TIMELINE

# Horticulture: the font for the baptism of genetics

*Robert C. Olby*

This year marks the centenary of the rediscovery of the laws of heredity, and their introduction to the English-speaking world. Here I introduce the main events and the characters who figure in this story before turning to the task of this essay — to ask why it was that support in England for the emerging science of genetics, or Mendelism as it was then called, came chiefly from horticulture, and was only belatedly accepted into the mainstream of British academic biology.

The familiar story of the beginnings of the science of genetics is inaccurate. We all know how poor Mendel's classic study of hybridization[1] contained the keys to the mystery of heredity, but his work was neglected for 35 years. Then, like several claps of thunder, came announcements of the rediscovery of Mendel's laws of heredity by three botanists — Hugo de Vries in Holland[2], Carl Correns in Germany[3] and Eric Tschermak in Austria[4]. There followed the drama of the Cambridge zoologist, William Bateson (FIG. 1), who, according to his wife's account, read Mendel's paper for the first time travelling on the train from Cambridge to London to address the Royal Horticultural Society (RHS). He consumed the text avidly, transformed his lecture there and then, and on the 8 May 1900 unfolded to his audience the wonders of Mendel's work and its affirmation by de Vries[5]. Bateson became the apostle of Mendel. Around him collected a group of dedicated young scientists, many of them women, who worked to explore the application of the Mendelian experiment to a variety of animals and plants.

Bateson agreed with the great German evolutionist, August Weismann, that acquired characters are not inherited, and he fought to convert LAMARCKIANS with the gospel of Mendelism. But Mendelism, it seemed, allowed only for the varied reassortment of hereditary characteristics already present. Fortunately, de Vries was developing another concept to which he gave the name 'mutation', that is, an abrupt change in an organism due to a change in the constitution of the particles that are the bearers of the characters, or the loss of such particles[6,7]. He considered his mutation idea much more important than the Mendelian laws he had rediscovered, for mutation opened up a vista of evolution by discontinuous variation and the potential to develop new varieties of plants for horticulture and agriculture[8].

### The revisionist account

Recent historical research indicates the need to revise this standard account in several respects. First, we are now confident that two of the three rediscoverers had read Mendel's 1865 paper before they came to their rediscovery. It was the stimulus that caused de Vries to select from his numerous HYBRIDIZATIONS those that fitted the 3:1 Mendelian scheme of the segregation of dominant and recessive characters (BOX 1). Admittedly, he had already realized that this ratio could be broken down into the fundamental 1:2:1 ratio of the binomial

Figure 1 | **William Bateson, the apostle of Mendelism in Britain (left) and Maxwell Masters, editor of the *Gardeners' Chronicle* (right).**
Photographs courtesy of the John Innes Centre, Norwich, UK and the Royal Horticultural Society, London, UK, respectively.

Box 1 | **Mendel's principles and Correns's 1896 notes**

**Mendel's observations**

Mendel showed that the apparent confusion of data concerning hybrid offspring could be resolved by treating the characters as independent units, following the transmission of each character difference separately (his character-pairs) and by growing statistically significant numbers of plants in each generation. Because he could recover the contrasted characters in their pure form in hybrid progeny he concluded that a segregation between the co-mingled germinal material in the formation of the germ cells must have occurred. This is the doctrine Bateson termed "the purity of the gametes". Hence the great variability of many cultivated plants is mostly the result of the enhanced opportunities for crossing that cultivation permits. He allowed that in some hybrids a segregation process may not take place. Such hybrids would breed true and might so introduce new species. The cases he studied did not breed true, but over others he left a question mark.

**Correns's notes on Mendel**

Correns's notes on Mendel are found in his protocols for his experiments with peas. Among the 330 pages of notes recording sowing times, results, calculations, drawings and drafts of papers, there is a bundle labelled 'Crosses with Pisum'. Here there is a page, dated 16 April 1896, devoted to Mendel's paper:

*Mendel distinguishes dominant and recessive characters.*
*The dominant and recessive characters are expressed already in the first generation in such a way that the former are present in 3, the latter in 1 individual, respectively.*

expansion — indeed he had noted the 1:2:1 ratio in his 1896 notes on his reading of work by Galton[9]. But thinking about such a ratio, looking for it, observing data that approximate to it, is one thing, realizing that it has a very special significance — as did Mendel — is quite another, for de Vries's extensive researches yielded a variety of numerical data. In Correns's case, we have the actual notes (BOX 1)[10] he made on Mendel's paper in 1896! Four years later, when he had observed several generations of the segregating offspring, he had, according to his later recollection, first read the paper a 'few weeks after' arriving at the correct explanation of his own data.

Second, there is crucial evidence that does not fit with the recollections of Beatrice Bateson about that train journey her husband took to London[11]. Although Mendel's work figures prominently in the published version[12] of the talk in 1901, the report published in 1900, four days after the lecture, makes no mention of Mendel. However, the report[13] does refer to de Vries's evidence that breeding of the offspring of cross-bred plants "leads to the reproduction of the parent species in such proportions (3:1) that the facts can be expressed by a modification of Galton's law". It should be no surprise that these (Mendelian) data were viewed through the lens of the well-known 'Ancestral Law of Inheritance' (BOX 2)[14] formulated by Darwin's cousin, the statistician and eugenist Francis Galton, which applied to NON-BLENDING AND BLENDING characters[15]. And so Bateson read and incorporated into his lecture the work of de Vries as he travelled to London on the 8 May, but placed it in a Galtonian and not a Mendelian context.

Third, examination of the papers of the three rediscoverers reveals that only two of them — de Vries and Correns — understood clearly Mendel's distinction between the transmission of a characteristic and its expression. The tendency of hybrid offspring to revert to one or other parental species concerns hereditary transmission, whereas the expression of a characteristic has to do with the interactions of the hereditary elements in development. Tschermak, like many nineteenth-century biologists, including Charles Darwin, thought of these elements as possessing 'hereditary potency', which was conceived to determine both transmission and expression.

Fourth, the political implications of heredity were being much discussed internationally at the time of the rediscovery of Mendel's work, and the establishment of institutions in a number of countries was due to interest in human heredity as a basis for eugenics. However, the birth of Mendelism as an experimental science in England owed most to the horticultural community, and to the evolution committee of the Royal Society. As for the RHS, hybridization was serving it well in the trade's pursuit of novelty, fuelled by visions of the rewards to be won in what was becoming an expanding and increasingly valuable market. Where there had been only single flowers, double flowers were produced; white flowers were produced where there had been only coloured; and Mendelism offered the promise of rationalizing the art of breeding itself.

### The importance of hybrids

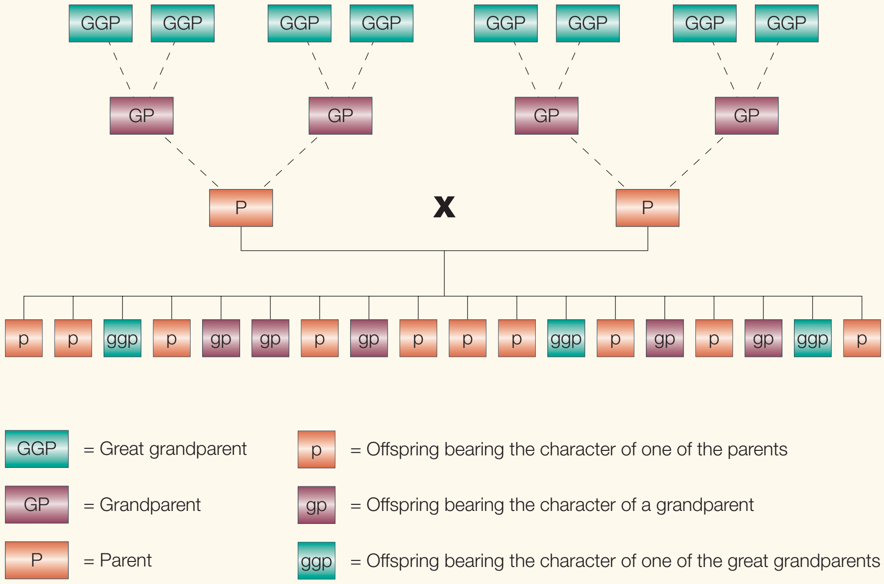
Mendel entitled his paper 'Experiments on plant hybrids', de Vries his 'On the law of the segregation of hybrids', and Correns his 'G. Mendel's law concerning the behaviour of the progeny of hybrids'. Why hybrids and not heredity? How and why did hybrids and experimental hybridization become important in nineteenth-century science? Their significance had been realized by animal breeders since the eighteenth century, but their practical importance to plant breeders was not fully recognized until the latter decades of the nineteenth century. Most garden and house plants owe their success to the hybridization of exotic plants brought from distant parts of the world. Classic examples are orchids, daffodils and begonias

Figure 2 | **John Dominy and the first orchid hybrid he created, *Calanthe dominii*.**
Photographs courtesy of the Linnean Society, London, UK, and the Hunt Botanical Library, Pittsburgh, Pennsylvania, USA, respectively.

### Box 2 | Galton's law of ancestral heredity for non-blending characters

Galton's law states that our heritage is, on average, constituted from that of our ancestors according to the following proportions: parents jointly contribute one half, grandparents one quarter, great-grandparents one eighth… Where character differences do not blend they are distributed among the offspring, such that the characters of the parents will be found in 50% of the offspring, those of the four grandparents in 25% and those of the great-grandparents in 12.5%.

- The distribution of the non-blending characters in the descendant gives: 10p : 5 gp : 3ggp out of a population of 18.
- The ratio is: 0.55 : 0.277 : 0.16
- With large numbers the ratio should approach the Galtonian law of: 0.5 : 0.25 : 0.125
- Galton showed that data he took from the Basset Hounds Studbook approximated to these proportions.




(FIG. 2). Mendel himself had experience of cross-breeding fuchsias before he began his experiments. Although animal breeding retained its commercial importance in nineteenth-century Britain, it was not given as much attention from experimentalists as were plants, because plants were easier and less costly to handle.

The main concern behind Mendel's research programme, however, seems to have been an attempt to resolve the debate over the role of hybrids in the formation of new species[16,17]. If hybrid offspring revert, what general law governs the process? If some do not, can they form new species? Mendel showed that in the garden pea, hybridization produces genetic recombination yielding variability and new combinations of characters. However, in this case, he rejected the suggestion that hybrids may simply BREED TRUE from the start and so produce new true-breeding forms. For some other species he left the verdict undecided. Nevertheless, he could see the error of those like Darwin, who believed that changed conditions of life are the fundamental determinant of variation. Cultivated plants are not more variable than their wild relations because they have experienced different conditions, but because of the increased opportunities they have for crossing with other species.

Among the applied sciences, it was horticulture that used hybridization most effectively in the pursuit of the trade. A striking example is provided by the famous firm of James Veitch and Sons. After financing 22 plant hunting explorations, they began hybridizing orchids, begonias and many other species. Their success made this firm one of the greatest in the world[18]. However, hybrids do not normally breed true. Many house and garden plants can be reproduced vegetatively, so avoiding this problem. But in agriculture, where crops like maize and wheat can be grown only from seed, hybrid varieties long remained unpopular, because farmers could not save seed from their own crops. Also, the alleged harmful effects of inbreeding discouraged crop researchers in agriculture from Mendelian programmes[19–23]. Instead, the majority favoured the existing technique of MASS SELECTION.

> "That no generally applicable law of the formation and development of hybrids has yet been successfully formulated can hardly astonish anyone" (Gregor Mendel)

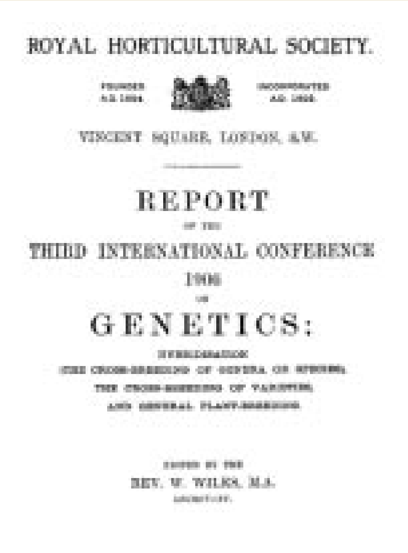
Hence it was the RHS that embraced the science of hybridization, influenced by members of its scientific committee, which included the society's dedicated and effective secretary, the Rev. William Wilks, and the committee's chairman, the plant TERATOLOGIST, Dr Maxwell Masters (FIG. 1). It did so in 1899 — just at the time when the trade was intensively engaged in hybridization programmes, and on the eve of the rediscovery of Mendel's laws. This temporal coincidence has not, I believe, been remarked on before.

#### The Royal Horticultural Society

The RHS was no mere pressure group of middle-class activists, but a prestigious and highly visible society dedicated to the interests of the art and trade of horticulture[24]. Among its leading members were scientists such as Sir Michael Foster, the financier Sir Henry Schröder, and its president Sir Trevor Lawrence, son of the famous surgeon Sir William. The trade was represented by Sir James and later by Sir Harry Veitch, Arthur Sutton, George Bunyard and Charles Hurst. In the 1880s its membership was around 1,000, but by the turn of the century it had risen to 11,000, and six years later on, to 16,000. After its recovery at the end of the 1880s, it directed its efforts to the trade it represented, but it did not lose its aristocratic character. Instead, the two constituencies of its membership formed an effective alliance for their common cause — the promotion of horticulture.

William Bateson, anxious to tap the knowledge of the society's members, contacted its scientific committee in 1897. He did this formally as a member of the Royal Society's evolution committee. This approach prompted Secretary Wilks to suggest holding an international meeting on plant hybridization in 1899. It took place in July and was a great success[25]. The following April, Bateson gave a lecture on hybridiza-

**Box 3 | The Third International Conference 1906 on Genetics**


ROYAL HORTICULTURAL SOCIETY.

VINCENT SQUARE, LONDON, S.W.

REPORT

THIRD INTERNATIONAL CONFERENCE

1906

GENETICS:

REV. W. WILKS, M.A.

An excerpt from William Bateson's Inaugural Address to the 1906 International Conference, in which he coins the term 'genetics':

"…the science itself is still nameless, and can only describe our pursuit by cumbrous and often misleading periphrasis. To meet this difficulty 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. After more or less undirected wanderings, we have thus a definite aim in view."

(Photograph courtesy of the Royal Horticultural Society, London, UK.)

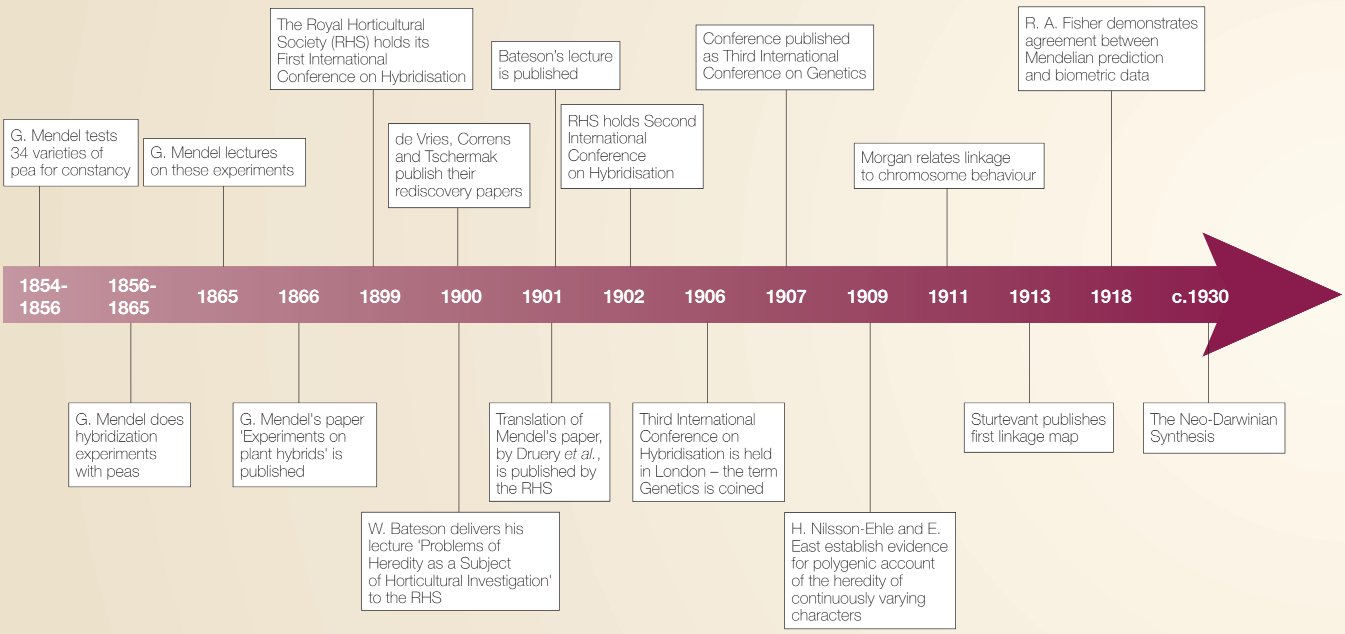
tion to the scientific committee, but without any knowledge of the two papers read by de Vries at the March and April 1900 meetings of the Académie des Sciences in Paris. On the 8 May came Bateson's address 'Problems of heredity as a subject of horticultural investigation', which, when revised, gave to the English-speaking world the first brief account of Mendel's work for a general audience. Stimulated by the new knowledge, Wilks arranged for his colleague, the fern hybridist, Charles Druery, to make a draft translation of Mendel's paper. After revision, this was published by the RHS in its journal along with an introduction and some notes by Bateson[26]. Four years later it was again Secretary Wilks who suggested holding another international conference on hybridization. At this sumptuous event in 1906, the conference president — Bateson — gave genetics its official baptism when he coined the word 'genetics' to describe the new science[27] (BOX 3). Papers were given by seven Mendelians, and Veitch Gold Medals awarded to five of them by the RHS. As this was the third international conference on hybridization, Wilks named the published proceedings 'The Third International Conference 1906 on Genetics'.

### The response of the biologists

The characteristics that Mendel studied statistically were all of the non-blending type — they were either dominant or recessive. Their variation was discontinuous and their origin was therefore assumed by Bateson to be due to saltations (macromutations). But natural selection was, and is, claimed to act on continuously varying characteristics, shaping them gradually to show adaptation. So the Mendelians and the Darwinians did not become bed-fellows, and instead a violent controversy arose, which only began to be resolved in the 1920s (TIMELINE).

Today it is all too easy to look back and judge these scientists as perverse for not accepting that Mendelism was in harmony with the biometrical data and with evolution by natural selection. In fact, Mendel provided the solution to Darwin's great problem — how rare variants in a large inter-breeding population can avoid being rapidly diluted to vanishing point. Mendel showed that the characters he brought together in a hybrid are determined by elements that do not melt together forever, but separate cleanly when the germ cells are formed. Their integrity, no matter how rare, is preserved.

**Timeline | Mendel, Mendelism and genetics**



But de Vries, Bateson and his circle of Mendelians pressed for a reform of Darwinism, in which new species originate by mutational events — events that natural selection has either to accept or reject, but is deprived of the power to fashion in a gradual and stepwise manner over a long period of time. These two functions of natural selection are often referred to as the 'gate-keeper role' and the 'creative role'. (Today this issue is again very much alive.)

The enthusiastic response of the horticulturists to the work of the Mendelians provides a striking contrast with the response of the botanists and zoologists. When the International Congress of Botany met in Vienna in 1905, Austria's first Mendelian, Erich Tschermak, spoke on his research, but his was a lonely voice, and at the subsequent event in Brussels five years later Mendelism was not even mentioned. The zoologists were more forthcoming. At the Seventh International Congress of Zoology in 1907, they awarded the prize of Emperor Nicholas II to the French Mendelian, Lucien Cuénot, for his essay[28] on 'New experimental researches on the question of hybrids'. However, it was the only entry received on time, and they also printed an essay[29] on experiments in support of Lamarckian heredity that was received too late for the prize. A new section on CYTOLOGY and heredity was introduced, where opportunity was given for the discussion of Mendelism, especially in relation to cytology. This is important, for it was through the connection with chromosomes and sex determination that Mendelism entered the mainstream of biology, a connection consistently denied by Bateson until 1922.

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[30]. The BIOMETRICIANS offered the most direct challenge to him, but influential members of the scientific establishment who were also unenthusiastic about biometry, either rejected Mendelism or considered it of marginal importance and irrelevant to the concerns of the evolutionist. These included Edward Poulton, Professor of Zoology at Oxford, William Thiselton-Dyer, Director of the Royal Botanic Gardens, Kew (who were both subsequently knighted) and, last but not least, Alfred Russel Wallace, co-discoverer with Darwin of evolution by natural selection.

> "The Sacred College has convened and orthodoxy has spoken through its chosen mouthpiece."

In his critical survey of 1908, Wallace[31] belittled Mendel's achievement, and quoted Darwin to the effect that "hybridization… 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". 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[32]. Bateson's co-worker, Reginald Punnett[33], replied that: "The Sacred College has convened and orthodoxy has spoken through its chosen mouthpiece." Weismann's public comments were cautious, but writing to his translator, William Parker, he expressed his dislike of mathematics, and his expectation that reduction division in animals introduces complications that are not present in plants[34], because, as the great botanist Edward Strasburger claimed, there is no reduction division in plants!

### Conclusions

There were several reasons why these biologists were so unreceptive to Mendelism. First, Bateson was confrontational and often scornful in his comments on the Darwinian science they supported. Second, although neither Mendel nor Bateson considered non-blending characters to be the only ones deserving of study, that was the impression their work gave in the hands of many of their expositors. This was reinforced by the emphasis Bateson and de Vries placed on discontinuous variations, allied with their scepticism over the creative role of natural selection. At the same time, Bateson and other experimentalists judged the descriptive comparative embryological approach to the study of evolution to be fatally flawed. This approach was still popular among Darwinians, despite the failings of the theory of recapitulation (ontogeny repeats phylogeny) on which much of the work was based[35].

What a contrast to the horticultural scene. Many of the traits prized for their variability — flower colour, symmetry of organization, number of floral parts and shape of fruit for example — were or initially seemed to be subject to a simple Mendelian form of inheritance. The work of the breeder lent itself to an experimental approach, and the trend in biology at the time was moving away from descriptive and towards experimental

### Glossary

BIOMETRY
The study of biology using quantitative, statistical methods.

BREED TRUE
When individuals breed true their characteristics are reproduced faithfully in their offspring.

BLENDING AND NON-BLENDING
Where there exists a gradation in the expression of an hereditary trait in the individuals of a population, the variation is termed continuous and the inheritance is blending — for example, height in humans. Where there is no such gradation, but an abrupt change from one state of the trait to another, the variation is termed discontinuous and its inheritance is non-blending — for example, round or wrinkled peas.

CYTOLOGY
The study of cells, the units of the tissues studied by the histologist.

HYBRIDIZATION
Formerly used to refer to the crossing of pure species, whereas cross-breeding referred to the crossing of varieties and races. This distinction was still in use when the RHS held its conferences on the subject.

LAMARCKIANS
Those who held that adaptive variations are the result of the action of the environment in directly modifying both the organism and its hereditary constitution. In the 1890s Lamarckians sought to promote experimental investigations in support of their case.

MASS SELECTION
Practised in maize breeding, where the best ears of corn were selected and their seeds mixed for sowing.

MUTABILITY
The rate of production of mutations of any kind by an organism or associated with a given chromosome.

RECURRENT MUTATIONS
Identical mutations that appear independently are called recurrent mutations. The problem with measuring the rate of recurrent mutation from experiments was the rarity of the events.

TERATOLOGY
The study of malformation in animals and plants.

approaches. Breeders wanted the 'physiology' of heredity, not its biometrics.

Before the first decade of the century came to a close, Mendelian heredity had been applied successfully to continuously varying traits, but this did not clear the way for the reconciliation of the opposing sides. The inadequate understanding of the nature of mutation remained. Although estimates of MUTABILITY in the chromosomes of the fruitfly were published in 1919, it was not until 1923 that the idea of mutation as RECURRENT[36] and measurable in the form of a statistical value for a given mutant in a population began to appear in the literature. Until mutation ceased to be considered unpredictable and for the most part saltatory, and so long as mutants were associated with what were considered unimportant or useless characters, there was no way in which Darwinian evolution and Mendelian genetics could come to terms with each other. But Mendelism and horticulture did not have to wait, even though the benefits of Mendelism were only slowly realized.

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## Links

**FURTHER INFORMATION** Mendelweb | Genetics timeline | Mendel's 1865 paper "Experiments in plant hybridzation." | Galton's 1898 paper "A diagram of heredity." | Bateson's 1899 paper "Hybridization and cross-breeding as a method of scientific investigation." | Bateson's 1900 paper "Problems of heredity as a subject for horticultural investigation." | Bateson's 1902 book "*Mendel's Principles of Heredity, a Defence*" | The Royal Horticultural Society of London | Robert Olby's homepage

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SCIENCE AND SOCIETY

# Genomics in the public domain: strategy and policy

*Rebecca S. Eisenberg*

The public domain has been conspicuous in media accounts of public and private sector initiatives to complete the sequence of the human genome. The issue of whether the human genome will be freely available to the public or privately held as a proprietary resource has captured the attention of the scientific, trade and popular press, the financial markets, and even heads of state. Although some media commentary has framed the issue as a conflict between ethics and greed, strategic considerations go a long way towards explaining the timing and quality of information disclosures on both sides of the public–private divide.

Some descriptions of the relationship between Celera Genomics Corporation and the Human Genome Project have painted a black-and-white picture of a private firm racing to profit from patents while the publicly funded project struggles to keep the genome in the public domain. In fact, both sides of the picture are variegated. Even as it has built a proprietary database and filed patent applications, Celera has repeatedly promised that it will eventually make the raw sequence of the human genome available to scientists free of charge[1], although the timing and details of this commitment are unclear and seem to have shifted. At the same time, although the public sponsors of the Human Genome Project have consistently affirmed the importance of prompt and free public access to raw genomic sequence data (BOX 1), the United States government reportedly holds more patents on DNA sequences than any private firm[2]. Public and private strategies for publication and patenting have overlapped throughout the brief history of genomics research[3]. An important factor contributing to this convergence has been the policy of the United States gov-