• *ABSTRACT*

A re-examination of the case of Mendel suggests that he was neither ignored in the 1860s nor simply re-discovered in 1900. In 1900, the concern for priority among De Vries, Correns and Tschermak, and the controversy between Bateson and the biometricians over species variation, led scientists to reconstruct the relevance of Mendel's hybridization experiments with Pisum *in terms of their own work on natural selection. By contrast, an examination of the original paper indicates Mendel's concern, not with variability, but with the very process of speciation via hybridization.*

The Reification of Mendel

Augustine Brannigan

The case of Gregor Mendel presents one of the great perennial problems in the history of genetics. How could a series of outstanding experiments which were conducted over a period of years and which laid the foundation for the modern field of genetics fail to have come to the attention of the scientific community? A series of historical papers has tried to account for the 'long neglect' of Mendel's work by drawing attention to such things as the forbidding mathematical approach, the obscurity of the publication, the low status of the researcher, the prematurity of the problem and the misinterpretation of the results. None of these solutions is completely convincing. The present paper offers an alternative hypothesis: that the relevance of Mendel's achievement changed over time from the point at which it was initially conducted in the 1850s and 60s to the point at which it reappeared in 1900. Specifically, it is suggested that Mendel's revival in 1900 took place in the context of a priority dispute between Correns and De Vries, and that this dispute led scientists to overlook the original intent of

Social Studies of Science (SAGE, London and Beverly Hills), Vol. 9 (1979), 423-54

the earlier research. Furthermore, the revival of Mendel in England emerged in the context of a controversy between the biometricians who had adopted a model of continuous variation and evolution by the selection of individual differences, and the 'saltationists' like William Bateson who had adopted the model of evolution by the selection of 'mutations' or discontinuous variations. In the context of this controversy, Mendel's work was erroneously employed to dismiss biometrical models of inheritance and to underwrite the efforts of the mutationists. However inaccurate such positions turned out to be, Mendel's achievement emerged at a point in time when the problem of inheritance was an acute question in evolutionary theory, especially in light of Darwin's failing model of pangenesis. On the other hand, it appears that, in his own day, Mendel's work was undertaken in the tradition of the hybridists who viewed the process of inheritance not as a *subfield* in the general theory of evolution but as itself a potential explanation of the origin of species. These facts tend to support the opinion that in 1866 Mendel's work figured as normal science in the hybridist tradition, while in 1900 the revival of Mendel's discovery of segregation constituted a relatively revolutionary achievement.[1]

The Contexts of Mendel's Revival

In 1900 Hugo De Vries announced the results of his experiments describing 'the law of segregation of hybrids.' That law was based on De Vries' reformulation of the Darwinian hypothesis of pangenesis presented in his *Intracellular Pangenesis* (1899). De Vries divided Darwin's hypothesis into two parts: a *material unit hypothesis* which held that qualities inherited by the organism are represented by discrete material particles in the germ cell, and a *transportation hypothesis* which held that parts of the organism throw off particles which often become incorporated into the germ cell, and result in the inheritance of changes acquired during ontogenetic experiences. However, De Vries dismissed the transportation hypothesis on the grounds that it was not empirically supported. August Weismann had as early as 1883 propounded the theory of the absolute independence of the germ plasma from the other somatic cells; and prior to this, Francis Galton's transfusion experiments had thrown doubt on the existence of mobile 'gemmules' and their effects on the germ plasma and inheritance. Consequently, De Vries' reformulation of Darwin's provisional hypothesis focused exclusively on the existence of discrete particles of inheritance.

De Vries undertook a programme of experimentation during the 1890s to explore the behaviour of these particles during the process of inheritance. However, his chief interest in these experiments was to determine the process by which species emerged. In De Vries' mind, the most important hereditary solution to this problem was the process of mutation. From at least 1886, when he discovered new species of evening primrose in a field near Hilversum, De Vries had entertained the hypothesis that speciation occurs through the appearance of new species by discontinuous variations of traits. De Vries concluded that the new species of primrose (*Oenethera lamarckiana*) found side by side with the traditional but markedly dissimilar form of the same species had appeared as a result of a mutation.[2] During the decade prior to his segregation paper, he conducted large numbers of hybrid experiments with over 30 species, in which he observed the 'splitting' or segregation of monohybrids in, for example, opium poppies and *oenethera lamarckiana*; second generation hybrids characteristically reverted to a recessive character in about one quarter of the plants. It was his conjecture during this period that evolution resulted from what he termed 'progressive mutations' — that is to say, by mutations in which the effect of an 'active pangen' was not held in check by a 'semi-latent pangen.'[3] Different populations presumably could be described in terms of the activity or latency of the pangens and hence classified according to their mutability. Since De Vries was most interested in the origin of species, progressive mutations (that is, mutations which has arisen *without* 'antagonistic pangens') were of far more interest to him than hybrids characterized by segregation and reversion to parental stocks. Consequently, though De Vries clearly recognized the ratio of dominance and the principle of gametic segregation, these were of secondary interest in his *Mutation Theory*, which he published in 1901-03. Nonetheless, he published his law of the segregation of hybrids, which specified two important conclusions:[4]

> 1. Of the two antagonistic characteristics, the hybrid carries only one, and that in complete development. Thus in this respect the hybrid is indistinguishable from one of the two parents. There are no transitional forms.
> 2. In the formation of pollen and ovules, the two characteristics separate, following for the most part simple laws of probability.

Actually, De Vries wrote three articles announcing his conclusions. His first communication was published in *Comptes Rendus de L'Academie des Sciences* at Paris. Here De Vries made no mention of the fact that his laws of segregation and ratios of dominance were identical to the conclusions of a certain Gregor Mendel which were published 34 years earlier. However, in a more extended report which appeared in May, and which had actually been the first of the three reports to be prepared, De Vries noted that 'these two statements in their most essential points, were drawn up long ago by Mendel for a special case (peas).'[5] In a footnote he suggested that 'this important treatise is so seldom cited that I first learned of its existence after I had completed the majority of my experiments and deduced from them the statements communicated in the text.'[6] Exactly how seldom was Mendel cited?

The Mendel Citations

Mendel's paper on *Pisum* was cited several times in different places prior to its wide acclamation in 1900. In 1869 it was quoted in Hermann Hoffmann's *Untersuchungen zur Bestimmung des Werthes von Species und Varietat*. Mendel's conclusions were summarized as follows: 'Hybrids possess the tendency in the succeeding generations to revert to the parent species.'[7] One finds a similar interpretation in the second major book to appear, *Die Pflanzenmishlinge* by W. O. Focke in 1881. Focke cited Mendel's *Pisum* work 15 times, though again he interprets Mendel as reporting the sort of thing already known from the work of earlier hybridists like Andrew Knight — specifically, that hybrids tend to revert to the form of the parents and do not exhibit a fusion of characteristics as a result of the cross. Focke also mentions that 'Mendel believed that he found constant numerical proportions between the types of hybrids.'[8] Focke's reference was copied by George John Romanes and cited in a list of plant hybridists in an article entitled, 'Hybridism,' which appeared in the Ninth Edition (1881) of the *Encyclopedia Britannica*. There was no specific discussion of Mendel.[9] Another reference to Mendel to appear in 1881 was recorded by Benjamin Daydon Jackson in *The Guide to the Literature of Botany: Being a Clarified Selection of Botanical Works*. This reference was also lifted directly from the citation in Focke. The *Guide* listed some 6,000 references to botanical works not contained in the *Thesaurus* compiled by Pritzel, another popular reference guide, but again there was no discussion of Mendel's contribution.[10]

The next reference to Mendel's paper appeared in L. H. Bailey's 1892 article, 'Cross-Breeding and Hybridizing.' Bailey had not read Mendel's work, but like the others, merely lifted the reference to Mendel from Focke's 1881 book.[11]

Among the other references we find to Mendel in this period is one recorded by I. Schmalhausen in the appendix to his master's thesis at the University of St. Petersburg in 1874. Though Schmalhausen read Mendel only after having completed his research, he appears to have understood his concept of the segregation of elements in the gamete, and the resulting ratio of the characteristics in the hybrids. Also, Schmalhausen pointed out the similarity of Mendel's work to Naudin's views on segregation.[12]

The only other references to Mendel which have been uncovered to date appeared in 1872.[13] One was in a dissertation written at the University of Uppsala by Albert Blomberg in which Mendel's *Pisum* experiments were discussed, and again compared to Naudin's work on segregation. The other citation was by Anton Besnard and appeared in a paper on *Heracium* plants published in *Flora* in 1872. We shall deal with the interpretations and comparisons of Mendel in a moment.

While De Vries suggests that he became acquainted with Mendel's work *after* the bulk of his experiments was completed, some historians have expressed reservations about this claim. Glass points out that L. H. Bailey sent a copy of his 'Cross-Breeeding...' to De Vries in 1892, clearly a date which follows De Vries' *Intracellular Pangenesis*, but which probably does not postdate the 'bulk' of the experiments.[14] In response to H. F. Roberts' queries in 1924, De Vries suggested that he first came across Mendel's work as a result of the citation in the bibliography of Bailey's 1895 *book*, though it appears that Mendel was only mentioned in the 1902 and subsequent editions.[15] However, this confusion is easily understood when we learn that De Vries communicated to Bailey that he had come across Mendel as a result of the citation in Bailey's 1892 *paper*. These two courses could easily have been confused in De Vries' mind. However, the confusion does not end there, for T. J. Stomps related that in 1900 De Vries received a copy of Mendel's paper from a friend, Martius Wilhelm Beijerinck, a professor of bacteriology at the University of Delft, 'who had himself suspected the operation of something like unitary mutation in bacteria.'[16]

Certain historians suspect that De Vries may have had no intention of mentioning Mendel's earlier work and that perhaps the crucial factor in his recognition of Mendel was the swift reaction by Correns and Tschermak to the *Comptes Rendus* article. Both Correns and Tschermak had independently become aware of the phenomenon of segregation and the ratios, and had read Mendel's paper during the winter of 1899-1900. However, if De Vries had learned of Mendel prior to 1900, and if he had planned to suppress this fact, his plans were interrupted by the communications of Correns and Tschermak. Correns related to Roberts that he received a reprint of De Vries' *Comptes Rendus* article on 21 April 1900, and that he had immediately composed his own finding which he had prepared for publication by the evening of the 22nd![17] Tschermak had conducted his research for a doctoral dissertation which he had defended on 17 January 1900. Upon receipt of De Vries' reprint, he too immediately arranged the publication of his results, and succeeded in having them accepted in the *Journal for Agricultural Research* in Austria. When De Vries received pre-prints of these papers, he appears to have edited the galleys of his second and third publications before they appeared in print. Sturtevant speculates that the unusual number of printer's corrections in the longer German version of De Vries' paper are probably indicative of a difficulty in following De Vries' hasty corrections to the galleys.[18] Also, in the second French version of the paper submitted to the *Revue Generale Botanique*, mention of Mendel's original paper and of the forthcoming contributions of Correns and Tschermak appear to be awkwardly appended to the article, as though they were an afterthought.

In his own announcement of segregation results in the *Berichte*, Correns exhibits two distinct reactions to De Vries. First of all, he frames his announcement so as to indicate that though he had lost priority in the discovery to De Vries, both had lost out to an earlier researcher, even though the initial intent of that research, and its contemporary importance, were somewhat less than identical. In other words, he neutralizes his loss in what would have otherwise been a priority dispute between he, De Vries and Tschermak. This is accomplished decisively by labelling the discovery 'Mendel's Law.' This is perhaps the single most important fact in the reification of Mendel as the founder of genetics. This action effectively undermined the priority of De Vries' claim to the discovery, and at the same time lent a decisiveness to Mendel's experiments which they would not have had had the community not had the benefit of Weismann's cytological conclusions, and experienced the weakness of Darwin's hypothesis of pangenesis. Correns glossed these differences in context by suggesting that Mendel had come to the same conclusions that he and De Vries had in 1900, 'as far as it was possible in 1866':

> I also, in my hybridization experiments with races of maize and peas, had arrived at the same result as De Vries, who had experimented with races of very different sorts of plants, among them also with two maize races. When I found the orderly behaviour, and the explanation therefore...it happened in my case, as it manifestly now does with De Vries, that I held it all as being something new. *I then, however, was obliged to convince myself that the Abbot Gregor Mendel in Brünn in the sixties, through long years of and very extended experiments with peas, not only had come to the same result of De Vries and I, but that he had also exactly the same explanation, so far as it was at all possible in 1866.*[19]

Secondly, Correns exhibits a certain amount of suspicion regarding the frankness of De Vries and his unacknowledged reliance on Mendel. He insinuated that not only had De Vries come to the same conclusions but suggests in a stroke of understatement that the names given to the terms are 'coincidentally' the same: 'This one may be called the *dominating, the other* one the *recessive* anlage. Mendel named them in this way, and by a strange coincidence, De Vries now does likewise.'[20]

This, of course, was no coincidence; De Vries was familiar with Mendel, as he admitted in his second two papers. However, in light of De Vries' programme of research, it is probably fair to say that De Vries sincerely believed that his own theory of the role of mutations was far more important than the observations of Mendel on the segregation of antagonistic pangens. After all, his programme pointed to the process of species formation, while Mendel's conclusions appeared to point to species preservation; one was a theory of evolution, the other merely a theory of inheritance. De Vries' opinion of Mendel's contribution did not change in the ensuing years of the development of genetics. Indeed, on 31 October 1901, De Vries repeated an earlier suggestion he had made to William Bateson:

> I prayed you last time, please don't stop at Mendel. I am now writing the second part of my book which treats of crossing, and it becomes more and more clear to me that Mendelism is an exception to the general rule of crossing. It is no way *the* rule! It seems to hold good only in derivative cases, such as real variety-characters.[21]

Consequently, De Vries' later failure to mention Mendel in his 1907 *Pflanzenzuchtung*, and his refusal to sign a petition calling for the construction of a memorial to Mendel in Brünn, probably ought not to be taken as evidence of De Vries' jealousy of Mendel, as Tschermak suggested, but as confirmation of his conviction that Mendel's importance was over rated. Nontheless, Mendel's paper was republished in *Flora* in 1900 with a recommendation of its great importance. Also, Tschermak succeeded in having Mendel's paper republished in 1901 in *Ostwald's Klassiker Exakten Wissenschaften*. When Bateson received a copy of De Vries' work, he immediately looked up the Mendel paper, and soon had it translated and published in the *Journal of the Royal Horticultural Society of London* in 1901. In England it was seized upon at once as evidence supporting the model of evolution through the selection of discontinuous variations. This was the second major step in the reification of Mendel in 1900.

Though Mendel's work is often cited in retrospect as a decisive contribution to genetics, it is clear that in England, those who initially found it so decisive were likewise those who were most frustrated by the account of variation and inheritance found in Darwin, and who were exploring alternative accounts, especially in the notion of discontinuous variation and mutation. One of the great ironies in the history of evolutionary theory is that, though Darwin's work on *The Origin of Species* was probably instrumental in the establishment of evolutionary thinking in Victorian England, few naturalists actually subscribed to Darwin's view of the natural selection of individual differences.[22] Such variations were thought to be too easily 'swamped' by crossing.

The Controversy Over Variation in Evolutionary Theory

Darwin, as well as other naturalists, believed that there were two sorts of variability: on the one hand, individual differences, and on the other, sports or mutations. Darwin believed that evolution could not progress by the natural selection of sports for several reasons: their progeny were frequently infertile; they often experienced pathogenic imbalances in the internal organs or tissues ('monstrosities'); and they occurred far too infrequently. In addition, they were subject to processes of 'swamping' just as much as selected individual variations. On the other hand, individual variations were typically heritable, they did not suffer infertility, and most importantly, they occurred in large numbers in every generation, and hence gave natural selection a great pool on which to operate.

As noted earlier, one of the drawbacks of the reliance on small individual variations was that these were very easily swamped. A given variation, unless isolated from the population, would not be perpetuated in an organism's progeny because the interbreeding of the progeny with the rest of the stock in subsequent crosses would result in the decrease in the number of elements in the germ cells which controlled the new variations. Each new generation would, therefore, tend to contain less of the germ material underlying the new characteristic. As Darwin himself noted, this process, as well as natural aversion and infertility, tended to keep species quite distinct from one another.[23] However, in geographically isolated areas, such as the Galapagos Islands, different conditions of existence together with these minor variations might be able to facilitate the perpetuation of even small variations. However, many of Darwin's supporters thought that he was confining himself unnecessarily with such a theory. T. H. Huxley, Francis Galton, William Bateson, W. K. Brooks — and even some of Darwin's antagonists, like Mivart — thought that evolution by this slow and gradual process was highly unlikely. Most thought that it was more probable that evolution occurred through the operation of selection on discontinuous variations, saltations or sports. Additionally, this model of selection was not subject to the charge that had been made by certain physicists, particularly W. Thomson (later Lord Kelvin), who criticized the theory because it presumed a far longer period of geological time than geophysical theories allowed for the formation of the earth. Discontinuous variations presumably would allow speciation to occur at a far quicker rate than continuous variations.[24]

Darwin was not unaware of these problems. In 1865 he proposed an idea in a brief paper written for Huxley, which integrated a mass of diverse information about reproduction in sexually and asexually reproducing populations. This was his 'provisional hypothesis of pangenesis', which appeared in extended form in 1868 in *The Variation of Plants and Animals under Domestication*. William Provine summarizes the theory as follows:

> Basically the theory stated that each part of the organism throws off 'free and minute atoms of their contents, that is, gemmules.' The gemmules multiply and aggregate in the reproductive apparatus, from which they are passed on to the following generations. The theory was designed so that the 'direct and indirect' influences of the 'conditions of life' might become embodied in the hereditary constitution of the organism. If an organism were affected by the environment, the effected parts would throw off changed gemmules which would be inherited, perhaps causing the offspring to vary in a similar fashion.[25]

Thus, Darwin, by giving a role to the effects of the conditions of life, guaranteed at least in his own mind the large numbers of heritable differences, with a tendency to vary in the same direction over time, both of which conditions would be required to overcome the blending problem. However, it does not appear that many found this hypothesis convincing, for the search for models of discontinuous variation continued. We have already mentioned the efforts of De Vries and his search for mutative variation. Francis Galton, Darwin's cousin, had attempted an empirical test of pangenesis by performing blood transfusions on different varieties of cats, but failed to find any evidence of transmission of characteristics from one animal to another, and hence concluded that there was no evidence of 'gemmules' floating in the bloodstream.

Galton's attempt to produce a more viable theory of inheritance took the following course. Though he admitted the omnipresent evidence of variability, his observations on things like human stature led him to believe that the variability always distributed itself in the long run around a fixed median average. He expressed this in his 'Law of Regression', which stated that the deviation of a new organism in some characteristic will be a fraction of the parental deviation from the same population norm for that characteristic. Specifically, the new organism will inherit two-thirds of the parental deviation from the norm. Hence, the population variability will be 'in a constant outgrowth at the centre,' and a 'constant dying away at the margins,' thereby preserving the average at a fixed point. With this situation, Galton concluded that speciation *had* to depend on sports or discontinuities in variability, for mere individual differences were controlled by a regression to the median.[26]

However, Galton's two chief students, Karl Pearson and W. F. Weldon, who were studying his new 'biometrical' techniques, thought otherwise. While Galton assumed that the population median remained constant, Pearson and Weldon suggested that *if* the exceptional offspring continued to be crossed with other exceptional offspring, a new variant would arise in which the ancestral mean for the characteristic would shift over time as the 'ancestors' came to include more organisms with the same characteristic. This could occur either through isolation of a subgroup, or the elimination of that part of the population whose characteristic was disadvantageous. Pearson and Weldon became the leading advocates of the biometrical approach, and employed it to defend the original Darwinian argument regarding the utility of continuous variation.

During this same period, William Bateson was developing his own ideas about the process of deviation. His study of the small isolated lakes of the Russian steppes convinced him that variations *were not* continuous with the changing conditions of life. He discovered that, though there existed a change in salinity from lake to lake, there was no corresponding consistent change in the animal forms inhabiting the lakes. In 1894, he published his voluminous *Materials for the Study of Variation, Treated with Especial Regard to Discontinuity in the Origin of Species*.[27] Bateson had gathered 886 cases of discontinuous variation, and on the basis of these expounded his views on the validity of a model of discontinuous evolution. With Weldon's negative review of the book in *Nature*, a series of what were at times heated personal confrontations developed between Bateson and the biometricians, which ended only with Weldon's death in 1906. This antagonism likewise resulted in a power struggle for the control of the Evolution Committee set up by Galton under the auspices of the Royal Society. Though initially dominated by the biometricians, Bateson's differences with Weldon and Pearson led them, along with Galton, to resign in January 1900. They subsequently directed their energies toward the establishment of a new journal for the advancement of biometry. *Biometrika* appeared in 1902.

In 1897, Bateson initiated a series of hybrid experiments to explore discontinuity in variation in hybrid crosses. Though he did not discover Mendel's ratios, he did have a vivid sense of what ought to be explored. In July 1899, he presented a most prescient paper, entitled 'Hybridization and Cross-Breeding as a Method of Scientific Investigation.' It read in part:

> What we first require is to know what happens when a variety is crossed with its *nearest allies*. If the result is to have scientific value, it is almost absolutely necessary that the offspring of such crossing should then be examined *statistically*. It must be recorded how many of the offspring resembled each parent and how many shewed characters intermediate between those of the parents. If the parents differ in several characters, the offspring must be examined statistically, and marshalled, as it is called, in respect of each of those characters separately.[28]

As mentioned earlier, Bateson heard of the Mendel paper via De Vries. Given the above statement, Mendel could hardly have expected a more sympathetic reader than Bateson. However, the publication of Mendel's work did nothing to depolarize the splits in the evolutionary community. Mendel's law of segregation was bandied about by Bateson and his group as evidence of discontinuous variability, and hence of speciation through the process of discontinuous evolution. Consequently, the initial reaction toward Mendel's paper among the biometricians was negative. Only later was it realized that a Mendelian model could account for *continuous* changes in the (phenotypic) characteristics. This emerged with the realization that certain characteristics could be controlled by more than a single factor. Even Mendel had pointed this out in his discussion of crosses with red and white flowered species of *Phaseolus*. He noted that the flowers of hybrids were not segregated discretely into either red or white, but that most plants were various gradations from crimson to pale violet. Rather than treating this as a disconfirmation of segregation, Mendel suggested that 'the colour of flowers and seeds is composed of two or more totally independent colours that behave individually exactly like any other constant trait in the plant.'[29]

During the early period of the controversy, there was *some* recognition that Mendelism and Darwinism were not mutually exclusive. In 1902, G. Udny Yule published a paper in which he outlined how the multiple factor hypothesis made it possible for Mendelism to account for continuous variations and hence made it compatible with biometry and Darwinian evolution. However, so entrenched were personalities on each side of the issue that 'Yule's excellent paper had little effect upon the widening gap between the Mendelians and the biometricians. Not until R. A. Fisher's first genetical paper in 1918 was there an important attempt in England to follow the lead suggested by Yule.'[30] This indicates that there was a large element of propaganda in Bateson's use of Mendel to settle his score with the biometricians, for even when the basis of a synthesis was suggested, its importance was missed.

Clearly, Bateson found Mendel's law of segregation the answer to his problem of discontinuity. However, it is not always obvious that he completely adopted Mendel's concepts. Provine points out that in his criticism of Pearson's hypothesis of 'homotyposis',[31] Bateson does *not* rely on Mendel's model to construct his rebuttal. While Pearson argued that sperm cells and ova were undifferentiated like cells, Mendel believed that the germ cells were differentiated. However,

> Bateson did not use the criticism from Mendel's theory because he did not believe that Mendel's 'differentiating elements' were material bodies. As early as 1893, Bateson had developed a 'vibratory theory of heredity,' which did not fit with a materialist view of heredity, and he maintained this theory with some misgivings to the end of his life. It even caused him to reject the chromosome theory of heredity. . . Evidently, Bateson misunderstood or rejected what Mendel had said.[32]

When we reflect on the special value which Mendel's theory had for Bateson in the context of his dispute with the biometricians, it is less than clear that Mendel's work was simply 'revived' from dormancy. In the controversy over continuous-discontinuous variation, Mendel's paper had a relevance which was not available in 1865. Can we conclude, then, that Mendel was simply 'rediscovered' in 1900? Evidence suggests that Mendel's paper had a rather different valence in the context in which it was initially written.

Was Mendel Rediscovered?

Mendel had read the report of his research on the effects of cross-breeding of seven different traits in successive generations of peas between 1856 and 1865 at the meetings of the Brunn Natural Science Society in February and March 1865. Weinstein suggests that the belief that Mendel was virtually unknown prior to 1900 can be traced to the statements of the rediscoverers in 1900.[33] Consequently, it has been widely believed that Mendel's audience in 1865 responded politely but non-comprehendingly to his work on pea hybrids. Loren Eiseley, for example, conjectured: 'Stolidly the audience had listened...Not one had ventured a question, not a single heartbeat had quickened...Not a solitary soul had understood him.'[34] A. D. Darbishire noted likewise that 'the publication of Mendel's paper in 1865 [sic] was the throwing of pearls before swine.'[35] However, recent research indicates otherwise. Reports of Mendel's two lectures indicate he received very positive and rather accurate coverage in the local papers. In the daily *Neuigkeiten* it was reported that Professor G. Mendel gave a long lecture of interest to botanists on the results of his 'artificial pollination of related species by the transfer of pollen from the pollen parent to the seed parent.' The report continued, in part:

> [Mendel] pointed out that the fertility of the cross-bred or hybrid plants was proved, but that it did not remain constant, and that the hybrids continually tended to revert to the parental forms... He demonstrated specimens of relevant generations, according to which characters shared in common were transmitted reciprocally, but differing characters led to the production of quite new characters...Particularly worthy of notice were the numerical comparisons in regard to the character difference introduced into the hybrids in their relation to the parental forms. The enthusiastic interest of the listeners showed that the subject of the lecture was appreciated, and its delivery very acceptable.[36]

The second lecture appears to have been just as successful. The *Neuigkeiten* reported that Mendel spoke about 'the production of germ cells, fertilization, and the formation of seeds in general.'[37] Following the second lecture, G. Niessl, the secretary of the Society, added that he had observed 'hybridization with the help of a microscope in fungi, and algae, and that further observations in this field would not only substantiate existing hypotheses but produce interesting explanations.'[38] Vitezslav Orel reports that 'minor commentaries also appeared in other German and Czech newspapers. No doubt Mendel's lectures did not remain unnoticed.'[39] Further evidence for Mendel's reputation is found in the various obituaries written following his death in 1884. On January, the *Brunner Zeitung* crowned a list of Mendel's achievements with the observation, 'Above all it is necessary to point out to his experiments with plant hybrids.'[40] The *Tagesbote* noted similarly, 'Epoch-making were his experiments with plant hybrids.' And the January report of the Agricultural Society's journal noted, 'Downright epoch-making were his experiments with plant hybrids. What he has done and created will remain in unforgettable memory.'[41]

In light of these observations it is hard to maintain the opinion that Mendel was an obscure figure in the 1865 context. However, it is nonetheless clear that his work did *not* evoke an international revolution in biology comparable to that which began to emerge in 1900. The 1865 lectures were submitted as one long paper which was published in the 1866 volume of the proceedings of the Brünn Natural Science Society. The journal, though relatively new, was mailed to 138 international addresses, two of which were in England: the Royal Society and the Linnean Society. Likewise, Mendel's seven-year correspondence with the renowned Swiss botanist, Carl Naegeli, awoke no sense in Naegeli of the evolutionary relevance of Mendel's work. Naegeli, an advocate of a true blending model,[42] probably thought Mendel's views on the segregation of material in the germ cells were erroneous, or were atypical. Naegeli was himself trying to cross-breed species of *Hieracium*, a plant species which appears to fertilize in cross pollination, but which is self-fertilizing. He succeeded in getting Mendel to attempt hybridization experiments with this species; Mendel, of course, found that this plant appeared to contradict his conclusions with *Pisum*.[43]

Consequently, we begin to realize that the value of Mendel's paper was not always compelling, even for his contemporaries like Naegeli. Sir Ronald Fisher remarks on this fact in his noted paper, 'Has Mendel's Work Been Rediscovered?' To this question he offers the following conclusion:

> Each generation found in Mendel's paper only what it expected to find; in the first period, a repetition of the hybridization results commonly reported, in the second a discovery in inheritance supposedly difficult to reconcile with continuous evolution. Each generation, therefore, ignored what did not confirm its own expectations.[44]

From this point of view, *Mendel was not really rediscovered*; presumably a 'rediscovery' would consist in seeing that one's own views were merely *duplications* of findings recorded earlier. It is Fisher's judgement that Mendel's work, on its own terms, was a suspicious or problematic illustration of the arithmetic ratios governing the inheritance of dominant traits; according to Fisher, Mendel's ratios were far too accurate to have occurred by chance. But was this what was 'rediscovered'? Certainly, the first generation (represented by Naegeli and Focke) perceived the results as identical to those 'commonly reported,' not only by Mendel's predecessors but by this contemporaries like Naudin. These made his work no 'discovery' at all — merely normal science duplication or confirmation, and not all that unproblematic. The second generation (represented by William Bateson) perceived discontinuous evolution. This might have been a latent consequence of his position, but was certainly not the focal point of the study for Mendel. Fisher's position reinforces the impression that Mendelism was not revived in 1900, but constructed then for the first time. However, Fisher should not be read as supporting the conclusion that discovery is merely a 'perspective' — that is to say, that everybody saw what he expected because of his unique point of view. The point is that, as noted earlier, the processes which made Mendel's Law so important in 1900 were historically unique. Furthermore, in 1865, Mendel's conclusions were not so entirely unprecedented as we usually think.

The Normal Mendel: His Predecessors and Contemporaries

The present interpretation of Mendel's work contrasts with that of Gasking, Glass and Barber, the main proponents of the 'long neglect' school. Gasking, for example, suggests that 'Mendel was ignored because his whole way of looking at the phenomena of inheritance was foreign to the scientific thought of his time.'[45] His 'whole way' differed in that his experiments were directed to (a) observing the inheritance of *particular* traits in hybrids and (b) observing these patterns as arithmetic proportions. Regarding the first point, Gasking notes that the thinking of the hybridists before Mendel was directed toward the specific essence of plant species and how this intermingled in cross-breeding, and reconstituted as the sex cells formed.[46] Hence, there was no appreciation of the focus on the various *individual* traits of plants and the particular form of their inheritance; hybridists were searching for whole new plant transmissions — that is, the origin of whole new species through breeding. Furthermore, according to Gasking, biometrics, the application of mathematical models to biological patterns, was unfamiliar before Mendel's time and did not achieve popularity until years later with Galton's work.

However, these claims are palpably misleading. Galton's first noted work, *Hereditary Genius*, appeared in 1869, only three years after Mendel's paper was published. Nothing occurred over those three years which would have particularly favoured the reception of *his* arithmetic method. As for the claim that focus on *particular* traits had not been examined by others beforehand, this too is erroneous. In 1868 Darwin published the results of his studies of hybridization and breeding in domestic species; it specifically focused on the inheritance of individual traits. And in this respect Darwin's work was far from novel. The inheritance of specific traits had always been the preoccupation of breeders and horticulturalists; their work had appeared as early as the 1790s, and had proved so useful to Darwin in the presentation of his case. Therefore, not only was Mendel's work *not* out of tune with the times, but the link between Mendel and his predecessors may have been much more concrete than is generally thought. This has been emphasized repeatedly in a series of articles published by Conway Zirkle,[47] who has observed that:

> ... much of Mendelism was known before Mendel published, and we can list the earlier pertinent contributions which were probably known to him. We may even find good evidence that Mendel was familiar with the greater part of this work.

Zirkle outlines the five aspects of Mendel's theory: the principle of dominance; the principle of segregation; the 3:1 ratio of dominance to recessive traits; the perpetuation of these patterns over f_{1+n} generations; and the principle of independent assortment. He then shows that work published in the *Transactions of the Horticultural Society of London* in 1799 and in 1824, and later quoted frequently in C. F. von Gaertner's classic 1849 work on hybridization, explicitly anticipated various aspects of Mendel's work. Thomas Andrew Knight, John Goss and Alexander Seton, all working with the common pea, reported observations on both the dominance of certain traits over others and the segregation of these traits in second generations of the hybrids. For example, after crossing green and white peas, Seton noted that the hybrids 'were all completely one colour or the other, none of them having an intermediate thing.'[48] Likewise, in 1826 Augustin Sageret cross-bred two sorts of melons with five different characteristics of each parent. The result was not a blending of the various traits of the offspring but the independent assortment of the traits: 'the resemblance of the hybrid to its two ascents consisted not in an intimate fusion of the diverse characters peculiar to each one but rather a distribution, equal or unequal, of the same characters'.[49] Gaertner referred to Sageret's work 30 times. After reviewing the evidence, Zirkle observes: 'We may conclude that Mendel knew of the results obtained by Knight, Sageret and Gaertner and had the work of Seton and Goss called to his attention.'[50] And what of the 3:1 ratio? 'A precise hybrid segregation raito had been published 11 years before Mendel's paper.'[51] Its author was a fellow cleric who lived in nearby Silesia, a beekeeper by the name of Johann Dzierzon. Dzierzon crossed German with Italian bees and found that the unmated hybrid queens produced German and Italian drones in equal numbers in a definite one-to-one ratio. His findings were published in 1856 and read, in part:

> If [the queen] originates from a hybrid brood, it is impossible for her to produce pure drones, but she produces half Italian and half German drones, but strangely enough, not according to the type — not a half and a half intermediate type — but according to number, as if it were difficult to fuse both species into a middle race.[52]

This work was not widely known to evolutionary biologists but was familiar to professional beekeepers. However, it would hardly be likely that Mendel, who raised and bred honey bees for two decades, would have been *unfamiliar* with Dzierzon's research. He himself kept records of the inheritance of various traits of his own hybrids. Alas, the evidence indicates that the idea that inheritance of particular traits could occur in discrete proportions might well have been suggested to Mendel by this earlier work by a fellow apiarist and cleric.

Consequently, on the basis of Zirkle's research it would seem difficult to argue that Mendel was ahead of his time, or that his points were unorthodox compared to the existing tradition in horticulture. If anything, Mendel's reputation was modest not because he was so radically out of line with his times but because his identity with his contemporaries was so complete! His observations on segregation and independent assortment were recorded by his predecessors and the focus on inheritance ratios was pioneered by his contemporary.

Also, as pointed out by Blomberg and Schmalhausen, Mendel's results were not unlike those of Charles Naudin, the Parisien who in 1860 won the 'prix des sciences physiques' awarded by the Academie des Sciences for his work on hybrids. Though he failed to describe the ratios of inheritance, Naudin clearly understood that the segregation of traits in his monohybrids resulted from the union in the sex cells of dissimilar germ material producing plants which reverted to the paternal, maternal or a mixed type. It is of note here that Darwin and Naudin corresponded with one another from 1862 to 1882. Darwin expressed reservations about Naudin's work, for, according to Darwin, it was incapable of explaining 'distant reversion' — that is, the reappearance of ancestral traits in their distant hybrid progeny.[53] Consequently, it is hard to imagine why Darwin, even if he had read Mendel, would have been any more favourably disposed towards him than Naudin.

Therefore we must conclude that the reasons offered to explain 'why Mendel's work was ignored' appear to be quite unconvincing (and, as we shall see, redundant). Mendel was clearly integrated into the tradition of hybridists. Indeed, his paper seems to begin in some debt to his predecessors and ends with a fulsome preoccupation with their questions. And as for the 'statistical' approach, this is hardly a forbidding aspect of his paper inasmuch as the great proportion of Mendel's data simply illustrate the 3:1 arithmetic proportions found in the various generations of hybrids. There is nothing especially mysterious or disentitling in this practice; indeed, if, as Fisher has suggested,[54] Mendel's results were doctored in favour of illustrating a clear 3:1 ratio, this should have only made the argument all the more forceful!

However, it would be a grave error to treat Mendel as no different from his predecessors. His work was far superior in two respects. First of all, not only had he observed evidence of segregation but he had observed the *ratios* in which the characters appeared in both hybrid and di-hybrid crosses. Secondly, he had formulated an explanation of these observations in which he attributed the ratios to the *segregation* of factors in the sex cells, and the *dominance* of certain characters over other characters. Neither achievement had occurred before. However, the question still remains as to how Mendel himself regarded his own investigation. Did he realize the value it had in the context of evolutionary theory? I would suggest that it appears from Mendel's paper that he probably did *not* appreciate the role his work could play in the theory of evolution laid down by Darwin (that is, natural selection). Yet he did see his contribution as a contribution to evolutionary theory. After describing broadly his manner of research, he adds: 'this seems to be the one correct way of finally reaching a solution to a question whose significance for the evolutionary history of organic forms must not be underestimated.'[55] However, when he writes up his results, one does not find reference to the contemporary figures in the field of evolutionary theory. Had Mendel fully appreciated the significance of his contribution to the controversy raging in England, it is not improbable that he would have sent it to one of the leading British journals, as opposed to the local society — but he did not. However, this is not especially problematic when we realize that the problem of hybridization and its relationship to evolution had been a perennial theme in the Natural Science Society since its founding by Mendel and others in 1862.[56]

Even so, if Mendel was certain of the significance of his work within the framework of Darwinian evolution, it is unclear why he never sent copies of his paper to Darwin, Wallace, Huxley, Hooker, Agassi or any other proponents of the theory of evolution with whose work he would have necessarily been familiar if he were to have appreciated the subsequent value of his own contribution (that is, its 1900 significance) — but he did not. Likewise, if the value of his work was obvious, it is unclear why it did not find its way indirectly by referral and citation to the attention of those hotly debating the issues of evolution in the mid-1860s. It did not, yet it enjoyed a certain currency just the same (as the hybridization results commonly reported). And this was the way in which it subsequently came to light in 1900. At that time its significance as a clue to the process of discontinuous evolution and particulate inheritance was apparently obvious — above all to Bateson, who quickly put it to work for him in his debate with the biometricians.

Lastly, if Mendel was really conscious of the significance of his ratios, it is unclear why this was never vividly expressed in the original paper itself. In that paper, Mendel certainly does formulate his findings as general observations stated in italics. For example, 'transitional forms were not observed in any experiment.'[57] Also:

> It becomes apparent that of the seeds formed by hybrids with one pair of differing traits, one half again develop the hybrid form while the other half yield plants that remain constant and receive the dominating and recessive character in equal shares.[58]

Hence the regularities are stated explicitly — and, in fact, further on, having reviewed the experimental results for peas, he refers several times to the *lawful* character of the regularities: 'the law of development discovered for *Pisum*,' 'the law of simple combination of traits,' 'the same law as in *Pisum*,' and 'the law valid for *Pisum*.' However, this usage seems to be offered tangentially — that is, it does not seem to draw attention to the fact that the identification of the law is the whole point of the paper, and that such a law governs inheritance generally. In other words, *this is never explicitly stated either in or as the conclusion*. Unlike Darwin, who prefaced his treatise with a discussion of the relevance or importance of his own work, 'that mystery of mysteries,' evolution, and his proposed solution, Mendel only obliquely ties his research to 'the evolutionary history of organic forms.' When Mendel refers to the larger issues of evolution and to other theorists,[59] he discusses not his *own* work, or even that of Darwin, Huxley, or Wallace, but the work of C. F. von Gaertner, Koelreuter and Wichura — the hybridists who had explored hybridism as a clue to the question of speciation. If Mendel had been thinking of evolution and heredity in the way later researchers thought of it, he is certainly less than frank in communicating this to his readers. The significance of his work to the larger issues of evolution and natural selection appears to be obscured by his discussion of the work of other hybridists.

A solution to this paradox might be offered by the observations of G. Niessl, the secretary of the Brünn Natural Science Society in the early 1860s, and still an active official there at the turn of the century. In 1902, he suggested that it was believed in the 1860s that Mendel's work was in *competition* with, as opposed to *complementary* to, that of Darwin and Wallace: 'His work was well known but ignored in the prejudice of the then exclusively *different divergent* views...for the principle of the then generally acknowledged hypotheses of Darwin were almost exclusively decisive.'[60] In other words, it seems that the Darwinian model (focus on selection processes) appeared inconsistent with the Mendelian model (focus on combination of traits). Also, Vietzslav Orel suggests that Mendel did not ever use the terms 'heredity' or 'hereditary' in his analysis, and that when later evolutionists wrote about Mendel, they were assuming that his work figures under the broader umbrella of evolutionary theory — that is, that heredity theory was a subfield in the explanation of the evolution of new species. Consequently, as Correns admits, they were attributing to Mendel a status different from what he himself pictured. As Correns noted, 'these sentences are not formulated by Mendel himself, but were derived from reality only at their rediscovery.'[61] In other words, Mendel seems to have believed, like De Vries, that an account of heredity would be *equivalent* to an account of evolution; that is, Mendel was seeking an explanation for the process of evolution which did not require a theory of selection! This reading of Mendel was apparently overlooked in 1900, when for Bateson and company a theory of selection was already taken for granted in the debate with the biometricians, and when the question of inheritance was the crucial missing link or *sub*theory that consolidated the broad model of evolution. In other words, the work of Mendel was revolutionary in the context of latter-day evolutionary theory, where it constituted a model of heredity, an evolutionary subfield; but in 1865, when viewed as an account of evolution based on a model of hybridism, it appears to have had only mixed success. To appreciate this last point, one needs to re-examine Mendel's discussion of Gaertner, Wichura and Koelreuter.

The Hybridist Tradition Referred to by Mendel

In his introductory remarks to the 1886 paper, Mendel refers to the work of Koelreuter, Gaertner, Herbert, Lecoq, and Wichura, who had 'devoted a large part of their lives' to the problem of hybridization. These hybridists had all conducted numerous experiments on the creation of hybrid plants through the artificial fertilization of stable, closely related species, and had studied the persistence of changes in the progeny. Koelreuter, in the latter half of the 18th century, had, in fact, produced some 500 hybrids involving some 138 different species. Gaertner, in the early and mid-19th century, conducted some 10,000 hybrid crosses with 700 species belonging to 90 different genera of plants, and obtained some 350 hybrid plants.[62] Wichura, whose memoir on the hybridization of certain species of willow plants appeared in 1865, succeeded in making some 35 successful crosses between 21 different species of willows.[63] And Herbert reported the results of numerous crosses in different species of ornamental flowering plants and in certain vegetables. These hybrid crosses were undertaken to explore the role of hybridization in the development of new species. Though the hybridists all appear to have noted the frequency of *reversion* to the grandparent species in the progeny of self-fertilized hybrids, and noted likewise the infertility or the characteristically low fertility of true breeding hybrids, it would be a mistake to conclude that they all took this as evidence of the impossibility of new forms resulting from hybridization. This is far from the case. Roberts notes that 'Koelreuter had shown that fertile hybrids could be produced between plants of different kinds.'[64] Also, Koelreuter's studies of the cross pollination of similar species by insects 'tended to cast doubt, and to require the substitution for the doctrine of the *fixity* of species...the principle of the *comparative* stability of organic forms.'[65] Lecoq observed, in a similar vein, that the process of artificial fertilization would allow the gardener the power to mix and produce species almost at will:

> The most difficult thing was and always is the shattering of the stability of the first type, the breaking of its habit; just as soon as an impulse thereto is present, then variation begins to know the limits of which no human eye and no human understanding suffices. With the mighty lever of hybridization in the hand, the power of the gardener is an almost unlimited one.[66]

Herbert exhibited the most radical scepticism towards the natural unit or type concept of species. He held that:

> There is no substantial and natural difference between what botanists had called species and what they had termed varieties, the distinction being merely in degree, and not absolute...Any discrimination between species and permanent varieties of plants is artificial, capricious, and insignificant.[67]

However, these views were based as much on Herbert's belief that species characters would be effected by common soil, climate and the like as his belief in the power of hybridization in producing new species.

Given the preoccupation of these hybridists with species formation through cross-fertilization, Mendel's own intention to contribute to the discussion of 'the evolutionary history of organic forms' becomes more intelligible.

What evidence in the 1866 paper suggests that the role of hybridization in speciation was of central concern to Mendel? Mendel introduces his discussion of the arrangement of the experiments with the observation that when varieties are crossed which have traits in common, these traits are passed to their progeny unchanged 'as numerous experiments have proven.'[68] However, pairs with differing traits 'form a new trait.' 'It is the purpose of the experiment to observe these changes for each pair of differing traits, and to deduce the law according to which they appear in successive generations.'[69] Mendel goes on to describe the traits he selected for hybridization, and to report the results for the first and subsequent generations. These results show that his hybrids were, in the first generation, either *all* like the male or all like the female plant, and in the second generation, again like the original male *and* the female. There were no transitional or intermediate forms like those reported by Koelreuter, Gaertner or Wichura. However, he later suggests that there is a difference between his crosses with *Pisum*, which always demonstrate segregation and the reversion to parental forms, and the hybrids discussed by Gaertner and Wichura which breed true and which constitute new species:

> We encounter an *essential difference* in those hybrids that remain constant in their progeny and propagate like pure strains. According to Gaertner, these included the *highly fertile* hybrids Aquilegia atropurpurea [etc. . . .]; according to Wichura it includes the hybrids of willow species. This is of particular importance to the evolutionary history of plants, because constant hybrids attain the status of *new species*. The correctness of these observations is vouched for by eminent observers and cannot be doubted.[70]

Having made this observation, Mendel goes on to describe how such stable hybrids might be organized at the level of the germ cell so as to be able to propagate purely.

> When a germinal cell is successfully combined with a *dissimilar* pollen cell we have to assume that some compromise takes place between those elements of both cells that cause their differences. The resulting mediating cell becomes the basis of the hybrid organism whose development must necessarily proceed in accord with a law different from that for each of the two parental types. If the compromise be considered complete, in the sense that the hybrid embryo is made up of cells of like kind in which the differences are *entirely and permanently mediated*, then a further consequence would be that the hybrid would remain as constant in its progeny as any other stable plant variety.[71]

Clearly this passage was written by someone who appreciated the possibility of speciation via hybridization and had a valid sense of the processes which might make this possible. Consequently it is hardly surprising that in the last four pages of the paper, Mendel discusses what would be the otherwise unintelligible transmutation experiments of Koelreuter and Gaertner, and proposes a solution to the observation that certain of these experiments took longer than others to succeed. Mendel also reported his *own* experiments on this subject. The hybridists took certain closely related species, cross-fertilized them, and continued to fertilize the progeny with pollen from the species whose re-creation was the object of the crossing. Mendel points out how the transmutation can be accounted for by his model of segregation and random combination of elements in the germ cell. He notes particularly that if there are a small number of plants and a large number of traits which are originally dissimilar, it will take longer than if the traits are quite close and there are large numbers of plants from which to choose each successive generation. 'The transformation of widely divergent species cannot be completed before the fifth or sixth experimental year.'[72] However, the transmutation *is* possible.

Mendel concludes the paper with a reference to the fact that because Gaertner found the transformed hybrids to remain stable, he argued against 'those scientists who contest the stability of plant species and assume continuous evolution of plant forms.'[73] Presumably Gaertner was arguing against people like Herbert and Lecoq who seemed to believe that artificial fertilization and the cultivation of hybrids made species *infinitely* variable and unstable. It appears that Gaertner (and presumably Mendel, who ends his paper with this discussion) finds species and varieties to be *relatively* stable, but certainly not immovable — and hence certainly not incapable, through hybridization, of producing new *stable* hybrids, which, as Mendel had observed earlier, 'attain the status of new species.'

Conclusion

These aspects of Mendel's paper indicate that his work was well within the tradition of the hybridists whose experiments he discussed. Mendel's paper is a brilliant formulation of the reasons for the observations of reversion and the rise of new traits. It describes the segregation of external characters in terms of the separation of trait elements in the germ cell, and their random recombination during fertilization. It also explains the patterns or ratios in the self-fertilized progeny in terms of the dominance and recessive character of the traits. Furthermore, Mendel represents these patterns in a cogent though simple mathematical way:

> If n designates the number of characteristic differences in the two parental plants, then 3^n is the number of terms in the combination series, 4^n the number of individuals that belong to the series, and 2^n the number of combinations which remain constant.[74]

Mendel also describes the process by which new hybrids can arise and breed true, though he criticizes the earlier hybridists for their assumptions regarding the fluidity of species. Specifically he attacks the opinion that 'through cultivation, species stability is greatly upset or entirely shattered.'[75] Presumably he is referring to Lecoq, who suggested that the first step required to induce variation in plants is 'the shattering of their stability, and the breaking up of their habit.'[76] This was achieved by varying the external conditions such as climate, temperature, soil moisture, and so on. Lecoq was not alone in his belief about the external conditions. As Roberts points out, 'it was the view of Herbert that fertility in hybrids depended much upon circumstances of climate, soil and situation.'[77] Mendel attacked this view also. 'It is not clear why mere transportation to garden soil should have such thorough and persistent revolution in the plant organism as its consequence.'[78] Hence, it is apparent that Mendel's work is erected on the tradition of the hybridists, though he certainly does not take all of their conclusions for granted. His own results with *Pisum* preclude this. However, this does not mean that he had initiated an entirely new science or was attacking an entirely new problem. Though the basics of genetics are suggested by his description of the fertilization of the germ cell with its separate elements contributed by each parent, it appears that for Mendel this constitutes a theory of hybridization, where hybridization constitutes a solution to the process of the evolution of organic forms.

When read by his contemporaries like Focke, Mendel was perceived *quite correctly* to be addressing the problems addressed by his predecessors in the field of hybridization. However, these interpretations paid no attention to the model of the reproductive process which Mendel inferred from his hybrids. This does *not* appear to be the main point of the paper, but appears to be one of the assumptions made in order to make the ratios intelligible. Consequently, it is no mystery that Mendel does not dwell on the 'genetic' model in his conclusion but discusses, instead, the hybridists' efforts to tansmutate different species. By contrast, when De Vries discusses splitting or segregation, this is unmistakably the focal point of his discovery.

In summary, it appears that Mendel was not an obscure historical figure, long neglected for three and a half decades.[79] Nor was Mendel entirely misread by those who were most familiar with his work. Nor was Mendel accurately read by those who claimed to have rediscovered his work in 1900. In 1900, Mendel's work was read as a contribution to the dispute between Bateson and the biometricians over continuous/discontinuous variation. Only later was the purely 'genetic' orientation of his paper formulated. Yet in 1865, this 'genetic' orientation was a relatively minor consideration; it appears more to have been assumed than 'discovered' — and, even if discovered, the main point of the 1866 publication pertains to the role of hybridization in the evolutionary history of organic forms. In other words, in 1866 Mendel's research was a contribution to the model of evolution based on hybridization and the perpetuation of characters; while in 1900 it constituted a link between the phenomenon of variation and the mechanism of natural selection. This paper has tried to outline the social forces affecting the reconstruction of Mendel in 1900, and the in vivo orientation of Mendel in 1866.

• *NOTES*

The author would like to express his gratitude to Professors Lindley Darden, David L. Hull and James L. Turk for commenting on an earlier draft of this article. Also, the article has benefited enormously from recommendations of the anonymous readers for *Social Studies of Science*, especially from the reader who was kind enough to send me a galley copy of Robert Olby's paper, 'Mendel No Mendelian?', since published in *History of Science*, Vol. 17 (1979), 53-72. Olby's conclusions reinforce the interpretation of the present article.

1. Thomas S. Kuhn suggests not only that there are two types of discoveries in science, 'normal' and 'revolutionary', but that a particular achievement might constitute a normal discovery for one group while being a revolutionary discovery for another. See Kuhn, *The Structure of Scientific Revolutions* (Chicago: The University of Chicago Press, 1962), 51. The implications of this insight are significant for a sociological model of the problem of scientific discovery: a theory of discovery should concern itself *not* with determining what makes discoveries happen, but with what makes certain happenings discoveries.

This present study is one of a series of investigations which I am undertaking into the social basis of scientific discovery. In a related paper I am concerned to show the more sociological implications of this interpretation of Mendel. These are fourfold. First, Mendel's case has been used to recommend the salience of the idea of an historical *zeitgeist*: Mendel was 'ignored' because of his unorthodox conception of the problem, and consequently went unnoticed. Inasmuch as the evidence I examine shows that Mendel was not ignored, this position is untenable. So too is the 'culturological' model of social change put forward by A. L. Kroeber in 1917, and substantiated by Ogburn and Thomas in 1922 and Leslie White in 1944. These authors argued that changes take place in society as a result of 'historical maturation'. Their chief evidence was the record of multiple, simultaneous discoveries. Chief among the examples explored by Kroeber was the case of the re-discoverers of Mendel's paper (De Vries, Correns and Tschermak), who all claimed in 1900 to have independently come to the same results which Mendel had published in 1866. My research indicates that a close examination of the materials suggests that these 're-discoveries' were not as equivalent, as innocent or as simultaneous as the records of multiple discoveries would lead us to believe. The third implication which I have explored is Reichenbach's distinction between the context of discovery and the context of justification. Mendel's case has sometimes been cited as an illustration of its relevance (cf. S. Cannavo, *Nomic Inference* [The Hague: Martinus Nijhoff, 1974]). Presumably Mendel's situation in 1865 was the context of discovery, while the rediscovery in the limelight of public scrutiny in 1900 was the context of justification. When we see the direction of 'Mendelism' during these two different periods, this interpretation of Mendel is unwarranted.

The fourth and most important implication of this approach to Mendel is the model of discovery which it recommends. Specifically, the case of Mendel draws us toward an attributional model of discovery in which the central question is a phenomenological one: how was this event constituted as a discovery? Most models of discovery in the current literature point to psychological, causal relationships. Discoveries are pictured as the outcome of gestalt shifts, the perception of anomalies, retroductions, unconscious synthesis, strong inference, and so on. All these models equate the question of discovery with the question of how an idea gets 'into an individual's head'. I ask the question of how the ideas get into the society. The answer which I explore takes the following form. Following Wittgenstein and Winch, what needs to be explained are 'the criteria of intelligibility' by which native speakers are able to interpret events as discoveries. The commonsense perception of discoveries involves tacit judgements and/or attributions regarding the validity of the achievements, their substantively scientific derivation and embeddedness in courses of research action, their patent unprecedentedness, and their possibility structure in the tradition. This model of discovery has been sketched in a forthcoming article, 'Naturalistic and Sociological Models of the Problem of Scientific Discovery', to appear in the *British Journal of Sociology*, Vol. 30 (1979).

Two of the important implications of the model I propose are the following. First, it provides a more substantively scientific account of priority disputes. Often the evidence suggests that priority disputes in science are not motivated primarily by contradictions in the normative and reward structures of science, but by quarrels over related formulations of a theory. In such disputes, scientists are recommending competing models of the same phenomena. In other words, they are seeking recommendations for their ideas because they appear to be *better*, not recommendations of themselves because they claim to be *first*. Secondly, the model I propose coheres well with some compelling formulations offered by others — specifically Walter

Weimer, who speaks of theories as 'injunctive utterances'. I would suggest similarly that discoveries be looked at as 'performatives', and that as sociologists we should pay attention to the transformations theories undergo as they are turned into announcements. G. Nigel Gilbert has already reported some seminal contributions to this area, in his 'The Transformation of Research Findings into Scientific Knowledge', *Social Studies of Science*, Vol. 6 (1976), 281-306. By paying attention to discoveries as announcements, I conjecture that we will uncover the procedures by which the problem of recognition is addressed in the ways it is 'textualized' by the author. These several matters are explored in a manuscript which the author is currently preparing for publication.

2. See Herbert Wendt, translated by James Cleugh, *In Search of Adam* (New York: Collier Books, 1962), 358-59.

3. Lindley Darden, 'Reasoning in Scientific Change: Charles Darwin, Hugo de Vries and the Discovery of Segregation', *Studies in the History and Philosophy of Science*, Vol. 7 (1976), 154ff.

4. Hugo de Vries, 'The Segregation of Hybrids', translation of 'Das Spaltungsgesetz der Bastarde' by Evelyn Stern, in Curt Stern and Eva R. Sherwood (eds), *The Origin of Genetics* (San Franciso: Freeman, 1966), 107-17, at 110.

5. Hugo de Vries, quoted in H. F. Roberts, *Plant Hybridization Before Mendel* (Princeton, NJ: Princeton University Press, 1929), 328.

6. Ibid.

7. Bentley Glass, 'The Long Neglect of a Scientific Discovery: Mendel's Laws of Inheritance', in Johns Hopkins — History of Ideas Club, *Studies in Intellectual History* (Baltimore, Md: The Johns Hopkins Press, 1953), 148-60, quoted at 154.

8. Ibid.

9. It is ironic that Romanes borrowed Darwin's copy of Focke, and that neither apparently read the section on 'Leguminosae', for some of the pages in Darwin's copy had not been cut. Both Romanes and Darwin merely read the historical introduction. See Robert Olby, *The Origins of Mendelism* (London: Constance Co., 1966), 195.

10. Alexander Weinstein, 'How Unknown was Mendel's Paper?', *Journal of the History of Biology*, Vol. 10 (1977), 341-64, especially 341-42.

11. See Conway Zirkle, 'The Role of Liberty Hyde Bailey and Hugo de Vries in the Rediscovery of Mendelism', *Journal of the History of Biology*, Vol. 1 (1968), 205-18.

12. See A. E. Gaissinovitch, 'An Early Account of G. Mendel's work in Russia (I. F. Schmalhausen 1874)', in Milan Sosna (ed.), *G. Mendel Memorial Symposium 1865-1965* (Prague: Academia Publishing House of the Czechoslovak Academy of Science, 1966), 39-40. Schmalhausen's report read, in part: 'His experiments and mathematical considerations in the second part of the work (*Befruchtungszellen der Hybriden*) lead him to conclusions which are basically similar to the theoretical considerations of Naudin' (ibid., 40).

13. Weinstein, op. cit. note 10, 343.

14. Glass, op. cit. note 7, 149.

15. See Roberts, op. cit. note 5, 323.

16. L. C. Dunn, *A Short History of Genetics* (New York: McGraw Hill, 1965), 16.

17. See Roberts, op. cit. note 5, 337.

18. A. H. Sturtevant, *A History of Genetics* (New York: Harper and Row, 1965), 27.

19. See Roberts, op. cit. note 5, 339. (Italics in original.)

20. See Stern and Sherwood, op. cit. note 4, 121. (Italics in original.)

21. See William B. Provine, *The Origins of Theoretical Population Genetics* (Chicago: The University of Chicago Press, 1971), Bateson quoted on 68.

22. David L. Hull et al., 'Planck's Principle', *Science*, Vol. 202 (17 November 1978), 717-23, esp. 720-21.

23. See Malcolm J. Kottler, 'Charles Darwin's Biological Species Concept and Theory of Geographic Speciation: The Transmutation Notebooks', *Annals of Science*, Vol. 35 (1978), 275-97. Also see Gerald L. Geison, 'Darwin and Heredity: the Evolution of his Hypothesis of Pangenesis', *Journal of the History of Medicine*, Vol. 24 (1969), 375-411.

24. See Fleeming Jenkin's discussion of swamping and the question of geological time in his review of *The Origin of Species* from the *North British Review* of June 1867, reproduced in David L. Hull, *Darwin and His Critics* (Cambridge: Harvard University Press, 1973), 302-44.

25. Provine, op. cit. note 21, 9-10.

26. Ibid., 14ff.

27. William Bateson, *Materials for the Study of Variation* (New York: Macmillan, 1894). Also see Lindley Darden, 'William Bateson and the Promise of Mendelism', *Journal of the History of Biology*, Vol. 10 (1077), 87-106.

28. See Provine, op. cit note 21, 56.

29. Gregor Mendel, 'Experiments on Plant Hybrids', translated by Eva R. Sherwood, in Stern and Sherwood, op. cit. note 4, 35.

30. See Provine, op. cit. note 21, 28.

31. Pearson argued that organisms produce 'undifferentiated like organs' or 'homotypes' (e.g. blood cells, fish scales, body hair) which exhibit a degree of variability within the organism, but a degree smaller than that found for the race as a whole. Since the various ova and sperm cells are homotypic, they would unite to produce organisms the degree of variability between which would be no greater than the degree of variability in the homotypes of the parental organism. This model of heredity paid no special attention to the character of the germ cells and specifically the segregation which Mendel suggested occurred in them. See Provine, ibid., 58ff.

32. Ibid., 61.

33. Weinstein, op. cit note 10, 360.

34. Loren Eiseley, *Darwin's Century* (New York: Anchor Books, 1961), 206.

35. A. D. Darbishire, *Breeding and the Mendelian Controversy* (London: Cassell, 1911), 189. Cited by Robert Olby, 'Mendel No Mendelian?', *History of Science*, Vol. 17 (1979), 53. For an even more outlandish account, cf. H. Wendt, *In Search of Adam* (New York: Collier, 1963), 355.

36. Quoted in Vitezslav Orel, 'Response to Mendel's Pisum Experiments in Brno since 1865', *Folia Mendeliana*, Vol. 8 (1973), 199-211, see 202.

37. Ibid., 203.

38. Ibid.

39. Ibid.

40. Ibid., 204.

41. Ibid., 205.

42. See Ernst Mayr, 'The Recent Historiography of Genetics', *Journal of the History of Biology*, Vol. 6 (1973), 125-54, see 140.

43. The Hawkweed plants which Mendel raised at the suggestion of Naegeli were apometic plants: these plants appear to cross-fertilize while they in fact reproduce asexually — that is, without fertilization. Naegeli's focus on this plant to study heredity was unfortunate. Likewise the attention De Vries paid to the apparent new mutations in *Oenothera* was unwarranted; the peculiar behaviour of this species is produced by its balanced chromosome rings. (See Mayr, ibid., 137.)
44. Sir Ronald Fisher, 'Has Mendel's Work Been Re-discovered?', in Stern and Sherwood, op. cit. note 4, 139-72, quote at 171.
45. Elizabeth Gasking, 'Why was Mendel's Work Ignored?', *Journal of the History of Ideas*, Vol. 20 (1959), 60-84, see 60.
46. Ibid., 66.
47. Conway Zirkle, 'Gregor Mendel and His Predecessors', *Isis*, Vol. 42 (1951), 97-104, see 98.
48. Ibid., 99.
49. Cf. ibid.
50. Ibid., 100.
51. Ibid.
52. Quoted in Zirkle, ibid., 102.
53. Olby, op. cit note 9, 62-67.
54. Fisher, op. cit. note 44, 164.
55. Mendel, op. cit. note 29, 2.
56. See Orel, op. cit. note 36, 201.
57. Mendel, op. cit. note 29, 11.
58. Ibid., 15.
59. Ibid., 41, 44, 47.
60. Quoted in Orel, op. cit. note 36, 205.
61. Quoted in Orel, ibid., 207.
62. See Roberts, op. cit. note 5, 168.
63. Ibid., 180.
64. Ibid., 81.
65. Ibid., 82.
66. Quoted in Roberts, ibid., 155.
67. Quoted in Roberts, ibid., 96.
68. Mendel, op. cit. note 29, 5.
69. Ibid.
70. Ibid., 41. (Italics in original.)
71. Ibid., 42. (Italics in original.)
72. Ibid., 45-46.
73. Ibid., 47.
74. Ibid., 22.
75. Ibid., 37.
76. Quoted in Roberts, op. cit. note 5, 154.
77. Ibid., 95.
78. Mendel, op. cit. note 29, 37.
79. One of the overlooked reasons that Mendel's case has touched such a poignant note in us is that his case has always been presented as an enormous tragedy which, like Galileo's case, curries our moral indignation. In both cases, great contributions went unrewarded by the local communities. In other words, the suppression of Galileo by the Church and the apparent obscurity of Mendel elicit a common

moral reaction over the patent injustice experienced by each. The same common sense of injustice animates the general interest in such cases of scientific deviance as Kammerer's midwife toad (cf. A. Koestler, *The Case of the Midwife Toad* [New York: Random House, 1972]), the Piltdown scandal, and the suppression of Velikovsky. All these cases are of inordinate interest to the scientist and the layman alike inasmuch as they raise for science the moral concerns of fairplay and justice which dominate everyday life. Perhaps the moral basis of such cases explains the fact that Mendel's story has figured so importantly in the writings of so many authors for so long, in spite of *the lack* of evidence that for Mendel 'the law valid for *Pisum*' was a revolutionary contribution to the theory of evolution.

Augustine Brannigan graduated from the University of Toronto in 1978, and is currently Assistant Professor of Sociology at the University of Calgary in Calgary, Alberta. Professor Brannigan's manuscript on the *Social Basis of Scientific Discoveries* will be appearing in Britain in 1980. He is currently working on two investigations related to the attributional model of discovery. These concern 'A Latent Function of Priority Disputes' and 'The Problem of Narrative in Sociobiology'.
Author's address: Faculty of Social Sciences, Department of Sociology, The University of Calgary, 2920 24 Avenue, N.W., Calgary, Alberta, Canada T2N 1N4.