CHAPTER 3

1866 TO 1900

The period between the publication of Mendel’s paper and its rescue in 1900 from oblivion was dominated by the development of the theory of evolution and its implications. So far as heredity was concerned, it was largely a period of the production of theories. There were, however, several real advances which helped to make Mendel’s results acceptable. Here we may mention the germ-plasm theory with its emphasis on the effects of germinal material on the body rather than the reverse; the resulting challenge of the inheritance of acquired characters; the striking increase of knowledge of the cytological details of fertilization and cell division; and the increasing emphasis on the importance of discontinuous variation. This chapter will be concerned chiefly with these topics.

The outstanding figure of the time was August Weismann (1834–1914), who was professor of zoology at Freiburg for many years. From 1862 to 1864 he published several papers on the embryology of Diptera, and these seem to have led to much of his later theoretical work.

In these flies, the so-called pole cells are set aside in early cleavage divisions, subsequently to develop into the germ cells. Their early separation from the somatic cells, and their relatively independent development, seem to have suggested the germ-plasm theory to Weismann (1883), although he was also aware of a similar idea expressed by Nussbaum. According to this scheme, the germ line is the continuous element, and the successive bodies of higher animals and plants are side branches budded off from it, generation after generation. This is, of course, only a way of looking at familiar facts, since Weismann recognized that in the higher plants and in many animals the visible distinctness of the germ line only appears late in development and, in fact, that many cells that will not normally give rise to germ cells still retain the potentiality of doing so. Nevertheless, the idea was a fruitful one, since it led to an emphasis on the effects of the hereditary material on the soma and to a minimizing of effects in the reverse direction—a point of view already foreshadowed by Aristotle. This in turn led to a challenging of the hypothesis of the inheritance of acquired characters, which had already been questioned by Du Bois Reymond in 1881. But it was the writings of Weismann that really showed that the hypothesis was unnecessary and improbable, and that the supposed evidence for it was weak. In the special case of the inheritance of mutilations, already questioned by Aristotle and Kant, Weismann carried out an experiment. He cut off the tails of mice for twenty-two successive generations and found no decrease in the tail length at the end of the experiment.

Weismann suffered from eye trouble, and finally had to give up microscopic work and experimental studies,[*] although he kept the latter going in his laboratory through the work of students and assistants. His own work, however, came to be largely theoretical. He was in close touch with the activity of the time in the cytological study of the chromosomes and played a large part in the theoretical developments in that field—which may be discussed conveniently at this point.

The importance of the nucleus in the cell theory had gradually become evident, though not universally recognized; but with the observations of O. Hertwig (1875) and of Fol (1879) on the fertilization of the egg of the sea urchin, the role of the nucleus in fertilization and cell division was placed beyond doubt.

There followed a few years (about 1882 to 1885) during which a whole series of investigators laid the foundations of our knowledge of the behavior of the chromosomes in mitosis and meiosis. This rapid development seems to have been due mainly to two events. The microtome was improved at about this time (by Caldwell), and made possible the production of serial sections of uniform thickness, thereby improving the quality of microscope preparations. At about the same time, van Beneden discovered the advantages of Ascaris for the study of chromosomes, and this animal (the threadworm of the horse) became one of the standard objects for such studies.

During these few years Flemming and Strasburger recognized chromosomes. Van Beneden showed that the daughter halves of the mitotic chromosomes pass to opposite poles at mitosis; that, in Ascaris, the fertilized egg receives an equal number of chromosomes from each parent; and that the meiotic divisions result in halving the number present in the fertilized egg. Here, then, was the first demonstration of the double na-

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[*] Both Mendel and Correns also suffered from eye trouble brought on by excessive work with strong light.

ture of the soma and the simplex condition of the germ cells (a relation deduced by Mendel from his genetic results but not recognized by his contemporaries). It had, however, been anticipated by Weismann, who supposed that the function of the polar body divisions in the egg was to prevent an indefinite accumulation of ancestral hereditary units and predicted that a similar reduction would be found in the formation of the sperm.

In 1883 there appeared a remarkable essay by Roux, in which he argued that the linear structure of the chromosomes and their point-by-point division into equal longitudinal halves were such striking and widespread phenomena that they must have some selective value. This, he suggested, lay in their effectiveness in assuring that each daughter cell received the same complement of chromosomal material. He saw this as a strong argument in favor of identifying the chromosomes as the bearers of the units of heredity. These units were also here first specified as being arranged in a linear series—the visible slender strands of the dividing chromosomes.

Roux applied these ideas to the cleavage divisions of the fertilized egg of the frog. He was the “father” of experimental embryology and had carried out experiments which he believed had shown that the two cells arising from the first division are equivalent, but that the second division leads to differences in the potentialities of the daughter cells.[*] He therefore concluded, in the 1883 essay, that at the second division the process of mitosis does not lead to exactly equal complements of hereditary units in the daughter cells. This was the beginning of the hypothesis that differentiation is due to somatic segregation—the sorting out of hereditary elements at somatic cell divisions.

These ideas were at once adopted by Weismann, who elaborated them into an intricate theory of heredity and development. According to this scheme, the chromosomes are the bearers of the hereditary material. Weismann supposed that each chromosome remains intact in successive generations, and is simply passed on through the germ line from generation to generation. Since an individual may resemble several different ancestors in one respect or another, he concluded that each chromosome carries all the hereditary elements necessary to produce a whole individual. The different chromosomes of an individual may have been derived from many different ancestral lines, and they therefore differ among themselves. Each is potentially able to determine the characteristics of a whole organism, but in the development of a particular part, only one

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[*] Later experiments have not borne out this conclusion about the second division.

chromosome is effective at any given time and place. There is, in a sense, a competition between the various chromosomes, and the nature of each characteristic depends on the outcome of this competition at each critical time and place in the developing embryo. Each chromosome was supposed to be made up of smaller units, and these in turn of still smaller subunits. These were distributed unequally at somatic divisions, forming the basis of differentiation.

This theory was elaborated in great detail and was widely known and discussed, but it was not accepted in detail, because it was so hypothetical and seemed to offer so little basis for experimental testing. There can be no question of the importance and widespread influence of much of Weismann's work, but the elaboration of his scheme of heredity and development led to widespread resistance to even the sounder parts of his interpretations. As Wilson expressed it in 1900:

> Weismann's . . . theories . . . have given rise to the most eagerly contested controversies of the post-Darwinian period, and, whether they are to stand or fall, have played a most important part in the progress of science. For, aside from the truth or error of his special theories, it has been Weismann's great service to place the keystone between the work of the evolutionists and that of the cytologists, and thus to bring the cell-theory and the evolution theory into organic connection.

One of the workers of the time who was greatly influenced by Weismann but was unwilling to accept all of his conclusions, was de Vries. In his *Intracellular Pangenesis* (1889), de Vries developed a theory of heredity different from Weismann's. He pointed out that there are two parts to Darwin's hypothesis of pangenesis—the view that there are persistent hereditary units which are passed on through successive generations, and the view that these are replenished by gemmules derived from the somatic tissues. Following Weismann and others, de Vries rejected the second of these views, but he retained the first. This might have led to an interpretation like Weismann's, but de Vries added an essential point, namely, that the units (which he called "pangens") are each concerned with a single character, and that these units may be recombined in various ways in the offspring. This was a clear approach to the Mendelian point of view, and helps to explain why, eleven years later, de Vries was one of the three men who discovered and appreciated Mendel's paper.

There was a difficulty about Darwin's views on the effectiveness of natural selection, if one supposed that most characters blend in hybrids, and that it is just these characters that are important in selection, either natural or artificial. The difficulty is that a favorable variation will, on this basis, be rapidly diluted by crossing to the parental form, and systematic change of the whole population will be painfully slow, if possible at all. It was not until well after 1900 that this difficulty (the "swamping effect") was cleared up, as we shall see in Chapter 9. But it led to an increasing interest in "sports," which, as Darwin had realized, showed little tendency to "blending" or "swamping." This interest is apparent in the writings of Galton as early as 1875.

Bateson, in *Materials for the Study of Variation* (1894), expressed the growing dissatisfaction with the view that selection was a sufficient explanation of evolution. He felt that too little was known about the facts of variation, and that the current phylogenetic theories were of little value. As he put it:

> In these discussions we are continually stopped by such phrases as "if such and such a variation then took place and was favorable" or "we may easily suppose circumstances in which such and such a variation if it occurred might be beneficial," and the like. The whole argument is based on such assumptions as these—assumptions which, were they found in the arguments of Paley or of Butler, we could not too scornfully ridicule. "If," we say with much circumlocution, "the course of Nature followed the lines we have suggested, then, in short, it did." That is the sum of our argument.

This dissatisfaction with the then-current views led Bateson, Korschinsky, and de Vries to lay great emphasis on the importance of discontinuous variations. As we can now see, they overemphasized the distinction between the two kinds of variation; but the immediate result was to focus attention on sharply separable variations, and these were more easily susceptible of exact study. Again, it was no accident that de Vries was one of the discoverers of Mendel's paper, and that Bateson was perhaps the most important of the early advocates of the Mendelian approach.

During the period in question, a quite different approach to the study of heredity was developed by Francis Galton. Galton, who was a cousin of Darwin, had carried out an experiment to test the theory of pangenesis. He performed extensive blood transfusions between different strains of rabbits and found no effects on their descendants in either the first or the second generation. Darwin admitted that he would have expected effects but felt that his gemmules were not necessarily to be expected in the blood, since the theory was supposed to apply even to organisms without a circulatory system. Galton agreed that the experiment was not decisive.

Galton's theoretical contribution arose from his feeling for the importance of quantitative study. He felt that almost anything could be measured. He attempted to develop a quantitative scale for beauty; and he carried out a study on the effectiveness of prayer, by examining mortality rates for crowned heads (whose subjects prayed for their health), and by comparing the frequencies of shipwreck for vessels that did and did not carry missionaries. Like Mendel, he also studied meteorology.

He developed the idea of correlation as a result of tabulating the relationship between the height of parents and that of offspring in human families. He saw what was needed in geometrical terms and referred the algebraic problem to the mathematician Dickson, who then produced the regression coefficient.* Galton used this to give a simple numerical value for the degree of resemblance between parents and offspring, thus initiating a whole field of study. He tabulated a large series of data on the colors of pedigreed basset hounds, and based his *Law of Ancestral Inheritance* on the results. These results showed that, on the average, an individual inherits ¼ of his characteristics from each parent, ⅟₁₆ from each grandparent, ⅟₆₄ from each great-grandparent, and so on. This ingenious approach was followed by many of his successors, but failed to give the hoped-for insight into the mechanisms involved. As it happened (through no fault of Galton's), it led to a long and bitter controversy that wasted much time and printer's ink in the early years of this century (Chapter 9).

The question has often been raised: Would any biologist have appreciated Mendel's work if he had seen the paper before 1900? My own candidate for the most likely person to have understood it is Galton, because of his interest in discontinuous variation, his mathematical turn of mind, and his acceptance of Weismann's view that the hereditary potentialities of an individual must be halved in each germ cell.

One of the "eager controversialists" referred to by Wilson was Haacke, who published a series of anti-Weismann papers between 1893 and 1897. These papers, which have been overlooked by many of the more recent authorities (but not by all—see Correns, 1922), contain the nearest approach to the Mendelian interpretation before the rediscovery. They make difficult reading, because the results and conclusions are so buried in a mass of polemics.

Haacke crossed normal albino mice with waltzing mice that were colored. In F_1 he got only colored normals, and in F_2 (which he called the "third generation," the parent strains being considered the first) he rec-

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* This account is from Galton's autobiography. It appears that the correlation coefficient had already been developed by Bravais in 1846.

ognized the occurrence of the recombination types. The analysis is based on his supposition that all structural characters (including the waltzing habit, presumably due to some structural change) were inherited through the centrosomes, and all chemical characters (that is, coat color in this case) through the nucleus. There follows a surprisingly modern-sounding hypothetical scheme. He designates the plasma (= centrosomes) of the waltzer as *t* (for *Tanzmaus)* and that of the nonwaltzer as *k* (for *Klettermaus);* and the nucleus of the albino as *w*, that of the colored mouse as *s*. He specifies that, at the reduction division, *t* separates from *k*, and *w* from *s*, resulting in four kinds of eggs or of sperm: *ts, tw, ks,* and *kw.* Fertilization of these will then result in sixteen kinds of individuals, which he lists: *ts, ts; ts, tw; ts, ks;* and so on to *kw, kw.* He points out which of these will breed true and which will not—in other words, a straightforward Mendelian analysis for two pairs of genes—except that no ratios are given. Here he makes what at first glance is an astonishing statement: “Ob die Anzahl der Chromosomen bei den Mäusen bekannt ist, weiss ich nicht, man würde daraus die möglichen Kombinationen aufstellen können.” This statement sounds at least ten years ahead of the thinking of the time—but study of the context indicates that Haacke was misled by the Weismannian idea that each chromosome contains all the hereditary material needed to produce an individual, and he needed the chromosome number to calculate the probability of getting all chromosomes in a gamete purely maternal or purely paternal. He was unaware of the 1 : 1 segregation in heterozygotes and, in fact, apparently visualized various kinds of heterozygotes, at least for color.

Only after this hypothetical analysis are we told that he had raised over 3000 mice in his experiments, and that they were in “the most beautiful agreement” with the theories he developed. No numbers are given, and no ratios.[*] He does, however, insist that the separation of *t* from *k* and of *w* from *s* must be complete, since extracted waltzers and albinos both breed true when mated to their own kind.

The paper from which this summary has been abstracted appeared in one of the best-known biological journals of the time (*Biologisches Centralblatt,* vol. 13, 1893), so that it is difficult to see why it was overlooked so long. One reason is surely the polemic nature of the paper, which led to the data and conclusions being emphasized primarily as ammunition against Weismann rather than for their own sake.[†] Another

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[*] The actual data were published much later, well after the rediscovery of Mendel’s work *(Arch. Entw.-mech.,* 1906).

[†] One gibe at Weismann is perhaps worth citing. Haacke argued that Weismann might have gotten further if he had made crosses between the various kinds of fancier’s

reason is their use to support the unpopular (and erroneous) idea of the genetic importance of the centrosomes. Finally, the failure to give actual counts made the data seem as speculative as the discussion in which they are imbedded.

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mice to study the inheritance of coat colors, "instead of cutting off the tails of his unfortunate mice and those of their children and of their children's children unto the twentieth generation."