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THOMAS HUNT MORGAN

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A Biographical Memoir by

A. H. STURTEVANT

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T. H. Morgan

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THOMAS HUNT MORGAN was born September 25, 1866, at Lexington, Kentucky, the son of Charlton Hunt Morgan and Ellen Key (Howard) Morgan.

In 1636 the two brothers James Morgan and Miles Morgan came to Boston from Wales. Thomas Hunt Morgan's line derives from James; from Miles descended J. Pierpont Morgan. While the relationship here is remote, geneticists will recognize that a common Y chromosome is indicated. The family lived in New England—mostly in Connecticut—until about 1800, when Gideon Morgan moved to Tennessee. His son, Luther, later settled at Huntsville, Alabama. This Luther Morgan was the grandfather of Charlton Hunt Morgan; the latter's mother (Thomas Hunt Morgan's grandmother) was Henrietta Hunt, of Lexington, whose father, John Wesley Hunt, came from Trenton, New Jersey, and was one of the early settlers at Lexington, where he became a hemp manufacturer. Ellen Key Howard was from an old aristocratic family of Baltimore, Maryland. Her two grandfathers were John Eager Howard (Colonel in the Revolutionary Army, Governor of Maryland from 1788 to 1791) and Francis Scott Key (author of "The Star-spangled Banner"). Thomas Hunt Morgan's parents were related, apparently as third cousins. Francis Scott Key's mother was Ann Phoebe Penn Dagworthy Charlton, daughter of Arthur Charlton of Frederick, Maryland; Henrietta Hunt's maternal grandmother was Mary Charlton—who seems to have been a sister of Ann.

The pedigree indicates that the greatest portion of Morgan's ancestry was of English origin, but besides that of the immigrant James Morgan there are at least two other Welsh strains, a number of surnames that seem to be Scotch, and at least one infusion each of Irish, French, and German—a mixture similar to that usually found in the ancestry of Americans whose families have been long in this country.

Charlton Hunt Morgan was American Consul at Messina in 1860, and at that time assisted Garibaldi—a circumstance long remembered by Italian patriots, with the result that his son felt especially close to Italy, and was received there with great cordiality. Shortly after his return, in 1861, Charlton joined the Confederate Army, being a member of the group known as "Morgan's Raiders," that was commanded by his brother, General John Hunt Morgan. Charlton was wounded at the battle of Shiloh, and was several times captured.

Thomas Hunt Morgan was interested in natural history as a boy. Some of his summers were spent in the mountains at Oakland, in extreme western Maryland, where he collected fossils. As a young man he was employed for several summers in geological and biological field work in the Kentucky mountains. In 1886 he received the B.S. degree at the University of Kentucky, and then proceeded to Johns Hopkins University, having first attended the marine laboratory at Annisquam, Massachusetts, during the summer of 1886. His own account of how he came to go to Johns Hopkins is as follows: "My days at Johns Hopkins were probably not very different from those of other students who were attracted there by the rather vague rumors that reached us as undergraduate students in far distant colleges. In my own case it was through Joseph Castle who had preceded me by a couple of years. Perhaps the fact that my mother's family were Baltimoreans had some effect; but little did I know then how little they appreciated that a great university had started in their midst, and I think this was typical of most of the old families of that delightful city" (from a letter written about 1943).

He always felt that he owed much to the atmosphere at Johns

Hopkins under Daniel Coit Gilman—and the similar one he encountered later at Bryn Mawr under President M. Carey Thomas.

At Johns Hopkins Morgan was a student of William Keith Brooks, and it was Brooks who influenced him in his choice of embryology as his first field of study. To Brooks also must be attributed the encouragement of his long interest in marine organisms. However, he was also greatly influenced, in his student days, by H. Newell Martin and by W. H. Howell. From them he learned to appreciate the value of physiological approaches to biology; and I think he was inclined to turn to them rather than to Brooks at times because he felt that the latter was somewhat too metaphysical for his tastes.

Among his fellow students at Hopkins were E. G. Conklin and R. G. Harrison—who remained among his closest friends for the rest of his life. Also in the Hopkins tradition, although he had already left there before Morgan arrived, was E. B. Wilson, later to be Morgan's close associate and personal friend. These three men were, I think, the ones among his contemporaries with whom he felt the closest ties.

Morgan received his Ph.D. from Johns Hopkins in 1890, and was then Bruce Fellow for a year—part of this time being spent in research in Jamaica and the Bahamas. In 1891 he was appointed Associate Professor of Biology at Bryn Mawr, succeeding E. B. Wilson. He remained at Bryn Mawr until 1904. Among his associates here were R. G. Harrison and J. Loeb, with both of whom he maintained close associations for many years thereafter. Here also he had a number of students who made great contributions to biology; especially to be noted are Nettie M. Stevens, whose work in regeneration and particularly in cytology was outstanding, and Lilian V. Sampson, whose early work was in embryology and regeneration, and to whom Morgan was married in 1904. In 1904 Morgan was appointed Professor of Experimental Zoology at Columbia, a position he held until 1928. During this period he was closely associated with E. B. Wilson. They were a remarkable pair, and those of us who were graduate students under them can appreciate the atmosphere of the labora-

tory more easily than we can describe it. Harrison (1936. *Science,* n.s., 84:565), writing about Wilson, says: ". . . Wilhelm Ostwald, in his interesting book on great men of science, classified them, according to their talents, as romantics and classics. . . . To the romantic, ideas come thick and fast; they must find quick expression. His first care is to get a problem off his hands to make room for the next. The classic is more concerned with the perfection of his product, with setting his ideas in the proper relation to each other and to the main body of science. His impulse is to work over his subject so exhaustively and perfectly that no contemporary is able to improve upon it. . . . It is the romantic that revolutionizes, while the classic builds from the ground up.

"Wilson is a striking example of a classic, and it is interesting to note that for many years his nearest colleague and closest friend was an equally distinguished romantic."

The two men did not always agree on scientific questions, but the disagreements were openly discussed and each respected the other's opinions. All this was apparent to the students in the department—and gave them an example of the scientific spirit at its best.

In 1928 Morgan was appointed Professor of Biology at the California Institute of Technology, a position he held until his death. His undertaking here was to organize a Division of Biology—a subject not then taught at the Institute. He preferred research to administrative work, but this seemed to him an opportunity not to be missed, for he was dissatisfied with the way in which biology was still so largely dominated by morphology in most institutions; here he had a free hand to develop the subject in the way he wanted, in an institution where physics and chemistry were outstanding, and where the primary emphasis was on research and the training of research men. He felt—and the event justified this feeling—that he could count on the support, in this undertaking, of the three guiding spirits of the California Institute: George Ellery Hale, R. A. Millikan, and Arthur A. Noyes.

Morgan was always interested in marine biology. As indicated

above, the summer before he began graduate work was spent at the marine laboratory at Annisquam. Two years later (in 1888) he spent his first summer at Woods Hole, where he continued to work nearly every summer for the remainder of his life. Here he made many friends, and played a large part in the scientific activities of the several laboratories situated there. He was made a Trustee of the Marine Biological Laboratory in 1897; he took an active and constructive part in the development of that laboratory from that time on.

Ten months in 1894 and 1895, and also the summer of 1900, were spent at the Zoological Station at Naples, which he had visited in 1890. Here he collaborated with Hans Driesch in the use of experimental methods in the study of embryology. This association was important in influencing the course of his later work. He found Driesch congenial and stimulating, and remained on close friendly terms with him—even though he found himself wholly out of sympathy with Driesch's later vitalistic views and preoccupation with philosophy.

After moving to California in 1928, Morgan continued to go to Woods Hole in the summers, but he also started a marine laboratory at Corona del Mar as an integral part of the new Division of Biology of the California Institute of Technology. Here, for the first time, work with marine forms became for him an all-year occupation.

Morgan's first work was in descriptive embryology, directed (as was the fashion at the time) toward the solution of phylogenetic problems. His doctoral dissertation, on the embryology of the Pycnogonida (sea spiders), and work on the embryology of *Balanoglossus,* belong to this period. Early work on the development of Amphibia and ascidians was also descriptive, but directed rather toward determining the exact history of specific embryonic regions. Later embryological work was almost entirely experimental in nature; this interest is apparent in his report of work done on the eggs of fish and of sea urchins and starfish in 1893. However, it was in the summer of 1894, at Naples, that this interest was strongly reinforced,

largely by his association with Driesch. The early experiments here were concerned with the determination of the median plane of the embryo, with the old problem of "concrescence" in the vertebrate embryo, and with the development of isolated blastomeres. In one of these papers (1894, *Anat. Anz.*) he reported the effects of fertilizing fragmented eggs of sea urchins, and reached the conclusion that Boveri had been mistaken in supposing that non-nucleated fragments could be fertilized with foreign sperm and would then develop and give rise to embryos like those of the paternal species. There resulted a controversy which was ended only by a posthumous paper by Boveri (1918, *Arch. Entw. Mech. Org.*, 44) in which he finally concluded that Morgan had been correct in his interpretation. It may be argued that this controversy was unfortunate, for it was largely responsible for Morgan's relative lack of appreciation for Boveri's later brilliant work. This was one of the respects in which Wilson was a useful counterpoise for graduate students at Columbia, for his admiration of Boveri was infectious.

In 1896 Morgan reported on the induction of artificial asters in sea urchin eggs by the use of hypertonic sea water. This was an outgrowth of earlier observations by the Hertwigs, Loeb, and Morgan himself. It was important in connection with Boveri's theory of the self-duplicating nature of the centrioles, and in the developments that led to Loeb's work on artificial parthenogenesis. There was at the time a rather general feeling that Loeb had taken more credit than was due him for the discovery of artificial parthenogenesis. A study of the literature of the period suggests that in fact the idea was "in the air," and that it was only a question of who would first find a technique that would lead to reasonably normal cleavage of the treated eggs. In later years Morgan sometimes talked about this matter; he clearly felt that Loeb had been secretive about his own work and had used every opportunity to find out just what Morgan was doing. However, Morgan was not as resentful as were some other members of the Woods Hole group on his behalf, and he and Loeb

were on close friendly terms during the period when I knew them—from 1913 until Loeb's death in 1924.

While he was still a graduate student Morgan had begun experiments on the regeneration of earthworms, and in 1897 he published the first of a long series of papers on regeneration in a wide variety of animals—planarians, Crustacea, coelenterates, teleost fishes, Amphibia, etc. At the time of his death he was studying regeneration in brittle stars. His book on the subject (1901), like some of his other books, was not intended as a summary of a well understood field. I once heard him say, semi-seriously, that the only book worth writing was one in a field that was developing so rapidly that the book would soon be out of date.

The work on experimental embryology and regeneration was directed largely toward the problem of differentiation: how does a relatively undifferentiated egg or tissue come to produce the orderly and regulated series of successive structural complications that lead to the fully formed adult? Here again there was a difference in attitude between Morgan and Wilson. The latter was inclined to lay great emphasis on the segregation of preformed materials in the egg during cleavage, whereas Morgan had little faith in the effectiveness of "formative stuff." His experiments with Lyon on the effects of centrifuging eggs (1907) represented an attempt to test this hypothesis experimentally.

Morgan was interested in the determination of sex as early as 1903, when he published a critical review of the literature. This was followed by a suggested interpretation of gynandromorphism in the honey bee (1905; the correctness of the interpretation was finally shown in 1951, by Rothenbuhler, Gowen, and Park, *Genetics,* 36:573). Then, beginning in 1906, came his work on the complicated life-cycle of the phylloxerans and aphids. He showed that the facts, which at first seemed quite inconsistent with the chromosome interpretation of sex determination, were in fact intelligible only in terms of that interpretation. This was one of Morgan's most brilliant achievements, involving great skill and patience in the collecting and

care of the animals, insight in seeing what were the critical points to study, and ability to recognize and to follow up unexpected facts. The results were of importance in serving to demonstrate the role of the chromosomes in sex determination, at a time when that importance was seriously questioned by many biologists.

Morgan's interest in genetics seems to have stemmed, at least in large part, from a visit to de Vries's garden in Holland (probably in 1900). In 1903 he wrote "No one can see his experimental garden, as I have had the opportunity of doing, without being greatly impressed." What impressed him was the occurrence of numerous sharply distinct types, differing from the parental forms in numerous respects, and breeding true to the new characteristics. It is, of course, now known that these types arise because of the very special and peculiar genetic properties of *Oenothera,* and that they do not furnish evidence for the kind of conclusions that were drawn by de Vries. But to Morgan they seemed to offer a means of escape from what seemed to him the sterile and somewhat teleological speculations of the extreme advocates of natural selection. This remained with him in later years; he could be persuaded that selection can in fact operate through the sorting out of numerous modifying genes, and that there is nothing mysterious or teleological about the process of natural selection—but it was always a point of view with which he was basically dissatisfied.

Morgan began work on *Drosophila* in an attempt to induce mutations; but before he took up that material he had already begun his strictly genetic work, using mice (beginning in 1908) and rats (1909). He was at first quite critical of parts of the Mendelian interpretation, beginning in 1905 with his questioning of the "purity of the germ cells"—i.e., of the principle of segregation. As late as 1909 he wrote: "In the modern interpretation of Mendelism, facts are being transformed into factors at a rapid rate." His argument here was that the interpretation was "preformationist," whereas he felt that an "epigenetic" interpretation was more hopeful. The point seems to have been that he felt the Mendelian factors to be arbitrary

inventions, made up to fit the facts, with no independent evidence for their existence, and not capable of experimental demonstration. One may suspect that he was influenced by his negative reaction to the highly speculative scheme of heredity developed by Weismann. It was characteristic of the man that these reservations about the reality of the genes as discrete and sharply separable units were quickly and completely discarded as soon as he became more familiar with the experimental results.

Morgan's first paper on *Drosophila* appeared in 1910. *Drosophila* seems to have been bred as a laboratory animal for the first time by C. M. Woodworth, who was later Professor of Entomology at the University of California. In the academic year 1900–1901 Woodworth was a student at Harvard University. He had cultures of *Drosophila* breeding in the laboratory, and called the attention of W. E. Castle to its availability as a convenient object for breeding experiments. Castle began experiments on the effects of inbreeding, ultimately published in 1906 (Castle, Carpenter, Clark, Mast, and Barrows, *Proc. Amer. Acad. Arts and Sci.*, 41:729–86). Meanwhile the material had been used for behavioral studies in the Harvard laboratory by Carpenter, whose 1905 paper (*Amer. Nat.*, 39:157–71) marks the beginning of the published experimental work on *Drosophila.*

It has usually been stated that Morgan got his original cultures of *Drosophila* from F. E. Lutz, who was at the Carnegie Laboratory at Cold Spring Harbor from 1904 to 1909, and later at the American Museum of Natural History. Lutz worked with *Drosophila* at least as early as 1907; and both he and Morgan have indicated in print that Morgan got his original material from him. However, Dr. F. Payne (in a personal communication) questions this. Payne was a graduate student at Columbia from 1907 to 1909, and during that time undertook experiments that involved breeding *Drosophila* in the dark (published 1910 and 1911, *Biol. Bull.*, vols. 18 and 21). These experiments were begun in October, 1907. He reports that Morgan was very insistent that he collect the beginning strains him-

self by exposing fermenting fruit, rather than by getting cultures from Lutz. It may be noted that Quackenbush also bred *Drosophila* in the Columbia laboratory, and that it appears from his paper (1910, *Science,* n.s., 32:183) that his strains stemmed from collections made in 1908 at Woods Hole. It may also be pointed out that it was evidently common knowledge at this time that *Drosophila* could readily be collected from decaying fruit and used to start laboratory cultures. Moenkhaus (1911, *Jour. Morphol.,* 22) used material that he had himself collected in Indiana, and he stated that these experiments were begun in 1903. (It may be noted that Payne had taken his A.B. and A.M. degrees at Indiana University, where Moenkhaus was working, before he came to Columbia.) Stevens (1910, *Jour. Exper. Zool.,* 5), in her account of the chromosomes of *Drosophila melanogaster* (then known as *D. ampelophila*) stated that she had bred the species in the Bryn Mawr laboratory in the winter of 1906–1907, but did not state how she obtained the material. Lutz (1911, Carnegie Inst. Washington, Publ. 143) stated that his experiments were begun at least as early as 1907, with wild-caught material. His reports in the *Carnegie Year Books* suggest that the work was in fact begun in 1907.

It is not clear when Morgan himself began work with *Drosophila.* We have seen that Payne, in his laboratory, began in 1907 and kept cultures going into 1909, and that Quackenbush worked with cultures established in the summer of 1908. Morgan's first paper on the material was read before the Society for Experimental Biology and Medicine on May 18, 1910. This first paper reports on the original white-eyed mutant and the F_1 obtained from him; in July, 1910, appeared the paper demonstrating the sex-linked inheritance of white eyes—the first of the major discoveries made with *Drosophila.* The July paper says that the original white-eyed male appeared "in a pedigree culture of *Drosophila* which had been running for nearly a year." This shows that Morgan had been rearing *Drosophila* at least since the summer of 1909.

Morgan stated several times (in personal communications) that he

began work with *Drosophila* in the hope of inducing mutations. He used "wide ranges of temperature, salts, sugars, acids, alkalis," and radium and X rays. It is now known that the two latter should have been effective, but the techniques for the detection of mutations were inadequate, and the few that were found after exposure to radium were attributed to chance rather than to the treatment. Mutations were found, but the conclusion was that they were not induced by the treatments used. It appears from the first paper mentioned above that selection (for a dark thoracic pattern) was also carried on in the very early experiments.

The cytological studies on the sex-chromosomes, leading to the discovery of the X-chromosome mechanism of sex determination (suggested by McClung in 1901, corrected and demonstrated by Stevens and by Wilson in 1905), had indicated the male as the heterozygous sex in several orders of insects (Orthoptera, Heteroptera, Homoptera, Coleoptera, Diptera); whereas the genetic data on sex-linkage (beginning with Doncaster in 1906) had indicated the female as the heterozygous sex in Lepidoptera and also in canaries and in fowls. Both results were thus known in enough forms to suggest that they were generally applicable—and yet they were flatly contradictory. It was against this background that Morgan's discovery of sex-linkage in *Drosophila* was made in 1910. Here was a case, in every way similar to those known in birds and moths—but here the male was the heterozygous sex, and this was in a group in which Stevens had already shown that the male was the heterozygous sex as judged by the chromosome picture.[1] This was a major step in the development of the chromosome theory of inheritance—

[1] It was apparent from the published pedigrees that color-blindness in man "follows the same scheme as does white eyes in my flies" (Morgan, *Amer. Nat.*, Feb. 1911, p. 77). This apparently was the first definite specification of sex-linkage of the *Drosophila* type in man, although an equally brief passage by Wilson (June, 1911, *Arch. mikr. Anat.*, 77:249) has recently been cited. It seems clear that both Morgan and Wilson understood the point. It is now scarcely possible to decide who should be given priority—and one may be certain that neither of them was concerned about priority at the time.

and in a few months Morgan followed it with another major step.

New mutant types kept appearing in his cultures, and a second sex-linked one (now known as "rudimentary") was soon found. Here, then, were two separate mutant types, one with white eyes and the other with rudimentary wings, and according to the chromosome theory each of the genes concerned should be in the X chromosome. On crossing the two strains and rearing an F_2 generation, Morgan found that recombination occurred in the F_1 female that was heterozygous for both genes. As he saw, this indicated that there was some sort of exchange of parts between homologous chromosomes. There had been speculations that this might occur, and Janssens had presented cytological evidence indicating to him that it did in fact occur. This cytological evidence was not conclusive, and the idea was not generally accepted—although it was becoming clear that only in some such way as this could the chromosome interpretation of Mendelian inheritance be saved. This crucial experiment of Morgan's (reported at a meeting of the Society for Experimental Biology and Medicine on October 19, 1910) was thus a great step forward.

White and rudimentary happen to lie far apart in the X chromosome, with the result that it was not apparent in this first cross that they were linked—i.e., that they did not segregate independently in the doubly heterozygous female. But in 1911 cases of linkage had been recognized—most obvious in the relation between yellow body and white eyes—and Morgan then laid down the essence of the modern chromosome theory of heredity. The basis of linkage is nearness together in the chromosomes, and recombination between linked genes is due to exchange of parts between homologous chromosomes in some such way as that suggested by Janssens.

In the winter of 1910–1911 Morgan took C. B. Bridges and the writer—both then undergraduates— into his laboratory, and gave us desks in what came to be known as the "fly-room." This was a rather small room, with eight desks crowded into it, in which the three of us reared *Drosophila* for the next seventeen years. There was a steady stream of other students using the room also—rarely were

there fewer than five people working there at any one time. The post-doctoral foreign students who came to Columbia to work on *Drosophila* were regularly given desks here—e.g., O. L. Mohr, H. Nachtsheim, C. Stern, G. Bonnier, T. Komai, E. Gabritschevsky, T. Olbrycht, A. Zulueta, Y. Imai, T. Dobzhansky. In addition there were, at one time or another, F. N. Duncan, E. Cattell (later Mrs. H. J. Bagg), Mrs. T. H. Morgan, E. Altenburg, J. S. Dexter, A. Weinstein, J. W. Gowen, D. E. Lancefield, and E. G. Anderson. Others, who did not have desks in the "fly-room," but worked actively with the group and were often in and out, are too numerous to mention individually—but among them H. J. Muller must be especially indicated, since his share in the early developments was especially important.

This group worked as a unit. Each carried on his own experiments, but each knew exactly what the others were doing, and each new result was freely discussed. There was little attention paid to priority or to the source of new ideas or new interpretations. What mattered was to get ahead with the work. There was much to be done; there were many new ideas to be tested, and many new experimental techniques to be developed. There can have been few times and places in scientific laboratories with such an atmosphere of excitement and with such a record of sustained enthusiasm. This was due in large part to Morgan's own attitude, compounded of enthusiasm combined with a strong critical sense, generosity, open-mindedness, and a remarkable sense of humor. No small part of the success of the undertaking was due also to Wilson's unfailing support and appreciation of the work—a matter of importance partly because he was head of the department.

Because of the close cooperation in the work it is very difficult to trace the individual contributions to the developments in this period.[2] But in 1915 there appeared *The Mechanism of Mendelian Heredity,*

[2] This statement is not to be taken as applying to the conclusions described above as having been reached by 1911. These were certainly due to Morgan and not to the newly formed group.

by Morgan, Sturtevant, Muller, and Bridges. This was the first serious attempt to interpret the whole field of genetics in terms of the chromosome theory. It was a landmark in the history of the subject, for all significant later developments have taken that theory for granted.

In 1915 Morgan obtained a grant from the Carnegie Institution of Washington for the support of the *Drosophila* work; this grant was continued until his death. Part of it was used to support the maintenance of the living stocks of mutant types, which had become—and still remains—a time-consuming job requiring careful and technically trained workers. The rest of the grant was used to support Bridges and the writer (and, later, J. Schultz) as full-time assistants. What this meant was that we had research positions. Morgan did not direct our work. This was characteristic; he did his own work, and had no desire to develop a group working under his direction. The same attitude was evident in his relations to graduate students; he rarely assigned problems—the student was expected to find his own problems—and he did not lay out the approach to problems in any detail, though he was always ready to talk to a student about his work. We referred to Morgan as "The Boss;" but this was a term of affection and respect, not at all intended to imply that he was a taskmaster.

During the Columbia period the whole group regularly moved to Woods Hole each summer—except for the summers of 1920 and 1921, and the intervening academic year, which were spent in California (at the Hopkins Marine Station, Pacific Grove, at Stanford University, and at the University of California, Berkeley). The *Drosophila* cultures were shipped in barrels, and experiments were never interrupted for these summer moves. Morgan always had other experiments under way—with chickens, pigeons, mice, rats, or plants—and this material was carried by hand on the Fall River Line. At Woods Hole, Morgan himself always carried on some experiments with marine organisms, even while he was actively working with *Drosophila.*

During Morgan's later years at Columbia his own experiments with *Drosophila* gradually decreased in number, and after the move to Pasadena in 1928 they practically ceased. He remained very active in the discussions of the work, and in his support and encouragement of the rest of the group. But his own work—which never ceased—came to be more and more with other material and other problems.

To this period belongs a series of other types of work. The earlier studies of experimental embryology and of self-sterility in *Ciona* were continued at Woods Hole, and later also at Corona del Mar. In regeneration there was the work on fiddler crabs, which resulted in a solution of the problem of why the males have one large claw and a smaller mate, the "right- and left-handed" specimens being equally numerous. Here also came the experiments on the inheritance of the number of tail feathers in pigeons, and the important studies on the inheritance of hen-feathering in fowls and the effects of castration on hen-feathering. There were also numerous projects that did not yield published results. Morgan at one time or another collected and studied numerous strains of the plants *Coleus, Verbena,* and *Calochortus.* He also studied the Bidder's organ of the toad, the seasonally developed secondary sexual characters of the salamander *Triturus,* regeneration of the arms of brittle stars, crosses between different geographical races of deer mice, and rapid changes in color of the living "goldbug" (*Coptocycla*), and other questions with a wide variety of organisms.

Morgan was a good naturalist. He knew a surprising number of animals, and knew how and where to collect them, and he was remarkably skillful at keeping them alive and in good condition in the laboratory. I have made up a list of the various forms on which he published results. There are over fifty kinds of animals and one plant (burdock) on the list, which reads in part as follows: Protozoa (*Stentor*), coelenterates (*Gonionemus, Tubularia,* ctenophores, etc.), flatworms (both land and fresh-water), nemerteans, annelids (earthworms and marine forms), gephyreans, Crustacea (crabs,

crayfish), insects (phylloxerans and aphids, *Drosophila*), pycnogonids, mollusks (gastropods and bivalves), echinoderms (sea urchins, sand dollars, starfish), ascidians, *Balanoglossus, Amphioxus,* teleost fishes, salamanders, frogs, toads, birds (pigeons, peafowl, chickens, phalarope), mammals (mice, rats).

He was inclined to use simple techniques and equipment. The early *Drosophila* cultures were reared in a miscellaneous assortment of milk bottles, that were accumulated by various more or less unorthodox methods. It was customary to put a piece of paper in each culture bottle, and Morgan was very likely to use for this purpose the envelopes in which his current correspondence came. The flies were examined with hand lenses. He was aware of the necessity of elaborate and expensive equipment in much of modern experimental biology; but it was always somewhat difficult for him to support requests for such equipment. This was in line with his usual policy in money matters; when his own pocket was involved he was very generous, and many a student was helped financially by him (though he did not like this to be known); but he was very saving—sometimes it seemed almost miserly—when the source was institutional. He always tried to stay as far as he could under any budget that he administered, and was reluctant to ask for an increased budget.

Morgan was the recipient of many honors and awards, including the Darwin Medal (1924) and the Copley Medal (1939) of the Royal Society, and the Nobel Prize in Medicine (1933). He was a member of many scientific societies, including the Royal Society (Foreign Member), and the American Philosophical Society. He served as president of the following: American Morphological Society (1900), American Society of Naturalists (1909), Society for Experimental Biology and Medicine (1910–1912), National Academy of Sciences (1927–1931), American Association for the Advancement of Science (1930), Sixth International Genetics Congress (1932).

Morgan was married in 1904 to Lilian V. Sampson, who survived him. There were four children, who also survived him: Howard K.

Morgan, Mrs. Douglas Whitaker, Mrs. Henry W. Scherp, and Dr. Isabel M. Morgan (now Mrs. Joseph D. Mountain). He died at Pasadena, California, on December 4, 1945.

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KEY TO ABBREVIATIONS

Acad. Nat. Sci. Phila. Jour.=Journal of the Academy of Natural Sciences of Philadelphia
Amer. Breeders' Assn. Rep.=American Breeders' Association Reports
Amer. Jour. Physiol.=American Journal of Physiology
Amer. Jour. Psychol.=American Journal of Psychology
Amer. Med.=American Medicine
Amer. Med. Assn. Jour.=Journal of the American Medical Association
Amer. Nat.=The American Naturalist
Amer. Phil. Soc. Proc.=Proceedings of the American Philosophical Society
Anat. Anz.=Anatomischer Anzeiger
Anat. Rec.=The Anatomical Record
Arch. Entw. Mech. Org.=Archiv für Entwicklungsmechanik der Organismen
Arch. Zellforsch.=Archiv für Zellforschung
Bibliogr. Genet.=Bibliographia Genetica
Biol. Bull.=Biological Bulletin
Biol. Zentralblatt=Biologisches Zentralblatt
Calif. Inst. Tech. Bull.=Bulletin of the California Institute of Technology
Carnegie Inst. Wash. Year Book=Carnegie Institution of Washington Year Book
Columbia Univ. Biol. Ser.=Columbia University Biological Series
Encyc. Brit.=Encyclopaedia Britannica
Ent. Soc. Amer. Annals=Annals Entomological Society of America
Franklin Inst. Jour.=The Journal of the Franklin Institute
Harper's Mag.=Harper's Magazine
Johns Hopkins Univ. Circ.=Johns Hopkins University Circulars
Johns Hopkins Univ. Stud. Biol. Lab.=Studies from the Biological Laboratory of the Johns Hopkins University
Jour. Exp. Zool.=The Journal of Experimental Zoölogy
Jour. Gen. Physiol.=The Journal of General Physiology
Jour. Hered.=The Journal of Heredity
Jour. Morph.=Journal of Morphology
Jour. Phil. Psych. Sci. Meth.=The Journal of Philosophy, Psychology and Scientific Methods
Linnean Soc. Lond. Proc.=Proceedings of the Linnean Society of London
Med. News=Medical News
Nat. Acad. Sci. Biog. Mem.=National Academy of Sciences Biographical Memoirs
Nat. Acad. Sci. Proc.=Proceedings of the National Academy of Sciences
N. Y. Acad. Sci. Annals=Annals of the New York Academy of Sciences
Physiol. Rev.=Physiological Reviews
Pop. Sci. Mo.=Popular Science Monthly

Quart. Jour. Micr. Sci.=The Quarterly Journal of Microscopical Science
Quart. Rev. Biol.=The Quarterly Review of Biology
Roy. Soc. Lond. Obit. Not.=The Royal Society of London, Obituary Notices
Roy. Soc. Lond. Proc.=Proceedings of the Royal Society of London
Sci. Mo.=The Scientific Monthly
Smithsonian Inst. Ann. Rep.=Smithsonian Institution Annual Report
Soc. Exp. Biol. Med. Proc.=Proceedings of the Society for Experimental Biology and Medicine
Torrey Bot. Club Bull.=Bulletin of the Torrey Botanical Club
Yale Rev.=The Yale Review
Zeit. indukt. Abstamm.-u. Vererblehre.=Zeitschrift für induktive Abstammungs-und Vererbungslehre
Zool. Anz.=Zoologischen Anzeiger
Zool. Bull.=Zoological Bulletin

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