A PORTRAIT OF LEWIS JOHN STADLER 1896 - 1954

G. P. RÉDEI, UNIVERSITY OF MISSOURI, COLUMBIA, MISSOURI.

According to his wishes no funeral services were held for L. J. Stadler, and his body was cremated shortly after his death.

There has been no need to offer memorials - all ephemeral - to a scientist of his stature; he has created a monument "aere perennius" by his scientific contributions. Yet on the 15th anniversary of his death the geneticists of the University of Missouri wished to pay homage to the man who brought their discipline to success on this campus by his talent, enthusiasm, wise guidance and inspiration generously extended to his colleagues. Thus these Annual Genetics Symposia were initiated in 1969 and were dedicated to him.



- - L. J. Stadler (right) with G. H. Shull (middle) and with D. F. Jones (left). The photograph was taken at the Brookhaven National Laboratories in the fall of 1949. - -

RÉDEI

6

Besides his well-known professional association with Missouri, L. J. Stadler, a native of Missouri, remained a Missourian during his whole life. He was born in St. Louis on July 6,1896, and died there on May 12, 1954. With brief interruptions he pursued his studies in Missouri and obtained his Ph.D. in the Department of Field Crops of the University of Missouri in 1922. He then started his academic career at the University as an assistant and advanced to the rank of Professor of Field Crops by 1937, a title which he retained to the end of his life.

He was exposed to maize genetics during his graduate years at the University of Missouri. The Columbia campus learned early to appreciate the new science of genetics. Back in 1909 the fourth annual meeting of the American Breeders Association (predecessor of the American Genetic Association) was held on our campus. "A course called genetics and evolution was first taught at the University of Missouri in 1912-13 by Dr. George Lefevre, Professor of Zoology. In 1923-24 the course was replaced by a course in genetics, also in the Zoology Department" (LONGWELL 1970). From 1919 to 1924, W. H. Eyster, a former student of Dr. E. G. Anderson* at Cornell University was engaged in maize genetics investigations in the Botany Department. When Eyster left, Stadler took over the project, by then part of the program of the Agricultural Experiment Station.

The graduate student Stadler spent the summer session of 1919 at Cornell where he was associated primarily with H. H. Love and studied biometry. At the same time he first met R. A. Emerson. There was a much more important association of Stadler with Emerson in 1925/26. This academic year he spent partly at the Bussey Institute with E. M. East,** and partly at Cornell in the laboratory of Emerson. His studies with East and Emerson were made possible by a National Research Fellowship that he obtained as a result of publishing two very well received papers on crossing-over in maize (STADLER 1925, 1926).

Though his early contributions to crossing-over clearly reveal the skills of the author, another series of experiments were initiated in 1924 which made Stadler's name famous. In the Annual Report of the Missouri Agricultural Experiment Station for the year 1925/26 (Bull. 244, pp. 38-39) we read the following:

A GENETIC ANALYSIS OF MAIZE (L. J. Stadler) Variation in the Intensity of Linkage in Maize. -- Studies of the variability of crossing over in the C-sh and Sh-Wx regions in maize were continued, with special reference to family differences, constancy of crossing over within the individual, and the effects of X-rays. The effect of X-rays on crossing over in this material is of special interest because crossing over in these two regions in maize has been found remarkably constant within the individual, regardless of differences in age and temperature, etc. In the fruit-fly X-rays influence crossing over decidedly in regions not susceptible to the effects of age and temperature. Young tassels of heterozygous plants were irradiated at various dosages, the treatments being given during the period of maturation of the male germ cells, as determined by cytological examination. Irradiation at the greater dosages resulted in the death of a considerable proportion of the pollen and in some cases in distortion of the tassel. There was no significant difference in crossover percentage in treated and untreated tassels of the same plants at any dosage used.

The Frequency of Mutation in Maize. -- Preliminary studies of the frequency of mutation in the genes for several endosperm

^{*}Visiting Professor on campus since 1967.

^{**} Later the major professor of Dr. E. R. Sears who has been affiliated with the genetics faculty on this campus since 1936.

characters have been made. The method followed eliminated contamination as a source of error and permitted the production and examination of populations practically unlimited in size, thus making it possible to determine the rate of mutation in genes not selected because of their high mutability. Plants dominant for the gene under investigation were pollinated by recessive plants. All F_1 grains showing the recessive character were tested by backcrossing to the recessive parental stock. The production of a wholly recessive ear in this backcross was taken as evidence that the female gamete from which the recessive seed was produced lacked the dominant gene, as a result of mutation in the germ cell lineage previous to the first division of the megaspore. In 1924, among about 2000 grains so pollinated as to show mutation of R (a gene for aleurone color) two colorless grains were found. Both were tested in 1925 and found to be homozygous recessives, indicating a rate of mutation for R of the order of 1 per 1000. Among about 3000 grains which could have shown mutation of C (another gene for aleurone color) one colorless grain was found, but this did not germinate and could not be tested. In 1925 a more extensive trial was made, using as pollen parents stocks recessive for the genes c, sh, wx, su, and pr, in various combinations. Among 55,618 kernels which could have shown mutation of C 5 colorless kernels were found, and among 93,106 kernels which could have shown mutation of Sh, 2 shrunken kernels were found. Only about 10,000 grains could have shown mutation of Su, Pr, and Wx, and no mutations of these genes were found. These data are provisional, pending the results of the back-cross tests. Although linked genes were under observation in some 60,000 cases, in no case did the simultaneous loss of linked genes occur, indicating that the loss of chromosome was not an important factor in this material.

From these trials it appeared that mutation in some genes occurred frequently enough to be susceptible to quantitative experimental investigation by the method outlined. Multiple recessive stocks for determining the rate of mutation in 13 genes for endosperm characters have been prepared in quantity.

This brief summary of a year's activity touches on most of the problems Stadler pursued in detail in later years.

The following year (1926/27) he gives this resume of his progress:

The Frequency of Mutation. -- The effect of various environmental factors, particularly X-rays and radium radiation, on the frequency of gene and chromosome mutation has been studied. this purpose the most favorable material is a self-fertilized species in which the gametes united at fertilization are both derived from a single cell in which mutation may be induced. Preliminary experiments were made with barley, which was chosen among the grasses because its chromosome number was low and its genetic constitution was fairly well known. The plants were treated in large numbers as newly sprouted seed. At this stage the first leaves were differentiated (as they are in the embryo but the axillary buds were not. There are, therefore, in each seedling several separate cells from each of which a tiller and inflorescence will be developed. Chromosome and gene changes induced by treatment in any one of these cells will show their effects in the progeny of a single head. The absence of these effects in the other head progenies from the same plant shows that the change occurred in the ontogeny of the plant, thus eliminating the possibility that the new character resulted from irregular segregation. The tolerance limits of barley seedlings at this stage under intermittent X-ray irradiation of various degrees of hardness and under 12- and 24-hour exposures to radium were determined. It was found that considerable quantities

of lead, uranium, thorium, etc., could be introduced into the seed itself without serious injury. This was done in order that when the seed was irradiated a secondary radiation of known characteristics might be produced within the cell itself. This method permitted the application of beta rays as well as characteristic gamma rays to the protoplasm. (Bull. 256, Published Sept. 1927).

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-- The first record in Stadler's notebook (July 30, 1924) of an unsuccessful experiment with the application of X-rays to plants. --

In the Missouri Agricultural Experiment Station Annual Report 1927/28 on page 63 we read: "The attempt to induce mutations by X-ray and radium treatment of barley, as described in Missouri Agricultural Experiment Station Bulletin 244, pages 38 and 39, 1926 was successful." This reference is apparently erroneous since in Bulletin 244 only the above reproduced passages are found concerning the use of X-rays in genetic studies. There can be no doubt, however, that the experiments on mutation induction with barley must have started in 1926 in order to produce results before June 30, 1927.

It can not be determined when Stadler came to the idea of using ionizing radiation. In his first journal paper on crossing-over we see references to the work of MAVOR (1923) and associates and that of PLOUGH (1924), initiated in the early twenties, dealing with modification of recombination through the use of X-rays and radium (STADLER 1925). It seems certain that Stadler, who read German fluently, was familiar with the "Radiomorphosen" of Emmy STEIN (1922) produced in Antirrhinum, a higher plant.

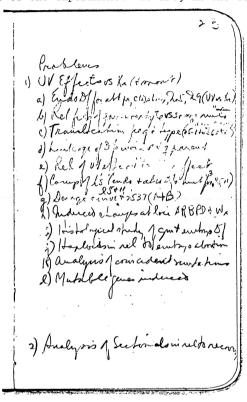
The oldest record of Stadler on the use of X-rays for plant treatment, found in his notebook is dated July 30, 1924.

The research laboratories of the world learned of his work on induced mutation only after the publication of MULLER's (1927) similar results with animals. The dignified STADLER (1928) graciously appraised the status of priority thus: "The experiments, which were independent of and coincident with those of Muller, though by no means so comprehensive and thorough, confirm Muller's discovery of the power of X-rays to induce mutation and show its application to plants."

By 1930 Stadler obtained X-ray mutants by the hundreds. The conclusions of this early period are best read in the original: "The possibility is not excluded that the recessive condition resulting from the X-ray treatments is merely the absence of the dominant gene; that is, the mutation induced is simply the destruction of a gene. But the outward effects and the genetic behaviour of the mutations, so far studied, are identical with those of "normal" recessive genes, and this conception may be applied equally well to "normal" recessive mutation.....Dr. Randolph has found several lacking an entire chromosome and others lacking a portion of the chromosome...Characters of value in breeding are more likely to be found in the varietal collection than in the progeny of X-rayed plants, and here they will occur without the many undesirable gene mutations and chromosome aberrations characteristic of the X-rayed progenies." (STADLER 1930).

Stadler has been accused of biased views concerning the genetic effects of X-rays because some research workers engaged in studies with other organisms obtained results not entirely consistent with his evaluation of the effect of ionizing radiation on the genetic material of maize. It is inappropriate to consider here the various arguments. Let us rather look at a series of experiments conducted by STADLER (1944a) on the effect of X-rays on dominant mutation in maize. Losses of a dominant gene (\underline{A}) were studied in the aleurone, and mutations from a to A were sought. "The sectors varied rather widely in size, the average number of aleurone cells included being 112..... The approximate number of aleurone cells in the entire endosperm was determined similarly by counts of aleurone cells in representative areas. The number of aleurone cells in seeds of average size was found to be about 160,000. It may be roughly estimated, therefore, that at the time of treatment the number of cells per seed whose genetic alteration could be detected by sectors in the mature aleurone is about 1400 (160,000/112).....On the basis of 1400 cells per seed, each containing 3 a genes capable of dominant mutation, this represents approximately 16 million chances for detectable dominant (3,832 seeds x 1,400 cells x 3 alleles = 16,000,000; anmutation." average ear of inbred corn contains about 300-400 kernels.) Several such experiments were carried out, and "in populations which, with the X-ray doses applied, were capable of yielding 900,000 losses of \underline{A} by deficiency or by mutation to a colorless allele" no changes from $\overline{\underline{a}}$ to A were observed. "The population irradiated was large enough to have yielded, under the influence of homozygous \underline{Dt} , about 400,000 such mutations." (\underline{Dt} , a mutator factor capable of inducing a to \underline{A} changes, was discovered by RHOADES (1938). The experimental design is elegant and critical, and the dimensions must be impressive even for the

modern-day microbial geneticist. There also were other lines of good circumstantial evidence: genetic transmission of the mutants, chromosome losses visible in pachytene*, reduced pollen tube growth** etc. (STADLER 1933, STADLER and ROMAN 1948). On the basis of the experimental observations available at that time, the statements contained in his posthumous paper (STADLER 1954) appear as wise today as they were 15 years ago: "When we conclude from an experiment that new genes have evolved by the action of X-rays, we are not simply stating the results of the experiment. We are, in the single statement,



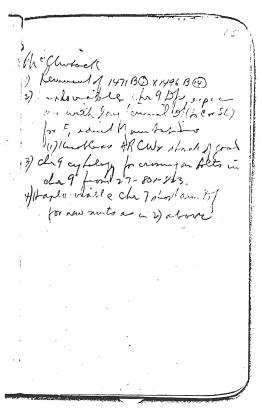
--Dr. Stadler always carried in his pocket a "black book" in which every year he prepared notes and outlines on research problems for himself and for all associates. These notes were made in 1939.--

combining two distinct steps: (i) stating the observed results of the experiment, and (ii) interpreting the mutations as due to specific mechanisms. It is essential that these two steps be kept separate, because the first statement represents a permanent addition to the known body of fact, whereas the second step represents only an inference that may later be modified or contradicted by additional facts. When the two steps are unconsciously combined we risk confusing what we know with what we only think we know."

^{*}The method was worked out by his associate Dr. Barbara McClintock.

^{**}The method of his later associate Dr. G. F. Sprague was adopted.

Many other important discoveries resulting from the study of the genetic effects of X-rays can not be mentioned here. I feel that an early little paper (STADLER 1929) can not be bypassed, however. Irradiation of the polyploid series of Avena and Triticum showed "in both genera that the mutation frequency (as measured by the visible effects) decrease sharply with increasing chromosome number....The mode of origin of the species of higher chromosome number is unknown, but it may be assumed that the triple component of 21 pairs of chromosomes ultimately represents a combination of 3 groups of seven pairs each, and these three groups are identical in some of their genes." These prescient statements were amply verified later by the cytogenetic studies



-- Page 115 of "black book" 1940 lists materials to be given to Dr. Barbara McClintock --

of Dr. E. R. Sears and his associates.

In the mid-thirties a new mutagenic agent, ultra violet light was introduced in the laboratory (STADLER and SPRAGUE 1936a,b,c). UV light had been repeatedly used for mutagenesis since almost the turn of the century. Stadler was aware of the work of ALTENBURG (1934) in Drosophila and of the use of this agent on plant material by NOETHLING and STUBBE (1933). The first report in the series mentions the findings of GATES (1928) that the bactericidal effectiveness of the various wave-lengths of UV irradiation parallels the absorption curves of nucleoproteins rather than those of amino acids. -- The early experiments demonstrated that monochromatic light of a wave-length of

 $254~\text{m}\mu$ was the most effective on maize pollen grains (STADLER and SPRAGUE 1936c). Subsequent studies carried out with the cooperation of F. Uber from the Department of Physics were quite revealing: The

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⁻⁻In 1941 L. J. Stadler was Visiting Professor at the California Institute of Technology. There he was closely associated with Norman Horowitz and others and developed a deep interest in biochemical approach to genetics. This is an excerpt of his note-book from that period (1941). The following year he published an abstract of his research (STADLER 1942).---

problem "is the determination of the genetic effectiveness of different ultra-violet wave-lengths as a possible clue to the chemical nature of the substance which absorbs the radiation producing genetic effects. If, for example, the absorbing substance determining chromosome breakage is nucleic acid, it might be anticipated from the known absorption spectrum of this substance that wave-lengths of about 260 mµ will be the most effective in producing breaks, and the effectiveness will decline on the long wave-length side to a negligible value at 310 mu." (STADLER 1939). The carefully performed genetic experiments with six endosperm markers exposed to nine narrow bands of the UV spectrum gave good matching between the thymonucleic acid (DNA) absorption spectrum and the frequency of marker loss (STADLER and UBER 1942). These experiments were done before the now often cited discovery of AVERY, MacLEOD and McCARTY (1944).

Stadler's main interest in UV was also determined by his observation that this agent did not induce large numbers of chromosomal breaks, deficiencies and rearrangements (STADLER 1941).

From 1925 on Stadler was keenly interested in the nature of spontaneous mutation at selected loci (cf. STADLER 1951). This work produced extensive quantitative information on differential mutability of 13 gene loci and resulted in a fruitful approach to the study of gene structure.

From Indian reservations of the southwestern United States 22 different R stocks of corn were collected and analyzed (STADLER and FOGEL 1943, 1945). The R genes affect seed and plant color in various ways. "Plant-color mutation has a pronounced effect upon aleurone-color mutability of the gene or gene-complex concerned. This is shown by the much-lowered aleurone-color mutability of the mutant $R^{\rm g}$ allele as compared with the $R^{\rm r}$ allele. This result is not consistent with the hypothesis that the $r^{\rm r}$ and $R^{\rm g}$ mutations represent independent alterations of distinct components of the gene or gene complex $R^{\rm r}$." (STADLER 1946). "Differences in seed-color mutation frequency are due in part to intrinsic differences in mutability of the various R alleles....Differences in mutation rate between different races are also due in large part to the effects of modifying factors....The varying modifier genotypes....modify plant color mutation rate apparently independently of their effect upon seed-color mutation rate." (STADLER 1948). These modifiers were genetically analyzed and "three of the seven marked segments proved to have detectable effect on mutation frequency." (STADLER 1949).

The R complex was a fortunate choice for studies on gene structure. The particular mutability of identifiable alleles was easily tested, hence the unusual behaviour of one allele (RE-14) was recognized. In the heterozygote RE-14/R the RE gametes mutate at a lower rate than those of Rr constitution. In the backcross progeny the Rr gametes in RE/R mutate at a higher rate than those of the Rr gametes in the homozygous sibs." (STADLER and EMMERLING 1956). Stadler suspected that the R locus is made up of two interrelated elements affecting plant (P) and seed color (S), respectively, and that these components may be separated by unequal crossing-over, as the Bar locus in Drosophila. The hypothesis was then studied with the best possible genetic tests. "The nearest useful marker to the left of R is "golden" (symbol g), 14 units distant. There is no known gene locus to the right of R, but a knob-like terminal appendage described by LONGLEY* (1938) may be used for the same purpose." (STADLER 1951). Plants of $\mathbb{R}^r/\mathbb{R}^g$ and $\mathbb{R}^r/\mathbb{R}^r$ constitution produced \mathbb{R}^r mutants with or without recombination of the outside markers in approximately equal frequency likely to be unequal crossing-over (STADLER and NUFFER 1953, STADLER and EMMERLING 1956).

^{*}Dr. A. E. Longley has been Visiting Professor on the University of Missouri campus since 1967.

"Stadler's experimental studies are models in their clarity of conception and simplicity in design; he excelled as a theoretician and analyst" writes M. M. RHOADES (1957) in the Biographical Memoirs of the National Academy of Sciences.

Professor Stadler was not only a theoretician, however; he published several papers relevant to practical agriculture, worked out the method of gamete selection (STADLER 1944b) for corn breeding, and

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PRESIDENT FRANKLIN D ROOSEVELT

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L J STADL R

(Straight tolegram rate -- charge to personal account of L. J. Stadler)

-- In 1940 Stadler sent this telegram to President Roosevelt. At the same time he mailed \$100 to a relief agency and invited Dr. Emil Heitz, a German expatriate to join his group as Visiting Professor.--

developed the "Columbia" variety of oats which was long widely grown by the farmers of the southern Corn Belt. The wheat varieties "Lewis" and "Stadler" which were developed by Dr. Charles Hayward and Dr. J. M. Poehlman with the use of ionizing radiation, were named in his honor.

L. J. Stadler's interest went far beyond theoretical and applied genetics. A browse through the still existing personal correspondence is enough to learn that he was a genuine humanitarian deeply concerned with the problems of the society.

It is partly this human concern that made him an inspiring educator. At the University of Missouri he never taught formal courses, but he trained graduate students. Several of whom contributed significantly to genetics. Luther Smith, Herschel Roman, John R. Laughnan, Seymour Fogel, Myron G. Neuffer and Margaret Emmerling received the Ph.D. degree under his guidance, and several others studied with him for various periods of time.

Dr. Stadler never held an administrative position at the University of Missouri, but by virtue of his intellectual leadership he "built an internationally recognized establishment through his own work and by bringing to the University a succession of brilliant and promising young scientists, most of whom later went elsewhere to establish

HEARINGS ON SCIENCE LEGISLATION

(S. 1297 and Related Bills)

HEARINGS

BEFORE A

SUBCOMMITTEE OF THE

COMMITTEE ON MILITARY AFFAIRS

UNITED STATES SENATE

SEVENTY-NINTH CONGRESS

FIRST SESSION

PURSUANT TO

S. Res. 107

(78th Congress)

S. Res. 146

(79th Congress)

AUTHORIZING A STUDY OF THE POSSIBILITIES OF BETTER MOBILIZING THE NATIONAL RESOURCES OF THE UNITED STATES

PART 3

OCTOBER 22, 23, 24, 25, and 26, 1945

Printed for the use of the Committee on Military Affairs



UNITED STATES
GOVERNMENT PRINTING OFFICE
WASHINGTON: 1945

(pages 576-580)

78860

PREPARED STATEMENT OF DR. L. J. STADLER, PROFESSOR OF FIELD CROPS, UNIVERSITY OF MISSOURI; AGENT, UNITED STATES DEPARTMENT OF AGRICULTURE

My testimony will be concerned chiefly with the value to the national welfare of basic research in biology, outside the field of medicine. This can be discussed most concretely in terms of actual examples from our own national experience.

--In 1945 L. J. Stadler testified eloquently in Congress as to his views on the role of science in the society and its significance for the economy. Among other statements he said:.."I think the public will support pure science when it is brought to see the value of pure science, just as it supports liberal education when it is brought to see the value of liberal education.--I do not think the remedy for the situation is to provide a special buffer for the protection of science from the dangers of public support...The remedy is rather to meet the issue squarely--to apply scientific method at its best and defend it on the ground of its demonstrated social value...The total expenditure for corn breeding by the federal Department and the State experiment Stations through the entire 25-year period 1920-45 was in the neighborhood of \$5,000,000. The return of this investment...on the basis of the farm price per bushel is more than \$2,000,000,000."--

landmarks in their fields. Most of these people could not be held because the strength of the group was based on one scientist's reputation rather than a strong department" notes former Dean of Agriculture John H. LONGWELL (1970). The "Genetics Group" included for various periods of time D. Anderson, J. G. Carlson, K. W. Cooper, H. V. Crouse, A. C. Faberge, M. M. Green, B. Griffing, E. Heitz, J. D. Krivshenko, C. C. and Gertrude Lindegren, Barbara McClintock, A. D. McLaren, D. Mazia, E. Novitski, J. O'Mara, J. Schultz, E. R. Sears, J. R. Singleton, R. W. Singleton, G. F. Sprague, Lotti M. Steinitz-Sears, C. P. Swanson, F. M. Uber, and M. S. Zuber.

2. The Gene

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--In 1950 Stadler was visiting professor at Yale University, where he taught Plant Science 128. The outline of the course appears still up-to-date. This draft is an excerpt of the content of the second lecture in the series.--

There were several graduate and undergraduate students who worked for L. J. Stadler in the corn nursery or in the laboratory. Several of them are well known geneticists today: G. Braver, Sam Goodsel, G. Lefevre, J. D. Mohler, E. L. Pinnell, L. M. Sandler, S. Zimmering.

INDIANA UNIVERSITY

BLOOMINGTON, INDIANA

DEPARTMENT OF ZOÖLOGY

Dec. 29, 19 45

Dr. L. J. Stadler, Advisory Panelon Neutation, 202 Genetics Euroding, University of Missouri, Columbia, Missouri, Lean La. Stadler:

It is very good news that there is a chance for the support of fundamental work on mutation, since this is one of the fields most basic to biological science as a vehole, including cancer theory, and since, despite this fact most studies of this subject have till now been struggling along with funds much smaller, in comparison with their needs, then those in other biological fields. University administrations, and those of general research foundations, can hardly be expected to have a of this situation, sincert is not common knowledge even among not our opists, It is therefore especially fortunate that the present hard on this subject consists of feethous all of whom are themselves among those that have been most active in research in this direction, and who are consequently in such a good fosition to know what the needs of the work are individually a such a good fosition to know what the needs of the

Mutation and the zene have constituted the chieffields of escared of the present writer for about a third of a century on this work he has been concerned mainly with the joneral principles, wherever they may be found. And although for reasons of training and technical convenience he has used Drosophila almost entirely as the material in his personally, conducted experiments of these without converted in this most not be ause of any primary interest in this material

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(Professor of Boology)

--Excerpts of a nine-page long letter of H. J. Muller, requesting Stadler's support for the continuation of his "third of a century" mutation research.--

18 RÉDEI

Though L. J. Stadler was not a titled administrator, he was an efficient organizer. In the mid-thirties his genius for research and leadership were recognized by a \$80,000 grant from the Rockefeller Foundation to build a home for the genetics group. With a supplemental \$66,000 provided by the University, Curtis Hall* was erected to house most of the geneticists on campus.

Professor Stadler's contributions to the University of Missouri were aptly appraised by Henry E. Bent, then Dean of the Graduate School, in an introduction to the "Stadler Memorial Lecture" given by George W. Beadle on February 3, 1955:

"It is difficult to imagine the operation of the University of Missouri without a president and many administrative and business officials. Yet these do not constitute the real University. It is impossible to imagine a university carrying on without buildings and equipment, both books and scientific apparatus. But these are inert objects until brought to life by the touch of a human mind. It would be a strange institution which did not have a large body of students with their endless activities, social life, recreation, lectures and final examinations. But none of these constitute a great university or even a part of a great institution until it has a company of scholars composing an outstanding faculty.

Lewis Stadler reminds us that the real University of Missouri is essentially a company of scholars, that all administration, all buildings and books serve merely to make these scholars more effective. That all students who come to the campus for an education come here for the influence which faculty can have upon them---upon their abilities to observe and reason, to form judgements and choose values and to put these together in effective, creative activity."



--Stadler with his students and associates. From left to right, upper row: E. A. Graner, L. J. Stadler, J. G. O'Mara, E. R. Sears, bottom row: J. R. Laughnan, M. R. Tomes, E. Weaver, H. V. Crouse, and H. R. Roman.--

^{*}Named after the zoologist W. C. Curtis, former Dean of the College of Arts and Science and an admirer of Stadler's scientific contributions.

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