The last third of Mendel's paper

Leigh Van Valen
Dept. Ecology & Evolution
University of Chicago
1101 E. 57 St.
Chicago, Ill. 60637

It isn't immediately apparent, to the uninitiated, that the inheritance of continuously varying traits can be explained in a Mendelian context. After the discovery of Gregor Mendel's reconceptualization [dare I say paradigm shift?] of inheritance, by Hugo de Vries and Carl Correns in 1900, the pre-existing conflict between biometricians such as Francis Galton and the now apparently triumphant advocates of discontinuity, such as William Bateson, continued without interruption.

The multifactorial explanation for continuous inheritance is variously attributed to Yule (1902), Bateson (1902), Bateson and Saunders (1902), Shull (1908), Nilsson-Ehle (1908 or 1909), Emerson (1910), East (1910), or East and Hayes (1911). All these workers did indeed see how Mendelian inheritance could underly continuous variation, and most authors provided examples which they interpreted in this way. (Bateson [1902] may, though, have referred to multiple alleles rather than to multiple loci; his writing is unclear.) Environmentally induced variation, then called fluctuating variability, was well known, although because it usually or always was regarded as a nuisance its explicit incorporation into the theory came later.

However, Mendel had already done both theory and experiment by 1865, when he reported on his work to the Naturforschender Verein in Brünn, which published his paper the next year. The last third of his paper discusses, not crosses between several pea strains, but crosses between two pairs of strains of *Phaseolus*, beans. In one cross, now regarded as intraspecific within *P. vulgaris*, the beans were as well behaved as his peas. So were shape traits in the other cross, between species now known as *Phaseolus coccineus* and *P. vulgaris*, despite semisterility of the hybrids.

Contrarily, flower color (and the apparently related color of seed pods) showed incomplete dominance in the F_1 and exploded from the true-breeding parental crimson and white into a near-rainbow in the F_2 and later. This "*remarkable color change*" (Mendel's emphasis) differed drastically from his expectation based on peas.

[Thus, contrary to received opinion, Mendel didn't regard dominance as universally applicable. He qualifies its domain of applicability again later: "Furthermore, when the differing traits include *dominating* ones. . . " He also explicitly, if casually, supported evolution: "This feature is of particular importance to the evolutionary history of plants, because constant hybrids attain the status of *new species*."]

Mendel had, though, done crosses among peas that involved as many as three traits. His straightforward interpretation of them comes immediately before his presentation of the bean crosses. He interpreted the "puzzling phenomena" of flower color by a direct extension, or interpolation, of his explanation for multi-trait crosses. The results for color "could probably be explained by the law valid for *Pisum* if one might assume that in [*Phaseolus coccineus*] the color of flowers and seeds is composed of two or more totally independent colors that behave individually

* * *

exactly like any other constant trait in the plant. Were blossom *A* composed of independent traits $A_1 + A_2 + \ldots$, which produce the overall impression of crimson coloration, then, through fertilization with the differing trait of white color *a*, hybrid associations $A_1a + A_2a + \ldots$ would have to be formed; and the situation with the corresponding coloration of the seed coat would be similar." East (1910) also used the trope of independent colors, in his case with respect to maize, apparently without knowledge of Mendel having done so.

He then said "that the explanation attempted here rests on a mere supposition, with nothing more to commend it than the very incomplete results of the experiment just discussed." However, some tentativeness also extended to his proposed laws: "Yet even the validity of the laws proposed for *Pisum* needs confirmation, and a repetition of at least the more important experiments is therefore desirable."

Mendel didn't start with any continuously varying characters, presumably because of his requirement that his parental stocks be true-breeding. However, when one nevertheless intruded itself on him he was able to extend his earlier conceptual framework and develop the basis for the kind of analysis that we still use.

References

Bateson, W. 1902. Mendel's Principles of Heredity. A defense. Cambridge University Press. 212 pp.

_____ and E.R. Saunders. 1902. Royal Society, Reports to the Evolution Committee 1 (for 1901), 160 pp. London: Harrison & Sons.

East, E.M. 1910. A Mendelian interpretation of variation that is apparently continuous. American Naturalist 44: 65-82.

_____ and H.K. Hayes. 1911. Inheritance in maize. Connecticut Agricultural Experiment Station, Bulletin 167: 1-142 + 25 plates.

Emerson, R.A. 1910. Inheritance of sizes and shapes in plants. A preliminary note. American Naturalist 44: 739-746.

Mendel, G. 1866. Versuche über Pflanzen-Hybriden. Verhandlungen des Naturforschenden Vereines in Brünn 4 (for 1865), Abhandlungen: 3-47. [The best translation of this paper is in Stern, C., and E.R. Sherwood. 1966. The Origin of Genetics: A Mendel Source Book. San Francisco: W.H. Freeman. 179 pp. The publisher is, or at least has been, unusually uncooperative with respect to permitting academic use of this important document.]

Nilsson-Ehle, H. 1908. Einige Ergebnisse von Kreuzungen bei Hafer und Weizen. Botaniska Notiser (1908): 257-294.

——. 1909. Kreuzungsuntersuchungen an Hafer und Weizen. I. Lunds Universitets Aarskrift (Ny Följd), 2(7): 1-122.

Shull, G.H. 1908. The composition of a field of maize. Report of the American Breeders' Association 4: 296-301.

Yule, G.U. 1902. Mendel's laws and their probable relations to intra-racial heredity. New Phytologist 1: 193-207, 222-238.