Robert Heath Lock and His Textbook of Genetics, 1906

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ABSTRACT Robert Heath Lock (1879–1915), a Cambridge botanist associated with William Bateson and R. C. Punnett, published his book *Recent Progress in the Study of Variation, Heredity, and Evolution* in 1906. This was a remarkable textbook of genetics for one appearing so early in the Mendelian era. It covered not only Mendelism but evolution, natural selection, biometry, mutation, and cytology. It ran to five editions but was, despite its success, largely forgotten following Lock's early death in 1915. Nevertheless it was the book that inspired H. J. Muller to do genetics and was remembered by A. H. Sturtevant as the source of the earliest suggestion that linkage might be related to the exchange of parts between homologous chromosomes. Here we also put forward evidence that it had a major influence on the statistician and geneticist R. A. Fisher at the time he was a mathematics student at Cambridge.

ROBERT HEATH LOCK (1879–1915; Figure 1) is a largely forgotten figure today but was highly influential in the nascent field of genetics in the early 1900s. As an undergraduate, he had counted William Bateson as one of his lecturers and had graduated in Botany in 1902, soon afterward becoming a Fellow of Gonville and Caius College, University of Cambridge. Caught up in the excitement of the development of Mendelism in Cambridge, as championed in particular by Bateson, he nevertheless kept his distance from Bateson and wrote his own book-length treatment of genetics, *Recent Progress in the Study of Variation, Heredity, and Evolution*. This book appeared at the end of November 1906 (Lock 1906) and in subsequent editions in 1909, 1911, 1916, and 1920. Although it was not the first book to embrace the new science of genetics, following the rediscovery of Mendel's paper, it was the first in English that can be described as a textbook. As such it was widely used and admired in Britain and the United States. Its influence, both acknowledged and inferred, was substantial, but it was essentially forgotten after the First World War (1914–1918) and the death of its still young author, in 1915, from heart failure following influenza.

An indication of the book's importance is that it was used as a text by E. B. Wilson in his lectures at Columbia University, inspiring H. J. Muller to take up the study of genetics (Crew 1969; Carlson 1981, p.27) and leaving its mark on T. H. Morgan and A. H. Sturtevant as we shall see. Another famous American geneticist Sewall Wright read it in graduate school (Provine 1971, p.25).

There is also the possibility that the second edition was the primary source of information about genetics and evolution for the undergraduate R. A. Fisher, who entered Gonville and Caius College in October 1909. Fisher, famous as a statistician, held the Arthur Balfour Professorship of Genetics at Cambridge from 1943 until 1957 and in addition to his genetical work he had (and continues to have) a great influence on evolutionary biology through his book *The Genetical Theory of Natural Selection* (Fisher 1930; see the *Perspectives* by Edwards 2000, in *GENETICS*, Vol. 154, No. 4). In July 1909 Lock had presented a copy of the second edition of his book to the college library, and I shall offer evidence that this actual copy was used by Fisher. If this is true then the role of Lock's book on the development of genetics through its influence on Fisher will equal that through its influence on the Columbia school of *Drosophila* geneticists in the United States.

In asserting that *Variation, Heredity, and Evolution* was the first textbook in English of Mendelian genetics, I should mention two other books for the avoidance of misunderstanding. Bateson's *Mendel's Principles of Heredity* of 1902, unlike its namesake of 1909, was no textbook, but principally "A Defense of Mendel's Principles of Heredity" against the criticism of W. F. R. Weldon, a prominent member of K. Pearson's group of biometricians who were opposed to

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Figure 1 R. H. Lock, from the 4th (1916) edition of *Recent Progress in the Study of Variation, Heredity, and Evolution*.

Bateson's Mendelian line of thought. Second, R. C. Punnett's *Mendelism* (1905) was, in its first edition, a tiny octavo volume of vii + 63 pages with neither contents nor index: essentially just a single chapter. It was subsequently expanded into a substantial textbook in its third edition of 1911, and by the time of its seventh and last edition in 1927 it had acquired a considerable reputation.

Mention should also be made of J. P. Lotsy's *Vorlesungen über Deszendenztheorien* of 1906. Lock wrote in his Preface (p. viii):

> Whilst I was still engaged upon my task [of writing], the first volume of Dr. Lotsy's admirable "Vorlesungen über Descendenztheorien" made its appearance. But for the fact that most of the following pages had then already been written, I might have hesitated to pursue my project, since a book not altogether unlike the present might be produced by the comparatively simple process of making a series of judicious extracts from Dr. Lotsy's work.

Bateson reviewed Lotsy's first volume in *Nature* of June 14, 1906 under the heading *A TEXTBOOK OF GENETICS*, this being the first time his word "genetics" appeared in print:

> As the moment is favourable, may it be suggested that the branch of science the rapid growth of which forms the occasion of Prof. Lotsy's book should now receive a distinctive name? ... the physiology of heredity and variation is a definite branch of science, and if we knew nothing of evolution that science would still exist. To avoid further periphrasis, then, let us say genetics.

(On July 31 Bateson also proposed "genetics" in his presidential address to the Third International Congress on Hybridization and Plant Breeding 1906, with such success that when the *Report* was published, the title of the congress was changed to "Genetics" retrospectively.) Lock intimated in the preface of his book (p. vii), dated October 23, 1906, that he would have liked to have used "genetics" in its title. "Since, however, the meaning of the word 'genetics' is not yet clearly understood by everybody, it seemed better to adopt in the present instance a somewhat more descriptive title."

Lotsy's book seems to have had little impact in the English-speaking world. Thompson (1908, p. 564) records it as "a valuable treatise," but it was rarely referenced, not even by Waddington (1939) in his extensive bibliography with many entries in German. Bateson (1909) lists it, but apparently without reference to it, as did Doncaster (1910), while Sturtevant (1965) does not include it.

Although Lock has been almost completely forgotten, many readers will in fact have come across his name in those tables often reproduced showing the results of experiments with peas in the first decade of the 20th century when early Mendelians sought to confirm Mendel's results. Such tables, which usually give the name "Lock" without initials and without a reference, originate from the one he published in "The present state of knowledge of heredity in Pisum" (Lock 1908). He there mentioned: "Many of the original crosses upon which the most recent of these results are based were made by Mr. Bateson. I desire to record here my indebtedness to him for handing over to me, in 1905, the greater part of his material relating to Pisum."

In this *Perspectives* I first give a biography of Lock, necessarily scanty given his neglect for nearly a century, and then a description of his book. There follow two sections discussing its influence, first on the Columbia school and second on R. A. Fisher.

R. H. Lock, 1879–1915

The posthumous fourth edition of *Variation, Heredity, and Evolution* (1916) carries a biographical note by "B. L.," Lock's widow Bella, formerly Bella Sidney Woolf (1877–1960), eldest daughter of Sidney Woolf, QC. Her brother Leonard married Virginia Stephen, the second daughter of Sir Leslie Stephen and better known today under her married name of Virginia Woolf. The details of Lock's early life, given below, are based largely on this biographical note.

Robert Heath Lock was born on January 19, 1879 at Eton College where his father, the Reverend John Bascombe Lock, was a master. His mother Emily was the daughter of Edwin Baily of Cirencester. He was educated at Charterhouse School and entered Gonville and Caius College with an entrance exhibition on October 1 1898, by which time his father, a mathematician, had moved to Cambridge and then become bursar of the college. The son prospered in the Natural Sciences Tripos, attending Bateson's lectures "On the practical study of evolution" and being placed in the first class in both part I (1900) and part II (Botany 1902). While still an undergraduate Lock accompanied Bateson abroad, who wrote to his wife Beatrice from Tours, France, in April 1902, commenting on Lock, "My little companion ... [who] knows no French of any kind, and when I say no French I mean it. 'What is French for 'to eat?' ... German, he reads with fair ease. He has a prodigious memory for verse: knows most of Hamlet, Macbeth and Gilbert and Sullivan by heart,

and can recite more ephemeral verses than ever I heard of" (Cock and Fordyce 2008, p. 290).

His Tripos results gained Lock the Frank Smart studentship of the college for two years, which he spent at the Royal Botanic Gardens at Peradeniya in Ceylon (Sri Lanka), where another Caian (as members of the college are called) who had also been a Frank Smart student, J. C. Willis, was director. During this time, Lock engaged in an extensive correspondence with Bateson. Described by Cock and Forsdyke (2008, p. 290), these authors remark "In principle, the correspondence was all that a free and open scientific correspondence should be."

Returning to England, Lock was elected a Drosier fellow of the college on January 11, 1905, finding himself next in seniority to R. C. Punnett, who had been elected in 1901 (for Punnett, see the *Perspectives* by Edwards 2012, *GENETICS*, Vol. 192, No. 9). The interval of three years reflected not only their difference in age but the timing of their graduation, Lock entering Caius in the term after Punnett graduated. Though they did not overlap then, they did in the academic year 1901–1902 when Punnett was junior fellow and Lock a fourth-year undergraduate. Very probably their friendship started at that time. On p. 43 of *Variation, Heredity, and Evolution* (1906) Lock refers to "my friend Mr. R. C. Punnett," and there is much evidence of friendly banter between them later on in the Fellows' Betting Book. Punnett had joined Bateson as a collaborator at the start of 1904, so when Lock returned at the end of the year he would soon witness their famous discovery of "partial coupling" in the sweet pea (later "linkage"; for details see Edwards 2012). Lock was also appointed curator of the University Herbarium in the Botany School.

As bachelor fellows, Punnett and Lock both lived in college, and will have done much of their writing in their college rooms. These were in the 16th century buildings of Caius Court (M2 and K3, respectively). The preface of Punnett's book *Mendelism* is dated May 1905, so that for the first months of 1905 he was writing *Mendelism* and Lock was writing *Variation, Heredity, and Evolution* within a few yards of each other and in daily contact as resident college fellows. There was surely an understanding between them that they were engaged in quite different tasks, Punnett writing a short essay on just Mendelism, published in Cambridge, and Lock a survey of recent progress in genetics and evolution published in London by John Murray, Darwin's publisher. "The idea of writing this little book," he wrote in his preface (p. vii), "occurred to me while reading Mr. W. C. D. Whetham's volume on *The Recent Development of Physical Science*." "I found the story of the modern progress of physics so interesting as to encourage the belief that a similar account of the subjects with which I was myself more particularly familiar might prove of a like interest to other people."

Lock held his fellowship for six years, though not resident for the last two-and-a-half. In August 1906 he attended the Third International Conference on Hybridization and Plant Breeding (later styled "Genetics") in London with Bateson, Punnett, R. H. Biffen (another former Frank Smart student) and T. B. Wood (also a Caian). The "Newnham College Mendelians" (Richmond 2001) were also well represented, so Bateson, who was president of the congress, was supported by a substantial Cambridge contingent of his colleagues, helpers, and former students, mostly from Caius and Newnham. Further information about the "Cambridge Mendelians" is given by Richmond (2006a) and also in her account of the 1909 Darwin Celebration by the University (Richmond 2006b).

In the spring of 1908 Lock returned to Peradeniya as assistant director of the gardens under Willis. "We understand," says the Caius College magazine, "that he is to have complete charge of the Economic Development of the Gardens." There he met his Trinity College contemporary Leonard Woolf and, on the voyage out, Leonard's sister Bella who was visiting him. At the end of June 1909, Punnett also traveled to Ceylon (to study mimicry) on a three-month trip, visiting Lock. No doubt their conversation naturally turned to the appointment of a first director of the newly founded John Innes Horticultural Institute then under consideration. Lock was one of three who had been short listed from among 30 applicants (Cock and Forsdyke 2008, p. 382) but the council deemed none satisfactory and ultimately, in November, Bateson, who had not applied, was offered the directorship. He accepted. There are further letters from Lock to Bateson during this period.

In 1910 Lock returned to England on short leave and married Bella on July 7. Two days previously he had dined in college and settled a bet with Mr. Duncan Jones, whom he had bet on March 11, 1906 "will be engaged to be married before him." He had won, and Mr. Duncan Jones paid (with the customary wine after dinner). Returning to Ceylon with Bella, Lock conducted experiments on rubber tapping and rice breeding, but was also heavily engaged in administrative work, especially as acting director when Willis was on leave.

In 1911 Willis moved to Rio de Janiero as director of the botanic gardens there, but Lock, not wishing to succeed him in Ceylon, returned to England in 1912, spending the first few months after his return writing a second book *Rubber and Rubber Planting* (1913). In June 1912 Bateson was invited to return to Cambridge for the newly created Arthur Balfour Professorship of Genetics, but he declined it and suggested Punnett (see Edwards 2012). Had the professorship been filled by a board of electors rather than Arthur Balfour and the prime minister, Lock might have stood a chance, but Punnett was effectively the sitting tenant and the possibility might never have crossed Lock's mind. Only with hindsight can we see what a good choice he might have been.

He then took up a post of inspector at the Board of Agriculture and Fisheries. When the First World War broke out in 1914 he sought to join the forces, but was asked instead to add the chairmanship of a Vegetable Drying and

Fruit Preserving Committee to his existing duties, a government body charged with furthering work on food preservation as a wartime necessity.

Struck down by a severe bout of influenza in February 1915 from which he never fully recovered, and overworked with his wartime duties, Lock died from heart failure at Eastbourne on June 26, 1915 at the age of 36. He is buried in the Ascension Burial Ground, Cambridge, where also lie his parents John and Emily. His widow, Bella, went on, as Bella Woolf, to be a successful author.

Robert and Bella Lock had no children, but Robert's three brothers were also educated at Caius College, and two of them started family lines that have ensured four and five generations of Locks at Caius, a tradition that had started with John Bascombe in 1867.

Recent Progress in the Study of Variation, Heredity, and Evolution

In the preface to *Variation*, *Heredity, and Evolution* (p. ix) Lock is at pains courteously to distance himself from his teacher Bateson. After thanking a number of his friends he continues:

> Adequately to acknowledge Mr. Bateson's influence upon these pages is a more difficult matter, and not the less so because I have deliberately refrained as far as possible from consulting him while the book was in course of preparation, in order that it might retain if possible some traces of individuality. It is therefore clear that he is in no way responsible for its deficiencies. But, apart from the fact that I am conscious of having quoted his ideas at more points than could possibly be acknowledged *seriatim*, I owe to Mr. Bateson both my first introduction to the science of genetics, and a continual fund of encouragement in the prosecution of studies connected with it.

Lock's book is indeed characterized by a transparent willingness to give both sides of every controversial point, and this is especially true of the saltationist view of evolution championed by Bateson as opposed to the gradualist Darwinian mechanism. Cock and Forsdyke (2008, p. 382) mention in connection with the John Innes directorship that "Bateson's fair-mindedness had been sorely tried by [Lock's] support of de Vries and even, on occasions, of Pearson." "Fair-mindedness," however, is a quality that one comes to associate more with Lock than with Bateson. Bella's biographical note reveals a character that is sensitive, thoughtful, and considerate. She quotes "an old college friend" as writing about the photograph of Lock (Figure 1) "I think, in a very charming way, it reflects the outstanding feature of his moral and mental personality. He liked cleverness, but wouldn't put up with it for a moment if it were superficial. His love of truth was something more than the habit of a trained scientist." In contrast to Punnett, who worked happily with Bateson (see Edwards 2012), Lock kept his distance. After his death Bateson reread Lock's book with a view to writing an obituary notice for him: "I have made a start on my notice of Lock. I don't like the book better on closer acquaintance" (Cock and Forsdyke 2008, p. 459).

Variation, *Heredity, and Evolution* is an astonishing work for its time, partly because of the encyclopedic knowledge of its 27-year-old author and partly because of its original and influential musings on the relationship between the phenomenon of partial coupling discovered by Bateson and Punnett and the chromosomal theory of heredity (see the next section). The 10 chapters of the first edition bring together discussion of evolution by natural selection, biometry (at quite an advanced level) including the law of ancestral heredity, the theory of mutation, Mendelism (including the contributions of Yule and Pearson), cytology, and the implications of genetics to human affairs. Chapter topics are listed in the contents, and reproduced below in an appendix. The historical background is amply covered: Darwin, Wallace, and Mendel of course, but Malthus and Lamarck and Galton and other still more distant figures. Of recent writers Lock is thoroughly familiar with de Vries, Weismann, Johannsen, Tschermak, Correns, Wilson, Boveri, Yule, and Pearson, as well as with his Cambridge contemporaries Bateson, E. R. Saunders, Punnett, and Biffen. Some indication of the extent of Lock's reading can be gauged from the list of 80 references at the end of a paper he published just before returning to England in the autumn of 1904 "Introductory: The work of Mendel and an account of recent progress on the same lines; with some new illustrations. Part I of Studies in Plant Breeding in the Tropics" (Lock 1904).

The second edition (1909) adds bibliographies to each chapter. An important addition is made to Chapter VIII: where the first edition briefly alludes to "some coupling" between two Mendelian factors, the second discusses Bateson and Punnett's case of *partial gametic coupling* in the sweet pea, the first observation of what came to be known later as *linkage* (see Edwards 2012). Chapter X "Eugenics" is entirely new, amplifying some remarks contained in the concluding chapter of the first edition. Lock's views are typical of the period. He summarizes Galton's arguments and adds that "The point of view which has been adopted in the present chapter is very well summed up in the following paragraph by Prof. Karl Pearson," which starts "As we have found conscientiousness is inherited, so I have little doubt that the criminal tendency descends in stocks" and continues in like vein. No reference is given, but the paragraph is from *The Scope and Importance to the State of the Science of National Eugenics* (Pearson 1909), the Robert Boyle Lecture in Oxford in 1907. The views expressed in the lecture are more extreme than those customarily attributed to Pearson.

The third edition (1911) differs little from the second. The fourth, posthumous, edition (1916) was a revision by Lock's friend Leonard Doncaster, who inserted substantial alterations and additions at three points. We note the first two, to do with linkage, in the next section. The third concerned sex determination and sex linkage, particular interests of Doncaster (1914). Doncaster had himself written a small book *Heredity in the Light of Recent Research* (1910) in which he recorded his debt to Bateson (1909) but added "I have not hesitated to make use of Lock's *Recent*

Progress in the Study of Variation, Heredity and Evolution, Thomson's *Heredity* [see below], and some other books dealing with general aspects of the subject." His own third edition (1921) lists Lock's book in a fifth edition, 1920, which he had revised but little further.

Lock wrote to Bateson on March 8, 1909 that his first edition had sold so well that the publisher was proposing a second (Cock and Forsdyke 2008, p. 382). The first edition had already been reprinted twice, in April 1907 and March 1909. Copies of all editions are not hard to find.

There was a sympathetic full-page review of the first edition in *Nature* by "F.A.D." (1907; probably Dixey), and a hostile one in *Biometrika* by W. P. Elderton (1907), a statistical colleague of Pearson's. J. Arthur Thompson, in his *Heredity* (1908, p. 563), thought the book "a useful introduction especially to biometric methods and Mendelian experiments," while Alfred Russel Wallace's (1908) opinion merits a full quotation:

> In conclusion, I would suggest to those of my readers who are interested in the great questions associated with the name of Darwin, but who have not had the means of studying the facts either in the field or the library, that in order to obtain some real comprehension of the issue involved in the controversy now going on they should read at least one book on each side. The first I would recommend is a volume by Mr. R. H. Lock on "Variation, Heredity and Evolution" (1906) as the only recent book giving an account of the whole subject from the point of view of the Mendelians and Mutationists. ... .

This quotation is printed on the fly leaf of the second (1909) and subsequent editions of *Variation, Heredity, and Evolution*.

The influence of *Variation, Heredity, and Evolution* on the Columbia school

The 2000 reprint of A. H. Sturtevant's *A History of Genetics* (1965) says, on the back cover:

> In the small "Fly Room" at Columbia University, T. H. Morgan and his students, A. H. Sturtevant, C. B. Bridges, and H. J. Muller, carried out the work that laid the foundations of modern, chromosomal genetics. The excitement of those times, when the whole field of genetics was being created, is captured by this book, written by one of those present at the beginning. ... it is worth remembering that the world's first genetic map was created in 1913 by A. H. Sturtevant .. .

Appendix A in the book gives a chronology, recording for 1906 "Lock: suggested the relation between linkage and the exchange of parts between homologous chromosomes" (2000, p. 137). In the text, Sturtevant wrote (2000, p. 43) "The possibility that linkage might result from genes lying on the same chromosome had been suggested by Lock in 1906, in his elaboration of de Vries' idea that exchange of material between homologous chromosomes could account for independent segregation." The reference is to the American edition of *Variation, Heredity, and Evolution* (Dutton, New York 1906; identical to the British one) and Chapter IX Recent Cytology. Lock was, of course, familiar with the recent discovery of partial coupling of characters in the sweet pea found by Bateson and Punnett in 1904 and 1905, later called linkage, and on p. 187 he briefly alludes to it. Then on p. 252, after describing de Vries's (erroneous) hypothesis for independent segregation, Lock writes:

> In cases where the phenomenon of correlation or coupling has been observed we must suppose that there is some mechanism which causes the representative particles of the respective characters concerned to remain in company during the process by which the other allelomorphs are being reassorted between the chromosomes. Of this process of coupling the cytologists have not yet been able to observe any visible indication in the behaviour of the chromosomes, any more than they can really see the redistribution of the supposed factors carried by the chromosomes. But apart from this it must be allowed that the facts of the experiment and of microscopic observation fit in with one another in a remarkable way, and that the Mendelian theory throws considerable light on the minute features of cell anatomy.

E. B. Wilson, professor of zoology at Columbia, used Lock's book for his course "Heredity, variation and the chromosomes." The minds of the geneticists of the Columbia school, for whom *Variation, Heredity, and Evolution* had been their textbook, were thus exposed to the germ of an idea about a chromosomal explanation for linkage.

H. J. Muller had taken general biology in his freshman year, much of it taught by J. H. MacGregor, and

> After his first successful year, Muller spent the summer as a hotel clerk in New Jersey. He knew that in the fall he would be taking Wilson's course on the cell, and he knew from MacGregor that the text for it would be R. H. Lock's *Recent Progress in the Study of Variation, Heredity, and Evolution* (1906). Muller read the book while he hid, out of sight, under the stairwell of the hotel when the bell wasn't ringing, and he again experienced the electrifying thrill he had when he first read Mendeleev's periodic tables. Here was a system that brought evolution, cell biology, and plant and animal breeding into one common scheme (Carlson 1981 p. 27).

In the words of Crew (1969), it was Lock's book "that did so much to attract Muller to genetics." Carlson (2013) attended Muller's course "Mutation and the gene" in 1955 and prints a page of his lecture notes recording: "1906. R. H. Lock. Recent progress in the study of variation and evolution (*sic*)—The completely modern viewpoint for its time." Muller (1943) himself wrote that in 1908 he took E. B. Wilson's "thrilling one semester course on heredity and the chromosomes, variation and evolution. In this course, the text chosen by Wilson was Lock's extraordinary book of 1906—too far "ahead of its time" to be sufficiently remembered now—which, with less caution and fewer qualifications than employed by Wilson himself, advocated the sufficiency of Mendelism, multiple factors, the chromosome theory (including exchange of linearly arranged genes during parasynapsis, after de Vries), and the natural selection of mutations, as the basis of all heredity and evolution."

Muller (1916) did not mention Lock in his Ph.D. thesis "The mechanism of crossing-over," and neither had Morgan (1911) when he advanced his hypothesis that "partial coupling—linkage—is a reflection of 'associations of factors' that are located near together in the chromosomes." By then Morgan was able to rely on the cytological observations of Janssens (in 1909; see the *Perspectives* by Koszul *et al.* 2012, in *GENETICS*, Vol. 191, Num. 2). But when all four of the Columbia school combined to publish *The Mechanism of Mendelian Heredity* (Morgan *et al.* 1915) in Chapter I they wrote "In the same year [1906] ... Lock called attention to the possible relation between the chromosome hypothesis and linkage" (p. 5) and did not there mention Janssens. Consciously or subconsciously, they had absorbed Lock's point. But memory of Lock was fading: they gave him no initials, either there or in the index, and his book is not in the bibliography. By the time Whitehouse (1965) wrote his *Toward an Understanding of the Mechanism of Heredity* with its substantial historical content, Lock had disappeared almost completely, squeezed out between de Vries and Morgan rather than perceptively linking the two. Besides Sturtevant (1965) perhaps only Cock (1983), in his study of Bateson's reaction to the chromosome theory, remembered: "Lock, in particular, gave vigorous support to the chromosome theory as early as 1906." Indeed, in his second edition (1909, p. 201) when he added a report of the segregation ratios proposed by Bateson and Punnett on their "reduplication hypothesis" (see Edwards 2012), Lock did not mention the hypothesis by name. His account of their idea evinces skepticism and concludes "There is good reason for hoping that we shall soon be able to describe the facts of correlation [*i.e.* partial coupling] in terms as definite as those which can now be applied to the phenomena of segregation." Janssens was just round the corner.

Wilson attended the 1909 Darwin Centenary Celebrations in Cambridge, staying with the Batesons (Cock and Forsdyke 2008, p. 321) and receiving an honorary degree from the university. It seems probable that Lock was in Ceylon at the time and missed the opportunity to meet the most influential user of his book.

From a historical point of view, it was unfortunate but understandable that when Doncaster inserted new material about linkage in Lock's fourth edition (pp. 200–202, 269–271) he removed Lock's suggestion for the phenomenon of coupling, quoted above, and replaced it with a description of Morgan's work.

R. A. Fisher's Sources of Information About Genetics, 1909–1911

> I first came to Cambridge in 1909, the year in which the centenary of Darwin's birth and the jubilee of the publication of *The Origin of Species* were being celebrated. The new school of geneticists using Mendel's laws of inheritance was full of activity and confidence, and the shops were full of books good and bad from which one could see how completely many writers of this movement believed that Darwin's position had been discredited (Fisher 1947).

"The fiftieth anniversary of the publication of *The Origin of Species* was being celebrated, apart from other things, by the publication of Bateson's book *Mendel's Principles of Inheritance*" (Fisher 1959; actually *Mendel's Principles of Heredity*). Fisher bought the book. He also received as a college prize the book of essays *Darwin and Modern Science* (Seward 1909) published by Cambridge University Press as part of the Darwin Celebrations ("a remarkable collection of able essays," Fisher was to say in 1959).

This is all the definite information there is about Fisher's reading in genetics, and includes Mendel's paper, which was given in translation in *Mendel's Principles of Heredity*. But among the "books good and bad" that he encountered then, or soon after, we must surely include Punnett's *Mendelism* in one of its first two editions (1905, 1907). Punnett, as we have seen, was a resident fellow of Caius, and Fisher certainly came to know him during his undergraduate days (Mazumdar 1992, p. 99). However, Fisher may not have met Lock. The only time when they might both have been in college was when Lock dined there on July 5, 1910 just before his wedding (see above). But Lock had presented his second edition (1909) to the college library in July, and even if Punnett had not drawn attention to it Fisher would surely have come across it. An undergraduate who notes "books good and bad" on a subject of consuming interest to him in the Cambridge bookshops is hardly likely to ignore his own college library. Be that as it may, Fisher never referred to Lock's book in his writings, but then he never referred to Punnett's either.

There is some evidence that Fisher used this particular copy of Lock's second edition. The book has been moderately well used, and of all the potential Caius undergraduate readers of it, Fisher seems the most likely. But more direct evidence appears on p. 87. Lock there reproduces a diagram from Wallace's *Darwinism* (1889, p. 58). Neither axis is labeled, and in the Caius copy someone has added "No of birds" for the *x*-axis and someone else (the hand is different) an indistinct "length of wing" or some such for the *y*-axis. As one who is familiar with Fisher's spidery handwriting, often very small because of his extreme short sightedness, I believe "No of birds" (Figure 2) is in his hand. I can cite other instances of Fisher having annotated library books in Cambridge, including one other in the Caius library. There is also of course the possibility that Fisher remembered the diagram from Wallace, whose *Darwinism* he had read by 1915 (Fisher 1915).

By the time Fisher gave his talk "Mendelism and Biometry" on November 10, 1911 (printed in Bennett 1983, p. 51) he was to varying degrees familiar with the work of Weismann, de Vries, and Johannsen. His first example of Mendelism is the Andalusian fowl, which he could have got from any of the three books of Bateson, Punnett, and Lock. He is familiar with the work of Pearson, and in particular with the problem of parent–offspring correlation and the differing views of Pearson and of Yule (whom he does not mention by name). The only source among the books so far mentioned seems to be Lock (1909), Chapter VIII

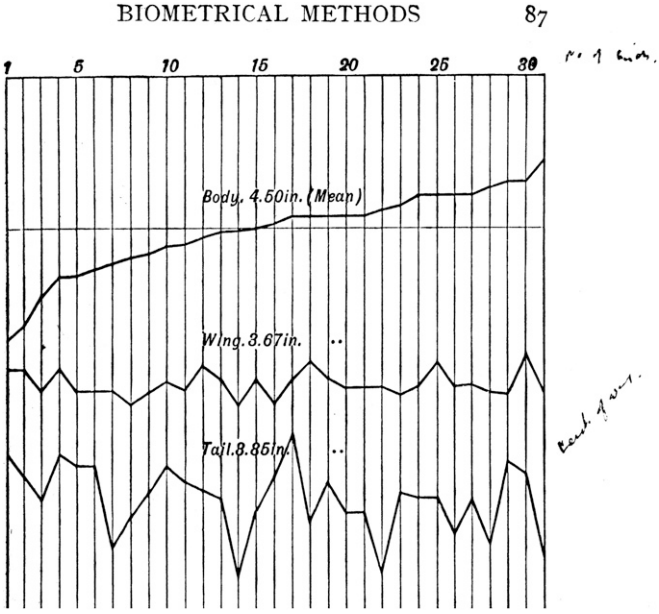

Figure 2 From the 2nd (1909) edition of *Recent Progress in the Study of Variation, Heredity, and Evolution*, annotated "No of birds" in a hand probably R. A. Fisher's.

Mendelism (*continued*) with a section "Mendelism and Biometry"—the very title of Fisher's talk—"researches of Yule and Pearson" (p. 227). Fisher mentions the good fit of Mendel's data to his hypothesis, revealing an apparent familiarity with Weldon (1902), a paper in *Biometrika* (see Edwards 1986, Magnello 1998). This seems to be a direct result of perusing *Biometrika* itself. He has read Galton's *Hereditary Genius* (1869). Lock (1909) devoted a whole new Chapter X Eugenics (p. 282) to Galton and his work.

In addition to this evidence for Lock's book in its second (1909) edition having been an important source for Fisher, it contains a number of quite suggestive remarks bearing on some of Fisher's later work. We have already noted the opening of the topic of the correlation between relatives, which matured into Fisher (1918). On the subject of classification Lock wrote in his introduction (p. 10)

> ... though at first sight it may appear almost paradoxical, ... it is quite possible for groups to be perfectly distinct, although individual members of them may have deviated so far, each from its proper type, as to render impossible the task of deciding from their appearance which group any of these individuals belong to.

In Fisher's (1925, p. 37) *Statistical Methods for Research Workers* we find the same thought:

> When a large number of individuals are measured in respect of physical dimensions, weight, colour, density, etc., it is possible to describe with some accuracy the *population* of which our experience may be regarded as a sample. By this means it may be possible to distinguish it from other populations differing in their genetic origin, or in environmental circumstances. Thus local races may be very different as populations, although individuals may overlap in all characters;

Furthermore, this follows two pages after a figure (his figure 3) constructed on the same strange principle as Wallace's diagram referred to above, which was reproduced by Lock (p. 87). As Fisher was still a fellow of Caius when writing *Statistical Methods* he would have had ready access to Lock in the library.

A remarkably prescient remark is made by Lock on p. 99, to the effect that the standard deviation "happens to be determinable with greater accuracy from an actual series of variates" than the mean quartile, and in a footnote he gives the root-mean-square derivation. Fisher (1920) explored the whole question in intricate detail and proved that *The whole of the information respecting* σ [the standard deviation of a normal distribution], *which a sample provides, is summed up in the value of* σ_2 [the sample standard deviation calculated from the mean-square deviation from the mean]. This is the first appearance of the notion of statistical *information* and led to the concept of *sufficient* statistics. Fisher (1950) notes that the paper arose from an examination of a statement by A. S. Eddington, but that does not preclude an initial stimulus from his reading of Lock.

Finally, when "quasi-linkage," or association between Mendelian factors on different chromosomes, was first discussed (Michie 1953, Wallace 1953) Fisher suggested the word "affinity" to describe it (Wallace 1958). Lock (1906, p. 185, 1909 p. 197) had written of "the existence of some kind of affinity occurring in the same individual between allelomorphs which belong to distinct pairs."

But perhaps equal to all these pieces of evidence is the unique feature of Lock's book that it brought together (to quote from its chapter headings) evolution, the theory of natural selection, biometry, the theory of mutation, Mendelism, cytology, and eugenics, all in a single volume. Nowhere else could the young Fisher have found such a guide to the subjects that fascinated him over and above his student work for the Mathematical Tripos. He had to look no further than his college library for the book, which would lay out the ground that he was to till so fruitfully in *The Genetical Theory of Natural Selection* (1930). Lock's *Recent Progress in the Study of Variation, Heredity, and Evolution* was, I suggest, as much an inspiration for R. A. Fisher as it had been for H. J. Muller.

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Appendix

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