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Thomas Hunt Morgan

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The Hunt-Morgan House is associated with two nationally or internationally famous Americans. It was the home of General John Hunt Morgan, a Confederate general and cavalry leader whose exploits as head of "Morgan's Men" placed him high on the Union's "most wanted" list. Probably better known, and certainly better known outside the United States is his nephew, Dr. Thomas Hunt Morgan, a professor of biological sciences whose pioneer studies in the field of classical genetics opened up a new and exciting area of biological research, and laid the foundations for the vast amount of work in biochemical and molecular genetics that has developed since the end of World War II.

Dr. Morgan's father was Captain Charlton Hunt Morgan who rode with the general's band during the War Between the States, and his mother was Ellen Key Howard whose grandfather, Francis Scott Key, was the author of "The Star-Spangled Banner." Dr. Morgan was descended from the early Anglo-Saxon stock who founded and built up the country during colonial days, and in height, appearance, and manners he was very much a southern gentleman. In his ancestral lines were several old, aristocratic families of Pennsylvania and Maryland. He was born on 25 September 1866 in the Hunt-Morgan House, which has sometimes been called Hopemont. Apparently, he was named for his uncle, Lieutenant Thomas Hunt Morgan, a member of Morgan's Raiders, who had been killed in a skirmish at Lebanon, Kentucky, in 1863.

In 1880, Dr. Morgan entered the Agricultural and Mechanical College of Kentucky (now the University of Kentucky) as a student in the preparatory department. Two years later he became an undergraduate and received his Bachelor of Science degree, with highest class honors, in 1886.

Dr. Morgan had shown an early interest in natural history, and was an avid collector of birds, birds' eggs, and fossils before he was 10 years old, so it was only natural that as an undergraduate his chief interest would be in that subject. He was fortunate to study under A. R. Crandall, a professor in the Department of Natural History, from 1878 to 1888. Apparently, Professor Crandall maintained high academic standards, for Dr. Morgan had to take a year of organic and inorganic chemistry as a prerequisite to a major in the department. He later wrote of Professor Crandall (letter to President Frank L. McVey at the time of a University of Kentucky Convocation on 25 September 1936 in honor of Dr. Morgan) "I have never met with a finer character or better teacher. I realize the very great debt I owe to these earlier experiences."

During his student days, the college, including the preparatory school, had an enrollment of a little more than 300 students and about 20 faculty members. Lexington was a very small town in a distinctly rural environment and was not then ringed, as it is today, by residential suburbs and shopping centers. It was a paradise for the student of natural history. Dr. Morgan was an excellent student and was valedictorian of his class at the graduation exercises, but he had a lighter side as well, and accumulated a number of demerits for tardiness at chapel and for disorder in class and in the halls. His only low mark was in French, and for a most unusual reason. Professor François M. Helveti, the instructor in French, had been a soldier in the Union army during the War Between the States and had been captured by General Morgan's men and forced to ride backwards on a mule from Cincinnati to Lexington. Such an indignity provoked a hatred for the Morgan family that prevented him from being objective when it came to Dr. Morgan's grade in French.

In the autumn of 1886, Dr. Morgan entered The Johns Hopkins University for graduate work in biology. This was a fortunate choice, as The Hopkins was, under the leadership of Daniel Coit Gilman, one of the superior graduate schools in the United States and one of the few institutions in the country that offered the degree of Doctor of Philosophy. It was a fortunate choice, too, because it had an excellent faculty in biology which included Professor William Keith Brooks and several others of note, and a group of fellow students, such as H. V. Wilson, E. G. Conklin, S. Watase, and R. G. Harrison, who became leaders in the biological sciences at the turn of the century. Professor E. B. Wilson, later a colleague of Dr. Morgan at Columbia University, had preceded him as a graduate student at The Hopkins by just a few years.

In 1888, the State College of Kentucky awarded Dr. Morgan the degree of Master of Science on the basis of work done there during his senior year plus work done for two years in absentia while he was a graduate student at The Johns Hopkins University. On 5 June 1889, the Board of Trustees of Kentucky elected him to a professorship, and the Annual Register of the State College of Kentucky for 1888–1889, with the announcements for 1889–1890, listed Thomas Hunt Morgan as Professor of Natural History. However, on 13 June 1889, Dr. Morgan wrote to President James K. Patterson declining the appointment as he had just accepted an appointment as Fellow in Morphology at The Hopkins and hoped to apply for his degree of Doctor of Philosophy at the end of the year. He wrote that the fellowship generally led to the Bruce Fellowship for one or more years and that by accepting it he could devote himself for one or two years entirely to research in zoology. He received his doctoral degree in 1890 and remained for one postdoctoral year as a Bruce Fellow. At that time he had no thought of being a geneticist. His field was experimental embryology, and his doctoral dissertation was entitled "Embryology and Phylogeny of the Pycnogonids (sea spiders)."

Bryn Mawr College in Philadelphia offered him a professorship in 1891 and he accepted it. He taught there for 13 years and, as in his graduate studies at The Johns Hopkins University, was preceded there by Professor E. B. Wilson, who left the year Dr. Morgan joined the faculty. His Bryn Mawr experience was a very significant one, as during his later years he became engaged to Miss Lilian Vaughan Sampson, a graduate student in biology and an excellent violinist. She was a first-class biologist in her own right and published a number of articles in technical scientific journals after she was married. Their marriage took place in June 1904 and they became the parents of four children.

In 1904, Dr. Morgan was called to the new Chair of Experimental Zoology at Columbia University in the City of New York. In a sense, this appointment was the turning point of his professional career because it gave him facilities that he could never have had at Bryn Mawr. His teaching load was lighter, the library was much better, and he had many first-class graduate students. In addition, there was a much larger group of stimulating biologists in the faculty, including Professor E. B. Wilson, whose field was closely allied to Morgan's. The inclusion of both men in the same department was mutually very beneficial.

One of the great benefits that Dr. Morgan derived from his Columbia professorship was access to three unusually brilliant graduate students who were there at the same time, and who, along with their professor, formed a harmonious team which, in a sense, was the forerunner of the numerous scientific teams of the present day. They were H. J. Muller, C. B. Bridges, and A. H. Sturtevant. In recognition of their assistance, Dr. Morgan shared his Nobel Prize money with the two who were still with him in 1933 when he received it.

In 1920, the California Institute of Technology was formed from a smaller and less renowned technical school near Los Angeles. In 1928, it expanded to include biology, and Thomas Hunt Morgan was appointed Chairman of the Division of Biology, Director of the Wm. G. Kerckhoff Laboratories, and a member of the Executive Council of the Institute. There, he had an even greater opportunity to develop the science of genetics than he had as a professor at Columbia University. Naturally, the Division of Biology tended to emphasize genetics as he added his former students Dr. Bridges and Dr. Sturtevant to the staff as well as several other geneticists from other institutions. He remained as Chairman of the Division and Director of the Kerckhoff Laboratories until 1941, when he retired at almost 75 years of age. "Retirement," however, is a relative word, and Dr. Morgan continued his biological research after he gave up his more formal duties, and until a short time before his death, which occurred 4 December 1945, at the age of 79 years.

Dr. Morgan was one of a group of biologists responsible for establishing the well-known Marine Biological Laboratory at Woods Hole, Massachusetts. Especially during the early part of this century it was a tremendously active research laboratory for aquatic biology, and many famous biologists of that period spent their summers there. Dr. Morgan built a home at Woods Hole in 1907 which he maintained until 1944, and he spent every summer there during that period with two exceptions. The house had a double living room 80 feet long and 25 feet wide, and a large dining room and kitchen. On the second floor were six bedrooms, two sleeping porches, and one household bathroom. The third floor had four huge unfinished rooms for the maids. No architect was used, and the total cost for lumber and labor was $3,000. While there, he entertained many of the famous biologists of Europe. In addition to his periodic visits to the Marine Biological Laboratory, he made other trips to collect material and to consult with investigators in other laboratories. They included the West Indian island of Jamaica, the Stazione Zoologica in Naples, and the Universities of Berlin, Zurich, Helgoland, and other places.

During his academic career, Dr. Morgan published 14 books with a total of almost 5,000 pages. His first, published in 1897, was on the development of the frog's egg, and his last, in 1934, was on embryology and genetics. Perhaps the one that had the greatest impact on biology was "The Mechanism of Mendelian Heredity" authored by T. H. Morgan, A. H. Sturtevant, H. J. Muller, and C. B. Bridges. It was originally published in 1915 and was revised in 1923. It brought together and summarized the evidence which that team had been accumulating in support of Mendelism and the chromosome theory of heredity, and from then on the chromosome theory was well accepted and no longer under suspicion except by a few diehard biologists. In addition to the books, Dr. Morgan published more than 300 articles in technical biological journals.

Experimental embryology was a fashionable biological subject in the 1880's and 1890's and Dr. Morgan was one of its leaders. According to Muller (1946), he was "an outstanding member of what may be called the heroic generation of American biologists—those whose work raised American biology to a position second to none among the countries of the world." During that period, biology was in a very unsettled state. In many ways it had not attained the status of a science, and it tended to be confounded and obfuscated by philosophical or pseudophilosophical speculations that all too frequently were substituted for experimentation and the objective procurement of facts.

One of the big controversial problems was the fundamental one of the essence and substance of life. The two principal theses were *mechanism* and *vitalism* and they were mutually antagonistic. The former hypothesized that living things were fundamentally the same as nonliving, that that they were composed of the same kinds of molecules, and that they operated according to the same laws that controlled the reactions of inanimate objects. The vitalists, on the other hand, assumed that life is partly self-determining, that it cannot be explained by the laws of chemistry and physics alone, and that its functions and behavior are not purely mechanistically determined. The vitalists refused to explain life in concrete terms with the result that subjects such as embryology, heredity, regeneration, organization, and evolution frequently seemed to be enshrouded in an air of mystery.

Dr. Morgan was an experimentalist who believed in exact observation. He was one of a group of biologists of that period who detested and scorned speculation and all generalization based on inadequate information, and who felt that the important need was for more data, more information, before conclusions could be drawn or generalizations made. This attitude was frequently called "mechanistic," especially by those not in rapport with it. Morgan's philosophy on that subject can be readily understood from a biographical note he published in Science (Morgan 1912) about Miss N. M. Stevens, a former student of his at Bryn Mawr College; she was a first-class cytologist who made some significant observations on chromosomes and the inheritance of sex in animals. He wrote "She was a trained expert in the modern sense—in the sense in which biology has ceased to be a playground for the amateur and a plaything for the mystic."

Early work of Dr. Morgan involved, among other problems, the importance of the structure of the egg to the development of the individual. It was a problem that interested him all his life. In the preface to his "Experimental Embryology" (Morgan 1927), he wrote "A transparent egg as it develops is one of the most fascinating objects in the world of living things. The continuous change in form that takes place from hour to hour puzzles us by its very simplicity. The geometric patterns that present themselves at every turn invite mathematical analyses. The constancy and orderliness of the whole series of events, repeating themselves a thousandfold in every batch of eggs, assures us of a causal sequence conspiring to create an object whose parts are adjusted to make a machine of extraordinary complexity."

Some of the early embryological studies were fascinating because of the meticulousness of the observations and the ingeniousness of the methods used to devise critical experiments. During the early stages of the development of the embryo, the first cell to be formed, the zygote, divides into 2, those 2 divide into 4, then into 8, 16, 32, and finally into a mature individual that consists of hundreds of thousands or millions of cells. A study of this development requires great patience and keen observation, for growth and differentiation are very precise and follow a rigid pattern, any deviation from which would result in an abnormal individual. The pattern, however, may differ with different species or kinds of animals.

Those most frequently studied are lower marine invertebrates because their eggs are readily obtainable in tremendous quantities and are not too difficult to study under the microscope. Various zoologists in Europe and the United States studied different organisms; Morgan's main observations were on the frog, and culminated in 1897 in a small book on "The Development of the Frog's Egg." He traced the normal development of the egg, cell by cell, from its beginning until late in the development of the tadpole.

During that period of biological research, many zoologists were studying the egg under abnormal conditions to determine whether they could learn more about normal development by studying the abnormal rather than the normal. Various means were used to produce unusual conditions. Eggs were kept compressed in certain planes, cells or parts of cells were destroyed with hot needles, developing embryos were raised in sea water lacking or containing too much of certain salts, eggs were subjected to violent centrifugal force before or during development, nuclei were removed from cells, pieces of the egg were sliced off, and both nucleate and enucleate egg fragments were fertilized and allowed to develop as they would. Morgan tried all these methods on frogs and other animals, such as sea urchins and marine polychaete worms, and from these studies many valuable principles of development were discovered and understood. Morgan's interests in the field of experimental embryology were extensive throughout his life, and the problems he attacked were many and varied.

Early in the twentieth century, Morgan turned from his study of experimental embryology to the newly emerging field of genetics or the science of heredity. In 1865, Gregor Mendel, living in a monastery in Brunn, a town then in Austria, now in Czechoslovakia, presented a talk before the natural history society of that town in which he explained in considerable detail the results of a series of experiments he had conducted on the breeding of peas; he also suggested a theoretical explanation of his results. His talk was published the following year in the transactions of that society, but did not attract the attention of the biological world.

At the end of the century, similar experiments were being carried on independently by Hugo de Vries in Holland, Carl Correns in Germany, and Eric von Tschermak in Austria. They all obtained the same results and came to the same conclusions, and in 1900 each published his own data and conclusions. In the meantime, they came across Mendel's original work and realized that their conclusions had been anticipated by 35 years.

When the rediscovery of the principles that Mendel had originally discovered became known to the biological world, there was a mixed reaction. Some biologists saw in them the answer to all problems of heredity and evolution, but others were very skeptical or even hostile to their acceptance. Some people thought they were not true and some thought that even if they were true they were not universal, but applied only to the garden pea or to just a few organisms.

It is very interesting to note that Dr. Morgan was one of a group of biologists who were critical of parts of Mendel's scheme. Morgan started his work in genetics in 1908 (Stubbe 1933), and in 1909 he gave a talk at a meeting of the American Breeder's Association in Columbia, Missouri, in which he expressed a doubt that the hereditary factors, which we now know as "genes" existed at all. He proposed instead, that the condition of two contrasting characters, such as round or wrinkled peas, might be the result of alternative states of stability or conditions which determine the traits of which an individual is composed, rather than the result of the clean and absolute segregation of material bodies such as genes.

The principal event that changed Morgan's attitude towards genetics was the discovery of a white-eyed fly. Within three years of the rediscovery of Mendel's laws, a graduate student by the name of W. S. Sutton, who was studying at Columbia University, observed the striking parallelism in the behavior of chromosomes during cell division and the formation of germ cells and the hereditary factors that Mendel had hypothesized. He emphasized that it could not be purely coincidental, and maintained that these hereditary factors must be located in the chromosomes, thus laying the foundations for the chromosome theory of heredity. Not all biologists accepted such a revolutionary doctrine.

At about the same time, several zoologists were concerned with the problem of the determination of sex. It had been shown by some that females in many animals apparently had two members of a certain chromosome, now designated the "X chromosome", whereas the males had only one, and it was suggested that this difference determined whether the animal was a male or a female. However, other zoologists found that in other animals the reverse condition seemed to be true, the male having two such chromosomes and the female only one. Confusion reigned, and the problem of sex determination seemed to be a very baffling one.

Most of Dr. Morgan's work in genetics was done with a tiny two-winged fly called *Drosophila melanogaster*; its popular names are pomace fly, fruit fly, or vinegar fly. If a person should put some bananas outdoors in the spring or summer, he would probably soon find some of these flies flitting around them. If he collected and examined them, he would find that they would invariably have eyes of a certain shade of red. Such flies, collected under natural or "wild" conditions are said to have "wild-type" characteristics or traits. This peculiar shade of red is then called the wild-type eye color. Morgan had had a number of such wild-type flies in his laboratory for many generations. It was, therefore, a great and pleasant shock when one morning he found a white-eyed male in a laboratory stock bottle. Of course, there was only one thing to do with such a fly—mate it immediately to a wild-type-eyed virgin female to see what would happen. Probably to his surprise, Dr. Morgan found that wild-type and white eyes behaved exactly as they should if they were determined by a pair of those hereditary factors or genes at the basis of the Mendelian laws of heredity. Furthermore, not only did they behave according to Mendel's laws, but they also followed a pattern that would indicate that they were located on the X chromosome, or were "sex-linked," to use the technical expression. Their pattern of transmission from one generation to another was the same as the pattern that Miss Stevens had observed for the X chromosome of *Drosophila*.

It was then finally recognized that birds and butterflies show one type of sex inheritance and sex-linkage, and the Diptera, mammals, and other animals show another, and that these two types are fundamentally the same except that in one the female has the odd chromosome, and in the other, the male has. It was also seen that Morgan's example of white eye inheritance in the fruit fly follows the same pattern of heredity as do certain sex-linked traits in human beings, such as hemophilia and a certain kind of color blindness.

Very soon after the discovery of the white-eyed male, a male appeared with short wings. This trait happened, by chance, also to be sex-linked and thus to follow the same pattern of transmission that was followed by the white-eyed character. Experiments soon showed that these two genes, white eyes and short wings, were linked together, which is just what they should have been if they were on the same chromosome. Dr. Morgan then crossed these two types together and found that although they were linked and therefore tended to be inherited together, they would sometimes show recombinations. Such recombinations of otherwise linked genes had been found in other organisms by other biologists but had never been satisfactorily explained.

Morgan reasoned that the chromosomes must break and interchange similar pieces at some time early in the divisions that produce the germ cells in animals. This theory of crossing over was supported by observations that had been made by F. A. Janssens, a Belgian cytologist, in 1909. He had shown that in a very early stage of these divisions, cross-shaped chromosome configurations could be seen under the microscope that were exactly what one would expect to find if the chromosome broke and crossed over as Morgan hypothesized (Morgan 1911a, 1911b). Recent observations have substantiated these ideas and have shown that crossing over involves exchanges of pieces of half chromosomes, as Janssens had originally suggested, and not whole ones, a very minor point.

The crucial point is that these observations caused Dr. Morgan to reverse some of his former ideas about Mendel's laws. Instead of being skeptical of them, he now accepted them wholeheartedly and spent most of the rest of his life confirming and expanding them. Only a great man would have done so, as many people, confronted with evidence opposed to their hypotheses would tend to find ways to look for confirmatory evidence, rather than give up their cherished hypotheses.

After demonstrating sex-linkage and showing that two sex-linked genes are linked to one another, Morgan extended his genetic studies. From 1909 to 1912, he and his group found many new mutations in *Drosophila.* After 1910, they attacked the problem of crossing over with great vigor, and published the first edition of their masterful "The Mechanism of Mendelian Heredity" in 1915. Morgan's greatest contribution was the study of linkage and crossing over. He demonstrated beyond doubt that genes located on the same chromosome sometimes separate from one another and that they do so more frequently if they are farther apart on the chromosome. With this demonstration, linkage maps, based on breeding data, could be constructed and the whole chromosome theory was substantiated.

While Dr. Morgan's earlier work was in the field of experimental embryology, and while the work for which he is best known was the genetic study of *Drosophila,* it should also be mentioned that he carried on extensive research on regeneration, and on the life cycle and cytology of the phylloxerans, a group of plant lice. These studies were important in influencing the thinking of the time.

Dr. Morgan's list of honorary degrees is extensive. He received the Doctor of Laws degree from The Johns Hopkins University (1915), the University of Kentucky (1916), McGill University (1921), the University of Edinburgh (1922), and the University of California (1930). The University of Michigan awarded him the degree of Doctor of Science in 1924, and the University of Heidelberg (Germany) gave him the degree of Doctor of Philosophy in 1931. In 1933, he received the degree of Doctor of Medicine from the University of Zurich (Switzerland), and two years later the University of Paris awarded him the degree of Docteur Honoris Causa.

He was President of the National Academy of Sciences from 1927 to 1931, of the American Association for the Advancement of Science in 1930, and of the Sixth International Congress of Genetics in 1932. He was a member of the American Philosophical Society, the Academy of Natural Sciences of Philadelphia, the American Society of Naturalists, and other American scientific organizations. He was an honorary member of many European societies including the Royal Society of London, the Paris Academy of Science, Belgian Society of Zoology, Royal Society of Science of Uppsala, Vienna Academy of Science, and other scientific societies in France, Norway, Denmark, Ireland, Finland, Brussels, Moscow, St. Petersburg, and Munich. He was one of the members of the editorial board of GENETICS from the time it was founded in 1916 until his death.

Of his many important scientific contributions, the greatest was the work in genetics that clinched the acceptance of Mendel's laws, established the chromosome theory, and developed the concept of the linkage and crossing over of genes on a chromosome. It was for this work that he became the first man without a medical degree to be awarded the Nobel Prize in Physiology and Medicine.

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