The Real Objective of Mendel's Paper: A Response to Monaghan and Corcos

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ABSTRACT: Mendel's work in hybridization is *ipso facto* a study in inheritance. He is explicit in his interest to formulate universal generalizations, and at least in the case of the independent segregation of traits, he formulated his conclusions in the form of a law. Mendel did not discern, however, the inheritance of traits from that of the potential for traits. Choosing to study discrete non-overlapping traits, this did not hamper his efforts.

KEY WORDS: Hybridization and inheritance, laws of inheritance, Mendel.

> Each generation, perhaps found in Mendel's paper only what it expected to find. ... Each generation, therefore ignored what did not confirm its own expectations. Only a succession of publications, the progressive building up of a corpus of scientific work, and the continuous iteration of all new opinions seem sufficient to bring a new discovery into general recognition.
>
> Fisher (1932)

In a recent issue of *Biology and Philosophy* Monaghan and Corcos (1990) claimed that Mendel's objective in his research was to find the empirical laws that describe the formation of hybrids and the development of their offspring over several generations, and not the laws of inheritence that are generally credited to him. Moreover, they claim that the "Mendelian" laws of segregation and independent assortment are not stated in Mendel's original paper. We wish to suggest, in this note, that for all the novelty of their positions (and that of Olby (1979) whom they follow and extend), these conclusions are unwarranted if the text of Mendel's paper and the context of his work are carefully scrutinized.

Biology and Philosophy **6**: 447–451, 1991.

Monaghan and Corcos' argument is three-pronged (1990, p. 268): (i) Mendel's experiments "were not concerned with heredity and its laws but were concerned with the formation and development of hybrids and the laws related to this"; (ii) "Mendel was using empirical methods in designing and carrying out his experiments"; and (iii) Mendel "did not explain his results by employing invisible particulate determiners." As an alleged corollary they also claim that the laws of segregation and independent assortment are not given by Mendel. It is important, immediately, to note that the last claim is logically independent of the rest of their positions. Whether or not Mendel was searching for, or thought that he had found, the laws of inheritance, he might (or might not) have stated them. As far as this last claim goes, all that is required to demonstrate the untenability of Monaghan and Corcos' position is to show that statements of Mendel's laws are present in his paper.

We begin by turning to the first set of claims. Indeed, as Olby (1979) has observed, Mendel phrased his problem in terms of the formulation of hybrids and their progeny. The reason for this is the historical context: in the first half of the nineteenth century, Moravia was a center of intensive breeding activity which provoked considerable interest in intellectual circles (Orel 1977, 1984). The breeding methods of Robert Blakewell that were imported from England and promoted by Geisslern (known as the "Moravian Blakewell") were those of the production of hybrids between divergent strains showing desired traits, and then inbreeding such hybrids intensely to maintain the desirable traits and transmit them to the progeny over several generations. A difficulty that arose was that the traits did not breed true. When Mendel addressed such problems he was, therefore, directly addressing a problem of heredity. Conceptually, moreover, it could not have been otherwise. If hybrids are formed through reproduction, and pass traits on (with whatever success) through reproducton, and these are the traits being studied, what is being studied, *ipso facto*, is the inheritance of traits. The problem of inheritance is, in some sense, more general than the problem of hybridization. But that hardly means that studying hybridization is not studying inheritance.

Monaghan and Corcos claim that Mendel was using empirical methods in the design of his experiments. This is hardly surprising given that he was searching for general laws in an experimental field that had not previously been systematically numerically investigated. Indeed, in the textbook of experimental physics written by Baumgartner and Ettinghausen, with both of whom Mendel came into contact, the authors emphasize that the aim of research was to work from observed phenomena towards the "highest laws," that is, those fundamental laws which could not be derived merely by means of (passive) induction, but required experiments (Orel 1984, p. 31). This is what Mendel seems to have been doing. Furthermore, he was clearly searching for as universal generalizations as possible. He was thus looking for laws, for theoretical insight into the underlying processes involving the inheritance of traits (a point we will return to in the next paragraph). From the outset Mendel makes it clear that although he had worked primarily with one specific experimental organism, his interest is in

universal generalization. He states: "A final decision [about the status of any principles he discovers] can be reached only when the results of detailed experiments from the most diverse plant families are available" (1966, p. 2). The inclusion of some experiments with beans at the end of his paper, as well as his further unsuccessful experiments with *Hieracium* underscore this point and further suggest that even if he did not initially set out to formulate general laws, such a concern manifested itself as the work was in progress.

Mendel makes clear that he was not interested in hybrids *per se*, but in the *inheritance of traits in hybrids*. Explaining the design of his experiments, Mendel claims: "It was the purpose of the experiment to observe these changes [of characters in progeny of hybrids] for each pair of differing traits, and to deduce the law according to which they appear in successive generations. Thus the study breaks up into just as many separate experiments as there are constantly differing traits in the experimental plants" (1966, p. 5). Monaghan and Corcos (1990, p. 270) claim that Mendel was not interested in "individual characters" – hence he was interested in the hybrid *per se*. They seem to confuse "individual" with "specific": Mendel was interested in individual traits, though not in any specific trait. Mendel does refer to the "hybrid trait" but his disinterest in the hybrid itself is evident when, after noticing the existence of such traits, he chooses to ignore them during further studies. For example, he observed but ignored hybrid vigor. He notes: "the stem of the hybrid is usually longer than the longer of the two parental stems, a fact which is possibly due only to the great luxuriance that develops in all plant parts when stems of very different lengths are crossed" (1966, p. 10). He does not follow up on this observation. He also notes but does not explore another such observation: "*Hybrid seed coats* are often more spotted; the spots sometimes coalesce into rather small bluish-purple patches. Spotting frequently appears even when it is absent as a parental trait" (1966, p. 10, italics in the original). Thus properties specific to hybrids are only marginally interesting to him.

We agree with Monaghan and Corcos that the case for Mendel explaining his results by employing invisible particulate determiners is not strong. The distinction between a potential for a trait and the trait proper was formulated by Johannsen only around the beginning of this century (see Falk (1986)), but as has been pointed out by Sandler (1983) and others, Mendel limited his attention to those traits for which there was an identity for the potential for a trait and the trait itself, excluding from his experiments all other traits. Consequently, he did not have to hypothesize invisible determiners. However, Mendel did invoke "factors" in trying to to account for constancy of traits (1966, p. 24). Perhaps what is most important here, is to note (with Monaghan and Corcos) that Mendel made no claims about the "factors" being particulate.

We turn now to the question whether Mendel stated the laws of segregation and independent assortment. Monaghan and Corcos are correct to the extent that there is no clear statement of the law of segregation in Mendel's paper. However, he does state that "in the ovaries of hybrids as many kinds of germinal cells (germinal vesicles), and in the anthers as many kinds of pollen cells are

formed as there are possibilities for *constant* combination forms and that these germinal and pollen cells *correspond in their internal make-up to the individual forms*" (1966, p. 24; the latter emphasis added). He goes on to add: "this assumption would be entirely adequate to explain the development of hybrids in separate generations if one could assume at the same time that the different kinds of germinal and pollen cells of a hybrid are produced on the average in equal numbers" (1966, p. 24). These statements come close to stating the law of segregation to alleles since the "forms" referred to are identified by the observed traits.

However, contrary to the claim made by Monaghan and Corcos, Mendel clearly states the law of independent assortment and emphasizes it by italicization of the relevant passages. Where Monaghan and Corcos are misled is in their assumption that the law of independent assortment must refer to gametes: "It states that the genes of each pair assort to the gametes independently" (1990, p. 288). While this is no doubt true, it is not necessary to resort to "gametes" in stating the law of independent assortment. A much more usual statement, from a fairly recent textbook, states: "Different segregation gene pairs assort independently" (Suzuki and Griffiths (1976, p. 16); see also, for example, Russell (1980, pp. 146–148)). Now compare this to Mendel: "*the behavior of each pair of differing traits in a hybrid association is independent of all other differences in the two parental plants*" (1966, p. 22; italics in the original). There are numerous similar statements in Mendel's paper. All the modern statement of this law does is to state it in the form of genes or alleles because subsequent work has shown the complexity of gene expression at the phenotypic level. Of course, some textbooks do mention gametes (e.g. Suzuki, Griffiths, Miller and Lewontin (1984, p. 24)) in the interest of adding more information. However, the example given above shows that such a reference is not necessary. Moreover, in the period after Mendel's "rediscovery" and the establishment of Mendelism, most conventional accounts of Mendel's work state this law virtually in Mendel's terms. For example, Morgan states "when races differ from each other in two pairs of characters, each pair considered by itself alone gives the 3 : 1 ratio, and the inheritance of one pair is independent of that of the other" (1919, p. 59).

In conclusion we note that Mendel was studying and reporting on inheritance simply because hybridization is conceptually inseparable from inheritance and that Mendel clearly stated the law of independent assortment although his "version" of the law segregation is not that clearly stated. Indeed, had Monaghan and Corcos been correct in their claims, we would have been faced with a curious problem: that Mendel's "rediscoverers" attributed to Mendel important laws that they had only discovered themselves. This would have been remarkable given the usual quest for priority in scientific matters. It would have presented a nobler image of science. However, the picture that emerges from Mendel's work (and its rediscovery) continues to be much less selfless.

ACKNOWLEDGEMENT

We would like to thank Garland Allen for useful comments on an earlier draft of this note.

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