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THE EMERGENCE OF GENETICS

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A nineteenth-century biologist would have been perplexed if he were asked to explain what a 'geneticist' studies. A 'genetic' study implied a developmental one, tracing the history of, for example, the growth of intelligence from birth to maturity. Those who studied hereditary transmission were regarded as students of the broad field of 'inheritance', which was concerned as much with questions of development and evolution as with transmission. The narrower conception of inheritance, in which attention was focused on hereditary transmission, was referred to as 'heredity' in the latter part of the nineteenth century, and it was this conception of the field which was understood by the term 'genetics'. Yet, like psychology, which has a long history rooted in the philosophy of mind, genetics has a long history located in theories of 'generation'. A problem for the historian is, then, to settle on a strategy for relating the genetics of the twentieth century with the study of inheritance and of hybridism in previous centuries.

If we turn to definitions of inheritance in the earlier period we find that they rely on the analogy with the inheritance of estate, thus emphasising the transmission of the possessions of one individual, some of which he may have acquired in his own lifetime. The use of the term 'inheritance' was thus metaphorical, and to an extent misleading. As J. Arthur Thomson (1861–1933) pointed out, the use of phrases borrowed from the inheritance of property is 'apt to cause obscurity and fallacy when applied to the inheritance of characters which literally constitute the organism and are inseparable from it'.[1] In the biological literature, inheritance was not really a subject in its own right, rather it was a feature of a fundamental property of living things, namely generation. Discussions of inheritance tended, as a result, to be closely concerned also with theories of fertilisation and development. From the Greeks came the material theory of Hippocrates, several versions of which were offered in the eighteenth century. Charles Darwin resurrected the theory in the nineteenth century and called it 'Pangenesis'. The 'seed' or representatives of the various parts of the body of both male and female was accumulated in the gonads. Such a process allowed for the inheritance of acquired characters since acquired structures, just like congenital structures, could supply their representatives. Many other features of generation could also be explained by the theory, for example, regeneration and development. From Aristotle came the form and matter theory. The female contributed the matter and nourishment of the embryo, the male the form. This theory rested in turn upon his conception of substance, according to which the existence of an organism depended upon the intimate union of matter and form. Such a conception allowed the development of the organism to be envisaged as a progressive transformation starting with the apparently formless matter of the egg. This 'epigenetic' theory contrasted with the 'preformationist' theory according to which a miniature of the adult was formed which was not transformed but simply enlarged in development, and with the theory of 'pre-existence' which claimed that all individuals were present at Creation in miniature form, packed one within the other like Russian dolls.[2]

The eighteenth century witnessed several attempts to subject such theories to experimental test by hybridising species and varieties. Although to our eyes the results constitute a refutation of pre-existence, whether on the male (spermist) or female (ovist) side, such data were not interpreted in this way. Thus Charles Bonnet (1720–93) and Albrecht von Haller (1708–77) both selected those data which, taken in isolation, supported their own preformationist views. By the nineteenth century, however, preformation no longer held sway, so that the results of hybridisation could be evaluated in the light of epigenetic development. Now clearly, if the specific form of the offspring was not already present in the 'germ' before fertilisation, it should be possible by hybridisation to change this form, a change which might affect not only the immediate offspring, but subsequent generations also. This possibility opened up the debate on the transmutation of species, for it would then appear that hybridisation could lead to species multiplication, or if not multiplication, at least the transmutation of one existing species into another. Much of the experimental study of hybridisation in the eighteenth and the nineteenth centuries was conducted to test this point.

1. THE HEREDITARIANS

Between the eighteenth and nineteenth centuries, the medical literature shows a development from preoccupation with discussions of the evidence for the inheritance of acquired characters and the effects of the imagination of the mother upon the foetus, to concerns about the effects of consanguinity (in-breeding) and the urbanisation of society leading, it was widely believed, to hereditary 'degeneration'. It was within the debate on the possibilities or the limits to progress of man, his 'perfectibility', that a new school of thought arose, which we may describe as 'hereditarian'. The hereditarians were opposed to the claims of the 'perfectibilists' because they rejected the assumption of the perfectibilists that the effects of civilisation and amelioration of society were in the course of generations acquired by heredity. Into this debate entered the historian, Henry Thomas Buckle (1821–62), arguing both against those who claimed the inheritance of acquired characters and those who denied it. He perceived that selective citation of pedigrees could be used to support almost any claim. Consequently, in order to account for the development of modern civilisation in Europe he turned to the *social structure* of European nations, rather than to their biology or climate. As the most prominent hereditarian, Francis Galton (1822–1911) opposed this nihilism by reconceptualising inheritance as a statistical relation between populations of successive generations. This definition took the subject out of its old context of generation, extricating it from its association with embryology, and establishing a clearly-defined research programme concerned only with the data of hereditary transmission. As Ruth Cowan has pointed out, Galton's new conception of the subject was signalled by his replacement of the old metaphor 'inheritance' by the term 'heredity', after the French term '*hérédité*'.[3]

Galton's work was debated chiefly within the context of inheritance in man, and had virtually no impact upon the work of the hybridists and animal and plant breeders until the 1890s. Gregor Mendel (1822–84) appears to have remained completely ignorant of Galton's work, and it was only when Mendel's papers were discovered in 1900 that attempts were made to relate the work of these two pioneers. Many biologists sought to link the new field of cytology with the data of hybridism and heredity. Darwin's hypothesis of Pangenesis of 1868 was really a pre-cytological hypothesis based on the analogy between a higher organism and the colony of polyps in a coral, but his admirer, Hugo de Vries (1838–1945) transformed it into the hypothesis of Intracellular Pangenesis, in which the hereditary determinants, or 'Pangenes' were stored in the nucleus from which they migrated into the cytoplasm in order to form the characters for which they were severally responsible. Such migration, however, did not extend beyond the cell wall.[4] Continuity between cellular and individual generations was therefore traced to the source of pangenes, the nucleus. August Weismann (1834–1914) and Oscar Hertwig (1849–1922) also used the results of cytology in formulating theories of heredity, but it would be a mistake to assume that the development of the understanding of cell division, the formation of germ cells and their fertilisation, led inevitably towards a Mendelian type of hereditary theory. On the contrary, the same cytological assumptions served to support quite distinct theories of inheritance.

With the discovery of Mendel's papers in 1900 we enter a new period, during which the principles of the animal and plant breeders were as far as possible reinterpreted in Mendelian terms. Mendel's papers served as a significant achievement which was emulated in experiments with an increasing range of species. A number of these did not appear to follow the Mendelian scheme without introducing ancillary hypotheses such as linkage and the compound character, and it was only gradually that Mendelian heredity became established as a *general* theory of heredity. In the first phase of the subject in the present century it was widely believed that there were at least two forms of heredity – Galtonian and Mendelian – indeed many biologists, particularly those in Germany, held that Mendelian heredity concerned only unimportant characters, and that characters of evolutionary significance to the species were subject to a different form of hereditary transmission in which acquired characters could be inherited. These characters were 'carried' not by the nucleus but by the cytoplasm.

Although the claims made for Mendelism by the Mendelians were enthusiastic, they were nevertheless tentative. Confidence was tempered by the recognition that examples of the presence of Mendelian heredity were as yet limited and scattered. The subject which the Mendelians studied they therefore called 'Mendelism' rather than 'heredity'. Their subject was launched more confidently and effectively when Bateson coined the term '*genetics*' in 1906. Three years later the Danish biologist, Wilhelm Johannson (1857–1927), introduced the term '*gene*' in his widely read textbook, *Elemente der exakten Erblichkeitslehre* (1909), and made the fundamental distinction between 'genotype' and 'phenotype' thus adding considerable precision to what Galton had called the effects of 'nature' and 'nurture'. Meanwhile, the successful welding together of Mendelian heredity and the cytology of chromosomes had to await the work of the Columbia school under T. H. Morgan (1866–1945) in the years 1911 to 1913, by which time it could be said that genetics was established. This essay, therefore, does not go beyond the year 1913.

2. THE BREEDERS AND THE HYBRIDISTS

Charles Darwin greatly prized the knowledge of the practical breeders of his time and was convinced of the power of inheritance by the willingness with which sheep breeders paid out large sums of money for the privilege of using the rams owned by Robert Bakewell (1725–95). Little did he know that these breeders were being 'milked' by Bakewell who at the time was facing bankruptcy and needed all the money he could get! Nor were the successes of the animal breeders a guarantee that the theoretical assumptions behind their practices were well founded. Thus Nicholas Russell has pointed out the practice of horse breeders in the seventeenth century of importing fresh Arab stallions rather than relying on indigenous stallions of Arab blood[5]. This expensive procedure was due to their belief that the transmission of Arab qualities depended upon the stallion having been reared in the oriental climate. Equally, their lack of concern about the qualities of the mare stemmed from their assumption of the predominant influence of the male in hereditary transmission.

The fear that changed conditions of life would destroy breed characters was based on the then-current theory of adaptation according to which the distinctive characters of the breed represented adaptations to the locality in which that variety lived. Under changed conditions the breed would acclimatise, but in the process it would 'degenerate' losing the breed's special characteristics. By the end of the eighteenth century breeders had found definite evidence that degeneration did not occur. Arab horses and Merino sheep bred in England retained their breed characteristics. This discovery led animal breeders to attach much more importance to hereditary constitution and much less to the effects of the environment.

Although by the nineteenth century the animal breeders achieved a clearer understanding of their art, they pictured heredity in terms of characters of different 'strengths' in the 'blood', the longer the character had been in the breed, the greater its strength. Thus older breeds were held to be 'prepotent' over more recent breeds. Sometimes a character that had not been seen in a breed for generations would suddenly reappear producing what was called a 'reversion' to a long-lost breed – as in Darwin's hybrid pigeons. Here the plumage of the wild rock dove was produced in domestic brown and white breeds. The breeders were clear that crossing yields variability, and that selfing of hybrid offspring was essential to achieve constancy of type. However, they had no theoretical grounds for being able to predict how long such a process would take and no expectation that it could be achieved rapidly as in Mendel's pea experiments.

Among the hybridists, those experimenting with plants contributed the most useful results. Carl Linnaeus introduced a controversy in the 1760s when his prize essay on plant sexuality was published.[6] Here he claimed that hybridisation occurs in nature and leads to the production of new species. This assertion was tentatively supported by the Swabian botanist, J. G. Gmelin (1709–55) who called for experiments to decide the question. There followed a long line of responses, first J. G. Koelreuter (1733–1806) followed by Carl Friedrich von Gaertner (1772–1850), Charles Naudin (1815–99), D. A. Godron (1807–80) and William Herbert (1778–1847). They all admitted that new varieties could thus be formed, but only Herbert in his work on the Amaryllidaceae claimed that new species also are yielded by hybridisation.[7] The others were too impressed by the strength of reversion which brought hybrid progeny back to one or other of the originating species to accept Linnaeus's claim. As for those hybrids which did not revert, Gaertner was convinced that they suffered a general weakening such that they were unlikely to form the starting point of new species. Mendel, as we shall see, appears not to have taken so pessimistic a position.

The result of the plant hybridists' studies was the clear demonstration of the very different behaviour of the immediate offspring of hybrids (known as F1) and the behaviour of their progeny (F2). The former were uniform, the latter variable. Many individuals of the latter generation tended to revert to the originating partners in the cross. Naudin found examples of complete reversion in the F2 generation, and he speculated that it had been achieved by the separation of the specific essences in the formation of the pollen grains and the germinal vesicles. Unions in fertilisation between the specific essences thus separated would produce the reversions observed. This theory of germinal segregation was like the Mendelian theory, but differed in that Naudin treated the specific essence as a whole rather than considering the character differences themselves as independent units in heredity. Nor was complete reversion the only result of hybrid reproduction, for some of Naudin's experiments gave what he called *variation désordonnée.* Gaertner, too, concluded that the species acts as a whole although he found evidence of apparently independent transmission of characters.

Ernst Mayr has argued that the distinction between typological and populational thinking in biology marks an important feature of the differing approaches to biology throughout its history.[8] Naudin and Gaertner treated species as 'types' following the 'essentialism' of the old systematists, whereas Mendel and plant breeders like Henry Louis de Vilmorin (1843–99) and Henri Lecoq (1802–71) saw no fundamental difference between species and varieties and looked to the individual characters for the stable units. As for the basis of heredity, they did not look to particles but to fluids and forces. Naudin spoke of heredity 'ploughing the furrow more deeply, generation after generation' so that new varieties gained strength with the passage of time. Variation was treated as a force opposing heredity, not as a feature of heredity itself.

3. MENDEL'S EXPERIMENTS

The inspiration of the famous experiments of the Moravian priest, Gregor Mendel (1822–84), has been a subject of much debate among historians, as has been the meaning and significance of the papers he wrote. Sir Gavin de Beer (1899–1972) claimed that the science of genetics could be traced directly to Mendel and that its birth took place in 1865, the year in which he described his experiments with the edible pea (*Pisum sativum*). Vitszlav Orel has urged the importance of the attention devoted in Moravia to practical animal and plant breeding in providing Mendel with an informed and enthusiastic environment in which to pursue questions concerning the nature of hereditary transmission. L. A. Callender and Robert Olby, on the other hand, have argued that however important this environment may have been for making the techniques of breeding accessible to Mendel, his work was addressed to an unresolved question concerning hybridisation, namely whether or not hybridisation leads to the production of new species, as Linnaeus had claimed.[9] This question was of major concern to botanists, as is seen in the number of prizes which were offered by scientific academies for answers to it. Among the prizewinners were Naudin and Gaertner.

This question focused Mendel's attention upon hybrid descendants (F2 and beyond) rather than upon the immediate hybrids (F1). When he surveyed the literature he failed to find any reports which classified hybrid offspring accurately with respect to each of the differentiating characters in the cross, yet he saw that without such information it was impossible to draw any firm conclusions as to the power of hybrids to give rise to new species. Having guessed that the characters which show constancy of type behave independently, Mendel planned a brilliant set of experiments in which he grew statistically significant numbers of each generation, not a small sample merely to exemplify the variety of forms in a generation, as was the custom among breeders and hybridists hitherto. The result was his discovery of the approximation of the frequencies of the contrasted characters in the F2 generation to the integral ratio of 3:1. From his study of the next (F3) generation he was able to show that the fundamental ratio in F2 was 1:2:1, which the phenomenon of dominance obscured. As a student of mathematics and physics he was thrilled to find that this ratio represented, on the one hand, the terms in a binomial expansion $(A + a) = A^2 + 2Aa + a^2$, and on the other, the terms in the expansion of 'hybrid' series, or the 'development' of the hybrid in its offspring – $A + 2Aa + a$. When he considered two pairs of contrasted characters, the different classes of offspring and their proportions reflected the terms produced by combining two binomials. This fact, he considered, clinched the case for the independence of the characters he dealt with.

The manner in which the parental characters were recovered in unadulterated form in the hybrid offspring convinced Mendel, as it had convinced Naudin, that there is a process of segregation between the elements brought together in the hybrid, but it was clear to Mendel that the species or variety did not act as a whole. His atomistic conception of the independence of the characters fitted with his belief in the material basis of heredity located in the constituents of the germ cells and the fertilised egg resulting from their fusion. Yet it is not obvious from any of his writings that he intended his fundamental concept – the character pair – to be translated into a pair of elements, factors, or *Anlagen*, as in the theory of the gene. J. Heimans and J. H. Bennett were the first to point out this distinction between Mendel's theory of heredity and the gene theory to which it gave rise. Nor is it credible to claim that Mendel's 1865 paper was simply a contribution to the laws of heredity. As the opening and the closing sections show, the paper was addressed to the question of species multiplication by hybridisation. The results with *Pisum* suggested that a limited number of constant forms carrying new combinations of existing characters could be produced, but that the character of the immediate hybrid (F1) was not preserved.

Mendel seems to have been convinced that other hybrids exist which do not follow the law found for *Pisum*. These allegedly showed no reversion, they were 'constant hybrids'. Despite the scepticism of the chief authority, Carl von Gaertner, on this point, Mendel was hopeful that such hybrids did exist in nature and could be produced by experiment. Before he communicated with the eminent authority on the hawkweeds (*Hieracium*), Carl von Naegeli (1817–91), Mendel had decided to explore the behaviour of this genus, aware though he was of the exceeding difficulty of hybridising its species. In 1865 he had argued that just as the contrasting character pairs separate in germ cell formation in the hybrids of *Pisum*, so in other genera this separation might not take place, but instead the contrasted characters remain attached in a lasting union. In such cases 'constant hybrids' would be produced at once which, by virtue of their constancy, would constitute new varieties or species. His experimental test of other so-called constant hybrids proved negative, but the hawkweeds mystified him. Not all members of the first generation of hybrids were the same. This, as Callender has pointed out, was not what he expected. Some of them gave rise to constant forms – a vindication of his hope to discover such forms, and thus to account for the great polymorphism of this genus, the feature about the hawkweeds which had attracted him to them in the first place.

4. THE DISCOVERY OF MENDEL'S WORK

The neglect and 'rediscovery' of Mendel's work has been a subject of much debate. Compared with his fellow-countryman, Christian Doppler (1803–53) who, like Mendel, started his professional life as a teacher, Mendel made very little effort to publicise his work. Those who knew it found it supportive of the belief that hybrid offspring revert to their originating species. His paper on hawkweeds, though better known than his work on the pea, was too brief and inconclusive to have much impact. Within the context of middle-European botany in Mendel's day it is hardly surprising that the remarkable significance of his work was unappreciated.

In 1900 three botanists, Hugo De Vries (1848–1935), Carl Correns (1864–1933) and Erich Tschermak von Seysenegg (1871–1962), claimed to have rediscovered Mendelian ratios and the Mendelian explanation of germinal segregation, and to have gone on to discover Mendel's paper of 1865. Mendelian heredity has thereafter become the most famous example of 'rediscovery' and 'multiple' discovery in science. Attempts to establish these claims on the basis of a thorough reading of the documents have only been made recently.

The results throw doubt on most of the claims made by the three 'rediscoverers'.

First we must ask what constitutes the discovery of Mendelian ratios. Darwin and other nineteenth-century biologists reported data which we can identify with the advantage of hindsight as exemplifying Mendelian ratios. However, when Mendel reported a Mendelian ratio, he perceived that the numbers he gave represented an *approximation* to a specific ratio such as 3:1, and that such a result indicated the operation of a statistical law of some kind. When De Vries reported the numbers 3167 and 1082 for yellow and white maize seeds in 1899 he merely remarked that these maize hybrids were capable 'of reproducing the types of their two parents'.[10] In truth the concept of a Mendelian ratio is not a simple and unadulterated fact, but a theory-laden fact. It is the theoretical component that identifies certain data among a host of results as peculiarly significant.

From the documents available we can be fairly confident that both Correns and Tschermak were aware that the numerical results they recorded had some special significance. Therefore they knew that they had made some sort of discovery. This prompted them to undertake a literature search, the result of which was that they independently discovered Mendel's 1865 paper. Then they realised that they had really rediscovered what Mendel had already found. Very likely Correns had understood how germinal segregation could yield these ratios. The same cannot be said for Tschermak. In the first place he did not have the data showing how the 3:1 ratio was composed of a 1:2:1 ratio until the summer of 1900. In the second place, he treated the numerical predominance (3:1) like the total predominance observed in all F1 individuals and called 'dominance' by Mendel. For Tschermak these were *both* manifestations of the combining power or 'valency' of the two contrasted characters. He appears not to have accepted Mendel's view that F1 dominance and F2 reversion are due to different causes, the latter to the operation of a stochastic process. One would expect that De Vries, being the first to announce the discovery of ratios in 1900 and to offer the explanation in terms of segregation, could claim independence from Mendel. But as Onno Meijer has conclusively shown, there is no evidence to support such a claim other than De Vries's own recollections. Rather, it appears that it was not until he received a reprint of Mendel's paper early in 1900 that he was able for the first time to organise his results on a rational plan based on Mendel's theory.

Augustin Brannigan has argued that scientific discovery is a process of 'social attribution' rather than an intellectual or psychological process.[11] Clearly the public recognition of Mendel's work as a discovery of importance to science was the work of the scientific community, and hence a social process in which the 'rediscovery' in 1900 was the first step. It involved attributing the discovery to Mendel, which was clearly a social act. At the same time Mendel, Correns and

Tschermak seem to have realised by themselves that they had made a discovery of some importance. This was surely a psychological process. Equally the attribution of the status of discovery to Mendel's work on *Pisum* involved experimental work to corroborate it, and intellectual activity to integrate the new results with the old. The recognition of the fundamental importance of Mendel's work was not therefore simply a process of social attribution.

5. HEREDITY IN MAN

It was above all social and political questions which exposed the need for sound knowledge of the nature of hereditary transmission in man. Among those who were concerned about the state of modern urban society were Prosper Lucas (1833–85), Augustin Morel (1809–73) and Francis Galton. Although all three advocated some policy to guide human reproduction, it was Galton who introduced the name *eugenics* in 1883 to refer to the study of the means by which the race of man might be improved.

His starting point was the long-term stability of racial characters. Despite the fact that not all offspring are like their parents, the characteristics of a race are preserved constant over many generations. This must mean that the physiological basis of racial constancy is not what common sense would have us believe. The link connecting parent and offspring is not through their *bodies* but through the elements from which they are formed. He drew the analogy with a necklace, the chain being like the germinal material, the pendants on the chain like the bodies of individuals of successive generations. Equally, we do not inherit all the characters of one parent or grandparent, but some characters from one parent and some from another. Heredity must be due to many independent bearers or particles. To discover the laws of heredity it was necessary to investigate large numbers of related individuals, not just the members of a few families. Whatever these laws might be, they must express the statistical relations between generations.

It is well known that Galton discovered the tendency of offspring on average to be pulled back towards the mean of the population. Exceptional parents had on average less exceptional offspring, yet average parents were here and there throwing out more exceptional offspring and the two effects were balanced thus yielding racial stability. If a population was to evolve, he concluded, it would have to suffer a sudden change which would introduce a new racial mean to which future generations would cling. Galton was thus an advocate of the quantitative study of populations (biometry) and of a saltatory (mutationist) theory of evolution.

Methodologically and conceptually Galton had stepped well beyond the position reached by such authorities as Lucas and Morel, who were the best-known writers on human heredity before him. Unlike them he demanded sufficient data for statistical treatment, and in opposition to them he viewed variation, reversion and inheritance as belonging to the same phenomenon – heredity. Variation did not oppose heredity, as Lucas claimed, but was a feature of it. Degeneration was not, as Morel claimed, due to the effects of environmental pollutants, but to the reproductive pattern of urban societies. For the law of heredity Galton turned to the widely accepted hypothesis of *fractional* heredity, according to which the contribution of each ancestor to the offspring is halved in each generation. Thus the parents contribute between them one half the heritage, the grandparents one quarter, etc. He claimed that the statistical relations which he had found between the generations – the regression coefficients – were in harmony with this fractional or *Ancestral Law* as he called it. Although the first data he used to establish the law concerned a *continuously* varying character (stature), he went on to attempt to establish the same law also for 'alternative' or non-blending characters (eye colour in man and the coat colour of basset hounds). The law, he explained, was expressed in a different way in the two cases. In blending characters the law related to the blend of the differing ancestral expressions of the character in each individual although it still had to do with averages of many individuals. In the case of non-blending characters, it was expressed in the number of individuals which showed exclusively the character of a particular ancestor. This meant that the Ancestral Law was *the* law of heredity.

Galton was thrilled to learn that the cell divisions leading to the formation of the egg involve throwing out half of the germinal material, thus offering a possible material basis to the fractions in his Ancestral Law. Equally the discovery of the ova of the child in the foetal stage reassured him that he had been right to claim that the physiological link between generations was through the reproductive cells and not through the body cells. Galton's success in developing the statistical tools with which to investigate the data of human heredity and his vigorous promotion of eugenics, which included furnishing liberal funds in support of research, resulted in his becoming known as the founder of eugenics, although, as Victor Hilts has described there was a previous tradition of eugenic thought to which the phrenologists, among others, belonged.[12] Galton's notion of hereditary filiation through the 'stirp' was not known outside Britain, and August Weismann's development of the 'continuity of the germplasm' in 1889 was independent of him. Unlike Galton, Weismann was deeply immersed in biology, and as a true Darwinian he believed that the evolution of species had been due entirely to natural and what he called 'germinal selection' acting on the abundant variations which were shuffled and distributed by the mixing process of bisexual reproduction.

In Continental Europe the debate over the role of selection and the possibility of the inheritance of acquired characters were major subjects of controversy up until the Second World War. In Britain the selectionists were a small band, but there grew up around Galton a vigorous group of 'hereditarians' which set about demonstrating selection in action. This was the 'biometric' school led by Karl Pearson (1857–1936) and by the hard-working experimental zoologist Raphael Weldon (1860–1906). The climate of opinion concerning the role of selection at this time was also sceptical in Britain, and has been described by Peter Bowler in his book *The Eclipse of Darwinism* (1986). Dissatisfaction with the speculative, descriptive embryology which relied upon the theory of recapitulation was allied to the growing demand for experimental approaches to the questions of evolution. Foremost among such experimentalists was William Bateson (1861–1926). He sought to demonstrate the truth of Samuel Butler's aphorism: 'The origin of species is the origin of varieties', by an investigation of clearly-marked 'discontinuous' variations. He saw in hybridisation an experimental technique for exposing the behaviour of these variations. By 1900 he was convinced that they were the source of new varieties because they persisted when outbred and, having originated in one step, were not dependent upon natural selection to accumulate their divergence from the existing population gradually over many generations. When he read De Vries's French paper on hybrids (which did not mention Mendel), Bateson thought the numerical ratios might represent a modification of Galton's Ancestral Law for non-blending heredity. Only after he had read Mendel's own paper did he realise that here was a new theory which he could deploy very effectively in his fight for experimentalism and in his attack on the biometric school.

The controversy which took place between the biometricians and the Mendelians has been the subject of much discussion. Mackenzie and Barnes claim that empirical, scientific data did not determine the attitudes of the contestants, but rather that socio-political factors were decisive. William Provine emphasised personal animosities, and Bernard Norton, while recognising that the broad cultural milieu throws some light on the debate, concluded that there did not exist clear differences between the social groups to which the contestants belonged, and that differences in fundamental views concerning philosophy and methodology of science were of far greater significance.

It would, in any case, be misleading to assume that the biometric-Mendelian controversy marked the only significant difference of opinion over the nature of heredity in the first decade of this century. Other disagreements were not charged with personal animosity, and were less dependent upon the presence of a few major figures. When Weldon died prematurely in 1906 the controversy over heredity in animals and plants died down, but it continued in the field of human heredity, the disputants being Pearson and C. C. Hurst (1870–1948). Yet opinion was divided over the relative merits of Mendelian, Galtonian and Weismannian heredity. We are apt to assume that because Weismann believed in the presence of reduction division, which was both quantitative and qualitative and because Mendel assumed a process of germinal segregation, that the two theories were complementary. Indeed, this was how Correns viewed them. Others saw the situation differently.

First, it is clear that Weismann assumed the presence of many determinants of one character trait, not just a single pair in each cell. The representation of such determinants in the organism depended upon a process of 'germinal selection' which did not lead to the sort of clear predictions which follow from Mendel's scheme. In his *Lectures on Evolution* (1906), Weismann was not particularly enthusiastic about Mendelian heredity.[13] Authors like J. Arthur Thomson followed Weldon, who had offered a rival explanation of dominance and segregation in terms of the expression or latency of determinants. He argued that just as the recessive character is hidden in F1, so in F2 the recessive character is hidden in all the dominant segregates, but expressed in all the recessive segregates, and there has been no segregation of determinants. The reappearance of ancestral characters long lost from the breed could be attributed to the stimulating effect of cross-breeding causing the expression of the latent determinants.

6. GENETICS AS A DISCIPLINE

It was in the course of Bateson's struggle to fund his Mendelian research that he hit upon the term 'genetics'. First in a letter to Adam Sedgwick in 1905, and the following year at the Third Conference on Hybridisation and Plant Breeding in London, he publicised the word, defining it as: 'The elucidation of the phenomena of heredity and variation: in other words, to the physiology of Descent, with implied bearing on the theoretical problems of the evolutionist and systematist, and application to the practical problems of the breeders, whether of animals or plants'.[14] When the conference proceedings were published; genetics was adopted as the alternative title. The subsequent growth of genetics was brought about by a combination of factors. Firstly, there was the undoubted success of the Mendelian theory and method as the basis for a research programme. Then there was the interest of academic agriculturalists who were striving to make their subject genuinely scientific and who found in Mendelian experimentation a fruitful avenue to pursue. Last, but not least, there was a strong interest in the possible social applications of genetics. This eugenic concern was an important stimulus to the support of the subject in its early days, witness the Eugenics Laboratory at University College London (1906), the Balfour Chair of Genetics at Cambridge (1912) and the Eugenics Record Office at Cold Spring Harbor (1906).

In Germany, the subject of heredity remained broad in conception, embryological and physiological aspects being included. Heredity was not to be confined to transmission genetics other aspects being ignored. Clearly *Erblichkeitslehre* was not the same as *genetics*. Whilst the American geneticists, led by

T. H. Morgan, attributed all heredity to the chromosomes in the nucleus, the Germans argued for the importance of determinants in the cytoplasm. They rejected his 'nuclear monopoly', and argued not just for the cytoplasmic determination of the plastids, which are responsible for the colour of foliage, and could be considered a special case, but also for the determination of important specific and generic characters by a structure in the cytoplasm which they called the 'Plasome'. Although Correns became the director of the Kaiser Wilhelm Institut für Biologie in 1913, he did not convert it into a Morgan-style laboratory, for he was himself more interested in non-Mendelian than in Mendelian heredity.

It has been argued persuasively by Jan Sapp and Jonathan Harwood that the historiography of genetics has been constructed in a misleading manner owing to the concentration of studies upon Anglo-American genetics.[15] A broader approach embracing the work of German-speaking scientists reveals a rather different picture. Nor is it true that British genetics was as completely devoted to Mendelian genetics and nuclear transmission as some accounts would suggest. Bateson urged his followers to treasure their exceptions. He devoted much time himself to the study of graft hybrids and to plastid inheritance. Indeed, he does not seem to have been convinced that segregation is a unique event identified with germ cell formation.[16]

It is clear at the same time that British geneticists did not all follow closely the Morgan model. Thus J. S. Huxley was successful in demonstrating the action of 'rate genes' in his study of eye colour in the fresh water shrimp (*Gammarus*) and R. Scott-Moncrieff, continuing earlier studies of the genetics of flower colour by the Bateson school, was able to display the close parallel between genetically distinct strains of snapdragon (*Antirrhinum*) and the chemically distinct organic pigments in their flowers. The mode of gene action in terms of the catalysis of specific biochemical reactions was clear in these early studies.[17]

The literature on the early history of genetics has been adversely affected by the Whiggish tendency to read into the texts the concepts of modern genetics. Thus Mendel's theory was allegedly about the transmission of factors or genes and Mendelian segregation was the segregation of genes. Equally, Mendel was making a contribution to the Darwinian theory of evolution by showing that new characteristics are not diluted and lost in bisexual reproduction. In fact there is now strong evidence that Mendel was not talking about what later became known as genes, and he was not sympathetic to Darwin's views on variation and heredity. Mendel's remarks on transformism, though guarded, would seem to align him with the theological tradition of evolution by species multiplication from a limited set of created stocks as held by Linnaeus and by William Herbert, Dean of Manchester. On the other hand, there is no doubt that Mendel's conception of heredity was revolutionary. Weismann and Galton had sought to distance themselves from *personal* notions of inheritance as discernable in the body of the individual, but they did not abandon the assumption that the germinal matter contains determinants representative of each individual. Admittedly these determinants were subject to repeated fractionation until in subsequent generations they became mere traces. Even then it was possible for long-forgotten ancestral traits to reappear. Hence the establishment of purity of type ought to be a long and difficult task, rather than an often rapid process as the Mendelian theory predicted. The establishment of genetics on the basis of Mendelian heredity therefore marks a clear discontinuity in the history of hereditary theory and practice.

Another tendency which has produced misleading accounts of the establishment of genetics is that of placing so much emphasis on the Biometric-Mendelian debate. Quite apart from this controversy, Mendelian heredity was not at once seen as the model for all hereditary phenomena, even by its supporters. Nor was Bateson alone in his scepticism towards chromosomes. As Scott Gilbert has shown, it was research and debate over the determination of sex which led to the resolution of uncertainties about the relation between chromosomes and genes, and which set ground rules in the United States for the demarcation of genetics from embryology.[17]

NOTES

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16. See L. Doncaster, *An introduction to the study of cytology* (Cambridge, 1920), p. 219.
17. R. Scott-Moncrieff, 'The classical period in chemical genetics', *Notes and records of the Royal Society*, 36 (1981), 125–54.
18. Scott F. Gilbert, 'The embryological origins of the gene theory', *Journal of the history of biology*, 11 (1978), 307–51.

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