One hundred and one mendelians

MSc dissertation, Mike Buttolph

1. Summary

This dissertation presents a new detailed analysis of the history of mendelian genetics in the first decade following its inception in 1900. It shows that there is more to that history than the 'rediscovery' of Mendel and a debate between the new mendelians and the 'biometricians', and shows once again that history focussed on 'big fish' may mislead.

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3. Introduction

3.1 The fish of history

E H Carr says that on the commonsense view of history "The facts are available to the historian in documents, inscriptions and so on, like fish on the fishmonger's slab.", but he only sets up this view so that he can tell us later that: "The facts are really not at all like fish on the fishmonger's slab. They are like fish swimming about in a vast and sometimes inaccessible ocean; and what the historian catches will depend, partly on chance, but mainly on what part of the ocean he chooses to fish in and what tackle he chooses to use – these two factors being of course determined by the kinds of fish he wants to catch. By and large, the historian will get the kinds of facts he wants." (1961:9, 23).

In studies of science it is common practice to use large-mesh nets, so getting big fish, and some others in the side-catch. This yields a manageable number of the most prominent facts as the basis of the story.

A typical example is the volume edited by Thomas F Glick, on the comparative reception of relativity, where in the first chapter Stanley Goldberg discusses other Americans, but focuses on the reactions of R C Tolman, R D Carmichael and P W Bridgeman. In the second chapter, Sánchez-Ron structures his account of the reception of special relativity in Great Britain around J H Poynting, J Larmor, N R Campbell and G A Scott (Goldberg 1987, Sánchez-Ron 1987). The same point could be made in relation to *The comparative reception of darwinism* (Glick 1988), and *The reception of the galilean science of motion in seventeenth-century Europe (*Palmerino and Thijssen 2004), two further 'reception studies' chosen at random.

It is the same with other historical approaches. It is clear in any list of biographical studies, and "The texts most often studied by rhetoricians are those that foment scientific revolutions, such as those by Charles Darwin, Isaac Newton, and James Watson and Francis Crick. … Many studies of revolutionary rhetoric use the current historical status of texts not only as a method of selecting the text but also as a measure of its success." (Paul, Charney and Kendall 2001:375).

This issue is generally recognised, and no-one openly advocates the 'big fish' approach for studying science. History based on the 'big fish' whose thoughts and actions played a causative role in the creation of the world of today is 'Whiggish history'. This is everywhere condemned, as bad history, and as morally inappropraite in a democratic age. Yet somehow those who study science still find justification and funding and publishers for more stories about Lavoisier, Darwin and Einstein.

Many of the products of this scholarship are immensely valuable, but they do not present a comprehensive account and may create an overall impression that misleads. There are other stories to be told too. As Herbert Butterfield told the British Society for the History of Science in 1949:

> Some of the surprises, some of the most remarkable reversals of judgment, that have taken place during the last fifty years have been the result of a much more detailed study of a host of intervening scientific workers whose names have been comparatively unknown. A knowledge of these minor people alters the place which we now give in history to Leonardo da Vinci or Galileo or Sir Isaac Newton. (Butterfield 1950:51).

3.2 Relativity for three players

Generally the 'big fish' versions of history do not claim to be comprehensive, but there is an implication that what they say is right, even if incomplete.

In an essay entitled *Two experiments that 'proved' relativity*, Collins and Pinch (1993) described the Michelson-Morley experiment of 1887 and the results of the Eddington Solar eclipse expeditions of 1919. Neither of these gave clear, unequivocal proof of relativity, and the authors claimed that those who accepted relativity at that time did so on the basis of insufficient evidence: "[relativity] is a truth which came into being as a result of decisions about how we should live our scientific lives, and how we should licence our scientific observations; it was a truth brought about by agreement to agree about new things. It was not a truth forced on us by the inexorable logic of a set of crucial experiments." (1998:54). For Collins and Pinch this was an example of a process of social construction by which "the scientific community ... brings order to chaos, transmuting the collective Golem Science into a neat and tidy methodological myth." (1998:149).

But could a different story be told if we had more than the three big fish, Michelson, Morley and Eddington? Of *Two experiments ...* David Mermin said: "Hardly a hint is given that this essay follows a single tiny strand in an enormous tapestry of fact and analysis." ... "Michelson-Morley was only a small part of a network of theory and experiment to which relativity brought clarity and coherence." ... "Their description of the accumulated evidence in its support during its first three decades was so incomplete as to suggest that its acceptance in 1933 was based on sparse and superficial evidence." (Mermin 1996a p1; 1996b p15; 2001 p85). Mermin likens the physics of the early twentieth century to a rich, complex tapestry, and accuses Collins and Pinch of ignoring all but one or two strands thereof.

The essence of Mermin's complaint is not that Collins and Pinch had constructed a shortened, truncated story, but that the story was actually wrong. The physics of the early twentieth century never looked like that to anyone; there was never a time when scientists had only the work of Michelson and Morley, and Eddington, upon which to base a judgement of relativity. All of them had, at every stage, a vast range of data and analyses of greater or lesser significance. They drew upon these when forming their views, each coming to a conclusion based on the data and analyses known to them, their experience, judgement and values.

This is the way in which science has always been done. As Kuhn (1970) has emphasised, it is a process of great complexity, involving a delicate balancing of gains and losses for which no common scale is available. It cannot, for example, be reduced to the simple falsification of an existing theory to usher in a new and better one, and it cannot be reduced to the evaluation of a candidate theory on the basis of two items of information, no matter how important they appeared to the scientists of the time, or appear to us now.

If Collins and Pinch have failed to give a true picture of how things really were in early relativity physics, how could improvements be made? The essence of the failure is in the inadequacy of the data to which they appealed, and a comprehensive data-set is a necessary (though not sufficient) condition for success. A practical difficulty arises in the amount of work that would be involved in acquiring the data-set, but it is achievable with modern communications and information technology.

An example is provided by Stephen Brush's study *The reception of Mendeleev's Periodic Law in America and Britain* (1996). "After spending considerable time perusing the crumbling pages of late-ninetenth-century chemistry journals and books" (1996:618), he generated a list of some two hundred journal references that refer to the Periodic Law, and rather more text- and reference-books, showing which of them mention the Periodic Law, in English, French and German.

3.3 Three stories of genetics

The early history of mendelian genetics has been told many times, but in only three different ways. First there are general histories (many written by scientists) which set out to record, with no particular emphasis, the history from 1900 onwards.[1]

A more specialised story has been constructed as the 'biometrician-mendelian' debate, with William Bateson on one side and Karl Pearson and Raphael Weldon on the other, which is discussed in some detail below.

Finally, the earliest history is usually presented as the story of Mendel's work (1866) brought to light in the year 1900 after thirty-five years of neglect, sometimes with themes of the prematurity of the original work, or the simultaneity of three acts of 'rediscovery'[2,3] . Most of these take the form of examinations of the contributions of the

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[1] See for example, Bowler 1989, Carlson 2004, Darden 1991, Dunn 1965, Sturtevant 1965a, 1965b

[2] In March 1900 de Vries published experimental results showing mendelian heredity, but without acknowledging Mendel (de Vries Database). In May Correns published results of his own (Correns Database), and took the opportunity to emphasise that de Vries must have known of Mendel's work. For example, he gave prominence to Mendel's name in his title *G. Mendel's Regel über das Verhalten der Nachkommenschaft der Rassenbastarde.* He also said that when he recognised the significance of Mendel's work, he had not felt it necessary to claim priority for this 're-discovery'. The usual German words for 're-discovery' would be *die Wiederentdeckung* ('again-discovery') or *die Neuentdeckung* ('new-' or 'latest-discovery'). However, Correns used the rather unusual term *Nach-Entdeckung*, which literally means 'after-discovery.' By this he seems to have been emphasising that both he and de Vries had 'found again' the conclusions that Mendel had published in 1866. The translation 're-discovery' was generally used at the time (for example, Bateson Database:14, 104; Davenport in Ward 1903:46).

[3] There is a further complication here, in that Robert Olby (1979) has contended that Mendel's original work does not encompass the basic ideas that were supposedly found in it by the rediscoverers and those

three ‘rediscoveres’, Carl Correns, Erich Tschermak and Hugo de Vries[4]. In spite of claims made at the time, there is now general agreement that in 1900 each of them had results from experimental breeding that exhibited ‘mendelian’ inheritance, but did not understand this until they read Mendel’s original paper. This point is of no great significance for present purposes; here the three ‘rediscoverers’ are regarded as ‘mendelians’, and further characterised as *retrodicters*, see below.

The second and third of these historical approaches, in particular, describe what was done by a small number of ‘big fish’ - Bateson, Pearson and Weldon, or Correns, de Vries and Tschermak. The general studies give accounts of the leading figures, including these six, but are far from comprehensive in their coverage.

Nothing comparable with Brush’s study of the Periodic Law has been done for mendelism. As long ago as 1981, Daniel J Kevles said that most of the existing scholarship

> does not go much beyond treatments of the principal actors or conceptual developments. Certainly it leaves unexplored the history of the overall corps of men and women, including the commoners in research, who came to form the Anglo-American genetics community. ... The story of these commoners, their significance in research, training programmes and the governance of the community, is a subject of interest in its own right. The commoners also form a useful arena of arbitration for the historiographic issues under consideration here.” (1981:193, 201).

Kevles makes important points of his own[5], but he raises several issues that can only be resolved by a comprehenisve study of the commoners. Amongst other things, he suggests that in England the opponents of mendelism might have included a number of biologists who were not biometricians, wonders whether William Bateson was atypical of British biologists in his embrace of mendelism, seeks to know whether the angry sharpness of the biometrical-mendelian debate extended through the entire British genetics community, and asks who were the early converts to mendelism in the United States and Great Britain, and how their positions are to be accounted for (1981:200, 201).[6]

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who followed them. If that is so, there never was any ‘rediscovery’. However, the continuing use of the term seems justified by convention, no matter how poorly-based.

[4] For Correns see Corcos and Monaghan 1987b, 1987c, Renner 1961, Rheinberger 1995, 2000a, 2000b; for Tschermak see Harwood 2000, Monaghan and Corcos 1986, 1987, Ruckenbauer 2000, Tschermak-Seysenegg 1951; for de Vries see Corcos and Monaghan 1985a, 1987a, Darden 1985, Heimans 1962, 1978, Kottler 1979, Lenay 2000, Meijer 1985, Pas 1976, Stamhuis 1995, 1999, Stomps 1954, Theunissen 1994, Zevenhuizen 2000, Zirkle 1968.

[5] And intimates that he was then making a statistical analysis of early writings on genetics (1981:201 n18, n19), though it seems that this was never published.

[6] These are not the only issues that Kevles raises, but they are the ones to which my analysis provides answers, see section *8. Conclusions*.

More recently Kim (1994) has offered a new survey of the early development of genetics. Although he focusses primarily on the 'biometrician-mendelian debate' (see below), he does not restrict himself to the three 'big fish' – Bateson, Pearson and Weldon – who are usually pulled from this particular area of ocean, but examines too the work of *paradigm articulators* on both sides of that argument. His heirarchy has the 'big fish' as *elite protagonists*, the paradigm articulators (who extend and elaborate the theory to which they subscribe, but without evaluating that theory), and the *critical mass*. This last encompasses the less committed, less vocal, biologists, who none-the-less contributed experimental data in support of mendelism, and played a crucial role in the closure of the biometrician-mendelian debate (1994:35). Kim does not discuss the membership or activities of the critical mass supporting mendelism, and does not seem to envisage a critical mass in support of biometry. I shall identify and characterise the most important members of the mendelian critical mass, and I agree with Kim's implication that there was no identifiable biometric critical mass.

In a perceptive review of Kim, Marga Vicedo points out that his focus on the 'biometrician-mendelian debate' obliges him to situate his soldiers in opposing trenches, whereas the battleground of hereditary and evolutionary studies at the turn of the century "presented a much more fluid and diverse landscape" (1995:376). I shall offer a fuller picture of that landscape, at least in the sense of populating it with more of the soldiers involved.

Vicedo also points out that Kim does not justify his selection of Lock, Hurst, Biffen and Punnett as the 'paradigm articulators' of mendelism (1995:376). Whilst that is true, I think a case could be made that these were Bateson's *leading* articulators. However, my contribution to the discussion will be to offer a complete list of Bateson's articulators, a total of 26 people (including E R Saunders, Vicedo's own nomination).

Finally, I quote Vicedo's closing appeal for more work: "The major weakness results from the fact that to be persuasive [Kim's] project needs more research, research that is not yet available. Sturtevant (1965a) named 22 researchers as the 'early'mendelians, those who made major contrtibutions between 1900 and 1905. ... Before we can defend global characterizations of the work done on heredity and evolution at the turn of the century, we still need many more detailed studies of individual researchers There is still much work to do." (1995:380). Here I present a study of many more researchers, though without as much individual detail as Vicedo had in mind.

This present study is a general history. It covers the leading figures, but also the paradigm articulators and the more important members of the critical mass, or commoners, to give an inclusive, rounded account of what happened in the first few years of the twentieth century. In particular, it seeks to show how mendelism was constructed, tested, extended and legitimised, and by whom, in the decade 1902 to 1911. It also seeks to reveal how this field of work appeared to a well-informed biologist, abreast of recent developments, at the end of that decade – as a complex network of theory and experiment to which mendelism had brought clarity and coherence.

4. The biometrician-mendelian debate

4.1 Biometry and mendelism[7]

A biometrical research programme was established in England at the end of the nineteenth century with the object using mathematical approaches to discover more about the process of evolution, and specifically the mechanism of inheritance. Starting with work of Francis Galton, the approach was characterised by making measurements of one or a few characteristics in succeeding generations, the data then being subjected to sophisticated statistical analysis. The leader of the biometric school was Karl Pearson (1857-1936), based at University College London, with expert biological support from Walter Frank Raphael Weldon (1860-1906) at Oxford. It was an essential feature of biometric thinking that the heredity of each individual can be traced back through all previous generations, the more distant ancestors exerting a diminishing influence.

This established research programme was challenged when Mendel's work was 'rediscovered' in 1900 by de Vries, Correns and Tschermak (see Database entries). Thereafter the principal champion of mendelism was William Bateson (1861-1926) at Cambridge. It was an essential feature of mendelian thinking that the heredity of each individual is determined exclusively by the immediate parents. The mechanisms postulated by mendelism and biometry are quite distinct, but the complexities of biological processes are such that it was not easy for either school to show either that it had a superior research programme, or that its results better represented the realities of nature.

4.2 The 'debate literature'

The 'biometrician-mendelian debate' focusses upon the relationships and exchanges between Bateson, Pearson and Weldon, with 'walk-on' parts for one or two dozen more British and American scientists of the time. It continued during the first decade of the twentieth century, and was at times viciously personal. It now has a substantial literature of its own (Allen 1976; Ankeny 2000; Farrall 1975; Frogatt and Nevin 1971; Kim 1994; MacKenzie 1979, 1981; MacKenzie and Barnes 1974, 1979; Magnello 2004; Olby 1989; Provine 1971; Roll-Hansen 1980; Rushton 2000; Spencer and Paul 1998; and Swinburne 1965). It is also a major feature of more general historical surveys (see for example,

[7] *Mendelism* was first used in 1905, as the title of a small book by R C Punnett (Rieger, Michaelis and Green 1968:282), but he gave no definition. Robert Olby offers the following definition, in the context of a detailed examination of what it was that Mendel brought to the world: "a Mendelian … subscribes explicitly to the existence of a finite number of hereditary elements which in the simplest case is two per hereditary trait, only one of which may enter one germ cell."[7] (Olby 1979:68). In fact, a formal definition of the term is not straightforward, first because there has never been general agreement about the precise nature of Mendel's contribution (Hartl and Orel 1992; Monaghan and Corcos 1990; Olby 1985:234-254); and second, because the doctrine was continually developed and extended (Darden 1991), so that the word meant different things at different times. Here *mendelians* are identified as those who believe that there is mendelian inheritance (see para 5.2 *Data and mendelian interpretation, logically arrived at*), so for that purpose *mendelism* is in the eye of the beholder, and the detailed wording of a definition is not crucially important.

Daniel J Kevles's *Genetics in the United States and Great Britain, 1890-1930,* 1980:442-445; 448-450) and of histories of genetics for the general reader (see, for example, Chapter 17 'A death in Oxford' in Henig 2000; Chapter 7 'Mendel Wars' in Schwartz 2008).

The prominence of this episode in historical and sociological writings seems to have created some impressions that are not entirely accurate. The 'debate literature' gives the overall impression that the two schools were fairly evenly matched but, as I shall show, during the period of the debate there was more and expanding support for mendelism. Some one hundred researchers contributed to this support, and most of these were not part of Bateson's immediate circle (Kim's 'paradigm articulators').

It is claimed in the 'debate literature' that the debate ceased on the death of the biometricians' biologist, W F R Weldon in 1906. This contributes to the impression that both schools were evenly matched, with any apparent victory of mendelism having nothing to do with superior explanatory power or effectiveness as a research programme. In fact, the debate did not decline until the end of the decade, and was not caused by Weldon's death - see below, *7.6 The real challenges to biometry*.

The 'debate literature' focusses on an embattled William Bateson and a few supporters repeatedly assailed by Pearson and Weldon (and a few supporters), but this gives the false impression that mendelism was seriously threatened by biometry. In fact, most of the evidence against mendelism at that time was provided by people who had no interest in biometry – see below, *7.7 The real challenges to mendelism*.

4.3 The challenge of biometry to mendelism

Eileen Magnello (2004) suggests that the 'debate literature' gives a false impression of the challenge that biometry posed to mendelism. Biometry was a challenge in the sense that it represented a different research approach, but not in the sense that some kind of 'defeat' of mendelism was part of the biometric agenda. In fact, both Pearson and Weldon accepted the reality of mendelian inheritance at an early stage. In a letter of 28 November 1901 to Pearson, Weldon said that Mendel "cooked his figures, but he was *substantially* right." (quoted in Magnello 2004:23 n 29). Pearson carried out constructive work on mendelism (see, for example, Pearson 1904a). When a letter in *Nature* claimed that "the facts of Mendelian segregation were still being disputed by the biometric school of evolutionists", Pearson wrote to say that this was untrue, that biometry was "no more pledged to one hypothesis of heredity than to another" (Pearson 1904b).

Pearson and Weldon were the leading biometricians, but others of their school also treated mendelism seriously. Ethel Elderton ("Assisted by Karl Pearson") published a memoir on the resemblance of cousins which starts with a theoretical representation of the transmission of a mendelian recessive detrimental character. Her analysis of survey data shows that an individual resembles cousins to the same extent as uncles and aunts, and she concludes that the physiological bearing of this equality of resemblance "appears to us of fundamental importance as indicating that a determinantal theory of heredity, emphasising alternate inheritance, must take precedence of any theory of simple blending for the bulk of the characters here dealt with". (Elderton 1907:3-4, 20). In other words, here is mendelian inheritance[8]. There are other examples of biometricians who published constructive discussions of mendelism, including Snow (1910) and Harris (1912).

Where there were direct confrontations between mendelians and biometricians the ultimate issue was often a matter of judgement. In 1906 Amy Barrington and Pearson published a biometric account of the inheritance of coat colour in cattle, and the data were then given a mendelian interpretation by James Wilson (see Wilson Database, and *Retrodicters* for more detail). Pearson contested Wilson's interpretation saying, *inter alia,* that the original paper had said "the close approximation to the Mendelian number of the roans is noteworthy, but the appearance of 4(WW) is again impossible … " (Pearson 1908, with a rejoinder from Wilson). For Pearson, the "4(WW)" anomaly is "impossible" and so defeats any mendelian interpretation; for Wilson the four white calves in a total of 332 can be dismissed as due to error.

Eileen Magnello traces the idea that the biometricians were opposed to mendelism to statements to that effect published by William Bateson in 1902, and W E Castle in 1903. These claims became established, and were repeated throughout the twentieth century by biologists including J B S Haldane, Lancelot Hogben, Julian Huxley, A H Sturtevant and Sewall Wright, and by historians including Joan Fisher Box, Bernard Norton, Robert Olby, R G Swinburne and William Provine (Magnello 2004:20, n7, n8).

There were undoubtedly personal antagonisms at work, with Bateson and his circle feeling themselves assailed by Pearson and the other biometricians. This might make for interesting history (and sociology), but it is not evidence that biometry threatened to falsify or otherwise defeat mendelism. There is no evidence either for the oft-repeated accusation that Pearson delayed scientific progress for years (see Magnello 2004:20 n 7 for details), which itself is irreconcilable with the claim that the violent exchanges with the biometricians furthered the consolidation of genetics (Powell, O'Malley, Müller-Wille, Calvert and Dupré 2007:9).

The 'debate literature' gives the false impression that biometry was a serious threat, but at the same time fails to reflect some real problems confronting mendelism, which are discussed below - see *7.7 The real challenges to mendelism.*

5. The database

The centre of this study is the *Database*, listing 101 researchers who signified acceptance of the new science of mendelism in the early years of the twentieth century - they are the first 'mendelians'. This section describes the way in which the Database was constructed, sets out delineations between those included and those excluded, and explains how some other issues have been resolved.

[8] This memoir has original data which are interpreted as showing mendelian heredity, and so would qualify the author to be regarded as a 'mendelian' on the definition I set out below, were it not for the statement at p 4: "But the Mendelian theory cannot be considered as demonstrated …".

5.1 Database construction

There is a large literature on the early history of mendelism but, as discussed in the *Introduction*, it deals with the work of a limited number of people. These more famous people (Bateson, Correns, Davenport, Garrod, Morgan, de Vries et al.) make up roughly a third of the Database. Another third comprises people who are not well known, but have featured in one or a few historical studies (for example, Darbishire (see Ankeny 200), Guyer (see Bungener and Buscalia 2003), Nettleship (see Rushton 2000), Tammes (see Stamhuis 1995) et al). The last third of the Database consists of people to whom I can find no reference in the historical literature, including, for example, Bacot, Beach, Gerould, Leake and van der Stok.

The only sources that have produced any significant number of references for the Database are *A bibliography of plant genetics* (Warner, Sherman and Colvin 1934) and the 1913 revision of Bateson's *Mendel's principles of heredity*. I have read all the papers in the Database, and many others in the process of identifying those to be included. My intention was to identify 100 'mendelians', with a reserve in case it later transpired that a mistake had been made. I have not yet found any mistaken entries, and so the Database has 101 individuals, which provides a title for the paper that chimes with a popular children's book (and Disney film).

More seriously, I should make it clear that the Database includes every 'mendelian' that I have been able to identify in the years up to and including 1911. I have no doubt that there are some that I have failed to find; for example, in the Italian literature I have found only authors who say that their data do not fit mendelian predictions (see Frasetto 1910:170). However, I do not believe that the omissions are very numerous, or that their inclusion would substantially change the conclusions. The Database includes almost everyone who made a significant contribution of data, together with a claim that it showed mendelian inheritance, before 1912.

5.2 Data and mendelian interpretation, logically arrived at

The publication that qualifies its author for inclusion in the Database has passed three tests. It presents a body of data, from which the author is able to demonstrate mendelian heredity. Examples are given below of inadequate data, claims that are not supported by the data, and authors who do not accept the mendelian inheritance exhibited by their data.

These publications thus reflect two processes in the development of the new science – the induction of new recruits, and the augmentation of the supporting factual evidence.

There is no requirement that mendelian heredity is the right and only conclusion to be drawn from the author's data. The intention is to identify those who subscribed to mendelism, and so the test is, as the lawyers would say, *subjective* – it is decided by the state of mind of the person concerned, whether mistaken or not. This approach gives a proper reflection of recruitment to mendelism, though it does entail accepting some rather insignificant contributions of data to the mendelian *corpus.*

Several people are included in the database on the basis of their re-analyses of data previously published. Coutagne, Guyer, Spillman and Weinberg re-analysed data previously published by themselves without a mendelian interpretation. Gerould, Plate and Punnett published new mendelian interpretations of data that had been published earlier by others with different mendelian interpretations. This is discussed further below - see *6.9 Retrodicters.*

Those who republished data that had previously been published with essentially the same mendelian interpretation are excluded. For example, in 1911 Rosanoff and Orr published *A study of heredity in insanity in the light of the mendelian theory,* with data from the records of the King's Park State Hospital New York. However, the same data set, with the same mendelian interpretation, had been published earlier that year by Cannon and Rosenberg (Database). Cannon is included in the database, Rosanoff is not.

Second authors are included in the bibliographic reference. Presumably they subscribed to mendelism, but they are not classed as 'mendelians'.

5.3 Mendelian and non-mendelian inheritance

All the authors listed say explicitly that they have data that exhibit mendelian inheritance. However, none of them says that there is no other mechanism of inheritance, and many of them report non-mendelian inheritance in the same paper – see below. This may appear to involve the recruitment to mendelism of people who did not really subscribe to the new science. As we shall see, one of the trends discernible in this period was the demonstration that mendelian inheritance operates not only in peas (as Mendel had shown in 1866), but in other plants, in animals, and in humans.

This trend encouraged predictions that mendelism would have wide application. However, for the purpose of correctly identifying 'mendelians', the crucial point is this: no-one seriously suggested that there was no other mechanism of inheritance in operation. The 'mendelians' claimed only that there are *some* processes of inheritance that conform to Mendel's law.

Where the author has reported non-mendelian inheritance, or has expressed reservations about mendelism, an attempt has been made to reflect this in the entry in the 'outcome' column - see, for example, the entries for Blaringhem, Durham and Woods.

5.4 Dates

Each paper represents the first occasion on which that author has presented a data-set with a mendelian interpretation. In a few cases it has been necessary to make judgements as to the point in time at which an individual should be regarded as a mendelian. C B Davenport accepted mendelism over a period of more than a year, on the basis of a series of empirical results, and the persuasion of William Bateson (Shor 1971). He published results from his own experimental crosses of mice in January 1904 and concluded: "Mendel did not discover all the important laws of inheritance, and that further investigation will unquestionably reveal other and still broader principles of heredity." (Davenport 1904a: 114). The following week he published his own analyses of the data of other authors on polydactylism in humans and cats, and deaf-mutism in humans, concluding: “while Mendelian principles seem applicable to some cases of crosses between sports and the normal species, there seem to be others where neither Mendel’s nor Galton’s Law of Inheritance holds.” (Davenport 1904b:153).

In these two papers of early 1904, the overall tone suggests that, while there is mendelian inheritance, it is not of any real significance. It seems to me that he emerges as a committed mendelian in November 1905, when he publishes an analysis of the inheritance of black coat colour in the sheep of a herd kept by Alexander Graham Bell, and says: “The conclusion of the whole matter is that black wool color in sheep behaves like a Mendelian recessive character.” (Davenport: Database).

There are a few other cases in which acceptance of mendelism took place over a period of time. A D Darbishire experienced a somewhat painful conversion from biometry to mendelism (Provine 1971; Ankeny 2000). T H Morgan accepted mendelism at an early stage (“the theoretical interpretation that Mendel put on his results is so simple that there can be little doubt that he has hit on the real explanation” (1903:285)). However, this was not based on any original work of his own. Mendelism was thereafter carried forward in a way that he found unconvincing, and he made some very sceptical comments at a meeting of the American Breeders’ Association in 1909: “In the modern interpretation of Mendelism, facts are being transformed into factors at a rapid rate. If one factor will not explain the facts, then two are invoked; … ” (1910:365). Then everything changed for Morgan over a few weeks in the summer of 1910, when he analysed data from experimental crossings of a white-eyed mutant found in his laboratory stocks of *Drosophila*. The 22 July issue of *Science* carries his mendelian explanation of those data, and on that basis he is here considered a mendelian as of 1910.

The dates shown are those of publication, except in the case of papers read at meetings, where the date is that of the meeting. For showing recruitment to mendelism, the oral presentation of a paper seems a satisfactory dating point. The question of adding to the data supporting mendelism is more complicated. Reading a paper at a meeting makes it known to some people interested in the subject, though not of course to everyone. On the other hand, the date when a paper is read is a fixed point, but the time from meeting to publication is somewhat arbitrary. In the Database, Johnson’s paper was read in 1907 and published in 1912.

5.5 Exclusions: revisionists

As discussed elsewhere, the early years of mendelism involved extending and developing the theoretical framework that had first been set out in 1866. Some authors made suggestions for changes so fundamental that the results were not extensions of mendelism, but new theories. Revisions involving major *ad hoc* additions without justification, or abandonment of essential mendelian principles such as segregation, have been disqualified. Two examples are provided by Laughlin’s revision of mendelism to include an antibody against the determiner for pigmentation (1911, 1912), and a scheme of the Scots obstetrician David Berry Hart, which had human sexual characters as mendelian unit characters, but without segregation of the determinants (1909).

5.6 Exclusions: the data-deficient
It was acceptable at this time to publish scientific results with little or no supporting data. For example, by way of evidence that there is mendelian inheritance when *Oenothera rubricalyx* is crossed with itself, Gates says only that "this type splits in the Mendelian ratio of 3:1, giving approximately 75 per cent *O rubricalyx* and 25 per cent *O rubrinervis*." (Gates:Database). C J Davies (1910), gives several original examples of mendelian inheritance from the breeding of domestic animals, but with no details. For example: "Blue skin and face in Wensleydale sheep is believed to come from the combination of black and white factors, and blues mated together give approximately 50 per cent blue, 25 per cent white and 25 per cent black-faced lambs. Black and white gives all blues." (1910:83).

The question arises as to whether the publication meets the requirement for *presenting* data. In borderline cases, this point was decided on the basis of whether the data were accessible to scientific scrutiny. Gates's data were in a paper read at a scientific meeting and published in the *American Naturalis*t (Gates:Database); they were acceptable to the journal editor, accessible to questions at the meeting and to written criticism addressed to the journal. Davis's data appeared in his book *The theory and practice of breeding to type*, which was addressed to dog breeders. Gates is here regarded as a 'mendelian', but Davis is not.

This is not to say that publications addressed to breeders are all excluded. The Database has several publications from the *American Breeders' Association,* but in those cases the adequacy of the data is not an issue.

5.7 Exclusions: the logic-deficient
The data must also be 'adequate' in the sense that they contribute to the author's commitment to mendelism. Houser was unable to show mendelian inheritance in experimental breeding of tobacco plants. In spite of this, he said:

> Before going into this discussion, which is more or less speculative, it may be well to state that, notwithstanding our inability to single out the unit characters concerned; notwithstanding their apparent blending in the first generation and their subsequent apparent failure to segregate, it is the belief of the writer that the Mendelian law offers the best explanation of the hereditary transmission of such qualities as productiveness. (1912:161).

Houser is not regarded as a 'mendelian' because, although he accepts that there is mendelian inheritance, there is no logical support for this from his data.

5.8 Exclusions: recalcitrants
We see the operation of the 'subjective' test of commitment to mendelism in a few cases in which authors published data showing mendelian inheritance, but rejected that interpretation. For example, Louis B Prout (1907) published data showing mendelian inheritance, but said: "the colour dimorphism of *Xanthorhoë ferrugata* does not obey Mendelian law.", and the mendelian interpretation was provided later by Doncaster

(1907). Prout published original data, and the data exhibited mendelian inheritance, but he cannot be regarded as a 'mendelian'

6. The mendelians

6.1 The personnel of mendelism

In 1902 Bateson defended mendelism against what he saw as an unreasonable attack by Weldon. He was concerned that few people had the direct experience of the subject that would enable them to judge Weldon's claims ("The facts of variation and heredity are known to so few that anything passes for evidence") and that this criticism might dissuade newcomers ("but coming from Professor Weldon, there was the danger – almost the certainty – that the small band of younger men who are thinking of research in this field … would look elsewhere for lines of work." Bateson Database: xi, vi).

Ten years later, despite Bateson's concerns (and perhaps despite his attacks on Weldon), one hundred researchers had published original data exhibiting mendelian inheritance, as recorded in the Database.

As discussed below (see *6.7 The mendelians: paradigm articulators*), within that 100 were 66 people who had no particular allegiance either to Bateson or to biometry. These are the scientifically competent, research-active members of Kim's 'critical mass'. There acceptance of mendelism, on the basis of their own researches, represents a commitment by a large proportion of those who had studied the subject. For them, the criticisms based on biometry were interesting (though largely incomprehensible because of the mathematics required), but only one of many issues to be considered and weighed in coming to conclusions. For them, the biometrician-mendelian debate was a side show; noisy and brightly lit, perhaps, but still a side show.

As discussed below, the 'reach' of mendelism was extended in the decade to new organisms and new characters. No-one managed this expansion[9], there was no overall plan to fill in gaps or achieve a measure of universality. Rather investigators chose either organisms that were peculiarly convenient for their purpose, or organisms with which they were already familiar. The first few entries in the Database show Allen working with the mouse, Bateson with Primula and Baur with Antirrhinum. All these choices were simply matters of convenience. Allen's choice of organism had been made by his PhD supervisor, W E Castle, and Allen did no further work in genetics. Bateson did more work on primula, but he also worked on a wide range of other organisms. Baur set out to make "a full analysis of the Antirrhinum species by hybridisation" ("ich will eine völlige hybridologische Analyse der Spezies durchführen." (1910:38)), and studied it for more than twenty years. The totemic instance of an organism selected for geneticist convenience is Morgan's fruit fly (Database).

[9] Though its significance was evident at the time. C B Davenport (1904c:322) described as "epoch-making" what he took to be the first demonstration of mendelian inheritance in animals, Bateson's work using fowls (though Bateson himself said: "Cuénot's paper seems to be the earliest application of Mendelian principles to animals" (Bateson 1903:80, n 1).

The second group is exemplified by Bacot working on the moth Moth *Typhæna comes* and Balls on cotton. Bacot was an amateur lepidopterist who realised that his broods exhibited mendelian inheritance. Balls was employed in Egypt to improve the cotton crop, and sought to enlist the new mendelian principles for this purpose. In a similar way, medical practitioners such as Garrod and Weinberg reported what they found in their human patients. They all used the organism at hand.

Each group chose their organisms as a matter of convenience, the difference is that only the first group had a more-or-less free choice. The second group looked for mendelian inheritance in the organisms they already had, but they did not look for it thereafter in other organisms with which they were not already familiar. This is only a rough classification, but the first group consists of those we should now think of as *geneticists* – Bateson, Baur, Morgan – and the second as *species specialists* – Bacot and Balls. The numbers of geneticists and species specialists in the database are about the same.

6.2 Agriculturalists

In the United States, mendelism was rapidly accepted and nurtured by the agricultural community (Kimmelman 1983, Paul and Kimmelman 1988), whereas Palladino has suggested that in Britain the relationship was not so close, identifying a school of thought that had mendelism as an explanation for botanical experiments, but not as the basis of practical plant breeding (1993:319).

The thesis of Kimmelman and Paul is borne out by the Database, in which almost half (17 of 37) of the contributions by American authors are from those working in agriculture or horticulture. The figure for British nationals is one third (12 of 38). Though this is lower than the figure for the USA, it still suggests that the British agricultural community was well engaged with the new science in its formative years.

6.3 Cytologists

Although most of the evidence listed in the Database was from experimental breeding, five authors reported cytological observations in support of mendelism - see the Database entries for W A Cannon, Farmer, Guyer, Stevens and E B Wilson[10].

At this time various objections were being raised against mendelism. Many authors published data that did not meet mendelian predictions (see *7.7 The real challenges to mendelism*). Others, including some 'mendelians', suggested that it was only pathological or trivial characters that are inherited in mendelian fashion:

> It is evident that we have here to do with abnormal forms that rarely or never occur in nature as self-sustaining species. (Wallace 1908:137).

[10] As with other forms of evidence, there were cytological observations that were interpreted as inconsistent with mendelism, see, for example, Fick 1907:140).

> The characters which behave Mendelianwise are in the main superficial, unimportant attributes of the organism, … (Tower 1910:335).

As a scientific theory, mendelism had been constructed on the basis of the results of breeding experiments. Confirmations from further breeding experiments were significant, but could not easily resolve these and similar criticisms. This situation is similar to that described by Ian Hacking, when the electron microscope revealed new structures within red blood cells. Initially it was thought that they were artefacts of electron microscopy, but they were also found to be visualisable by fluorescence microscopy, and then further characterised by other physical and chemical methods. (Hacking 1983:20-201).

Cytology provided support for mendelism based on a technology quite distinct from experimental breeding. Furthermore, the cytological observations held out the prospect of showing a mechanism underlying mendelian heredity.

6.4 French mendelians

There are seven French mendelians[11], which is rather more than might have been expected when it has been generally felt that mendelian genetics was not well received in that country (see, for example, Buican 1973, 1983; Gayon and Burian 2000). Writing of France in the era 1900-1930, Gayon and Burian say that "by 1930, only one biologist, Lucien Cuénot, had carried out significant genetic research" (2000:1097). Depending on how 'significant' is defined, this may well be true; but that adjective shows that this is yet another 'big fish' account of history. If we look not for people who did 'significant' work, but for all those who made original contributions exhibiting mendelian heredity, we find 6 more good French mendelians by the year 1911, only one short of the German contingent.

6.5 Mathematicians

A major innovation of mendelism was the careful counting of the kinds of offspring produced in large-scale experimental crosses. This gave rise to a lot of data, and editors sometimes allowed these to be printed in large tables. Virtually all of the papers listed in the Database present numerical data, but very few have analyses using anything beyond arithmetic and the most elementary algebra.

In part this is because the Database has only authors who contributed new data, but not those whose contributions were exclusively mathematical. Of these, two were of major importance.

George Udney Yule was a 'paradigm articulator' for biometry (see below), but he

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[11] In addition, the Database has 38 citizens of the British Isles (including 6 Scots of whom one (James Wilson) was resident in Dublin, and one Irish citizen (Augustine Henry) resident in Cambridge), 37 Americans, 8 Germans, and 5 Dutch, together with Tschermak (Austrian), Gates (Canadian, resident in the USA), Haecker (Hungarian by birth and resident in Germany), Toyama (Japanese), Nilsson-Ehle (Swedish) and Lang (Swiss).

accepted mendelism at an early stage and published the first attempt to synthesise it with biometry (1902)[12].

G H Hardy, a Cambridge mathematician, formulated what is now known as the 'Hardy-Weinberg' equation (Hardy 1908)[13]. This shows the proportions of characters occurring in succeeding generations where there is mendelian inheritance. Essentially the same equation was published a little earlier by Wilhelm Weinberg (Database), though this second paper was not recognised in the English-speaking world until 1943 (Stern 1943).

The earliest use of complicated mathematics by a 'mendelian' is Darbishire's paper of 1903, but that was not for mendelian purposes. Darbishire worked for Pearson and was another 'paradigm articulator' of biometry. However, gradually and rather painfully, with advice from Bateson, he came to see that his results were consistent with mendelian predictions (see Provine 1971, Ankeny 2000). In this paper he first offers a biometric analysis of his results, complete with computations of correlations (Database:11-13). Then he discusses mendelian explanations, for which he requires nothing beyond averages and arithmetic.

It is instructive to consider what impression this paper would have made upon biologists of the time – most of them could have followed the second part perfectly well, but not the first.

Weinberg's is one of two other papers in the database with any kind of advanced mathematics (the equation that he produced covered the case of multiple alleles, whereas Hardy had a much simpler formulation based on only two).

Brownlee used mendelian theory to develop a tool by which anthropologists could determine the racial sources of a present-day population. By way of validation, he applied his mendelian scheme to data of hair colour published by Beddoe (1885) and later authors. Using chi-square tests, he showed that some of Beddoe's data were consistent with mendelian inheritance: "he has by direct observation made an unconscious Mendelian analysis." (Database:195). He later extended the approach to cover also eye colour (Brownlee 1912).

The fact that Brownlee's paper was published at the end of the decade is significant. By then mendelism had become quite widely accepted (see 7. *Black-boxing*, where Brownlee's use of mendelism as a tool is considered), and began to attract the attention of more publics, including mathematicians. The American J Arthur Harris had worked with Pearson and always saw himself as a biometrician[14]. In 1911 he published *A simple test of the goodness of fit of mendelian ratios.* He does not say whether or not he believes that

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[12] Tabery says that Yule's proposal was for a reduction of mendelism to the law of ancestral heredity, not a synthesis (2004 :88).

[13] Hardy knew nothing of mendelism, but responded to a request from R C Punnett (Punnett 1950:9).
[14] A festschrift-volume is entitled *J Arthur Harris: botanist and biometrician* (Rosendahl, Gortner and Burr, 1936).

mendelism has any validity, and his motive seems to have been to introduce some mathematical rigour into the expanding mendelian literature, where a wide range of numbers were routinely "simplified" into ratios of 1:2:1, or 3:1.

Other statistical analyses of mendelism at the time included Snow's *On the determination of the chief correlations between collaterals in the case of a simple mendelian population mating at random* (1910) and Hatai's *The mendelian ratio and blended inheritance* (1911). Pearson had started to publish sophisticated mathematical analyses of mendelism, usually in comparison with ancestral heredity, in 1904 (1904a, 1904b), and these continued through the decade and after – see Pearson 1911, Pearson and Heron 1913 (a new statistical analysis of the work of several earlier authors).

6.6 Medical practitioners

The most well-known medical practitioner in the Database is Archibald Garrod, who is sometimes seen as the pioneer of biochemical genetics (Beadle 1958). The mendelian interpretation of his data on alkaptonuria was provided by Bateson but, although Garrod accepted it, he himself had little interest in genetics (Bearn 1993:69). In Britain, Drinkwater, Gossage, Nettleship and Priestley Smith also published evidence of mendelian inheritance of disease conditions or abnormalities in humans[15].

The mendelians of the United States include only one medical practitioner, Gertrude L Cannon, who with A J Rosanoff had found that the "neuropathic make-up", including "imbecility, epilepsy, hysteria, and various mental eccentricities that are not usually included under the designation insanity" is "recessive to normal, in the Mendelian sense" (Database:275, 279). This was one of several contemporary contributions to a literature that would grow and be used to support the development of eugenics. Cannon and her co-author thank Charles D (sic) Davenport for his guidance, advice and assistance (Database:279) Charles Benedict Davenport was to be a leader of the eugenics movement in the United States, and had already published *Eugenics. The science of human improvement by better breeding* (1910) (See Kevles 1985: *Chapter III. Charles Davenport and the worship of great concepts*).

6.7 Paradigm articulators

As discussed in the *Introduction*, Kim identifies three classes of people involved in the 'biometrician-mendelian debate', including the *paradigm articulators*, characterised by their scientific competence together with a commitment to one or the other side in the 'debate' (Kim 1994:35).

Kim gives some examples, but he does not offer an exhaustive list of paradigm articulators, for biometry or for mendelism. Bateson's group, he says, consisted of such researchers as Biffen, Lock, Hurst and Punnett, and to these are added James Wilson [16], Drinkwater, Nettleship and Gossage, a total of 8 (1994:35, 37 fig 2).

[15] Brownlee, Galloway and Henry were also medical practitioners but they did not present data on disease conditions or abnormailities.

[16] Variously shown incorrectly by Kim as "F Wilson" and "James F Wilson".

All of the 100 other people in the database were scientifically competent and it would be surprising if any of them did not know something of Bateson's work. Confronted with a choice, virtually all of them would have supported Bateson rather than Pearson and Weldon. However, many of them, especially those (the majority) outside the British Isles, had little or no contact with Bateson or his immediate circle. Their commitment was to mendelism, but not necessarily to Bateson. They are properly classified as part of Kim's *critical mass* (see the *Introduction*).

However, there are mendelians in the database in addition to the eight people named by Kim who were associated with Bateson and should be regarded as paradigm articulators. The matter is not clear cut: to take one example, Bateson was on very good terms with Erwin Baur. He visited him in 1909, describing him in a letter home as "the best Mendelist *ausserhalb* [outside] England, I think" (Harwood 1993 p 244). The two established a good working relationship, and Baur adopted Bateson's "presence-and-absence" hypothesis in explaining some of his results (see, for example, Baur 1910:38, 91-92). Although they were intellectually close, it seems improbable that Baur saw himself as articulating Bateson's paradigm.

Taking everything into consideration, those who seem to have the requisite commitment to Bateson and his programme are - Balls, Bruce, de Vilmorin, Doncaster, Durham, Garrod, Gregory, Henry, Keeble, Lock, Marryat, Mudge, Salaman, Saunders, Sollas, Staples-Browne, Wheldale and T B Wood, giving, together with the 8 identified by Kim, a total of 26 articulators of the batesonian paradigm.

Kim identifies[17] Castle, Darbishire, C B Davenport, Farabee, Pearl, Schuster, Shull and George Udney Yule as the paradigm articulators that gathered around Weldon and Pearson, a total again of 8 (1994:35, 37 fig 2). Seven of these eight are listed as mendelians in the Database, having abandoned Pearson as described in *7. The real challenges to biometry*. The eighth, Yule, is noted above (see *Mathematicians*). Yule is only excluded from the Database because he published no data of his own. Like all the other biometrician paradigm articulators, he eventually fell out with Pearson, in his case on a dispute about Johannsen's pure lines (the issue that eventually damaged biometry beyond retrieval, see *7.6 The real challenges to biometry*) (Porter 2004:272-273).

Apart from these 34 paradigm articulators, and Bateson himself (an *elite protagonist* in Kim's hierarchy), there are 66 other people in the Database. They are a well-informed, research-active part of Kim's *critical mass* who all subscribed to mendelism. Not directly involved in the 'biometric-mendelian debate', they have no place in the 'debate literature' but I shall suggest in the *Discussion* that they had significance.

6.8 Recidivists

A few authors subscribed to mendelism at the outset, but then rejected it.

[17] Vicedo (1995:375-376) questions Kim's characterisation of Davenport and Pearl as biometric paradigm articulators, illustrating again the difficulty of making clear-cut distinctions in this matter.

After 1903, W E Castle's experimental crossings of rats suggested to him that there might be blending or cross-contamination of unit characters. This was fundamentally at odds with mendelism, which postulates pure, discrete unit characters (genes) which are transmitted from generation to generation without modification by companion genes. By 1910, his views were inconsistent with mendelism, but in *Piebald rats and selection: a correction* (1919) he conceded that his results were explained by the mendelian mechanism that had been suggested by other authors.

F A Woods was a lecturer in biology at MIT, but earlier he had carried out researches with Pearson in London. Publishing the results in 1903 he recognised mendelian inheritance (Database). In 1906 he published data on over eight hundred members of European royal families, finding that mental and moral qualities usually do not blend, but show at least partial alternative inheritance. However, he did not find dominance and recessiveness in his data and so dismissed mendelian inheritance as a possible explanation (1906:274).

Hugo de Vries was one of the rediscoverers, but never thought that mendelian heredity was of any great significance. As late as 1922 he wrote: "The glorification of Mendel is a fashionable article in which everyone, even those without much understanding, can join: this fashion will surely pass." (de Vries to F A F C Went, 14 September 1922, quoted in Theunissen 1994:248). Meijer (1985) concluded that he was not a mendelian, though on the basis of a definition different from that used here.

Their changes of view having been acknowledged, it remains the case that all three met the criteria for inclusion in the Database on the date shown.

6.9 Retrodicters

The Database lists seven mendelians who made re-analyses of data that had been obtained before the original authors knew of mendelism – Brownlee, Bruce, Coutagne, Guyer, Haacke, Spillman and Weinberg. To these should be added the three 'rediscoverers', Correns, Tschermak and de Vries, since each of them had acquired their data before they discovered Mendel's work and realised that their results were consistent with his findings. However, they (and Haacke, see below) had not actually published the findings in advance of the interpretation.

These ten contributions are *retrodictions* – explanations applied to data acquired before the explanation became available.

An eleventh mendelian, James Wilson, made a mendelian interpretation of data published by biometricians, who knew of mendelism but explicitly rejected it. Three authors published new mendelian explanations for data that had already been explained in mendelian terms (see Database entries for Gerould, Plate and Punnett). These retrodictions, in so far as they were in fact 'better' explanations than the originals, helped to establish mendelism on a firmer footing, though they do not contribute new data to the mendelian *corpus*.

6.9.1 Retrodicters who re-analysed their own earlier data

Together with the three 'rediscoverers', four people put forward new mendelian interpretations of data that they themselves had obtained before 1900 – Coutagne, Guyer, Haacke and Spillman.

Guyer and Spillman both said that they had been close to discovering mendelism independently of the announcements made by the "rediscoverers", on the basis of cytological observations and experimental breeding respectively. In 1903, Guyer said: "In studying the germ cells of hybrid pigeons some years ago (1897-1900), the writer observed certain phenomena which led him to much the same opinion regarding the separation of qualities in germ cells as that expressed by Mendel, although at the time the results of Mendel were wholly unknown to him." (Guyer Database:490). Also in 1903, W J Spillman described the 'rediscovery' and said: "Meanwhile, the writer, working on hybrid wheats in this country, announced the law (but not the theory) in November 1901." (Database:269, Spillman 1902).

In contrast, Georges Coutagne simply republished his data from experimental breeding of silkworms with a new mendelian interpretation (Coutagne Database).

The rediscoverers, and Wilhelm Haacke, had obtained their data before they knew of mendel, but had not published it. The stories of the rediscoverers are well covered elsewhere (see the references given in the *Introduction*). Haacke had data showing mendelian heredity before 1900 but did not publish them then. He had carried out breeding experiments with large numbers of mice and followed the inheritance of two pairs of characters, colour or albinism, and waltzing or normal gait. He observed segregation of these characters; Sturtevant says of his observations that they "contain the nearest approach to the Mendelian interpretation before the rediscovery." (1965b:22). From his results Haacke developed a theory whereby heritable elements in the cytoplasm control structural characters such as gait, and elements in the nucleus control chemical characters such as colour of fur (Haacke 1893). However, he published no data to support his conclusions. When he did publish the data in 1906, he interpreted them as a confirmation of mendelism (Haacke Database).

6.9.2 Retrodicters who re-analysed the data of others

Two authors re-analysed data that were originally published by other people in the nineteenth century. The Glasgow medical practitioner John Brownlee made a detailed re-analysis of data first published in *The races of Britain* by John Beddoe in 1885. He showed that the distributions of the characteristics that Beddoe had recorded, particularly colour of hair, were consistent with mendelian inheritance, and went on to suggest that the kind of analysis that he had made could be used to trace the racial origins of groups in a population (Brownlee Database).

In 1876 Darwin published the results of experiments, "continued during eleven years" (1876:15), that he had made to compare the vigour of plants produced by cross- and self-fertilisation. 'Vigour' was measured by the height of the plant, and the numerical data obtained for seven species were passed to Francis Galton for statistical analysis. Galton showed that the plants from cross-fertilisations were consistently taller than those from self-fertilisations, and furthermore that the ratios of those heights “ranges in five cases within very narrow limits. In *Zea mays* it is as 100 to 84, and in the others it ranges between 100 to 76, and 100 to 86.” (1876:18). Galton described the result as “a very remarkable coincidence”, (Darwin 1876:18), but neither he nor Darwin offered an explanation.

In 1910 the Cambridge agriculturalist A B Bruce pointed out that Darwin’s results showed the same narrow range of ratios in many more than five cases. He showed that, if the decline in plant height was due to the accumulation of mendelian recessive characters, the ratios of height would be as 100:83, 100:75 and so on, as the number of character pairs increases (Bruce Database).

6.9.3 Retrodicters who re-analysed data published earlier with biometric explanations

There are also two cases in which new mendelian interpretations were made of data published after 1900, but laden with biometric theory by their original authors.

Wilhelm Weinberg re-analysed data that he himself had first published before he knew anything of mendelism. In 1889 he had started working as a general medical practitioner in Stuttgart. He specialised in obstetrics, and published five papers on the inheritance of a tendency to multiple births (Weinberg 1901, 1902a, 1902b, 1903a, 1903b). The analyses he made of these data at the time were essentially biometric, emphasising blending inheritance (Crawford 1995:2148). He was introduced to mendelism by a lecture given by Heinrich Ziegler in 1905 (Stern 1962:2) and three years later published a new mendelian analysis of his earlier data (Weinberg Database). In this paper he also derived his version of the ‘Hardy-Weinberg equation’ (see *Mathematicians*).

In 1906 Amy Barrington and Pearson published a biometric account of the inheritance of coat colour in cattle, based on data on 2172 calves and their parents drawn at random from volumes of the *Short-horn Herd-book*. In 1908 James Wilson published a mendelian interpretation of the same data (Database), though this was contested by Pearson in a letter to *Nature* (Pearson 1908, with a rejoinder from Wilson). The difference between the two authors was largely due to Pearson’s absolute reliance on the accuracy of the data in the *Herd-book*, whereas Wilson’s practical knowledge of stock and stockmen led him to suspect that there were errors in the data due to carelessness or dishonesty [18]. This case is slightly different from the others, in that the original authors knew about mendelism when they published their data, though like the other authors, Barrington and Pearson had no expectation of a mendelian outcome.

6.10 Retrodiction and theory-ladenness

There are many examples at this time of authors who clearly intend to fit their data to a mendelian explanation. Some extreme cases were considered for inclusion in the

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[18] An essentially similar difference had been at the root of a dispute between Pearson and Hurst at a meeting of the Royal Society in 1905, where Hurst presented a mendelian interpretation of data on the inheritance of coat colour in horses drawn from the *Stud Books* (Punnett 1950:8-9).

Database but rejected - see paras *5.5 Exclusions: revisionists* and *5.7 Exclusions: the logic-deficient* above. Some of those that have been included in the Database give unconvincing support for mendelism (see, for example, the Database entry for Gertrude Cannon). There are counter-examples: the data published by Louis B Prout clearly shows mendelian inheritance, but he says explicitly that he favours biometry – see *5.8 Exclusions: recalcitrants*. Given these patent inclinations for and against mendelism, the suspicion arises that authors might have been biased in the data that they collected, or that they selected for publication, that the data were *theory-loaded* or *theory-laden*.

However, the criticism that data are 'laden' with a particular theory cannot apply to data that precede the theory. The analysis of data by a later theory provides a *retrodiction*, as distinct from the *predictions* from a theory applied to new data. The classic example of a retrodiction is the anomaly in the perihelion of the planet Mercury. The phenomenon had been known since 1859, but there was no explanation for it until Einstein's theory of general relativity of 1905 (Einstein 1920:124-126).

There are different views on the relative values of predictions and retrodictions. Retrodictions derive from 'old' data, a possible criticism of the work done by Brownlee and by Bruce on data from 1885 and 1876 respectively. However, retrodictions are not subject to the bias of theory-ladenness. Furthermore, the capacity to explain something unexplained by existing theories over a period of years may be seen as a particular strength in a new theory. On the other hand, an explanation based on a new theory must be regarded as provisional, because it might be supplanted by a better explanation from a competing theory in due course (Brush 1994).

6.11 Retrodiction and postmaturity

The three 'rediscoverers' published their retrodictions in 1900, and Coutagne, Guyer and Spillman in 1903. This accounts for 6 of the 25 papers published in the first five years (1900-1904) of mendelism, almost a quarter of the total. That seems a high proportion, though it is not clear what should be the 'average' or 'normal value' for such a parameter. An unusually large proportion of retrodictions could result from the accumulation of an unusually large amount of data, not adequately explicable within the existing paradigm. That in turn suggests that the new paradigm is overdue, that the new theory is *postmature* (Zuckerman and Lederberg 1986).

Recently Miller (1992) re-examined two claims that DNA is the genetic material. In 1944 Avery, MacLeod and McCarty did not succeed in persuading other scientists of this, but less than ten years later, Watson and Crick did so. Miller says that the attempt by Avery *et al* to promote the importance of DNA was premature because at that time anomalies were just beginning to be noticed against a framework of fairly solid expectations, and the cautious tone that they adopted in their claim was entirely appropriate.[19] On the other hand, with far more data available, by the time Watson and Crick advanced their claim in 1953, an "explanatory synthesis was awaited", and they were justified in adopting a more confident tone.

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[19] On the cautious tone of Avery et al, see also Cresto 2007.

Given the data that were accumulated in the years following 1866[20], it seems quite credible to think of the year 1900, the year of 'rediscovery', as a better time for the reception of and explanatory synthesis of knowledge of heredity.

Zuckerman and Lederberg say that postmaturity "is a matter of retrospective conjecture" (1986:629), but the concept might be made rather more concrete by measuring the proportion of retrodictions that occur in the literature engendered by new theories.

One might expect *prima facie* that postmature discoveries are more likely to be made simultaneously by more than one investigator. As we have seen, in the case of mendelism three 'rediscoverers' were involved[21].

Finally, if it is accepted that the rediscovery of Mendel's work was in fact 'postmature', there is a nice symmetry with the old contention that his original work was premature (Glass 1974, Zirkle 1964).

7. Mendelism

7.1 The aspirations of mendelism

Mendelism was widely seen as a means of advancing the status of biology, so that it would become, and be seen as, more scientific and more serious. In 1900, biology was regarded as a collection of facts, and the best that could be hoped for was that they could be interrelated and classified in a rational way.

In this respect, the situation in biology was rather like that thirty years earlier, when Mendeleev's periodic law brought lawfulness to chemistry: "Teachers saw an urgent need to show their students that chemistry is not just a huge collection of facts to be memorized but that, in the words of the English chemist M M Patterson Muir, 'law and order pervade [its] vast domain'. Once the student can connect the atomic weight of an element with its position in a general classification scheme, 'he gains a basis on which he may rest a superstructure of facts as they are presented to him'" (Brush 1996:600).

The early mendelians foresaw that their work would bring biology to a new status, no longer near the base of the hierarchy of the sciences. Bateson said: "Following the clue which [Mendel's] long lost papers provided, we have reached a point from which classes of phenomena hitherto proverbial for their seeming irregularity can be recognised as parts of a consistent whole. The study of Heredity thus becomes part of an organised branch of physiological science, already abundant in results, and in promise unsurpassed." (1909: v).

[20] See, for example, Delages 1903, Olby 1985, Roberts 1929, Robinson 1979 and Stubbe 1972

[21] This has long been regarded as an exemplar of simultaneity: in 1961 Robert K Merton described the case of the simultaneous discovery of Mendel's work as "too well known to need review" (1961:480).

Others saw that Mendelism would bring to biology the certainties of contemporary celestial mechanics:

> One of the corollaries of Mendel's law is that each pair of contrasting characters in a hybrid works out its effects, for the most part, independently of all other pairs. As in Newton's 'Law of the Coexistence of Motion', the final result is but the summing up of the various component movements taken separately." (Brainerd Database:941).
>
> As Galileo, Newton and Kepler discovered laws that are since used for the accurate determination of celestial phenomena, likewise Mendel and other investigators have disclosed laws for genetic transmission. … The guesses of Aristotle are being replaced by the laws of causation. We are nearing the dawn of genetic science and let us utilize its light while approaching." (Simpson Database:250, 255).

7.1.1 Mendelism as chemistry

Others saw chemistry as the hallmark of scientific certainty, of falsifiability: chemistry as more certain. Lucien Cuénot constructed a scheme based upon the enzymic syntheses of pigments to explain the inheritance of coat colouration in mice – see below. He said that this scheme has the advantage of substituting for the idea of dominance, which is nothing but a statement of fact, an explanation based on chemistry, open to experimental verification. ("Elle a encore l'avantage de substituer à la notion de dominance, … notion qui n'est que l'expression du fait constaté, une explication d'ordre chimique, susceptible de vérification expérimentale." Cuénot 1903:XXXIX).

The periodic law's prediction of the existence of gallium and scandium before they were discovered was "now regarded as among the most remarkable achievements of modern science" (*Elements of chemistry*, by F W Clarke, quoted in Brush 1996:611-612). The promise of predictive power held out by mendelism was a great attraction for anyone with experience of experimental breeding. Bateson drew attention to this in 1902[22], predicting that breeders would "forecast the character of the race in regard to each such pair of characters taken severally, but this is an immeasurable advance on anything we knew before. … Soon every science that deals with animals and plants will be teeming with discovery, made possible by Mendel's work. The breeder, whether of plants or of animals, no longer trudging in the old paths of tradition, will be second only to the chemist in resource and in foresight." (Database:196, 208).

7.1.2 The certainties of chemistry

The aspirations of the mendelians to chemistry-like certainties are frequently shown in analogies that they draw with chemical entities:

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22 Bateson said that he had compared Mendel's law to Mendeleev's in a lecture in 1900, but this did not appear in the published version (Olby 1985:128). However, the lecture was reprinted in 1902, and says at the end: "and I venture to think that I used no extravagant words when, in introducing Mendel's work to the readers of the Royal Horticultural Society's Journal, I ventured to declare that his experiments are worthy to rank with those which laid the foundation of the Atomic laws of Chemistry." (Database:35)

> Some remarks may be made in this place concerning the meaning of coupling. … The theory at present advanced by Mendelian biologists makes in my notation $m/n = 2^p - 1$ when p is a positive integer. I confess that I cannot follow the arguments on which this is based. The facts seem to me much more in line with the conditions of stability in chemical solutions. If there be a solution, say, of Na_2SO_4 and HCl, the relative proportions of the four possible substances depend on the rate at which … (Brownlee 1912:460).
>
> It may be that there is a kind of biological isomerism, in which, instead of molecules of the same formula having different physical properties, there are isomers capable of forming the same character, although, through difference in construction, they are not allelomorphic to each other. … Several of these units which produce the same character may become attached like a chemical radical and again behave as a single pair." (East Database:1, 72).
>
> Mendelian phenomena force on us the conclusion that organisms display a number of unit characters, each of which behaves in much the same way as a radical does in chemistry … The sexual act would appear to resemble a chemical synthesis in some respects … In chemical reactions the tendency is for the most stable combinations to be formed, so in nature (161). (Dewar and Finn 1909:151, 152, 161).

7.1.3 Chemical analogies

The analogy of genes with chemical entities was also good for teaching purposes. In 1909 George Shull described *A simple device to illustrate mendelian inheritance*, in which acid, alkali and a solution of litmus are arranged in containers so that, on mixing, red and blue colours behave as mendelian unit characters. J P Lotsy had a more sophisticated teaching tool in which no indicator was needed, but instead the yellow colour of platinum chloride represented the dominant allele, the yellow colour persisting in the combination with white potassium chloride, and then segregating again in the next 'generation':

	weißes KCl zu gelbem $PtCl_4$	
So erhalt ich	\ /	
	Gelbes K_2PtCl_6	(ursprüngliche Hybride, in
	/ \	welcher "gelbe" dominiert)
Nehmen wir an, daß dies	/ \	
auseinander fällt in	KCl und $PtCl_4$	(Reine Fortpflanzungszellen
	(weiß) (gelb)	der Hybride)

(Lotsy 1906, 112-113)

Finally, the mendelians also used chemical analogies when emphasising (*contra* the biometricians) that genes persist and are unaffected by their histories:

> The number of generations through which a character of a variety has remained pure alters the probability of its dominance … no more, so far as we are yet aware,

than the length of time a stable element has been isolated alters the properties of a chemical compound which may be prepared from it." (Bateson Database:129)

The genotype-conception is thus an 'ahistoric' view of the reactions of living beings – of course only so far as true heredity is concerned. This view is an analog to the chemical view, as already pointed out; chemical compounds have no compromising ante-act, H_2O is always H_2O, and reacts always in the same manner, whatsoever may be the 'history' of its formation or the earlier states of its elements." (Johannsen 1911:139)

7.1.4 Biometrician chemistry

Pearson thought that the mendelian use of a chemical analogy might ultimately suit his case rather than theirs. As we have seen, the mendelians often compared unit characters to chemical entities, to emphasise that the unit character is fixed, and passes through combinations to emerge unchanged. Pearson pointed out in 1911 that modern physical chemistry regarded populations of molecules as statistically but not literally identical, and he contemplated the possibility that "the attempt of some biologists to replace vital variation by 'unit' characters be really a retrogressive change, and the persistence and absence of individuality to which they appeal as comparable with chemical changes be ultimately a false analogy, because the sameness of chemical theory is a statistical experience which may ultimately admit differentiation within the class." (1911b:156).

7.2 The reach of mendelism

7.2.1 Organisms

In the years to 1911, breeding experiments with peas confirmed and extended Mendel's original results – see the Database entries for Correns, Keeble, Laxton, Tschermak and de Vilmorin. In addition, the database shows that the reach of mendelism was extended to encompass many other plant species, and animals including humans.

7.2.2 Hybrids of species

In 1900 Correns thought that mendelian inheritance occurred in only a limited number of situations, and specifically that it probably occurred only in hybrids between varieties (Database:107). In 1909 Blaringhem too said that crosses between varieties showed mendelian heredity, but crosses between species did not (Database). However, Baur, Brainerd and Lotsy were all able to demonstrate that species crosses in plants followed mendelian predictions (Database entries).

7.2.3 Characters

Most of the characters whose inheritance was studied were easily visible, mainly colouration, but also the form of leaf or the height of plants, brachydactyly in humans, and so on. The exceptions are

Time of ripening in wheat (Biffen)
Immunity to rust in wheat (Biffen)
Immunity to aphids in cherry and plum trees (Beach)
Time of ripening in cotton (Balls)
Nervous diseases (Crouzon),
Insanity (Gertrude L Cannon)
Blood groups (von Dungern)
Tendency to multiple births (Weinberg)

7.2.4 Material, constitutional and physiological characters

There was a general awareness that most easily-visible characters were relatively unimportant, and those who worked with other characters emphasised their greater significance. Discussing early and late ripening in wheats, Biffen said: "We have thus one pair of 'constitutional' as distinct from morphological characters obeying Mendel's laws. As many of these are of far greater importance to the agriculturalist than the merely morphological characters, a number are being investigated in detail. The most important of these is the disposition to withstand the attacks of parasitic fungi …" (Biffen Database:282) – and see below, *Applications of mendelism.*

Coutagne distinguished between morphological characters which strike the eye of the naturalist, and serve to define species, ("les caractéres morphologiques qui frappent l'oeil du naturaliste, et servent à définir les espèces …") and physiological characters "concerned on the other hand with the intimate biological function of organs" ("concernant au contraire le fonctionnement intime des organes") (Coutagne 1904:234, 233).

Others sought theoretical schemes giving material form to the characters transmitted by mendelian inheritance. Von Dungern and Hirschfeld speak throughout of the characters they study as "structures", that is, the group-specific structures of the red blood cells, though these structures are not anatomically visible ("gruppenspezifischen Strukturen der Blutkörper, … diese Strukturen nicht anatomisch sichtbar sind",von Dungern Database:284 n 1). Silverstein (1989:296) says that this was "perhaps the first interpretation of Mendelian inheritance in terms of the formation of specific molecular entities.".

Lucien Cuénot saw that even a simple visible character such as coat colour in mice must be produced by some underlying physiological process. His early work (Cuénot Database), was developed into a scheme by which a colour-precursor ("chromogène ") is acted upon by one or both of two enzymes, producing black and yellow pigments: (" … deux diastases, l'une pour la pigment noirâtre, l'autre pour la pigment jaune … " Cuénot 1903:XXXVIII). And the capacity to make these three materials (chromogen and two enzymes) must be carried in the hereditary material:

> The germ plasm of a grey mouse must contain the potential for the three substances which, by their interactions, later produce the hair-pigments; and these three substances are undoubtedly present potentially in the same number of material particles of the germ plasm …
> "Le plasma germinatif d'une Souris grise doit contenir en puissance les trois substances qui, par leurs réactions réciproques, produiront plus tard les depôts pigmentaires des poiles; et sans doute ces trois substances sont contenues à l'état potentiel dans autant de particules matérielles du plasma germinatif … " (Cuénot 1903:XXXVIII).

Cuénot says that this scheme has proved to be accurate in predicting the outcome of hybridisations (Cuénot 1903:XXXIX).

Here we have the first steps in understanding of the essentially chemical mechanisms by which inherited factors are expressed in the organism.

7.3 The evidence for mendelism

The Database shows that in 1900 the three 'rediscovery' papers were published, but has no entries for 1901. That is not to say that no-one wrote about mendelism in that year, but rather that no-one came forward with any new evidence. The delay seems to be due simply to the time required to make and analyse breeding experiments[23]. Bateson, for example, had been carrying out breeding experiments for some years before 1900, but the first evidence that he published for mendelism was from crossings of plants grown in 1901 and 1902 (Database:182).

The numbers of papers in the Database for the ten years 1902-1911 were:

7, 7, 8, 10, 11, 9, 11, 11, 13, 11.

The number for each year is small and no major pattern seems apparent other than a gradual increase.

The result of all this was a series of 101 pieces of evidence for mendelism. How is this collection to be regarded? "All science is either physics or stamp collecting" claimed Ernest Rutherford (Blactkett 1962:108). Most stamp collections are put together by individuals who seek and select their stamps. The literature of mendelism is more akin to an archaeological or geological collection, in that its objects had all been discovered, and donated by the discoverer. Generally the donors were not selected, but came forward without invitation. They had in common a desire to see the collection expand and serve useful purposes, and more or less knowledge of the subject. The curators received, examined and catalogued the items. They then selected some of the better specimens and displayed them, in a good light and with expert commentary, in an exhibition. The result was a general review of mendelism, such as Bateson's *Mendel's principles of heredity*

[23] There have been much longer delays in the acceptance by the scientific community of other new ideas. Darwin's theory of evolution by natural selection was ignored by the learned societies in Britain for some years, but that seems to have been largely a matter of the avoidance of controversy (Burkhardt in Glick 1988).

(1913), Darbishire's *Breeding and the mendelian discovery* (1911) and Walter's *Genetics: an introduction to the study of heredity* (1913).

Other curators selected a smaller number of items for a special audience, or to illustrate one particular point. Exhibitions of these kinds are found in Bateson's presentation to medical practitioners at the Royal Society of Medicine in 1908 (Bateson 1909), and Spillman's review of selected items to give support to his revision of mendelism based on 'teleones' (Spillman 1910).

In all these cases the curators sought to attract the attention of the public (or a public), to advance the subject in which they were interested, and to attract the attention of others who might themselves contribute to the collection.

Without pressing the analogy any further, we can see that the body of knowledge of a given science could be seen as a 'collection' (though it is not obvious that the analogy does not hold for physics). In 1911 the 'mendelism collection' comprised items submitted by one hundred and one donors. Since many of those had made multiple donations, the one hundred and one donors had contributed perhaps two or three hundred items (that is, individual data-sets each exhibiting mendelian inheritance). With the passage of time, some of these items might have been found to be fakes, or to have been included in the 'mendelism' collection in error; but these were few [24]. If anything, the balance of the traffic was in the opposite direction – specimens believed by the original discoverer to be ineligible (or to be part of some other collection, such as 'biometry') were later found to be good 'mendelism' after all, and admitted to the collection [25].

7.4 The applications of mendelism

The early mendelians believed that the new science would have important practical applications. Vernon Kellogg said that experimental breeding "with the Mendelian principle in mind will enable the professional silk grower to determine speedily the simple or compound nature of the characteristics of the eggs, larvae and cocoons; ... and will save him much waste of time in empirical work." Kellogg Database:63). Gilbert said that his work with tomatoes demonstrated "the economic and commercial use of Mendelism. Desirable unit characters may be transferred from one plant to another almost at will. Mendelism has an unlimited commercial application" (Gilbert Database:187-188).

Bateson foresaw that the discovery of dominance and recessiveness was of major practical significance for the breeding of varieties with desired characters. "Wherever there is marked dominance of one character, the breeder can at once get an indication of the amount of trouble he will have in getting his cross-bred true to either dominant or recessive character. He can only thus forecast the character of the race in regard to each

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[24] I know of no examples. Even 'recalcitrants' such as W E Castle and F A Woods, never withdrew the mendelian interpretations that they put on their data in 1902 and 1903 respectively – see Database.

[25] For example, the re-presentation with mendelian explanations of data-sets that had initially been seen as unconformable (see the discussion of Doncaster's re-interpretation of Prout), or had been given biometric interpretations (see Database entries for Weinberg and James Wilson).

such pair of characters taken severally, but this is an immeasurable advance on anything we knew before." (Database:196). Castle made the same point: "The law of Mendel reduces to an exact science the art of breeding in the case most carefully studied by him, that of entire dominance." (Castle Database:541).

Bateson and Castle were both writing in 1902. Five years later it was clear that dominance was rather a mixed blessing: "The breeding of pure types [of cotton] suitable for the needs of the manufacturer and the cultivator will possibly prove a little difficult, owing to the fact that many of the characters of economic importance are dominant." (Balls Database:216). Shoemaker found it difficult to follow the inheritance of commercially-important *lint length* in cotton, since it varies only slightly. He demonstrated mendelian heredity of leaf form, but the types were difficult to stabilise, and concluded that this work "does not seem to hold out any great hopes of fixing intermediate types of lint, should Mendel's law also apply to that character." (Shoemaker Database:119)

However, there were successes. As early as 1903, Biffen recognised that in wheat immunity from the disease 'rust' is "a definite Mendelian character" (Database:282). The great significance of this was immediately clear, especially since rust resistance was recessive rather than dominant, and so could be fixed into a new wheat fairly easily. Bateson described Biffen's work "as perhaps one of the most important instances to which Mendelian method has yet been applied." (1913:25).

Making use of the inheritance of resistance as a mendelian recessive gene, Biffen bred a new rust resistant winter wheat, *Little Joss*. It was released for agricultural use in 1910, and was very successful in reducing losses from disease and raising yields. Bell (1976) says that this work was "an achievement of outstanding merit as Little Joss attained an important place in English wheat growing because of its valuable field characters, while it later remained on the national list of recommended varieties issued by the National Institute of Agricultural Botany until 1956."

7.5 The acceptance of mendelism

7.5.1 Accounts of what Mendel had done

In 1900 few people knew anything of mendelism. A researcher who wanted to claim that data were, or were not, consistent with Mendel's law would first have to explain what that law was. Mendelism gradually became better known and better understood, and by the end of the decade there were several substantial audiences for whom no explanation was necessary. In addressing those audiences, it was sufficient to refer to *mendelian heredity* or *mendelian results*, without further explanation. Mendelism had achieved credibility, had become 'black-boxed' (Latour and Woolgar 1979:242, Latour 1987: 131). This process can be followed in a decline in the perceived need for explanations of mendelism, and in changing uses of *Mendel* and derivatives.

As we should expect, early papers all give descriptions of Mendel's rediscovered work – see the database entries for Correns, de Vries, Tschermak (all 1900), Bateson, Castle and Cuénot (all 1902) and Spillman (1903). Thereafter, botanical audiences were expected to know about Mendel[26], but some of the papers addressed to zoologists continued to explain what mendelism is. For example, in claiming that there is mendelian heredity in mice, Allen in 1904 and Haacke in 1906 both have over a page on the essentials of mendelism (and Haacke was writing for the well-informed readership of the *Archiv für Entwicklungsmechanik der Organismen*). As late as 1909, Standfuss gives well over two pages (of 15) to explain mendelism when writing about Lepidoptera (Database:34-36). It is not a coincidence that these papers are both addressed to German audiences; by 1906 or 1909, mendelism was generally well understood in the English-speaking world.

Finally, and perhaps unsurprisingly, the physicians and social workers seem to have represented the last bastion, when Gertrude L Cannon addressed a two-page explanation of basic mendelism to them in 1911, so that they might the better understand the mendelian inheritance of insanity (Database:272-274).

7.5.2 Developing *mendelian* understanding

The word *Mendel* and derivatives such as *Mendelian* is used in 25 of 101 titles in the Database. Its first use in a title was by Correns in 1900 (Correns Database). In this and other early uses the title was clearly intended to advertise an exposition and explanation of something new (see, for example, Bateson and Castle (both 1902), Spillman (1903)), perhaps in relation to a named phenomenon – Cuénot's *La loi de Mendel at l'hérédité de la pigmentation chez les souris*, Guyer's *The germ cell and the results of Mendel*.

In the five year period 1902-1906, the word *Mendel* is used in this way in 8 titles. The adjectival form *Mendelian* appears once, in W A Cannon's *A cytological basis for the Mendelian laws* (1902).

In the following five years, 1907-1911, the adjective is used in ten titles, twice as many as include the noun *Mendel*. Clearly many authors now believe that their audiences will understand the qualifying term *mendelian*. This is consistent with the decline in the perceived need for *explanations* of mendelism discussed above.

The way in which the biometricians used these terms shows a similar trend. There were several references to *Mendel* in the early titles of Weldon and Pearson (Weldon 1902a, 1902b. 1902c, 1903; Pearson 1904a, 1904d), but Pearson was an 'early adopter' of the adjective *mendelian* (1904b, 1904c).

7.5.3 Introducing *mendelian* tools

The term 'black box' is used to simplify discourse, but black boxes are generally seen as serving some purpose. Having achieved the status of 'black box' for the purposes of discourse, by 1911 the term *mendelian* came to signify also something that has applications, as a *tool* or *technique*. All prior uses refer to mendelian *heredity*, that is, to

[26] There is the occasional exception. In his paper on wheat hybrids of 1906, Keyser gives an outline of Mendel's researches in one paragraph (Database:89).

the inheritance of characters according to Mendel's law. In 1911 for the first time there are descriptions of mendelian *tools* – the *mendelian formula* used to analyse racial origins (Brownlee Database), the *mendelian study* showing 'the economic and commercial use of Mendelism' (Gilbert Database:188).

The biometricians did not discuss *mendelian tools*, which is consistent with the view that mendelism has only a narrow validity.

7.5.4 The challenge of *genetics*

At the outset, *mendelism* was a set of regularities in inheritance in peas, but it soon extended far beyond that. As Bateson said in 1906, "the physiology of heredity and variation is a definite branch of science", and he suggested that it be called *genetics*. Bateson had his new word incorporated into the title of the International Conference held in London in that year (Wilkes 1907) and used it in the titles of a review of 1907 and of his inaugural lecture (1908). However, it was not used in any title in the database, and there seem to be only three appearances of *genetics* in the titles of research papers before 1912 (Castle and Philips 1909, Wheldale 1909, and Jennings 1911). It would be interesting to know why there was such a slow take-up of a term which has now supplanted *mendelism* [27] almost completely.

7.6 The real challenges to biometry

Those whose data did not conform to mendelism did not turn to biometry, but there was traffic in the other direction: several of those who started as biometricians eventually became 'mendelians', and are shown as such in the Database. The outcome of this trend is summarised, in rather personal terms, by H S Jennings (1910:143): "Note how quickly the biometricians that devote themselves to careful biological investigations fall away from the Pearsonian faith. Darbishire, Davenport, Tower, Shull, Johanssen, Pearl; are there any biologists of achievement that still hold with Pearson?"

These losses of biological talent were a problem for Pearson, but the most important loss to biometry was the sudden death of Weldon. Several commentators have this as the closing event in the dispute with the mendelians: "And so the controversy was to continue until the death of Weldon in 1906. At this point it rapidly subsided: there were to be no more direct confrontations." (MacKenzie and Barnes (1974:12). Essentially the same point is made in Bowler (1989:119), MacKenzie (1981:246), (Magnello 2004:28) and (Provine 1971:88). Kevles says that the dispute diminished in intensity not only because Weldon died, but "Quite possibly it was also because two of the chief contestants [Pearson and Bateson] acquired more secure institutional status … " (1980:450).

None of these writers give either evidence or authority for their claim about the consequences of the death of Weldon. It may be that they all simply repeat, without attribution, what was said by the earliest of them, William Provine. It may be that Provine took it, without attribution, from what Punnett had written in 1950: "Then

[27] The first and last books entitled *Mendelism* were those of Punnett (1905, seventh edition 1927) and James Wilson (1916, second edition 1929).

suddenly Weldon died; the controversial stage fizzled out and genetics entered into its own." (1950:9). Provine discusses Weldon's death and its supposed results on p188 of his book, and has on this same page (footnote 75) a reference to Punnett 1950 for a different point.

The externalist approach taken by the originators of the 'debate literature' privileges non-scientific over scientific factors as determining the course and conclusion of the debate. The only evidence that the debate came to an end because Weldon died seems to originate in the memoirs of one of the scientists involved in the debate, written fifty years after the event. Punnett was Bateson's closest ally and was certainly involved in the debate; but, as we shall see, neither of these men was actually involved in its closure.

As early as 1976, Garland Allen entered the objection that "The further suggestion, that the controversy ended largely because Weldon died, does considerable injustice to any understanding of how historical change comes about." (Allen 1976:111).

Weldon had been the most devoted biometric biologist, but it would be surprising if the death of one individual were a sufficient cause for the termination of a serious research programme. In fact, biometry did not decline in 1906; Pearson and his allies continued to write about mendelism for some years after Weldon died (see for, example, Harris, 1911; Pearson 1909; Snow 1910). However, after 1909, three years after Weldon died, there were conceptual developments that seriously devalued the biometric approach to heredity.

Pearson always maintained that biometry had nothing to do with theories of inheritance. As noted above, he wrote to *Nature* in 1904 to say that that biometry was "no more pledged to one hypothesis of heredity than to another." The biometricians' *law of ancestral inheritance*, was: "not a biological hypothesis, but the mathematical expression of statistical variates." (Pearson 1930:21). On the face of it, this put the biometricians in a strong position – they collected data on some chosen characteristic in related individuals, made mathematical analyses and reported the results. It was difficult to contest the rightness of the data, or of the analyses.

It took some time for the biologists to realise that biometry did in fact incorporate an hypothesis of heredity – that the characteristics that a parent transmits to the next generation are accurately and unambiguously represented by the characteristics of that parent's own body. The idea itself seems reasonable, and is consistent with the familiar process by which parents have goods or ideas which they pass by inheritance to their offspring – the *transmission-conception* of heredity (Johannsen 1911:130). But as Johannsen said in this address to the American Society of Naturalists, "The transmission-conception of heredity represents exactly the reverse of the real facts, just as the famous Stahlian theory of 'phlogiston' was an expression diametrically opposite to the chemical reality." (1911:130).

The crucial difference between genotype and phenotype was set out in Johannsen's *Elemente der exakten Erblichkeitslehre* (1909). Raymond Pearl[28] described the implications of this idea for biometry in 1911, when he wrote:

> Now as a matter of fact, practically all the work that has been done upon inheritance by Pearson and his co-workers seems to the writer to involve from its very beginning a fundamental biological assumption. This assumption is that the correct determination of the correlation in respect to external, somatic characters between genetically related individuals is an adequate measure of the intensity of inheritance between these individuals. But the validity of this assumption has never been demonstrated, and presumably never can be, because the assumption itself is contrary to demonstrated biological facts, which can at any time be experimentally verified. The facts to which I allude are those upon which rest the demonstration of the existence of the *genotype* as contrasted with the *phenotype* in inheritance (Pearl 1911 (1915):64-65).

Johannsen emphasised that biometry as a research programme on heredity could not survive the new thinking: "The famous Galtonian law of regression and its corollaries elaborated by Pearson pretended to have established the laws of 'ancestral influences' in mathematical terms. … such interesting products of mathematical genius may be social statistics *in optima forma*, but they have nothing at all to do with genetics or general biology! Their premises are inadequate for insight into the nature of heredity." (1911:138).

The genotype/phenotype distinction became a live issue around 1910, but the outline of the idea had been discerned in Mendel's work as soon as it was 're-discovered'. Disputing with Weldon in 1902, Bateson had said: "Mendel, on the contrary, disregards the 'condition of the character' in the parent altogether; but is solely concerned with the nature of the characters of the *gametes*. … [and] has proved that the inheritance from individuals of *identical ancestry* may be entirely different:" (Bateson Database:186 footnote, 185).

In 1907 Lucien Cuénot drew a clear distinction between genotype ("caractère-unité") and phenotype ("caractère descriptif"), and said that failure to see this distinction had caused researches in heredity based on statistical analyses to give only approximate results; clear results will only be obtained by defining first the unit-characters at work:

> It is because of a failure to appreciate the difference between a descriptive character and a unit character that all the researches on heredity based on the interpretation of statistics, on some mathematical apparatus with which they are surrounded, give results that are only approximate, or even completely incorrect:.
>
> ("C'est pour n'avoir connu la distinction profonde à établir entre caractère descriptif et caractère unité, que toutes les recherches sur l'Hérédité basées sur l'interprétation de statistiques, de quelque appareil mathématique qu'elles soient entourées, ont donné des résultats seulement approchés ou même parfaitement inexacts:" (1907:XI).

[28] Raymond Pearl (1879-1940) was an American biometrician who had fallen out with Pearson in 1910 (Kim 1994:130).

The history of the recognition of this defect in biometry is briefly given by Kim (1994:139-140) and will not be further described here (though it would repay a more detailed study). For present purposes the essential point is that the realisations that biometry incorporated an (unspoken) hypothesis of heredity, and that the hypothesis was incorrect, were quite sufficient to cause a loss of interest in biometry.

Contemporaneous with these developments was a quite separate defeat for biometry, in the dawning realisation that mendelism could explain blending inheritance. Mendel and the early mendelians had focussed their attention on the inheritance of discrete character pairs, such as roundness and wrinkledness in peas, presence and absence of colour in the coats of mammals. It had been generally assumed that mendelism could not deal with 'blending' inheritance, the inheritance of 'quantitative' characters, where there was a range of results such as height in humans. Bateson discussed this point in 1902, though he formulated it in terms of the removal of cases which "obey the Mendelian principle … finally and irretrievable from the operations of the law of Ancestral Heredity." (Database:106). In 1909 Bateson was still distinguishing Mendel's system from that of Galton on the basis of their applying to discrete and blending inheritance respectively, but he also intimated that mendelism might provide an explanation for blending inheritance (1909:54-56).

And so it turned out. Nilsson-Ehle in 1908, East in 1910 and Tammes in 1911 showed that mendelian inheritance of multiple genes control continuously-varying, blending, characters in oats, maize and flax respectively (see Database entries).

In the few years between 1908 and 1911, biometry was shown to have a shaky theoretical foundation, and was supplanted as the means of explaining the one important biological phenomenon that had not previously yielded to mendelism. It is difficult to conceive of anything that Weldon might have done to alter this course of events had he survived.

This reading has the debate about biometry determined on the basis of scientific developments, in America, Denmark, Sweden and Holland, finds no place in the 'debate literature', focussed as it is upon external factors, events in England, and the activities of Bateson, Pearson, Weldon and their paradigm articulators.

7.7 The real challenges to mendelism

7.7.1 Challenges based on theory

Whereas the biometric challenge to mendelism has been exaggerated, other very real challenges have been underestimated.

Like every other scientific innovation, mendelism was received critically. It was rejected by some on theoretical grounds: see, for example, O F Cook (1907:336-338, 1908), Yves Delage (1909:185-186), Dewar and Finn (1909:Chapter V), Felix le Dantec (1904:513, 517), G Archdall Reid (1910:Chapter VII) and Alfred Russel Wallace (1908:140).

These writers deployed a variety of theoretical objections to mendelism, and these would form the basis of an interesting study. For present purposes we simply note that none of them brought forward an argument against mendelism based on biometry, because biometry has no theory of heredity, being instead, in Pearson's words, 'the mathematical expression of statistical variates' (1930:21).

7.7.2 Challenges based on observations

In addition to these theorisers, there were those (including the biometricians) who had empirical data that could not be fitted to mendelism. This present study has involved reviewing a large number of papers setting out empirical data, to distinguish those that gave mendelian interpretations from those that did not. The focus of the study is upon the first group, the 'mendelians', but, without any claim that the result is comprehensive or representative, the process has also identified authors in the second group, the 'non-mendelians', including Bellair (1913), Delcourt and Guyénot (1913), Fick (1907), Frasetto (1910); Hammerschlag (1910); Harman (1909); Hart (1909); Holmes and Loomis (1909); Laughlin (1912); McCracken (1905, 1906, 1907); Prout (1907); Saunders (1907); and Whitman (1904).

These authors tried to fit mendelian interpretations to their observations, but could not do so. Some seem to have been disappointed that their results did not conform to mendelian expectations – Hart and Laughlin devised *ad hoc* extensions of mendelism to try to account for their results (see para 5.*5 Exclusions: revisionists*). On the other hand, Prout and Saunders seem to have been well satisfied that their results were inconsistent with mendelian expectations.

These unconformable cases represented a real challenge, each one being, in a small way, an apparent falsification of mendelism [29], but there has been no substantial historical analysis of these and similar cases. Having found their data unconformable with mendelism, none of the authors offered biometric interpretations instead [30], and so the matter is not referred to in the 'debate literature'.

8. Conclusions

The foregoing provides an account of the development of mendelism after its inception in 1900. The intention has been to include all those who presented data in support of mendelism, but there may be omissions. Each mendelian author is represented by only one paper, and many who wrote with authority on the subject have not been considered

[29] At least two of the data-sets were later re-analysed and shown to be consistent with mendelian expectations (Doncaster (1907) and Lundborg (1912) on the data of Prout and Hammerschlag respectively).

[30] Indeed, it would have been surprising if these biologists and medical practitioners had been able to deploy the requisite mathematical skills to do so. This was not due to the fault of Pearson, but, as Eileen Magnello says, the result was that: "Pearson's inability to write or speak in the language of the early Mendelians meant that he was not able to communicate his ideas successfully to this group of scientists." (1998:94).

because they offered no data of their own The focus upon those who supported mendelism has entailed only the briefest treatment of those who did not. The last of these issues has not received anything like the study that it merits, except in so far as biometry represented a challenge to mendelism, and there the case has been overstated.

The comprehensive nature of this study does show us things that we did not know before. We can answer, for the first time, some of the questions that Kevles asked in 1981. The opponents of mendelism in England did indeed include a number of biologists who were not biometricians; William Bateson was not atypical of British biologists in his embrace of mendelism; the angry sharpness of the biometrical-mendelian debate does not seem to have extended through the entire British genetics community; and the early converts to mendelism in the United States and Great Britain can now be identified, at least in so far as their conversions were the result of their own researches (Kevles 1981:200, 201).

In the *Introduction*, reference was made to Stephen Brush's herculean study of the reception of the Periodic Law. In conclusion he says: "I have confirmed the traditional account: Mendeleev's Periodic Law attracted little attention (at least in America and Britain) until chemists started to discover some of the elements needed to fill gaps in his table … " (Brush 1996:618).

The present study has confirmed some aspects of the traditional account, but is more interesting for the aspects that are not confirmed. First and foremost, it displays the large amount of work that was being done outside the confines of the 'biometric-mendelian debate', by people who were not involved, and in fields upon which the debate did not impinge, most particularly cytology. Even if the batesonian mendelians who were involved in the debate are widely defined, they were still outnumbered two-to-one by mendelians who were not.

The wider focus presented here also raises questions about the traditional account of the neglect of mendelism in France, and the possibility that the initiation of mendelism in 1900 was not only a case of simultaneous discovery, and 'rediscovery', but also of postmaturity. To the extent that traditional accounts are not confirmed, analysis of a wide swathe of the contemporary research literature can produce new answers, in contrast to Brush's experience.

This is only one account of early mendelism, but from it emerges a picture of a research programme that was widely discussed, and to which increasing numbers of scientists subscribed. Mendelism failed in some challenges and succeeded in others, and was changed and extended as a result. There were instances of successful application for agricultural purposes. At the end of its first decade, mendelism had brought clarity and coherence to much of contemporary biology.

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