

## GENETICS OF CONTINUOUS VARIATION

Galton's use of correlation methods for the analysis of parent-offspring resemblances, resulting in the "Law of Ancestral Inheritance," was described in Chapter 3. This approach was followed by Weldon and by Pearson, the latter, in particular, contributing more sophisticated mathematical techniques, as did Fisher and others more recently.

Karl Pearson was a mathematical physicist by training, and wrote a book, *The Grammar of Science* (1892), that had a great deal of influence. According to Pearson, science is simply description—by which he meant description in quantitative terms—and he was very suspicious of the idea of causality. He was an extreme philosophical idealist; he was also convinced that there is nothing to which the scientific method cannot be applied.

Weldon was a contemporary of Bateson at Cambridge, and the two were at first close friends but later became bitter enemies. According to Bateson's letters, this enmity must have begun about 1890; by 1895 it appeared publicly in a controversy about the origin of the cultivated races of *Cineraria*, in the course of which each accused the other of deliberately misrepresenting the published statements of an authority that each cited in favor of his own view.

This personal quarrel, which came to involve Pearson as an ally of Weldon, seems to have been a chief reason for the anti-Mendelian stand of both Weldon and Pearson. Bateson felt that they were trying to strangle the new development, and he resisted vigorously. The controversy was pursued in debates and published works for years, and certainly delayed the utilization of the powerful methods of statistics in much of genetics.

In 1902 Yule suggested that the "Law of Ancestral Inheritance" could be thought of as due to the operation of the Mendelian principles in a random-breeding population. In 1904 Pearson disputed this conclusion

and attempted to prove that the observed parent-offspring correlations, which had been found in many kinds of organisms, were quantitatively in flat contradiction to the Mendelian scheme. In 1906 Yule showed that Pearson's conclusions rested on the specific assumption of complete dominance for all pairs of genes concerned, and that if dominance was sometimes incomplete, the Mendelian scheme could give correlations throughout the actually observed range. It is now clear that linkage between wholly dominant and wholly recessive genes is a possible alternative interpretation.

In 1905 Darbishire urged that there was no reason why both approaches might not be useful, and both were, in fact, used at about this time by Davenport and others. But the most important influence leading to the general use of statistical methods was that of the Danish botanist Johannsen, beginning in 1903 and culminating in his *Elemente der exakten Erblchkeitslehre* (1909). Johannsen, like Bateson and others, pointed out that the results of the biometrical school were only valid statistically, were of no help in individual families, and gave no insight into the mechanisms involved. But he did recognize the value of statistical methods, and used them extensively. There are twenty-five chapters in his book, and Mendelism does not appear until Chapter 22, the previous ones being concerned almost entirely with the development and use of statistical methods.

Johannsen's work was especially important in emphasizing the distinction between inherited and environmentally produced variations; the words *phenotype* and *genotype* (as well as *gene*) were introduced by him. The distinction was not new. It had, for example, been discussed by Galton under the heading "nature vs. nurture," but it was Johannsen who made it a part of general thought. There had been classifications of variability, as "individual," "fluctuating," "continuous," "discontinuous," and so on, but these were based on the magnitude of the differences rather than on their causes. With Johannsen it became evident that inherited variations could be slight and environmentally produced ones could be large, and that only experiments could distinguish them.

Johannsen's own experiments were largely with beans, and concerned the inheritance of the size of seed in self-fertilized lines. Self-fertilization is the normal method of reproduction here; therefore his plants were in general homozygous—belonging to what he called "pure lines." He found that selection was without effect within such lines, and that two different lines might be only slightly different in size (with much overlapping), but would maintain this slight difference generation after generation. He recognized that the situation was different in cross-fertilizing

forms, but was inclined to minimize the effects of selection, and to agree with de Vries that it could produce nothing really new.

In his original paper, Mendel had suggested the beginnings of the theory of multiple genes and had recognized (in connection with flowering time in peas) the confusing effects of environmental differences; but it was not at once evident that continuously varying characters could be studied effectively by Mendelian methods.

In 1902 Bateson pointed out that it should be expected that many genes would influence such a character as stature, since it is so obviously dependent on many diverse and separately varying elements. This point of view was implied by Morgan in 1903 (*Evolution and Adaptation*, p. 277), and by Pearson in 1904. It was developed by Nilsson-Ehle in 1908 and 1909, especially as a result of his experiments with wheat and oats. Nilsson-Ehle applied the idea of numerous separately Mendelizing pairs of genes—plus the confusing effects of environmental differences—to quantitative characters such as size, length of awns, winter-hardiness, and so forth, but his actual detailed analyses concerned somewhat simpler cases, such as color and presence or absence of ligules.

Lock and Castle had both reported crosses in which quantitative differences supposedly gave no increased variability in  $F_2$ , but in 1910 East and R. A. Emerson, separately, reported cases in several different plants in which the  $F_2$  was much more variable than the  $F_1$  and interpreted them as being due to the segregation of several pairs of genes. Their joint paper (1913) on maize is a classic in the field and marks the bringing of the inheritance of quantitative characters into the general scheme of Mendelism.

There is another method of studying the inheritance of quantitative characters, namely, the use of selection. This, of course, has a long history; we are here concerned with the relation between it and Mendelian genetics. De Vries was inclined to minimize the effects of selection, and argued that it could produce nothing new. Johanssen had a similar view; but this was so contrary to the point of view of Darwin, Weismann, and the whole generation that followed Darwin, that it was not generally accepted. There followed a series of selection experiments by numerous workers. Those of Johanssen have been discussed, and the circumstance of their being done with self-fertilizing homozygous strains has been pointed out.

The most extensive and most widely discussed selection experiment of the time was that which Castle carried out with rats, beginning in 1914. The "hooded" type here is white with a colored area on the head and usually a narrow, colored line on the back. Castle selected for an in-

crease in the colored area in his "plus" line, and for a decrease in his "minus" line. Selection was effective and ultimately yielded individuals far beyond the limits of the variability of the original series. Both extremes, when crossed to self-colored rats, gave self (that is, uniformly colored) in  $F_1$ , and 3 self to 1 hooded in  $F_2$ . Castle argued that this pointed to a gradual change in the hooded gene, rather than to an accumulation of modifying genes—a conclusion not accepted by most geneticists. Considerable discussion resulted—some of it (including one paper of mine) rather heated.

Finally Castle crossed the two selected lines, separately, to wild type and examined the grades of the extracted hooded  $F_2$  rats. In each case these were less extreme than their hooded grandparents, that is, more like the original, unselected strain. After two more crosses to wild type and extractions, the two lines were nearly identical, and by 1919 Castle concluded that most of the effects of selection had been due to sorting out and accumulation of modifying genes at loci other than that of the hooded gene, although it seemed probable that a small part of the result was due to minor changes in the hooded gene.

With this result there came to be general agreement that selection operates chiefly through the sorting out of modifiers already present, especially after the demonstration in *Drosophila* (by Payne, Sturtevant, and others) that such modifiers could be located on chromosome maps by using marker genes. With the realization that modifiers are numerous, it came to be recognized that they are often linked to each other. It is to be expected also that plus modifiers will be linked to minus ones sometimes, thus greatly complicating the analysis. Since practical breeding of domestic animals and cultivated plants depends to a large extent on selection, knowledge about the nature of its action has been of importance in agriculture and horticulture; though perhaps this importance has been more in the understanding of the principles than in the practice of the art of selection.\* This art has, however, profited much from the application of statistical methods that grew out of the work discussed in this chapter. Here the work of Fisher has been especially important.

Finally, an understanding of the way selection works has been of the first importance in the application of genetics to the problems of evolution (Chapter 17).

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\* The understanding of the principles may, of course, lead to practical results. As an example, the increased vigor of hybrids was observed long ago by Kölreuter, and even earlier, in the particular case of the mule; but it was the application of Mendelian methods by Shull (1908) and Jones (1917) that led to the most important agricultural uses, beginning with "hybrid corn."