Mendel's Opposition to Evolution and to Darwin

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Although the past decade or so has seen a resurgence of interest in Mendel's role in the origin of genetic theory, only one writer, L. A. Callender (1988), has concluded that Mendel was opposed to evolution. Yet careful scrutiny of Mendel's *Pisum* paper, published in 1866, and of the time and circumstances in which it appeared suggests not only that it is antievolutionary in content, but also that it was specifically written in contradiction of Darwin's book *The Origin of Species*, published in 1859, and that Mendel's and Darwin's theories, the two theories which were united in the 1940s to form the modern synthesis, are completely antithetical.

Mendel does not mention Darwin in his *Pisum* paper (although he does in his letters to Nägeli, the famous Swiss botanist with whom he initiated a correspondence, and in his *Hieracium* paper, published in 1870), but he states unambiguously in his introduction that his objective is to contribute to the evolution controversy raging at the time: "It requires a good deal of courage indeed to undertake such a far-reaching task; however, this seems to be the one correct way of finally reaching the solution to a question whose significance for the evolutionary history of organic forms must not be underestimated" (Mendel 1866). So it is not plausible that Mendel could have been writing in ignorance of Darwin's ideas, which had aroused the worldwide furor.

Of course, neither Darwin nor Mendel used the word "evolution." It is a term that came into vogue as a synonym for Darwin's "descent with modification" shortly after the publication of *The Origin of Species,* when it assumed application to fully developed organic forms, in contrast to its earlier embryological connotation. However, Gavin de Beer has observed that it is in exactly this sense that Mendel employs the German expression "Entwicklungs-Geschichte," and he comments: "Here, therefore, was Mendel, referring to evolution and laying down an experimental programme for its study by means of research in breeding hybrids" (de Beer 1964). Some years later, Robert Olby (1979) also emphasized the evolutionary orientation of Mendel's paper: "The laws of inheritance were only of concern to him [Mendel] in so far as they bore on his analysis of the evolutionary role of hybrids."

Olby's (1979) article, entitled "Mendel No Mendelian?," led to a number of revisionist views of Mendel's work and his intentions, although no agreement has been reached. For instance, some writers, unlike de Beer, Olby, and Callender, overlook or minimize the evolutionary significance of Mendel's paper, while others maintain that Mendel had little or no interest in heredity, an interpretation that has been opposed by Hartl and Orel (1992): "We conclude that Mendel understood very clearly what his experiments meant for heredity." If there is any consensus at all about Mendel, it is, quite extraordinarily, that he was an evolutionist, but it is inconceivable that a priest could have been openly supporting a theory that Darwin had been hesitant to publish because of its heretical religious and political implications.

Mendel does not make a definite statement about his stance, but it is argued that there is evidence, both from the historical background and in Mendel's paper itself, that indicates that the latter was an ad hoc attempt to refute Darwin's ideas and that Mendel's position was one of theological orthodoxy. (Mendel was a well-integrated member of his monastic community and a zealous defender of the faith, not a dissident.) Furthermore, if Mendel's paper is seen in this light, the many incongruities (or apparent incongruities) that have been the subject of discussion throughout the twentieth century disappear.

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Evidence From the Historical Background

It is known that Mendel possessed a copy of the second German edition of *The Origin of Species* published in 1863, many passages of which he marked (de Beer 1964; Orel 1971), and his paper distinctly reflects certain important aspects of Darwin's thought, as de Beer (1964) has pointed out. Also, Mendel was most probably familiar with the earlier German edition owned by the natural history society to which he belonged (Orel 1971). In 1861, the parent body of this society had discussed *The Origin,* a year after the publication in a German journal, to which Mendel could have had access, of the "word-by-word translation" of Darwin's chapter entitled "On the Geological Succession of Organic Beings," in which Darwin clearly formulated his theory of descent with modification through natural selection (Orel 1971). [Mendel was obviously interested in Darwin's ideas. Hugo Iltis, Mendel's first biographer, notes that Mendel bought all Darwin's later works as soon as they were published in German, adding: ". . . and not Darwin's books alone, for almost all the Darwinian literature of the 'sixties and 'seventies is to be found in the monastery library at Brünn" (Iltis 1932).]

This would have given Mendel at least 4 years in which to carry out his experiments and prepare his paper for presentation in February and March 1865. Evidently this would not be sufficient time if the experimental program was conducted as Mendel records, but recently doubt has been cast on the veracity of Mendel's account. Federico Di Trocchio (1991), in an article entitled "Mendel's Experiments: A Reinterpretation," observes: "To understand Mendel's work we are forced to admit, as was tentatively suggested by William Bateson, that most of the experiments described in *Versuche* are to be considered fictitious." Di Trocchio (1991) claims that Mendel did not perform the seven monohybrid experiments that he reports, the basis of the law of segregation: ". . . Mendel never carried out these experiments in the garden, but rather only on the pages of his notebooks." He suggests that this could also be true of both the dihybrid experiment and trihybrid experiment, from the results of which the law of independent assortment was derived, and he states: ". . . we are to-day forced by a series of anomalies and incongruities to admit that Mendel's account of his experiments is neither truthful nor sci-

entifically likely, and that the strategy he really followed must have been completely different" (Di Trocchio 1991). Di Trocchio argues that the numerical data for the mono-, di-, and trihybrid experiments were obtained by progressively disaggregating those from polyhybrid crosses conducted for about three hybrid generations, that Mendel may have used the 3:1 ratio as his criterion for the selection of the seven traits, and that he did not report all his data "because he was well aware that other *Pisum* characters did not follow the law, having already ascertained that they produced strange ratios (i.e., that they were linked)" (Di Trocchio 1991). Di Trocchio adds: "Had he [Mendel] described the real course of his experiments he would have had to admit that his law worked for only a few of the hundreds of *Pisum* characters—and it would thus have been considered more of an exception than a rule" (Di Trocchio 1991). (The possibility that Mendel reported marginal totals without saying so was first raised by Fisher in 1936.)

Therefore, 4 years would have been adequate time for Mendel to perform whatever experiments were necessary and to write his paper, especially as he was familiar with the prior work in the field, of which, however, he makes no acknowledgment, although many of the earlier investigators had also used garden pea and reported very similar results: "It is well known that practically all the points proved by Mendel in his main paper had been made by others before—J. Goss and A. Seton in 1822 reported the results of their pea-crossing experiments, indicating dominance in the first hybrid generation and reappearance of recessives in the second. Knight verified their results in 1824, adding such observations as the 'scattering' of 'indivisible' characters in the generations following hybridization. [Knight also reported backcrosses and a 2 year trial period, as Mendel was later to do in his paper.] A. Sageret (1826) had further substantiated the independent reappearance of Knight's 'indivisible' characters in successive generations; only some characters reappeared in all generations (the dominants). This work was known to Mendel when he planned his experiments" (Gedda and Milani-Comparetti 1971). Mendel's attention had been drawn to these papers by Gärtner's book *Experiments and Observations upon Hybridization in the Plant Kingdom,* which was published in German in 1849 and which extensively reviewed investigations into plant crossing. Mendel

possessed a copy, and his marginalia and notes on the flyleaf suggest that he studied it in detail several times (Orel 1984). Olby (1985) comments: "These notes are important because they show Mendel at work, hunting for clearly-marked character differences between the various forms of peas."

There is no record of any previous experiments by Mendel that might have led to the initiation of the famous *Pisum* program. ["But despite all that has been discovered and preserved we have no direct information on the sources of Mendel's inspiration . . ." (Olby 1985).] Also, Mendel does not provide a time schedule for his experimental program or even state the date of commencement of the project, observing in his paper only that it occupied "a period of eight years." However, in his second letter to Nägeli, obviously a defensive response to the latter's criticism ["I am not surprised," Mendel wrote, "to hear your honor speak of my experiments with mistrustful caution" (Stern and Sherwood 1966)], Mendel elaborates on several issues, stating categorically that the experiments were conducted from 1856 to 1863, when "they were terminated in order to obtain space and time for the growing of other experimental plants" (Stern and Sherwood 1966). Nevertheless, throughout this period, Mendel maintained a lively correspondence with his brother-in-law, Leopold Schindler, and yet he never alluded to his scientific work, although making frequent references to the events of the day (Iltis 1932). And it is clear from Nägeli's reply to Mendel's first letter, with which Mendel had enclosed his paper, that Nägeli considered the latter to be no more than an outline: "I shall not remark on any other points in your communication, for without a detailed knowledge of the experiments on which they are based I could only make conjectual comments" (quoted by Stubbe 1972).

It was in May 1856, when he was purportedly setting out on his experimental program, that Mendel failed in his second attempt to become a certificated teacher, an event that was preceded and followed by illness. Olby (1985) writes: "Evidently Mendel was very ill and it was presumably the same illness which had plagued him at times of stress when he was a schoolboy and a student. Dr. Joseph Sajner, who has made a special study of Mendel's illness, calls it an 'unstable psychological constitution'. Mendel had already been ill earlier in the year, no doubt owing to the stress of his studies, and when faced with the 'Vi-

enna ordeal' again his nerves gave way." [It was in 1856 also that the controversy over procreation (whether only one parent or both parents make a material contribution to the embryo), which was the greatest biological conflict before the Darwinian revolution, was only just "coming to a head" (Orel 1982).] At that time, Mendel was a supply teacher at Brünn Modern School, which had just recently been founded. In 1857 and 1858, Mendel received commendations from the education authorities for his "zealous and successful endeavours" (Iltis 1932) in promoting the working of the school, and he remained in his office until 1868. Thus, Mendel could have had very little time to devote to his botanical pursuits, particularly in the important early stages.

The myth has prevailed that Mendel worked in isolation, the bibulous gardener usually being cited as the only helper and held responsible for the "too good" results, but it appears that the experiments were a communal enterprise, to which the monastic hierarchy must have been very kindly disposed to allow such appropriation of time and space usually set aside for other purposes. Abbot Napp, the head of the monastery, was keenly interested in natural history, and, like Mendel and other monks, he was a member of the agricultural society that had discussed *The Origin of Species* in 1861. Orel (1984) observes: "Perhaps it is as well that, during his studies and early experiments, Mendel enjoyed both the moral and material support of Abbot Napp, who understood his motivation if anyone did."

Hugo Iltis, a teacher in Brünn like Mendel before him, names two other monks involved in the experimental program and refers to a senior member of the staff at the school where Mendel taught, Alexander Makowsky, the noted natural historian "who from 1860 onwards collaborated with Mendel" (Iltis 1932) (i.e., after the publication of *The Origin of Species*). Alipius Winkelmayer, one of the monks who assisted Mendel, was Mendel's contemporary, having entered the monastery soon after Mendel, and he, like several other monks, had a taste for botany. For instance, Thomas Bratránek and Matthaeus Klácel, two of the monastery's leading scholars, "though not professional botanists, were distinguished amateurs of that branch of science" (Iltis 1932). Corcos and Monaghan (1990) comment: "His [Mendel's] colleagues were highly intellectual and, like him, were teachers and members of learned societies."

So Mendel's fellow monks must have not only understood his work but regarded it with great approval, for 2 years after Mendel's paper was published they elected him abbot of the rich and influential monastery to succeed an outstandingly good administrator. His priorities necessarily realigned, Mendel spent the rest of his life in an office of power and privilege. It was a position to which he had aspired. In a letter to his brother-in-law, 4 days before the election, Mendel had written: "It is still uncertain which of us will be the lucky one. Should the choice fall on me, which I hardly venture to hope, I shall send you a wire on Monday afternoon" (quoted by Iltis 1932).

After becoming spiritual leader of his monastery, Mendel journeyed to Rome to be received by the Pope (Sootin 1959). In 1872, four years after his election, he was made Commander of the Order of Franz Joseph, the published citation for the award referring not only to Mendel's teaching career but also to his political service (Orel 1984).

Some of Mendel's notes for addresses as abbot have survived. Zumkeller (1971) writes: "For precisely because these sermon outlines are but little polished, they give us a clearer idea of the personal religious sentiment and thought of the preacher. One fact imposes itself at the very first reading of these texts: Here speaks a man of true faith and a pastor who thinks with the Church. He endeavors zealously to acquaint his audience with the unadulterated Christian doctrine ... Decades ago, some writers endeavored to present Mendel as a freethinker, who searched for truth 'without deference to dogmas.' It has long been recognized that this opinion is incorrect. The discovery of these sermon outlines of the Abbot Mendel should cut the ground forever from under such imputations."

In 1870, there had been a proclamation of the infallibility of the Pope, and later encyclicals announced the infallibility of the Bible. It was not until 1951 (almost a century after the publication of *The Origin of Species*), when Pope Pius XII relaxed the dogmatic interpretation of the Bible, that open discussion of evolution was officially permitted by the Catholic Church (George 1982).

Evidence From Mendel's Paper

The Origin of Species was an onslaught on the doctrine of special creation, which Darwin (1859) referred to as the belief that

"at innumerable periods in the earth's history certain elemental atoms have been commanded suddenly to flash into living tissues," and Darwin's themes were evolution, population, and heredity, a conceptual framework that is mirrored in its entirety by Mendel's paper. ["As a consequence of his evolutionary approach, Mendel adopted, as Thoday (1966) has correctly pointed out, the method of population analysis ... " (Mayr 1982).] Heredity was a vital component of Darwin's theory, for he reasoned that for variation to be evolutionarily important it must be heritable, although he was forced to admit: "The laws governing inheritance are quite unknown" (Darwin 1859). Thus, it is highly significant that only a few years later Mendel elaborated his very definite atomistic theory of heredity—a theory, moreover, that results only in stasis: "The pure process of Mendelian heredity does not produce any evolutionary change at all: the population stays the same" (Ridley 1985).

The populational orientation of Mendel's paper is also significant. Population thinking was Darwin's most original and revolutionary concept, a concept that made the introduction of natural selection possible (Mayr 1972), and its genesis has been well documented, but it was not until the publication of Darwin's iconoclastic book that it was unveiled to public view. Therefore, Mendel must have either independently adopted a populational approach from the outset or planned his experiments with knowledge of Darwin's ideas, for it is obvious from the design of the reported experimental program that there could have been no change in his research objective after its initiation.

At that time, the existence of constant (true-breeding) hybrids, which several experimentalists had reported, was of great interest, as Mendel emphasizes in his *Pisum* paper: "This feature is of particular importance to the evolutionary history of plants, because constant hybrids attain the status of *new species*" (Mendel 1866; emphasis in original). And it was Mendel's concern with constant hybrids that spurred him to enter the fray again a few years later with his *Hieracium* paper: "The question of the numerous and constant intermediate forms has recently acquired no small interest since a famous *Hieracium* specialist has, in the spirit of the Darwinian teaching, defended the view that these forms are to be regarded as [arising] from the transmutation of lost or still-existing species" (Mendel 1870). But Mendel him-

self does not report constant hybrids in his *Pisum* paper: " . . . he [Mendel] did not find any constant hybrids" (Monaghan and Corcos 1990). In fact, Mendel's paper can be seen as an attempt to provide a theoretical explanation for the phenomena of reversion and transformation, both of which were held to support the orthodox doctrine of special creation. [L. A. Callender (1988) has differentiated between what he calls the orthodox doctrine of special creation (which asserted that all existing species were directly created by the hand of God and which denied the existence of constant hybrids) and what he calls the modified version proposed by Carolus Linnaeus in the middle of the eighteenth century, which claimed that constant hybrids could arise.] Ernst Mayr (1982) remarks: "It is highly significant that, as in the case of Darwin, it was the species question which inspired Mendel in his work on inheritance."

However, Mendel's experimental material did not fulfill the criteria considered necessary by theoretical biologists of the time for hybridization pertaining to the origin of species (Gasking 1959): Mendel chose domestic varieties, not wild species, although he often uses the word "species" in his paper, obviously tendentiously, in reference to his garden peas. L. C. Dunn (1965a) comments: "Kölreuter and Gärtner, to whom he [Mendel] refers, worked with true species hybrids differing in many variable intergrading characters from which such a rule as Mendel envisaged could not have been derived." And Corcos and Monaghan (1993) write: "Hence, what Mendel was discussing as the transformation of one species into another was really the transformation of one variety into another." It has been argued that the classification of peas was uncertain at the time and that Mendel states in his paper that their position in a classificatory system was "completely immaterial to the experiments in question," an attitude that has been labeled "cavalier" (Hartl and Orel 1992). However, the important point is that Mendel is not consistent, referring to his experimental plants as "varieties" in some contexts and as "species" in other contexts, as Corcos and Monaghan (1993) have noted: "In this paragraph [detailing the selection of plants for his experimental program] Mendel uses the word 'variety' for his breeding lines, and yet in his 'Introductory Remarks' he wrote about hybrids between species." Mendel also called his peas "varieties" in his first letter to Nägeli, in

which he enclosed his paper (Stern and Sherwood 1966).

The late eighteenth- and early nineteenth-century experimentalists in plant crossing are seen to fall into two distinct groups: those who investigated the "essence of the species as a whole" (Mayr 1982) and those (such as Gallesio, Knight, Goss, Seton, and Sageret) who followed the course of individual plant characters and who, therefore, like Mendel, worked of necessity with varieties. Nevertheless, Mendel obviously felt that his conclusions had relevance to the former group, several of whom he mentions in his paper (Kölreuter, Gärtner, Herbert, Lecoq, Wichura), while making no acknowledgment of the pioneers in his own field. Mayr (1982) observes: "Even though Mendel occasionally calls himself a hybridizer and in his paper often refers to Kölreuter, Gärtner, and other plant hybridizers, he himself does not at all belong to that tradition."

Ever since Kölreuter's work with the tobacco plant in the 1760s, hybridizers had sought to settle the question of immutability and creation by experiment, and, as Callender (1988) has suggested, a proper understanding of such important theoretical categories as reversion and transformation, two phenomena that Kölreuter claimed to have discovered in the course of his experimental investigations that refuted the existence of constant hybrids, is essential to an interpretation of Mendel's paper. In this context, reversion was the return of a hybrid by self-fertilization to the two original types crossed, while transformation was the conversion of one species into another already existing species by repeated backcrossing of the hybrid with one or the other of the two original parental forms. The purpose of such experiments was not to disprove the fixity of species, as so it may appear today, but to support the orthodox doctrine of special creation, since no new species was produced.

Joseph Gottlieb Kölreuter (1733–1806) and his successor Carl Gärtner (1772–1850), to whom Mendel repeatedly refers, were firm believers in the orthodox doctrine of special creation ["Constant hybrid plant forms, they maintained, could not and did not exist" (Callender 1988)], and Darwin had cited them in *The Origin of Species* as adversaries. [Darwin described Gärtner as "so good an observer and so hostile a witness" (Darwin 1859).]

The first half of Mendel's (1866) paper (pp. 1–23) is devoted exclusively to the acquisition of his "generally applicable

law" quantifying reversion (in which the population reverts to the pure parent forms, while the hybrid represents an ever-decreasing proportion of the progeny), while the final pages (pp. 44–48) are devoted exclusively to transformation experiments. Mendel (1866; emphasis in original) writes: "Finally, the experiments performed by Kölreuter, Gärtner, and others on *transformation of one species into another by artificial fertilization* deserve special mention. Particular importance was attached to these experiments; Gärtner counts them as among 'the most difficult in hybrid production.' " Mendel then proposes the application of his "law valid for *Pisum*": "If one may assume that the development of forms proceeded in these experiments in a manner similar to that in *Pisum*, then the entire process of transformation would have a rather simple explanation." And in the penultimate paragraph of his paper, Mendel (1866) states: "The success of transformation experiments led Gärtner to disagree with those scientists who contest the stability of plant species and assume continuous evolution of plant forms. In the complete transformation of one species into another he finds unequivocal proof that a species has fixed limits beyond which it cannot change. Although this opinion cannot be adjudged unconditionally valid, considerable confirmation of the earlier expressed conjecture on the variability of cultivated plants is to be found in the experiments performed by Gärtner." The last sentence obviously indicates that Mendel thought that the "generally applicable law" he had acquired supported Gärtner's position. However, it has been interpreted as meaning the exact opposite, as L. A. Callender has pointed out: "Despite its clarity this paragraph has been a source of endless confusion in the literature. If this statement is to be taken literally, as Mendel most assuredly intended it to be taken, then it says quite simply that he gave *conditional acceptance to the view, expressed by Gärtner, 'that species are fixed within limits beyond which they cannot change'*. Nothing could be clearer. Nevertheless, interpretations of this passage have been given which are remarkable for their extreme departure from accepted use in both the German and English languages" (Callender 1988; emphasis in original).

Thus, Mendel's concerns can be seen as consistent with the traditional science of his day (Max Wichura's book on true-breeding willow hybrids had been published as recently as 1865) and also with

the tumultuous times in which his paper appeared, when the Darwinian revolution was demanding a complete reassessment of man's concept of himself and his world in a way that no earlier revolution in the physical sciences had. David L. Hull (1973), discussing the impact of Darwin's book, writes: "Seldom in the history of ideas has a scientific theory conflicted so openly with a metaphysical principle as did evolutionary theory with the doctrine of the immutability of species." And Augustine Brannigan (1979), in an article entitled "The Reification of Mendel," comments: "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!" One of Mendel's contemporaries was Gustave Niessl [in fact, Hugo Iltis records that Mendel "owed a good deal to Niessl's insight and clarity" (Iltis 1932)], who was secretary of the natural history society to which Mendel had presented his paper in 1865, and he was still an active official at the turn of the century when Mendel's paper was revived. Brannigan (1979; emphasis in original) observes: "In 1902, he [Niessl] 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." [The problem of hybridization and its relationship to evolution had been a frequent theme since the founding of the society by Mendel and his friends and acquaintances in December 1861 (Brannigan 1979).]

Mendel also compares his *Pisum* "law" with the reversion experiments reported by Kölreuter and Gärtner. After stating that the monohybrid seeds and plants have been followed through four to six generations (and just before presenting his formula extrapolating to *any number* of generations), Mendel (1866) writes: "The observation made by Gärtner, Kölreuter, and others, that hybrids have a tendency to revert to the parental forms, is also confirmed by the experiments discussed."

Therefore, no constant hybrids arise in the monohybrid experiments, and Mendel concludes that the same "law of development" applies in the dihybrid and trihybrid experiments: "Therefore there can be no doubt that for all traits included in the experiments this statement is valid: *The progeny of hybrids in which several essentially different traits are united represent the terms of a combination series in which the series for each pair of differing traits are*

combined. This also shows at the same time that *the behavior of each pair of differing traits in a hybrid association is independent of all other differences in the two parental plants*" (Mendel 1866; emphasis in original). So no constant F_1 hybrids occur in any of Mendel's experiments. Although true-breeding forms appear among the progeny of the hybrids (F_2) in the dihybrid and trihybrid experiments, they are only the result of a recombination of existing alternatives. Nothing new comes into being at either the phenotypic or genotypic level, for Mendel's abstract symbolic notation implies that Darwin's "elemental atoms" are discrete entities that remain immutable throughout both time and space, irrespective of how many generations or character pairs are involved. [Interestingly, Mendel refers to the internal determinants he postulated in order to account for his "doctrine of hybridization" (Sinoto 1971) as "elements": ". . . those elements of both cells that cause their differences" (Mendel 1866). Meijer (1983) writes: "Whenever Mendel discusses the material composition of the germ-cells, he uses the word 'elements' ('Elemente')."] This is in marked contrast to Darwin, who argued that there is a continual production of small heritable variations upon which his mechanism of natural selection could act. Callender (1988), in his article entitled "Gregor Mendel: An Opponent of Descent with Modification," observes: ". . . Mendel, of course, denied the very basis of the evolutionary process, modification of hereditary characteristics." And Callender elaborates: ". . . it is a striking fact that the multitude of commentators who have so consistently held that Mendel was in essential agreement with the theory of evolution have singularly failed to demonstrate in his theory of heredity any mechanism by which descent with modification might have come about. Indeed, only the merest handful have ever drawn attention to the fact that a concept of hereditary mutation is entirely absent from the whole of Mendel's published work."

Of particular significance is the single trihybrid experiment, from which Mendel obtains the expected result despite the recalcitrant data. In this experiment, Mendel includes the color of the seed coat with the familiar traits of seed shape and cotyledon color that he had used for the dihybrid experiment, although the seed coat is maternal tissue and therefore its appearance following each artificial fertilization is determined solely by the maternal genetic constitution and not by an equal

contribution from both parents (Mayr 1982). (William Bateson, in his book *Mendel's Principles of Heredity,* first published in 1909, wrote: "The seeds of course are members of a generation later than that of the plant that bears them. Thus when a cross is made the resultant seeds are F_1, showing the dominant character yellowness or roundness, but the seed-skins are maternal tissue.") Consequently, the appearance of the seed coat relevant to Mendel's formulae is not observable in combination with the two embryonic traits in the same plant or in the same year. Mendel does not mention this, nor does he state the very complex procedures necessary to overcome the serious difficulties, reporting only that this "experiment was conducted in a manner quite similar to that used in the preceding one" (Mendel 1866), all of which cast doubt on whether he actually performed the experiment, thus substantiating Di Trocchio's (1991) claims.

Mendel says nothing at all about a tetrahybrid experiment, although his populational generalizations immediately following the trihybrid experiment are projections from four pairs of character differences: "For instance, when the parental types differ in four traits the series contains $3^4 = 81$ terms, $4^4 = 256$ individuals, and $2^4 = 16$ constant forms; stated differently, among each 256 offspring of hybrids there are 81 different combinations, 16 of which are constant" (Mendel 1866). Mendel then extrapolates to any number of traits, even those he had excluded at the outset because they did not fulfill his criteria for selection: "The complete agreement shown by all characteristics tested probably permits and justifies the assumption that the same behavior can be attributed also to the traits which show less distinctly in the plants, and could therefore not be included in the individual experiments. An experiment on flower stems of different lengths gave on the whole a rather satisfactory result, although distinction and classification of the forms could not be accomplished with the certainty that is indispensable for correct experiments" (Mendel 1866). This suggests that Mendel acquired his seven traits by prior experiment, which again correlates with the methodology Di Trocchio argues Mendel must have used to obtain his data. Mayr (1982) comments: "The 22 varieties [which Mendel (1866) reports he "planted annually throughout the entire experimental period"] differed from each other by far more than the seven selected traits,

but Mendel found the other traits unsuitable because either they produced continuous or quantitative variation not suitable for the study of the clear-cut segregation he was interested in, or else they did not segregate independently." It also supports Fisher's (1936) evaluation of Mendel's paper, of which L. C. Dunn (1965b) wrote: "The impression that one gets from Mendel's paper itself and from Fisher's study of it is that Mendel had the theory in mind when he made the experiments reported in the paper. He may even have deduced the rules from a particulate view of heredity which he had reached before beginning work with peas. If so, the outcome of his experiments constitutes, in Fisher's words, not discovery but demonstration."

In his conclusion, Mendel (1866) discusses the combination series he has acquired, in which "the members of the series tend equally toward both original parents in their internal makeup" [conversely, Darwin (1859) had argued that when "hybrids are able to breed *inter se,* they transmit to their offspring from generation to generation the same compounded organization"], and he declares: "One sees how risky it can sometimes be to draw conclusions about the internal kinship of hybrids from their external similarity."

As Arnold Ravin (1965) has pointed out, Mendel's theory was based upon the assumption of equality throughout all stages of the life cycle: equal gametes that unite at random to form equal zygotes that grow into equal plants, reproducing equally generation after generation. This, of course, is the antithesis of Darwin's theory of differential survival and differential reproductive success. Also, Mendel focused on discontinuous variation: "Mendel's concept of discrete characters was completely opposed to Darwin's idea of continuous variation" (Orel and Kuptsov 1983). Mayr (1982) remarks: "Even though Darwin acknowledged the existence of discontinuous variation as a separate category, he considered it evolutionarily unimportant."

When Mendel's paper was revived at the beginning of the twentieth century, the purity of the gametes was highlighted by William Bateson (1901; emphasis in original) in his introduction to the first English translation: "The conclusion which stands out as the chief result of Mendel's admirable experiments is of course the proof that in respect of certain pairs of differentiating characters the germ cells of a hybrid, or cross-bred, are *pure,* being carriers and transmitters of either the one

character or the other, not both." The same point had been made by Mendel in his second letter to Nägeli: "The course of development consists simply in this; that in each generation the two parental traits appear, separated and unchanged, and there is nothing to indicate that one of them has either inherited or taken over anything from the other" (Stern and Sherwood 1966). Eiseley (1958) comments of this passage: "Heredity and variation in the old Darwinian sense could, therefore, not be synonymous. The unit factors had a constancy which the Darwinians had failed to guess."

Darwin and Heredity

Darwin, of course, believed throughout his life in blending inheritance, like all his contemporaries ["In Darwin's time everybody except Mendel ... thought that inheritance was blending" (Dawkins 1986)], and in the inheritance of acquired characters for both corporeal structures and behavior. In fact, Darwin put forward his own theory of heredity, "Pangenesis," in 1868 in order to account not only for the production of variation but also for the inheritance of acquired characters. It is generally thought that this was a retreat on Darwin's part in the face of mounting criticism of his mechanism of natural selection, but historians have shown that Darwin's ideas on heredity were developed over the years in concert with his theory of descent with modification ["... the hypothesis represents the crystallisation of Darwin's thoughts over a period of a quarter of a century, thoughts that began with his wonder at the ability of a planarian to regenerate after division" (Olby 1985)], and it is clear from the first edition of *The Origin of Species* that Darwin took the inheritance of acquired characters for granted. Darwin devotes a whole chapter to instinct, and in his discussion of the hive-bee (Mendel, incidentally, also worked with bees), he states: "The motive power of the process of natural selection having been economy of wax; that individual swarm which wasted least honey in the secretion of wax, having succeeded best, and having transmitted by inheritance its newly acquired economical instinct to new swarms, which in their turn will have had the best chance of succeeding in the struggle for existence" (Darwin 1859).

Mendel's theory was obviously constructed to deny all Darwin's ideas about heredity and thus his theory of descent with modification. George (1982) ob-

serves: "The final blow, or so it seemed—to pangenesis, inheritance of acquired characters, inequality of parental contribution and blending inheritance—occurred in 1900 when Mendelian and de Vriesian theories of inheritance reached the scientific world." Mendel's onslaught, however, unlike that of de Vries, was mounted in the early 1860s, when the world was agog with Darwin's ideas and when biological knowledge and theory were entirely different.

Darwin's belief in the inheritance of acquired characters was increasingly played down in the twentieth century—after the acceptance of August Weismann's theory of the isolation of the germ plasm from somatic influence—so much so, in fact, that the inheritance of acquired characters became the central theme of acrimonious debate between French and English biologists and philosophers, who lined up on opposing sides behind their heroes. Although, as Maynard Smith (1982) has pointed out, it was not Lamarck's theory of heredity that Darwin rejected but his idea that evolution could be explained by an inner drive toward complexity.

It was the hereditary aspect of evolutionary theory that most fascinated Darwin. In a letter to T. H. Huxley, some years before the publication of *The Origin of Species,* Darwin had remarked: "Approaching the subject from the side which attracts me most, viz inheritance, I have lately been inclined to speculate" (Burkhardt and Smith 1990). Darwin drew a sharp line of demarcation between the inheritance of what later came to be known as Mendelian characters and those acquired by natural selection. In the first edition of *The Origin of Species,* he states: "Looking to the cases which I have collected of cross-bred animals closely resembling one parent, the resemblances seem chiefly confined to characters almost monstrous in their nature, and which have suddenly appeared—such as albinism, melanism, deficiency of tail or horns, or additional fingers and toes; and do not relate to characters which have been slowly acquired by selection" (Darwin 1859). This passage appears unaltered in the sixth (and final) edition, published in 1872.

Darwin began *The Variation of Animals and Plants under Domestication* (in which he presented his theory of heredity) in 1860, a year after the publication of the first edition of *The Origin of Species,* and it was first published in 1868, two years after the appearance of Mendel's *Pisum* paper and a year before Mendel's presentation of

his *Hieracium* paper. [Interestingly, Mendel made numerous marginalia in Darwin's chapter on inheritance (Orel 1971) (the German edition of *The Variation* was published in the same year as the English edition), and, as we have seen, he mentioned Darwin in his *Hieracium* paper.] In this massive, two-volume work, the first part of the long-promised addition to *The Origin* (the second part on the variability of organic beings in a state of nature was never written), Darwin devoted only five pages to Mendelian-type inheritance. The section, entitled "On certain characters not blending," concludes: "All the characters above enumerated, which are transmitted in a perfect state to some of the offspring and not to others—such as distinct colours, nakedness of skin, smoothness of leaves, absence of horns or tail, additional toes, pelorism, dwarfed structure, etc.— have all been known to appear suddenly in individual animals and plants. From this fact, and from the several slight, aggregated differences which distinguish domestic races and species from one another, not being liable to this peculiar form of transmission, we may conclude that it is in some way connected with the sudden appearance of the characters in question" (Darwin 1875).

In the section of *The Variation* entitled "Prepotency in the transmission of character," Darwin presented in careful detail experiments very similar to Mendel's. [As Mayr (1983) has pointed out, Darwin was not only a meticulous observer but "also a gifted and indefatigable experimenter whenever he dealt with a problem, the solution of which could be advanced by an experiment."] He writes: "Now I crossed the peloric snapdragon (*Antirrhinum majus*), described in the last chapter, with pollen of the common form; and the latter, reciprocally, with peloric pollen. I thus raised two great beds of seedlings, and not one was peloric ... The crossed plants, which perfectly resembled the common snapdragon, were allowed to sow themselves, and out of a hundred and twenty-seven seedlings, eighty-eight proved to be common snapdragons, two were in an intermediate condition between the peloric and normal state, and thirty-seven were perfectly peloric, having reverted to the structure of their one grandparent" (Darwin 1875).

The occurrence of intermediate types is very significant, for it categorically rules out the possibility of establishing a definite ratio between only the two types resembling the parental forms, as it is well known that Mendel did in his paper: "*Transitional forms were not observed in any experiment*" (Mendel 1866; emphasis in original). [Hugo de Vries, one of Mendel's "rediscoverers," later commented: "The lack of transitional forms between any two simple antagonistic characters in the hybrid is perhaps the best proof that such characters are well delimited units" (de Vries 1900).] Thus, the difference between Darwin's and Mendel's ideas about inheritance was not only a question of interpretation: Mendel's "facts" were different from Darwin's—and from those of all his contemporaries. [For instance, Meijer (1983; emphasis in original) notes: "Mendel's *views* appear to have been very different from Nägeli's, and also his *facts* were different."]

Darwin (1875) began the conclusion to his theory of heredity: "The hypothesis of Pangenesis, as applied to the several great classes of facts just discussed, no doubt is extremely complex, but so are the facts."

At the time when Darwin and Mendel wrote, it was impossible for a scientist to be anything but speculative about the nature of inheritance, for it was not until 1869 that Friedrich Miescher elucidated the chemical composition of the cell nucleus, and it was even later that it was understood that the nucleus of the zygote is formed by the fusion of the egg nucleus and a male nucleus derived from a spermatozoon.

A. R. Wallace, the codiscoverer with Darwin of the principle of natural selection, lived to see the great cytological advances at the end of the nineteenth century—and the rise of Mendelism. George (1971) states: "... in 1910, in the 'World of Life' Wallace made his last comments on Mendelism. He still objected to the idea because the Mendelian characters were abnormalities and, therefore, detrimental to the species under natural conditions. He stressed, once more, their rarity: 'The phenomena on which these theories are founded seem to me to be mere insignificant byproducts of heredity, and to be essentially rather self-destructive than preservative. They form one of nature's methods of getting rid of abnormal and injurious variations. The persistency of Mendelian characters is the very opposite of what is needed amid the ever-changing conditions of nature.'"

Mendel's Wrinkled Pea Seeds

Interestingly, molecular studies have recently revealed that the wrinkled-seed character that Mendel chose for his first monohybrid experiment (and also for both the dihybrid and trihybrid experiments) is caused by an insertion sequence that prevents normal expression of a gene for an enzyme (the presence of which gives rise to the alternative character, roundness), and this has important implications to Mendelian theory.

Madan Bhattacharyya and his colleagues point out that the phenotype description of wrinkled pea seeds that Mendel provided fits only two loci described among commercial cultivars, *r* and *rb*, and that the latter would have been unavailable to Mendel, and they comment: "It has been widely accepted that the wrinkled-seed character described and studied by Mendel (1865) was an allele of the *r* locus" (Bhattacharyya et al. 1990). The insertion is thought to be located in an exon of the SBE1 gene, which codes for an enzyme called the starch-branching enzyme 1, and it is estimated that it would cause loss of the last 61 amino acids of the SBE1 protein, resulting in defects in starch, lipid, and protein biosynthesis in the seed (Bhattacharyya et al. 1990). Therefore, wrinkled pea seeds are abnormal pea seeds, the equivalent of Darwin's "sports" and Garrod's "inborn errors of metabolism," and round pea seeds are normal pea seeds. There are no instructions "for" wrinkledness—only defective instructions for roundness. In other words, there are not two different units of information, one coding for wrinkledness and the other for roundness; there is only one unit, the wild-type gene coding for roundness, with or without an insertion sequence.

Furthermore, the insertion sequence is 0.8 kb long, and, whereas the normal SBE1 gene transcript in round seeds is 3.3 kb, the aberrant transcript in wrinkled seeds is 4.1 kb, suggesting that the nuclear DNA of the homozygous recessive wrinkled pea seeds contains the entire information for the enzyme (i.e., for roundness), although it cannot be expressed. [J. R. S. Fincham (1990) writes: "The size difference was shown to segregate from crosses with the *r* locus, as if the *r* mutation were due to an insertion of an extraneous sequence into the wild-type *R* gene."] Thus, the information for roundness is not being eliminated at meiosis (although, of course, disjunction of chromosomes with their different complements occurs), and consequently all gametes for both phenotypes (and for the heterozygote) must carry the information for roundness, a fact that calls into question the validity of the first Men-

delian law, the law of segregation. As Dover (1986) has observed in a different context: "The traditional algebraic representation of the Mendelian segregation of genes from one generation to the next is, strictly speaking, a description of the segregation of chromosomes." [The second Mendelian law, the law of independent assortment, was disproved many years ago, as Mayr (1982) has noted, despite its persistence as textbook orthodoxy: "Finally, free assortment is also [in addition to the short-lived "law of dominance"] not a valid 'law,' because it was discovered soon after 1900 that characters could be 'linked,' by having their determinants on the same chromosome."]

Although there is no evidence of excision of the insertion sequence that produces wrinkled pea seeds, there are increasing reports of somatic and germ-line excision of such elements in fruit flies and other organisms, leading to reversion to wild type. Thus, organisms scored as mutants in one generation can give rise to normal progeny in subsequent generations. This, of course, has important implications to all aspects of Mendelian theory: gametic transmission of information, fixed ratios, predictions of long-term stability, the definition of "rate of mutation," and even Mendelian terminology. (Most of these mutant organisms, like Mendel's wrinkled pea seeds, are labeled "homozygous recessive" in the Mendelian system, according to which information for complex normal characters has been lost and cannot be reacquired.)

These findings would correlate with Darwin's observation preluding his report of his experiments with normal and peloric snapdragons: "... plants bearing peloric flowers have so strong a latent tendency to reproduce their normally irregular flowers, that this often occurs by buds when a plant is transplanted into poorer or richer soil" (Darwin 1875). [Fincham (1990) points out that transposable DNA elements have been characterized from several plant species, including antirrhinum, and it is known that excision events are strongly dependent upon the environment, occurring, for instance, less frequently in plants grown inside a greenhouse than in those grown outside, where the temperature is lower.]

It is possible that other recessive characters Mendel chose could also be caused by insertion sequences in wild-type genes and that the departure from the expected phenotypes that Mendel recorded but ignored in formulating his theory could be

explained by somatic excision of the elements. For instance, in the experiment with yellow/green seeds (which Mendel used for his second monohybrid experiment and, like the round/wrinkled character pair, for both the dihybrid experiment and trihybrid experiment), Mendel observed a "partial disappearance of the green coloration" (Mendel 1866) in some seeds.

Now, in retrospect, it can be seen exactly what Mendel did: he deliberately chose characters exhibiting a most unusual pattern of inheritance ("this peculiar form of transmission," as Darwin referred to Mendelian-type inheritance) because he wanted to demonstrate stasis, formulated a highly improbable theory, and then extrapolated to all other modes of inheritance. But it is today known that the genome is extraordinarily fluid, as a consequence of a variety of mechanisms of non-reciprocal DNA transfer within and between chromosomes, and it is obvious, as the early opponents of Mendelism maintained (Wallace was by no means alone in his objections), that the type of transmission upon which Mendel focused (that represented largely by human diseases and laboratory mutants) is the exception and not the rule: "The ubiquity of genomic turnover mechanisms both within and between genes (single-copy and multigene families) means that few genes will be found that are refractory to the mechanisms involved. It is conceivable that strict Mendelian genes and stable Mendelian populations in Hardy–Weinberg equilibria do not exist except as observed over short periods of time and amongst small numbers of progeny" (Dover 1986).

Conclusion

1. Mendel's sole objective in writing his *Pisum* paper, published in 1866, was to contribute to the evolution controversy that had been raging since the publication of Darwin's *The Origin of Species* in 1859.
2. Mendel could have come into contact with Darwin's ideas as early as 1860, when the first German edition of *The Origin of Species* was published and a chapter was printed in a journal that was available to him. This would have given Mendel a time frame for his experimental program that correlates with the methodology Di Trocchio (1991) claims he must have used to obtain his data.
3. The content of Mendel's paper shows

that he was familiar with *The Origin of Species,* Darwin's themes of evolution, population, and heredity being echoed by Mendel, and that he was opposed to Darwin's theory: Darwin was arguing for descent with modification through natural selection, Mendel was in favor of the orthodox doctrine of special creation.
4. Darwin's theory was based on differential survival and differential reproductive success, Mendel's on equality throughout all stages of the life cycle: equal gametes that unite at random to form equal zygotes that grow into equal plants, reproducing equally generation after generation.
5. Darwin's concepts were continuous variation, mutation, and "soft" heredity; Mendel espoused discontinuous variation and "hard" heredity without mutation.
6. The theoretical significance of Mendel's first monohybrid experiment (with seed shape) and of both the dihybrid and trihybrid experiments (in which the same trait was included) is questionable in light of molecular studies showing that the wrinkled-seed phenotype is caused by an insertion sequence that prevents normal expression of the gene for an enzyme, the presence of which gives rise to the antagonistic character, roundness (Bhattacharyya et al. 1990).

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