Perspectives

Anecdotal, Historical and Critical Commentaries on Genetics

Edited by James F. Crow and William F. Dove

Reminiscences of T. H. Morgan

A. H. Sturtevant

THIS *Perspectives* was transcribed from a talk given August 16, 1967, at the Marine Biological Laboratory, Woods Hole, Massachusetts. According to Michael Ashburner,

> The provenance of this account is given in the following note from Professor Andrew G. Szent-Györgyi, Brandeis University. According to Ed Lewis, the four Russian geneticists who attended Sturtevant's lecture were S. I. Alikhanian, B. L. Astaurov, N. P. Dubinin, and D. Belyaev. The transcript of this taped lecture was checked for Professor R. A. Zimmerman by Sturtevant himself (R.A.Z. to A.G.S.-G., January 13, 1968).

COMMENTS BY ANDREW G. SZENT-GYÖRGYI, JUNE 26, 2000

In 1967, embryology, invertebrate zoology, neurobiology, and physiology were the major summer courses of the Marine Biological Laboratory at Woods Hole. The morning lectures of the physiology course were attended by a large number of investigators. Since the audience was coming from all over the States and abroad, people were eager to give the talks. Over half of the morning lectures were given by the summer scientists and also by visitors attending the various Gordon Conferences or visiting friends of the scientific community. Their only compensation was to be invited (without their expenses paid) to the picnic at Tarpaulin Cove. The interesting situation was that more people wanted to give lectures than the days of the formal part of the course, which was concluded by the end of July. In the second half of the course, the faculty and the majority of the students stayed and spent an additional four to five weeks to do research under the aegis of one of the faculty. So in my first year of being in charge I had decided to extend the lecture period to the research phase as long as interesting lecturers could be enlisted. I had asked the students whom they were interested in listening to. Tom Blumenthal, who was, I think, a graduate student at the University of Indiana, had the brilliant idea to propose A. H. Sturtevant. Sturtevant had a laboratory in the basement of Old Main. When I approached him, he apologized that he could not give a research talk, he was over 80 years old, but would a lecture on his experiences with T. H. Morgan be satisfactory? He also needed two weeks for preparation. Of course I jumped at the opportunity and scheduled him for August 16th, 1967.

On the afternoon of August 15th I received a phone call from Mat Meselson on behalf of the National Academy of Sciences, who was hosting, I think, four Russian geneticists. They accompanied Krushchev on his trip to the States, possibly to indicate that by that time Lysenko's influence was waning and Mendelian geneticists were tolerated in the Soviet Union. Meselson asked if the Soviet guests could visit the physiology course. One can imagine my answer and delight. I informed Mat that Sturtevant was scheduled to lecture the next day at 9 AM in the Auditorium and the guests should be there. They were accompanied by Dr. Robert A. Zimmerman of Harvard Medical School, who also had the foresight to tape the lecture. The four elderly Russians, formally dressed, sat in the first row to listen to one of the pioneers of genetics, a creator of ideas for which they had suffered, risked their careers, and even, like Vavilov, survived a concentration camp. This was one of the most satisfying coincidences that made the very hard work of teaching in the course particularly worthwhile.

REMINISCENCES OF T. H. MORGAN

When Dr. Szent-Györgyi asked me to talk here, I wanted to do something historical, and for Woods Hole the appropriate person to talk about seemed to me to be Thomas Hunt Morgan. There are several reasons for that choice. One is the part that he played in the development of notions about the particulate nature of the genetic material. Another is the fact that he was deeply involved in the early history of this laboratory. And the third is that I worked quite closely with him for some 35 years so that I can perhaps give you a more or less first-hand account of some of the material.

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T. H. Morgan was born 101 years ago in 1866 in Lexington, Kentucky. He graduated from the University of Kentucky in 1886. The summer following his graduation, he went to the Marine Laboratory at Annisquam, on the coast north of Boston. This was the last year of the Annisquam Laboratory. In the next year, in 1887, the group which had organized and managed that laboratory came to Woods Hole. Annisquam was the immediate predecessor of the Marine Biological Laboratory, and it was there that Morgan first became familiar with marine forms. This acquaintance "took," and from that time on, the study of marine forms was one of the particular interests of his life. He did his graduate work at Johns Hopkins under William Keith Brooks, who was also a marine biologist. Brooks was an extraordinary teacher who trained a whole generation of outstanding American zoologists. E. B. Wilson had preceded Morgan by 10 years there, and contemporary with him were E. G. Conklin and Ross G. Harrison, and those three, especially Wilson and Conklin, were also deeply involved in the early developments here at Woods Hole.

Morgan's first year at Woods Hole was the summer of 1888, and in that summer he worked at the U.S. Fisheries. But he came back to the MBL in 1890 and spent a very high proportion of the summers here for the rest of his life. He was made a trustee of the laboratory in 1897, and he remained a trustee for the rest of his life; 1897 was the year in which the "Young Turks" took over the laboratory and its management, and Morgan was one of the new trustees elected at the time of that change. I'm not going to go into the history of that revolution, but I would like to point out that it really was a revolution in terms of the management of scientific organizations. The director at that time was C. O. Whitman, and Whitman's idea was that a scientific organization should be owned and managed by the people who were working in it. He resisted any plans to fit this laboratory under the wing of any other organization, any university, or any foundation. This was a new idea, and it was a very difficult one to implement. One of the reasons he was able to do it was that he had this extraordinary group of people working here and, as it happened, they came from different universities. Whitman was at Chicago, Wilson was at Columbia, Morgan at that time was at Bryn Mawr, and Conklin was at Pennsylvania. They were all first-rate people and they got along very well together, and the fact that they came from different universities was a great strength in the organization.

Morgan succeeded Wilson as chairman of the department at Bryn Mawr in 1890, and in 1904 Wilson persuaded him to accept a professorship at Columbia. For 24 years the two of them worked there in very close association. In 1928, Morgan went to the California Institute of Technology to organize a new department of biology starting from scratch. What intrigued him about this opportunity was that he was able to build up a department in the way in which he wanted it, in an institution where physics and chemistry were strong and where the whole atmosphere was one of research, and the training of students was designed to train them as research men. Morgan remained at Caltech until his death in 1945, but still regularly came back to Woods Hole each summer. So much then for the statistics of his life.

Most of you know that T. H. Morgan was a geneticist, but I would like to point out that even without his genetics—or shall we say, even if he had never seen a Drosophila in his life—his place in the history of biology would be a high one. Like most biologists—zoologists—of the period, he was trained in comparative anatomy and especially in descriptive embryology. His thesis was done on the embryology of the Pycnogonidae, the sea spiders, based on material collected here at Woods Hole. This paper was based on topics of descriptive embryology with the emphasis on phylogeny. This was the custom of the time—this is what a zoologist did.

But Morgan, like some of his other contemporaries at Johns Hopkins, was strongly influenced by H. Newell Martin, who was a physiologist and was a student of T. H. Huxley. I think that it was from Martin that Morgan got his slant toward a physiological approach to biology. He early got interested in experimental embryology. This was a movement which had been started in Germany, largely by Wilhelm Roux. And Morgan spent a summer or two at Naples—the first visit was in 1890. And then he spent a year abroad, most of it in Naples, in 1895. There he came to know—developed direct contact with—many of the people who had developed experimental embryology, such as Driesch, Dorn, Boveri, and Herbst. He was already an experimental embryologist, but it was this experience which really set him on that course. It was a very active group, both abroad and in this country, and it must have been an exciting time because they had a new sort of approach and problems were to be found at every turn. The kinds of problems that Morgan and the others had worked on had to do with the question of the extent to which development is dependent on, is influenced by, specific formative stuffs that were supposedly present in the egg, and, if these are involved, how do they operate? Is it a question of a sorting out of them into different parts of the egg?

A big problem that was early of very considerable importance—still is—but was early studied, was the extent to which the different parts of the embryo are independent of each other in development. Problems of this sort were studied by cutting the eggs and separating the blastomeres, by the use of a centrifuge for reorganizing—rearranging—the material in the egg, and by other methods. These were perhaps most important in that period. Much of what went on was perhaps best described as just fooling around: Let's see what happens if you treat an egg in this way or that way or the other. Of course most of this didn't pan out, but it wasn't really expected to. But sometimes this sort of approach did yield results, especially for a man who had his eyes open and could recognize and follow up a result.

I would just like to tell one story in connection with that about T. H. Morgan. He was interested in this period—and for the rest of his life, also—in self-sterility in the ascidian, Ciona. For example, if you mix eggs and sperm from the same individual, normally nothing happens. But sometimes self-fertilization does occur. And one of the questions was, Why? What brings this about? How does it happen? And Morgan had a nice hypothesis: maybe the acidity of the water is responsible. Let's see what pH changes will do. But being Morgan, he didn't set up measured amounts or concentrations. What he did was to take a dish in which eggs and sperm were present and squeeze a lemon over it. And it worked. Then he studied it in more detail after that. This was one of the most successful experiments in the field.

As a graduate student, Morgan began studies on regeneration. He cut pieces off of animals or plants, studying the conditions under which the parts would be regenerated. This was a subject which he made particularly his own. He published a book on it which was a progress report and wasn't intended to be a definitive account. This was characteristic. I once heard him say, semi-seriously, that the only book that is worth writing is one in a field which is developing so fast that the book will be out of date before you can get it printed.

Perhaps the most characteristically physiological area that he worked in—it would now be listed, I think, as physiology—is his work on the effects of castration on the plumage of the Sebright fowl. In this particular breed, the male has essentially the same plumage as the female. He studied the genetics of this condition and found it was due to a single dominant gene. But he also studied the effects of castrating the male and found that this capon developed normal male plumage, not the hen-feathered type. This was later followed up by other people and carried a good deal further. But the initial observation was Morgan's. Another study that he carried out here at Woods Hole was that of the local fiddler crab, in which the male, as you know, has one large claw, while the mate on the other side is smaller, more like that of the female; half of them have the right claw large, half of them the left. I won't go into it, but he got an answer—I think it was the right answer. Anyhow, this was the kind of problem that intrigued him. This is only a partial catalog of the kinds of things Morgan did other than genetics.

Now we come to his studies on genetics. In the early days of Mendelism, there was a good deal of resistance to the ideas of Mendel, especially right here at Woods Hole. The director, Whitman, was an experimental geneticist and spent years in the study of hybrid doves and pigeons. He would have none of the Mendelian approach. This is understandable because in pigeons you get, to put it mildly, a mess. You don't get sharp segregation of the characters; they blend, and you get all kinds of intermediates, queer things that don't sort out in nice 3:1 ratios. I don't know why this is so characteristic of pigeons, but at this stage, the simple, clear-cut 3:1 yes-or-no kind of character was not apparent. People who had reported that sort of experience had to be opposed. And Morgan had the same attitude, not as strongly as Whitman, but there were problems, and he didn't see how to get around them. The suggestion was fairly early made that there were a great many separate genes affecting the same character, and by recombination amongst those you could get this sort of a tangle. This didn't suit Morgan. It seemed to him just making up hypothetical units to get you out of a jam—to save an initial hypothesis that itself wasn't too well established. There was a suspicion of this sort of approach. Of course, the fact that Morgan was not sympathetic to the ideas of Weismann about particles involved in heredity and development also entered here. Morgan's difficulty in accepting this was that it was too hypothetical. You didn't have any evidence for any particular particles, but you made them up and assigned them the properties that you wanted them to have in order to explain the results, and that was that. No one saw how you could approach the hypotheses experimentally, and this seemed to him sterile.

So about 1910, Morgan, I think, could fairly be described as anti-Mendelian. What cured him was the work with Drosophila. Morgan's first paper on Drosophila was published in 1910, and the first paper of significance that he published on it was also in 1910. It is not necessary to tell how he came to work with Drosophila or where he got his material, although certainly some of the early material was collected in grocery stores which existed then in Woods Hole. He did not domesticate Drosophila; that was done earlier by an entomologist from the University of California by name of Woodworth. Woodworth, working in 1900 and 1901 at Harvard, pointed out the promise of the material as a laboratory object to W. E. Castle, who was the first person to use it for genetic studies. He studied the effects of inbreeding on fertility. Later there were a good many other people who studied it from this point of view.

Morgan started his work with Drosophila, as he stated in print, and as he often told me, in the hope that he could induce mutations in it. He had gotten interested in mutations through a visit, which must have been about 1899 or 1900, to the gardens of Hugo DeVries in Amsterdam, where he had seen DeVries' Oenothera cultures. The story of the relation of Oenothera to the history of genetics is a long one, and I won't go into that. But this was, of course, the material in which "mutations"—with quotation marks around that word—were first studied in detail. Now this struck Morgan as interesting and important, and he wanted to try some of it himself. Well, he fitted into the tradition of the proverbial embryologist who tried everything he could think of—including radium and ultraviolet light. He got a few mutations. But they were just as likely to come from the controls as they were from the mistreated cultures. It is clear now that his techniques were simply not adequate to detect the increases in mutation frequency which should have come from radium. So he didn't induce mutations, or at least he didn't know that he had, but he got them and he began studying them, and the rest of the story evolved from these presumably spontaneous mutants. The first of these—not the first found, but the first really significant one—was the white-eye character, which was sex-linked. This was a major discovery.

The relation of Mendelism to the chromosome theory is again a long story that I will not go into today, but there had developed a paradox. The only cytological evidence seemed to be perfectly clear for the relation of the chromosomes to sex determination. It was consistently shown that males were heterozygous for sex, beginning with the work of Stevens and Wilson in 1905–1906—and this was known for a wide variety of organisms: insects, nematode worms, and many others. Though the evidence was not too convincing, it was also generally accepted at the time for mammals, including man, and for other groups, like the echinoderms. In all of these, it was the male that was carrying the unpaired chromosome. But there was also genetic evidence which flatly contradicted this and said that the female was the heterozygous sex. This also was thought to be general, because it was known in birds, both the canary and the fowl, and in moths. Abraxas, the currant moth, was the first one reported. So this also represented a general phenomenon, and there was a flat contradiction. Well, this contradiction was finally resolved with the discovery of the white-eye character in Drosophila. The male was found to be heterozygous for this sex-linked character in a group where the cytological evidence already said that the male was heterozygous. It was 1913 before convincing cytological evidence for female heterozygosis was produced in moths. So this was really a major discovery, and it was quickly recognized by Morgan and by Wilson—I don't know which first, probably they talked it over with each other—that this must also apply to man because there was good evidence that this was the kind of inheritance which would fit the published pedigrees for color-blindness in man.

In 1909, for the one time during his 24 years at Columbia, Morgan gave the opening lectures in the beginning biology course. And I was lucky enough to be in that class, as was C. B. Bridges. Nothing was said about genetics; we didn't even know that Morgan was interested in it—I doubt if we knew what the word genetics meant—but we were greatly interested in Morgan. And it so happened that in the following fall—it was just a few months after the white-eye discovery—Bridges and I got desks in his laboratory, the so-called "fly room" at Columbia, where the three of us worked together for the next 18 years. This was a room 16 × 23 feet in which there were eight desks. There was a place where we cooked fly food, and there were usually at least five people working in there. Bridges and I practically lived in this room; we slept and ate outside, but that was all. And we talked and talked and we argued, most of the time. I've often wondered since how any work at all got done with the amount of talking that went on, but things popped. There were other people, too; there was a string of doctoral and postdoctoral students; there were a good many postdoctoral foreign students who had desks in there. I won't name them, but I'm not sure that this wasn't really pretty much the beginning of the reverse flow of postdoctoral students. It had been the custom that Americans, of course, went to Europe, especially to Germany, for a while after they got their degrees. Fortunately, this still happens, but the custom is not as universal as it was in the earlier days. The reverse flow was a very thin trickle of foreign students coming to this country to do advanced work. Certainly one of the first places to which the reverse flow in biology was directed was to the fly room at Columbia.

There was another important member of this team that I should not forget to mention, namely H. J. Muller. Muller was a couple of years ahead of Bridges and me as a Columbia undergraduate, and he only very briefly had a desk in the fly room, but he was an instructor in the department and he was in and out all the time and took his full share in the general discussions and arguments and suggestions and criticisms. I don't think I can give you the atmosphere of that laboratory. I think it's something that had to be lived through to be appreciated. One of the major advantages of the place was the fact that both Morgan and Wilson were there, and the graduate students of each saw quite a lot of the other. They complemented each other in a great many ways and were very close friends. In the early days at Columbia, we fed Drosophila on bananas, and there was always a bunch of bananas hanging in the corner of the room. Wilson's room was just a few doors down the hall, and he was fond of bananas, so that this was another attraction that caused him to come for frequent visits.

During this period, Morgan came down to Woods Hole for the summer regularly. This did not mean any interruption in the Drosophila experiments. All the cultures were loaded into barrels—big sugar barrels—shipped by express, and what you started in New York, you'd finish here and vice versa. We always came down by boat—it was when the Fall River Line was still running—and Morgan also had going—always—all sorts of experiments that had nothing to do with Drosophila. He raised chickens, pigeons, rats, and mice and grew a variety of plants. And these were all loaded up and carried by hand on the Fall River Line and then brought back to New York again. And when he got here, he plunged deeply into work on marine forms, into embryology of one sort or another, even while his work with Drosophila was actively going on. This was the way Morgan worked; he wasn't happy unless he had a lot of different irons in the fire at the same time. I don't think I'll go into the details of just how the Drosophila work progressed. I'll simply point out that this was the beginning of the detailed proof that the genes were localized in the chromosomes and that they were separable, and it was at that time that the various relations were worked out.

I would like to say a few more words about Morgan as a person. He had an aristocratic background, but I don't think I've ever known anyone who was as free of snobbishness as he was, and he was certainly not self-conscious. This background meant, however, that he was at home in any company. I've seen him with college presidents and I've seen him with children. My own children were delighted with him. Every time they saw him this was an event, and he had something to talk about with everyone. I have seen him on a ferry boat on the Hudson River joke with the Italian bootblacks in the Neapolitan dialect and with complete success. I have stood in line with him at the Polo Grounds waiting to buy tickets to a World Series baseball game and watched him joke with fellow baseball fans standing in line, and they accepted him as one of them immediately despite the fact that he knew very little about baseball. And Morgan was a tease. You never thought very much of it—you had better get used to that because that was what was going to happen. And he was very good at it. He was never mean, but yes—you had to expect to be teased. One of my friends—close colleagues—said that he frequently found that when he argued with Morgan, just as he thought he had the argument won, he would suddenly discover, without his knowing how it happened, that he was now arguing on the opposite and losing side. He did do this! But on the other hand, he was always sympathetic and helpful, and any time that you wished to have a serious discussion with him on scientific or personal matters, he would be helpful.

In my senior year as an undergraduate, I got my bookkeeping mixed up and finished the required work in the middle of the year; I was graduated in February. I had an undergraduate scholarship and I didn't see how I was going to live for the rest of that year—I needed that scholarship. So I went to Morgan. He said, "Well, go and talk to the provost. I think maybe he can fix you up." So I did. No, he couldn't do anything like this with all the problems that he had, of course not. So I went back and told Morgan this and Morgan didn't say anything in particular, but about three of four days later, he said, "You had better go see the provost again." So I went and saw the provost who said, "It turns out that we do have a scholarship available." Now I was quite innocent, and it was only years later that I understood—of course, this had come out of Morgan's pocket. But that's simply the way he would operate.

Morgan's objectives, what he was trying to get at in general in his biological work was to produce mechanistic interpretations of biological phenomena. One of the things that irritated him most was any suggestion of purpose in biological interpretation. He always had some reservations about the idea of natural selection, because it seemed to him to open the door to interpretations of biological phenomena in terms of purpose. He could be talked into the conclusion that there was nothing that wasn't strictly mechanistic about this interpretation, but he never liked it. And you had to talk him into it again every few months. I think the two dirtiest words that he knew were "metaphysical" and "mystical". Metaphysical to him meant a philosophical dogma, an interpretation that wasn't open to experimental test. His title at Columbia was Professor of Experimental Zoology, and I know of no one else that I think was as thoroughly committed to the experimental approach to scientific problems.

Thank you.

M. A. thanks Professor Andrew G. Szent-Györgi, for making the text of this lecture available to us, and Dr. Sharon Endow for her mediation.