THOMAS HUNT MORGAN: KENTUCKY'S GIFT TO BIOLOGICAL SCIENCE

BY WENDELL H. STEPHENSON

A hundred years ago history embraced little more than the doings of kings and military chieftains; its substance was drawn largely from politics and war. The concept of the subject has broadened and deepened, especially during the last generation, and those who now record the past are interested in the whole kaleidoscope of complex society, from diplomatic, financial, and constitutional developments to economic, social, and cultural patterns. In this newer concept of the subject, the contributions of scientists have won a permanent place in historical literature. Among biologists of the past half century, Thomas Hunt Morgan occupied a pre-eminent position, and it is proper that the state of his nativity should recognize his merit.

Born in Lexington, Kentucky, September 25, 1866, Morgan was descended from Anglo-Saxon southern stock. His father was Charlton Hunt Morgan, captain of cavalry in the Confederate Army under his more distinguished brother, General John H. Morgan. His mother, nee Ellen Key Howard, was a granddaughter of Francis Scott Key, author of "The Star-Spangled Banner." It is significant that Thomas's birthplace was "Hopemont," the General Morgan shrine in Lexington: "Morgan's Men" in the days of the Confederacy wrought havoc with enemies of the South, and in a later generation another group of "Morgan's Men"—biological scientists—made war upon ignorance and superstition.

Lexington had been a center of culture in ante-bellum years; in the postwar era it became the seat of the college that

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eventually developed into the University of Kentucky. For six years, from 1880 to 1886, young Morgan was a student at the State College of Kentucky, as it was then called. During the first two years he was enrolled in the school's preparatory There were slightly more than three hundred department. students at preparatory and college levels when he became a freshman in the fall of 1882. James K. Patterson, the only member of the staff holding the doctorate, was not only president but also professor of metaphysics, civil history, and po-There were less than a score of teachers. litical economy. some of whom were assigned to duties in sub-freshman classes. Regulations aplenty filled several pages in the catalog, with infractions bringing demerits in their wake. These were designed "for the repression of neglect and misconduct," and a hundred during an academic year were sufficient for "ipso facto" dismissal. It is gratifying to learn that Morgan was never in danger of expulsion, but it is also a relief to know that his conduct was not perfect, for perfection in deportment might have spelled failure as a man. Demerits assigned during his junior year were for tardiness at chapel and disorder in the hall and "in section." These were not serious offenses, but they indicate that he was a normal college student.

As an undergraduate Morgan's chief interest was in natural history, a predilection which antedated enrollment at State College. Before he had reached the age of ten, he began collecting birds, eggs, and fossils, with woods, meadows, and railroad cuts near Lexington providing specimens. Even then he was a leader, for he headed groups of boys who made expeditions into the adjacent countryside. Summer trips to Oakland, Maryland, gave further opportunity to develop his knowledge of natural history; fishing for craws in ponds and branches, whether in Kentucky or Maryland, introduced him to an ele-

mentary aspect of aquatic life.

The professor in the department of natural history was A. R. Crandall, who attained the doctor's degree just prior to Morgan's senior year. Fifty years after graduation the student recalled that he had "never met with a finer character or better teacher." As a prerequisite for entering the department, a year of organic and inorganic chemistry was demanded, and the student then had before him in the sophomore, junior, and

senior years such subjects as anatomy, physiology, and hygiene, plant histology and physiology, microscopy, zoology, physical geography, geology, and paleontology, only a few of which were optional.

Morgan excelled as a student, whether in natural history or in other branches of learning—with one exception. There is a story to the effect that he came near failing French in his senior year despite adequate classroom performance. The professor of French and Germanic languages and literature, François M. Helveti, had been a Union soldier captured by "Morgan's Men" and forced to ride a mule, "about face," from Cincinnati to Professor Helveti had never forgiven this indignity, and could not be objective where a Morgan was concerned. Notwithstanding a low mark in French, Morgan led his class. The faculty, on April 7, 1886, assembled in President Patterson's office "to consider the first and second honors for graduation." Three names were presented: William Prewitt and Robert L. Prewitt, candidates for the bachelor of arts degree, and Thomas Hunt Morgan, candidate for the bachelor of science degree. By a five to four decision, Morgan was awarded highest honors and became valedictorian, and William Prewitt, with second honors, became salutatorian.

Two years later Morgan received a graduate degree from State College. A part of the work taken during his last year counted for graduate credit. The rules provided that, for the master of arts and master of science degrees, "a satisfactory examination is required on a course of post-graduate studies prescribed by the Faculty, and covering a period of two years." After studying for a biennium at the Johns Hopkins University, the faculty of State College, on June 4, 1888, "unanimously resolved to recommend" Morgan for the degree of master of science.

The Johns Hopkins University at Baltimore provided one of the superior graduate schools in the United States during the last quarter of the nineteenth century. Under the leadership of President Daniel C. Gilman, it acquired an enviable reputation, whether in the humanities, the social studies, or the sciences. While the school's patronage was widespread, it attracted a large clientele from the South, for it was regarded as a southern university in a southern city. Morgan was a

student there for a quadrennium, receiving the Ph. D. degree in 1890. Among his instructors were Henry N. Martin, with whom he studied general biology and physiology, and William N. Howard, who taught other courses in physiology and mammalian anatomy. One of the greatest teachers of zoology of that day was William K. Brooks, under whom Morgan carried on his studies in morphology, and who directed his dissertation on the Embryology and Phylogeny of the Pycnogonids (sea spiders). Brooks had the power of inspiring his students with the scientific spirit of research, just as his colleague in history, Herbert B. Adams, captivated other Hopkins students with a love for history. Not all the work for the doctorate was done in classrooms and laboratories at Baltimore, for Brooks took his students to the marine laboratory at Beaufort, North Carolina, a real experience for a man who had grown up in the interior. And, before leaving the Hopkins, a similar trip was made to the Cape Cod area to study marine life. It was during these graduate days, too, that Morgan became acquainted with a group of young biologists whose close association lasted for half a century, and who were to lead in the advancement of biological science during the next generation.

Morgan continued at the Hopkins as Bruce Fellow for a year after receiving his degree. Then, in 1891, he was appointed professor of biology at Bryn Mawr College, where he served until called to a new chair of experimental zoology at Columbia University in 1914. For nearly a quarter of a century he directed that department's research laboratory. In 1928 Morgan was appointed director of the William G. Kerckhoff Laboratories of the Biological Sciences at the California Institute of Technology, Pasadena. He retired from that position in 1941, but continued his research until shortly before

his death on December 4, 1945.

It is a mistake to suppose that Morgan's education was complete when he received the doctorate at the age of twenty-four, for he continued to search for new truth as long as he lived, profiting from the discoveries of other scholars as well as his own. He journeyed to Jamaica with student friends to study and collect specimens; made regular summer migrations to the marine laboratory at Woods Hole, on Cape Cod, Massachusetts; and spent considerable time in Europe to utilize research facilities not available in America. European sojourns

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began in the 1890's. The summer of 1893 was spent at the University of Berlin, the winter of 1893-1894 at the Stazione Zoologica at Naples, and the summer of 1896 at Zurich. Fascinated by Siena, Italy, he settled there for a six-weeks period. Another summer was spent at Helgoland, where he lived with German officers, and beat them at tennis.

It was while Morgan was teaching at Bryn Mawr that he became engaged to one of his graduate students, Miss Lilian V. Sampson. They were married in June, 1904, and went on a trip to California, where he collected birds, experimented with lizards, and worked on Ciona. Mrs. Morgan, a native of Maine, was a biologist in her own right. Her grandfather had inspired an interest in music and science. While playing the violin in chamber music became an avocation. the field of genetics continued to call, even after the arrival of four children. In 1907 Morgan built a house at Woods Hole, and with two exceptions the family spent their summers there until 1944. Always there was the usual biological baggage to be transported over the Fall River Line-suitcases of Drosophila and mice and baskets of bantam roosters, pigeons, or experimental plants. At their summer home there was the garden with its vegetables raised for food and for fun; the orchard with its apples, pears, and plums; and the cow for a summer supply of milk.

Relief from the tedium of research, writing, and teaching came from tennis, which Morgan played until an advanced age, and from various cultural interests. On his trips to Europe he saw the passion play at Oberammergau, attended operas and symphony orchestras, and visited art galleries. In New York City he listened to concerts and chamber music. He followed intellectual interests at home by constant reading. And, after an evening of writing, a detective story or a novel might carry him far into the night. Sunday afternoons at Woods Hole were reserved for walks with his family, and the evenings saw a companionable group of scientists from home and abroad gather to discuss advancement in biology. "Morgan worked long hours and hard," said a former student who visited in his home, but "found time to play and enjoy life with his family."

The great bulk of Dr. Morgan's writings is an eloquent tribute to his industry; the excellence and general acceptance of the content a memorial to his scholarship. Fourteen books, totaling nearly five thousand pages, and more than three hundred articles, some of them in collaboration, published in scientific magazines, represent an accomplishment that few men have attained in any field. Before he began concentrating upon heredity, he had already acquired an international reputation as an experimental zoologist, with significant contributions to embryology, regeneration, and cytology. In 1897 he published *The Development of the Frog's Egg.* Then came Regeneration (1901), followed by Evolution and Adaptation (1903). The first book that emanated from his Columbia professorship was Experimental Zoology (1907), a product of the newer method of treating a subject which until recently had been largely historical and descriptive.

From 1910 forward Morgan's researches lay principally in genetics and closely allied fields. Heredity and Sex appeared in 1913; The Mechanism of Mendelian Heredity, in collaboration with Alfred H. Sturtevant, Hermann J. Muller, and Calvin B. Bridges, in 1915; A Critique of the Theory of Evolution in 1916, with a revised and expanded edition, Evolution and Eugenics, in 1925; The Physical Basis of Heredity in 1919; The Theory of the Gene in 1926; Experimental Embryology in 1927; What Is Darwinism? in 1929; The Scientific Basis of Evolution in 1932; and Embryology and Genetics in 1934. Many of his books went through reprintings and new editions; some were translated into German, French, Spanish, or Russian; several were foundation lectures delivered at sundry universities.

The great contribution of Dr. Morgan was his clarification of the laws and the mechanism of heredity, and of the mutation of species. He and his associates were the first definitely to locate the genes, the guiding hereditary units of chromosomes which determine characteristics in animal and plant life. For experimental purposes he desired an organism that had a short life cycle. In 1909 he began to use *Drosophila melanogaster*, the vinegar or fruit fly, which completes the cycle from egg to adult in ten days, with as many as thirty generations appearing annually. The advent of a white-eyed male the next year was the mutation for which Morgan had been watching, for normal fruit flies have red eyes. By crossing the mutant with the red-eyed fly, and by inbreeding the hybrids, he could

follow the pattern of inheritance of a unit character. The second generation of flies were all red-eyed, whether male or female; but the third consisted not only of red-eyed males and females but also of white-eyed males. Other mutants eventually appeared, with pink and vermilion eyes; with olive and black bodies, instead of the usual brown; and with wings of different colors and shapes. Heat, radium, and X-rays were employed to produce mutations. Using millions of *Drosophila* for experimentation, crossbreeding and inbreeding and back-crossing established laws of linkage and crossover. In a very tangible way, the findings have contributed toward improved

plant and animal breeding.

In arriving at scientific truth, Morgan would employ speculation, theory, and hypotheses if they led "to further research and possible discovery." They were useless, however, when applied to problems that could not be subjected to observation and experimentation. He saw no value in the vague speculations of metaphysicians and mystics; their efforts to explain organic evolution by removing "the problems from the biological field have done more harm than good." Embryology would become an exact science only by "the use of working hypotheses controlled by quantitative measurements, or in a word experimental methods." He was ever alert for new discoveries. "It may not be desirable to accept everything that is new," he wrote, "but it is certainly undesirable to reject what is new because of its newness, or because one has failed to keep in touch with the times." To critics who viewed his findings as "rash or intemperate," he answered that he held "all conclusions in science relative, and subject to change." He deplored the view which looked upon genetics as a science distinct from biology; it would be hazardous for either geneticists or zoologists to ignore advancement in the broader field of biology. Solutions of problems came from hard, ceaseless toil with hand lens and microscope. In his own work, he must see for himself rather than depend upon the research of assistants.

Morgan's success as a teacher did not lie in ability as a lecturer. The student whose primary interest was college credit rather than a genuine love for the subject would probably not have appreciated his classroom technique. A graduate student at Columbia has left the following appraisal of the man and the teacher, recorded from the perspective of nearly thirty years later:

"In the lecture room, when he didn't forget to come, and when he didn't forget to think in advance about what he was going to say, his lectures were rather coherent. . . . He was familiar with past and current literature and hence could tell us what had been done and what was being done. Most of all, I liked his suggestions for further investigations. There was always a spontaneity to his remarks-not dull monotony. His imagination was always at work. . . . In the laboratory he was at his best, always ready to talk over worthwhile problems with worthwhile students. . . . In these discussions his suggestions and keen analyses of problems and conditions were immensely helpful and stimulating." The men who were taking graduate work assembled fortnightly at his house after dinner to read aloud and discuss biological works such as E. Metschnikoff's Prolongation of Life or Charles Darwin's Animals and Plants. At ten the group, including Mrs. Morgan, "adjourned to the dining room where discussions continued for another hour "

In time Morgan trained scores of young scientists in research technique. Bridges, Sturtevant, Muller, and many other laboratory assistants learned scientific methodology and made notable contributions to the field of genetics. They expanded the frontiers of biological science: discovered and explored and charted the unknown. Their names are as significant in social, cultural, and scientific history as are their prototypes of an earlier day who found a new geographical world, plotted its contours, and opened it to settlement.

Morgan's achievements brought merited recognition. It was appropriate that his two alma maters should be the first to honor him: the Hopkins awarded the LL.D. degree in 1915 and the University of Kentucky in 1916. The same degree was conferred by McGill University in 1921, the University of Edinburgh in 1922, and the University of California in 1930. The University of Michigan honored him with the Sc.D. degree in 1924, Heidelberg University with the Ph.D. degree in 1931, the University of Zurich with an M.D. degree in 1933, and the

University of Paris designated him Docteur Honoris Causa in 1935.

Some of the organizations to which Morgan belonged were professional societies, open either because of his interest in the field or because of his contributions to it. Such were the New York Academy of Sciences, the American Society of Zoologists; the American Society of Naturalists, and the Society of Experimental Biology and Medicine. From 1927 to 1931 he served as president of the National Academy of Sciences, and in 1929 he was chosen president of the American Association for the Advancement of Science. A recital of the European societies that elected Morgan corresponding member or foreign associate would become monotonous; it is sufficient to record that organizations in England, Ireland, Finland, Belgium, France, Bavaria, Russia, Denmark, and Italy recognized his merit. Perhaps it should be particularized that he was elected to membership in the Royal Society of London, which awarded him the Copley Medal in 1939 for his contributions to the science of genetics.

The greatest of all distinctions came in 1933 when he was declared winner of the Nobel Prize in Medicine "for his investigations concerning the eugenic functions of chromosomes." The prize carried a monetary value of 170,331 kroner, or nearly \$40,000 in American money. Awarded annually in the field of medicine, physics, and chemistry, it was the first time the prize in medicine had gone to a nonmedical scientist. The recipient regarded the award as a recognition of the work of the group associated with him, and with them he always wished to share the honor. On June 4, 1934, he presented a lecture at Stockholm on "The Relation of Genetics to Physiology and Medicine."

When the Nobel Prize was announced, President Frank L. McVey of the University of Kentucky telegraphed congratulations: "The University is honored by your great services as a scientist, philosopher and gentleman." Three years later, on the occasion of Morgan's seventieth birthday, the University honored him by a convocation at which one of his former students at Columbia, Dr. Ferbandus Payne, dean of the graduate school at Indiana University, made an address. A bronze plaque, marking his birthplace in Lexington, was

unveiled. Dr. Morgan could not attend the ceremonies. "To be quite frank," he wrote President McVey, "I am afraid that I should be terribly embarrassed, for on such an occasion, I am quite sure that my good friends will kindly overlook my deficiencies and perhaps exaggerate the little that I have accomplished." If any trait of character predominated, it was extreme modesty. He was Kentucky's gift to biological science, but the gift honored the state that gave it birth.