Beyond Mendelism and Biometry

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Abstract

Historiographical analyses of the development of genetics in the first decade of the 20th century have been to a great extent framed in the context of the Mendelian-Biometrician controversy. Much has been discussed on the nature, origin, development, and legacy of the controversy. However, such a framework is becoming less useful and fruitful. This paper challenges the traditional historiography framed by the Mendelian-Biometrician distinction. It argues that the Mendelian-Biometrician distinction fails to reflect the theoretical and methodological diversity in the controversy. It also argues that that the Mendelian-Biometrician distinction is not helpful to make a full understanding of the development of genetics in the first decade of the twentieth century.

Key words

Mendelism; Biometry; Weldon; Yule; Darbishire; de Vries; Johannsen; heredity; variation

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1. Introduction

A typical narrative of the development of genetics in the first decade of the twentieth century begins with the introduction of Gregor Mendel's work (1866) to the study of heredity in 1900 by the Dutch biologist Hugo de Vries (1848-1935), the German botanist Carl Correns (1864-1933), and the Austrian agronomist Erich von Tschermak (1871-1962), which inspired the Cambridge biologist William Bateson (1861-1926) and his associates to develop a Mendelian approach to heredity. However, the Mendelian approach was immediately resisted by the Biometric School, who advocated a statistical approach to heredity based on Francis Galton's work (1889). The leading proponents of Biometry were the UCL statistician Karl Pearson (1857-1936) and the Oxford biologist W. F. R. Weldon (1860-1906). The Mendelian-Biometrician controversy ended soon after the sudden death of Weldon in 1906. Thereafter, the Mendelian approach was developed in great depth and at a rapid speed and eventually incorporated into a highly successful theory of inheritance, classical genetics, by the efforts of the Morgan School in the 1910s. According to this historiography, the development of genetics in the early 1900s is to a great extent centred on the conflict between the Mendelians and Biometricians.

Much has been discussed on the nature, origins, development, and legacy of the debate between the Mendelians and Biometricians (see Provine 1971; Cock 1973; MacKenzie and Barnes 1975; Roll-Hansen 1980; Mayr 1982; Olby 1989; Kim 1994; Radick 2005). This paper challenges the traditional historiographical framework based on the Mendelian-Biometrician distinction. Section 2 reviews the historiography of the Mendelian-Biometrician controversy. Section 3 argues that the Mendelian-Biometrician distinction fails to reflect the diversity and change of the contenders' views on heredity in the debate. Section 4 argues that the Mendelian-Biometrician framework is problematic and not helpful to make a better understanding of the development of genetics in the first decade of the twentieth century.

2. The Historiography of the Mendelian-Biometrician Controversy

Precisely speaking, the Mendelian-Biometrician controversy initially referred to a heated and publicised debate over heredity at the seventy-fourth meeting of the British Association for the Advancement of Science in 1904. On the morning of 18th August 1904, Bateson delivered the presidential address of the Zoological Section. In his talk, Bateson defended a Mendelian approach to the study of heredity and criticised the statistical approach as 'a misleading instrument' (Bateson 1905, 578). The next morning, there were a series of talks devoted to discussion of the Mendelian approach, given by E. R. Saunders, A. D. Darbishire, and C. C. Hurst respectively. As Bateson's collaborators, Saunders and Hurst defended the Mendelian approach based on their studies of stocks and rabbits.

> The regularity with which all these phenomena [of heredity in garden stocks] occur plainly indicates that even these complex appearances result from a fundamentally simple system of Mendelian segregation. (Saunders 1905, 591)

> These results [of the experiments on rabbits] are in accordance with the Mendelian expectation… (Hurst 1905, 593)

As R. C. Punnett (1950, 7) recalled later, ‘Miss Saunders authoritatively announced her findings in the stocks. Hurst assured the audience of Mendelian phenomena in [rabbits].’ Even Darbishire, a former student and collaborator of Weldon, admitted that some results of his experiments seemed ‘confirmatory of the Mendelian interpretation’ (Darbishire 1905a, 592).[1]

Table 1. The Programme of Section D (Zoology), the British Association for the Advancement of Science at Cambridge, 1904

	18th August 1904	19th August 1904
Morning session	“Presidential Address” by William Bateson	“Heredity in Stocks” by E. R. Saunders
		“On the Results of Crossing Japanese Waltzing with Albino Mice” by A. D. Darbishire
		“Experiments on Heredity in Rabbits” by C. C. Hurst
		Discussion, opened by W. F. R. Weldon
Afternoon session	“The Coloration of Marine Crustacea” by F. W. Keeble	“Experiments on Heredity in Fowls” by R. C. Punnett
	“The Miocene Ungulates of Patagonia” by W. B. Scott	“An ‘Intermediate’ Hybrid in Wheat” by R. H. Biffen
		“Experiments on the Behaviour of Differentiating Colour-characters in Maize” by R. H. Lock
		“Experiments on Heredity and Sex-determination in Abraxas grossulariata” by G. H. Raynor and L. Doncaster
		“Experiments on Heredity in Web-footed Pigeon” by R. Staples-Browne

[1] It should be noted that the experiments that Darbishire discussed in his talk were expected to disconfirm the Mendelian theory (Pearson 1906, 41).

		Discussion, chaired by Sydney Hickson

The talks were followed by a discussion, in which Weldon harshly criticised the Mendelian approach. Weldon argued that 'until further experiments and more careful descriptions of results were available, it was better to use the purely descriptive statements of Galton and Pearson than to invoke the cumbrous and undemonstrable gametic mechanism on which Mendel's hypothesis rested' ("Zoology at the British Association" 1904, 539). The discussion resumed after the talks in the afternoon. Bateson responded to Weldon's criticism and argued that 'by the Mendelian hypothesis alone was it possible to draw together the vast number of observed facts which had seemed utterly incoherent' ("Zoology at the British Association" 1904, 539). Towards the end of the discussion, Pearson proposed a truce to the debate for three years, for he maintained that 'the controversy could only be settled by investigation, not by disputation' ("Zoology at the British Association" 1904, 539). The discussion ended with the remarks by Sydney Hickson as the chair of the section, who said that 'the debate had been of much value' ("Zoology at the British Association" 1904, 539).

Bateson and his associates claimed the victory of the debate. In Punnett's words, 'Bateson's generalship had won all along the line and thenceforth there was no danger of Mendelism being squelched out through apathy or ignorance' (Punnett 1950, 8). In contrast, Pearson was deeply disappointed by the meeting.

> The Presidential Address in the Zoological Section was chiefly an attack upon biometric work and methods, and the discussion which followed culminated in the President dramatically holding aloft the volumes of the Journal [i.e. *Biometrika*] as patent evidence of the folly of the school, and refusing the offer of a truce to this time-wasting controversy. (Pearson 1906, 44)

This confrontation, as well as the broader debate between the proponents of the Mendelian approach and those of the statistical approach in the first decade of the twentieth century, was not regarded as a particularly important episode of the history of genetics in the first two-third of the twentieth century. For example, neither Alfred H. Sturtevant's *A History of Genetics* (1965a) nor Leslie C. Dunn's *A Short History of Genetics* (1965) mentions it.[2] Historians began paying serious attention to the controversy in the 1970s. Both William Provine (1971) and P. Froggatt and N. C. Nevin (1971) provide the detailed analyses of the Mendelian-Biometrician controversy.[3] Donald Mackenzie and Barry Barnes (1975; 1979) use the Mendelian-Biometrician controversy as an example to show how the development of science can be explained by social factors. Lyndsay Farrall (1975) examines the nature of scientific controversy with a case study of the Mendelian-Biometrician controversy. Bernard Norton (1975) analyses the philosophical

[2] Sturtevant (1965a) does briefly mention that Francis Galton developed an alternative approach to the study of heredity, but says little about Pearson and Weldon. Nor is the Mendelian-Biometrician controversy mentioned at all.

[3] As an anonymous reviewer insightfully indicates, these accounts of the controversy seem to echo very closely some of Punnett's autobiographical account. It might be plausible to infer that Punnett's autobiographical account was a main source of these historiographical analyses in the 1970s, but more careful work is to be done.

foundations of Pearson's advocacy of Biometry. It is worth noting that in most of these works the Mendelian-Biometrician controversy refer to the persistent debate between the proponents of the Mendelian approach and those of the statistical approach rather than the confrontation in 1904.[4]

Since then, the Mendelian-Biometrician controversy has been one of the central issues in the history of genetics. The nature of the Mendelian-Biometrician controversy has been debated (e.g. Roll-Hansen 1980; Barnes 1980; MacKenzie 1981; Kim 1994). The theoretical, methodological, and philosophical positions of the contenders in the controversy have been examined (e.g. Cock 1973; Olby 1989). The historical significance of the controversy has been discussed (e.g. Mayr 1973; Hull 1985). These historiographical analyses of the controversy have been explicitly framed by the Mendelian-Biometrician dichotomy. However, such a historiographical framework based on the Mendelian-Biometrician dichotomy has been questioned. Marga Vicedo (1995, 374), for example, is sceptical of 'the monolithic and static categories of Biometry and Mendelism'. In a similar vein, Barnes (1996, 198) views the Mendelian-Biometrician dichotomy as a 'problematic historical construct'.

For the past two decades, the historiography of the controversy has been carefully revised. It has been shown that the so-called Biometricians differed in their theoretical and philosophical commitments (e.g. Sloan 2000; Ankeny 2000; Tabery 2004; Radick 2005; Pence 2011): some (e.g. Yule 1902; Darbishire 1905b; 1906) doubted the supposed incompatibility of Mendelism and Biometry, whereas others (e.g. Weldon 1905) attempted to find an alternative to the Biometric and the Mendelian theories.

In addition, the legacy of the controversy has been revisited (e.g. Radick 2005; 2016a; Jamieson and Radick 2013; 2017). Greg Radick, for example, has argued that the significance of Weldon's work has been unfairly downplayed. By doing so, he challenges a Mendelian-centric analysis of the early development in genetics. Radick indicates that Mendelism was not clearly superior to Biometry as traditionally understood.

> [B]iometry and Mendelism offered methods and theories of comparable research… moreover, biometry had experimental and physiological sides potentially as robust as Mendelism's… On a couple of issues, furthermore – and here we adopt a 'Whiggish' stance for the moment – Weldon was much closer to current consensus than Bateson was. (Radick 2005, 40)

All these analyses provide a more nuanced picture. The controversy is no longer simply construed as a battle between two groups of pig-headed dogmatists. The Mendelian-Biometrician distinction is more colourful than a black-white contrast. Nevertheless, these revised historiographical analyses are still framed by the Mendelian-Biometrician distinction. They still assume that the Mendelian-Biometrician controversy is basically a debate between two scientific

[4] In the rest of this paper, the Mendelian-Biometrician controversy is used in this broad sense.

communities: Mendelians and Biometricians. In the rest of this paper, I shall show such a historiographical assumption is problematic and not very useful and should be abandoned.

3. Methodological and Theoretical Diversity in the Controversy

In this section, I shall illustrate the methodological and theoretical diversity in the controversy by examining the works of Yule, Darbishire, and Weldon, all of whom have been traditionally characterised as Biometricians. I shall argue that recent analyses show that none of them can be labelled simply as either Mendelian or Biometrician.

3.1 Yule

George Udny Yule (1871-1951) is best known for his contribution to statistics. He read engineering at UCL where he attended Pearson's lectures on statistics. Later, he became a demonstrator of Pearson in 1893-1899, and lectured statistics at UCL in 1902-1912. There has been a disagreement on Yule's position in the Mendelian-Biometrician controversy. Given his close relationship with Pearson and his expertise in statistics, Yule is traditionally regarded as a Biometrician (e.g. Mayr 1973, 149; Tabery 2004, 77; Rasmuson 2010, 244; Roll-Hansen 2014, 1009), though he is occasionally viewed as an early Mendelian (Sturtevant 1965b, 203). In addition, Yule is often characterised as a reconciler (e.g. Cock 1973, 10; Falk 1991, 474; Gillham 2001, 310). All these interpretations mainly stem from the different understandings of Yule's paper 'Mendel's Laws and Their Probable Relations to Intra-Racial Heredity' (1902). In this paper, Yule appreciated the potential significance of the Mendelian approach.

> I am inclined to agree with Mr. Bateson as to the possibly very high importance in practice and theory of Mendelian phenomena… The assumed separation of characters in the germ cells of the hybrid on which Mendel based his explanation of the results he had observed, may, as Mr. Bateson suggests, very possibly be proved in the future to hold good over a much wider field than has yet been experimentally tested. Mendel's phenomena may bring us to revise fundamentally some of our conceptions of heredity, they may suggest new directions in which to seek for solutions of some problems of the cell, they may throw fresh light on the process of fertilization in general, and on the nature of variation. (Yule 1902, 194–95)

According to Yule, the Mendelian-Biometrician controversy was largely due to mutual misunderstanding rather than a genuine theoretical disagreement.

> Many of the conclusions at which Mr. Bateson arrives seem so entirely due to his misunderstandings of various passages in the writings of Mr. Galton and Professor Pearson that I propose, in the first place, to deal not with Mendel's work at all, but with that of the statistical or biometrical school. (Yule 1902, 195)

He argued that Mendel's principles could be 'a special case' of the law of ancestral heredityand provided a mechanism of heredity, which was missing from the Biometric theory.[5]

> The value of the work of Mendel and his successors lies not in discovering a phenomenon inconsistent with [the law of ancestral heredity], but in shewing that a process, consistent with it, though neither suggested nor postulated by it, might actually occur. (Yule 1902, 227)

That said, Yule also noted that the statistical approach was superior to the Mendelian approach in some cases.

> If, however, either dominance fail, or the rigid predetermination of the somatic attributes by the germ cell, or both, Mendel's Laws will cease to hold, but the Law of Ancestral Heredity will still apply. (Yule 1902, 228)

Finally, Yue concluded that the two approaches were not intrinsically incompatible and could be complementary to each other. Since neither provided a generalised theory of inheritance, there was a possibility that the two approach would be incorporated into a new and better theory of heredity in the future.

> It is, however, essential, if progress is to be made, that biologists – statistical or otherwise – should recognise that Mendel's Laws and the Law of Ancestral Heredity are not necessarily contradictory statements, one or other of which must be mythical in character, but are perfectly consistent the one with the other and may quite well form parts of one homogeneous theory of heredity. (Yule 1902, 236)

Yule's paper has been widely regarded as one of the earliest attempts to reconcile Mendelism with Biometry (Sturtevant 1965b, 203; Froggatt and Nevin 1971, 19; Bowler 1989, 120).[6] Nevertheless, there are different interpretations of Yule's reconciliation. Many (e.g. Cock 1973, 10; Kevles 1980, 443) maintain that Yule tried to propose a synthesis of the Mendelian approach and statistical approach, while James Tabery (2004) argues that Yule's work is better understood as a reduction of Mendelism to Biometry. No matter how Yule's work should be interpreted, it is evident that Yule's position cannot be easily characterised in terms of Mendelian or Biometrician. As Yule (1902, 236) himself emphasised, 'To make my own position clear, let me

[5] Yule (1902, 204) used the term 'the law of ancestral heredity' in a broader sense than Galton and Pearson. Galton (1889) and Pearson (1903) referred the law of ancestral heredity to an equation expressing a mathematical relationship of heritable contributions from ancestors, while Yule (1902, 202) formulated it as follows: 'the mean character of the offspring can he calculated with the more exactness, the more extensive our knowledge of the corresponding characters of the ancestry'.

[6] Yule's paper (1902) was published on 28 November 1902. On 23 October 1902, Hugh Richardson published a short paper "Theories of Heredity" in *Nature*, in which he proposed that 'both Galton's and Mendel's ideas… are not necessarily antagonistic, but may turn out to be as simultaneously true as the laws of Boyle and Charles' (Richardson 1902, 630).

repeat with regret, that I cannot include under the same heading the special laws as to the operation of Ancestral Heredity which were formulated by Galton and Pearson.'

3.2 Darbishire

Darbishire (1879-1915) studied zoology under Weldon at Oxford. He began undertaking the hybridisation experiments on Japanese Waltzing mice under the supervision of Weldon in 1902. The main purpose of the experiments was to test Mendelism. Darbishire published four reports on the results of the experiments. In the first report, Darbishire (1902, 102) argued that the Mendel's Law of Dominance did not apply to the mice of F1 generation.[7] In the second report, Darbishire (1903a, 172) showed that some results were 'in possible accordance with some form of Mendelian hypothesis', but he was still quite cautious.

> The first of these results although not inconsistent with the truth of Mendel's hypothesis cannot be taken as proof that this hypothesis applies; for a similar result is observed in such cases as that of human eye-colour where Mendel's Laws have been shewn not to hold. (Darbishire 1903a, 172)

In the third report, Darbishire (1903b, 282) noted that the results of some experiments did not confirm the Mendelian hypothesis that 'the (so-called "extracted") recessive individual which is produced by pairing two first crosses, is in every respect similar to the original pure recessive'. In the final report, Darbishire (1904) provided a detailed summary of the results of the experiments without making a general conclusion on Mendelism. Eight months later, Darbishire presented his work on Japanese Waltzing mice at the British Association and witnessed the heated debate. In his account of the debate, he characterised his position as neutral.

> [O]n a certain day there gathered together the life-measurers [i.e. the Biometricians] and the priestfollowers [i.e. the Mendelians]; and the great chief of the life-measurers [i.e. Weldon] was there, and the great chief of the priest-followers [i.e. Bateson] was there . . . There was also there one Petúrcha [i.e. Darbishire] . . . Petúrcha was young; he was not a chief, but he marvelled at the marvel. In the dwelling, at the appointed time, words fell from the mouth of the chief of the priest-followers which were not pleasing to the life-measurers; and that which the chief of the life-measurers said found no favour with the priest-followers; and each party said, "We are right"; and each party said, "You are wrong." But Petúrcha said, "Both may be right," and he found favour neither with the life-measurers nor with the priest-followers. And the wizards departed . . . without having laid bare the marvel . . . And Petúrcha . . . sent forth word saying, "There are two ways of busying with the marvel: the way of the wizards of the dead, and this is done by life-measurers; and the way of the wizards of the living, and this is done by the priest-followers; it is for a man to choose which way he will pursue; but if he thinks the way which he chooses not is wrong, his thoughts are

[7] In this report, Darbishire followed Weldon's formulation of Mendelism (1902a), which consisted of the Law of Dominance and the Law of Segregation.

> wrong. There is no strife between the two ways." But save from a few there came no answer.[8] (Darbishire 1917, 165–66)

Darbishire's neutral position was more explicitly expressed in two papers: "On the Supposed Antagonism of Mendelian to Biometric Theory of Heredity" (1905b) and "On the Difference between Physiological and Statistical Laws of Heredity" (1906). The central argument in these papers is that Mendelism and Biometry were not mutually exclusive and could be complementary to each other.

> It is the thesis of the present essay to demonstrate the compatibility of Mendelian and biometric theory and to account for their apparent antagonism. (Darbishire 1905b, 2)

For Darbishire, the two approaches differed in their objects of study.

> A confirmatory sidelight on the truth of my comparison is thrown by the consideration that of the two men whom I have quoted as representing the rival theories of heredity, the biometer is a mathematician, while the Mendelian is a zoologist; and it is entirely in accord with expectation that the former regards the phenomena of heredity from that point of view which does not presuppose knowledge of the unit, while the latter is concerned with the properties of the individual organism. (Darbishire 1905b, 17)

Darbishire argued that the Mendelian theory provided a physiological law of heredity, which was 'an attempt to account for the phenomena of heredity by picturing the way in which the characters of an organism are represented in the germ-cell which produces it' (Darbishire 1906, 18), while the Biometric theory provided a statistical law of heredity, which was basically 'a statement that the characters of the ancestry of a population reappear in certain definite proportions in that population' (Darbishire 1906, 16). In other words, Darbishire (1906, 18) suggested that the Mendelian approach could be understood as an attempt to explain the phenomena of heredity, while the statistical approach could be construed as an attempt to describe the pattern of heredity. It is in this sense that 'the briefest possible statement of the difference between the two that Mendelism treated of units, and biometry of masses of units' (Darbishire 1906, 19). And Darbishire claimed that the Mendelian theory was true of units, while the Biometric theory was true of masses.

As Darbishire himself admitted, there was a shift of his views on Mendelism and Biometry. He once believed in the antagonism of Mendelism and Biometry, but then was convinced that two approaches could be compatible. Darbishire finally became an advocate of both Mendelism and Biometry in 1905. Therefore, I argue that Darbishire's position cannot be simply classified into either of the Mendelians and Biometricians. As Rachel Ankeny (2000, 340) indicates, '[I]t is

[8] This is an excerpt of a little fable, so-called by its author Darbishire, which is an account of the infamous debate over heredity at the British Association Meeting in 1904.

erroneous to claim either that Darbishire became a converted Mendelian or remained a committed ancestrian or biometrician.'

3.3 Weldon

Traditionally, Weldon is regarded as a leading figure of the Biometric school. He studied mathematics with Olaus Henrici (1840-1918) and zoology with E. Ray Lankester (1847-1929) at UCL in 1876-1877 and obtained a degree in natural sciences from Cambridge in 1881. After a stay at the Naples Zoological Station, Weldon took up a lectureship at Cambridge in 1882. He succeeded Lankester in the Jodrell Chair of Zoology in 1889 at UCL, where he became a close friend and collaborator of Pearson. In the first few years of the 1900s, Weldon led the criticisms of the Mendelian approach to the study of heredity (Weldon 1902a; 1902b; 1903b; 1903a; 1904). He also maintained that the statistical approach was essential to the study of heredity (Weldon, Pearson, and Davenport 1901b, 3). However, as I (Shan 2020) have argued, the traditional historiography of Weldon is problematic. It is dubious that Weldon was a stubborn Biometrician. Since 1904, Weldon had begun working on a book project, entitled *Theory of Inheritance*. The book was never finished due to Weldon's death in 1906, and still not published. The manuscript of *Theory of Inheritance*, now stored at UCL Special Collections, contains Weldon's most systematic work on the study of heredity.[9] In the manuscript, Weldon explicitly stated two goals of the study of inheritance.

> The student of heredity has two main objects: the first is to discover what degree of stability is actually exhibited by the various races of animals or of plants, and to determine the extent to which deviation from the average characters of parents or other ancestors is associated into deviation in their descendants; the second object is to acquire such knowledge of the changes which occur during the growth and maturation of the germ-cells, their fusion and subsequent development, as may serve to indicate the process by which the obscure relation between parents and filial characters is brought down. The first object is to make a purely descriptive statement of the actual relation between the visible bodily characters of living things and those of their ancestors or their descendants; the second is to learn the process to which this relation is due. These two objects are pursued by different methods, and as it happens they are generally pursued by different men, so that few attempts have been made to consider the learning of what are actually known concerning relation between the visible characters of parents and those of their offspring upon the possible interrelation of structural changes revealed by minute study of the germ-cells and of embryonic processes in germinal. (Weldon 1905, f.3.r)

Here Weldon made three important claims. First, the study of inheritance is more than a pure description of the pattern of inheritance. Second, study of the mechanism of inheritance is as important as the statistical study of the pattern of inheritance. Third, an ideal theory of inheritance should encompass both a statistical description of the pattern of inheritance and a

[9] For an overview of the manuscript, see Shan (2020, 56–64).

mechanistic account of the hereditary process. These claims clearly distance Weldon's view from a typical Biometric view on inheritance. For example, Pearson maintained that a study of mechanism played a secondary role in science.

> Step by step men of science are coming to recognise that mechanism is not at the bottom of phenomena, but is only the conceptual shorthand by aid of which they can briefly describe and resume phenomena. That all science is description and not explanation… (Pearson 1900, vii)

And for Pearson, an accurate description of the pattern of inheritance would be all that one needs to know about inheritance.

> If either that [Galton's] law, or its suggested modification be substantially correct, they embrace the whole theory of heredity. (Pearson 1898, 411)

Thus, it is clear that Weldon's approach to the study of inheritance (1905) is not a typical Biometric approach, mainly developed by Pearson (1898; 1902; 1903). In addition, as I (Shan 2020) argue, the theory that Weldon attempted to develop in the manuscript was not a typical Biometric (descriptive) theory of inheritance, which was centred on Galton's law of ancestral heredity. It encompassed Galton's theory of hereditary determinant elements (1872a; 1872b) and Galton's law of ancestral heredity, incorporated with contemporary studies on regeneration, reproduction, embryology, cytology, and so on.

Moreover, the Weldonian theory could not be understood as an assimilation of Mendelism into the Biometric framework. As Weldon himself noted, what he ultimately aimed at was a new theory in which 'both views, the Galtonian and the Mendelian, will be reconciled' ("Current Theories of the Hereditary Process" 1905, 732). Therefore, characterising Weldon's position terms of the Mendelian-Biometrician distinction is not very helpful to understand Weldon's view on inheritance in order to assess its significance. In other words, the Mendelian-Biometrician distinction fails to capture Weldon's nuanced understanding of inheritance.

3.4 Summary and Remarks

Yule, Darbishire, and Weldon were all important figures in the Mendelian-Biometrician controversy. However, as I have shown, none of them can be simply labelled as a Mendelian or a Biometrician. Even if all of them eventually realised that Mendelism and Biometry could be compatible, they differed in their ways of reconciling the two approaches. Yule developed a mathematical model which renders Mendelism as a special case of Biometry, though he was not completely happy with Biometry. He anticipated a new theory in which both Mendelism and Biometry would play their roles. Darbishire tried to reconcile Mendelism with Biometry by highlighting the differences between two approaches. Unlike Yule, Darbishire did not provide 'a solution or model to reconcile the theories' (Ankeny 2000, 341). Weldon's project was most ambitious. His manuscript suggests that he was developing a new theory of inheritance. Thus, I argue that the theoretical and methodological disagreement among Yule, Darbishire, and Weldon shows that they are difficult to be characterised as the Biometricians. Accordingly, it is not too hasty to conclude that the Mendelian-Biometrician distinction is too coarse to reflect the theoretical and methodological diversity in the debate over heredity in the 1900s.

4. Mendelism and Biometry Reconsidered

Some might argue that my conclusion in section 3 is not decisive: the theoretical and methodological diversity in the Biometrician School does not show that Yule, Darbishire, and Weldon were not Biometricians. It is not unusual in the history of science that there are some disagreements between the members of a scientific community. For example, Priestley and Cavendish held different versions of the phlogiston theory of combustion, but they were both 'phlogistonists'. In a similar vein, it can be argued that Yule, Darbishire, and Weldon were Biometricians, though they maintained different versions of the Biometric theory or approach. Accordingly, it can be argued that the Mendelian-Biometrician distinction is not a sharp cut. Mendelism and Biometry should be construed as continua rather than as dichotomies. Moreover, the shift of the views can be characterised as paradigm-conversion, as Kyung-Man Kim (1994) has argued. Therefore, it can be argued that the Mendelian-Biometrician distinction is not undermined by the theoretical and methodological diversity.

In order to respond to this line of argument, I find it necessary to revisit the Mendelian-Biometrician distinction. What is the Mendelian-Biometrician distinction? What is Mendelism? And what is Biometry?

A popular characterisation of the Mendelian-Biometrician distinction is by appealing to Thomas Kuhn's philosophy of science. More precisely speaking, the controversy is often interpreted as a conflict between two paradigms in some Kuhnian sense.[10]

> The first group of scientists, the paradigm articulators, were those who articulated the still inchoate paradigms by extending and elaborating the theory by the elite of the group to which they belonged. They were not, however, supposed to evaluate their mentor's original theory – and, in this they were doing what Kuhn has called normal science… Weldon and Pearson succeeded in gathering around themselves a group of paradigm articulators, such as A. D. Darbishire, E. H. J. Saunders, G. U. Yule, Raymond Pearl, and Charles Davenport. On the other hand, Bateson's group consisted of such researchers as R. H. Biffen, R. H. Lock, C. C. Hurst, and R. C. Punnett. (Kim 1994, 35)

> Darbishire as part of a more skeptical younger generation was attempting to reconcile two competing paradigms [i.e. Mendelism and Biometry], or at least suggest that they were not mutually exclusive. (Ankeny 2000, 342)

> [Biometry and Mendelism] were [rival 'paradigms'] to the extent that they supplied different exemplars (Kuhn's own preferred meaning of 'paradigm'). (Radick 2005, 44)

[10] For a detailed paradigm-based analysis, see Kim (1994).

> This debate [i.e. the Mendelian-Biometrician controversy] has often been interpreted as a clash of mutually exclusive paradigms in which the Mendelians won the upper hand over the biometricians in the end. (Müller-Wille and Rheinberger 2012, 114)

It has been implicitly assumed that the Mendelian-Biometrician controversy is a case of scientific revolution in a Kuhnian sense. Much efforts have been made to examine the nature, origins, and development of the debate between two paradigms: what are the theoretical and methodological differences between Mendelism as a paradigm and Biometry as a paradigm (e.g. Provine 1971; Froggatt and Nevin 1971; Olby 1989)? Do social factors play a decisive role in the formation and development of two paradigms (e.g. MacKenzie and Barnes 1979; Roll-Hansen 1980; 1989)? Are Mendelism and Biometry two incommensurable paradigm (MacKenzie and Barnes 1979)? What are the theoretical and methodological differences within each paradigm (e.g. Sloan 2000; Pence 2011)? What best explains some contenders' 'supposed conversion' to the other paradigm (e.g. Kim 1994; Ankeny 2000)? Does the supposed victory suggest that the Mendelian paradigm was superior to the Biometric paradigm (e.g. Radick 2005; 2016a; 2016b; Jamieson and Radick 2013)?

However, I argue that such a Kuhnian paradigm-based characterisation of the Mendelian-Biometrician controversy is problematic. First, the Mendelian-Biometrician controversy cannot be understood as an episode of scientific revolution (or, revolutionary science) in the Kuhnian sense. For Kuhn, a revolutionary period is an intermediary period between two periods of normal science.[11] Although it might make sense to understand the establishment of classical genetics as the beginning of a normal science, it is highly controversial to argue that there is a pre-1900 paradigm in the study of heredity. As many (e.g. Wood and Orel 2005; Müller-Wille and Orel 2007; Gliboff 2013; Shan 2020) have pointed out, there were multiple lines of inquiry in the study of heredity in the nineteenth century. Moreover, these lines, as Staffan Müller-Wille (2021, 117) argues, 'were largely independent of each other and fail to form a coherent paradigm'. Thus, if we try to characterise the origins of genetics in a Kuhnian way, the first ever paradigm must be classical genetics, established by the Morgan School in the 1910s. Thus, an important implication is that the Mendelian-Biometrician controversy should be construed as a part of the pre-paradigmatic period rather than an episode of scientific revolution in the history of genetics. Therefore, if we try to understand the development of genetics in the first decade of the twentieth in a Kuhnian way, the period would be better characterised as a pre-paradigmatic period rather than a revolutionary (or paradigm-shift) period.

Second, it is problematic to characterise Mendelism and Biometry as two paradigms in a Kuhnian sense. Kuhn (1970; 1974) distinguishes two senses of paradigm: a paradigm in the broad sense, also called a disciplinary matrix, refers to a community-based consensus, while a paradigm in the narrow sense, also called an exemplar, refers to a concrete problem-solution. When talking of paradigms in the history of science, Kuhn typically means disciplinary

[11] According to Kuhn (1962), the history of science can be characterised as a cyclic progress: pre-paradigmatic period, normal science, revolutionary science, normal science, revolutionary science, and so on.

matrices.[12] Unfortunately, neither Mendelism nor Biometry is a disciplinary matrix. There was no explicit formation of the Mendelian principles of heredity in the early 1900s, even if Bateson's book was entitled 'Mendel's principles of heredity: A defence'. As Müller-Wille (2021, 119) argues, '[Mendelism] was the result of thoroughly contingent circumstances that fail to fit with a clear taxonomy of "paradigms".' Similarly, it is not easy to identify a set of symbolic generalisations, models, values, and exemplars that were explicitly and invariantly shared by the Biometricians in the early 1900s. Most of the Biometricians' works (e.g. Weldon 1902a; 1902b; Darbishire 1902) at the time were critical rather than constructive. The first articulation of the Biometric theory of inheritance was Pearson's paper "The Law of Ancestral Heredity" published in 1903. Therefore, it is difficult to regard Mendelism and Biometry as two disciplinary matrices in a strict Kuhnian sense.[13] As Müller-Wille (2021, 108) puts it, 'one should not overestimate the coherence and dominance of presumed "paradigms" … in biology.'

Some might argue that it is a just metaphor to call Mendelism and Biometry paradigms. The Mendelian-Biometrician controversy might still be interpreted as a conflict between two paradigms if paradigms are loosely construed as community-based consensuses. Kuhn's 'paradigm' just provides an account of community-based consensuses. Other accounts include Lakatos' 'research programme' (1978), Larry Laudan's 'research tradition' (1977), Haosk Chang's 'systems of practice' (2012), and my 'exemplary practice' (Shan 2020). Historians do not have to delve into these philosophical work and decide which one provides the best characterisation of community-based consensuses. It can be argued that historians could take a minimalist position by maintaining that the Mendelian-Biometrician controversy can be characterised as a confrontation between two community-based consensuses without committing to any philosophical account of community-based consensuses. Unfortunately, this move does help much. All of these community-based concepts assume that there is some consensus among the members. For example, a research programme includes a theoretical hard core, which is explicitly and invariantly shared by the members of the programme. However, both Mendelism and Biometrician lack an explicit 'hard core' in the early 1900s.

What is worse, a community-based account of the Mendelian-Biometrician distinction is not very helpful to have a good understanding of the development of genetics. It might easily lead to an impression that Mendelism and Biometry were two dominating research communities in the study of heredity at the time. But this was not the case. In the first decade of the twentieth century, the study of heredity flourished in various ways in different parts of the world. In Netherlands, de Vries (1903) tried to incorporate Mendel's work into his theory of pangenesis, though his attempt was eventually unsuccessful (Stamhuis, Meijer, and Zevenhuizen 1999; Shan 2020). In Germany, Correns made efforts to explore the scope of the Mendelian approach to the study of heredity (Rheinberger 2000). In Austria, Tschermak (1901a; 1901b; 1901c) attempted to develop a Mendelian theory of heredity in terms of valency (*Werthigkeit*). The American

[12] A paradigm as a disciplinary matrix typically consists of symbolic generalisations, models, values, and exemplars (Kuhn 1970, 181–87).

[13] It should be noted that Mendelism and Biometry can be analysed and characterised in terms of exemplary practices (Shan 2020). That said, such an analysis is not very Kuhnian.

physician Walter Sutton (1877-1916) and the German biologist Theodor Boveri (1862-1915) independently developed the chromosome theory of inheritance. The equilibrium principle was proposed by the English mathematician G. H. Hardy (1877-1947) and the German obstetrician-gynecologist Wilhelm Weinberg (1862-1937) independently. The Danish botanist Wilhelm Johannsen (1857-1927) coined the term 'gene' and introduced a distinction between phenotype and genotype, which later became 'the foundation stone of classical genetics' (Roll-Hansen 2009, 458).

The Mendelian-Biometrician controversy forms a part of this broader picture. Mendelism was a new approach to the study of heredity at the time. It received a mixed reception and weathered a great deal of criticisms. For example, Mendelism was poorly received in France. As Peter Bowler (1989, 122) points out, '[H]ardly any took up Mendelism as the basis for active research programmes, nor was there any significant effort to establish a role for the new science in the university curriculum.' Biometry was basically a statistical approach to the biological sciences (Weldon, Pearson, and Davenport 1901a; 1901b; Pearson 1902). The Biometric theory of heredity based on the law of ancestral heredity, put forward by Pearson and Weldon in the first few years of the twentieth century, was just an application of Biometry and also faced the challenges (e.g. Johannsen 1903) other than those from Bateson and his associates.

The different lines of development in the study of heredity, including Mendelism and Biometry, were mutually influenced by each other. For example, Johannsen's early work (1896) was influenced by Galton's statistical approach to evolution and heredity. His work on beans (1903) was inspired by the discussion between de Vries (1901) and Weldon (1902c). And his development of the concepts of genotype, phenotype, and gene was stimulated by Pearson's and Weldon's criticisms of his bean experiment (Roll-Hansen 2009, 486). On the other hand, Johannsen's bean experiment is regarded as 'the crucial experiment' in the Mendelian-Biometrician controversy (Roll-Hansen 1989). Like Johannsen, Tschermak was also closely involved in the Mendelian-Biometrician controversy. He had correspondence with Weldon, Pearson, and Bateson respectively, and seemed to act as a 'foreign consultant' in the 'British affair' (Simunek, Hoßfeld, and Breidbach 2012, 246).

In addition, as many (e.g. Froggatt and Nevin 1971; Olby 1989; Roll-Hansen 1989) have indicated, the Mendelian-Biometrician controversy was interwoven with a debate on the problem of variation in the study of evolution. The debate over variation is known as the Darwnism-Mendelism debate (Provine 1971; Bowler 1989; Stoltzfus and Cable 2014), also sometimes called the Biometry-Mutationism debate (Mayr 1982). Typically, Bateson, de Vries, and Johannsen are characterised as the Mendelians (or the mutationists), while Pearson, Weldon, and Yule are viewed as the Darwinians (or the Biometricians) in this context.

Bateson emphasised the significance of discontinuous variation in the evolution of species and argued that the phenomena of dominance in F1 generation were 'all examples of discontinuous variation' (1902, 7). In contrast, Weldon (1895, 380) contended that 'specific modification is at least generally a gradual process'. It was also the Biometric standpoint, as summarised by Pearson.

> [T]he main evolution has not taken place by leaps, but by continuous selection of the favourable variation from the distribution of the offspring round the ancestrally fixed type. (Pearson 1908, 39)

The debate over variation between Weldon and Bateson began in 1894, eight years earlier than their first public debate on heredity (Bateson 1902; Weldon 1902a). Bateson (1894, 2) argued that 'the forms of living things, taken at a given moment, do nevertheless most certainly form a discontinuous series and not continuous series'. Weldon (1894) quickly dismissed Bateson's arguments for discontinuous variations without a substantial and detailed discussion.

> [The arguments] in favour of Mr. Bateson's main contention therefore fail, when applied to any part of the process of evolution of which we can know anything. It remains to consider what experimental evidence is brought forward to prove that variation is in fact "discontinuous" in any living animals… No definition of what exactly is meant by "discontinuous" variation is given. (Weldon 1894, 26)

Note that Weldon accepted that there were some phenomena of discontinuous variation, but he did not think that discontinuous variation played any significant role in the process of evolution. In other words, what Weldon differed from Bateson is the significance of discontinuous variation in the study of evolution. To some extent, the debate over Mendelism and Biometry was an extension of their debate over variation. As Froggatt and Nevin (1971, 19) point out, 'Weldon [was] immersed in mutual problems of inheritance and evolution.'

In short, the debate over Mendelism and Biometry was not an isolated event that took place in England between Englishmen. It not only originated from the introduction of Mendel's work to the study of heredity and the development of the statistical approach in the biological sciences, but also was deeply rooted in the persistent debate over variation in the study of evolution. The development of the debate over Mendelism and Biometry was profoundly shaped by the theoretical and methodological development in the biological sciences at the time. For example, as I have shown in section 3.3, Weldon tried to incorporate contemporary studies of embryology, regeneration, and development into his theory of inheritance.

To sum up, I argue that not only is the Mendelian-Biometrician distinction problematic, it is but also not very helpful. The historiographical analyses of the controversy based on the Mendelian-Biometrician distinction focus too much on the debate itself and pay insufficient attention to its relation to other lines of development in the study of heredity at the time.[14] For example, despite Roll-Hansen's careful analyses (1980; 1989; 2009), the significance of Johannsen's work (1903) is still not well recognised. Nor is de Vries', or Tschermak's involvement of the Mendelian-Biometrician controversy sufficiently examined.[15] If our concern is just about the development of the debate between the so-called Mendelians and Biometricians in England, it might make sense

[14] Note that many scientists working on the problem of heredity at the time cannot be simply classified into the Mendelian school or the Biometric school. As Vicedo (1995, 375) indicates, 'At least in the United States, most researchers at the turn of the century were not Mendelian, Biometricians, Darwinians or Galtonians in the sense of having sworn allegiance to a single research programme, school or paradigm.'

[15] Michal Simunek, Uwe Hoßfeld, and Olaf Breibach's paper (2012) is an exception.

of the neglect of de Vries', Tschermak's, and Johannsen's involvement. None of them could be straightforwardly labelled as a Mendelian or a Biometrician. Nor did their work seem to make direct influence on the controversy in England. Nevertheless, if our concern is ultimately about the development of genetics or the biological sciences in the 1900s, we would better situate the debate on heredity in a broader context. Thus, framing the debate by the Mendelian-Biometrician distinction somehow prevents us from having a fuller account of the development of genetics, or the biological sciences in the 1900s. In other words, the Mendelian-Biometrician distinction is not helpful for us to have a good overview of the development of genetics in the 1900s.

5. Conclusion

The Mendelian-Biometrician distinction has been widely used to investigate the historical development of genetics (e.g. Froggatt and Nevin 1971; Provine 1971; Cock 1973; Bowler 1989; Schwartz 2008). However, it is not helpful for this purpose. As I have argued, the Mendelian-Biometrician distinction obscures the methodological and theoretical diversity in the debate on heredity in the 1900s. Nor does it provide a good understanding of the development of genetics in the 1900s.

In addition, the Mendelian-Biometrician distinction is used as a historical case in the history and philosophy of science. It has been often used to examine the nature of scientific controversy (e.g. MacKenzie and Barnes 1975; Roll-Hansen 1980; Barnes 1980). With the distinction, historians and philosophers assume that Mendelism and Biometry can be understood as two competing paradigms or community-based consensuses. Unfortunately, such an assumption is problematic. As I have argued, both Mendelism and Biometry were relatively new approaches to the study of heredity at the time. The advocates of two approaches loosely formed two camps. The theoretical and methodological hard cores of two approaches were still developing in the first few years of the twentieth century. Neither can be understood as an established paradigm, or a community-based consensus. Thus, the distinction does not serve as a solid historiographical basis for the philosophical examination of scientific controversy.

In conclusion, I argue that the Mendelian-Biometrician distinction as a conceptual tool would be better abandoned. It should be highlighted that I am not denying that there was a debate over Mendelism and Biometry. Nor am I arguing that the works of the contenders in the debate (e.g. Bateson, Pearson, Weldon, and Yule) are not worthy of examination. Rather I am arguing that the Mendelian-Biometrician distinction oversimplifies the views of the contenders in the debate over heredity and fails to be a useful conceptual tool for a historiographical analysis of the development of genetics in the 1900s.

A final point should be noted. I contend that the Mendelian-Biometrician controversy is an important episode of the history of genetics. There is still much more that we can learn from that historical episode. We will have a better understanding of the debate over Mendelism and Biometry if it is situated in a broader context. For example, the Mendelian-Biometrician controversy can be viewed as a case of the resistance to the emergence of the Mendelian approach. Weldon's unfinished project can also be viewed as an attempt to explore a new theory of inheritance rather than a mere solution to the Mendelian-Biometrician controversy. Even in order to examine the controversy, we do not have to assume that there are two paradigms or community-based consensuses in competition. We will have a more sophisticated understanding of the significance of the contenders' works if we no longer try to analyse them as an attack or a defence of a particular paradigm. We will also have a fuller understanding of the development of genetics and the biological sciences in the 1900s if we go beyond the Mendelian-Biometrician framework.

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