Mendelism: From Hybrids and Trade to a Science

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> 'The scientific and the practical have gone to Form a perfect and fertile hybrid.'
>
> Bateson (1906)[1]

It is a remarkable fact that when Mendel's work was rediscovered in 1900 the constituency in Britain that was most closely associated with and supportive of this new science was neither the Linnaean Society, nor the Zoological Society, nor the Royal Society, nor even the Royal Agricultural Society, but the Royal Horticultural Society. Mendel's work was first publicly reported in the Society's journal. De Vries's *Comptes rendus* paper was first reported at a meeting of the Society on May 8 1900. Mendel's work was first described in the paper Bateson published in 1901 in the Society's *Journal*, and it was a member of the Society, C.T. Druery, who translated Mendel's paper for the same journal at the request of its editor, the Rev. William Wilks. The first international Meeting given to Mendel and the theme of hybridisation was again an event organized and financed by the RHS in 1906. As president of that event the Society chose the Cambridge zoologist, William Bateson. Gold medals in honour of James Veitch, of the famous firm of James Veitch and Sons, were awarded to William Bateson, Wilhelm Johannsen, and Maurice de Vilmorin, of the firm of Vilmorin–Andrieux & Cie. A further three medals were awarded to three British Mendelians: Miss Saunders, R.H. Biffen, and C.C. Hurst. The formal proceedings opened with five papers by Mendelians. At the Banquet in the Society's Great Hall, Bateson publicly christened the study of the 'phenomena of heredity and variation' with the name 'Genetics'. The context of the introduction of Mendel to England was thus unquestionably horticultural. How can we account for this fact, and what significance has it for our understanding of the nature of early Mendelism?

Principles of 19th Century Breeding

We can distinguish four approaches to breeding in the nineteenth century:

1. *Mass selection* – used in agriculture for corn, wheat, etc.
2. *The Pedigree Method* of individual selection used by Hjalmar Nilsson in Sweden.
3. *Crossing plus Inbreeding* and selection, illustrated here from the example of Begonias and Orchids.
4. *Seedling Selection* – the selection of promising seedlings from populations raised without deliberate crossing. This is a slow process that relies on the occurrence of cross-fertilisations or the appearance of sports. Amateur French strawberry growers used it with some success.[2]

The first method focused on populations of plants rather than on single individuals. Their pollination was not rigorously controlled. Deborah Fitzgerald[3] and Barbara Kimmelman[4] have shown how American agricultural researchers, attempting to improve corn, for the most part, clung to various versions of this method, fearing the bad effects of inbreeding. Nor was this fear dispelled by the attempt of Edward East and Herbert Hayes in 1912[5] to explain on Mendelian principles the need for inbreeding as a 'purifying agent' alongside crossing. Not until 1919 did American corn breeding along Mendelian lines become prominent and successful with the double-cross technique of Donald Jones[6] from which hybrid corn was later produced. In England, and in Europe generally, mass selection was favoured. After 1900 R.H. Biffen used Mendelian methods to breed a rust-resistant variety of winter wheat, 'Little Joss', which became available to farmers in 1910, but its low yield prevented its widespread adoption.[7] In contrast to these failures of Mendelian research to have an impact on the farmer, the travels of M.A.Carleton for the US Dept. of Agriculture to Russia in 1895 and 1900 yielded important varieties of wheat, among them the variety Kharkov, which by 1921 was being cultivated on twenty-one million acres of American soil.

The second method – the pedigree method – originated with Louis de Vilmorin,[8] and was discovered independently by Hjalmar Nilsson in 1892.[9] As Nils Roll-Hansen has shown,[10] it formed the basis upon which Wilhelm Johannsen built his famous distinction between genotype and phenotype. It proved of economic value in the plant breeding of the Vilmorin firm, but it did not lead either the Vilmorins or Nilsson or Johannsen in the 1890s to rediscover Mendel's laws.

The third approach – crossing or hybridisation together with inbreeding – had long been practised by both plant and animal breeders. In England it was the

plant breeders who enjoyed singular success in the closing decades of the nineteenth century using this approach. They played a major part in the growth of the horticultural industry and contributed decisively to the resuscitation of the Royal Horticultural Society (RHS). This is best illustrated from the history of the firm of James Veitch and Sons.

James Veitch and the Hybridists

The firm of James Veitch and Sons was founded by John Veitch who came from Scotland to Devon in 1808 as gardener to Sir Thomas Acland. In 1832 he started the Killerton Nursery near Exeter. This formed the basis for the establishment that he, his son, James (1792-1863), and his grandson James Jr. (1815-1869), built between the 1830s and 60s, and was continued by other members of the family.[11] Between 1840 and 1905 the firm financed some 22 collecting journeys and supplied the specimens for 422 of the plates in *Curtis' Botanical Magazine*. James, father and son, sent out the majority of these plant collectors, among them:

1840-1857 William Lobb to Brazil
1843-1860 Thomas Lobb to Java
1859 & 1863-1866 Richard Pearce to Chile, Patagonia, Peru, Bolivia
1860 & 1864 John Gould Veitch to Japan and South Pacific, Phillipines & Australia
1840-1857 William Lobb to Brazil
1843-1860 Thomas Lobb to Java
1859 & 1863-1866 Richard Pearce to Chile, Patagonia, Perú, Bolivia & 1864 John Gould Veitch to Japan and South Pacific, Phillipines & Australia

Also sent out by Veitch & Sons in 1877-1878 was F.E. Burbidge – to Borneo.

Those conducted between the forties and the sixties furnished the major species with which Veitch's hybridists could work. The hybridists who worked with Veitch were the most famous in the industry:

Johnn Dominy (1816-1891)
John Seden (1840-1904)
John Heal

Dominy produced the first man-made orchid hybrid, *Calanthe* x *dominii* (*C. Masuca* x *C. furcata*). It flowered in 1856. Among his many orchid hybrids was the

handsome, winter-flowering *C.* x *vietchii*. Between 1860 and 1890 the number of recorded orchid hybrids increased from 4 to 200. By 1898 it was 800. Inter-generic hybrid orchids were being produced from 1887. So popular did orchid hybrids become that the *Orchid Review* introduced a companion volume entitled *The Orchid Stud-Book: An Enumeration of Hybrid Orchids of Artificial Origin* for the registration of hybrids. This work was edited by two Fellows of the RHS, Robert Rolfe and Charles Hurst, the latter a member of Bateson's circle of Mendelians. There are now some 80,000 registered orchid hybrids. It is not mere coincidence that the RHS in the 1880s had four orchid enthusiasts on its Council:

Sir Trevor Lawrence (President)
Sir James Veitch
Baron Sir Henry Schröder
A.H. Smee

Dominy trained John Seden in the art of hybridisation at Veitch & Sons. Seden began hybridising *Cypripediums* in 1873, and went on to raise some 500 orchid hybrids. But he is chiefly remembered for his hybridisation of the tuberous-rooted Begonias.[12] He started in 1873 with the five species brought back by James Veitch's collectors:

Begonia boliviensis exhibited at the International Horticultural Exhibition, Paris, 1867.

B. veitchii priced at 10s in 1878 [average weekly worker's wage £1.10].

B. pearcei named after Richard Pearce who collected for Veitch & Sons.

B. rosaeflora from which the first white begonia was developed.

B. davisii collected by Davis in Peru for Veitch and Sons.

The 18 hybrids he raised from crossing these species form the basis of the tuberous-rooted garden begonias we enjoy today. But even by the end of the nineteenth century, Maxwell Masters, in his opening address to the hybrid conference of 1899, could note that tuberous begonias had been so transformed by hybridisation that a French botanist had felt the need to found a new genus for them.[13] Veitch named the first of his hybrids *B. sedeni*. Messrs Veitch and Sons built their reputation on the many new varieties of ornamental plants, fruit, and vegetables they introduced as a result of their combined collecting and hybridising programme. Their business expanded until it must have become one of the largest of its kind in the world. There was the original nursery near Exeter, to which they added the famous Royal Exotic Nursery, in King's Rd. Chelsea, purchased in 1867 from Messrs Knight and Perry. By 1906 they also had Coombe Wood nursery at

Kingston Hill, Middle Green Farm at Slough, and nurseries at Fulham, Feltham and Langley.

The story told here of orchids and begonias could also be told of the sweet pea (*Lathyrus*), varieties of which were developed by Henry Eckford of Wem, in Shropshire,[14] beginning in 1870, the strawberry (*Fragaria*) which Thomas Laxton began hybridizing in 1865, and produced the long cultivated variety *Royal Sovereign* (*Noble* x *King of the Earlies*) in 1892,[15] Fuchsia – Dominy's cross between *F. fulgens and F. magelanica* (1855) was named *F. dominiana* by Veitch, *Streptocarpus* – Veitch's *Streptocarpus* 'original hybrids' were marketed from 1890, and *Gloxinia* – John Sedens' cross formed the basis of the Chelsea varieties marketed by Veitch. These innovative ventures in variety development gave the trade the means to entice the public and expand their markets. Unlike the situation in cereal development, where farmers wanted to save their own seed and therefore were ill-disposed to hybrids, the gardening public was for the most part not trying to save theirs, besides which, many of these plant hybrids could be propagated vegetatively. Also the choicer varieties, especially the orchids, were 'carriage trade', i.e., they were bought by the wealthy who had no need to be 'penny-pinching'. There thus opened up what Peter Galison in another context has called a 'trading zone'[16] in garden-loving Britain.

The Royal Horticultural Society

In several respects this Society differed from the many societies in Britain which existed to support research – the Eugenics Education Society, the Society for the Control of Inebriation, etc. Such pressure groups were dominated by the middle classes, and led by members of both the old and new professions. Founded as the Horticultural Society in 1804 at the instigation of three men – John Wedgwood, son of the famous potter, Josiah, Sir Joseph Banks, President of the Royal Society and Advisor on behalf of royalty to Kew Gardens, and William Forsyth, gardener to King George the third, this was an aristocratic society.[17] It gained a royal charter in 1809. In 1858 the Prince Consort became its president, and three years later it was permitted to adopt the title Royal Horticultural Society. After its golden years under the famous hybridist, T.A. Knight and Joseph Sabine, the Society twice came near to bankruptcy, due to its venture into leisure facilities for the entertainment of London's High Society, but thanks to the efforts of its secretary, Sir Daniel Morris, and his colleagues, the Society was rescued and its health restored. Later Sir Daniel recalled how he an his colleagues 'refused even to consider the renewal of the Badminton and tennis courts and garden parties of South Kensington.'[18]

The impact of this policy transformed and resuscitated the Society. It began to represent the interests of trade as well as those of members wealthy enough to own land, build hothouses, and employ gardeners. Admittedly, tradesmen were outnumbered on the Society's Council, but three members of the Veitch family were at one time or another members. In later years George Bunyard the fruit grower and Arthur Sutton of the famous seed company of that name became Council members. At the same time the Society's links with aristocracy and royalty were maintained. King Edward and Queen Alexander were Patrons, Lord Rothschild, the Earl of Ducie, and Joseph Chamberlain, M.P., were Vice Presidents, and Lord Balfour of Burleigh and the Earl of Tankerville were on its Council. To its annual flower show held at the Temple came High Society. Thus *The Times* described this show, held on the 23 May 1900, as 'one of the principal events of the London season,' graced with the presence of the Queen of Sweden and Norway, the Duchess of Connaught, the Duchess of Devonshire, Lady Warwick, and Lord Cross. Queen Alexander was received by the President, and Lady Bredalline.[19] The Society's first Chelsea Flower Show in the year 1813 was visited by King George V and Queen Mary, and this annual event has remained high on Society agendas.[20]

But this was far from being simply an organisation for High Society. Among its leading members were men with scientific standing. Consider the following:

Treasurer: Sir Daniel Morris – Assistant Director, Royal Botanic Gardens, Kew.

Chairman of the Scientific Committee – Maxwell Masters, F.R.S., author of *Plant Teratology* and editor of the *Gardeners' Chronicle* (from 1865-1907).

Editor of the *Orchid Review*, Robert Rolfe, and co-editor with Charles Hurst of the *Orchid Stud-Book*.

Secretary of the Scientific Committee: Rev. M.J. Berkeley, the respected authority on mycology, who had a wide knowledge of botany, and was familiar with German botanical research.

F.E. Burbidge, who wrote about his plant collecting in Borneo in the book *The Gardens of the Sun*, became Curator of the Botanic Gardens of Trinity College, Dublin, and received an honorary degree from that university in 1897.

C.T. Druery, the fern expert, fern hybridiser, and translator of Mendel's 1865 paper, secretary and president of the British Pteridological Society, discoverer of apospory.

Sir Michael Foster, Professor of Physiology, Cambridge University, expert on iris breeding.

William Wilks, M.A., Secretary of the RHS, 1882-1915, editor of many volumes of the *Journal*, and keen advocate within the Society of Mendelism.

The Society perceived as its most important tasks to support efforts at discovering and introducing new species and varieties with which the nurseryman could hope to capture 'market share' in what was a rapidly growing trade, and at the same time to set up and oversee an agreed nomenclatural system for the trade. The *Orchid Stud-Book* is an example of that function. Produced by the *Orchid Review,* both titles were edited by Fellows of the RHS.

The International Conferences on Hybridisation

In 1868 at the instigation of Maxwell Masters, the RHS formed a Scientific Committee the object of which was to deal with nomenclatural problems and 'to promote and encourage the application of physiology and botany to purposes of practical culture, and to originate experiments which may assist in the elucidation of such questions.' When Bateson became secretary of the enlarged committee of the Royal Society now called the «Evolution Committee» he asked to meet with the Scientific Committee of the RHS. This suggestion was accepted and in February 1898 Bateson explained his reasons for making this approach to the Council. He wanted breeders to maintain records of all their hybridisations, both successes and failures, because these would supply data on variation, heredity, and selection so vital if the process of evolutionary change was to be understood. This suggestion was enthusiastically supported by Masters. He persuaded the Scientific Committee of which he had become chairman to form a sub-committee which proceeded to circulate Bateson's request to horticulturists. At the same time, the secretary, the Rev. William Wilks, suggested holding an international conference on hybridisation.

The aim of the meeting between Bateson and the RHS Scientific Committee had been to cooperate over 'the investigation of the doctrines of evolution and heredity', Bateson distributing a memorandum listing the kind of data which he needed. He stressed the necessity of keeping records of all attempted crosses, and of recording all the steps which lay between the first hybridisation and the new form subsequently exhibited. Wilks' initiative in proposing an international meeting put the subject of hybridisation on the international stage. The resulting conference served both to advertise the remarkable results of commercial and amateur hybridisation and to bring together scientists and horticulturists. There were the marvelous exhibits of hybrid orchids of Messrs James Veitch, hybrid lilies of Messrs Wallace, hybrid ferns of C.T. Druery, Messrs Paul and son's hybrid roses and the greatly admired hybrid water lilies of Leopold de Rothschild. In his speech

at the conference banquet Lord Justice Lindley, son of the great botanist John Lindley, recalled the early days when the Society sent out plant collectors – John Potts, George Don, John Forbes, John Damper Parks, David Douglas, and Robert Fortune – that was in the first half of the century. Those day, he said, are passed. Now the Society was turning to scientific men and to hybridisation. (As a lawyer he saw before him 'a vista of patent hybrids!')[21] Now was the era of the hybrid, and the Society had now made the deliberate policy decision to promote the work of the hybridist rather than that of the plant collector. From the point of view the Society's finances this was a wise decision. For the introduction of Mendelism it could not have come at a better time.

The theme of the conference was the relation between science and practice. De Vries remarked how impressed he was by this desire to bring together men of science and of horticultural practice to exchange views...

> *...the same sort of bonds that have brought engineering and electricity and all applied sciences to act together, in order to allow such magnificent results, must be brought into action in order to unite scientific and practical horticulturalists in the realms of hybridisation.*

Bateson, echoed De Vries' view. There was a mood of expectancy, great things were around the corner. Yet a study of the papers presented gives no hint that any of the contributors were close to rediscovering the quantitative laws set out by Mendel in 1866, least of all Hugo de Vries. Both he and Bateson focussed on the origination of new forms. De Vries did express the concept of independent material bearers of characters which by hybridisation are transferred from one species to another. 'Thence must arise,' he explained, 'hybrids which would be just as stable as ordinary species, and which therefore, in certain cases, could imitate normal species.' Both De Vries and Bateson made a strong plea for experimental data, treated statistically.[22]

The most interesting paper expressing the mixing of the practical and the scientific was by Charles C. Hurst.[23] In the family nursery at Burbage, Hurst had facilities for orchid breeding and as a member of the trade and of the RHS – he was a Fellow from 1891 – he made contact with other orchid breeders. His efforts to apply Galton's law to his data from orchid hybridising met with little success, but show us how consciously he tried, as had Galton himself, to apply his ancestral law to cases of non-blending heredity. There is little to suggest that this conference was a prelude to the rediscovery of Mendelian heredity, but it does represent a public and international recognition of the scientific as well as practical

importance of experimental hybridisation and the presence of a growing concern to collect statistically significant data.

Less than a year following the 1899 Conference came the papers of the three rediscoverers of Mendelian segregation – published between March 26 and July 24 1900. Their researches arose out of specific questions in academic botany – xenia, hybrid vigour, mutation and prepotency. The Society's interest was more directly practical, but there was a common theme shared by Bateson and the horticultural community, the former how species arose, the latter how varieties were best formed. 'By what steps,' asked Bateson,

> *... by integral changes of what size - did the new form come into being? How did the new form persist? How was it perpetuated when the varying individual or individuals mated with their fellows? Why did it not regress to the form from which it sprang, or to an intermediate form?*

When Bateson spoke to the RHS Scientific Committee in April 1900 he clearly knew nothing of Mendel, and he addressed the same theme as he had at the 1899 conference. On the 8th of the following month he addressed the RHS on the subject, «Problems of Heredity as a Subject of Horticultural Investigation.» This paper, when published had Mendel as its centre piece, and as a consequence it has been generally assumed that it was at this meeting that Mendel's work was for the first time presented to an English-speaking audience. I am confident that this assumption should be rejected.[24] Instead I claim that it was not until Bateson received De Vries' second paper – shortly after May 8 – the one published in the *Berichte der deutschen botanischen Gesellschaft*[25] – that he understood the significance of Mendel's work and incorporated it in his revision of the paper he had already delivered. This texts was then published in the RHS's journal. As he later remarked, this text was written 'almost immediately after the rediscovery of Mendel.'[26] We know that Hurst received his copy of this second paper from De Vries after the 19th. of May, so we are reasonably confident that it was not available to Bateson when he travelled to London to give his talk on the 8th. During that summer, the editor of the RHS *journal*, the Rev. W. Wilks, thus came to learn about Mendel's work. According to Hurst's widow, Rona Hurst, Wilks then had Charles Druery make a draft translation of Mendel's 1865 paper. This formed the basis for the version published in 1901 in the Society's *Journal*. Clearly the translation was the work of several members of the Society, but chiefly Druery, and Bateson's involvement went little beyond writing the notes that accompany it. Also translated and published by the Society were De Vries' two papers from the *Berichte der*

deutschen botanischen Gesellschaft. (Later translators seem not to have been aware of the existence of these earlier translations.)

The key document in this matter is Masters' report of Bateson's address on May 8. This appeared in the *Gardeners' Chronicle* on May 12. It has all the appearance of the notes written by a reporter at the event. Like De Vries' *Comptes rendus*[27] paper, there is no mention of Mendel. Instead, the theme is Galton's law, its attempted application to non-blending heredity by Galton, and the difficulty of fitting this law to first generation hybrids in which the characters of one parent predominate. Masters then continued his report as follows:

> *The recent work of Professor de Vries (Comptes rendus, March 1900) however, shows that in certain such cases subsequent breeding from the cross-bred plants leads to the reproduction of the parent species in such proportions that the facts can be expressed by a modification of Galton's law.*[28]

The report then refers to Bateson's suggestions as to the help continued research on hybrids and their progeny might yield in making predictions as to the number of generations of selfing required to produce a true breeding variety. It ends with Batesons' appeal for the preservation of statistical records of hybridisations. The attention given to Galton in this report conforms with the enthusiasm Bateson expressed elsewhere at this time, and it reminds us of Hurst's attempts to use Galton's law in 1899. The reference in Masters' report to reproduction yielding the parent species in certain proportions shows that the Mendelian ratios obtained by De Vries were reported by Bateson on May 8 and noted by Masters, but without any knowledge of Mendel. After the May 8 meeting Bateson presumably received De Vries' second rediscovery paper in which Mendel's name was mentioned, and he could then have consulted the volume of the *Verhandlungen* of the Brünn Scientific Society in Cambridge University Library in which Mendel's paper appeared.

The year 1902 saw the publication of W.F.R. Weldon's critique of Mendel's paper.[29] This was no damp squib but an incendiary which set alight the fizzeling skirmishes already occurring between Mendelians and biometricians. In 1903 Bateson and Hurst presented an account of their researches and explained the application of Mendelian heredity to plant hybridisation.[30] The climax came with the confrontation between the Mendelians and biometricians at the British Association in 1904. I suspect that there is a link between this event of August and the decision taken in the winter of 1904[31] by the Council of the RHS to hold yet another international conference on the subject of cross-breeding. This conference

was much larger than its predecessor. The number of foreign guests was greater, and as president of the conference the Society chose a scientist – Bateson. More of the participants and speakers were scientists, most of them Mendelians, but De Vries and Correns could not come. Most of those who did were given special attention by the award of Veitch medals.

In his inaugural address to the conference Bateson introduced the term 'genetics' to identify the new science based on Mendelian principles.

> *... I suggest for the consideration of this Congress the term* Genetics, *which sufficiently indicates that our labours are devoted to 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 the systematist, and application to the practical problems of breeders, whether of animals or plants.*[32]

The result of this action was that the proceedings of this conference when published a year later became the third International Conference 1906 on Genetics although right up to the final programme issued at the conference it had retained its former title. The two earlier conferences on the same subject – in 1899 and 1902 – were thus retrospectively redefined by the editor, the Rev. W. Wilks, with the approval of the Society as the first and second international conferences on genetics. Wilks further linked the 1906 conference with Mendelism by publishing full-page photos of Mendel, the Altbrünn monastery, the Veitch Medal recipients, and a sample of Mendel's letters to Carl Naegeli followed by a five page account of his life and work. Thus notwithstanding the growing interest in the proposals and doctrines of the eugenists at this time, it was this powerful and prestigious society that gave both national and international recognition to Mendelian heredity.

The Response of Botanists & Zoologists

A Comparison of the response of the horticulturists to the work of the Mendelians with the response of the botanists and zoologists offers a striking contrast. When the international congress of botany met in Vienna in 1905, as we might expect, Vienna's first Mendelian, Erich Tschermak, spoke on his Mendelian researches, but his was a lonely voice, and at the subsequent event in Bruxelles five years later Mendelism was not even mentioned. The zoologists were more

forthcoming. They had offered the prize of Emperor Nicholas II on the occasion of the seventh international congress of zoology in 1907 for an essay on 'New experimental researches on the question of hybrids,' by Lucien Cuénot.[33] As the only essay submitted on time the congress had little choice but to award Cuénot the prize, but Standfuss' essay on the inheritance of acquired characters, notwithstanding its late arrival, they also published,[34] and I infer that they favoured his essay over Cuénot's. At this congress a new section was introduced on cytology and heredity, where opportunity was given for the discussion of Mendelism, especially its relation to cytology. Bateson was invited and attended this section.

During the first decade of Mendelism in England, Bateson's efforts to gain long term support for his research and a university position failed. It was a horticultural trust, intended for the education of gardeners, that was usurped for Bateson's genetics.[35] The biometricians had offered the most direct challenge to him, but influential members of the scientific establishment who were also not enthusiastic for biometry, either rejected Mendelism or considered it of marginal importance, and irrelevant to the concerns of the evolutionist. These included E.B. Poulton, professor of zoology at Oxford and an enthusiastic supporter of August Weismann, Thiselton-Dyer, Director of the Royal Botanic Gardens, Kew, and J. Arthur Thomson, Professor at Edinburgh, and last but not least, A.R. Wallace.

In his critical survey of 1908 Wallace belittled Mendel's achievement, and quoted Darwin to the effect that 'hybridisation...had no place whatever in the natural process of species-formation,' and that, he added, 'was the reason why Darwin did not prosecute the research further.' Wallace preferred Darwin's text to 'any amount of study of the complex diagrams and tabular statements which the Mendelians are for ever putting before us with great flourish of trumpets and reiterated assertions of their importance.' Wallace's anger grew as he wrote. For the Mendelians to 'set upon a pinnacle this mere side-issue of biological research,' was to invite ridicule. Their claims were, he declared, 'monstrous'.[36] Poulton, for his part, reported that all the eminent zoologists to whom he explained his grounds for indicting the Mendelian writings as 'injurious to Biological Science, and a hindrance in the attempt to solve the problem of evolution' had agreed with him.[37] Bateson's co-worker, R.C. Punnett, replied that 'The Sacred College has convened and orthodoxy has spoken through its chosen mouthpiece.'[38]

The Character of Mendelism

The ties between Bateson's circle and the horticultural trade can be correlated with major features of the science of genetics, in the first decade of the twentieth century. At that time those working in this field were known as Mendelians, because of the prominence they gave to Gregor Mendel and his laws. Starting with the adjective 'Mendelian' (1902),[39] the literature of the period introduced the noun 'Mendelism' in 1903,[40] and in 1905 it was the title of R.C. Punnett's little book.[41] A year later, Karl Pearson, a principle opponent of the Mendelians, asked with evident sarcasm: 'What is the essential feature of that which is called Mendelism by those who believe in it, and Mendelianism by those [of us] who do not?'[42] Indeed, it was the growing controversy between two warring groups that firmly established the labels 'Mendelians', and 'Biometricians.' For a succinct but flippant statement of what Mendelians stood for one could turn to one of Bateson's circle, R.H. Lock, who in 1909 wrote to Bateson enclosing the following Mendelian 'creed' which he had received from 'a scurrilous friend':

> I believe in Weismann, the author of soma and germplasm,
> And in Gregor Mendel, his antecedent,
> Who discovered Ds and Rs, who suffered obscurity,
> Was rediscovered by Bateson, and set on a pedestal from which are judged all the followers of Lamarck,
> I believe in De Vries, the creator of mutations,
> In the segregation of gametes, the continuity of germplasm,
> The disappearance of acquisitions, and the everlasting formula
> F_1, F_2, F_3.[43]

That, of course, was at the time an unpublished source. For the most authoritative statement on Mendelism published prior to the advent of the Morgan group, the acknowledged source was Bateson's *Mendel's Principles of Heredity* (1909). In this work Bateson deliberately left out discussion of the more theoretical questions raised by Mendelism – those dealing with evolution and the nature of species, reserving them for the volume containing his Silliman Lectures of 1907 which appeared belatedly in 1913.[44] Instead he concentrated in *Mendel's Principles* on presenting the 'concrete phenomena' that had been established in the new field. His justification for the volume was that 'our knowledge of the main facts has reached a definite stage'. Also, by introducing a chapter given to Practical Applications, he drew attention to the future commercial value of the science. His opening remark on this subject was indeed prophetic:

Such applications will probably far exceed any limits we can yet perceive. Among them we must foresee not merely advances in the art of breeding animals and plants, but a control over the destiny of our own species.[45]

Now, pause for a moment to compare *Mendel's Principles* with Morgan, Sturtevant, Muller & Bridges' *The Mechanism of Mendelian Heredity* (1915). In the Preface Morgan remarked on the 'curious situation' that had developed since 1900. He explained:

The students of heredity calling themselves geneticists have begun to draw away from the traditional fields of zoology and botany, and have concentrated their attention on the study of Mendel's principles and their later developments. Their terminology is often regarded by other zoologists as something barbarous, – outside the ordinary routine of their profession. The tendency is to regard genetics as a subject for specialists instead of an all-important theme of zoology and botany.[46]

There is nothing about practical applications in the *Mechanism of Mendelian Heredity*. The fruit fly (*Drosophila*) on which the Morgan group worked had even less commercial value than the sea urchin on which, as an embryologist, Morgan had previously worked. Morgan's initial concern being with the determination of sex, not with the generation of novelties, he concentrated on the one organism, using it as a *model organism*, much in the way that he had previously used the sea urchin in embryology. Bateson's concern, by contrast, was with the genesis of new species, much as the horticulturists were concerned with the production of novel varieties. Appealing to the *quantitative combining patterns between elements* in chemistry, and their place in a system of relations – the Periodic Table – the emphasis of the research of Bateson's circle was upon the replication among other species of the combining ratios that Mendel had achieved with the edible pea (*Pisum*). Using species of importance to the trade – the Sweet Pea (*Lathyrus*), Stocks (*Matthiola*) orchids (*Paphiopedilum*), tomatoes (*Lycopersicum*), snapdragons (*Antirrhinum*), thorn Apples (*Datura*), Begonias, flax (*Linum*), the house plant *Primula sinensis*, sage (*Salvia*), and chillies (*Capsicum*), these Mendelians explored the 'coupling' of characters (linkage) (chap.ix), the generation and inheritance of double flowers (chap. xi) – a feature of many of the new varieties produced in the trade –, the cause of 'rogueing' (chap. xvi) – a problem for the trade –, the inheritance of leaf shape, and the chemistry and inheritance of flower colour (chap. v). A number of these topics had been brought to Bateson's attention by horticulturists, and especially by Messrs Sutton & Sons, the King's Seedsmen, of Reading, whose

Arthur Sutton met with Bateson on many occasions. In addition, an important member of Bateson's circle, Charles Hurst, was the owner of the family nursery in Burbage near Leicester.

Although these researchers served to extend the Mendelian theory, they also exposed many of its limits and the need to introduce modifications to cover a variety of cases, a point about which Bateson warned his readers repeatedly. Bateson sought to introduce modifications to the Mendelian scheme that remained within the framework of quantitative combinations. Thus he preferred his hypothesis of germinal reduplication to Morgan's cytological hypothesis of linkage and crossing-over. His notion of an underlying periodic table of combinations found expression later in Vavilov's theory of the centres of origin of cultivated plants.

In 1909 Bateson confessed that apart from speeding up the process of fixing desirable varieties and the 'creation of new types by re-combination of pre-existing characters', what the new knowledge would do was to introduce 'a new standard of precision,' into the language and concepts of the breeder. Cross-bred and pure-bred, for example, had to be defined in terms of homozygosity and heterozygosity.[47] But as for the 'Fancier', he admitted 'Mendelism can as yet do comparatively little'. He added:

> *«Fancying» provides the chief interest in life for thousands of persons in this country. It is an occupation with which the scientific naturalist should have more sympathy. If the scientific world had kept in touch with the operations of the «fancy» much nonsense which has passed into scientific orthodoxy would never have been written. The study of Mendelian phenomena will do something to bring about a fruitful interchange of experience... But applied to the business of breeding winners in established breeds they cannot materially help, for almost always the points which tell are too fine to be dealt with in our analysis.*[48]

Bateson might have added, that these fine differences are probably determined by many Mendelian factors. It was characteristics of the traits that are of principal interest in agriculture, such as egg yield of poultry, size of fruit, crop yield, etc., to have polygenic inheritance. Bateson's Mendelian programme in its first decade did not include such cases, although Bateson claimed rightly as early as 1902 that Mendelism could account for them. Nor did Bateson forge a link with the cytologists. His dislike of any crude physical localization of determinants in the cell prevented him from appreciating the results of the work of Gregory, a member of his circle, on the hereditary and cytological characteristics of the first polyploid discovered among cultivated plants – *Primula kewensis* – the first polyploid to be

produced and recorded under cultivation. This was the fertile form of *Primula kewensis*. In 1899 Mr. Garrett, foreman at Kew, noted what must have been a spontaneously produced hybrid between *P. floribunda* and *P. verticillata*. This hybrid was exhibited at a meeting of the RHS in 1900 under the name *Primula kewensis*, where it won a First Class Certificate. Most of the stock was then passed to Messrs Veitch and Sons of Chelsea. All the plants of this hybrid were sterile because all the flowers were «thrum-eyed». In 1905 Messrs Veitch noted a single «pin-eyed» flower. They pollinated this with the thrum flowers and seeds were set. From this one flower all the fertile plants of *P. kewensis* have originated. The original cross was repeated in 1910 by J. Coutts, foreman at Kew. Shortly after this, Miss L. Digby, a student in Professor J. Bretland Farmer's department of botany at the Royal College of Science, London, undertook a study of the cytology of this hybrid with material supplied by Kew Gardens and by Messrs Veitch. The result was her discovery of the tetraploid state of the fertile form ($4x = 36$) in contrast to the diploid state of the originating species and the sterile form of *P. kewensis* ($2x = 18$). It was the link with the chromosomes, and the study of polygenic inheritance that enabled Mendelism to become what we know as genetics, a science central to biology.

Conclusion

The first decade of Mendelism under Bateson's guidance, was not yet genetics. It was the product of the fruitful interaction between Bateson and his circle and the horticultural community under the stimulus of the rediscovery of Mendel's laws. Although these Mendelians espoused eugenic aims, Bateson was decidedly sceptical of the claims of the eugenists. Eugenists and the Eugenic Education Society – an organization founded in 1907 and one tenth the size of the RHS – provided neither the driving force nor the financial and institutional support for the first decade of Mendelism in Britain. Only when in 1912 two prominent politicians, Lord Esher and Arthur Balfour, obtained the funds to establish the Balfour Chair of Genetics at Cambridge could it be said that political concerns about the degeneration of the British population may well have played a supportive role. France had its Vilmorins, but how many other horticultural companies that undertook systematic programmes of hybridisation? More importantly, I am not aware of a French equivalent to the RHS existing in the 1890s with which the Vilmorins could have worked.[49] As William Schneider has shown the French had their own form of eugenic concerns,[50] but I suspect one reason why Mendelism

gained little hold in France the first decade of the twentieth century had to do on the one hand with the absence of the French equivalent of Maxwell Masters and William Wilks and on the other hand with the lack of an equivalent to the Royal Horticultural Society. Finally, Lucien Cuénot was by no means the equivalent of the determined and provocative William Bateson, with whom British horticulturalists enjoyed such a productive symbiosis.

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