

RECOLLECTIONS OF THE EARLY DAYS OF THE GENETICAL SOCIETY

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FIRST of all, Mr President, I wish to thank you and the Committee of the Society for providing me with such an excellent and adequate excuse for leaving the darkening shadows of retirement for a brief while to take part in these 50th anniversary celebrations. For me it is a kind of resurrection and I find the experience most refreshing.

During the course of my life I have been required on several occasions to act as a stand-in to a star. I do so now for here in my place should be Julian Huxley but, unfortunately, he found it impossible to accept the invitation that finally reached me. He was one of the foundation members of the Society whereas I did not join until a year later. In those days Edinburgh was a very long way from Cambridge and London and news did not travel so fast. I share your disappointment at Julian Huxley's absence for he is a very attractive person. I cannot hope to entertain you as he could have done and so ask you in advance to excuse any shortcomings that I may display.

Because this Society was very much the creation of William Bateson it becomes necessary, I think, when considering its early history to give thought to the man himself. That he could convene a meeting of 26 interested people in June 1919 to consider the desirability and the feasibility of forming the Society can surely be accepted as proof that, at long last, he had finally overcome the strenuous opposition he had encountered in his sustained effort to establish in the United Kingdom the science which he had christened Genetics. As you will know, during the first decade of this century, while still at Cambridge, he had been much occupied in acrimonious disputation with the biometricians as well as with certain of his fellow zoologists and had been severely handicapped in his researches by a chronic lack of assistance, space and funds.

But he had attracted a small but earnest band of disciples who had successfully sought, under his leadership, to determine how widespread the Mendelian phenomena were, to unravel the complexities of the so-called compound characters and to enquire into the generality of the property of dominance. His missionary zeal had enthused such people as Miss Edith Saunders, lecturer in botany in Newnham College, who was actively interested in Stocks; Miss Durham, his sister-in-law, (the canary and the mouse); Miss Killby, (the goat); Miss Marryat, (the canary and *Mirabilis jalapa*): Miss Wheldale, (Antirrhinums) and R. P. Gregory, (the sweet-pea and Primulas). At the same time he had secured close co-operation with Leonard Doncaster, (the tortoiseshell cat and Lepidoptera) and with a number of fanciers such as R. Staples-Browne, (the pigeon) and horticulturalists. Among the last was Major C. C. Hurst, the son of the owner of a large horticultural nursery near Burbage in Leicestershire. In his teens he had contracted tuberculosis and so was prevented proceeding to Cambridge there to take a degree in biology, as was intended. Condemned to a robust open-air life he developed into a very competent field naturalist and, making

full use of the facilities of the nursery, became an authority on the orchid and the rose and a prominent member of the Royal Horticultural Society. He was one of the earliest among the Mendelians to use the domestic fowl and the rabbit as experimental material. He successfully challenged Karl Pearson's dictum that Mendelism did not apply to the horse and to man. He investigated the inheritance of eye-colour in man and of chestnut coat-colour in the horse. His book *Experiments in Genetics*, 1925 is a veritable mine of early genetic history.

By this group a great body of very useful data was amassed and the foundations for later developments were soundly laid. Bateson and Punnett worked with the fowl and the sweet-pea and with Bateson's move to the John Innes Horticultural Institution in 1910, there to become its first director, this material and the programme of research that involved it passed to Punnett. At the John Innes Bateson found himself, for the first time, amply supplied with the means of carrying out research on a relatively grand scale under favourable conditions.

In 1912 Punnett's impermanent chair of Biology in the University of Cambridge became adequately endowed and transformed into the Arthur Balfour Chair of Genetics and the subject thus attained the status of an academic discipline in this country. It is to be noted, in passing, that at no time during his tenure of this chair, 1912-40, did Punnett add a cytologist to his staff. It is to be remembered, however that his main work was with the domestic fowl and that at this time the fowl was by no means an attractive cytological material.

No sooner had Bateson and Punnett settled in than war broke out to disturb and impede the development of all scientific activity other than that which seemed likely to promote the war effort. And it was during this period that in America, largely as a consequence of the appearance in 1910 of the vinegar fly, *Drosophila melanogaster*, the dew-lover, on the genetical scene, great developments had been occurring. By 1911 the essence of the Chromosome Theory of Heredity had been elaborated by Morgan and his younger colleagues in the "fly-room" in Columbia University, where breeding experimentation was skilfully combined with cytological investigation. In 1913 Sturtevant had produced the first chromosome map and in 1915 there appeared *The Mechanism of Mendelian Heredity* by Morgan, Sturtevant, Muller and Bridges to become a milestone in the history of genetics. Like so many of my generation I was away at this time but even the turmoil of war did not hide from me the importance of the great advance that this book heralded.

It is of importance to recall Bateson's review of this book for it reveals much that explains the rate and the direction of the development of our science around the time of the foundation of this Society. He wrote "it is inconceivable that particles of chromatin or of any other substance, however complex, can possess those powers which must be assigned to our factors" and "The supposition that particles of chromatin, indistinguishable from each other and indeed almost homogeneous under any known test, can by their material nature confer all the properties of life surpasses the range of the most convinced materialism".

In 1916 came Bridges' paper on non-disjunction which surely provided the final and conclusive proof of the Chromosome Theory, making it inconceivable that the relation of chromosomes and genes was merely some

kind of accidental parallelism. Yet Bateson and Punnett both remained unconvinced as did also most of their followers. To them the logical study of heredity was the study of variations and of their mode of transmission. They were therefore almost exclusively interested in the search for ratios and gave scant attention to the nature of the factors, of the genes, that lay behind the characters they studied so diligently. It was not until 1949 that Punnett, in his address to this Society at its 100th meeting, disclosed the reason why Bateson and he had managed to miss the tie-up of linkage phenomena with the chromosomes. They had been greatly impressed by Boveri's paper on the Individuality of the Chromosomes and had concluded that any tampering with the chromosomes by way of breakage and recombination was not to be contemplated. Yet, as Stern pointed out in 1950, Boveri had actually discussed the pairing and exchange of parts of homologous chromosomes and the breeding evidence that was required to demonstrate this.

At the time of the foundation of this Society almost all those who were engaged in genetical experimentation were content to contribute to the advancement of the science by means of typical Mendelian hybridisation experimentation. There were a few exceptions. There was Lock, a Cambridge man who spent much time in Ceylon and who, in his elaboration in 1906 of de Vries' idea, had suggested that exchange of material between homologous chromosomes could account for independent segregation. It was his book, *Recent Progress in the Study of Variation, Heredity and Evolution*, 1906, used by E. B. Wilson of Columbia University as a text-book, that did so much to attract Muller to genetics. There was Gregory, whose sudden death in 1918 distressed Bateson so greatly. There was Leonard Doncaster whose experimental material was so difficult cytologically that Bateson was quite unable to see any relationship between the chromosomes and the hereditary characters studied by Doncaster. Neither Ruggles Gates nor Heslop Harrison, both active in the field of cytology, could hope to influence Bateson's thinking. Hurst, though not a cytologist himself, had followed the teaching of Strasburger and of Weismann and had accepted the Chromosome Theory. But he was a quiet, gentle person who disliked disputation with men whom he greatly respected and so was able to collaborate with Bateson and Punnett though disagreeing with their interpretations of the results they obtained. When Gregory and Lock died in 1918 and Doncaster in 1920 there was no one left who could hope to persuade Bateson that experimental breeding without cytological investigation was no longer enough. As editor of the *Journal of Genetics* Bateson was in a position actively to discourage those actively engaged in genetical research from following the lead given by these younger men. It is somewhat comforting to learn that Morgan himself had to be jockeyed by his younger colleagues, who dealt with the cytological aspects of the *Drosophila* work, before he came to accept without reservation the Chromosome Theory.

I have always found it interesting to remember that Thomas Hunt Morgan, E. B. Wilson and William Bateson had all come under the influence of one man, W. K. Brooks of Johns Hopkins University. The first two were trained by him and Bateson spent the long vacations of 1883 and 1884 at the Johns Hopkins summer laboratory at Hampton, Virginia, studying the embryology of *Balanoglossus*. At the time Brooks was writing a book on heredity and his notion "that there was a special physiology of heredity capable of independent study" strongly appealed to Bateson and profoundly

influenced his thinking. On his return to Cambridge he began, before 1890 and in the pursuit of his interest in discontinuous variation, a number of experiments in order to determine how these variations were inherited. He was now on the path that led him directly to Mendel's paper and thence to the leadership of the British genetical school. You will remember that Bateson, when suggesting the term Genetics as the most appropriate name for our science, used the phrase "the physiology of descent".

Morgan, like Bateson, had been trained as an embryologist but between the years 1910-28 he became the chief architect of the Theory of the Gene. It was most fortunate that Morgan and *Drosophila melanogaster* were introduced to each other by W. E. Castle at this particular time and that Morgan should have invited two undergraduates, Sturtevant and Bridges, to join him in exploiting the opportunities that this dipteran proffered. The possibilities of its genetic study were just then beginning to be apparent and the right men happened to be in the right place at the right time with the right experimental material. Chance can play an all important role in the pre-determination of successful scientific enquiry.

The foundation members of this Society were a very heterogeneous collection. They included many academics, botanists, zoologists, agriculturalists; members of the staffs of the John Innes, Rothamstead, Long Ashton, Wisley and Kew; representatives of the Ministry of Agriculture and of commercial horticultural firms and a number of amateur naturalists, fanciers and medical men. Among the academics was one whose presence surprised many people, myself among them. Professor E. W. MacBride, a zoologist and of Imperial College, was a member of the governing body of the John Innes and a died-in-the-wool Lamarckian. Garrulous and power-loving, he was tireless in his efforts to impede the development of genetics both in the universities and in the existing research institutions. He and Karl Pearson represented the very powerful opposition that every young geneticist and cytologist had to face. They stood at the entrance of the Royal Society like the leogryphs which guard the portals of a Burmese Buddhist temple.

Of these foundations members, as far as I can gather, only two still retain their membership, Lady Barlow and Sir Julian Huxley. Death has removed the majority of the others, Biffin, Cockayne, Francis and Leonard Darwin, Ruggles Gates, J. B. S. Haldane, Heslop Harrison, Walter Heape, C. C. Hurst, F. H. A. Marshall, Michael Pease, Punnett, T. B. Wood and Udney Yule, among them.

Because my recollections of the early meetings were for the most part distinctly vague and blurred, I wrote to a number of those who had joined during the years 1919-24—Crane, Engledow, Rona Hurst, Julian Huxley, Lancelot Hogben—asking for their help. But, as would be expected, I found that to all of us the run-of-the-mill meeting had left little lasting impression. Unless one is presenting a paper, the purpose of attending these meetings is not so much to listen to communications about matters of no immediate interest to oneself but to meet such as can impart information bearing directly upon one's own current problems. The communications can be read at leisure when they appear in print. But certain of these early meetings were remembered by all of us because they were out of the ordinary for one reason or another, such as the one in the Linnean Society's rooms when a real pea-soup fog descended upon the metropolis to prevent the

Cambridge contingent finding Burlington House. They spent the evening in a fog-bound railway carriage in the station and did not reach Cambridge until three o'clock in the morning.

The 4th meeting in the rooms of the Linnean in April 1920 was made memorable by Jack Haldane who thrilled his audience with an account of his observations on the sex-ratio and unisexual sterility in hybrids—Haldane's Law, if one sex is absent or infertile in a species cross, it is the sex which from other evidence may be inferred to be heterozygous in sex. To witness a first-class mind in action is always an exciting experience and this was the first time I had heard Haldane display his astonishing ability to take the results of the skill and enterprise of others and out of them distil a principle.

In 1921 Bateson went to Toronto to attend a meeting of the American Association for the Advancement of Science and while in America spent some time in Morgan's laboratory where he was shown in detail the *Drosophila* work. He was greatly impressed by what he saw and heard, though remaining doubtful about the explanation of linkage that was offered. He decided that he must add a cytologist to his staff if the work of the John Innes was to flourish, so that experimental breeding could be combined with studies of the chromosomes. Accordingly, on his return to Britain he invited W. C. F. Newton, who had been a pupil of Lancelot Hogben at Birkbeck College, to join him and to develop a cytological section. Before his early death Newton attracted Cyril Darlington to his section and was succeeded by him with the direct result that very shortly the John Innes was to develop into one of the outstanding centres of cytological research in the whole world. But Bateson did not live to see this outcome of his far-seeing and far-reaching administrative action and up to the time of his death in 1926 he clung to a number of reservations concerning the role of the chromosomes in organic inheritance.

In 1922 Morgan visited this country and attended the 11th meeting of the Society in June. The President of the Society, A. J. Balfour, at that time Lord President of the Council, was in the chair. With Morgan came A. H. Sturtevant. They arrived loaded with hat-boxes filled with *Drosophila* cultures and with lots of microscopic slides displaying the chromosomes. Morgan gave an account of the mutants of *Drosophila melanogaster* and Sturtevant compared genetically *D. melanogaster* and *D. simulans*. The enthralled audience had no difficulty in recognising how greatly *Drosophila* had contributed to the advancement of genetics, on account of its mutability, its reproductive habits, its suitability as a laboratory animal and its relatively simple chromosome constitution. To us it seemed that the vinegar fly was to be regarded as one of the most important immigrants to enter the United States—probably with bananas from South-East Asia. No one in the United Kingdom had been using an animal or plant that could possibly have yielded in so short a time the genetical and cytological information from which emerged the Theory of the Gene.

The President made a characteristically felicitous speech when thanking the visitors and commenting upon their communications—he had an attractive personality and an unusually pleasing voice which he knew how to use—and Punnett made a handsome retraction of the doubts he had hitherto entertained concerning the identification of the chromosome with the physical mechanism of Mendelian heredity. Undoubtedly this was the most important and the most successful of the early meetings. Morgan's

enthusiasm and his manifest enjoyment in sharing with others the emotional and intellectual satisfaction that follows upon discovery converted the uncertain and ensured that henceforward nothing and no one could seriously impede the development of cytology in relation to genetics in this country. It was conceded that leadership in the genetical field had passed to the United States.

The 11th Meeting at Tring was memorable not only for the truly remarkable demonstration of polymorphism and geographical variation in Lepidoptera by Lord Rothchild and Dr Jordan but also for the presence of Richard Goldschmidt. He gave a fascinating account of his *Lymantria intersexes*. You will remember that his very extensive and thorough analysis of the development of this condition of intersexuality led him to propose a developmental interpretation which became the prototype of several subsequently employed to explain the action of mutant genes. He postulated that the intersex began its development according to one of two alternative plans, the male and the female, the balance between the two sex-determining forces being decided by their relative "strengths". Then, at a critical point in the course of sex-differentiation, the turning-point, the alternative sex-determining force took charge. This interpretation, like that of Bridges, was in essence a quantitative one though no actual quantitative data were involved. The numerical values assigned to the male and the female determining tendencies were purely hypothetical and did not refer to any measured or defined units. Though unsatisfactory in many ways, this, to me, was an introduction to epigenetics and I found it very attractive for the notion of a turning-point in the development of the condition of intersexuality, though never subject to strict proof, was very useful in those days before chromosome aberrations could be thoroughly studied.

I well remember the 15th meeting in Oxford in June 1923 when Poulton staged a marvellous exhibit of sexual dimorphism and mimicry in Lepidoptera. It was impossible not to recall the Poulton-Punnett mimicry disputation and also Poulton's early condemnation of genetics in his *Essays on Evolution* (1908). In this book he had expressed the view that Mendelism was "injurious to Biological Science and a hindrance in the attempt to solve the problems of evolution"; that it would lead to "the contemptuous depreciation of other lines of investigation directly inspired by the work and teaching of Darwin and Wallace" and to "a widespread belief among the ill-informed that the teaching of the founders of modern biology was abandoned". *Times change and we change with them*, for here we find Poulton as the genial host to the Genetical Society, now 110 strong.

Because of my own particular interests and obligations as the head of an animal breeding research department in the University of Edinburgh, I especially enjoyed the meetings of the Society that were held at the Crystal Palace Poultry Show, 1921 and 1930 and the Cagebird Show in 1926. I was required, like Bateson himself, to maintain close contact with "practical men", to study their problems and attempt to solve these. At these shows we met these "practical men" who demonstrated their creations. I found it very profitable to listen to Punnett, Staples-Browne and other members of the Society as they debated matters of common interest with the exhibitors. I came to realize clearly that I was not alone in finding it difficult to communicate with these "practical men". *Drosophila* genetics depended very largely upon the knowledge of fly-husbandry possessed by the Morgan group,

especially by Bridges. Poultry genetics, canary genetics, budgerigar genetics similarly depended upon the knowledge of the husbandry of these birds possessed by those who used them as experimental material. Those of us who kept fowls, for example, were able to talk on equal terms with the actual breeders whose fowls kept them. You will remember that Mendel spent two years in getting to know his peas before he commenced his hybridisation experiments with them.

There was a meeting in the rooms of the Zoological Society in Regent's Park thirty one years ago that had a special significance for me. The 7th International Genetics Congress was to have been held in Moscow in 1937 with Vavilov as President. But Otto Mohr of Oslo, the chairman of the International Committee that managed the affairs of the congress between its meetings, had become increasingly perturbed by the lack of news from Vavilov. It became apparent that somehow or other genetics in the USSR had become entangled with politics and was being actively discouraged. Muller, who had spent four years in Russia did what he could to combat the developing Lysenkoism but in 1937 he had been warned by Vavilov to leave the country without further delay. The International Committee at last decided that the congress could not be held in Russia and I was asked to tackle the job of staging it in Edinburgh in 1939. I turned to the Society for help and this was bountifully given. At its meeting in June 1938 the sum of £100 was placed at my disposal. The story of this 1939 congress is certainly well worth the telling, but not here and now. Halfway through the congress week war broke out to cause much confusion and very considerable anxiety, especially among the German, Italian and Polish members. We compressed the scientific sessions without much difficulty but we were forced to jettison almost all of the social activities of the congress with the result that I was able to hand over to the Society £199 of unspent money, a true measure of the failure of the congress to achieve its prime purpose, that of providing an atmosphere in which scientific intercourse is promoted.

I suppose the story I have been trying to tell should come to its end with the joint meeting of the Society with the Society for Experimental Biology in the rooms of the Zoological Society in 1942. Haldane was in the chair and the subject for discussion was the Genetical and Physical Structure of the Chromosomes. Among the speakers at this symposium were M. J. D. White, Cyril Darlington, Pio Koller and D. G. Catcheside. There had been an occasional cytological communication, for example, that of Hurst on the chromosomes of the rose in 1923 and that of Darlington on the chromosomes of the cherry in 1925 (with Bateson in the chair). But not until 1942 was a whole meeting devoted to cytogenetics. It would seem that 23 years had to pass in the life of the Society before such a symposium could be accepted as entirely desirable and appropriate. The slowness of this growth was partly due to causes that are disclosed in the early history of this Society.

If I have failed to entertain you I ask you to remember that with advancing age one's agility diminishes so that it should not be surprising that I should fail to leap across the chasm that separates the generations.