sense. He was especially effective as a public speaker, and also through the press. He became widely recognized as a powerful influence in molding opinion on educational questions. As governor of the state for a two year term (1888-90) he secured passage of the Bennett Act whereby instruction in English was made compulsory in all Wisconsin schools including those in predominantly German speaking communities in the eastern part of the state. This brought down on his head the fire of the clergy in the Lutheran and Roman Catholic parochial schools, and was one of the factors that brought about Hoard's defeat in the next election. (A more important factor in his defeat was that, as governor, he was a thorn in the flesh of the Republican "Old Guard"; they not only deserted him, but also actively opposed him for reelection.)

Seventeen years later (1907) in recognition of his great interest in the education of youth, Hoard was appointed a member of the Board of Regents of the University of Wisconsin. It was during this period that he brought his greatest influence to bear upon the development of agricultural education in Wisconsin.

Hoard believed that the breeding, as well as the feeding, of dairy cattle should be a scientifically controlled operation. The Experiment Station, he argued, should be prepared to make recommendations to the farmer in both areas, based on sound research. Nutritional studies had already been established at Wisconsin under Dean Henry's leadership, and were yielding important results. Hoard sought a comparable program in breeding, particularly in the interests of dairy cattle improvement.

²Borglum is best known for his carving, in heroic dimensions, of Washington, Jefferson, Lincoln, and T. Roosevelt, on the side of Mt. Rushmore in the Black Hills of South Dakota, 1927.

H.L. Russell, who was dean of agriculture at the time, was eager to apply all the relevant scientific disciplines to agriculture, and promptly took up Hoard's proposal for a new unit in the College of Agriculture. So a department, then called Experimental Breeding, was established while Hoard was president of the Board of Regents. (Hoard was opposed to naming the new department "Genetics" because genetics was a term the public didn't then understand. Out of deference to Hoard, therefore, the name became Experimental Breeding. It was changed to Genetics in 1918, two years after Hoard's death.)

Hoard's enthusiasm for the subject of heredity proved to be both a help and a handicap to the new department. Hoard's Dairymen printed articles on animal breeding and thus furnished encouragement. Hoard was looking, however, for assistance of the kind that a dairy cattle breeder could use currently in improving the production of his herd. For reasons that are obvious to us, direct help of this sort couldn't be provided at that early time. It is said that Mr. Hoard was disappointed that early returns were not forthcoming from the unique College venture that he had initiated. I shall say more about the handicap that the new department had to overcome a little later because of Hoard's over optimistic expectations.

Russell Vigorously Supported Basic Research

The establishment of a Department of Genetics in the College of Agriculture was in accord with a general policy, strongly supported by Russell, whereby the sciences underlying agriculture were to be fostered directly in the College. Russell regarded natural science as a vast primary resource which, if aggressively developed, could serve the farming industry abundantly. He held that the successful application of science to agriculture depended in the long run, upon the maintenance of a pool of knowledge upon which workers in applied fields could draw continuously. Russell was concerned that the staff in agriculture should not merely utilize this reservoir in serving the farmers' needs but also should contribute actively to it.

His immediate problem was to find a man who could provide the leadership necessary to fulfill this dual responsibility in genetics. The man he selected was Leon J. Cole, then an instructor in Zoology at Yale University, in New Haven, Connecticut.

Leon J. Cole (1877-1948)

Cole was born in New York state and grew up in Michigan, as a city boy, who spent some of his vacations on a farm. His high school ambition was to become a naturalist. In later years he was wont to remark humorously that his idea of a naturalist at that time was one who could live out of doors, enjoy the animals, birds, and flowers, and to be paid for doing this.

(1) High School - Grand Rapids, Michigan

(2) 1901 B.A., University of Michigan, after transfer three years earlier from Michigan Agricultural College. (As an undergraduate at Michigan he was a member of the Harriman Expedition to Alaska. His association on this occasion with eminent ornithologists, mammalogists, and botanists, strengthened his interest in the natural sciences. Monographed the Pycnogonidae - sea spiders - a group of marine Arthropods.)

(3) 1901-02 Graduate assistant in Zoology, at Michigan.

(4) 1902-06 Graduate student, Harvard, with E.L. Mark, in Animal Behavior: Ph.D. 1906.

- (5) Summers during this period were spent at:
- (a) Bermuda Biological Station (1903)
 - (b) With a biological expedition to Yucatan (1904)
 - (c) At the Tortugas station in the Gulf of Mexico (1906, in part)
 - (d) At Woods Hole Marine Biological Laboratory in Massachusetts, 1901 and 1906 on a biological survey for the U.S. Bureau of Fisheries. During this period a monograph was completed on "The German Carp of the United States".
- (6) In 1906 Cole was appointed Chief, Division of Animal Breeding and Pathology, Rhode Island Agricultural Experiment Station. He began a study there of inheritance in pigeons. He had received no formal instruction in genetics but his interest in the field had been stimulated by W.E. Castle at Harvard during graduate study with E.L. Mark at that institution.
- (7) 1908-09 Appointed instructor in zoology, Sheffield Scientific School, Yale.
- (8) 1910 Called to the University of Wisconsin to found a new Department of Experimental Breeding (name changed to Genetics in 1918).
- (9) Cole was always ready to give time and thoughtful effort to scientific organizations and to the promotion of science at large. His broad biological interests and numerous personal contacts resulted in much work outside the Department relating especially to animal genetics. The following items are noteworthy in this context:
1. 1923-24 Chief of the Animal Husbandry Division of the Bureau of Animal Industry of the U.S. Department Agriculture, Washington, D.C.. The Secretary of Agriculture sought his help in raising the level of scientific work in this Division, and would have liked to retain him as Chief.
 2. 1925 Vice-chairman, Division of Biology and Agriculture, Natural Research Council. 1926-27 Chairman of same.
 3. Represented agriculture from 1929 to 1936 on Board of Biological Fellowships, NRC.
 4. 1924-7 President, Wisconsin Academy of Sciences, Arts, and Letters.
 5. 1940 President, Genetics Society of America.
 6. Served many years on the council, American Genetic Association (Publisher of J. Heredity) and also the Council of the American Society of Naturalists.
 7. Birds were his hobby; he was a pioneer in bird banding.
 8. He loved books, and devoted much time to the departmental library. On his retirement he gave the University his extensive reprint collection. This collection, now in the department library, supplemented by that of the late Victor Jollos, which was purchased by the University, gives fairly complete coverage of the genetics literature up to about 1935.
 9. He was member of several scientific societies, including the Genetics Society of America, American Society Zoologists, American Society Naturalists, Ornithological Union, Society of Mammology, Eugenics Society, American Society of Animal Production, Poultry Science Association, Bird Banding Association.
 10. The American Society of Animal Production presented his portrait to the Saddle and Sirloin Club in Chicago in 1939.
 11. 1945 Honorary D.Sc., Michigan State College of Agriculture and Applied Sciences.

12. Cole joined the staff when little biological research was in progress in the College of Agriculture. He devoted much effort to developing biological training at the graduate level. One of his most effective accomplishments in this respect was to organize, in cooperation with L.R. Jones of the Plant Pathology Department, the Graduate Biological Division. A principal objective of this organization was to foster high standards in graduate biological work in agriculture, and in medicine, as well as in the College of Letters and Science where it was already well established.
13. During Cole's nearly 30 years as chairman of Genetics 62 Ph.D. degrees were earned in the Department. Most of the leading American workers in animal breeding until the late 1930's were Cole's students. These students, in turn, trained the next generation of investigators in animal breeding.
14. Cole's research tended to be topical rather than programmatic. He was continuously interested, however, in the genetics of pigeons and doves. This work was begun in Rhode Island, maintained during his two year instructorship in zoology in Yale, and actively pursued during all the years at Wisconsin.

Cole's early exploration of species differences among pigeons and doves provided foundation material for Dr. Irwin's later classical studies of species relationships in Columbidae, using immunogenetic procedures.

In cooperation with Professor Halpin of the Poultry Department Cole made the first systematic experiments on inbreeding chickens.

Also some careful work was done to test the claims of others that sex could be controlled in mammals by vaginal douches. The claims that had been made were not validated.

Cole also studied the inheritance of lethal and other defects in farm animals as well as the genetic basis of disease resistance.

In 1912 Cole organized a crossbreeding experiment with cattle designed to study the inheritance of dairy and beef qualities. Aberdeen-Angus were crossed with Jerseys, and later with Holstein-Friesians. An F₂ generation was reared, and some backcrosses were made. The experiment was costly to support and was not carried out on a scale large enough to provide decisive results on the inheritance of milking ability. I will have more to say about it later.

After retirement from the chairmanship of genetics in 1939 Cole devoted much of his time to studying the genetics of color phases in foxes and mink. Together with one of his graduate students, R.M. Shackelford, several papers on this subject were published. Dr. Shackelford has continued the fur animal breeding work since.

15. Personally Cole was an exceedingly kind and generous man. He had a host of friends among students and colleagues. Shortly before his retirement Cole suffered a paralytic stroke from which he only partially recovered. He received scores of letters at this time in one of which this statement was made by a former student:

"As I look back on the scholars I have known, I seem to note that there are the two following extremes. At one boundary, we have those scholars who are more or less, shall we say, self-centered and selfish as regard their ideas and their theories, and the research problems that arise from these. At the other extreme, we have men who are the epitome of unselfishness, giving and allowing their students to take credit for ideas that were really the 'brain children' of the professor. The first type of man may be admired by his students, but there is little affection for the man himself...From my contacts with you, I have always felt that you were a fair

example of the second type of research man. The inspiration that you have been to others, your [generosity] in giving ideas and other support to your students, have caused you to be regarded by them with both admiration and affection."

The State of the Genetic Art in 1910

- 1900 Rediscovery and verification of Mendel's principles (published 1866) by DeVries, Correns, and von Tschermak.
- 1902 (a) Bateson coined the terms allelomorph, homozygote, heterozygote, F₁, F₂, etc.
 (b) E.C. McClung related an accessory chromosome occurring in some insects to sex determination.
 (c) W.W. Sutton pointed out the parallel between chromosomes and Mendelian phenomena. This was the beginning of what came to be known later as cytogenetics.
- 1903 W.L. Johannsen (Denmark) developed the pure line concept. Defined phenotype and genotype, and thus laid a foundation for a Mendelian explanation of selection.
- 1905 G.H. Shull and E.M. East, independently began experiments on inbreeding in maize.
- 1906 Bateson coined the term "genetics".
- 1908 (a) The first journal devoted to heredity founded - Zeitschr. ind. Abstamm. u. Vererb-lehre.
 (b) Nilsson-Ehle (Sweden) advanced multiple factor theory to explain inheritance of pericarp color in wheat.
 (c) A.E. Garrod published in Lancet a now classical paper entitled "The incidence of alkaptonuria, a study of chemical individuality."
- 1909 Bateson published Mendel's Principles of Heredity, the first book in English in this field.
- 1910 (a) Epstein and Ottenberg (U.S.) pointed out that human blood groups, discovered by K. Landsteiner, Austria, in 1900, follow Mendelian principles in inheritance.
 (b) Morgan described white eye, the first observed gene mutation in Drosophila melanogaster, and proposed a chromosome explanation of sex-linked inheritance.
- 1911 (a) Journal of Genetics established by Bateson and Punnett, in England.
 (b) The first two text books in genetics in German were published, Baur, E., Einführung in die experimentelle Vererbungslehre Goldschmidt, R., Einführung in die Vererbungswissenschaft (The first widely used genetics text book in English was W.E. Castle, Genetics and Eugenics, 1916. Second edition in 1918.)
- 1912 (a) R.R. Gates (England) showed that Oenothera semi-gigas, one of the variants on which DeVries had based his mutation theory was a triploid.
 (b) Jennings showed that with self-fertilization the percentage heterozygotes is halved in each generation.
- 1913 (a) C.B. Bridges reported non-disjunction of sex chromosomes in D. melanogaster as critical evidence for the chromosome theory.
 (b) A.H. Sturtevant published his classical paper on the linear arrangement of six sex linked genes in D. melanogaster [in J. Exp. Zool.].
- 1915 (a) Morgan, Sturtevant, Bridges, and Muller published "The Mechanism of Mendelian Heredity" - an epoch making book.
 (b) Castle and Sewall Wright reported the first linkage in a mammal (rat).
- 1916 Raymond Pearl demonstrated the greater effectiveness of pedigree rather than mass, selection in increasing egg production in the fowl.
- 1917 (a) O. Winge (Denmark) elaborated a theory of polyploid origin of new species by hybridization and then doubling of the chromosome complex.
 (b) Emerson found that variegated pericarp in maize was due to an unstable gene.
 (c) The first commercial hybrid corn was produced in Connecticut.

- 1919 Morgan published The Physical Basis of Heredity, summarizing *Drosophila* genetics, and elaborating the gene theory of inheritance.
- 1922 (a) A haploid *Datura* plant was discovered by A.F. Blakeslee and associates.
 (b) R.E. Cleland showed that the atypical cytogenetic behavior of certain *Oenotheras* was due to arrangement of the chromosomes in rings at meiosis.
- 1926 Belling reported the interchange of segments between non-homologous chromosomes.
- 1927 Artificial transmutation of the gene was demonstrated by Muller in *Drosophila* and by L.J. Stadler in plants.
- 1930 R.A. Fisher published "The Genetical Theory of Natural Selection".
- 1931 (a) B. McClintock and H. Creighton in maize, and Curt Stern in *Drosophila* proved crossing over cytologically.
 (b) Sewall Wright published a classical paper in Genetics entitled "Evolution in Mendelian Populations". This article gave a comprehensive picture of the interplay in evolution between mutation, selection, inbreeding, isolation, and migration.
- 1932 J.B.S. Haldane published "The Causes of Evolution".

These publications of Wright, Fisher, and Haldane established population genetics as a major area of research in heredity and evolution. They laid the basis also for a rational approach to important problems in the genetic improvement of livestock. The time, you will note, is 1930-32. Thus 20 years were to pass beyond the date Hoard obtained a department in the College of Agriculture initially intended to help farmers with dairy cattle breeding problems before a meaningful research program in this area could have been organized. Evidently Hoard was 20 years ahead of his time in this venture.

Chronology of Professorial Appointments 1910-1955

(The date given relates to appointment as assistant professor, or above. Several in the list served on the staff for varying numbers of years at ranks below the level of assistant professor.)

- 1910 L.J. Cole (Founder)
- 1919 E.W. Lindstrom (Went to Iowa State College, 1922.)
- 1922 R.A. Brink (Chairman, 1939-55)
- 1930 M.R. Irwin (also Bacteriology and U.S.D.A.. Chairman, 1955-64)
- 1934 L.E. Casida
 G.E. Dickerson (Instructor only, also Dairy Records; went to Regional Swine Laboratory, Ames, 1941.)
- 1936 N.P. Neal (also Agronomy)
 G.H. Rieman (also Plant Path. and Hort.)
- 1937 W.K. Smith (also Agronomy and U.S.D.A.)
- 1939 A.B. Chapman
- 1942 D.C. Cooper
- 1943 R.D. Owen (also Zoology. Went to Cal. Tech 1947.)
- 1947 J. Lederberg (went to Stanford, 1958)
 R.M. Shackelford (also U.S.D.A.)
- 1948 J.F. Crow (also Zoology. Chairman, 1965-71.)
- 1949 R.W. Hougas
- 1951 W.J. Tyler (also Dairy Husb.)
- 1954 W.H. Stone (Acting Chairman, 1965)
- 1955 S. Wright (Came to Wisconsin after retirement at Chicago as Leon J. Cole Professor of Genetics.)

Note on the appointment of Ray D. Owen

Previous to 1943 two courses in general genetics were offered at the University of Wisconsin. One was given by M.F. Guyer in the Zoology Department, and the other by L.J. Cole in Genetics [Cole retired as chairman in 1939]. Following Guyer's retirement from the staff, Lowell Noland who then became chairman in Zoology, raised the question with us in Genetics whether the two offerings could be combined into one course. Noland's proposal was approved, and arrangements were made for the appointment of Ray D. Owen, then a post-doctorate student in Dr. Irwin's laboratory to teach the combined course. Owen's appointment was as assistant professor of Genetics and Zoology. Owen was a superb classroom teacher, and got the new joint course off to an excellent start. Four years later we lost him to California Institute of Technology. We were fortunate, however, in securing as Owen's successor in the post, James Crow, whose continued success with the course is widely recognized.

A Center For Graduate Study

About 180 students qualified for the Ph.D. degree in genetics (or jointly in genetics and an allied field) between 1910 and 1958. Only 15 were awarded up to 1925.

Twenty more students received the Ph.D. in the 5-year period 1926-30.

Enrollment fell off during the depression years of the 30's, and was not resumed until the end of World War II (1945).

Roughly 1/3 of the graduate students in the 1910-1958 period earned the Ph.D. in animal breeding, including physiology of reproduction. Excluding local personnel in this context these included J.L. Lush, W.A. Craft, A. Nalbandov, Clyde Stormont, Jack Stimpfling, Elwood Briles, G.E. Bradford, G.E. Dickerson, and Ivar Johansson.

Another 1/3 of the graduate students during the period earned the Ph.D. in plant genetics. These included F.V. Owen who later developed a breeding program with the U.S.D.A. at Salt Lake City that saved the sugar beet industry in the United States from the ravages of a serious virus disease called Curly Top; L.F. Chao, who had a distinguished career in mainland China, and later as a refugee in Taiwan, in rice research; Peter Barclay, of the Grasslands Division, Palmerston, North, New Zealand, and C.R. Burnham, for many years engaged in maize cytogenetics at the University of Minnesota.

Among the Ph.D.'s during the period who have distinguished themselves since in basic research, again excluding local personnel, I would mention R.D. Owen, (Cal Tech) N.E. Morton, (University of Hawaii) Motoo Kimura, (Misima, Japan) Norton Zinder (Rockefeller Institute for Medical Research, New York), and E.W. Shrigley, retired member of Department of Bacteriology, Indiana Medical School.

I am sure that I speak for all those who were engaged in graduate instruction during this period that the deepest satisfaction in our academic lives has been to see a graduate student effectively launched on a rewarding professional career.

Experiment Station Research in the Genetics Department

The research challenge to staff members in a natural science department in an Experiment Station like that at Wisconsin is two-fold. There is an obligation to see that scientific advances that are significant for agriculture are brought to a stage at which they can be utilized in the farming industry. So we have much research that can be called adaptive, or technological. It relates to the use of knowledge for practical purposes. Secondly, investigations must contribute to the pool of knowledge relating to natural phenomena as such. The objective in this case is to know, not necessarily to use.

Adaptive and basic research are not mutually exclusive categories. They interpenetrate each other. Genetics at Wisconsin has been extensively involved in both areas.

When Cole arrived on the campus in 1910 he faced a 3-fold task. Provisions were to be made in the new department for (1) undergraduate and graduate instruction, (2) basic research in genetics and (3) the relating of genetical concepts to agricultural practice.

It was a pioneer undertaking. This was the first time in America that genetics had been challenged to justify itself both as (a) a distinct biological discipline and (b) as being significant for agricultural practice.

Cole's task, at that time, in relating genetics to agriculture was particularly difficult. Especially was this the case because the prime mover in setting up our department of genetics was Hoard, who envisioned the new experiment station unit in the first instance as a potential aid to cattle breeders.

Doubtless with Hoard's interest in mind, Cole initiated a crossbreeding experiment with cattle in 1912 that was to prove a source of difficulty to the department later on. The object of this experiment was to study the inheritance of dairy and beef qualities. Aberdeen-Angus were crossed to Jerseys and later to Holstein-Friesians. An F₂ generation was raised and some backcrosses also were made.

A cow is a costly experimental unit. Furthermore, the genetic bases of dairy and beef qualities are exceedingly complex. The number of animals in the experiment always was small because of the limited funds from a small Experiment Station budget that could be allocated to the project. It was not possible, therefore, to develop the experiment on a scale that could yield meaningful results to cattle breeders. The College of Agriculture Administration became increasingly skeptical concerning the value of the relatively expensive crossbreeding project.

I became acutely aware of this attitude during my second year, that is 1923-24, on the staff here. Cole had been called to Washington to serve for a year as Chief of the Animal Husbandry Division of the Bureau of Animal Industry. I was alone in the Department, and so frequently was in contact with the Administration on departmental business.

One of the things repeatedly mentioned to me during that year were the misgivings the Administration had regarding the soundness of the crossbreeding project. F. B. Morrison, who was handling Experiment Station matters, and was an animal husbandman, was particularly pointed about it.

I doubt if Cole ever realized the extent of the handicap to growth that the cattle crossbreeding experiment imposed on the Genetics Department.

The University was expanding at a rapid rate at that time. Student numbers doubled (from 4,000 to 8,000) in the 12 years from 1910 to 1922. Yet support for Genetics was increasing very slowly.

Furthermore, the Department of Plant Pathology which had been started by L. R. Jones in the College of Agriculture at about the time Cole founded Genetics, acquired four men of professorial rank during this period. Genetics had only two persons of professorial rank by 1922, Cole and myself. The College administration evidently was still waiting to be shown what Genetics could contribute of significance for the farmer.

I decided then that more effective ways must be found than the dairy cattle crossbreeding project to demonstrate the potential of genetics for Wisconsin agriculture, if the young Department of Genetics was to obtain the support needed for continued development.

Hybrid corn was just then coming over the agricultural horizon. As a graduate student of E. M. East at Harvard, I had become aware of the possibilities of the new corn breeding procedures which East and G. H. Shull had earlier developed. Furthermore, while still a student at Harvard, I had visited D. F. Jones's corn breeding nursery at New Haven, Conn., and had seen at first hand what could be accomplished in raising yield by selection in and between inbred lines and controlled hybridization of appropriately chosen stocks. Jones, it will be recalled, invented the double hybrid, i.e., the crossing of two F_1 hybrids to obtain seed for commercial use. Adoption of the double hybrid procedure made hybrid corn an immediate technical success.

There was no one on the campus at the time I came here who was interested in hybrid field corn, at least to the point of doing anything about it, although breeding projects had already been started in the neighboring states of Iowa, Illinois, and Minnesota. The attitude of the local corn breeders at the time was one of indifference. After consultation with R. A. Moore, who wasn't enthusiastic, but was not actively opposed, I drafted a cooperative field corn breeding project, between Genetics and Agronomy in 1923, the year Cole was on leave in Washington. Dean Russell approved the project at once, and allocated funds for a graduate assistant. The project was later expanded to include Plant Pathology and the U.S.D.A., and more substantial financing was provided under the newly enacted Purnell Act. J. G. Dickson, in Plant Pathology, and I were the main supporters of the corn breeding work in its earliest years. Then Norman Neal, who had been a graduate student of mine, and later A. M. Strommen, at Spooner, took charge. Under Dr. Neal's most capable leadership the venture thrived. In fact, it quickly became a spectacular agricultural success.

The first Wisconsin hybrid was released for production in 1933. Only eight years later approximately 90% of Wisconsin's corn acreage was planted to hybrid seed. Acreage of corn grown for grain increased significantly (four-fold in the Northern part of the state) and, eventually, average yield throughout the state was nearly tripled with the use of hybrids and the improved cultural practices that followed.

A conservative estimate of the increased value of the Wisconsin corn crop resulting from the use of hybrids, many of which were bred at Madison and Spooner, was 80 million dollars up to 1958.

Needless to say, after the advent of hybrid corn as a commercial crop no further questions were asked concerning the significance of genetics in a College of Agriculture.

Thus, the successful development of hybrid corn marked a turning point in the history of the Genetics Department. In fact, it marked a turning point in the attitude of the farming public toward the Experiment Station enterprise as a whole. The significance of research for agriculture in general was now much more widely recognized than heretofore. Genetics began to become a household word with recognition of the science as a public utility. The success of the hybrid corn project anchored the Department of Genetics in the Agricultural Experiment Station.

The Depression

But the country was now beset by a depression, the most drastic in its history. It extended from the stock market crash in 1929 to the outbreak of World War II, about 10 years later. It was a dismal period in all aspects of our national life, and involved untold hardship for many, many people, students included.

Student numbers in this University declined, particularly in the graduate school. Staff salaries were cut 17%, and positions that became vacant were not filled. All public services, including the University, were in severe financial difficulties.

The depression interestingly enough, however, was not a period of paralysis for the Department of Genetics. M.R. Irwin was recruited to our staff in 1930, as a joint appointee with Bacteriology and the U.S.D.A.. The initial objective in his case was research on brucellosis in cattle. Out of the work Professor Irwin started grew a program in immunogenetics that brought the University of Wisconsin to the first rank in this field. He was joined in immunogenetics eventually by R.D. Owen (1943) and by W.H. Stone (1954) as members of the regular staff. An important early achievement of this group that would have warmed the heart of W.D. Hoard was the development of a method of blood typing dairy cattle as an aid to verifying parentage.

And it was during the depression years also that the program in cattle breeding came into its own. L.E. Casida was appointed to an assistant professorship in 1934 to develop work in the physiology of reproduction in farm animals. G.E. Dickerson was appointed an instructor the same year primarily to strengthen the program of the Dairy Herd Improvement Association. Dr. Chapman joined the animal breeding group as Assistant Professor a little later (1930). The last animal in the ill-starred crossbreeding experiment with cattle had been disposed of in 1933. Under the leadership of Chapman, Dickerson, and Casida well planned investigations in dairy cattle breeding were now started using some privately owned herds and also large herds of the State Department of Public Welfare. Studies were made on the effects of inbreeding and selection on birth weight, growth and development, milk and butter-fat production, and fat percentage. Swine investigations were carried out in cooperation with the Department of Animal Husbandry and the Regional Swine Laboratory at Ames, Iowa. One outgrowth of this work was the Wisconsin Swine Selection Cooperative which provided a means whereby genetic concepts could be utilized for the improvement of swine on Wisconsin farms.

Potato Genetics

In the middle thirties a program for the improvement of quality and disease resistance of the potato was organized in response to a special appropriation for the purpose by the State legislature.

Dr. G. H. Rieman was appointed in 1936 jointly in the Departments of Genetics, Plant Pathology and Horticulture to lead the program. Dr. Hougas joined in the potato investigations as assistant professor of Genetics in 1949, and Dr. Peloquiun at a later date. The Certified Potato Seed Industry was raised to a new level of efficiency and a National Potato Introduction and Preservation Project was organized (located at Sturgeon Bay) through cooperation with the U.S.D.A. and regional and national potato breeding research committees.

Hougas and Peloquiun opened a new era in potato breeding with the publication in 1958 of a paper entitled "The potential of potato haploids for breeding and genetic research." The common potato is a tetraploid, with 48 chromosomes. They demonstrated the means whereby potato breeding could be carried out with much greater efficiency using 24-rather than 48-chromosome plants.

Alfalfa Breeding

The breeding work that culminated in the release in 1953 of the Vernal variety of alfalfa was begun in 1926. Vernal soon became the most widely used alfalfa variety in the U. S. and Canada. It is grown on 25% - 30% of the alfalfa acreage in the North Central states. The Wisconsin acreage is roughly two million. Dean Glenn Pound in a recent report on pay off of Experiment Station research to farming estimated that Vernal and the more intensive system of forage production it made possible has been worth about a billion dollars to Wisconsin farmers since introduction of the variety in 1953. This is a gain comparable in magnitude from that of hybrid corn. Dean Pound's dollar figure is mentioned to inform you of the magnitude of a pressing agricultural problem to the solution of which the young Department made a major commitment, fortunately with success.

The alfalfa breeding, like hybrid corn, was a venture that involved extensive cooperation between genetics staff and others outside the department. In both these instances, the cooperation was with plant pathologists and agronomists. I would like to mention particularly the close and effective help I had in the alfalfa investigations from the late F. R. Jones, plant pathologist, and from my departmental colleague W. K. Smith, and also Dale Smith, L. F. Graber, and others in Agronomy. Without the active participation of these men at one stage or another in the work, my own considerable efforts to meet an obvious agricultural need, namely for a more dependable source on Wisconsin farms of a high quality protein roughage for cattle, might well have come to naught.

I have always believed that basic work should have a higher priority than applied research in a Department of Genetics in an Agricultural Experiment Station that is organized like that at Madison. In some other departments like Agronomy and Horticulture for example, and in Animal Science, the balance between theoretical and adaptive investigations should, in my judgement, be in the other direction. From the account of the two types of work I have presented, however, you may well have received the impression that the relative emphasis given these two classes of research in the Department of Genetics during the period under discussion has not been in accordance with this point of view. I do not think that such a conclusion is justified. From Cole's arrival on the campus forward basic work has been kept to the fore in the Genetics Department. What I have sought to make clear, however, is that as a department in the College of Agriculture, Genetics was expected to be concerned also with the solution of farming problems as the need for direct help from us arose. I have tried to describe how we fulfilled our mission during the period in question in that respect. In doing this I believe we have also strengthened our position with regard to obtaining support for teaching and basic research.

Policy questions of continuing interest are involved in these relationships. The public thinks of research largely in terms of relevance to felt needs. The general interest is in the fruits of science. Basic research may be likened to the roots of a tree on whose shoots fruits eventually may be borne. Roots are not visible to the passer-by, nor is their state of health readily apparent. The roots must be nourished, however, if the plant is to be maintained in a fruiting condition. In an agricultural experiment station (also in a medical school) this means that both basic and applied research must be fostered in order to serve public needs adequately. Collectively, at least, an ambidexterity in staffing as between theoretical and practical interests is required to achieve the needed balance. Experience shows that this is not an arrangement that is readily developed and effectively maintained. Underlying it at the college and department levels are policy questions that must constantly be reviewed as circumstances change. The general well being of a department, as an administrative unit, may be determined by how well it is adapted in this relationship to prevailing conditions.

Sweetclover Investigations

In 1933 it was observed that a newly introduced sweetclover strain growing in our nursery, that was later identified as an annual form of Eurasian origin of Melilotus dentata, was free of the bitter, stinging taste characteristic of the common sweetclovers. This was the beginning of a series of investigations that led to an explanation of the so-called sweetclover disease in cattle, caused by feeding spoiled sweetclover hay or silage and to the eventual identification and synthesis of dicumarol in the Biochemistry Department and the development of a related compound as a rodenticide (Warfarin) and as a therapeutic agent useful in controlling thrombosis in humans. The sweetclover disease involved destruction of the clotting power of the blood by lowering prothrombin content.

W.K. Smith and I demonstrated in 1938 that the tendency of sweetclover to become toxic to cattle if the sweetclover has undergone substantial heating in the barn or silo had its basis in the same substance that made fresh sweetclover bitter, namely coumarin.

Smith also did the pioneer work in K.P. Link's laboratory in extracting the toxin from spoiled sweetclover hays. Furthermore, he adduced the first evidence that heritable differences occurred between rabbits in sensitivity to the sweet-clover toxin. The broad significance of this phenomenon became apparent later when it was observed that exposed rat populations sometimes became so refractory to Warfarin that the rodenticide was ineffective as a control of this pest.

A recent review of the published reports of the Wisconsin work in this area has reinforced earlier doubts that the importance of these pioneer findings on the sweetclover toxin has not been properly recognized. The material I will file with the Oral History Project should be helpful eventually in correcting the published record.

The Endosperm in Seed Development

Another kind of work that I found particularly interesting was that on the endosperm in seed development. I would like to mention briefly the work that the

late D. C. Cooper accomplished in this field. A series of joint studies on seed development were initiated in the late 1930's that led to a more complete understanding of the role of the endosperm in seed formation. It was shown, particularly by Cooper's histological work, that the success or failure of seed development turns primarily not on the embryo which embodies the line of descent, as previously thought, but upon the product of the secondary fertilization, the endosperm.

Recruitment to the Staff of Joshua Lederberg

Cole retired from the chairmanship in 1939 after suffering a paralytic stroke. From this time until his retirement from the staff eight years later (1947) he devoted much of his time to investigating the genetics of color phases in the fur animals, especially foxes and mink, with R. M. Shackelford, as a close collaborator.

It was agreed by the departmental staff that in filling the position that had become vacant by Cole's retirement a person should be sought whose central interest was in theoretical genetics. Lederberg, then a graduate student in E. L. Tatum's laboratory at Yale University had been brought to our attention as an exceptionally promising young man in this respect. He and Tatum had just published convincing evidence for the occurrence in bacteria of sexuality. This finding aroused wide interest among biologists, and it opened the way to genetic work with a major group of lower organisms.

(Lederberg was awarded the Nobel Prize in Medicine & Physiology, jointly with E. L. Tatum and G. W. Beadle in 1958, for this and subsequent studies. He was the first member of the Wisconsin faculty to become a Nobel laureate.)

There was substantial opposition, however, within the Genetics staff, to inviting Lederberg to join us at Wisconsin. Opponents to inviting him here felt that the appointee should be agriculturally oriented whatever his other qualifications were.

Lederberg's background was metropolitan. He was born in Montclair, N. J., in 1925. He had taken the B.A. (with honors) at Columbia, following a course which had included two years of study in the College of Physicians and Surgeons, and he was a candidate at that time for the Ph.D. at Yale. The view was expressed by certain of my colleagues that with a background of this sort it was folly to expect that Lederberg could adapt to a College of Agriculture environment. There were reports also that Lederberg was aggressive to an unpleasant degree. We were warned that we had better look out if we had had no experience in the Department in lion taming. Happily these fears proved groundless. Lederberg was an extraordinarily dynamic individual. He was also thoughtful and considerate of his colleagues.

Weeks passed before a consensus was reached with reference to inviting Lederberg to Wisconsin.

Two letters strongly endorsing Lederberg for the Wisconsin post eventually brought the needed support within the departmental group. One of these was from E.W. Sinnott (June 4, 1947) who was Professor of Botany and also Dean of the Graduate School at Yale. Sinnott had become personally acquainted with Lederberg at Yale. Furthermore, Sinnott had been a member of the staff at the Connecticut Agricultural College, at Storrs, and so was familiar with the kind of academic environment Lederberg would enter in the Department of Genetics at Wisconsin. I knew Sinnott personally and had deep respect for his judgment.

I recall sitting down at my desk one Saturday afternoon after a particularly discouraging staff meeting in the morning, over which I had presided as chairman, at which Lederberg's recruitment was discussed, with strong overtones of opposition, to write a 4-or 5-page letter to Sinnott seeking his help in resolving our problem. That letter apparently is not existent I didn't keep a copy, and most of Sinnott's correspondence evidently was destroyed after Sinnott's death.

The other crucial letter in support of Lederberg's candidacy was from R. D. Owen (August 13, 1947) Professor of Biology, California Institute of Technology, and formerly Assistant Professor of Genetics and Zoology here. Ray had taken his Ph.D. in the Genetics Department here, and was well known to, and highly regarded by, all his former colleagues. Although the views among Owen's colleagues at Cal Tech were not unanimously in his favor, Ray reported that the two persons who knew Lederberg best were enthusiastic supporters of his candidacy.

Owen's August 13, 1947 letter in particular convinced some former opponents among my colleagues that Lederberg was a good prospect.

Eventually a vote was taken that favored inviting Lederberg to join the Genetics group. Lederberg accepted the offer made him and joined us as Assistant Professor of Genetics, September 15, 1947.

Lederberg's appointment here was an inflection point not only in the development of genetics but also of the biological sciences in general on this campus. His brilliant pioneer work in bacterial genetics which earned him a Nobel Prize in 1958 provided the foundation on which the extensive program in molecular biology has since been built.

I should mention also that it was Lederberg who brought James Crow, then at Dartmouth, to our attention when a successor to Ray Owen was being sought.

Genetics in Medicine at Wisconsin

Genetics in the School of Medicine had its beginning with the appointment of Newton Morton as assistant professor in the Department of Anatomy. Dr. Morton started a research program there and gave a few lectures on genetics in the first year course in Anatomy.

The Department of Medical Genetics was organized in 1957. It consisted at that time of Joshua Lederberg (half-time with the Department of Genetics) as chairman, and Professor Morton. With Dr. Lederberg's resignation in 1958, Dr. James Crow joined the Department of Medical Genetics as chairman.

In August, 1959, Dr. DeMars came from the National Institutes of Health to start a program in somatic cell genetics and in virology. Dr. Oliver Smithies joined the group in 1960 with a joint appointment in Genetics, and worked on human biochemical genetics. Dr. Klaus Patau became an official member of the group in 1960.

Although Medical Genetics became an independent administrative unit its staff members continued to meet regularly with the staff in the Department of Genetics to discuss matters of general policy and to make recommendations for the development of genetics at the University.

The two groups joined together informally at an early stage as a Division of Genetics, and formed a single working group. Drs. Smithies and Crow were then joint members of both groups. The Division of Genetics had no administrative standing.

There was a growing realization within both groups, however, that the informal union represented by a Division of Genetics was not enough to secure the level of

effectiveness needed. An official unification of the two departments appeared desirable.

The geneticists in the two groups (Adler, Brink, Casida, Chapman, Fox, Irwin, Kermicle, Nomura, Opitz, Patau, Smith, Smithies, Stone and Susman) voted unanimously at a staff meeting on January 6, 1965 to seek administrative approval for uniting the two departments under a single chairman.

Professor Patau reported at a joint staff meeting on February 2, 1965 a favorable response by Deans Pound and Crow (then Acting Dean of the Medical School) and also Chancellor Fleming on preliminary discussions with them concerning unification. A committee consisting of Crow (chairman) Patau, and Stone was asked to formulate a specific proposal for joining the two departments. The proposal brought forward by this committee was approved by both genetical groups. The plan called for the organization of an "Institute of Genetics" into which the two departments would be merged.

Dean Pound and Chancellor Fleming endorsed this plan. The Executive Committee of the Medical School, however, turned it down. The Medical Committee suggested that "some form of organization be considered that would preserve the present departmental status".

A revised plan for unification was then drawn up, that was approved at a joint meeting of the two groups on June 30, 1965.

It was agreed then that the two departments together be termed the Laboratory of Genetics.

The plan approved was as follows:

- I. Genetics, in the College of Agriculture, and Medical Genetics, in the Medical School, shall function as a single unit as of July 1, 1965. The same person shall serve as chairman of both departments.
- II. The two departments will operate as a single department according to the usual university rules and procedures except for the following provisions.
 - (1) The chairman of the two departments shall be appointed jointly by the Deans of Agriculture and Medicine and be responsible to both.
 - (2) Funds will be budgeted in the departments from both the College of Agriculture and the Medical School. They will be accounted for according to these sources.
 - (3) A vote of the combined departments is binding on both and shall be regarded by the College of Agriculture and the School of Medicine as the wish of the respective departments.
 - (4) The combined departments shall record votes by roll call of the members if the Administration or at least one member requests it.
- III. Members of the two departments shall have the title of Professor of Genetics (or other appropriate rank) and each should be a faculty member of the College of Agriculture or Medical School according to his or her departmental membership.
- IV. Master's and doctor's degrees shall be granted as degrees in Genetics. This plan was approved October 18, 1965.

Conclusion

And so genetics arrived at essentially its present form of organization on the Madison campus.

I have barely touched on the later chapters in the 60-year story. The present total program in the Laboratory of Genetics, as you are well aware, is a complex

mosaic of activities concerned mainly with one or another aspect of the "new" genetics, and the numerous ramifications of genetics in biological, agricultural, and medical affairs. Stiff challenges in research still abound. For example, how did naked DNA, characteristic of viruses and bacteria, evolve into the chromosomes of higher organisms? What are the mechanisms of control of gene expression in animals and plants? Curiously, when I wrote these last words my pen went dry.

November 6, 1974