CHAPTER 1

BEFORE MENDEL

In discussing the history of a subject it is usual to begin with Aristotle—and he forms a convenient starting point for genetics, though the real beginnings, even of theoretical genetics, go farther back. As a matter of fact, much of Aristotle's discussion of the subject is contained in his criticism of the earlier views of Hippocrates.

Hippocrates had developed a theory resembling that later proposed by Darwin, who called it "pangenesis." According to this view, each part of the body produces something (called "gemmules" by Darwin) which is then somehow collected in the "semen"—or as we should now say, the germ cells. These are the material basis of heredity, since they develop into the characters of the offspring. The view was developed, both by Hippocrates and by Darwin, largely to explain the supposed inheritance of acquired characters. Aristotle devoted a long passage to criticism of this hypothesis, which he discarded for several reasons. He pointed out that individuals sometimes resemble remote ancestors rather than their immediate parents (which is in fact one of the arguments used by Darwin *for*, rather than *against*, pangenesis, since Darwin did not suppose that the gemmules necessarily came to expression in the first generation and did not suppose, as did Hippocrates, that they were released from the parts of the body at the moment of copulation). Aristotle also pointed out that peculiarities of hair and nails, and even of gait and other habits of movement, may reappear in offspring, and that these are difficult to interpret in terms of a simple form of the hypothesis. Characters not yet present in an individual may also be inherited—such things as gray hair or type of beard from a young father—even before his beard or grayness develops. More important, he pointed out that the effects of mutilations or loss of parts, both in animals and in plants, are often not inherited. Aristotle, like everyone else until much later, accepted the inheritance of acquired characters; but he was nevertheless aware that there was no simple one-to-one relation between the presence of a part in parents and its development in their offspring. His general conclusion was that what is inherited is not characters themselves in any sense but only the potentiality of producing them. Today this sounds self-evident, but at that time it was an important conclusion, which was not always fully understood, even by the early Mendelians.

Aristotle was a naturalist and described many kinds of animals—some imaginary, others real and described in surprisingly accurate detail. He knew about the mule and supposed that other animals were species hybrids—that the giraffe, for example, was a hybrid between the camel and the leopard. According to him, in the dry country of Libya there are few places where water is available; therefore many kinds of animals congregate around the water holes. If they are somewhere near the same size, and have similar gestation periods, they may cross; this is the basis for the saying that "something new is always coming from Libya."

Some later authorities disregarded Aristotle's reasonable limitations on what forms might be expected to cross, as in the conclusion that the ostrich is a hybrid between the sparrow and the camel. There is a long history of such supposed hybrids—notably of the crossing between the viper and the eel, and of the hybrid between the horse and the cow. Zirkle records accounts of both of these as late as the seventeenth century.

The knowledge of sex in animals goes far back before the beginnings of history and was understood quite early even in plants—at least in two important food plants of the Near East, namely, the Smyrna fig and the date palm, both of which are dioecious (that is to say, have separate male and female trees). Zirkle shows that a special Near Eastern deity (the cherub) was supposed to preside over the date pollination, and that representations of this deity can be traced back to about 1000 B.C. There is, in fact, evidence that male and female trees were grown separately as early as 2400 B.C.

The condition found in these two trees was definitely related to the phenomenon of sex in animals, by Aristotle and others, but it was much later that it was realized that plants in general have a sexual process.

That the higher plants do have sexual reproduction and that the pollen represents the male element seems to have been first indicated as an important generalization by Nehemiah Grew in 1676. A sound experimental basis was first given by Camerarius (1691 to 1694). From that time on, the view was rather generally accepted, especially after Linnaeus presented more evidence and lent the prestige of his name in 1760.

More or less casual observations on natural or accidental hybrids in plants were made over a long period, beginning with the observations of Cotton Mather on maize in 1716. However, the systematic study of plant hybrids dates from the work of Kölreuter, published from 1761 to 1766. His work laid the foundations of the subject and was familiar to Darwin and to Mendel, both of whom discussed it a hundred years later.

Kölreuter made many crosses, studied the pollination process itself, and also recognized the importance of insects in natural pollination. He used a simple microscope to study the structure of pollen and was the first to describe the diversity of pollen grains found in seed plants. He also made studies on the germination of pollen. These studies on germination were carried out on pollen in water, with the result that the pollen tubes plasmolyzed almost immediately. This led Kölreuter to conclude that the fertilizing agent was the fluid released on the stigma, rather than a formed element from a particular pollen grain.

In another respect he reached a wrong conclusion that delayed the development of a clear understanding of fertilization, namely, the view that more than one pollen grain is necessary for the production of a normal seed. This view was based on experiments with counted numbers of pollen grains, which seemed conclusive to him. The result was generally accepted for some time, and even Darwin adopted it *(The Variation of Animals and Plants under Domestication*, Ch. 27) on the authority of Kölreuter, and of Gärtner, who later confirmed the experiments. Kölreuter supposed, as a result of his experiments, that he could recognize "half-hybrids," that is, individual plants derived from pollen that was partly from the seed parent and partly from a different plant. Like Aristotle and other predecessors, he thought of fertilization as resulting from a mixing of fluids, basing this in part on his direct observations of germinating pollen.

His observations on the hybrids themselves were of importance. He recognized that they were usually intermediate between the parents (he was nearly always using strains that differed in many respects), but he did record a few cases where they resembled one parent. He recognized the sterility often found in hybrids between widely different forms and showed that in some of these the pollen was empty. He emphasized the identity of the hybrids from reciprocal crosses—which is rather surprising, since plastid differences might have been expected in some of such a large number of reciprocal species hybrids.

Kölreuter reported a few instances of increased variability in the offspring of hybrids but laid no emphasis on this observation. He also observed the frequent great increase in the vegetative vigor of hybrids and suggested that it might be of economic importance, especially if hybrid timber trees could be produced.

Following Kölreuter, there were a number of men engaged in the study of plant hybrids. Detailed accounts of their work are given by Roberts (1929), but perhaps the most satisfactory general account of the state of knowledge in Mendel's time is to be found in Darwin's discussion in *The Variation in Animals and Plants under Domestication* (1868).*

Darwin collected a vast amount of information from the works of the plant hybridizers, from works on the practical breeding of domestic animals and cultivated plants, and from gardeners, sportsmen, and fanciers. He himself carried out numerous experiments with pigeons and with various plants. The book is still interesting, as a source of information and of curious observations. Darwin was looking for generalizations, and extracting them from masses of observations was his special ability. But, in the case of heredity, the method yielded very little. He recognized two more or less distinct types of variations—those that came to be known as continuous and discontinuous, respectively. The latter, sometimes called "sports," he recognized as sometimes showing dominance, and as being often transmitted unchanged through many generations. But he felt that they were relatively unimportant as compared to the continuously varying characters, which could be changed gradually by selection and which gave intermediate hybrids on crossing. He concluded that crossing has a unifying effect. Since hybrids are generally intermediate between their parents, crossing tends to keep populations uniform, while inbreeding tends to lead to differences between populations; this same conclusion is shared by modern genetics, though the arguments are not quite the same as Darwin's.

He reported crosses which led to increased variability in the second and later generations, but he was interested in them chiefly because of their bearing on the question of reversion to ancestral types. He also recognized the increase in vigor that often results from crossing and observed the usual decline due to continued inbreeding. He carried out numerous detailed experiments in this field, which are elaborated in one of his later books, *(The Effects of Cross and Self Fertilization in the Vegetable Kingdom*, 1876).

On the origin of variability, Darwin had little to say that sounds

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* Darwin's books were extensively altered in successive editions, and it is not always safe to consult a later edition and then to assign the views given therein to the date of the first edition. Although I have not seen the first edition of the book, I have no reason to suppose that its date is misleading in this connection.

modern. He thought that changed conditions, such as domestication, stimulated variability and also affected the inheritance both in selection within a strain and in crosses between strains. The effects of selection were familiar to him, but he was not aware of the basic distinction between genetically and environmentally produced small variations.

Darwin's own theory of heredity (pangenesis) was not generally well received, but it did apparently serve to suggest the particulate theories of Weismann and of de Vries, which paved the way in 1900 for the appreciation of Mendel's work.

The development of ideas about inheritance in animals and in plants was rather independent, for in plants the early experiments were directed largely toward the demonstration of sexual reproduction, which needed no demonstration in animals. This led to the study of hybrid plants, but in animals the development was largely in the hands of practical breeders, who were more concerned with selection than with crossing. One of the striking things about Darwin was that he had a detailed firsthand knowledge of both animals and plants, and of the literature on both. In his work we find the modern custom of discussing theory without regard to the distinction between animals and plants. It is true that this had been done before—by Aristotle, for example—but not to the extent that Darwin introduced. It may be noted that the previous hybridizers referred to in Mendel's paper (Kölreuter, Gärtner, Herbert, Lecoq, and Wichura) were all botanists. Since Mendel referred to them, we may suppose that they influenced his work; therefore there follow brief accounts of the last four, since Kölreuter has already been discussed.

Gärtner's work was published largely in 1839 and in 1849. He made a large number of crosses. Roberts says that "he carried out nearly 10,000 separate experiments in crossing, among 700 species, belonging to 80 different genera of plants, and obtained in all some 350 different hybrid plants." In general, he confirmed much of Kölreuter's work, but added little that was new, except for an insistence on the greater variability of F_2 (the second generation) compared to F_1 (the first generation). He did not often describe the separate characters of his plants but rather treated them as whole organisms—a habit common to many of the older hybridizers. Mendel gave a good deal of space to a discussion of Gärtner's results. He interpreted them as due in part to the multiplicity of gene differences between the plants crossed—which in F_2 resulted in great rarity of individuals closely resembling the parents. Gärtner also carried out experiments with several plants that involved back-crossing hybrids in successive generations to one of the parental species, in an effort to see how many such backcrosses would be needed to eliminate the characters of the other parent. Mendel did a few experiments of this kind with peas and found, as he expected, that the result depends on the proportion of dominant genes in the parent to which the back-crossing is done. He suggested that this factor must always complicate experiments of the kind carried out by Gärtner (and earlier similar crosses made by Kölreuter).

The work of Herbert, published between 1819 and 1847, dealt chiefly with crosses among ornamental plants. Perhaps his most important contribution was his discussion of the idea that crosses between species are unsuccessful or yield sterile hybrids, while crosses between varieties yield fertile offspring. He pointed out that there is no sharp line here, and that the degree of structural difference between two forms is not an invariable index of the fertility of their hybrids. In short, the argument is a circular one: infertility between species and fertility between varieties can be concluded only if fertility and sterility are made the criteria by which species and varieties are defined.

Lecoq (published 1827 to 1862) was interested in the breeding of improved agricultural plants. He made many crosses and discussed the results of other hybridizers, but seems to have added little that advanced the subject.

Wichura's chief paper appeared in 1865, after Mendel's experiments were completed; he therefore could scarcely have influenced the planning of Mendel's crosses. His work was on the crossing of willows; perhaps the most striking passages have to do with the necessity for extreme care in preventing unwanted pollen from confusing the experiments, and his strong insistence on the identity of reciprocal hybrids—the latter being a point that Lecoq had believed was not correct.

Two other people in this period should be discussed, since both have been cited as having in some respects anticipated Mendel's point of view.

Maupertuis was even earlier than Kölreuter, his work having been published between 1744 and 1756. He reported on a human pedigree showing polydactylism, and discussed albinism in man and a color pattern in dogs. He also developed a theory of heredity somewhat like Darwin's pangenesis. Glass (1947) has reviewed this work in detail; he sees Maupertuis, in some respects, as a forerunner of Mendel. This is, to my mind, based largely on the interpretation of rather obscure passages in terms of what we now know. In any case, it is clear that Maupertuis had little or no effect on later developments in the study of heredity.

Naudin, a contemporary of Mendel, published his accounts between 1855 and 1869. He studied a series of crosses involving several genera of plants. In several respects he made real advances. Like several of his predecessors, he emphasized the identity of reciprocal hybrids. He also emphasized the relative uniformity of F_1 as contrasted to the great variability of F_2; and he saw the recombination of parental differences in F_2. But there was no analytical approach, no ratios were recognized, and no simple and testable interpretations were presented. The expression "laws of Naudin-Mendel," sometimes seen in the literature, is wholly unjustified.

Mendel's analysis could not have been made without some knowledge of the facts of fertilization—specifically, that one egg and one sperm unite to form the zygote. This was not known until a few years before his time and was not generally recognized even then. Darwin, for example, thought that more than one sperm was needed for each egg, both in animals and in plants.

Direct observations on fertilization had to wait for the development of microscopes. Leeuwenhoek saw animal spermatozoa under a microscope in 1677 and thought that one was sufficient to fertilize an egg—but this was neither directly observed, nor generally accepted, for animals, until two hundred years later (see Chapter 3).* In the lower plants, fertilization was observed by Thuret in 1853 (Fucus), Pringsheim in 1856 (Oedogonium), and De Bary in 1861 (fungi). In seed plants, the work of Amici was especially important. In 1823 he recorded the production of the pollen tube, which in 1830 he traced to the ovary and even to the micropyle. In 1846 he showed that in orchids, there is a cell already present in the ovule, which, inactive until the pollen tube arrives, then develops into the embryo. This work was confirmed and extended by Hofmeister and others, so that Mendel could write in his paper: "In the opinion of renowned physiologists, for the purpose of propagation one pollen cell and one egg cell unite in Phanerogams into a single cell, which is capable by assimilation and formation of new cells, of becoming an independent organism." Nevertheless, there was not general agreement on the point. Naudin (1863) repeated the experiments of Kölreuter and of Gärtner, placing counted numbers of pollen grains on stigmas and concluding that a fully viable seed required more than one grain. It appears, from his let-

* Leeuwenhoek also saw conjugation in ciliated Protozoa (1695), but this observation was not understood until the unicellular nature of these animals was made out two centuries later.

ters to Nägeli, that Mendel himself also repeated this experiment (using Mirabilis, as had Naudin) and found that a single grain was sufficient. He did not publish this result, and does not refer to this approach to the question in his paper.