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CALVIN BLACKMAN BRIDGES

1889-1938

BY

T. H. MORGAN

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Calvin B. Bridges

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Calvin Blackman Bridges was born in Schuyler Falls, New York, on January 11, 1889, and died in Los Angeles, December 27, 1938. His father, Leonard Victor Bridges, who was brought up on a small farm near Plattsburg, married Charlotte Amelia Blackman in 1887, and Calvin was their only child.

His mother died when Calvin was two years old. His father died a year later. The Grandmother Bridges had already brought up a large family but considered it her duty to take charge of Calvin. He went to a small district school when it was convenient. When he was about 14 years old his grandmother insisted that he should be "educated," and he was allowed to go to Plattsburg. He was not ready for high school and had to spend two preliminary years in grammar school. He graduated from high school in 1909 when he was 20 years old. He had made a fine record. During the years at Plattsburg he drove to school part of the time with neighbors and worked and lived much of the time in town. He worked as "printer's devil" on the Plattsburg Press, and it was said "there is a boy who is going to amount to something." When he had spare time he was always at his books, but he was a "regular boy," good-natured and obliging.

One summer during his high school years he worked on a geological survey of Valcour Island with Professor George H. Hudson of the Plattsburg Normal School. There is extant a letter by Professor Hudson written when Calvin applied for a scholarship at Columbia University in which he says: "He is in many respects a very remarkable young man. He has always kept on the honor roll of his school and yet read very extensively outside of the lines of his school work." The list of the books he read, in Calvin's handwriting, exists and it certainly covers a very wide range of subjects. Hudson also says: "He has the questioning mind, is apt in the forming of hypotheses

and quick to see when they are weak. His great desire is to undertake research work.”

At the end of his high school work Calvin was urged to try the regional examination for a four year scholarship at Cornell which he passed. He also took an examination for a one year scholarship at Columbia University and passed this also. Wishing to live near his aunt, Mrs. Billings, who lived in New Jersey, he accepted the Columbia scholarship. During his three years at college he received some aid from scholarships, but earned much of his living in other ways. During one of the summers he tutored two young boys and during another he went “on the road” to sell a book entitled “Standard Dictionary of Facts.”

My first contact with Bridges was in 1909 when he took a course I gave in general biology and another in embryology (1910); and later, as a graduate student, a course in experimental zoology, largely devoted to genetics, and another course in experimental embryology. He attended also Professor E. B. Wilson’s course on The Cell.

Bridges graduated (B.S.) from Columbia College in 1912. In the same year he married Gertrude F. Ives, and was survived by his wife and three children, Philip, Betsey and Nathan. From 1910 to 1915 he served as part-time assistant in my work on *Drosophila*. In the course of this work (Morgan and Bridges 1913) certain exceptions turned up that Bridges began to study intensively. In 1913 he published briefly his results under the title of “Non-Disjunction of the Sex Chromosomes of *Drosophila*”. A much more extended paper appeared in 1916 entitled “Non-Disjunction as Proof of the Chromosome Theory of Heredity”. This work, offered as his doctoral dissertation at Columbia University, included not only genetic evidence but corresponding evidence from a study of the chromosomes that tallied with the genetic results. This paper went far towards convincing skeptics and conservatives that chromosomes are the bearers of genetic factors. It is true there was abundant evidence before 1916 showing that chromosome behavior furnishes an interpretation of heredity. It is today hard to believe that it was nearly ten years before this relation was generally accepted.

Sex-linked inheritance, as connecting genetic interpretation with known transmission of the sex chromosomes, had been established since 1910. The interpretation of crossing over, supported by less certain cytological evidence, had also been advanced in 1910, and covered what seemed to be exceptions to Mendel's laws. Crossing over opened up a new field of research in inheritance, and for 30 years formed the basis on which much of Bridges' work rested. He greatly improved the technique of locating the genes, and in the course of the following years he so thoroughly built up the genetic maps that these stand today as the most complete data we have on the location of the genes in the chromosomes.

In 1915 I received a grant from the Carnegie Institution of Washington to carry on investigations in heredity. Bridges and Sturtevant were appointed to undertake independent research work. For twelve years we three worked together in a small room in the Zoological Department of Columbia University. As the work on *Drosophila ampelophila* (as the vinegar fly was then called) became widely known, a succession of international fellows joined us, as well as some of the more advanced graduate students and fellows of Columbia University. It was not unusual for six of us to carry on in this small room; the only space at our disposal. Those were the days when bananas were used as fly food and in one corner of the room a bunch of bananas was generally on hand—an adjunct to our researches which interested other members of the laboratory in a different way. As there were no incubators, a bookcase and a wall case were rigged up with electric bulbs and a cheap thermostat, which behaved badly at times, with consequent loss of cultures. The use of milk bottles came into the program at an early date, but where they came from was not known, or at least not mentioned. At a later date we were bold enough to ask for a case of new bottles.

This picture of the conditions under which we worked is not intended to suggest that we were handicapped. On the contrary, our proximity to each other led to cooperation in everything that went on. The discovery of a new mutant was immediately announced, and its location in the gene chain anxiously awaited.

The Carnegie group worked at Columbia University until 1928, and from 1928 to 1938 at the California Institute of Technology. The annual grants from the Carnegie Institution of Washington contributed greatly towards the success of the genetic work on *Drosophila*.

The improvements that have gradually evolved have been to a large extent the outcome of Bridges' unusual inventive faculty. The hand lens was replaced by a binocular microscope of his designing; the wall cases have been supplemented by incubators with fans and expensive regulators; the banana has given place to a synthetic medium consisting of agar agar, corn-meal, molasses, and yeast. Even the symbols by which the *Drosophila* mutant races were named are in large part attributable to Bridges' interest in a suitable nomenclature. I recall one instance in which invention went too far. In order to save space in the incubators Bridges drew a plan for a milk bottle with a square base. But they were so closely packed that when the room temperature approached the lethal degree, the heat generated in the bottles went over the top. Unwilling to give up the new bottles Bridges got a large auger and bored holes through the carefully prepared insulated walls of the incubator.

Bridges had his own system of bookkeeping. The data were often filed on bits of scrap paper, but it was almost uncanny to see how quickly he could find any information that was called for. He has left hundreds of cards, carefully filed, which contain all the data collected in this laboratory relating to each mutant or aberration. Many of these data have never been published, and it is doubtful now if anyone will ever assemble them for publication. These data were used, however, in the calculation of loci and description of mutants and aberrations, in DIS 9, which appeared shortly after Bridges' death. This issue of *Drosophila* Information Service was one of the last things on which Bridges worked, and in it, fortunately, he brought down to date practically all his work in statistical genetics.

In 1916 Bridges and I brought together the then known data on the mutants and linkage relations of the first or X chromosome of *Drosophila*, in 1919 those of the second chromosome

were published, and in 1923 we published the data which had accumulated on the third chromosome group of mutants. Later (1935) Bridges gave a complete account up to date of the fourth chromosome (*Journal of Biology*, Moscow, U.S.S.R.).

The first gynandromorph of *Drosophila* was discovered in 1910. From that time onward such exceptions were watched for and recorded. In time Bridges and I had a considerable number on hand which we described in a Carnegie Publication in 1919. Bridges reported (1939) that we had at that time studied "about 100 gynandromorphs and found that the maternal X was eliminated about as often as the paternal X. In experiments in which all flies were counted 40 gynandromorphs occurred in 88,000 flies." In addition to our explanation of elimination of one of the X chromosomes, during early development, a few other exceptions were found that called for a different explanation; namely, the presence of two separate nuclei and reduction products in the egg.

Later, Bridges discussed a few individuals showing spots on the body which, from genetic evidence, were composed of haploid cells, and, in some of these mosaics, the regions included body parts that enabled one to diagnose their sex. The spots were clearly female in constitution, and this was surprising at the time since in other insects, where haploid individuals were known (bees, etc.), they were males. Bridges' finding in *Drosophila* was, however, consistent with the female sex formula: two X plus two sets of autosomes. In the spots the same balance is present, that is one X and one set of autosomes, so that the haploid somatic tissue is female.

During the years 1921-1925 Bridges made an extensive study of certain types of intersexes in *Drosophila*. He showed clearly by cytological analyses that they were due to chromosome aberrations of a type that had not been established previously for intersexes of other insects. The intersexes showed complex mixtures of male and female parts. In the first culture in which they were found (1920) there were 37 of them in addition to 9 regular males and 96 females. They were completely sterile, but certain of their sisters, when bred, gave intersexes and were shown by genetic and cytological evidence to be triploid (3N)

females. The breeding experiments with such females showed that a certain proportion of their mature eggs contained one full set of chromosomes, one X and one of each autosome, and, in addition, part or all of one extra set. Those mature eggs that contained a diploid set of chromosomes, would, if fertilized by a normal X-bearing sperm, again give $3N$ females, and if fertilized by a Y sperm would give intersexes. The formula for the intersexes is $3A + 2X + Y$. They differ from standard females only in having an extra set of autosomes, and this fact, as Bridges points out, "proved that autosomes (A) are as much determiners of the normal sex differences as are the so-called sex chromosomes. Autosomes turn the scale toward maleness." This idea of genic balance he had already developed in 1921 in connection with changes induced by loss or gain of a fourth chromosome. The theory was applied to the interpretation of certain other abnormal-appearing types of individuals, notably superfemales and supermales. A superfemale, he showed, arises when an individual has three X chromosomes and two autosomes. A supermale arises when one X and three sets of autosomes are present. Three types of females may exist in which the balance between X's and autosomes is the same as in the normal ($2X + 2A$) female, namely $3X + 3A$ and $4X + 4A$, besides the normal. These conclusions of Bridges were not theoretical speculations, but in every case the interpretation rested on genetic evidence, and in triploids and diploids on a cytological demonstration of the presence in the individual in question of the constellation of the chromosomes that was postulated.

Bridges paid a great deal of attention to the problem of genic balance, pointing out that it is fundamental for an understanding not only of the balance concerning sex, but for all other characters as well. The fact is that today there is demonstrable evidence that there is not a single gene for femaleness and another for maleness, but several, perhaps many, genes distributed through the chromosomes and affecting the development of certain characters in one way or in the opposite way. This conception in its broadest aspects has always been insisted on by the group working on the genetics of *Drosophila*, although it is also true that a change in a single gene often leads to strik-

ing changes in the individuals containing such a mutant gene. They argued that both the old and the new gene influence the end result, not by acting alone but by collaborating with other genes, and, in the last analysis, with all or most of the genes to different degrees. Each gene is thought of as a differential.

Bridges' early discovery (1917) that certain genetic data could be interpreted as due to deficiencies in the chromosome construction has led in recent years to a factual demonstration of such deficiencies. In some of his latest work (1937-1938) he made use of this discovery in the interpretation of overlapping deficiencies in analyzing the characteristics of certain mutant types. It would be hard to find in the history of genetic research a more convincing demonstration of the combination of actual evidence and masterly interpretation of it. As early as 1919 Bridges described "duplication" as a chromosomal aberration, and here, as in his other work, his conclusions rested not on vague hypotheses but on experimental proof. Much later he also reported the occurrence of "repeats" in the normal chromosome which will have to be seriously considered in future interpretations of certain types of genetic behavior.

The many interesting problems connected with losses (deficiencies) and additions (duplications) of groups of genes present interesting problems in which genic balance is involved, and the possibility, that now exists, of detecting deficiencies and duplications in the salivary chromosomes and correlating the observations with the genetic location of mutant genes is well under way, and during the last two years of his life, was receiving Bridges' close attention.

In 1925 the data, that had been collected in the course of genetic experiments, was brought together under the title "The Genetics of *Drosophila*," by T. H. Morgan, C. B. Bridges, A. H. Sturtevant. Not until 1934, when the first number of *Drosophila* Information Service edited by Bridges and Demerec appeared, was a similar summary made. Bridges spent a tremendous amount of hard work in summarizing the data, particularly those of the stocks that the Carnegie group had built up at Pasadena, and the reports include also much unpublished data that Bridges himself had on hand. Fourteen numbers of

Drosophila Information Service have appeared, the latest in February 1941.

In recent years Bridges spent much time in correlating the loci of the genetic maps with the bands of the salivary maps. He made an elaborate study of the salivary chromosomes, and more than doubled the previously known number of bands. His maps have become the standard ones for *Drosophila melanogaster*. As I have pointed out elsewhere, the identification of the salivary bands with the loci on the genetic map would not have been possible were it not that during the preceding twenty-three years the genetic (crossover) maps had been built up to a point where such comparisons have a real demonstrable basis. While many workers had contributed to bring the genetic maps to their status of 1933, it was Bridges in particular who had made a more detailed and critical study of the maps than had any other one of his contemporaries. His maps are now standard all over the world. During the year 1938, Bridges continued the revision of the maps of the salivary chromosomes; that of the X-chromosome has been published in the *Journal of Heredity*, January 1938. During the summer of 1938 he nearly finished the right half of the second chromosome in collaboration with his son Philip, who has now put it into shape for publication. He intended to leave the left half of that chromosome until the revision had extended to the other chromosomes because he had found that this half probably contains a number of "repeats", i.e., sections of duplicating parts. This idea is the last of the many new contributions that Bridges made to the "higher Mendelism" and may prove of unusual interest in the future development of genetics.

The original discovery of the banded nature of the giant salivary chromosomes of diptera goes back to Balbiani's record of 1881. But the regularity of the sequences of the bands, the union of homologous chromosomes in pairs, and distinction of regions that stain and those that do not stain was reported in 1933 by Heitz and Bauer.

Painter, also in 1933, using *Drosophila melanogaster* material, contributed the all-important proof that there is a close correspondence between the sequence of the banding of the chromo-

some and the sequence of the genes as determined by genetic theory and practice. Without the already existing information as to the position of the genes in definite chromosomes it would have been impossible to establish this relationship, although Painter and Muller had already in 1929 laid the basis for comparisons of this kind by demonstrating that certain genetic translocations could be visibly detected as such in the chromosomes involved in such transfers.

It became increasingly important after Painter's comparisons between the genetic and the salivary maps that identification of the bands be extended to the limit of microscopic vision in order to determine more definitely the relation of individual bands to the loci of the genes, since the determination of the correspondence between the sequence of the genes and that of the bands does not tell us whether there is an identity between them. Most of the bands are faint ones while some of the darker bands are double, etc. For this kind of work Bridges was eminently fitted. His eyesight was unusually acute but he did not depend on this alone and spent much time in the study of the best methods of illumination, and the most suitable staining and preserving technique to bring out the fainter bands. As a result his new maps more than double the number of the previously known visible bands. He was also interested in the problem as to whether the stretching of the chromosome, when the nucleus is burst under pressure, may introduce artifacts. It is unfortunate that he died when in the midst of this detective work, but his methods will enable others to take up the story where he left off.

As a member of the Carnegie group each year's progress was reported in the Year Book of the Carnegie Institution of Washington. These twenty-three reports give in briefest summary the results that Bridges had obtained. Whether the elaborate data on which these reports rested, can ever be fully utilized is questionable; but Bridges accomplished so much other work, that these will not be needed to place him amongst the leading geneticists of his time.

Bridges was a very friendly person. He was simple and unaffected and always helpful to anyone who came to him for

advice. In the course of twenty years he was largely instrumental in building up stocks of *Drosophila* in which mutant genes of each chromosome are spaced so that they can be used as markers for each chromosome. These stocks are especially useful in studying crossing over, translocation and other special problems. More than 900 separate stocks are carried at present. Many of them have been distributed to investigators all over the world. Bridges spent much thought and time in building up this material and distributed it freely without even claiming credit from others for its use. In fact, one of his most admirable traits was his freedom from priority claims of any kind. His death was a serious loss to genetics and to his many friends.

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KEY TO ABBREVIATIONS

- Amer. Nat. = American Naturalist.
 Anat. Rec. = Anatomical Record.
 Arch. Entw.-mech. = Archiv für Entwicklungsmechanik der Organismen.
 Biol. Bull. = Biological Bulletin.
 Biol. Zentral. = Biologisches Zentralblatt.
 Bull. Inst. Gen. = Bulletin, Institute of Genetics, Academy of Sciences,
 U. S. S. R.
 Carnegie Inst. Wash. Publ. = Carnegie Institution of Washington, Publi-
 cations.
 Carnegie Inst. Wash. Yr. Book = Carnegie Institution of Washington,
 Year Book.
 Jour. Biol. (Moscow) = Journal of Biology (Moscow).
 Jour. Exp. Zool. = Journal of Experimental Zoölogy.
 Jour. Franklin Inst. = Journal of Franklin Institute.
 Jour. Gen. Physiol. = Journal of General Physiology.
 Jour. Heredity = Journal of Heredity.
 Peking Nat. Hist. Bull. = Peking Natural History Bulletin.
 Proc. Birth Con. Cong. = Proceedings, Birth Control Congress.
 Proc. Nat. Acad. Sci. = Proceedings, National Academy of Sciences.
 Proc. 6th Int. Cong. Genetics = Proceedings, Sixth International Con-
 gress of Genetics.
 Proc. Soc. Exp. Biol. Med. = Proceedings of the Society for Exper-
 imental Biology and Medicine.
 Trans. Dyn. Develop. = Transactions on the Dynamics of Development.
 Zeit. Abst. Vererb. = Zeitschrift für Induktive Abstammungs und Vererb-
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