



The Thomas Hunt Morgan Era in Biology

by Judith R. Goodstein

This story of the genesis of biology at Caltech is excerpted from Millikan's School: A History of the California Institute of Technology (© Judith R. Goodstein) and is reprinted here with permission of the publisher, W. W. Norton & Company. Probably no one was in a better position to write Caltech's history than Judith Goodstein, who, since becoming the Institute's first archivist in 1968, has had an inside track on learning what went on when. In the years since, she has built the archives, now housed in expanded new facilities in the Beckman Institute, into a notable resource in science history—and also knows where all the bodies are buried. Research for the book, which appropriately appears in time for Caltech's Centennial, was supported by the Haynes Foundation. In addition to her post as archivist, Goodstein has also been a faculty associate since 1982 and registrar since 1989. She earned her BA from Brooklyn College in 1960 and PhD from the University of Washington in 1969. Millikan's School will be available in bookstores in October or may be ordered from the publisher with the coupon on the back cover.

Thomas Hunt Morgan, with flies, at Columbia University in 1917.

The establishment of a Department of Biology, rather than the traditional departments of Botany and Zoology, calls for a word of explanation. It is with a desire to lay emphasis on the fundamental principles underlying the life processes in animals and plants that an effort will be made to bring together, in a single group, men whose common interests are in the discovery of the unity of the phenomena of living organisms rather than in the investigation of their manifold diversities.

-THOMAS HUNT MORGAN, 1927

Why did Caltech officials pursue a biologist so near retirement to establish the school's division of biology?

The biochemist Henry Borsook liked to tell about a conversation Thomas Hunt Morgan had with the physicist Albert Einstein, a campus visitor in the early thirties. At a point in the conversation, Einstein supposedly asked, "What in hell are you doing in a place like this?" "The future of biology rests in the application of the methods and ideas of physics, chemistry, and mathematics," replied Morgan. The physicist persisted. "Do you think you will ever be able to explain in terms of chemistry or physics so important a biological phenomenon as first love?" "What did you say to that one?" Borsook asked Morgan afterward. "I tried to explain something about the connection between sense organs and the brain and hormones." "You didn't believe that yourself, did you?" Borsook asked. "No," said Morgan, "but I had to say something to him."

What he "had to say" says a lot about his plans, however. Thomas Hunt Morgan was 62 when he came to Caltech in 1928. By then, he had earned a worldwide reputation as a remarkable teacher, a clear writer, and an impressive researcher. In 1933, he would win the Nobel Prize for his discovery of the chromosomal mechanism by which character traits are passed on from parent to offspring through the interaction of genes.

All of that work had been accomplished in one room at Columbia University that held a bunch of bananas hanging in the corner and eight desks crammed into a space measuring 16 feet by 23 feet. In the fly room, as it was known, Morgan had elevated the lowly fruit fly, the *Drosophila*

Contributing to the squalor was Morgan's habit of squashing his flies (after he'd finished counting them) on his counting plate, which he left unwashed on his desk.



melanogaster, into the most famous experimental organism in the world.

Why did Caltech officials pursue a biologist so near retirement to establish the school's division of biology? The answer to the question begins with the ways and means of Morgan's *Drosophila* group at Columbia.

According to the Russian geneticist Theodosius Dobzhansky, Morgan ran the fly room by his own rules. Traveling on a Rockefeller-financed International Education Board fellowship, Dobzhansky in 1927 arrived in New York from Leningrad thinking that Morgan was "just next to God" and his laboratory "close to Heaven." To his dismay, he found what he called "a very small, poorly equipped, and positively filthy" laboratory, run by a man obsessed by "pathological stinginess." The Morgan operation made Dobzhansky's laboratory facilities back home in Russia look very good in comparison. Morgan's longtime co-workers Calvin B. Bridges and Alfred H. Sturtevant sat and worked in the same room, along with graduate students, postdoctoral fellows, like Dobzhansky, and assorted visitors, ranging from Yoshitaka Imai, a Japanese geneticist, to Alexander Weinstein, a recent fly-room PhD. Often, all the desks were occupied, including the two reserved for guests.

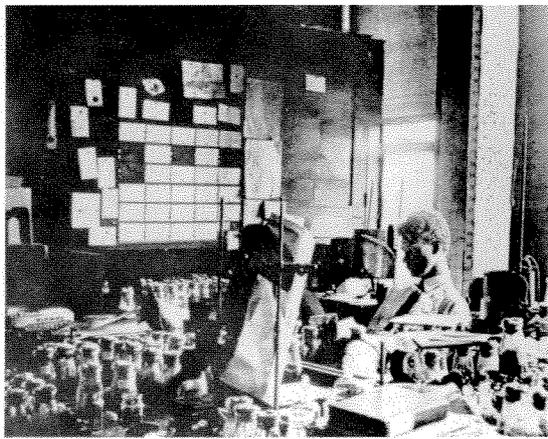
Cleanliness was unknown here. The workers competed for space with cockroaches that reproduced in awesome numbers. Contributing to the squalor was Morgan's habit of squashing his flies (after he'd finished counting them) on his counting plate, which he left unwashed on his desk. As the pile of lifeless flies grew, so did the

mold it attracted. Along one wall stood a kitchen table used by the student hired to wash bottles and prepare fly food. This area of the room was Morgan's only concession to hygiene.

Bridges, an unremitting tinkerer, sat at a desk covered with odd-looking pieces of apparatus he had made from items at hand. Capable of long periods of routine work and intense "fits and spurts" of ingenuity, Bridges gradually overhauled Morgan's primitive laboratory techniques: he designed a binocular microscope (most workers used a hand lens to examine flies; Morgan used a jeweler's loupe), invented new ways to etherize flies, developed new incubators, improved culture bottles, and whipped up alternative foods for flies.

Bridges had his faults, but jealousy, according to Morgan, was not one of them: "In fact, one of his most admirable traits was his freedom from priority claims of any kind." Morgan first met Bridges in 1909 when he took Morgan's courses in general biology and embryology. Hoping to find research work, Bridges put himself through Columbia on scholarships and odd jobs. Morgan hired him in 1910 to wash glassware, but gave him a desk and promoted him to the job of breeding flies and looking for mutants after Bridges spotted a fly with bright eyes in a dirty bottle. Bridges excelled at finding new mutants, which he "immediately announced." This skill (Sturtevant insisted he "had the best 'eye' for new types") paid off in 1916, when he published, in the first issue of *Genetics*, a detailed paper dealing with flies that had extra and missing chromosomes. Not only could Bridges explain

Left: Morgan's fly-room crew didn't flinch from eating among their specimens. Here a lunch celebrates the return of Sturtevant (front left, holding beer bottle and cigar) from the Army in 1919. Clockwise around the table from *Pithecanthropos* wearing Sturtevant's old uniform are Muller, Morgan, Lutz, Mohr, Huettner, Schrader, Anderson, Weinstein, Dellinger, and Bridges (with book). Right: Calvin Bridges, who began his career with Morgan as a bottle washer, was promoted to the job of breeding flies, and given a desk, which he covered with hand-made pieces of apparatus as well as bottles of flies.



these exceptions; he provided convincing proof of the chromosome theory of heredity. Bridges delighted in building up and studying the *Drosophila* stocks and mapping the position of mutant genes in each chromosome. He "was so good at this that he contributed many more mutants than did the rest of us," Sturtevant once admitted.

Sturtevant owed his desk in Morgan's laboratory to a childhood passion for recording the pedigrees of horses. A book on Mendelism that he read as a college sophomore opened new worlds, he later wrote, "for I could see that the principles could be applied to the inheritance of colors in the horses whose pedigrees I knew so well." He wrote up an account of his findings and submitted it to Morgan, his biology teacher. Much impressed, Morgan urged the young man to publish the account, which he did in due course. Sturtevant always believed this was the reason why in the fall of 1910 Morgan invited him into the laboratory and gave him a desk and some *Drosophila* to work on. By that time, Sturtevant knew for sure that he wanted to do genetics.

Sturtevant was the bookish one. Piles of books and reprints, stacked high, covered his desk. In the course of cleaning the room one summer, so the story goes, a workman found it necessary to rearrange some of Sturtevant's papers, uncovering a shriveled mouse.

It didn't take Dobzhansky long to discover what made the fly room tick. He later told an interviewer, "So this one room had six people working in it, a situation which doubtless had a

great many advantages, particularly for a foreign guest. You can ask anyone a question you wish to enlighten yourself on any problem which arises. You also listen to the conversation between the people. As far as training is concerned, nothing better can really be imagined." Jammed with people and paraphernalia, Morgan's laboratory, in short, was an ideal training ground for budding experimental biologists, good for everything from selecting projects on which to base PhD research to testing new techniques and analyzing experimental data.

Sturtevant tells a similar story. "Everybody did his own experiments with little or no supervision," he wrote on one occasion, "but each new result was freely discussed by the group." Morgan's *Drosophila* group did not go in for organized coffee breaks, nor did it set aside a certain time of the day for laboratory discussion. "Instead," recalled Sturtevant, "we discussed, planned, and argued—all day every day." He added, "I've sometimes wondered how any work got done, with the amount of talk that went on." But Morgan did have one cardinal rule: you had to pick your own research topic.

To do otherwise could be academically fatal, as one aspiring *Drosophila* geneticist, Edgar Altenburg, discovered. Having been given desk space in the fly room, Altenburg asked Morgan to suggest a fruit fly problem for graduate work. Close by Morgan's office was the aquarium room. He took Altenburg there, dipped his finger in a tank of stagnant water, and held it up to the light. "There are a lot of *Daphnia* in here," he said to Altenburg. "Why don't you work on them?" Humiliated by the experience, Altenburg quickly switched to plant genetics.

Dobzhansky nearly made the same mistake. Once unpacked, he wasted no time in asking Morgan "to suggest a topic." "After all I was coming from afar, and although I knew what they had published earlier, I didn't know what they were doing at the time, less still . . . what they were planning to do" in the future, he said, adding, "I did not know how foolish that was." At first, Morgan brushed him off with a joke. When Dobzhansky asked him again for something to read, "the Boss" reached into his desk, took out a reprint dealing with the effects of temperature on the development of *Drosophila* (a subject of no interest to the Russian biologist), handed it over to the newcomer, and turned away. A zoologist by training and a geneticist with an expert's knowledge of the natural variations in lady beetles and with a keen desire to study problems of evolution, Dobzhansky quickly made his peace with Morgan's managerial style.

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Morgan “thought that everybody should work on the problem which he sees fit,” and Dobzhansky knew he was “perfectly capable of choosing” what he wanted to do in Morgan’s laboratory. It was a perfect fit.

Morgan was a southerner, born in Lexington, Kentucky, in 1866. His maternal great-grandfather was Francis Scott Key, author of “The Star-Spangled Banner,” and his father’s brother, John Hunt Morgan, had been a notorious Confederate general. Preferring natural history to politics, Thomas Hunt Morgan in his youth combed the backwoods and byways of rural Kentucky and western Maryland, collecting fauna and fossils. One summer, he earned his keep working for the U.S. Geological Survey, tracing coal seams. After graduating in 1886 with a BS in zoology from the University of Kentucky, Morgan spent the summer months working in a marine biological laboratory at Annisquam, Massachusetts, and then enrolled as a graduate student at Johns Hopkins, earning his PhD—his dissertation involved studying different species of sea spiders—in 1890. By the time Morgan joined the Columbia University faculty, in 1904, he was known far and wide for his work in experimental embryology and regeneration.

But the studies that brought lasting fame to Morgan were those connected with *Drosophila*. He had begun breeding fruit flies in 1908 in an effort to determine what role—if any—chromosomes played in the transmission of physical traits from one generation to the next.

Morgan began his research with *Drosophila* just as biologists were beginning to appreciate for the first time the long-neglected findings of the 19th-century Austrian monk Gregor Mendel. Mendel’s genetic experiments on plant hybrids, published as a short report in 1866, led him to conclude that traits in garden peas such as seed shape, pod color, and plant-stem length were determined by fundamental units of inheritance, which he called “elements.” Alternative forms existed for every hereditary trait as well: round seeds and wrinkled; green pods and yellow; short stems and long—one of which always stood out decisively in the pea plant. Today every school-child knows how Mendel, toiling alone in his monastery’s vegetable patch, theorized the existence of dominant and recessive traits, through repeated crossings of innumerable pea plants. Yet Mendel’s work was ignored and forgotten until 1900, when it was rediscovered independently by three botanists.

Nevertheless, many researchers, Morgan included, were initially reluctant to accept the notion that Mendel’s “elements” (the term *gene*

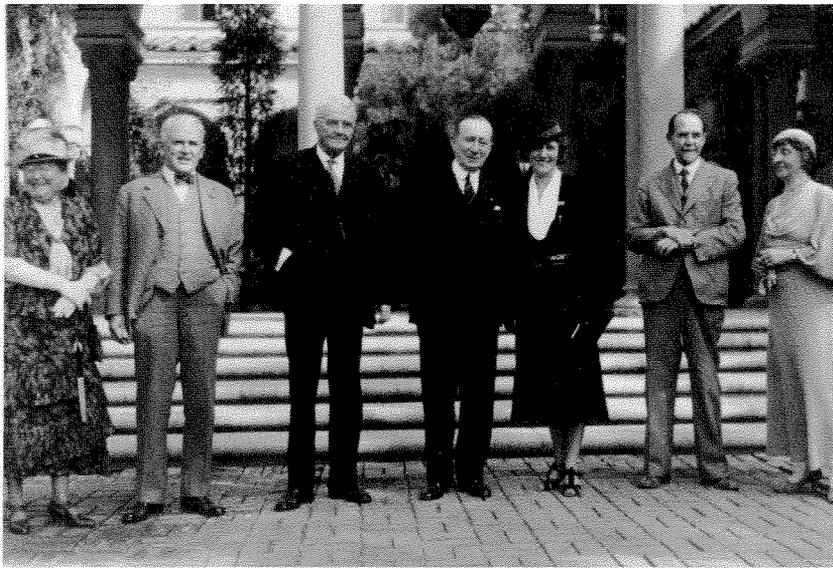
was coined only in 1909) were parts of chromosomes, unless they had evidence rooted not in statistical studies of monastery peas but rather in observable laboratory phenomena. Thus, the question facing Morgan and like-minded colleagues was twofold: First, how far could Mendel’s work be taken as an authentic description of heredity in organisms? Second, how correct was the theory that chromosomes were indeed the physical basis of inheritance? The validity of the chromosome theory took Calvin Bridges—first Morgan’s student and later his collaborator—only a few years (1914-16) to establish. The evidence needed to convince Morgan that Mendel’s “genes” were indeed carried on chromosomes took longer to accumulate.

Of this period (1910-11) in Morgan’s scientific life, the biologist John Moore has remarked, “Whereas it was difficult for Morgan to accept the data of others in suggesting that genes are parts of chromosomes, it was not nearly so difficult when his own data showed the same thing.” In the end, Morgan’s studies with *Drosophila* convinced him of the necessity of associating specific hereditary characteristics with specific chromosomes. He equated Mendel’s elements of heredity with invisible genes at known locations in visible chromosomes and in the process created a new science of genetics.

Fruit flies have been called the geneticist’s best friend. They reach maturity quickly, reproduce themselves frequently, and are inexpensive to rear. Shortly after he had begun research on *Drosophila*, in the autumn of 1910, Morgan recruited Bridges and Sturtevant, both then still undergraduates, to help with the fly work. Two years later, he brought a graduate student, the physiologist Hermann J. Muller, into the fold, an association that was to have less happy consequences. Muller was a good scientific choice—his work was clearly outstanding—but he and Morgan made a poor match in temperament. From the first, Muller’s relations with the group, and with Morgan in particular, were strained. Part of the problem was the pecking order. Scientific decorum mattered a great deal to Muller, who came to feel that others in the fly room got credit for *his* ideas and experimental work. In conversations with the psychologist Anne Roe in the 1940s, Sturtevant testified that “Muller was a very essential part of that group,” adding, “We didn’t see eye to eye but I got a lot out of him.” By the time Morgan moved his laboratory, *Drosophila* stocks, and research group to Pasadena, in 1928, Muller had long since left Columbia and launched his own research team at

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On October 21, 1933, a luncheon at the Athenaeum hosted by Robert Millikan in honor of distinguished visitors Guglielmo Marconi, inventor of the wireless, and his wife (third and fourth from right) also turned into a celebration of Morgan's Nobel Prize, which had been announced the previous day. A pleased-looking Morgan stands second from right, next to Mrs. Millikan. Millikan, (second from left) is flanked by Mr. and Mrs. Allen Balch, who, in addition to financing the building of the Athenaeum, also gave \$1 million toward the biology laboratory that helped bring Morgan to Pasadena (although Kerckhoff got his name on it).



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the University of Texas in Austin, where he became the first geneticist to demonstrate that x rays cause mutations. Like Morgan, Muller eventually won the Nobel Prize, but the personal rift between the two was never entirely repaired.

The discovery that genes are arranged in a single line in chromosomes like beads strung together on a loose necklace was made by Sturtevant in 1911. At the time, he and Morgan had been talking about the meaning behind some diagrams by H. E. Castle of coat colors in rabbits. The diagrams, they decided, were meant to be a representation of the spatial relationships of the genes on a given chromosome. How nice it would be to figure out the geometrical relationship between genes and chromosomes! “I think I can do it,” Sturtevant told Morgan all of a sudden. “I suddenly realized,” he recalled 50 years later,

that the variations in strength of linkage, already attributed by Morgan to differences in the spatial separation of the genes, offered the possibility of determining sequences in the linear dimension of a chromosome. I went home and spent most of the night (to the neglect of my undergraduate homework) in producing the first chromosome map, which included the sex-linked genes *y*, *w*, *m*, and *r*, in the order and approximately the relative spacing that they still appear on the standard maps.

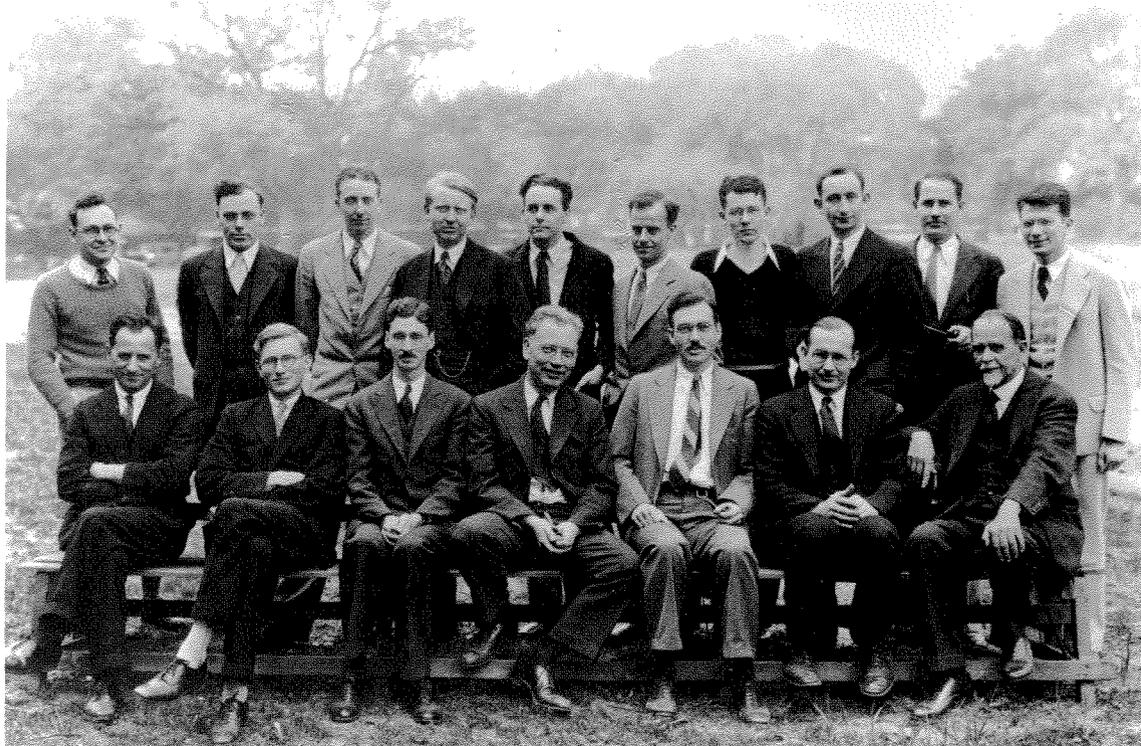
He published his results in 1913. Sturtevant later told an interviewer that the discovery of the linear arrangement was the most exciting thing he had ever done scientifically. He went on to

make other significant discoveries both at Columbia and at Caltech, but none came close to matching the thrill of his “first job on *Drosophila*.”

Two years later, Morgan, Sturtevant, Muller, and Bridges joined forces to produce the first textbook on *Drosophila* genetics, which they entitled *The Mechanism of Mendelian Heredity*. A landmark in the history of 20th-century biology, the volume quickly became the bible of the new science of genetics. In the hands of Morgan and his co-workers, the genetics of *Drosophila* involved a rigorous and experimental search for the secrets of life that lay sprinkled within the chromosomes of a tiny fly.

By this time, Morgan had largely turned his attention elsewhere. He left the day-to-day operations of the fly room in the care of his students, who were technical virtuosi of the first order. A great synthesizer, Morgan distilled their findings, popularized their work, and shouldered the responsibility for bringing their results to a wide, frequently nonscientific audience. In fact, by the time he left Columbia in 1928, Morgan could no longer follow in detail what his younger colleagues, Bridges and Sturtevant in particular, were doing.

This happens to scientists, even to the best of them. And it's often sad to observe. In Morgan's case, however, distance worked to his advantage. As one geneticist familiar with Morgan's working habits put it, “For Morgan himself the *Drosophila* work was only one aspect of a biologist's searching.” Professor of experimental zoology at Columbia for 24 years, Morgan in 1928 was still



In 1931 Caltech's Division of Biology included (front row, from left): H. Borsook, H. Dolk, H. Sims, A. H. Sturtevant, S. Emerson, H. Huffman, T. H. Morgan; (back row): H. Schott, C. Burnham, W. Lammerts, K. Lindström-Lang, E. Ellis, G. Keighley, J. Bonner, A. Tyler, G. W. Beadle, and J. Schultz. Missing from photo are E. Anderson, K. Belar, T. Dobzhansky, R. Emerson, and K. Thimann.

searching, as is plain from the following lines he wrote to George Ellery Hale, shortly after accepting the Caltech job:

... I am writing to you something of the ideas that are shaping themselves in my mind about the organization of our biological work.

Would it not be a good plan to think in terms of "The Biological Laboratories," rather than of a "Biological Department." This would allow greater freedom in giving each group an independent footing and allow greater flexibility in the future. As I have intimated to you, I think, I have no ambition to "boss the job," but rather to get together the best men available, to settle down to my own work, and then do all I can to coordinate and help matters forward along constructive lines.

Our program, when we get it going, should speak for itself. ... And, while I am anxious to emphasize the dynamic or physiological character of the work, I shall try to avoid the criticism that we are leaving the older and less important sides of biology in the background. This can best be done, perhaps, if we point out that we are not so much attempting to duplicate work that is being done well elsewhere, as in furnishing opportunities for the more advanced and less well developed lines of modern research.

Morgan's days of "the fly room" mentality were behind him. "Only through an exact knowledge of the chemical and physical changes taking place in development can we hope to raise the study of development to an exact science," Morgan told Caltech's elders in 1927, shortly after they had approached him about organizing

work in biology in Pasadena. "The best chance" for success, he indicated, would be "to put some physicists in the biological laboratory, and some biologists in the physical laboratory."

Morgan's prophetic remarks set the tone of biology at Caltech for the next half century. It was, for example, Caltech's physicist-turned-biologist, Max Delbrück, himself winner of the Nobel Prize in 1969, who helped lay the foundations of modern molecular biology and the brave new world that we've only begun to glimpse.

Morgan kept his word to Hale "to get together the best men available," starting with three he knew—Sturtevant, Bridges, and Dobzhansky. He also recruited as teaching fellows three graduate students from Columbia, including Albert Titlebaum. From the University of Michigan, he plucked Ernest Anderson and Sterling Emerson, both PhDs in plant genetics, but well versed in the genetics of animals as well. Anderson, 37, came as an associate professor of genetics; Emerson, 29, as an assistant professor. Another geneticist from Columbia, Alexander Weinstein, did not get to Caltech—in a way that says much about the school's early ways.

Weinstein, Morgan told Millikan in the spring of 1928, had been working in the fly room and had just successfully repeated Muller's use of x rays to induce mutations. If appointed to Caltech, he would continue the work in Pasadena and teach the introductory course in biology. Morgan was proposing to make Weinstein an assistant, perhaps even an associate, professor, at an annual starting salary of \$3,500. Emerson's starting salary was \$3,800 and Anderson's

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Morgan and Arie Haagen-Smit, who later pioneered studies in the chemical nature of smog and its sources, in 1938. Morgan had persuaded Haagen-Smit to come to Caltech as associate professor of bio-organic chemistry the previous year.

\$4,000. As professor of genetics, Sturtevant received \$6,500, placing him near the top end of the Caltech pay scale; Morgan was hoping to raise Sturtevant's salary to \$7,500. (As head of the new department of biology, Morgan himself made \$10,000, the same as Millikan and Noyes.)

A scientist "with distinct literary ability," broadly trained in biology, fluent in mathematics and physical chemistry, Weinstein ("a fine type, not aggressive") struck Morgan as the right man for the Caltech job. "I have hesitated a long time before bringing his name forward," Morgan admitted in his letter to the school's head, "but I think for the position proposed he is the most suitable man at present available."

No one on the faculty, save for members of the National Academy of Sciences, replied Millikan, made more than \$7,000 a year. In Sturtevant's case, Millikan agreed, Morgan might have to pay that much or more to get him, but he might first try less expensive inducements—paying traveling costs to meetings back east or moving expenses. Weinstein's case was scarcely different. Millikan had at least "three brilliant young men" in the assistant professor ranks, all making between \$3,000 and \$3,300. Offer him \$3,500, Millikan counseled, but then "give him a chance to match his pace to an associate professorship with these other men of about his age." In any case, he left all decisions about rank and salary in Morgan's hands.

Morgan did not change Sturtevant's starting salary. He offered Weinstein \$3,500 as an assistant professor, which the seasoned fly-room veteran refused, pointing out that Emerson, barely out of graduate school, was making more and that Anderson and Sturtevant, who were about his age, were getting higher faculty positions. Morgan bristled. "I . . . consider the matter finished, as I do not think we want to have a man who makes points like that," he informed Millikan by letter that May. Too cheeky perhaps for Morgan's taste, Weinstein went on to teach genetics at Minnesota, then branched out into zoology and the history of science at Johns Hopkins. He later taught physics at City College of New York and eventually wound up at Harvard.

Another possible appointment in biology was Leonor Michaelis, a prominent biophysicist at Johns Hopkins. Michaelis, however, had several strikes against him, according to Caltech's new biology head. One was his apparently pronounced ethnicity. In the same letter of 1928 to Millikan recounting his dealings with Weinstein, Morgan lamented that Michaelis already had "collected about himself a few young Jews." "He

In the genetics laboratory, the atmosphere of the original fly room was soon re-created.



himself is markedly Semitic," added Morgan. "I have my doubts whether we should want to start under all these conditions, and shall make no moves." Morgan recommended against hiring Michaelis. Fifty years later, Leonor Michaelis's daughter read the discussion about her father in the Caltech archives and said "it was shocking" to learn that the call never came because, as she put it, "he was a Jew." People, scientists included, rarely take the time to write shocking letters any more; they simply talk on the telephone instead.

Dobzhansky, who worked side by side with Morgan for many years, described him as a biologist with a razor-sharp mind, "a man of wide education which should have made him very broad, but curiously enough, did not." "In many ways," his Caltech colleague once recalled, "he was a very contradictory person." He'd had a number of Jewish co-workers at Columbia—Weinstein, Muller (he claimed one Jewish ancestor), Tyler (born Titlebaum, he changed it after moving to Pasadena)—and he brought many others to Caltech, including Henry Borsook, Jack Schultz, and Norman Horowitz, who many years later said,

The question of Morgan's alleged anti-Semitism bothers me. I was closer to him than most graduate students during 1936-39, because he and Tyler and I spent every weekend at the marine station. I never noticed any anti-Semitism whatsoever on his part. On the contrary, he was always nice to me, and I have always believed that it was he who got me a National Research Council Fellowship when I finished my PhD in 1939.

"But time and again he would make, especially when irritated, anti-Semitic remarks of the most crude sort," remembered Dobzhansky.

Morgan had a reputation for making outrageous remarks, for teasing those with different beliefs. "But he was never mean," insisted Sturtevant. Robert Millikan was often the butt of Morgan's gibes, for, unlike the atheist Morgan, Millikan was a pious Protestant. But Morgan's penchant for saying the wrong thing eventually caused an international flap in scientific circles. In 1934, Morgan went abroad, partly to pick up his Nobel Prize in Stockholm, partly to recruit new staff members. As Morgan had told a Rockefeller Foundation official beforehand, he wanted "to look over the ground at first hand and make sure that the men we have in mind are the kind we are looking for." While in London, Morgan attended an elegant reception hosted by the Royal Society. "He has announced to all who will listen," an eyewitness later reported, "that

the Rockefeller Foundation has given him money to secure the services of a physiologist. He is combing England and the Scandinavian countries to find one who is not Jewish, if possible." The informant added, "From the English reception of this announcement, I am inclined to believe that he will have difficulty in finding a first-rate Englishman who will be willing to go to Pasadena." Indeed, Morgan was unable to recruit anyone in England or Scotland. Just before sailing home, he hired a Dutchman, C. A. G. Wiersma, who evidently had the right pedigree. According to a Rockefeller official in Amsterdam, Morgan "gave somewhat the impression of being 'desperate.'"

In the fall of 1928, the founding members of Caltech's biology division assembled for the first time in Pasadena. Traveling by the Santa Fe Railway, Morgan and his wife, Lilian, also a biologist, left for Pasadena on September 6, 1928, after spending the summer, as always, at the Marine Biological Laboratory in Woods Hole, Massachusetts. Dobzhansky, his wife, and Miss Wallace, Morgan's illustrator and secretary, left Woods Hole and joined him in Pasadena several weeks later, carrying among them "the sacred flame," the *Drosophila* stocks. Morgan met them at the train station. Bridges turned up soon afterward. Emerson had gone fishing with his father-in-law in Canada meanwhile and arrived at the end of October, a month after the academic term had begun. Sturtevant's wife was expecting a baby, and Sturtevant "thought she had a right to be born in the East." They arrived two months late. Anderson was completing a research trip to Berlin and arrived even later, close to Christmas.

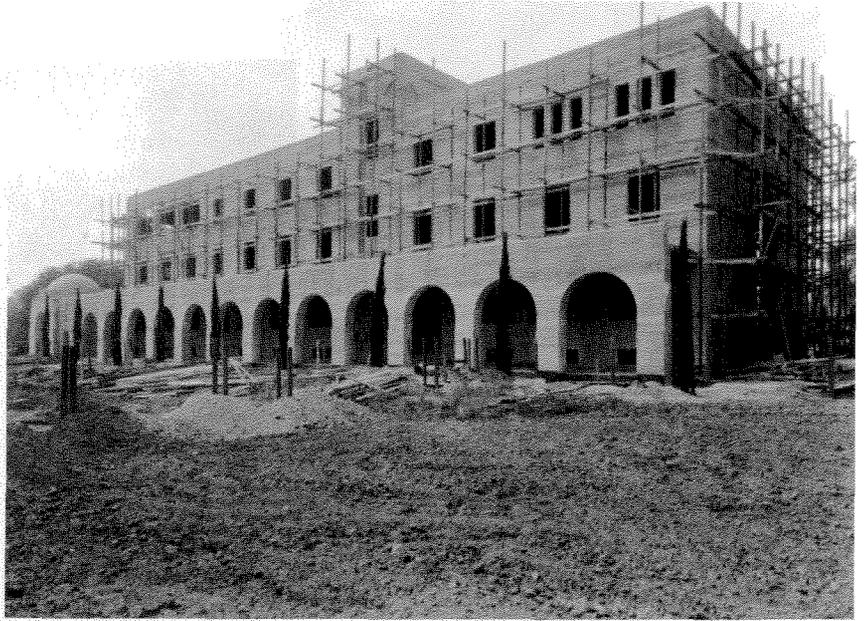
Finding the new biology building unfinished, Morgan and his group set up a makeshift laboratory in the chemistry building, in Arthur Noyes's office. By the time classes began, two rooms in Caltech's new Kerckhoff Laboratories of the Biological Sciences were ready for occupancy. Tucked away by itself in the northwest corner of the campus, the building was a brisk five-minute walk to the physics, chemistry, and engineering laboratories across the quadrangle. A student who took courses there in 1930 recalls that the building "was connected by a boardwalk to the rest of the campus. In the winter, the territory between Gates and Kerckhoff became a sea of mud, known generally on the campus as Lake Kerckhoff."

Caltech officials had promised the biologists that they would not have to teach any courses that first year. But under pressure from the undergraduates, they offered one—in beginning biology—in the spring term. Morgan and



Above: Russian geneticist Theodosius Dobzhansky, who joined Morgan at Columbia in 1927 and came with him to Caltech, enjoyed camping and often used the pursuit of biological specimens as an excuse to pursue his favorite pastime.

Above right: Kerckhoff Laboratory was still under construction when Morgan, his researchers, and his flies arrived in 1928. The sea of mud in front of it became known as Lake Kerckhoff.



Sturtevant divided up the lectures, while Anderson, Emerson, and Sturtevant ran the laboratory associated with it. Partial to Darwin, Morgan in his homework assignments often asked students to read a portion of his masterpiece, *The Origin of Species*, and to write a report on it.

In the genetics laboratory, the atmosphere of the original fly room was soon re-created. A long bench stood in front of the two windows. Dobzhansky and Sturtevant sat at opposite ends of it looking at their flies—Dobzhansky on the left, Sturtevant on the right. “The students sat in between and listened to the wise conversation and contributed to it when they could,” one former student remembers.

Intrigued by Muller’s x-ray work, Dobzhansky had used his time at Woods Hole during the summer to irradiate flies. He spent fall and winter in Kerckhoff studying the chromosomal aberrations caused by the x rays and arranging them on a chart, using genes as markers. “Just what I expected to see in chromosomes, I don’t remember,” Dobzhansky later told an interviewer, but he decided one day to look under a microscope at the rearrangements he had projected would be observed between the fly’s third and fourth chromosomes. Practiced in dissecting beetles, Dobzhansky removed the ovaries of a young female fly, embedded them in paraffin, and sectioned and stained them. It was a long, tedious process. He looked through the eyepiece. “Suddenly I saw an incredible thing,” he later recalled, “namely, I saw a chromosomal plate which had just one little dot . . . and a chromosome never seen before, a long rod, which clearly

meant that a piece of the third chromosome had become attached to the tiny fourth.” The ancient dream of geneticists—direct evidence of the serial order of genes on chromosomes—stared Dobzhansky in the face. “I don’t remember whether I emitted a loud yell,” he later said.

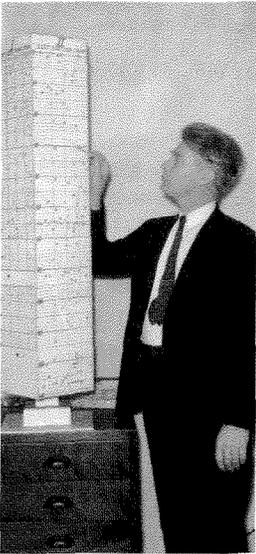
By spring 1929, Dobzhansky had produced the first cytological map of the fly’s long, rodlike third chromosome. To his joy, when he compared the linkage map, which summarized statistical data based on many genetic experiments, to the cytological map, he discovered that the two maps agreed with each other. The ability to predict the inheritance of certain characteristics, Morgan once said, justified the construction of genetic-linkage maps, “even if there were no other facts concerning the location of the genes.” Dobzhansky’s work in Kerckhoff Laboratory offered irrefutable, direct evidence of the correctness of Morgan’s classical theory.

Meanwhile, time was running out on Dobzhansky’s postgraduate fellowship. Morgan had succeeded in getting him a six-month extension, which meant he had to wind up his research and return home to the Soviet Union at the end of June 1929. One day, Morgan walked into the genetics laboratory and, according to Dobzhansky, “asked the question, ‘Dobzhansky’—or rather, he called me to the end of his days, he could not pronounce this name, which of course I don’t blame him, it’s a devil of a name—he called me ‘Dobershansky’—‘Would you like to join our staff as assistant professor?’” It took him no time at all to answer yes.

In educational matters, Morgan did not be-

Right: Morgan and Albert Tyler, then a grad student and later a member of the faculty, examine fertilized eggs of marine organisms at the Corona del Mar marine laboratory in 1931.

Left: Also in the early thirties, Calvin Bridges points out a mutant on his "totem pole," a map classifying mutations in a particular chromosome as "best, good, poor, dead" for the purpose of doing genetic experiments.



lieve in graduate courses; he believed in reading. But even in Morgan's day, graduate students took courses, whether required or not. Seminars abounded, including the general biology seminar each Tuesday night, which Morgan always attended (and at which he introduced the speaker).

In one of these seminars, in 1933, a visiting biologist reviewed a paper by two German researchers on the salivary-gland chromosomes of flies known as *Biblio*, or March flies, so named because they are commonly abundant in spring. The Germans had observed in the cell nuclei of the larval salivary glands rope-like structures, which they correctly interpreted as "giant chromosomes." A number of geneticists were in the audience that day, Morgan and Bridges included, but they did not get excited by the report. Their attitude changed overnight when Theophilus Painter, a geneticist at Texas, drew and published the first map of these chromosomes for *Drosophila* and pointed out how the banding pattern could be used to study the break points of any chromosomal rearrangements.

As Dobzhansky tells the story, Bridges showed up in his laboratory one morning just thereafter and said, "Dobzhansky, show me the salivary glands." Although he probably knew more about *Drosophila* than anyone else, Bridges had no experience in dissecting larval fruit flies. Indeed, he had never even seen the salivary glands. Dobzhansky dissected a larva and showed the results to his visitor. And Bridges jumped into the study of these giant chromosomes with a vengeance. He set about identifying and extend-

ing the number of visible bands of these chromosomes. He went on to produce a series of drawings that are still consulted by fly geneticists. "Bridges's map," the *Drosophila* whiz Edward Lewis remarked more than 50 years later, "is still a masterpiece."

Keen competition existed between the Caltech geneticists and Painter's research group at the University of Texas. In 1934, Painter wrote an indignant letter to the editor of the journal *Genetics*. According to Painter, the two groups were "in a sense competing," and the Texas group had already hit two "home runs": Muller's discovery of x-ray induced mutations, and Painter's own work on the salivary glands. But now he was upset that Bridges had reviewed his salivary-gland manuscript. (Did Morgan have a hand in this? he asked.) Worse still, Bridges's salivary-gland work was now "making a splurge in the newspapers"—the *New York Times* had sent a reporter to Cold Spring Harbor to cover Bridges's talk on his salivary-gland research—while his, Painter's, contributions had "been belittled." Painter's public howl strikes a familiar chord. It is not uncommon for scientists to believe that their work is underappreciated.

Painter's most pressing complaint, however, concerned a Science News Service press release about Bridges's work, which the magazine's editor had sent to Painter. From reading the marked-up copy, Painter could see that Bridges had corrected his estimate of the size of the salivary-gland chromosomes and that the new figures now agreed with Painter's—which had not yet been published. He felt that Bridges had

taken advantage of the situation. He wrote in his letter, "I do not intend to reflect in any way on Dr. Bridges. On the other hand, the men in . . . [our] laboratory are unwilling to allow competitors in our field to enjoy the privilege of examining our work a year prior to publication when we have no opportunity to see theirs."

"We are not interested in home runs," Morgan replied, after reading a copy of Painter's letter. As far as he, the dean of American biologists, was concerned, the two research groups were "cooperating," not competing. Far from admitting any wrongdoing, Morgan defended his group's honor, but held out a peace offering: articles submitted by Caltech would now be sent to Austin before publication. In a separate note to the editor, D. F. Jones, Morgan blamed Painter's "outburst" on Muller, noting, "[His] attitude has always been antagonistic to us . . . although he has generally managed to keep this under cover and we have consistently ignored it, treating him in the most friendly way, because we regarded his attitude as wrong and inexcusable." It is reported that Painter later mellowed in his view.

Painter's story bears telling because of Muller's experience several years later. At Caltech, Morgan had laid down the rule that getting papers published was an individual's responsibility, not the department's. But as Sterling Emerson once freely admitted, Morgan's group had no trouble getting him to submit their papers to *Science* and the *American Naturalist*, edited by J. McKeen Cattell, a personal friend. When Morgan submitted a colleague's paper, recalled Emerson, "it would come out in the next issue. It might be any time if you sent it in." Being friends of friends paid off, as Calvin Bridges discovered.

In 1936, Bridges was preparing a paper for *Drosophila* on the Bar gene, a spontaneously mutating gene that reduces the size of the fly's eye. As Bridges drew near the end, word reached the Caltech group that Muller was also working on this gene. Donald Poulson, a graduate student in the lab at the time, told an interviewer in 1978 what he remembered: "I don't know whether I should say anything about this, but I think it's current now—Dobzhansky had had a letter from Russia, from one of his friends, which said, 'Muller has solved the Bar story.'"

Morgan took matters in hand. Bridges's paper was submitted on February 21, to *Science*, and was published a week later. The habitually frugal Morgan, it seems, had wired the entire paper to the journal's editor. So much for Morgan's "cooperation" among *Drosophila* groups. Three months later, a special article by Muller on his own cytological analysis of the Bar gene appeared

in the same journal. Muller prefaced his technical remarks by calling "the attention of American readers . . . to the fact that essentially the same findings and interpretation" (presented in Bridges's paper) had already appeared in print in the Soviet Union under Muller's name and that of his two Soviet co-workers. In truth, rivalry is the handmaiden of science, and the quest to be first is a motivating force and a powerful stimulus to creative work. Good scientists are nearly always keen competitors.

Closer to home, Morgan made a magnanimous gesture when in October 1933 he received the Nobel Prize in physiology and medicine. From the proceeds of the prize, some \$40,000, he deducted his traveling expenses to Stockholm and back, and divided the rest of the cash prize three ways: one-third of the money went to his own children, one-third went to Bridges's children, and one-third to Sturtevant's.

Biology at Caltech in the thirties was special because of its emphasis on genetics, *the* essential science for the future of biology. Caltech had staked out its claim, and that was Morgan's doing. At other first-class universities, including Harvard and Princeton, genetics took a backseat to other branches of biology, such as comparative anatomy, embryology, and physiology. Caltech was unconventional not only in its choice of discipline but also in its methods of discovery. For one thing, Morgan's approach was completely experimental; no courses in descriptive biology existed. According to people in the department then, Morgan "said that as long as he had any say in this matter, there would never be a class in taxonomy or in morphology."

In setting the intellectual tone for the new division, Morgan was guided by his instincts, and by an outlook much broader than even his best pupils could muster. If he had an ideology, it "was that genetics was the root to finding out how life works," as Dobzhansky put it. Sturtevant said it in a slightly different way: "Morgan's objective in biology was the development of mechanistic interpretations. Anything teleological was sure to arouse his antagonism." There was, Morgan maintained, a rational, physico-chemical explanation behind all biological phenomena.

The Caltech plant physiologist and biochemist James Bonner remembers that when he was a graduate student in biology, in the early thirties, a fellow graduate student in physics, "Willy Fowler, who will of course deny this," said to him, "'Biology? How are you ever going to make a science out of that?'" Morgan came to Caltech to answer that question. □

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